Inter- and intraspecific variation of breeding biology, movements, and genotype in Peregrine Falcon *Falco peregrinus* and Gyrfalcon *F. rusticolus* populations in Greenland

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Submitted in fulfillment of the degree of
Doctor of Philosophy

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Dedicated to my father and best friend

William A. Burnham, Ph.D.

1947–2006

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Abstract

Peregrines *Falco peregrinus* and Gyrfalcons *F. rusticolus* were studied in Low and High Arctic Greenland, comparing populations within and between areas. Analyses of weather data from northwest Greenland (1979–2005) revealed a general warming trend, resulting in a lengthened breeding window for many bird species. Both falcon species depend on cliffs for nesting, and take a similar range of bird species as prey. However, Gyrfalcons lay six weeks earlier than Peregrines in Kangerlussuaq and one month earlier than Peregrines in Thule, and occupy more sheltered nest-sites. Being larger than Peregrines, Gyrfalcons also take some larger prey species. In addition, both species move to lower latitudes for the winter, but while most Gyrfalcons migrate relatively short distances, Peregrines are complete long-distance migrants to Central and South America. One Peregrine, satellite-tracked from its breeding site at 76.5° N, travelled ~12,500 km and >100° in latitude, one of the longest migrations ever documented for a raptor.

Around Thule in northwest Greenland (at 76.5° N), scientists had historically documented no breeding Peregrines, but six occupied sites were discovered during this study, comprising what is probably the most northern nesting population in the world. Over the same period, breeding Gyrfalcons have apparently disappeared from southern Greenland, and may have declined in central-west Greenland (67° N). The ultimate cause of this retraction may be climate warming, but the proximate cause is probably competition from an increasing Peregrine population.

Gyrfalcons tagged with satellite-received transmitters showed characteristics associated with both obligate and facultative migration. Their winter ranges varied greatly in size, with the largest, ~172,000 km^2, being the biggest ever documented for a raptor. Many individuals made long movements within a winter, and some spent up to a month at sea. They may have rested on ice and fed upon seabirds. Carbon dating of stratified faecal accumulation from Gyrfalcon nests in central-west and northwest Greenland showed use of sites for up to ~2,500 and ~650 years, respectively. The age of nest sites correlated significantly with the current distance to the Greenland Ice Sheet, and probably reflects colonization patterns following glacial retreat.

In central-west Greenland the ratio of Peregrine to Gyrfalcon pairs changed from 1:1 in the early 1970s to nearly 14:1 in 2005. Over this period, competition for nest sites and prey is likely to have intensified. The crucial prey for Gyrfalcons when they start nesting in early spring are resident ptarmigan, whose numbers are probably depleted by Peregrines during the months they are present. If recent trends in climate change continue, Peregrines may continue to increase in Greenland, and spread north into areas previously occupied only by Gyrfalcons. At the same time, Gyrfalcons may retreat north from many currently-occupied areas.

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Author's Note: Locations of both Peregrine Falcon and Gyrfalcon nest sites within Greenland are not provided in this thesis for reasons of security. While robbing of eggs and young from nests is much less frequent than in the past, it still occurs sporadically. Actual nest-site locations have been provided to The Peregrine Fund library (contact information follows this paragraph) from whom *bona fide* researchers can obtain this information in the future. Furthermore, raw satellite telemetry data for all birds tagged during this study will also be available through The Peregrine Fund library and may be accessed by *bona fide* researchers. The author may also be contacted for information on nest-site locations and raw PTT data. Contact information is as follows:

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Chapter 1: Introduction.

RESEARCH STATEMENT

The primary aim of this study was to compare the biology and ecology of Low and High Arctic Peregrine Falcon *Falco peregrinus* and Gyrfalcon *F. rusticolus* populations in Greenland (Figures 1.1 & 1.2). For each species, data were collected on territorial occupancy, nesting density, home range size, migration, nest site characteristics, DNA, and prey. Results were used to assess the level of competition and other relationships between the two species and their possible consequences. Migratory data derived from radio-tagged Gyrfalcons, using satellite-based receivers, were the first of their type to be collected, and provided a new perspective on the winter ecology of the species. In addition, carbon dating of nest-site material provided information on the extraordinarily long periods that particular nest-sites have been in use.

While current research leaves no doubt that anthropogenically induced climate change is occurring, its effects on falcon species in both the Low and High Arctic are unknown. To address this issue I analyzed previously unpublished climate data from Thule Air Base (High Arctic), Greenland, and summarized existing climatic data on both a local and regional scale. These findings are compared and contrasted with both historical data and contemporary data, which I collected, and possible long-term effects, such as increased competition between Gyrfalcons and Peregrines, are discussed. I predicted that warming climatic conditions would allow Peregrine populations to expand and move further north in Greenland, and that increased temperatures and competition with Peregrines would have an adverse effect on Gyrfalcon populations now or in the near future.

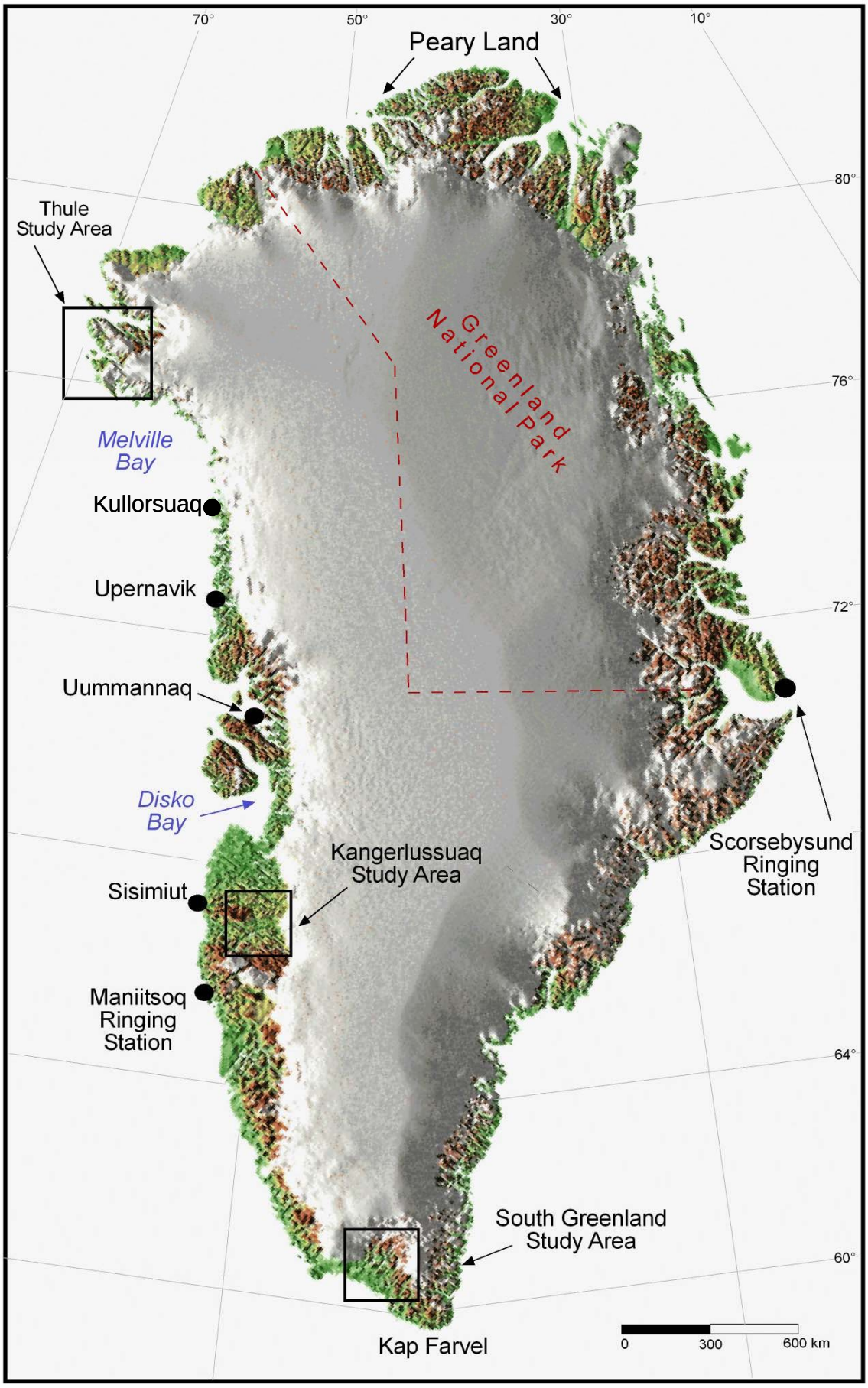

Figure 1.1. Map of Greenland showing study areas and pertinent place names.

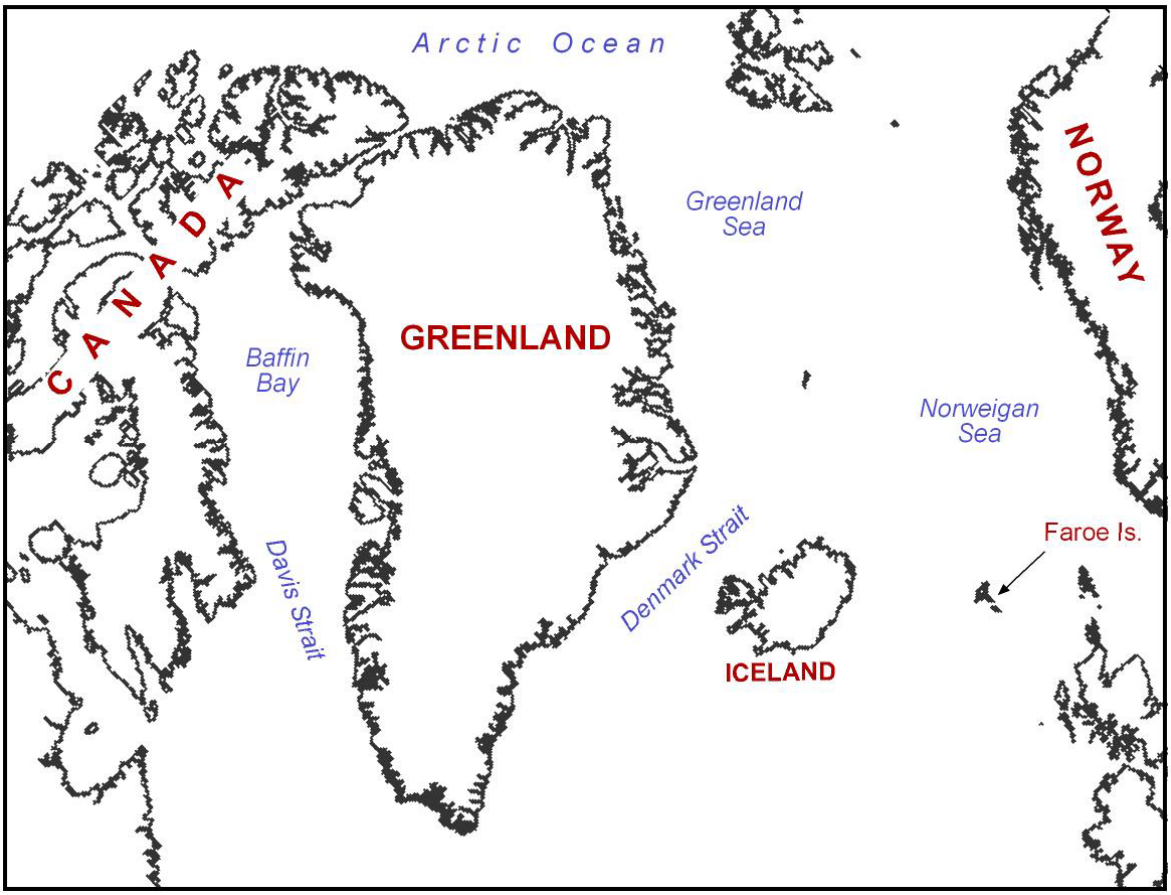

Figure 1.2. Map of Greenland and the surrounding Arctic region.

CLIMATE CHANGE

Changes in global climate are occurring at an alarming and potentially dangerous rate (Comiso & Parkinson 2004, Arctic Climate Impact Assessment 2004, Hansen *et al.* 2006, Richter-Menge *et al.* 2006, IPCC 2007). 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).

ARCTIC TERMINOLOGY

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 of 8–11 °C and the High Arctic a mean July temperature of 4–6 °C (Figure 1.3), with more temperate areas to the south frequently referred to as Subarctic (Bliss *et al.* 1973). Additionally, Bliss (1975, 1979, Bliss *et al.* 1973) provides further descriptions of these areas based on plants and herbivore species, with each area characterized by specific ecosystems.

The figure originally located here has been removed from this version of the thesis for copyright reasons

Figure 1.3. Temperature boundaries of the Low and High Arctic as defined by Bliss (1979). Low and High Arctic boundaries are defined by a mean July temperature of 8–11 °C and 4–6 °C, respectively (Bliss 1979). Map from Bliss (1979).

BIRDS AND CLIMATE CHANGE

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). Throughout the world, species from most major taxa have been shown to be impacted by climate change (reviews in McCarty 2001, Walther *et al.* 2002, Parmesan & Galbraith 2004, Parmesan

2006), 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).

The effects of weather and climate on bird populations have been well documented and discussed (Lack 1954, 1966, Newton 1998, 2003a). 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).

In the Arctic, the effect of climate change on bird species has been little studied. In the Canadian Arctic, the timing of breeding of Brunnich'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 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, 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 are frequent breeders 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), but little is known of Peregrines breeding in the High Arctic.

GYRFALCONS

The Gyrfalcon is the largest of the falcon species. It breeds in the circumpolar Subarctic to High Arctic, with some individuals migrating south to northern temperate zones during the late autumn and winter (Cade 1982). The species is well adapted to the harsh Arctic environment, and Nielsen & Cade (1990a) state that “its morphology, physiology, behavior, feeding ecology, population dynamics, and annual cycle” are all a result of these specialized adaptations. For example, the Gyrfalcon has well-developed down for insulation, and is the only species of falcon capable of covering its toes with its

feathers while remaining perched upright (Cade 1982, Nielsen & Cade 1990a). Plumage colour varies throughout the Arctic, from very dark grey to almost completely white depending upon regions (See Figure 1.4 for examples), which is also considered an adaptation to varying Arctic climates (see Cade 1980, Potopav & Sale 2005 for further plumage colour discussion).



Figure 1.4. Plumage colour of Gyrfalcons as referred to throughout the text. Although full spectrum of colours from white to dark occurred in Greenland these serve as representative samples for each individual plumage colour.

Although well studied in summer throughout much of its Low and Subarctic range (Cade 1982, Palmer 1988, Cade *et al.* 1998, Potapov & Sale 2005), limited information exists on Gyrfalcons during the winter months. In the Low Arctic, populations are easier to monitor, and adults frequently stay near their nest sites year round (e.g., Cade 1960, Plat 1976, Nielsen & Cade 1990a). In the High Arctic, summer information is restricted to notes made by early explorers, birding surveys/expeditions, or single seasons spent observing particular nests (e.g., Stone 1895, Muir & Bird 1984, Cabot *et al.* 1988, Lepage *et al.* 1998), while data on migration and winter movements are lacking.

POPULATION LIMITATION

Factors that influence the limitation of bird populations have been well studied (Lack 1954, 1966, Newton 1998). In particular, Newton (1979) thoroughly discussed the many factors that influence populations of raptors. Among Gyrfalcon populations, prey have been shown to limit breeding density, with populations following the cyclic pattern observed in ptarmigan *Lagopus* sp. populations in some regions (Mossop & Hayes 1994, Nielsen 1999), but not in others (Mindell & White 1988, Shank & Poole 1994). For Peregrines, a wide range of factors have been shown to influence breeding densities, including nest-sites and prey (Beebe 1960, Nelson & Myres 1975, Ratcliffe 1980), varying from region to region. As an example, Peregrines in Britain are more or less restricted to breeding where cliffs are present, but in those areas where cliffs are in surplus, breeding densities are primarily influenced by prey supply (Ratcliffe 1980).

Inter-specific competition can also limit bird populations, and species that have significant overlap in the use of resources, such as prey and nest sites, usually do not occur together in the same area (Lack 1971, Newton 1998). While Peregrines and Gyrfalcons have been documented breeding on the same cliff at the same time (White & Cade 1971, Mattox pers. comm.), Peregrines are almost always extremely aggressive toward Gyrfalcons (Cade 1955, Jenkins 1978). However, Peregrines are unlikely to dislodge breeding Gyrfalcons which settle earlier in the year. Furthermore, in the Arctic, both falcon species show significant overlap in avian prey species utilized, although the predominance varies between falcon species and area (Cade 1960, Burnham & Mattox 1984).

THESIS OVERVIEW

This research was part of a larger study initiated by The Peregrine Fund's Arctic Program, of which I served as Project Director until September 2007. I collected data from breeding falcon populations from 1993–2005 in the Thule study area (Figures 1.1 & 1.5)

and from 1999–2005 in the Kangerlussuaq study area (Figures 1.1 & 1.6). In 2000 and 2002 in Maniitsoq and in 2004 and 2005 in Scoresbysund, I collected data from migrant falcon populations (Figure 1.1). I also analyzed and tabulated anecdotal data collected on Gyrfalcons by W. Mattox who was studying Peregrines in the Kangerlussuaq region from 1972–1997. These data were previously unpublished and only appeared in annual field reports and field notebooks. A number of individuals assisted me in the field, as study areas were at times both remote and dangerous to work in, with extremely technical rock climbing necessary in some instances.

The Introduction (Chapter 1) lays the groundwork for my dissertation while the rest of the thesis is concerned with my findings on Peregrines (Chapter 2) and Gyrfalcons (Chapters 3 and 4), while Chapter 5 compares the biology of the two species, highlighting potential competition and other interactions between them, and any changes in status and breeding that may have been linked with climate change. Other falcon research from the thesis period which I initiated and oversaw, on the genetics of Gyrfalcons, has appeared elsewhere as a joint publication (Johnson *et al*. 2007).

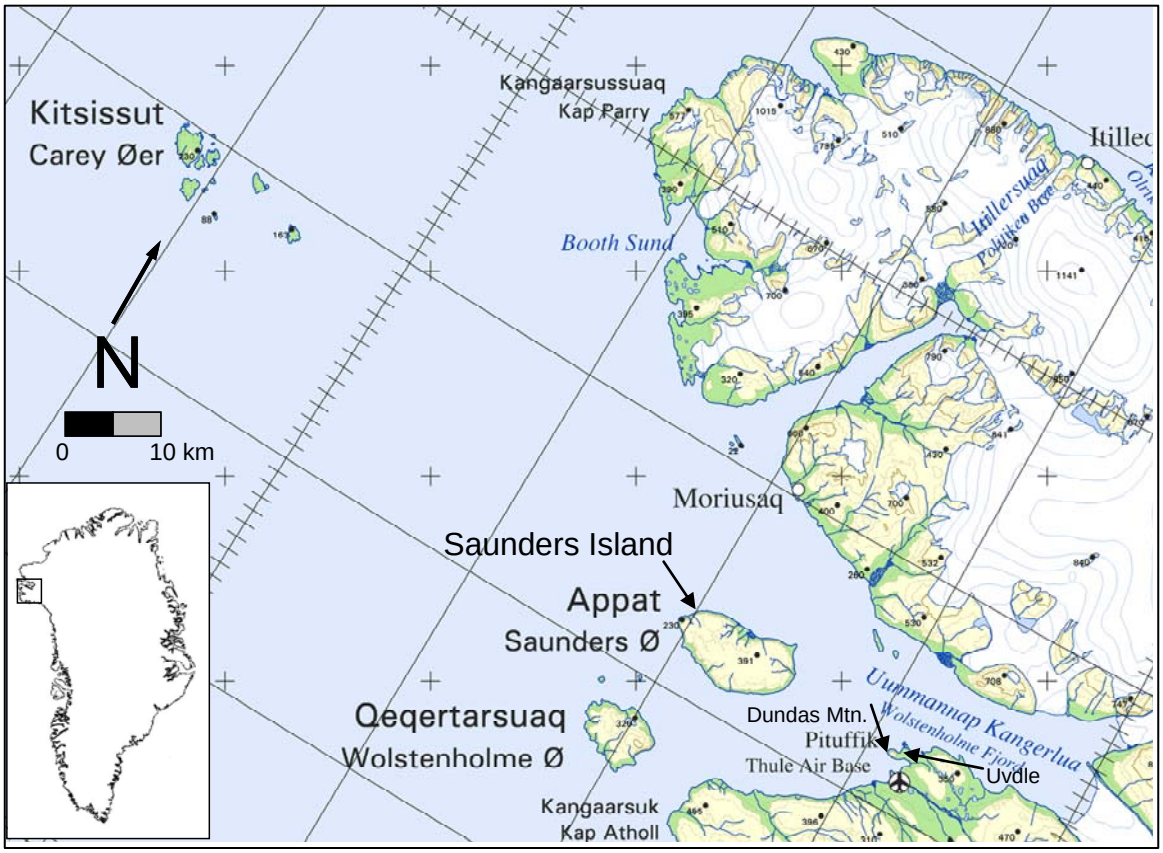

Figure 1.5. Map of the Thule study area.



Figure 1.6. Map of the Kangerlussuaq study area.

Chapter 2: Biology and population history of Peregrine Falcons in High Arctic Greenland.

INTRODUCTION

Peregrine Falcons *F. p. tundrius* breed throughout the mid and low latitude Arctic regions of North America and Greenland (Cade 1982). They are far less common in the High Arctic. 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 (Figure 1.1). Over that latitudinal range, meta populations are subjected to different ecological, environmental, 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. I 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 Thule area of northwest Greenland, existing long-term information and new data collected on Peregrines to the south in the Kangerlussuaq area in central-west Greenland, and previously collected information on Peregrines in southern Greenland (Figure 1.1).

From 1972 to 1997, under the leadership of W. Mattox, the first in-depth study of Peregrines in Greenland was accomplished in a large ice-free land mass centred around Søndre Strømfjord Air Base (now re-named Kangerlussuaq, 67.02° N, 50.71° W) (Burnham & Mattox 1984) (Figures 1.1 & 1.6). 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 (Figure 1.1) (Falk & Møller 1988). K. Burnham and W. Burnham collected data on Peregrine Falcons in the High Arctic of Thule, northwest Greenland, 75.9–77.6° N from 1993 to 2005 (Figures 1.1 & 1.5).

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

From 1993 to 2005 I spoke with local Greenlanders within the Thule area who were subsistence hunters and had intimate knowledge of the area. When shown photographs of Peregrine Falcons, all said they had never seen the bird and claimed it did not exist in the Thule area. In contrast, when shown photographs of Gyrfalcons, they knew exactly what they were and could commonly point out multiple locations on a map where nests existed. Confusion between Gyrfalcons and Peregrine Falcons was unlikely, with over 99% (n = >200) of observed Gyrfalcons in the Thule area being white. Further, the Greenlandic and Danish words for Peregrine Falcon, Kiinaaleeraq and Vandrefalk, respectively, are not known in the Thule area.

Historical separation

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

One of the first detailed accounts of birds in Greenland was presented by Sabine (1819), who visited the Thule 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. However, Peregrines were not reported farther north during the expedition. Walker (1860a), on the ship "Fox" from 1857–59, visited the southern Thule 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 falcons. From 1871 to 1873, on board the "Polaris," Hall (1876) regularly mentioned bird species seen and shot in the Thule area, 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 Thule area, and despite mentioning Peregrines further south in Greenland, made no reference of

Peregrines in northwest Greenland, only listing 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 (1950–51) provided reports of Peregrines in the Thule area: "According to Rev. J. Olsen (*in litt*.) and Vibe it breeds at Thule settlement, at Uvdle (slightly more eastward), and on Saunders Island." The "Thule settlement" almost certainly referred to Dundas Mountain, which sets 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) travelled the Thule area with local Greenlanders and recorded observations made on birds in the Thule area, of which Gyrfalcons, but not Peregrines, were seen. From 1978, Roby *et al*. (1981) make mention of "five potential Dovekie *Alle alle* predators observed at two study areas" in the Thule area, of which Gyrfalcons were one of the predators observed, but not Peregrines. Vaughan (1988) presents results on a survey of the birds of the Thule 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, even suggesting that Peregrines "perhaps" no longer breed near Thule Air Base. However, in 1987 and 1988 Peregrines were seen on Dundas Mountain, very near Thule Air Base (K. Falk pers. comm.).

As Salomonsen (1950–51) referenced, C. Vibe (1938) reported Peregrine Falcons on a cliff near the former village of Uvdle, which is about 14 km northeast of the "Thule settlement." In 1999, however, C. Vibe provided W. Mattox with a photograph of his reported Uvdle site (W. Mattox pers. comm.). I determined that the photograph does not depict the

small cliff above Uvdle, but Dundas Mountain, which is the "Thule settlement" and so both reported sites are one and the same.

Saunders Island is located 14 km west of Dundas Mountain (Figure 1.5). It is 391 m high and measures 16 km by 7 km with high cliffs around much of its perimeter. Hundreds of thousands of Thick-billed Murres *Uria lomvia*, Black-legged Kittiwakes *Rissa tridactyla*, and Northern Fulmars *Fulmarus glacialis* breed there (Boertmann 1994), and so could one or more pairs of Peregrines. Other than Salomonsen's general reference to the Peregrines on Saunders Island, 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 my study, despite careful checks every year.

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

STUDY AREAS

The Thule area is considered High Arctic and is known for its severe weather and harsh environment (Figures 1.1 & 1.5). Snowfall and strong winds (>160 km/hr) may occur in any month. Between 1951 and 1986 at 76.5 m elevation (76.5° N, 68.7° 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 Thule, pack ice usually breaks up in July and the ocean freezes over again by mid-October. Glaciers calving along the coast 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 ice-free land consists of rolling hills and valleys with streams emanating from the Greenland Ice Sheet or glaciers. The ice margin lies up to 26 km from the sea but reaches the sea in some locations. Most cliffs are adjacent to fjords, bays, or glaciers and have extensive talus slopes below. Ice-free land usually occurs below 600 m. Higher elevations are frequently ice covered. Vegetation is sparse and prostrate, typically no higher than five centimeters, as shown in Figure 2.1. Grasses and sedges are most common, with woody plant species such as willow *Salix* present only 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 Thule, 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 Dovekie, a small (160 g) planktivorous alcid that breeds in the Thule area, with ca. 33 million pairs (Egevang *et al.* 2003). Dovekies arrive at colonies in the Thule area in the first half of May, and leave them before the start of September (Salomonsen 1950–51, Thing 1976).

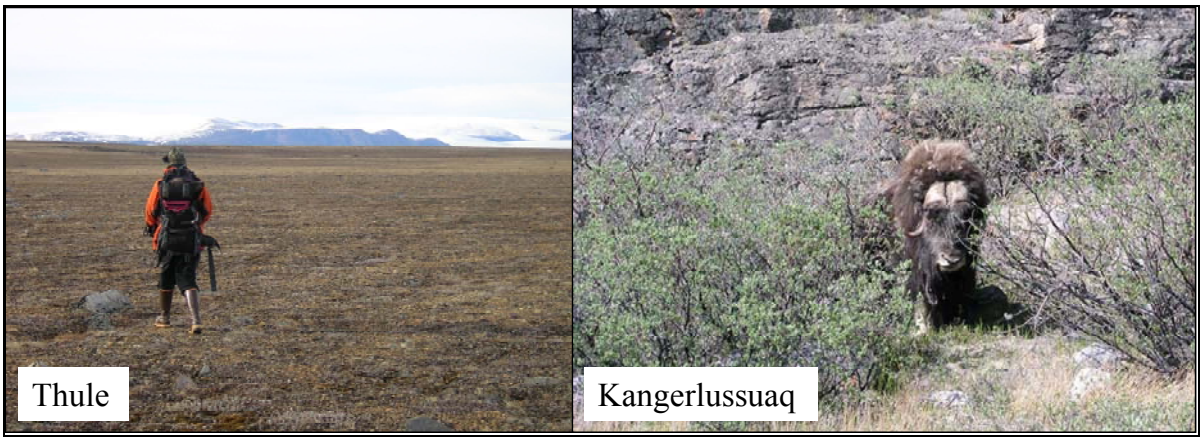

Figure 2.1. Photographs of typical tundra vegetation in the Thule and Kangerlussuaq areas in Greenland.

Approximately 1,170 km to the south of Thule, the Kangerlussuaq area is a large Low Arctic ice-free land area of rolling hills, which contain hundreds of lakes and valleys and is divided by Søndre Strømfjord (Figures 1.1 & 1.6). 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 *Salix* growing ≤2 m tall in Kangerlussuaq, as seen in Figure 2.1. The weather is more stable here than in the Thule 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 (Burnham & Mattox 1984). 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 (Figure 1.1). 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 and 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 area and Kangerlussuaq area 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 Thule, the amount of ice-free land decreases, with Peregrines only nesting on coastal cliffs starting in the Disko Bay area and with the density decreasing northwards (W. Burnham pers. comm.). In 2000 in the Uummannaq area (see Figure 1.1), north of Disko Bay, I participated in a large survey of the bird life in the area, covering a land mass of approximate 12,000 km^2, primarily made up of a very large system of fjords (Burnham *et al.* 2005). During the 18-day survey, in which 2,900 km were covered by boat and an additional 350 km by helicopter, only one territorial pair of Peregrines was found and an additional adult was seen flying at another location (Burnham *et al.* 2005). North of Uummannaq the amount of ice-free land and coastal cliffs continues to decline rapidly, with Melville Bay, between Kullorsuaq and the Thule 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, with Peregrines probably occurring in extremely limited numbers to the south between Upernavik and Kullorsuaq.

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

METHODS

Survey, capture, and breeding biology

After a thorough literature review, I contacted individuals with first-hand knowledge of birds (including local hunters) in the Thule area. A small aircraft was initially used 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. For further information on capture methods see Appendix A.

Nest site characteristics

In Thule, 10 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). 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) conducted by Dr. Jeff Johnson at the University of Michigan, Ann Arbor.

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 >2,000 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, I used a quail mass of 128 grams, 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 grams of food each day, respectively. These numbers were divided according to estimated crop size (e.g., 0.5 crop for female = 80.5 grams) 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 Kangerlussuaq and Thule and adult males from Kangerlussuaq. For the analysis on females, sub-adults (>1-yr-old falcons molting into 'blue' adult plumage), were included with adults. For females, t-tests were run between the means of individuals from Kangerlussuaq and Thule 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 taken from all Peregrine Falcons captured or ringed in the nest in Thule and Kangerlussuaq 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 (Figure 1.1), southwest of Kangerlussuaq, and Peregrines captured there were analyzed separately. 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/μL prior to PCR. All genetics work was in association with Dr. Jeff Johnson, University of Michigan, Ann Arbor.

Genotyping, sequencing, and statistical analysis

For specific methodology on genetic analysis see Appendix B.

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 Kangerlussuaq and Thule. 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 continuously each day (provided sufficient solar-power was available) to 7 hours on/106 hours off, depending upon the power source and battery life. 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 2.1 for summary information for each PTT.

Table 2.1. PTTs placed on Peregrine Falcons from 2001 to 2003 and a single stationary PTT (36321) deployed at Thule Air Base.

Year	Region	ID numbers	No. of PTTs	Brand	Duty cycle (on/off)	Weight	Power source
2001	Thule	10212, 10217, 10292	3	NS	daily (24h)	20 g	solar
	Kanger.	10219	1	NS	daily (24h)	20 g	solar
2002	Thule	35234, 35240	2	MT	10 h/24 h	18 g	solar
	Thule	35255, 36321	2	MT	5 h/38 h	30 g	battery
	Kanger.	35235–37	3	MT	10 h/24 h	18 g	solar
2003	Thule	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

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, Liabet & 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 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.

Statistical analysis

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 were 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 travelled 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 travelled, individual Peregrines may have travelled 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 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). I 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 from now on 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). When units stopped transmitting or were obviously no longer on the falcon, if >30 locations with LC 3–0 had been received and >25 days had lapsed from placement of unit on the falcon to failure, data were included to determine the breeding home range. 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 >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 and Eichenlaub (2000) were used. Argos data were imported into ArcView using the Argos-Tools extension designed for ArcView by E. Potapov and 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

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 Thule (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. The data were analyzed for the entire 27-year period and for the last 15 and 10 years, to look for trends, or slope, over time. All data were tested for auto-correlation using Durban-Watson and data were normally distributed. To avoid type-1 error Holm's Sequential Bonferroni 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

Falcon surveys were carried out from mid-July to early September from 1993 to 2005 along the coast and off-shore islands of Thule, with approximately 984 linear km of coastline and islands surveyed between 75.9° N, 66.5° W and 77.6° N, 71.17° W. Although the entire area was not travelled 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).

The historical breeding site, at Dundas Mountain, was occupied by Peregrines in all 13 years. No breeding Peregrines were ever seen on Saunders Island, the other location where Peregrines were reportedly seen in the past, although the island was surveyed annually and a 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 eight locations, Peregrines aggressively defended territories against humans, Northern Ravens *Corvus corax*, and Gyrfalcons, including Dundas Mountain. Young were produced at six of these locations in two or more years (Table 2.2). Of the two locations where reproduction was not observed, one (Parker Snow Bay) was reported by K. Kampp (pers. comm.) in August 1998 where an adult male Peregrine defended a cliff area from a Northern Raven. Although that general area of coastline (15 km) was surveyed each year from 1995 through 2005 and Peregrines were seen in 2000, 2002, and 2004, no territorial pairs were located. This is an area of high prey density. The other 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, respectively, had a median value of 33.3 km and mean of 38.8 km (n = 8, range 12.3–74.3) and median of 15.4 km and mean of 28.3 km (n = 6, range 12.3–67.2).

Table 2.2. Annual occupancy and reproduction of Peregrine nest sites in the Thule study area where young were raised in at least one year.

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
Y? = occupied but reproduction unknown; C = checked but unoccupied; N = not checked;
Gyr = occupied by breeding Gyrfalcons; F = failed, occupied by both adults.

Pairs, single adults, and single sub-adult Peregrines that were mildly defensive when approached or toward Northern Ravens and/or were seen multiple times at the same location were observed at seven other sites. These sites were all generally in areas with high densities of nesting Dovekies 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 (≥ seven days of age to flying) at least 28 times, giving 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 (Table 2.2, "≥"). Based on the observed young, the mean production was ≥2.17 young/occupied site (n = 41) and ≥3.18 (n = 28) young/successful site. Because inclement weather prevented boat travel, two of the known sites could not be visited/observed on two occasions each, but I 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 found not to be occupied (Table 2.2). In 2003 it was occupied by Gyrfalcons and in 2004 it was first occupied by 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 Thule. 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 my knowledge no adult females changed territories between years. No adult males were marked in the Thule area.

From 1993 to 2005, 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 Thule was 8 June ($n = 24$, sd ± 7) (Table 2.3). The average date for incubation to begin was 12 June ($n = 24$, sd ± 7) and for hatching 16 July ($n = 24$, sd ± 7). Assuming a 42-day nestling period (Sherrod 1983), the average fledging, or nest-leaving date, was 27 August ($n = 24$, sd ± 7). If young Peregrines at Thule 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 in Thule, and with the known departure dates of breeding females.

Table 2.3. Nesting chronology of Peregrine Falcons in Thule, Kangerlussuaq, and South Greenland 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 1st egg laid and start of incubation are calculated by subtracting 34 and 38 days, 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.

Date of:	South Greenland[a] median (min.–max.; *n* = nesting attempts) (Falk *et al*. 1986)	Kangerlussuaq[b] average (*n* = years) (Mattox 1997)	Thule[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 Kangerlussuaq collected from 1983 to 1997, W. Mattox, 1997 Field Report, Greenland Peregrine Falcon Survey
[c]Data for Thule collected from 1993 to 2005.

Ring recoveries from Peregrines marked in Thule 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 at Thule prior to 2005 were recovered.

Prey

Of 19 nests where prey remains were collected, Dovekie 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 Dovekie colonies to any nest being >30 km distant. However, Dovekies regularly make long flights to feed and pass within <1 km of each nest. In the five nests where Dovekie 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.

Dovekies and Snow Buntings thus appeared to make up the largest part of the Peregrine diet around Thule, with Dovekies 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 Black Guillemots and Black-legged 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 Thule, breeding pairs of Peregrines were located at cliffs with a mean height of 59 m (range = 25–137, median = 55, n = 33, sd ± 25) located <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, range = 20–78, median = 52, n = 28, sd ± 20) and cliff aspect, on average, was 213° (southwest) when corrected to True North (range = 225, median = 168, sd ± 75, n = 30) (Table 2.4).

Table 2.4. Nest site characteristics from Thule, Kangerlussuaq, and South Greenland. Nest sites in Thule and South Greenland (data collected 1979 to 1985) 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.

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

na–not applicable, information not collected.

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 (range = 50–500, median = 150, *n* = 21, sd ± 98) and depth 66 cm (range = 50–150, median = 51, *n* = 21, sd ± 30). 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° (range = 48–90, median = 78, sd ± 12), including the pothole nest site. Average horizontal angle of exposure (falcon viewing angle) was 134° (range = 70–180, median = 140, *n* = 19, sd ± 41). The average nest ledge aspect for each of 19

nests corrected to True North was 209º (range = 210, median = 213, sd ± 59, *n* = 19). Thirteen of the 19 had a south to southwestern exposure (Figure 2.2). 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.

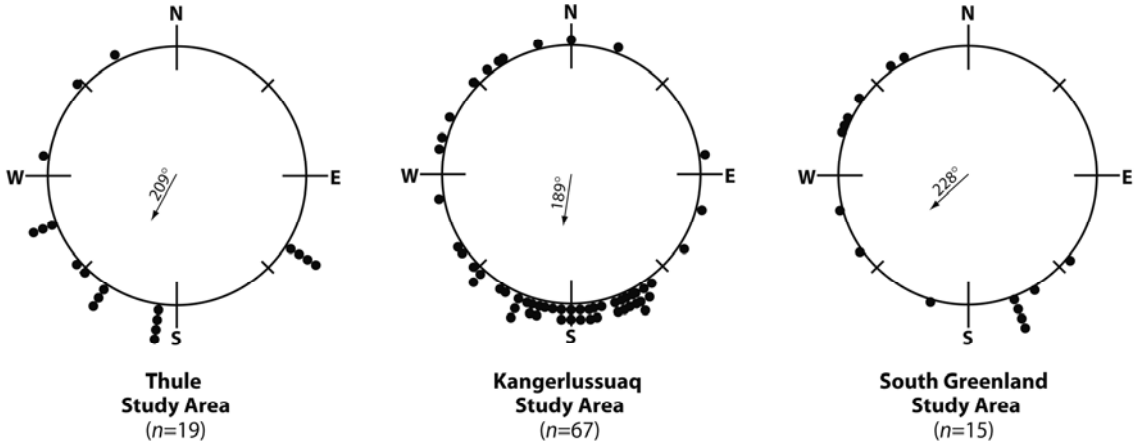

Figure 2.2. Nest ledge aspect of Peregrine Falcon nests in Thule, Kangerlussuaq, and South Greenland study areas. The average vectors are indicated, but the range of variation was large. Stacked dots may indicate the same nest was used multiple years. Data for Kangerlussuaq from Wightman (2001) and Wightman & Fuller (2005) and for South Greenland from Falk *et al.* (1986).

Morphometrics

Nineteen adult Peregrines (12 females and seven males) were captured from 15 June 2001 to 3 September 2004 in Kangerlussuaq, and nine adults (females) in Thule from 25 July 2001 to 25 September 2004. Adult female Peregrines from Thule had a significantly greater mass (T = 2.53, p = 0.02, df = 17) than females from Kangerlussuaq, but no significant difference in any linear measurements (Table 2.5). All five measurements taken on adult males in Kangerlussuaq were significantly smaller than those for females in the same area, as would be expected (Table 2.5).

Table 2.5. Mean ± sd (*n*) for five measurements taken on adult and sub-adult Peregrine Falcons from Kangerlussuaq and Thule. Measurements are in centimeters except for mass which is in grams.

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)
Thule					
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 Thule and Kanger.	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 Kanger.	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

The PCA yielded two components for adult females explaining 50 and 26%, respectively, of total variance (Table 2.6). 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 Kangerlussuaq 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 measurements and were excluded from the PCA analysis.

Included in the PCA were 17 adult females (Thule = 7, Kangerlussuaq = 10) and four adult males from Kangerlussuaq (Table 2.6).

Table 2.6. Results of two separate principal component analyses (PCA): (1) adult female Peregrine Falcons from Kangerlussuaq and Thule and (2) adult males from Kangerlussuaq, Greenland. Component loadings on each significant axis and percent of total variance explained are shown.

	Adult females (n = 17)		Adult males (n = 4)	
Variable	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.

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 Kangerlussuaq and Thule. For adult females from Kangerlussuaq and Thule there was a significant relationship ($r^2 = 0.66$, $p < 0.001$) between PC1 and body mass (Figure 2.3). Therefore, mass was a good predictor of overall body size for adult female Peregrines in Thule and Kangerlussuaq; heavier birds were usually larger. Additionally, as shown in Figure 2.3, females from Thule were generally heavier for their overall body size than were females from Kangerlussuaq. 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 Kangerlussuaq were almost all captured during the mid-to-early incubation period while females in Thule 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 Kangerlussuaq and Thule is genuine, but likely under-estimated in these data.

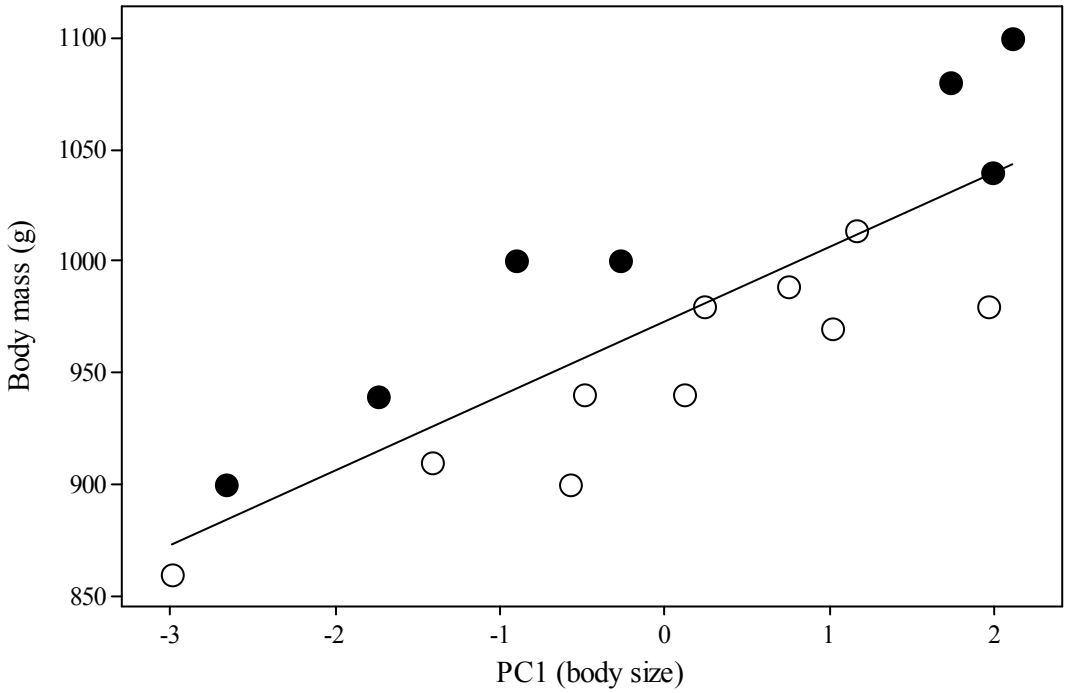

Figure 2.3. Significant linear relationship ($r^2 = 0.66$, $p < 0.001$) between PC1 (body size) and body mass (grams) in adult female Peregrines from Kangerlussuaq and Thule, Greenland. Open circles represent birds from Kangerlussuaq and filled circles from Thule.

Genetics

Genetic diversity

A total of 45 unrelated blood samples were collected from Kangerlussuaq ($n = 27$), Thule ($n = 15$), and Maniitsoq ($n = 5$). All eight microsatellite loci were polymorphic among the three sampling locations (Appendix C). 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, Thule; $H_E = 0.853$, $H_O = 0.400$). 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. I 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 Kangerlussuaq and 44 alleles from Thule (Appendix C). 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 Thule sampling locations (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 genetically indistinguishable.

Table 2.7. 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.

		Microsatellite DNA (8 loci)				Mitochondrial DNA (1,540 bp)			
Sampling location	Sample size (micro/mtDNA)	Mean alleles/locus	Allelic richness[a]	H_O	H_E	Number of haplotypes	Haplotype diversity (*h*)	Nucleotide diversity (*p*)	Tajima's D[b]
Thule	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, $p > 0.05$

Based on 1,540 bp of mtDNA cytb/control region sequence, 12 haplotypes were observed among Greenland Peregrine Falcons (Table 2.7), with two unique haplotypes observed in both Kangerlussuaq and Thule. 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 2.8, Figure 2.4). However, despite unique haplotypes within sampling locations, a single haplotype, A, was observed at high frequency among the three locations (60%; Figure 2.4). 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 sampling location, while nucleotide diversity (π) was similar across sampled populations (0.004; Table 2.7).

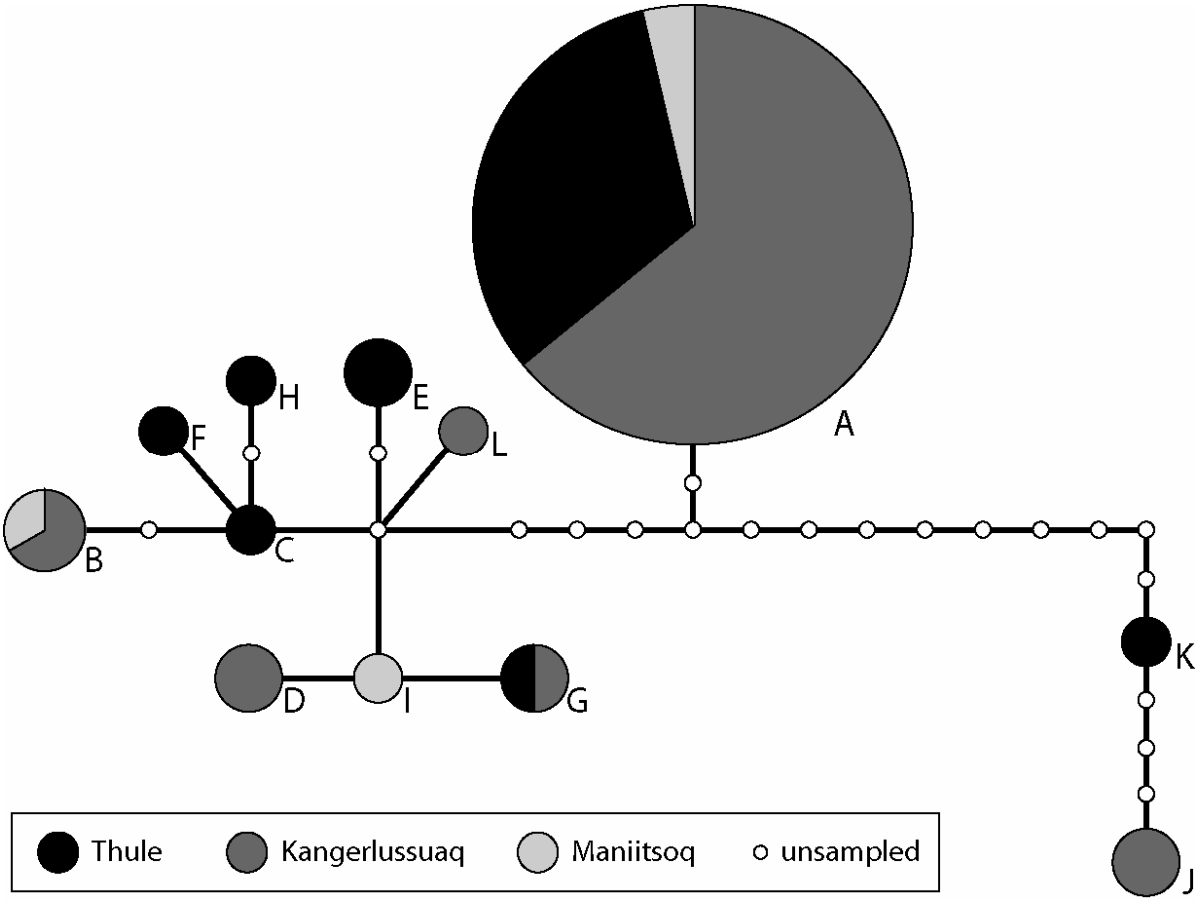

Figure 2.4. A minimum spanning cladogram inferred from maximum parsimony. Each circle represents a single haplotype where the size of the circle corresponds to the number of individuals observed with that particular haplotype. Solid lines represent parsimonious connections between haplotypes with a probability 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 2.8 for the exact number of individuals for each haplotype.

Table 2.8. 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 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.

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

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

No significant pairwise differentiation (F_{ST}) was observed between the three Greenland 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 (Figure 2.4). 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 & J) observed in Kangerlussuaq or Thule required a minimum of 12 point substitution steps to connect to their closest sampled haplotype (Figure 2.4), and both haplotypes contained a single indel not observed in other haplotypes (Table 2.8).

In Kangerlussuaq 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 placed on the female. 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 as one another 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 Kangerlussuaq and Thule, and further suggests that gene flow exists between the two locations.

Satellite-received telemetry

Transmitters: numbers deployed, longevity, and location classes

A total of 18 PTTs were placed on female Peregrines (13 adults, two sub-adults or second year birds, and three juveniles) in 2001 (4), 2002 (6), and 2003 (8) including six adults, two sub-adults, and two juveniles in Thule and seven adults and one juvenile in Kangerlussuaq. All adult females were breeding and captured at the nest either during incubation or rearing of young and fitted with PTTs. One Thule juvenile had the PTT attached in the nest shortly before fledging, the other two juveniles and two sub-adults were caught at ringing stations in their respective study areas. Of the 18 females tagged, 10 began migration with functioning PTTs, nine adults (six from Thule and three from Kangerlussuaq) and the pre-fledgling juvenile tagged in Thule. The fate of the other eight females with tags is unknown. 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 of the falcon or the bird had died with the unit attached. In other cases 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.

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 ± 189.9) (Table 2.9). 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. On average, locations with LC 3–0 made up 59.1% (n = 18, sd ± 6, median = 58.1%) of all the data collected, while the most accurate location classes, LC 3 and 2, made up an average of only 4.0% (n = 18, sd ± 3.7%, median = 3.1%). Locations with LC A, B, and Z made up an average of 41.2% (n = 18, sd ± 5.5, median = 41.9) of all the data collected. 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 (n = 18, sd ± 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 D.

Table 2.9. Number of days PTTs transmitted on female Peregrines.

	n	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

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 2.10). These percentages are much greater, specifically for LC 3–0, than for PTTs on Peregrines 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 receiving more receptions than winter months. Differences most likely were caused by limited snow cover during winter months when during some periods colleagues were unable to check the unit due to winds >150 knots and ambient temperatures <-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.

Table 2.10. 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.

	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]	2,284	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.

Breeding home range

Breeding home ranges were estimated for 13 individual adult female Peregrines, seven in Kangerlussuaq and six in Thule, from 2001 to 2003. For Peregrines 10212 and 10217 in Thule, breeding home ranges were obtained for two seasons, 2001 and 2003 and 2001 and 2002, respectively, and 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 2.11). For Peregrines in Thule, 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.

Table 2.11. Estimated home range size of adult female Peregrines in Thule and Kangerlussuaq, 2001–2003, and the estimated 'range' of the single stationary PTT in Thule Air Base.

		Kangerlussuaq home range in km^2	Thule home range in km^2 [a]		Stationary PTT in Thule in km^2 [b]
90% MCP LC 3–0	Mean±sd	1,475 ± 904	3,021 ± 2,106		104
	Median Range *n*	1,720 175–2,709 7	3,529 305–5,451 8		na
90% MCP LC 3–1	Mean±sd	72 ± 41	183 ± 199		19
	Median Range *n*	62 33–154 7	41 8–491 7		na
95% Kernel LC 3–0	Mean±sd	883 ± 770	2,007 ± 1,777		43
	Median Range *n*	643 158–2,524 7	1,562 427–1,659 8		na
95% Kernel LC 3–1	Mean±sd	144 ± 109	211 ± 259		5
	Median Range *n*	82 52–337 7	123 15–719 6		na
50% Kernel LC 3–0	Mean±sd	181 ± 189	252 ± 140		5
	Median range *n*	123 26–590 7	243 52–483 8		na
50% Kernel LC 3–1	Mean±sd	23 ± 25	31 ± 37		0.8
	Median range *n*	11 7–72 7	21 1–103 6		na

[a]Data represent home ranges from four Peregrines, with two years for two individuals.
[b]Locations from 3 June to 23 September, when adult female Peregrines have been shown to be in Thule.
na–not applicable, information for only a single unit.

Using 90% MCP, adult female Peregrines in Kangerlussuaq had on average 99 (n = 7) locations with LC 3–0 (Table 2.12) and an average estimated breeding home range of 1,475 km^2, while females in Thule had an average of 97 (n = 8) locations with LC 3–0 and an average home range of 3,021 km^2. However, individual breeding home range sizes between populations in the two areas overlapped (Appendix E). No correlation was found between number of locations and breeding home range size (Spearman Rho = 0.17, $p > 0.05$) and the apparent difference between the average breeding home range sizes of adult female Peregrines

in Kangerlussuaq and Thule was significant only at the 10% level (T = 1.89, p = 0.09, df = 9, not equal variances).

Table 2.12. Mean, standard deviation, median, and range of locations used to calculate home range figures in Table 2.11. Values for *n* vary between tests in Table 2.11 because some PTTs did not have sufficient locations for specific tests.

	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
Thule home ranges LC 3–0 (*n* = 8)	97	± 77	62	31–236
Thule home ranges LC 3–1 (*n* = 7)[a]	34	± 25	25	6–84
Thule 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 2.11.

When breeding home range size using locations with LC 3–1 were used to calculate 90% MCP, adult female Peregrines in Kangerlussuaq had an average breeding home range size of 72 km^2 (*n* = 7, average locations = 27), compared to 183 km^2 (*n* = 7, average locations = 34) for females in Thule. 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).

Using fixed 95% kernels with locations with LC 3–0, the average breeding home range size of adult female Peregrines in Kangerlussuaq was 883 km^2 (*n* = 7, average locations = 99) and 1,562 km^2 (*n* = 8, average locations = 97) for Thule females. Size of breeding home ranges overlapped slightly but in general, Thule females had larger ranges than Kangerlussuaq 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 Kangerlussuaq was 144 km^2 ($n = 7$, average locations = 27) and 211 km^2 ($n = 6$, average locations = 38) for females from Thule. Individual range sizes between geographical areas greatly overlapped, and again no difference was found between Kangerlussuaq and Thule (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 km^2 ($n = 7$, average locations = 99) in Kangerlussuaq and 243 km^2 ($n = 8$, average locations = 97) in Thule, 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 km^2 ($n = 7$, average locations = 27) for Kangerlussuaq and 31 km^2 ($n = 6$, average locations = 38) for Thule. 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 ± 51.0, median = 16.0, range = 1.5–159.0) 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 ± 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, I took the total number of locations used to calculate the size of the 90% MCP LC 3–1 (Appendix E) 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 E). 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 F). 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 ($T = 2.54$, $p = 0.02$) 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 not an effect of fewer locations used to calculate range size on MCP LC 3–1.

'Home range size' for the stationary PTT in Thule, 36321, 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 Thule area (see below section on outward migration and return migration). Despite this unit being stationary, estimated range size varied depending upon method of calculation from 104 km^2 using 90% MCP LC 3–0 to 0.8 km^2 using a 50% kernel with LC 3–1 (Table 2.11). 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 (Table 2.13 & 2.14). 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 km^2, 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 (Figures 2.5 & 2.6) while locations with LC 1 were generally within two km of the calculated centre (Figure 2.7). Locations with LC 0 were most commonly within 10 km of the calculated centre, although a number were off from 10 to 50 km (Figure 2.8).

Table 2.13. Home range sizes calculated using locations with LC 3, 2, 1, and 0 from a stationary PTT at Thule Air Base, Greenland, that operated from 30 September 2002 to 20 November 2003.

	LC3 area in km^2 (n = 91 locations)	LC2 area in km^2 (n = 303 locations)	LC1 area in km^2 (n = 611 locations)	LC0 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

Table 2.14. Average distance (km) each location varies 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.

	LC3 (n = 91 locations)	LC2 (n = 303 locations)	LC1 (n = 611 locations)	LC0 (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

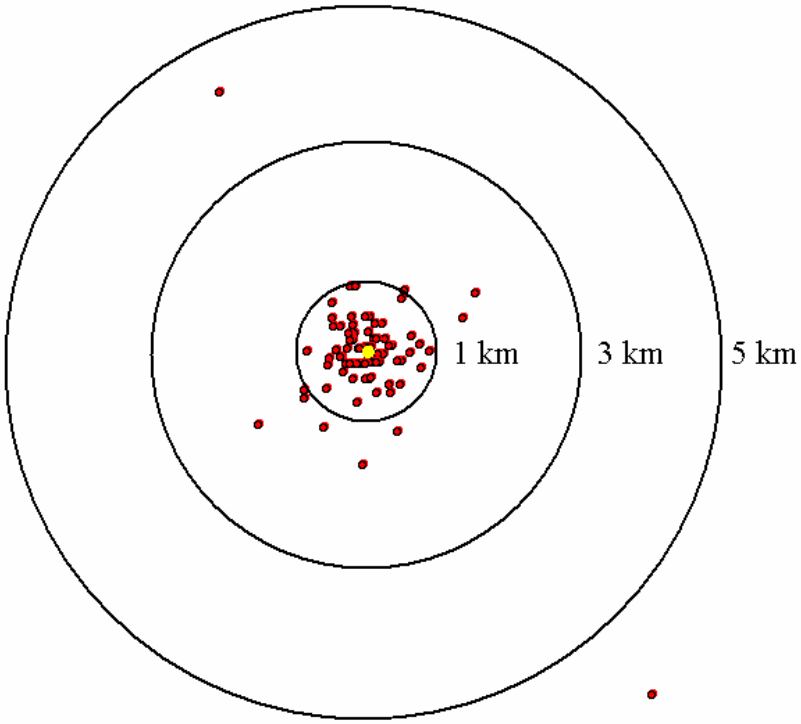

Figure 2.5. Distribution of 91 locations with location class 3 received from a stationary PTT at Thule Air Base, Greenland, which operated from 30 September 2002 to 20 November 2003. Yellow dot is centre.

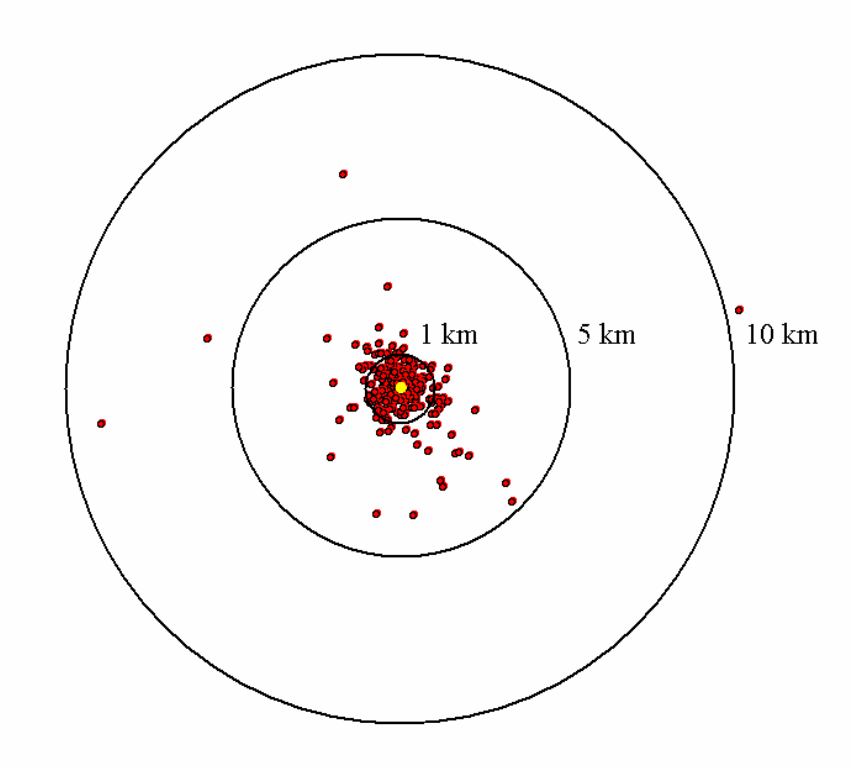

Figure 2.6. Distribution of 303 locations with location class 2 received from a stationary PTT at Thule Air Base, Greenland, which operated from 30 September 2002 to 20 November 2003. Yellow dot is centre.

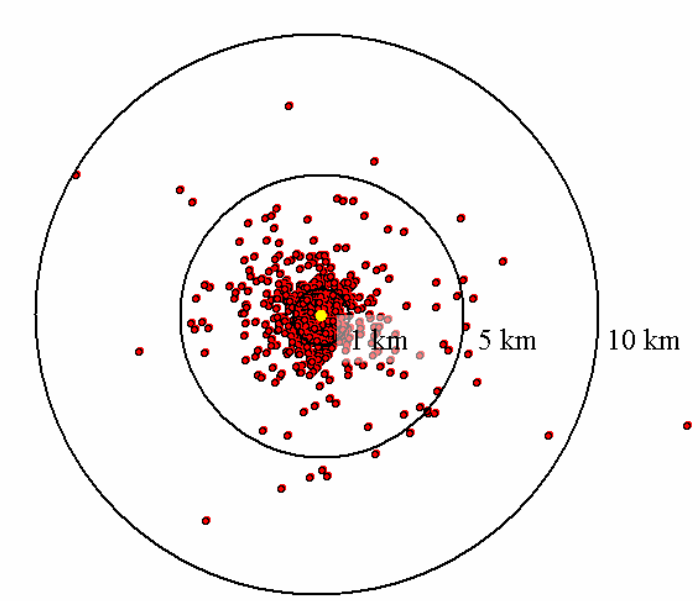

Figure 2.7. Distribution of 611 locations with location class 1 received from a stationary PTT at Thule Air Base, Greenland, which operated from 30 September 2002 to 20 November 2003. Yellow dot is centre.

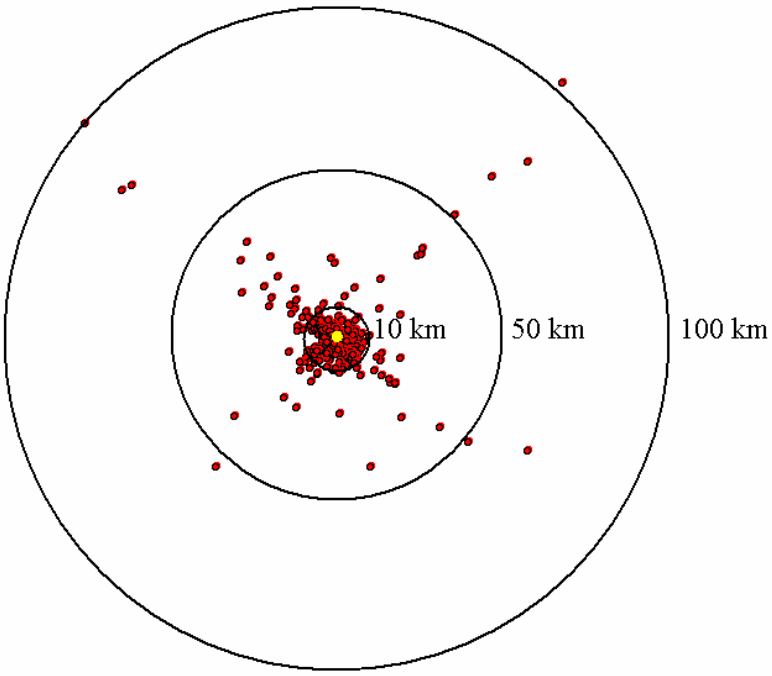

Figure 2.8. Distribution of 506 locations with location class 0 received from a stationary PTT at Thule Air Base, Greenland, which operated from 30 September 2002 to 20 November 2003. Yellow dot is centre.

Based on the above results, PTT locations are much less accurate than claimed by Argos, although some of this difference may be caused by the PTTs not being tested in the same conditions. Locations with LC 0 were on average 11 km from the actual position of the PTT. However, 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. Considering the very large range sizes estimated for Peregrines, the level of inaccuracy is tolerable only when using locations with LC 3–1.

Despite no significant differences being found, 11 of 12 measures of range size indicated larger ranges for females in Thule than in Kangerlussuaq. 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 Kangerlussuaq between 25 August and 5 October (average = 20 Sept., $n = 3$, median = 2 Oct.) and from Thule 8 to 23 September (average = 16 Sept., $n = 8$, median = 16 Sept.). In Thule 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 Thule 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 Thule with the pre-migration area approximately 58 km from the nest, and in Kangerlussuaq for Peregrines 35238 and 41438 with pre-migration areas approximately 122 and 136 km from the nest, respectively. Peregrine 10217 used the Carey Islands (Figure 1.5) as a pre-migration area while the two Peregrines from Kangerlussuaq travelled from their inland breeding areas directly west until reaching the coast.

For Thule, five complete outward migrations were obtained from four adult female Peregrines, with 10212 having complete outward migrations in 2002 and 2003 (Table 2.15). In Kangerlussuaq only one complete outward migration was obtained, from Peregrine 35238. For Thule, 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 Thule, and for one duty cycle before reaching the winter range, with normal functioning resuming after reaching the winter home range.

Table 2.15. Complete outward migrations of female Peregrine Falcons from Thule and Kangerlussuaq, Greenland (distances given as Great Circle Distances).

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)
Thule 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
Thule 10217	15 Sep 01–10 Nov 01	10,836	190	57	49 (86.0)	13–1,349	0, 3, 10, 34
Thule 36015	10 Sep 03–14 Nov 03	12,438	188	66	15 (22.7)	81–588	0, 3, 4, 6
Thule 36017	17 Sep 03–25 Nov 03	12,370	177	70	16 (22.9)	108–482	0, 1, 7, 6
Kanger. 35238	5 Oct 03–6 Nov 03	3,235	98	33	11 (33.3)	3–332	0, 1, 5, 3

[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.

The average distance for outward migrations of Peregrines from Thule was 10,794 km (n = 4, sd ± 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 greatest number of days with locations received during migration (Table 2.15). The overall distance falcons travelled varied widely from 7,532 to 12,438 km, with 36015 travelling the greatest distance and latitudinal shift (>100°), and 36017 the largest range of longitudinal shift (>41°). The

single adult female 35238 from Kangerlussuaq that completed the outward migration travelled 3,235 km while covering approximately 23.6° of latitude.

Of the four individuals that completed the outward migration from Thule, two (10212 and 10217) used the Central Flyway, including 10212 in consecutive years, while 36017 used the Eastern Flyway (Figure 2.9). Female 36014 from Thule used a combination of the two flyways, crossing diagonally from the southwest corner of Hudson Bay east into Florida. Peregrine 35238 from Kangerlussuaq used the Eastern Flyway.

The calculated average speed of migration for birds from Thule was 205 km/day ($n = 5$, sd ± 37, median = 190, range = 177–269) (Table 2.15). 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 Thule was 269 km/day (10212), and the slowest 177 km/day (36017). From Kangerlussuaq, falcon 35238 travelled at 98 km/day.

The individual measured speed of migration per day by Thule Peregrines ranged from >1,349 km, when 10217 crossed the Gulf of Mexico in a single day, to <13 km, again 10217 shortly after arriving in Mexico (Figure 2.9). Peregrine 36017 showed the least variation between the shortest and furthest distance travelled on any given day, >320 km, and 10217 showed the most fluctuation, >1,336 km (Table 2.15). Kangerlussuaq Peregrine 35238 had a minimum range from 3 to 332 km travelled per day. Considering the inaccuracy of satellite-based tracking using the Argos system (see above), 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.

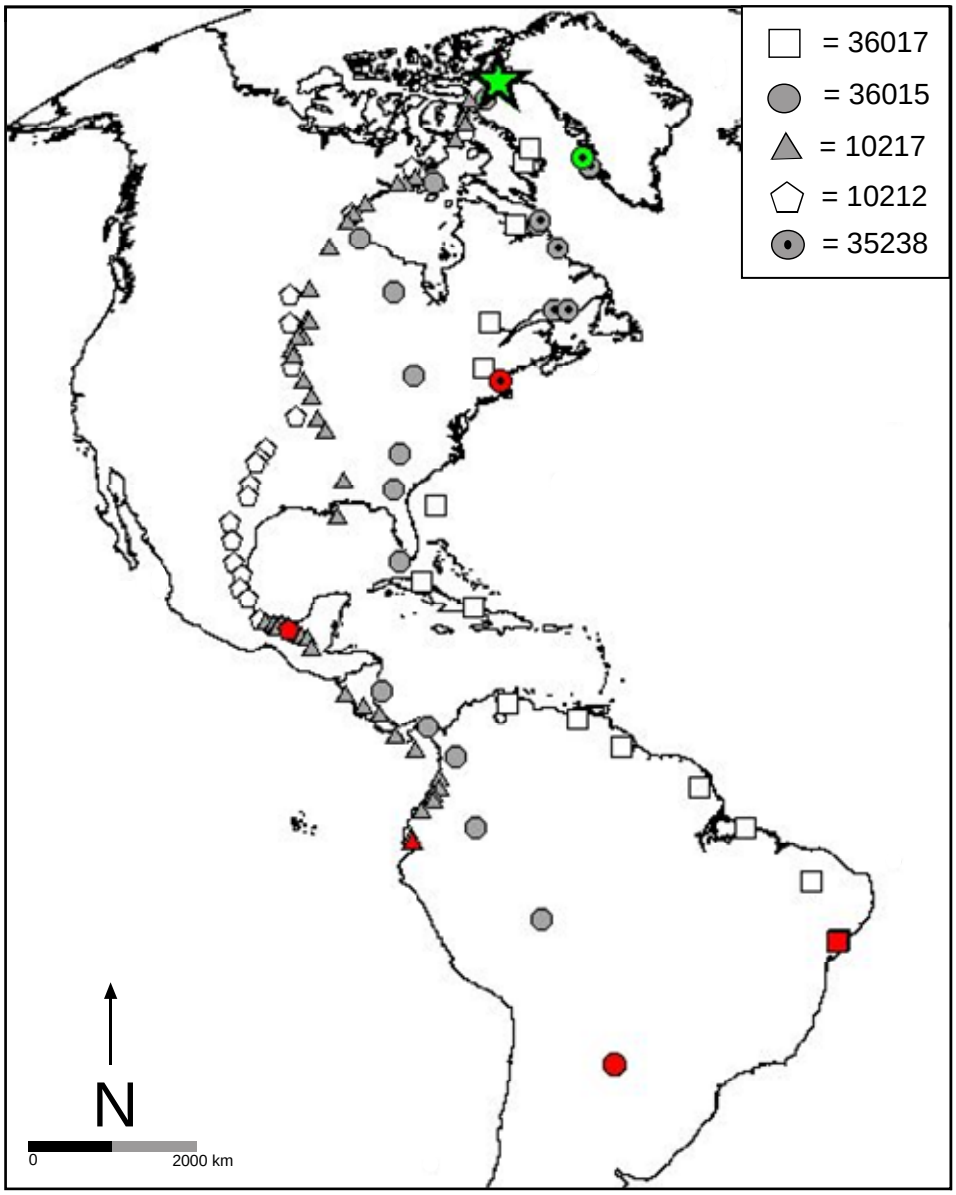

Figure 2.9. Outward migration routes for five adult female Peregrine Falcons tagged with PTTs in Thule (n = 4) and Kangerlussuaq (n = 1), from 2001 to 2003. The green star represents the starting location of females in Thule and the green circle with black dot the starting location for the female from Kangerlussuaq. Red symbols designate winter home ranges. Only days with locations with LC 3–0 are included and only a single location has been included for each day.

The time spent on outward migration by Thule Peregrines ranged from 28 to 70 days and had a significant positive relationship with total migration distance ($r^2 = 0.72$, $p = 0.02$) (Figure 2.10). Overall, Peregrines from Thule 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 Kangerlussuaq 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 travelled 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.

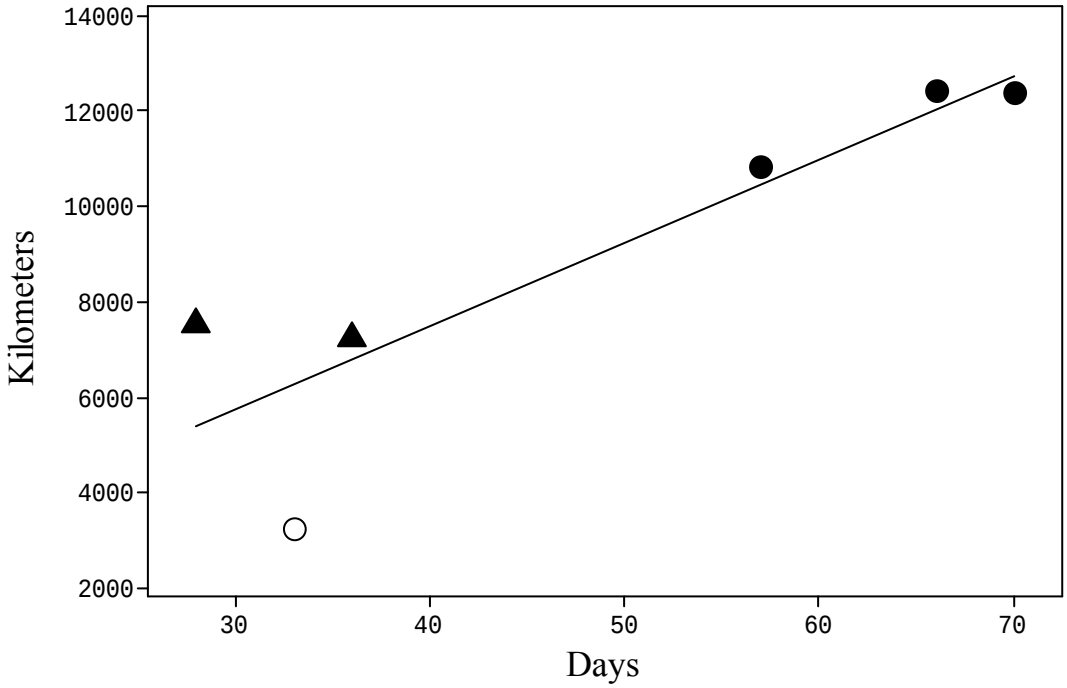

Figure 2.10. Positive significant relationship between overall migration distance and days spent on migration for adult female Peregrines from Greenland ($r^2 = 0.72$, $p = 0.02$). Filled circles are Peregrines from Thule, open circle from Kangerlussuaq. Filled triangles represent the same individual from Thule, 10212, in two separate years.

Peregrines from Thule clearly did not avoid crossing large bodies of water, with 10217, 36015, and 36017 all crossing the Gulf of Mexico or Caribbean Sea, with two of the three birds probably using islands. However, three Peregrines from Thule followed the west coast of Hudson Bay instead of crossing over the water. Peregrines 10212 and 36015 travelled closest to the most direct route possible from the breeding to winter range, the Great Circle Distance (GCD), travelling only 11.9 and 11.2% farther than the GCD, respectively. However, 10217

and 36017 travelled 23.1 and 24.1% farther than the GCD, respectively. Peregrine 35238 from Kangerlussuaq travelled 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 Thule varied from 13 October to 25 November. Median arrival date was 12 November ($n = 4$). Peregrine 10212 is shown twice in Table 11 (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 Thule. Peregrines 36015 and 36017 travelled the furthest distance from Thule and had the latest arrival dates, 14 and 25 November, respectively. Female 10212 had the earliest arrival dates while travelling the shortest distance. The arrival date for 35238 from Kangerlussuaq was on 6 November.

Incomplete data on outward migrations were collected from three other adult female Peregrines, two from Kangerlussuaq and one from Thule, and one juvenile female Peregrine from Thule (Table 2.16). Peregrines 35236 and 41438 from Kangerlussuaq travelled at speeds of 50 and 208 km/day, respectively. Peregrine 10212 from Thule travelled at 181 km/day, while the juvenile Peregrine from Thule, 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.

Table 2.16. Incomplete outward migrations from 2001 to 2003 of female Peregrine Falcons from Thule and Kangerlussuaq encompassing ≥10 days of travel (distances as Great Circle Distances).

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)
Thule 10212	14 Sep 01–6 Oct 01	4,156	181	23	22 (95.7)	7–913	1, 2, 10, 8
Thule 10292[c]	24 Sep 01–3 Oct 01	2,826	283	10	8 (80.0)	61–526	0, 2, 3, 2
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

[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.

All incomplete outward migration routes had a minimum of 10 days of locations collected, providing an accurate description of the initial migration route taken (Figure 2.11). The route for 10212 follows the same initial path as taken in 2003 when a complete migration was collected for the same bird (see Figures 2.9 & 2.11). The juvenile female Peregrine from Thule, 10292, took a route not used by other Thule Peregrines, travelling farther west into Canada before turning south, almost as if disoriented. Peregrine 35236 travelled the first 27 days of migration (605 km, 22 km/day) in Greenland before crossing the Davis Strait to Canada on day 28, covering 804 km in one day. Adult female 41438 from Kangerlussuaq crossed directly into Canada and went south.

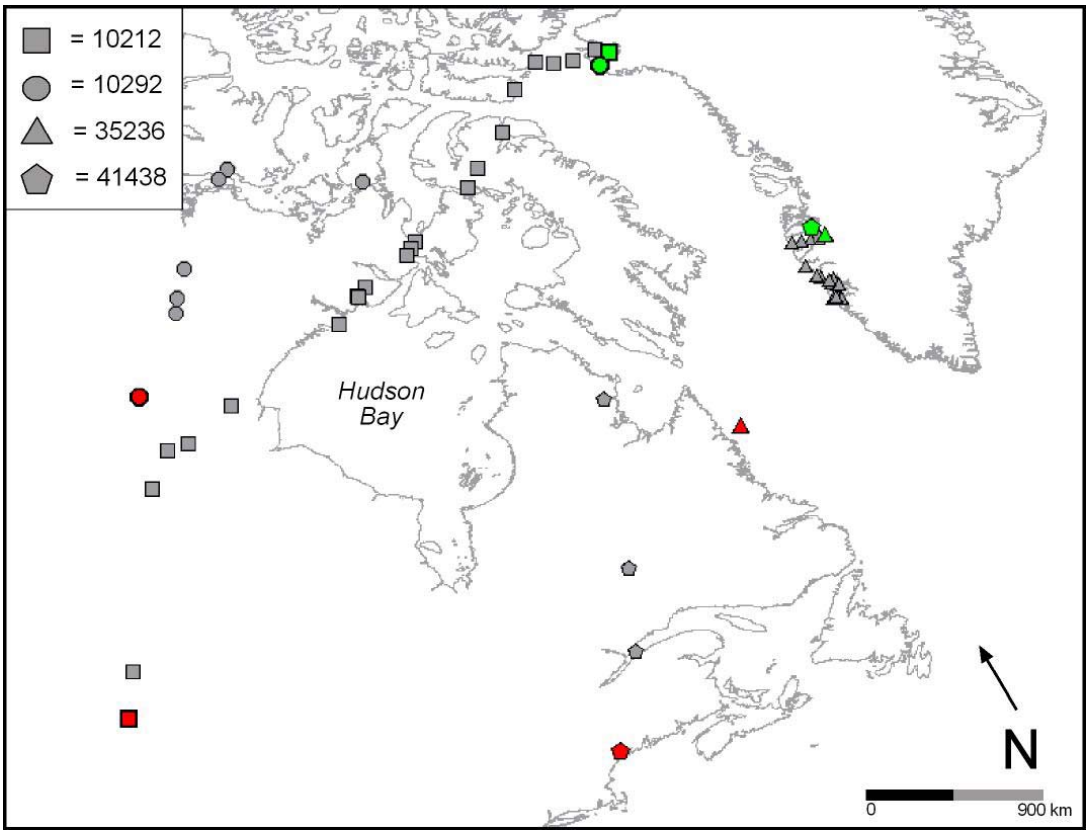

Figure 2.11. Incomplete outward migration routes used by three adult female Peregrines and one juvenile female Peregrine from Thule and Kangerlussuaq, from 2001 to 2003. Green symbols represent starting locations and red symbols the last location received for each bird. Only locations with LC 3–0 were used and only a single location was included per day.

Winter range

Adult females from Thule wintered in southern Mexico, Ecuador, Brazil, and Paraguay, with the lone individual from Kangerlussuaq wintering in the northeast United States (Figure 2.9). 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 2.17). On average, 43 (sd = 28) locations were received per individual Peregrine, with 10217 and 35238 only providing nine and eight locations, respectively. Additionally, locations for bird 35328 were received for only one month after it had reached the winter range and, although a winter range area is given in Table 2.17, it will be excluded from further analysis because the bird may have moved further south at a later date.

Table 2.17. Winter range in square kilometers for adult female Peregrine Falcons from Thule and Kangerlussuaq.

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
Thule 10212	2002/2003	961	1,230, *	286, *	0, 1, 9, 50
	2003/2004	779	1,070, *	134, *	1, 0, 5, 48
Thule 10217	2001/2002	511	1,724, *	216, *	0, 2, 0, 7
Thule 36015	2003/2004	907	907, *	178, *	0, 2, 9, 63
Thule 36017	2003/2004	1,659	2,193, *	512, *	1, 1, 9, 41
Kanger. 35238	2003/2004	4,147	12,541, *	2,587, *	0, 1, 3, 4

*not enough data to establish a meaningful value

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 ± 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.

Return migration

From 2001 to 2003, Peregrines marked in Thule 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 2.18, Figure 2.12). 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.

Table 2.18. Complete return migrations of female Peregrine Falcons from Thule, Greenland (distances as Great Circle Distances).

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)
Thule 10212	7 May 03–3 June 03	7,715	276	28	20 (71.4)	28–550	0, 0, 3, 15
Thule 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.

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. 10212 travelled 75 km/day faster on return migration in 2003 compared to outward migration the previous autumn, 2002, yet only 7 km/day faster than the outward

migration in 2003. Peregrine 10217 spent 55 days on outward migration and 57 on return migration, travelling at a speed of 201 versus 191 km/per day, respectively.

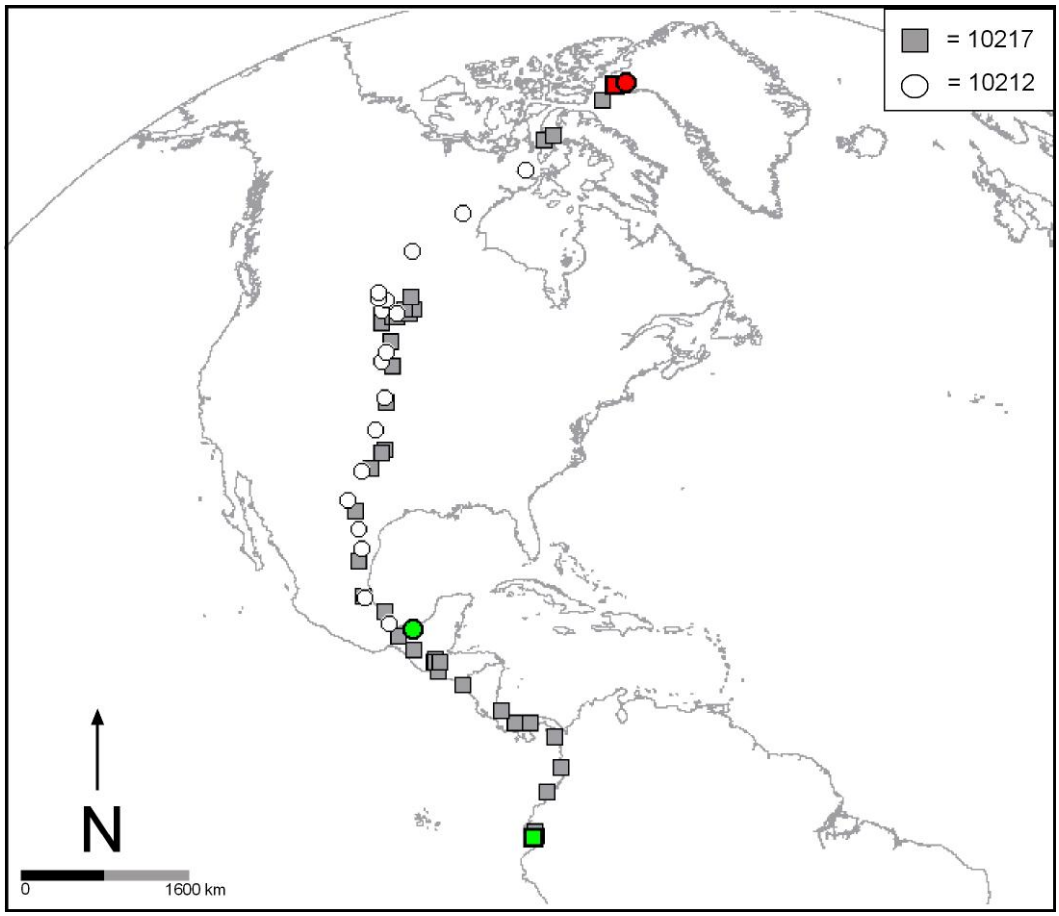

Figure 2.12. Return migration routes used by two adult female Peregrine Falcons fitted with PTTs in Thule. All days when locations with LC 3–0 were received were included a single time. Start of return migration is in green while end of return migration is in red.

Peregrine 10212 travelled 7,715 km on return migration compared to 7,532 km on outward migration (183 km difference) and 10217 travelled 11,071 km going north versus 10,836 km south (235 km difference). The difference between the actual distance travelled 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.

Climatic trends

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. Nevertheless, I felt it important to examine recent temperature trends from the Thule study area, where weather data have been collected, but to my knowledge, not previously analyzed. My analyses of the 27-year period of weather data from Thule Air Base for May through September show temperatures consistently increased for 46 of 54 regression analyses performed (Appendices G, H, & I).

Mean monthly temperature increased for all regression analyses except for July, in the 27-year period 1979–2005, and June, for the 10-year period 1996–2005. The month of May (1.8 °C) showed the largest temperature increase from 1979–2005, followed by September (1.4 °C) and August (1.2 °C), the last months of the summer season. For the 15-year period from 1991 to 2005, August showed the largest increase, 3.4 °C, with May (1.9 °C) and September (1.7 °C) being next largest. The 10-year period 1996–2005 showed the greatest overall temperature increases for four months, with August temperature increasing 3.9 °C, September 3.6 °C, May 1.8 °C, and July 1.8 °C. This trend is further supported by examining the slope of the regression line for the average of the mean monthly temperatures over the five months, with the slope increasing from 0.04 for the period from 1979 to 2005 to 0.12 from 1991 to 2005 and then to 0.22 from 1996 to 2005 (Figure 2.13, see Appendix G for regression equations, t, p, and r^2 values for mean monthly temperature analyses). In other words, the most rapid increases have occurred in the past 10 years.

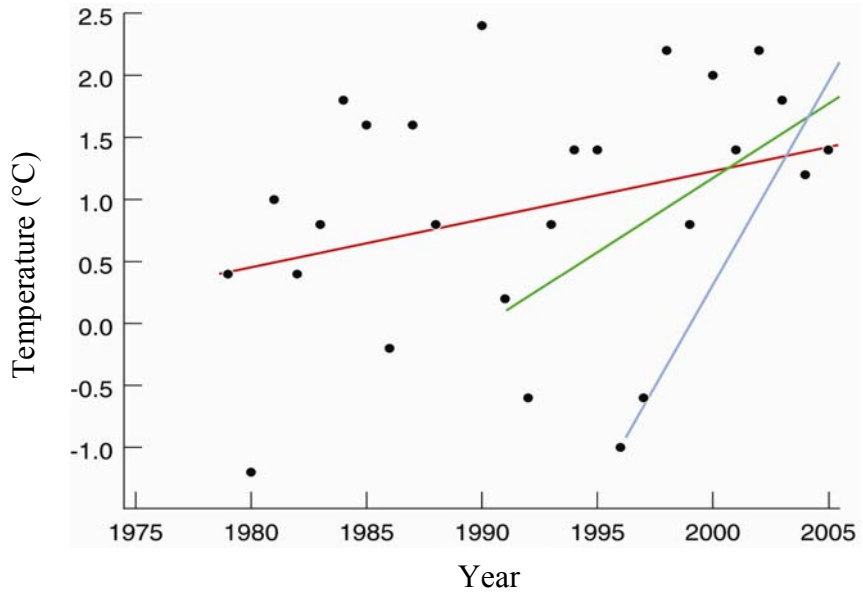

Figure 2.13. Trends in the average of the mean monthly temperatures (May–September) over time at Thule Air Base, Greenland, for the years 1979 to 2005 (red line), 1991 to 2005 (green line), and 1996 to 2005 (blue line).

Minimum monthly temperatures increased in 14 of 18 regression analyses. For the period 1979 to 2005, May showed the largest warming trend (5.3 °C) followed by September (1.6 °C), with the three months in-between having a negative trend. From 1991 to 2005 July showed the greatest increase in temperature, 2.3 °C, followed by September (1.9 °C) and May (1.9 °C). The period from 1996 to 2005 was characterized by a negative temperature trend in May, -1.4 °C, with August showing a large warming trend, 4.9 °C, and July (1.6 °C) and September (1.3 °C) a smaller increase in temperature. Averaging the five months together, the slope of the regression line increased during each period, from 0.02 during the period from 1979 to 2005 to 0.09 from 1991 to 2005 and 0.13 from 1996 to 2005 (Figure 2.14, see Appendix H for regression equations, t, p, and r^2 values for mean monthly temperature analyses). Again, the most recent 10-year period showed the steepest rise.

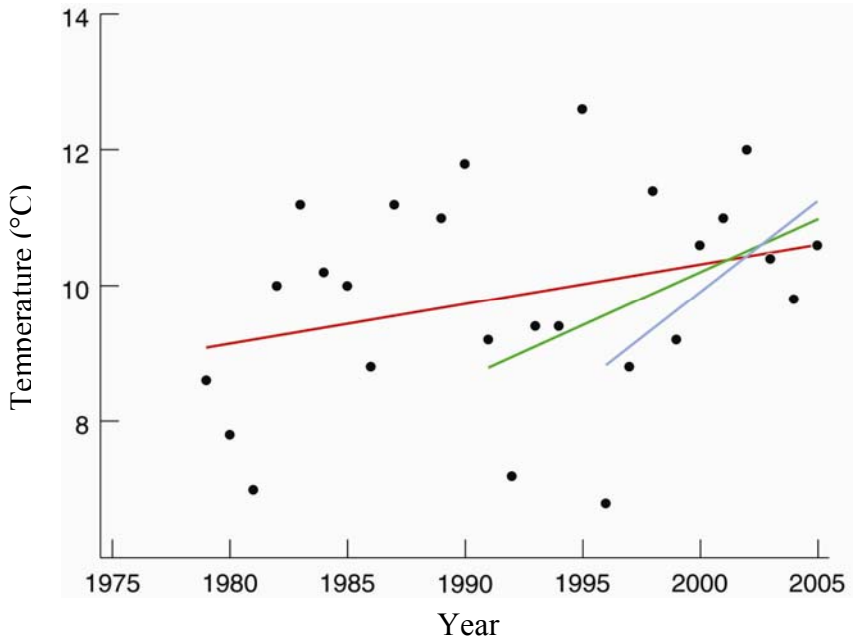

Figure 2.14. Trends in the average of the maximum monthly temperatures (May–September) over time at Thule Air Base, Greenland, for the years 1979 to 2005 (red line), 1991 to 2005 (green line), and 1996 to 2005 (blue line).

Mean maximum monthly temperature increased for 16 of the 18 regression analyses. For the period 1979 to 2005 August showed the largest increase, 1.9 °C, followed by May (1.9 °C) and September (1.2 °C). For the 15-year period from 1991 to 2005, all months had large increases, starting with May (3.1 °C), followed by August (2.8 °C) and June (2.6 °C). The period from 1996 to 2005 showed perhaps the largest increase for any of the temperature analyses, with May showing a positive trend of 8.5 °C followed by September (4.6 °C) and July (3.7 °C). Additionally, when examining the average of the maximum monthly temperatures over the five months, the slope increased the most of any of the three measurements, increasing from 0.06 from 1979 to 2006, to 0.16 from 1991 to 2005, to a high of 0.27 for the period from 1996 to 2005 (Figure 2.15, see Appendix I for regression equations, t, p, and r^2 values for mean monthly temperature analyses).

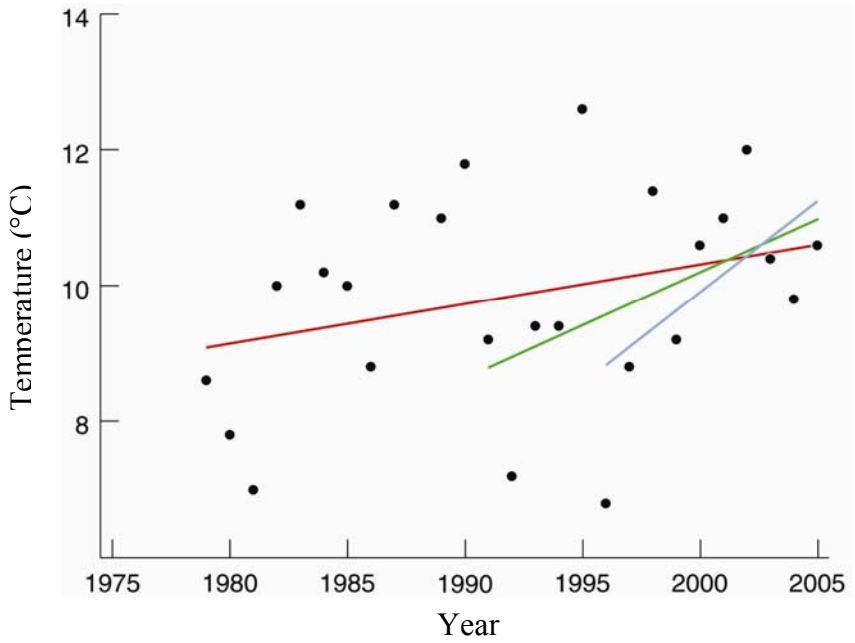

Figure 2.15. Trends in the average of the maximum monthly temperatures (May–September) over time at Thule Air Base, Greenland, for the years 1979 to 2005 (red line), 1991 to 2005 (green line), and 1996 to 2005 (blue line).

In summary, although no statistically significant increases were found in any of the particular monthly temperatures over time, there was clearly an overall warming trend in the Thule area. Of the five months analyzed using linear regression, September was the only month to never show a negative trend in association with any temperature variable over any of the time periods, with May and August only showing a negative trend in one instance each (Appendices G, H, & I). In general, the months May, August, and September showed the greatest amount of warming over all time periods. However, for the most recent 10-year period, from 1996 to 2005, August and September show perhaps the largest amounts of warming amongst all three temperature variables examined. Furthermore, for all three measured variables the 10-year period from 1996 to 2005 showed the greatest increases. These trends could have had the effect of lengthening the favourable summer season at Thule over the years covered.

Though none of the 46 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 46 or more of 54 to be positive is less than 0.0001%, clearly supporting an increasing trend in temperature.

DISCUSSION

It is difficult to determine where the world's most northern-nesting Peregrine Falcons are, but in the Western Hemisphere, the Thule area population (77° N) must be near the northern limit. For the Alaskan/Canadian Arctic, Peregrines have been reported nesting only as far north as Melville Island (c.75° N), but two birds have been reported seen as far as Axel Heiberg Island at 79.7° N (Ross 1974). In the Eastern Hemisphere, Dement'ev and Gladkov (1951) reported Peregrine breeding sites generally "in Novaya Zemlya to Matochkin Shar Strait (most northern point-Gemskerk Land-78° N)" and "Markham Land north of Taimyr Peninsula (75°30' N); and even further north (76° N) on Stalinets Island around Cape Tillo and Khatanga River (Krestovye Yary cliffs, 72°46' N)." 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 Kangerlussuaq and South Greenland 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 back 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 Peregrine population was ever recorded, DDE was detected in eggs during the 1970s by Walker *et al*. (1973) and Burnham & Mattox (1984), with Burnham & Mattox (1984) 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 Kangerlussuaq, 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 Kangerlussuaq, shows a decline in DDE levels beginning around 1980, to levels well below those associated with any reproductive impact (Jarman *et al*. 1994). Additionally, based on eggshell fragments and whole eggs collected between 1972 and 2003 in Kangerlussuaq and South Greenland, Falk *et al*. (2006) found that eggshells over that period increased in thickness by an average of 0.19% per

year. This finding corresponds well with what has been reported as a "stable" population from 1972 to 1982 by Burnham & Mattox (1984) and later an increasing population, reported by Mattox & Seegar (1984), 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 Kangerlussuaq 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 Kangerlussuaq. 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 contiguous United States and southern Canada have had on the increased sizes of arctic Peregrine populations is unknown. However, evidence from Figure 2.4, 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 Thule area appears to be much lower than those found by Restani & Mattox (2000) and Falk & Møller (1988, 2005) for Kangerlussuaq and South Greenland, 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 near Thule, these populations had much greater densities than Thule (Beebe 1960, White 1975). However, the Thule 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 Thule area pre-DDT, it seems probable that Peregrines have slowly colonized the Thule 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 Thule population is still increasing and not yet at capacity.

Nest site characteristics

Nest site characteristics in the Thule area differ from those in Kangerlussuaq and South Greenland 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, and snow banks and glaciers regularly occurring at elevations above 300–400 m, this is not a surprise. Nesting cliffs used in Thule, Kangerlussuaq, and South Greenland 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 Thule and South Greenland while they are oriented more to the south in Kangerlussuaq. However, Wightman (2001) reports for Kangerlussuaq 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 Thule severe winds of 100–130 knots occur during each breeding season, causing driving precipitation and potential chilling, 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 Thule area. When compared to Kangerlussuaq, nest ledges in Thule are much smaller, being on average 520 cm shorter in length and 99 cm shorter in depth. Furthermore, the horizontal angle of exposure in Thule is 25° and 10° less than South Greenland and Kangerlussuaq, 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 Thule 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 Thule. 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, 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 I 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 (1876) 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." However, no Peregrines or Gyrfalcons were collected or seen. Peary, from 1891 to 1896, spent many months in the Thule 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 Northern 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 Thule area, as they are still unfamiliar with them.

I have located both breeding and non-breeding Peregrines over a large area. Although I 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 Thule and Kangerlussuaq (67° N) study areas and the Thule and the South Greenland (60.5–61.0° N) study areas are separated by approximately 1,100 km and 9E 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 Thule 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 ephemeral 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 and Mattox (2000) found broods that produced 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 three 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), I calculated a 14-year average hatch date of 10 July and a 42-day-of-age average fledging date of 21 August (Table 2.3). For Thule, 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

Thule are about six-to-seven days later for each location from south to north, or 12–13 days for the whole ~17° latitudinal span.

Based on information from Kangerlussuaq, I estimate 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 at Kangerlussuaq and the dispersal of young from nest sites (Sherrod 1983), but less well for Thule (see below).

Home range size

While breeding home range and winter range sizes were calculated for adult female Peregrines from Kangerlussuaq and Thule by using PTTs, this information must be considered cautiously. Data from the stationary PTT in Thule (Tables 2.11, 2.13, 2.14) 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 2.11, 2.12, and

Appendix E). This procedure allows readers to draw their own conclusions based on the data, since in reality 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 Thule emerged as larger than in Kangerlussuaq (Table 2.11) 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 Kangerlussuaq being higher than in the Thule study area, possibly resulting in more territorial conflicts that may compress home ranges, while in contrast, the Thule population may be well below capacity level, facilitating larger range sizes. In addition, Thule Peregrines are primarily hunting passing Dovekies 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 Kangerlussuaq (1,475 km^2, $n = 7$) and Thule (3,021 km^2, $n = 8$) were both larger than those found by Ganusevich *et al.* (2004) (1,175 km^2, $n = 4$), 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. 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 km^2 for 13 adult females and one adult male wintering along the coast of the Gulf of Mexico. Using 90% MCP LC 3–0, I

calculated an average winter range size of 1,077 km^2, based on four winter range sizes with >10 locations (Table 2.17). I had too few locations with LC 3–1 to calculate the equivalent range size and my results do not allow for a meaningful comparison of winter range sizes between the two studies.

Timing of breeding and migration

PTTs show two adult female Peregrines arrived in Thule on 3 June (Table 2.18), one each in 2002 and 2003. Egg laying in Thule Peregrines begins about 7 June. Observations in Kangerlussuaq 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 at Thule by about one week.

In Thule, 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 Thule and began outward migration on 23 September. However, in 2002, a juvenile adult 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.). 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 Thule was 16 September (n = 8). Of the four adult females that completed the outward migration from Thule, 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 Kangerlussuaq, 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, I do not have same nest information on fledging date and departure date of adult females, and the 19-day post fledging period I give for Thule is a rough estimate, and may be off by up to several weeks. Given the much shorter breeding window in Thule it seems likely the post fledging period is shorter than in Kangerlussuaq.

Ringing recoveries 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 travelled 8,624 km at a speed of 172 km/day during outward migration. Thule females tagged during this study travelled an average of 10,794 km (n = 4) at a speed of 205 km/day (n = 5) during outward migration (Table 2.15), over 2,000 km farther and 30 km/day faster. This difference may be expected as the Peregrines in Thule 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 travelled at a speed of 201 km/day compared to 269 km/day in 2003, while both years wintering in the same location (Table 2.13). These results within Greenland extend the leapfrog migration pattern of Peregrines previously described by Newton (2003b).

As stated by O'Reilly and 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 travelled 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 Thule. Considering the separation 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. In conclusion, 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 juvenile survival, may benefit from having more time after fledging until outward migration is necessary and food supply declines.

Weather impacts

Weather has been demonstrated to affect breeding success of Peregrines in the Arctic (Bradley *et al.* 1997). Despite the harsh High Arctic conditions, Peregrine reproductive rates around Thule compare very favorably with those in South Greenland and Kangerlussuaq. 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, Falk & Møller 2005). For Kangerlussuaq, 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 Thule 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 Thule, although weather can be severe, long periods of precipitation were unusual in recent years. Weather-caused nest failures in Thule may now be no more frequent than for more southern West Greenland Peregrine populations, especially considering the greater protection afforded by nests in Thule. 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 importantly influence Peregrine populations. In Kangerlussuaq 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). 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, except for Snow Buntings which occur at low densities, the other more common passerine prey species and wetland species do not arrive until

mid-May, about the same time as Peregrines (Salomonsen 1950–51, Falk *et al.* 1986). Falk *et al.* (1986) also points out that fledging dates of Peregrines and passerines are similar for South Greenland and Kangerlussuaq. Salomonsen (1967) reports that Dovekies arrive in the first half of May in North Greenland, probably prior to Peregrines. Even when Peregrines do arrive, the locations where Dovekies may occur and be available as prey are influenced by sea ice, as Dovekies need open water to feed. Passerines arrive in June and are mostly gone by early September. Dovekies depart from nesting sites by mid-to-late August, and Dovekies and most other potential prey are gone from North Greenland by early September (Salomonsen 1950–51). 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 1950–51). Salomonsen (1950–51) calls Black Guillemots "extremely hardy and is the last bird in the autumn to yield to the ice."

Given the age of Salomonsen's (1950–51) 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 Black-legged Kittiwakes that "The departure has been delayed in recent years, owing to the amelioration of the climate." Additionally, from my own experience from 1993–2005 in the Thule area, in late-August through late-September I 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 Dovekies 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 at 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 in Thule for at least 30 years (longest resident at Thule). 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 I 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 Thick-billed Murres 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 to suggest that a warming trend in climate is occurring in the Arctic, as in many other regions (Overpeck *et al.* 1997, Morison *et al.* 2000, Hassol 2004). No evidence has yet been reported as to whether or how this may be affecting falcons. In Greenland, however, favourable ecological conditions would seem to be promoting the expansion of Peregrine populations, specifically in the Thule 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 has been occupied by Peregrines for >75 years in Thule. 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 yearly basis until the 1980s. One 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 Thule 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 were likely unsuccessful and a local population was never established, with adults dying off over time and only being replaced by new breeders when new immigration took place. Only in recent times (ca. late 1980s to present), 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 Thule have been occupied every year after the nest was initially found (Table 2.2), 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 Thule is expanding out from 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.

Overall body size of Peregrines, measured as PC1, is not significantly different between female Peregrines in Kangerlussuaq and Thule. However, the average mass of females between the two areas is significantly different; with Thule females weighing more than Kangerlussuaq individuals of the same body size (Figure 2.3). 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 Thule 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.

From the 1890s through the 1930s the Arctic warmed at a rapid rate (Kukla *et al.* 1977, Kelly *et al*. 1982), with Putnins (1970) identifying the period in Greenland from 1909 to 1929

as a consistent time of steady warming. The period from 1943 to 1955 was also characterized by Putnins (1970) as warming, except at Upernavik (560 km southeast of Thule) (which at the time was the closest weather station to Thule), where temperatures were first recorded in 1946 (Box 2002). Box (2002) identified several statistically significant temperature trends in west Greenland, with warming from 1873 to 1930 and 1985 to 2001, and a period of cooling from 1930 to 1990. This agrees with Kelly *et al*. (1982) who identified the 1940s as the beginning of a cooling period, with the Arctic as a whole cooling approximately 0.85 °C from the 1930s to 1960s (annual data) and temperatures only beginning to increase again in the late 1970s. Additionally, for the Canadian High Arctic and northwest Greenland, Bradley & England (1978) concluded that a major climate change occurred in approximately 1963–64, with the mean freezing level height (elevation) dropping up to 500 m in July and mean July maximum surface temperatures decreasing up to 2.7 °C, with levels staying low throughout the study which ended around 1976.

Temperature increases appear to have begun in the late 1970s to early 1980s in the Thule 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 Thule (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.

My 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, monthly minimum 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 (Appendices G, H, & I). Additionally, based on my analyses of the last 10 (1996–2005) and 15 (1991–2005) years of data compared to the entire 27-year period the warming trend has rapidly increased (Figures 2.13, 2.14, & 2.15), with the mean monthly temperature increasing 3.9 °C and 3.6 °C for the months of August and September, respectively, for the 10-year period from 1996 to 2005 (Appendix G).

Even though the above-mentioned temperature changes are relatively small, they could have an important impact on the climate in Thule, 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 Dovekies and other birds earlier access to breeding and foraging areas, both of which would have been covered by snow and sea ice, respectively. However, and perhaps most importantly, warmer autumns, specifically the month of September, may allow prey species for Peregrines to remain in the Thule 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 above-mentioned cooling period from the 1930s through the late 1970s likely made for a climate in Thule 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 Thule 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 Thule 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, effectively 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 in the Thule region (1993–2005) 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 Thule area, northwest Greenland. This population may compose the most northern nesting Peregrines in the world. Peregrine populations also exist in 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 Thule nest on coastal cliffs, primarily feeding on Dovekies that occur there in the tens of millions. Peregrines breeding to the south in Kangerlussuaq nest on cliffs in a large ice-free inland area and feed primarily on small passerines. The Thule 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 Thule and Kangerlussuaq 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 Thule Peregrines than those in Kangerlussuaq. The Peregrine population in Kangerlussuaq may be at carrying capacity for the habitat because almost all cliffs that appear suitable are regularly occupied. Genetically, Peregrines from both the Thule and Kangerlussuaq populations are essentially the same. Because of the significant lack of morphological and genetic differences, I conclude that the newly-discovered Thule 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 Thule females arrive at nest cliffs in the spring about two weeks later and depart from sites two weeks earlier than the Peregrines breeding in Kangerlussuaq. 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 Thule 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 Thule, females must immediately find a mate and territory and begin copulation to breed successfully. Additionally, on average adult females depart on migration approximately three weeks after young fledge from the nest, between two and three weeks earlier than females in Kangerlussuaq. 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 Thule and Kangerlussuaq. However, results from the stationary PTT at Thule 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 both on the number of locations used to calculate range sizes and the location classes of the locations used should also be given, 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, Kangerlussuaq Peregrines use the Eastern Flyway while Thule Peregrines use both the Eastern and Central Flyways and areas in-between. Peregrines from Thule flew southwest, passing to the east and west of Hudson Bay, then fanning out and travelled either over Mexico and Central America or across the Gulf of Mexico or Caribbean Sea. Thule Peregrines migrated at a more rapid speed than Peregrines from Kangerlussuaq (see discussion above), the possible advantage being to reach prime wintering areas before other falcons. Thule Peregrines carrying PTTs wintered in Central and South America, to include 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 Thule Peregrines show they breed about six to seven days later for each location south to north, or 13 days later over the whole ~17° latitudinal range. At least so 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 even occasionally may have attempted, or even successfully, bred. 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 almost global distribution and existence in arctic, temperate, and tropical environments, its predatory behavior, and its being a long-distance migrant to having no seasonal movements at all, there should be little surprise 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.

Chapter 3: Gyrfalcon colonization and extreme long-term use of nest sites in Greenland.

INTRODUCTION

It is well known that raptors may re-use nest sites for generations and some possibly for centuries (Newton 1979). Hickey (1942) referred to these nest sites as "ecological magnets." These locations are evidently so desirable that they are re-used again and again, even if the birds have no former familiarity with the location. For example, following extirpation of the Peregrine Falcon as a result of organochlorine pesticide use in large areas of North America and Europe, and the releases of captive-bred Peregrines, released falcons reoccupied former territories first, frequently reusing the same nest ledges as their predecessors (Newton 1979, Ratcliffe 1993, Oakleaf 2003).

Gyrfalcons and Peregrine Falcons both breed in the Arctic. Falcons do not build nests, but lay eggs in bowl-shaped depressions they scrape into existing substrates, including old nests made by other birds. Arctic Peregrine Falcons typically use open ledges on cliffs for nesting with little protection from the environment (Cade 1982). Gyrfalcons usually nest on cliff ledges overhung by rock, in potholes, or in sheltered stick-nests built by Northern Ravens (Burnham & Mattox 1984). These nesting situations provide protection from falling rock and the often extreme weather conditions, particularly during the early part of the Gyrfalcon breeding season. While stick nests are frequently damaged beyond re-use in a single season, some ledges and potholes are used long-term (Burnham & Mattox 1984). At re-used sites, faecal accumulation (whitewash) frequently occurs where Gyrfalcons roost and nest. Deposited over periods of years, the stratified accumulation of guano can become greater than one and a half meters thick in locations protected from erosion and where dry and cold environmental conditions enhance preservation (Figure 3.1). There are many such nest sites in Greenland.

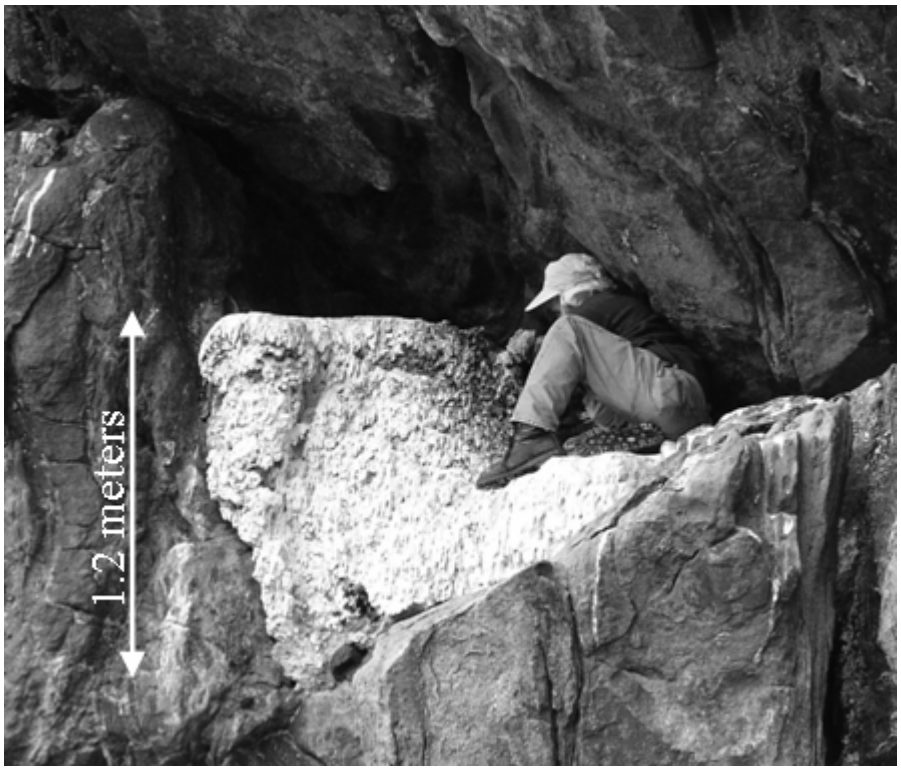

Figure 3.1. Gyrfalcon nest site in Kangerlussuaq, central-west Greenland, being sampled for radiocarbon dating.

The Greenland Ice Sheet covers 82% of the land mass of Greenland (Ohmura *et al.* 1999), and ice-free land occurs only along the island's periphery (Figure 1.1). Nest site availability for falcons may be affected by climate-induced glacial retreat and advance covering and exposing cliffs. Long-term use of nest sites by Gyrfalcons is a potential indicator for paleoenvironments and of stable glacial conditions. As the ice sheet retreated, areas at higher elevations, having a thinner layer of ice and snow, were exposed first. Land at lower elevations, including valley bottoms, had the thickest covering of ice and were exposed last (Fristrup 1966). I therefore hypothesized that guano in Gyrfalcon nests at lower elevations and closer to the ice sheet would have accumulated over shorter periods than that at nests at higher elevations and further from the Greenland Ice Sheet. To investigate this question I sampled and radiocarbon dated guano from Gyrfalcon nest sites in two areas, in Kangerlussuaq, central-west (66.50–67.00° N), and Thule, northwest (76.25–77.17° N), Greenland (Figure 1.1). These study areas were separated by about 9° latitude and 1,100 km.

STUDY AREAS

The Kangerlussuaq study area is located at the head of a 175 km long fjord and about 25 km from the ice sheet margin (Figure 1.5). The Low Arctic (see Chapter 1) tundra landscape in this area was sculpted by glaciation, with rolling hills and valleys, moraines and lakes, dissected by several meltwater rivers. Primary prey species for Gyrfalcons in Kangerlussuaq include both Rock Ptarmigan and Arctic Hare *Lepus arcticus*, with lesser quantities of passerines and waterfowl consumed (Booms & Fuller 2003). It is one of the largest deglaciated land areas in Greenland, and because of extensive past research, provides one of the most complete records of Greenland glacial history (Ten Brink & Weidick 1974, Eisner *et al.* 1995). From projected rates of deglaciation (see below), I can estimate that some gyrfalcon nest sites may have been uncovered about ca. 6,500–6,000 years before present (yr BP).

The Thule study area is centred around Pituffik/Thule Air Base, and the ice sheet margin lies up to 26 km from the sea, but reaches the sea at several locations (Figure 1.4). The environment is High Arctic (see Chapter 1) with an appearance of recent deglaciation. Gyrfalcons' primary prey species are Dovekies, Rock Ptarmigan, and Arctic Hare, with seabirds, waterfowl, and passerines taken in more limited quantities (see Chapter 4). Information on glaciation in Thule is more limited than for Kangerlussuaq, and glacial history is predicted more from inference of past climates than from moraine locations and measurement (Davies *et al.* 1963, Fredskild 1985, Kelly *et al.* 1999). Deglaciation sufficient to allow for potential consistent use of existing Gyrfalcon nest sites may not have occurred until 1,800 yr BP or more recently.

See Chapter 2 for further information on the Kangerlussuaq and Thule study areas.

METHODS

Gyrfalcon nest sites are distributed widely and irregularly throughout the two study areas. All sites are on cliffs and usually inaccessible without technical rock climbing equipment. The amount of faecal material build-up at sites varies greatly, as does the structure and size of the nest. The rock substrate upon which falcon guano accumulates is usually irregular, sloping, and seldom flat. Particularly on large ledges, the actual nest scrape is not always in the same location each year, nor is the associated faecal deposition resulting from breeding. Also, the rates of erosion are probably not constant across the nest, as some locations in the nest are more protected from weather than are others. Therefore, the guano is not of constant depth throughout the site, and it is difficult to know where the thickest and/or oldest deposits may lie. At nest sites where deposits seemed of more-or-less uniform thickness throughout, a single sample was collected where guano came in contact with the rock, while at other sites more than one sample was collected in an attempt to obtain the oldest guano. Bulk sample materials were collected from several centimeters of stratified guano, probably representing accumulation over decades or longer. Notes were made of sample depth (centimeters), cliff height (meters), and nest ledge elevation (meters above sea level, m asl). All nests sampled were occupied by Gyrfalcons within the past 25 years (W. Burnham pers. comm.).

When collecting samples, layers of faecal build-up were excavated carefully to prevent damage of the site for future use by gyrfalcons. At nest sites with only a few centimeters of feacal build-up, I dug vertically down into the guano, extracted samples at its base, and then refilled the hole to minimize damage to the nest site. At sites with substantial build-up, samples were taken from the side by using a masonry hammer and a small trowel to excavate horizontally until rock was reached. The amount of bulk material collected from the stratified samples varied, but in all cases was sufficient for dating using standardized radiocarbon procedures. Within the nest sites, feathers (from probable prey

and/or gyrfalcons) and bones (prey) were found during excavation. Three feathers that were easily identifiable as from Gyrfalcons were also radiocarbon dated.

Radiocarbon dating was carried out by Beta Analytic Inc, Miami, Florida, USA, using either the conventional radiometric technique (samples >30 gm) or accelerator mass spectrometry (AMS) (samples <30 gm and feathers). Guano samples were pre-treated using an "acid wash" while an "acid/alkali/acid" wash was used for feather samples. For the conventional radiometric technique, materials were analyzed by synthesizing carbon to benzene (92% C) and then measuring for ^{14}C in a scintillation spectrometer from which the radiocarbon age was calculated (Beta Analytic). AMS results were obtained by the reduction of sample carbon to graphite (100% C) along with standards and backgrounds (Beta Analytic). Graphite was then sent for ^{14}C measurement in an accelerator-mass-spectrometer to a research facility collaborating with Beta Analytic. The measured radiocarbon ages were returned to Beta Analytic where verification, isotopic fractionation correction using $\delta^{13}C$, and calendar calibration took place (Beta Analytic). Calibrations were made using calibration data published in Stuiver *et al.* (1998) using cubic spline fit mathematics, as described by Talma and Vogel (1993).

From 2002 to 2004, I collected 19 bulk guano samples and three feathers from 13 Gyrfalcon nest sites. Five guano samples and one feather were from four nests in Thule, and 14 guano samples and two feathers were from nine nests in Kangerlussuaq. To test for relationships between age of guano samples and nest variables (using JMP IN, vs. 4, SAS Institute Inc.), I analyzed the distribution of the variables and relationships using Spearman Correlation Analysis, as was most appropriate based on the non-normal distribution of the data. Conventional ^{14}C age was used as the maximum age for each sample.

RESULTS

The oldest conventional ^{14}C age bulk sample was from Kangerlussuaq and calculated to be 2,480 ± 40 yr BP (Table 3.1). Four nests in Kangerlussuaq showed evidence of occupation >1,000 yr BP, with the most recent nest being occupied a minimum of 570 ± 50 yr BP. In Thule, the oldest nest was a minimum of 650 ± 70 yr BP with two nests indicating use only within the past 50 years. Sites in Kangerlussuaq have been used over approximately 1,800 years longer than those in Thule. Sites with multiple samples collected showed an increase in ^{14}C age with sample depth. The three analyzed Gyrfalcon feathers were estimated at 170 ± 40 BP, 320 ± 30 BP, and 650 ± 40 BP. While the bulk samples of guano represent number of years of site use, the feathers were from a precise moment in time.

In general, marine organisms and animals that feed on them have less negative $\delta^{13}C$ values, while more negative $\delta^{13}C$ values are typically associated with land plants and systems based upon them (Moors *et al*. 1988). The $\delta^{13}C$ values for both feather and guano samples varied from a median of -20.7 (n = 6) for Thule to -21.6 (n = 16) for Kangerlussuaq. The difference is most likely a reflection of diet, with Gyrfalcons in Thule feeding on a mixed diet of marine and terrestrial prey and in Kangerlussuaq having an almost entirely terrestrial diet. However, no difference was found between Thule and Kangerlussuaq when using the $\delta^{13}C$ value from the oldest sample from each nest ($T = -0.62$, $p = 0.56$, $DF = 5$).

Table 3.1. Results of the ^{14}C measurements on guano material and feathers from Gyrfalcon nest sites in Kangerlussuaq, central-west, and Thule, northwest Greenland, collected from 2002 to 2004. Samples from the same nest site are designated by the use of A, B, C, or D following the number.

Nest site	Sample depth (cm)	Cliff height (m)	Elevation of nest (m asl)	Distance from ice margin (km)	$\delta^{13}C$ (‰) (PDB)	Year last used	Conventional ^{14}C age (yr BP ± 1σ)	Calibrated age range (yr BP ± 2σ)
Kangerlussuaq, central-west Greenland								
019	20-25	15	355	9	-22.7	1992	790 ± 60	790-650
053A	30-35	15	304	11	-22.4	1991	1290 ± 50	1,300-1,080
053B	15-20	15	304	11	-22.4	1991	1090 ± 80	1,180-900, 850-810
053C[a]	15	15	304	11	-22.5	1991	320 ± 30	470-300
068A	15-20	152	55	14	-22.9	2000	570 ± 50	650-520
068B	10-15	152	55	14	-20.7	2000	240 ± 60	450-260, 220-140, 30-0
082	25-30	76	441	5	-23.2	1999	830 ± 70	920-660
087A	30-35	46	365	54	-21.9	2002	2480 ± 40	2,740-2,360
087B	25-30	46	365	54	-20.9	2002	350 ± 40	500-300
087C	0-3	46	365	54	-24.2	2002	105.09 ± 0.66 pMC[b]	outside calibration range[b]
087D[a]	15	46	365	54	-21.3	2002	170 ± 40	300-60, 40-0
123	20-25	46	258	62	-21.1	~1985	1090 ± 60	1,160-920
163	100-110	152	395	72	-20.8	2003	960 ± 60	970-740
170	15-20	24	103	28	-21.3	2004	690 ± 60	710-550
201A	35-40	23	200	78	-17.8	2000	1430 ± 70	1,480-1,470, 1,430-1,250
201B	10-15	23	200	78	-21.3	2000	820 ± 60	910-660
Thule, northwest Greenland								
500A	3-6	46	152	14	-21.2	2003	122.08 ± 0.73 pMC[b]	outside calibration range[b]
500B	5-8	46	152	14	-23.3	2003	113.34 ± 0.71 pMC[b]	outside calibration range[b]
501	2-4	117	122	2	-23.2	2004	115.29 ± 0.66 pMC[b]	outside calibration range[b]
502	15-20	23	152	9	-20.2	2004	640 ± 50	670-540
503A	20-25	76	304	17	-19.1	2004	650 ± 70	690-530
503B[a]	20	76	304	17	-19.5	2004	650 ± 40	670-550

[a]Gyrfalcon feather samples.

[b]pMC (percent Modern Carbon) analyzed material was post-1950 and had more ^{14}C than did the AD 1950 reference standard due to atomic bomb testing and subsequent fall-out, 50 years used as conventional ^{14}C age while Calibrated Age Range is outside calibration range.

The maximum conventional ^{14}C age for each individual nest was significantly correlated with the distance from the ice margin (Spearman Rho = 0.56, $p < 0.05$, $n = 13$) (Figure 3.2), nest elevation (Spearman Rho = 0.61, $p < 0.05$, $n = 13$) (Figure 3.3), and sample depth (Spearman Rho = 0.88, $p < 0.0001$, $n = 13$) (Figure 3.4). The thickness of guano, represented by the depth at which all the samples were collected, is highly correlated with conventional ^{14}C age (Spearman Rho = 0.80, $p < 0.0001$, $n = 19$). Because of this significant correlation, sample depth could be used as a predictor of ^{14}C age. However, the margin of error would be much greater if using that method than if using radio carbon dating directly (e.g., 087A & 163, Figure 3.3).

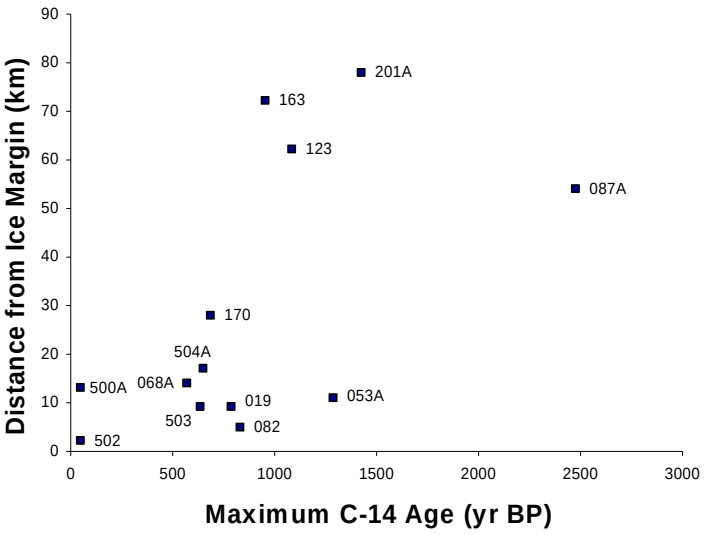

Figure 3.2. Relationship between maximum ^{14}C age and nest distance from ice margin (Spearman Rho = 0.56, $p < 0.05$, $n = 13$).

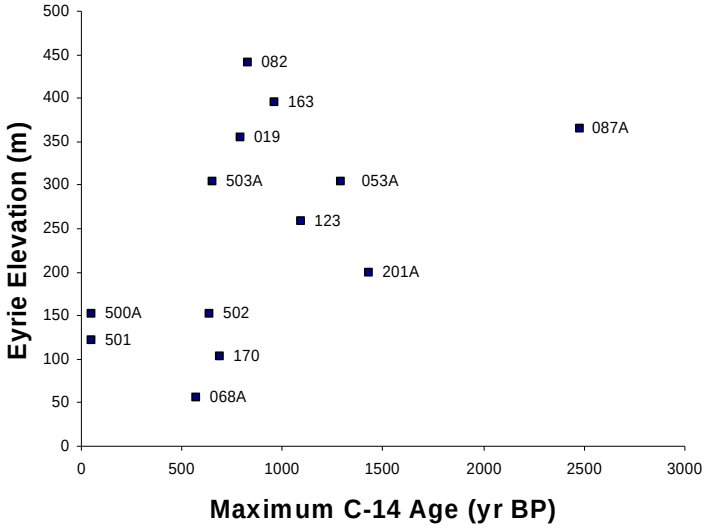

Figure 3.3. Relationship between maximum ^{14}C age and nest elevation (m above sea level) (Spearman Rho = 0.61, $p < 0.05$, $n = 13$).

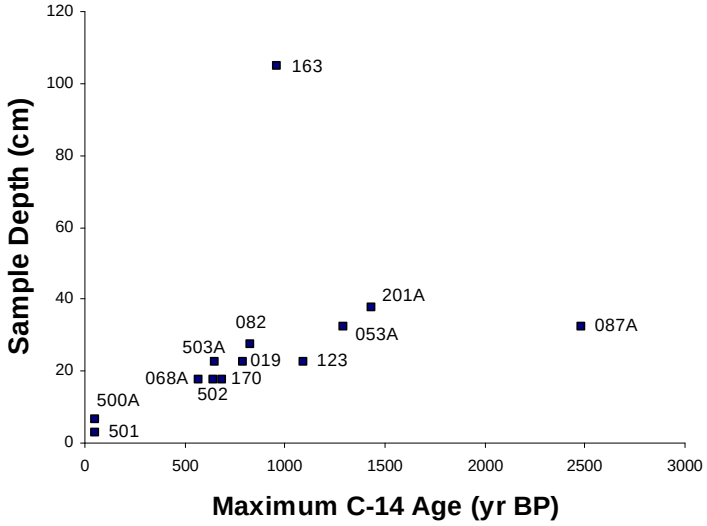

Figure 3.4. Relationship between maximum ^{14}C age and sample depth (Spearman Rho = 0.88, $p < 0.0001$, $n = 13$).

DISCUSSION

Radiocarbon dating of Gyrfalcon nest material from Kangerlussuaq and Thule, Greenland, indicate much longer occupancy times than can be determined from historical records. Sites from Kangerlussuaq were colonized approximately 1,800 years earlier than those in Thule, likely an effect of earlier deglaciation in the Kangerlussuaq area. These are some of the longest used raptor nest sites ever documented.

Similar studies of this type have been carried out on other Arctic and Antarctic species. These have included Snow Petrels *Pagodroma nivea* (Hiller *et al*. 1988), Thick-billed Murres (Gaston & Donaldson 1995), and Adélie Penguins *Pygoscelis adeliae* (Emslie *et al.* 2007), for which radiocarbon age has been calculated using solidified stomach oil deposits, peat moss deposits, and eggshell fragments excavated from ornithogenic sediments at abandoned colonies, respectively, and minimum dates for the establishment or colonization of bird colonies have been given (~34,000 yr BP, 1,500–3,800 yr BP, and ~45,000 yr BP, respectively). In addition, archaeological studies have sometimes revealed long-term use of raptor nest sites. For example, remains of Peregrine Falcons, probably adults and nestlings, were located during an archaeological investigation of prehistoric human occupation of a cave on Hunter Island, Tasmania (Bowdler 1984). Bones were found in layers 990 ± 90 to ca. 19,000 yr BP suggesting use by falcons during that time but not more recently.

There can be little doubt about the identity of the Gyrfalcon sites in Greenland. Only two falcon species breed in Greenland (Salomonsen 1950–51) and although Peregrines sometimes use former Gyrfalcon nest sites, these species typically select different nesting situations, as explained above. Cliff-nesting seabirds breed in different situations than do falcons. Gulls nest colonially and sites cannot be confused with falcon nests. Except for Iceland Gulls *Larus glaucoides* and Glaucous Gulls *L. hyperboreus*, all other avian species breeding in the research areas construct nests containing sticks, grass, and feathers, and/or breed on the ground. Ravens are the only other cliff-nesting species that nest in similar locations to Gyrfalcons, but they construct stick-nests. There can be no doubt that the accumulation of guano at sites sampled resulted from long-term use by falcons, and in particular Gyrfalcons.

The feather samples could be easily identified to Gyrfalcons. Although interesting because of their condition and long-term preservation, they did not contribute to knowledge on duration of nest site use or paleoenvironment beyond what could be inferred from guano samples. They did, however, provide confirmation of dates of past use.

Some nest sites provided much older radiocarbon dated samples than others. Newton (1979) attributed the repeated occupancy of nest sites to "the superiority of particular places over local alternatives." This superiority could result from a nearby abundance of prey, a superior hunting platform, a location in appropriate spatial relationship to other territorial pairs, or protection from mammalian predators or inclement weather (rain, snow, sun, and/or wind). Over time, the desirability of sites may change due to altered environmental conditions, including rock structure. This may be particularly true in areas of recent glacial activity and climate change.

The Greenland Ice Sheet gradually retreated about 175 km in the Kangerlussuaq area because of world-wide climate warming since the end of the last glaciation (~15,000 yr BP), but with frequent re-expansions (Ten Brink & Weidick 1974, Funder 1989). A slow retreat of the ice sheet (1 km/100 yr) occurred from ca. 15,000 to 10,000 yr BP followed by an oscillatory but more rapid retreat (3 km/100 yr) of nearly 100 km from ca. 9,500 to 6,500 yr BP (Ten Brink & Weidick 1974). By 6,000 yr BP the ice sheet had reached its present position, although between 5 and 10 km re-advances occurred from ca. 4,800 to 4,000 and from 2,500 to 2,000 yr BP (Ten Brink & Weidick 1974). Nearly present day sea level existed at that time. From lacustrine sediment records, Eisner *et al.* (1995) reports that Kangerlussuaq experienced a "climatic optimum" from ca. 4,400 to 3,400 yr BP with warmer and slightly moister conditions probably resulting in a denser vegetative covering of the area followed by a climatic deterioration with intermittent amelioration. Pollen

stratigraphy shows that the major vegetation types were already well established by the beginning of this period. A climatically stable period is believed to encompass 2,000 to 1,200 yr BP (Eisner *et al.* 1995). From lichenometrically dated samples, we know that the period from ca. 700 yr BP to the present was characterized by oscillatory advance and retreat of the inland ice within about a 3-km-wide zone (Ten Brink & Weidick 1974). Several minor advances then occurred again between 1880 and 1920 AD, followed by an incipient re-advance in the 1960s (Ten Brink 1975).

In Kangerlussuaq nest sites 019, 053, 068, 082, and 170 were probably covered by ice during re-advances of glaciers from the Greenland Ice Sheet between ca. 4,800 and 4,000 and from 2,500 to 2,000 yr BP. All five nest sites are in glacial valleys or river valleys and four of the five are on low cliffs. The fifth site (053) is near to the top edge of a deep valley. Furthermore, 068 and 170 are on small cliffs near low elevation rivers and even a 10 m rise in sea level could have affected use of these sites by Gyrfalcons. Nest sites 087, 123, 163, and 201 are less than 50 km from the ice edge and, based on the projected rate of ice-sheet retreat, these nest sites were ice-free by 6,500–6,000 yr BP. That does not preclude, however, the possibility of isolated snow banks and glaciers covering nest sites, particularly on small cliffs and at lower elevations, during periods of climatic cooling and glacial expansion. In addition, it was probably not until the "climatic optimum," from 4,400 to 3,400 yr BP, that the necessary vegetation was established to support the prey-base utilized by Gyrfalcons in Kangerlussuaq.

Information from Thule is far less complete and contentious than that from Kangerlussuaq. In Thule, Malaurie *et al.* (1972) used data from marine deposits of terraces to estimate deglaciation began ca. 8,000 yr BP, while Kelley *et al.* (1999) postulates that much of the area has been ice-free for at least 9,000 years. The recession of fjord glaciers is

believed to have begun before 6,000 yr BP, with driftwood dated from northern fjords ca. 5,900 yr BP (Fredskild 1973). Pollen analysis projects the "climatic optimum" occurring between 4,000 and 3,300 yr BP in North Greenland (Fredskild 1973). The climate deteriorated sometime after 2,700 yr BP but with periodic amelioration. Northern fjords were closed ca. 2,100 yr BP and vegetation acquired the High Arctic desert nature of today (Fredskild 1973). Archaeological evidence indicates unfavourable, cool conditions from 2,500 to 1,900 yr BP followed by three centuries with a warmer climate (McGhee 1972). Between ca. 1,800 and 900 yr BP conditions improved (Fredskild 1973). Based on sedimentation rates, the conditions are thought to have been moist to wet at Thule ca.1,120 yr BP, but vegetation character changed to drier grass heath by ca. 900 yr BP (Malaurie *et al.* 1972). From ca. 900 yr BP to the 20th Century, considerable climatic variability existed, but evidence from ice cores and oxygen isotopic records from Camp Century show that generally cooler conditions probably persisted in the Thule area until ca. 1,900 A.D (Johnsen *et al.* 1970). Meteorological records from Upernavik, Greenland (72° 50' N), show a 2 °C mean annual temperature increase through the middle of the 20th Century (Dowdeswell 1996). Throughout the High Arctic there is evidence for glacial retreat since the Little Ice Age from 400 to 500 yr BP.

In Thule, the existence of consistent long-term nest site availability is more recent than in Kangerlussuaq. The current limited amount of ice-free land, and the close proximity of the ice-margin to the sampled nest sites, emphasize this point. While some nest sites may have been ice-free as early as ca. 9,000 to 6,000 yr BP, they were possibly later re-covered by re-advances of the ice sheet. Furthermore, despite some nest sites being ice-free for extended periods of time, suitable environmental conditions for Gyrfalcons probably did not exist until between 1,800 and 900 yr BP or later. Even now, because of cool mean summer

temperatures, localized large snow banks and glaciers can develop in just a few years or decades and preclude the use of nest sites.

On the basis of paleoenvironmental investigations by others, I hypothesized that Gyrfalcon nest sites of higher elevations, and further from the ice margin, would show longer usage patterns than nest sites closer to the ice edge, and at lower elevations. Both predictions were confirmed using ^{14}C dating. Carbon dating of stratified guano accumulation at Gyrfalcon nest sites could thus be used to confirm and date when local environments were suitable for breeding by this species and when colonization likely occurred. Furthermore, past use of sites indicate that favourable environmental conditions existed for prey species as well. These results throw further light on local, and probably regional, paleoenvironmental conditions and glaciation in the Arctic.

CHAPTER 4: Ecology and biology of Gyrfalcons in Greenland.

INTRODUCTION

The Gyrfalcon is the largest of all falcon species and breeds in circumpolar High Arctic to Subarctic zones (Cade 1982, Ferguson-Lees & Christie 2001). Plumage colour varies greatly from white to dark grey, with the Gyrfalcons in the northern part of their range mostly white with little barring. Salomonsen (1950–51) considered the "white," "silver," and "grey" colour variants to be separate subspecies. In the Zoological Museum, Copenhagen, Denmark, there are more than 429 Gyrfalcon specimens that were collected in Greenland alone, primarily to investigate variation in plumage colour. Gyrfalcons were commonly shot during polar expeditions and specific collecting trips (e.g., Walker 1860b, Hall 1876, Hagerup 1891, Stone 1895). Explorers and collectors documented locations where falcons were observed breeding or migrating and helped to establish the range and migration timing of the species in Greenland. Beyond information collected incidental to other research and exploration, no investigations of Gyrfalcon ecology in Greenland were made until Mattox (Burnham & Mattox 1984) began a long-term investigation of Peregrine Falcons in 1972 in the Kangerlussuaq area. Even then, the Gyrfalcon was of secondary interest and noted anecdotally in most years. In a review article about the Gyrfalcon, Cade *et al.* (1998) commented that "fresh data from Greenland and Russia lag far behind" that from other locations.

The primary aim of my research was to collect data on the breeding biology and movements of Gyrfalcons in Greenland. These data allowed comparison of Low and High Arctic populations of Greenland Gyrfalcons and helped to determine the stability of these populations over time. They also provided the most complete description of seasonal movements of Gyrfalcons to date. Comparisons between Peregrine Falcon and Gyrfalcon populations within Greenland are left for Chapter Five.

Within Greenland, data were collected on Gyrfalcons from 1993 to 2005 in the northwest (Thule), from 1998 to 2005 in the central-west (Kangerlussuaq), in 2000 and 2002 in the southwest (Maniitsoq), and in 2004–2005 in the central-east (Scoresbysund) areas (Figure 1.1). Data were collected on distribution, nesting density, reproduction, prey numbers, nest site characteristics, seasonal movements, plumage colouration, and morphometrics.

Historical information

Gyrfalcons have historically been reported breeding along much of Greenland's ice-free coastlines from the far north in Peary Land (83° N: Manniche 1910, Koch 1925, Johnsen 1953) to Kap Farvel (60° N: Rafn 1933, Salomonsen 1950–1951) at the southern tip (Figure 1.1). Most records were sightings made and specimens collected prior to 1950. Hagerup (1891) reported the Gyrfalcon as "common in South Greenland, where it breeds." Bertelsen (1932) quotes Winge (1898) that "The Gyrfalcon is commonly distributed as a breeding bird along Greenland's west coast," while Muller (1906) called the Gyrfalcon "very common and occurring all over South Greenland" (south of Sisimiut, 67° N).

Bertelsen (1937) further reported that Fencker (1929) considered the Gyrfalcon as evenly distributed over the entire non-glaciated part of North Greenland (north of Sisimiut) to Upernavik (73° N) (Figure 1.1). In the Uummannaq District on the west coast (70–71° N), Bertelsen stated that “each year there are found 30 pairs in the District." He goes on to write that, although the Gyrfalcon has been observed all the way to Greenland's most northern tip, it seldom occurs above 78° N. Salomonsen (1950–1951) states that the Gyrfalcon breeds "rather locally in SW Greenland but in the Disko Bay region it increases considerably in number," referencing Bertelsen's and Fencker’s information. Salomonsen continues, "In Thule District, where the Gyrfalcon is a common breeding-bird northwards to Etah..." (75–78.3° N).

More recently for western Greenland, in 2000 I participated in re-surveying 28 Gyrfalcon nest sites reported by Bertelsen (1921) in the Uummannaq District (70–72° N) (Figure 1.1). Only three occupied sites were found, but four additional previously unreported active nest sites were discovered (Burnham *et al.* 2005). No previously reported nest sites were occupied near now abandoned seabird colonies. It was predicted that those sites in particular were abandoned in association with loss of prey. Occupied sites were in heath areas where Rock Ptarmigan likely existed. In 1974 W. Burnham and S. Sherrod surveyed reported Gyrfalcon nests in the Disko Bay area (69–70° N) (Figure 1.1), checking 14 of 18 known sites, and observed single adults near two locations but no breeding pairs (Burnham & Mattox 1984). The lack of reproduction was explained by a low prey year, and local hunters reported that nest sites were not usually used every year.

On Greenland's east coast the greatest breeding density reported was for the Scoresbysund (70.4° N) area north to Germania Land (77° N). Salomonsen (1950–51) wrote "According to Alw. Pedersone there are about 40 pairs breeding in the interior fjord country and 25 pairs at Liverpool Coast" (70.4–71.5° N). He went on to say that B. Christensen "observed in the first 18 days of September 1937 between 200 and 300 white Gyrfalcons passing Scoresby Sound." Salomonsen believed than the falcon bred only locally north of Germania Land.

Meltofte (1975) estimated 5–10 breeding pairs between 76 and 78° N in northeast Greenland. Cabot *et al.* (1988) reported Gyrfalcons in northern Germania land in 1987. After reviewing A. Pedersen's original publications (1926, 1930, 1934, 1942), T. Cade (pers. comm.) could find no indication of how the 40 pairs at Scoresbysund or 25 on the Liverpool Coast were determined. To Cade's knowledge, no systematic survey of nesting Gyrfalcons has ever been conducted in east Greenland or a precise count of autumn migrants done. Meltofte (1975) believed that the Gyrfalcon population in northeast

Greenland had decreased, and Elander and Blomqvist (1986) reported fewer migrants seen at weather stations in the 1970s than in the 1930s. In 1999 T. Cade and O. Nielsen surveyed approximately 6,000 km^2 of Jameson Land by helicopter and approximately 30 linear km of the Liverpool Coast by skis in May and dogsled in June (Burnham 1999). They found five occupied sites, but based on the number of unoccupied sites observed and reported by others, they felt that there could be 30 or more traditional Gyrfalcon territories in Jameson Land north to approximately 71.7° N and 20–25 territories on the Liverpool Coast. It is difficult to know how many of these sites might be occupied simultaneously, and the year they were surveyed followed a reported crash of Collared Lemming *Dicrostonyx groenlandicus* populations, which has been shown to be an important prey species (Fletcher & Webby 1978). In 2001 O. Nielsen (pers. comm.) returned to Jameson Land and did a 340 km survey on foot and located three occupied territories, one of which produced young.

Gyrfalcon populations (breeding pairs) are known to fluctuate widely, but the nature and cause are debated (Mindell & White 1988, Clum & Cade 1994, Cade *et al.* 1998, Nielsen 1999). Cyclic (Mossop & Hayes 1994) and irregular (Swem *et al.* 1994) fluctuations are reported and believed to follow ptarmigan population numbers in Iceland (Nielsen 1999) and the Yukon (Mossop & Hayes 1982). Gyrfalcons also prey upon lemmings and, in low lemming years, switch to Snow Buntings in northeast Greenland (Fletcher & Webby 1978, Gilg *et al.* 1997).

Vibe (1967) reported what he believed were climate-caused population fluctuations for several species in Greenland, including ptarmigan, which had six major population peaks between 1886 and 1954, an average interval between peaks of 11 years. The lemming population in Greenland apparently fluctuates on a four-year cycle, and 1998 was a peak year for Trail Island, northeast Greenland (B. Sittler pers. comm.).

Other than the occasional anecdotal mention in the literature and observations collected on individual nests or over small portions of a breeding season (Fletcher & Webby 1978, Fox & Stroud 1981, Cabot *et al.* 1988, Booms & Fuller 2003), the only demographic data on Greenland Gyrfalcons concern reproduction (young/successful pair) from Mattox's work in the Kangerlussuaq area. Because Gyrfalcon nestlings typically have fledged before Peregrine young are old enough to band, surveys for Peregrines in Kangerlussuaq provided only limited data on Gyrfalcons. Only during one four-year (1990–93) period did Mattox and associates accomplish a systematic search early in the season for Gyrfalcons (Yates *et al.* 1992).

From 1948 to 1992 only 14 recoveries of banded Gyrfalcons have occurred in Greenland, and limited data exist on seasonal movements or wintering areas (Lyngs 2003). No band recoveries have occurred outside Greenland, although the "white" Gyrfalcons seen in Iceland in winter are assumed to come from Greenland because that colour phase does not breed in Iceland (O. Nielsen pers. comm.).

STUDY AREAS

I examined populations of breeding Gyrfalcons geographically focused in the Thule (75.9–77.6° N) and Kangerlussuaq areas (66.5–67.5° N) (Figure 1.1). Capture and ringing stations were established in east Greenland in 2004 and 2005 in the Scoresbysund Commune (Kap Tobin, 70.4° N and Constable Pynt, 70.8° N) which effectively sampled in autumn Gyrfalcons breeding locally and to the north throughout the National Park, which extends along the East Coast from approximately 71° N to the northern tip of Greenland (Figure 1.1). These three locations are geographically separated by approximately: Thule to Kangerlussuaq 1,170 km, Kangerlussuaq to Scoresbysund 1,175 km, and Scoresbysund to Thule 1,550 km. Included in the separation between Scoresbysund and two west coast study areas, Thule and Kangerlussuaq, is the Greenland Icecap, which comprises

approximately 1,200 and 850 km of the respective distances between the locations. Between Kangerlussuaq and Thule, Melville Bay provides another likely uninhabitable area for Gyrfalcons, as the icecap borders the sea and very limited or no ice-free land exists.

Additional capture and ringing stations were operated during the autumns of 2000 and 2002 at Maniitsoq (65.4° N), central-west Greenland, and in the Thule area in 2002 and 2003. The Maniitsoq site is slightly south and coastal of the Kangerlussuaq area. The Gyrfalcons captured at these sites were most likely breeding locally or were migrants from northward in Greenland, possibly including the northeastern Canadian Arctic.

Scoresbysund north to Germania Land has many large ice-free areas, including islands, commonly separated by bays and fjords. Typically, the east coast of Greenland receives greater snowfall than the west coast. In the immediate Scoresbysund area the vegetation grows to less than a meter high and decreases in height and density moving north to Germania Land which is High Arctic. For further information on the Thule and Kangerlussuaq study areas see Chapter 2.

In all three study areas environmental conditions and potential prey species and densities have similarities, but also vary considerably. At the beginning of the Gyrfalcon breeding season, ptarmigan and Arctic Hares occur in all three areas but few other potential prey species exist. Snow Buntings may also occur in small flocks. Arriving later in the spring are Lapland Longspurs, Northern Wheatears *Oenanthe oenanthe*, and Greenland Redpolls *Carduelis flammea*, which breed in each area but at different densities. Also arriving in all three areas are Common Ringed Plovers *Charadrius hiaticula* and Dunlins *Calidris alpina*, with other species of shorebirds specific to each area. Although no species of shorebird exists at sufficient densities to be an important potential prey species for Gyrfalcons by themselves, Cabot *et al.* (1988) documented young from a combination of

Common Ringed Plover and Dunlin as an important prey for a pair of Gyrfalcons during the young-rearing stage in Germania Land. The only species of waterfowl common to all three study areas is the Oldsquaw (Long-tailed Duck) *Clangula hyemalis*.

In Thule and coastal Scoresbysund, from mid-May through August, very large numbers of seabirds occur. The Dovekie population alone in Thule is estimated at 33 million pairs (Egevang *et al.* 2003), while 3.5 million pairs are estimated for Scoresbysund (Kampp *et al.* 1987). Also present in both areas are Thick-billed Murres and Black-legged Kittiwakes, though Thule has much larger populations of both than does Scoresbysund (Boertmann 1994). Black-legged Kittiwakes are the only gull that could be an important prey species for Gyrfalcons. Black Guillemots are also common in both areas but numbers are difficult to quantify. Both King Eiders *Somateria spectabilis* and Common Eiders *S. mollissima* occur, but the latter is far more common. Snow Geese *Anser caerulsecens* breed in the Thule area and across very northern Greenland.

Unique to Scoresbysund and across north-east Greenland are Collared Lemmings and Least Weasels *Mustela rixosa*, but nowhere else in Greenland do they occur. An additional predator congruent with their range is the Snowy Owl. Inland, in the Scoresbysund area, Pink-footed Geese *Anser brachyrhynchus* breed, the goslings of which are preyed upon by Gyrfalcons (O. Nielsen pers. comm.). Further, throughout northeast Greenland, Barnacle Geese *Branta leucopis* are common breeders and during some years are important prey for Gyrfalcons (Fletcher & Webby 1977, Cabot *et al.* 1988).

In Kangerlussuaq, from June through September there is a great abundance of small migratory passerines, the Lapland Longspur occurring at the highest density (Rosenfield *et al.* 1995). There are also Mallards *Anas platyrhynchos* and Red-breasted Mergansers *Mergus serrator*, both of which are known Gyrfalcon prey (Booms & Fuller 2003).

Additionally, Greater White-fronted Geese *Anser albifrons* and Canada Geese are common breeders in this area.

METHODS

Survey and capture

After a literature review for the Thule area, individuals with first-hand knowledge of birds were contacted, including local hunters. Locations identified by hunters and during the literature review were then surveyed using a small aircraft to identify possible falcon nesting locations. Boats (motorized and kayak), helicopters, and dogsleds were used to observe sea cliffs and to gain access to areas more inland for walking surveys. In the Kangerlussuaq area, most Gyrfalcon nest sites located by Mattox were discovered incidentally while surveying for Peregrines. During this study, most sites were checked by helicopter. The Scoresbysund area was not surveyed, and data on individual Gyrfalcons were collected only at the capture sites. The same was true for the Thule and Maniitsoq capture locations.

When Gyrfalcons were seen, observations were made to determine if they were breeding, territorial, behaviorally attached to a location but not defensive, or just hunting or passing by. If breeding, nests were rappelled or climbed into, prey remains were identified, physical nest and cliff features were recorded, and young were ringed. Depending upon weather conditions, nests with breeding Gyrfalcons were visited more than once per season to record the number of nestlings/fledglings if possible. However, remote locations and inclement weather frequently precluded follow-up visits. As possible, breeding adult Gyrfalcons were captured, measured, and equipped with satellite-received transmitters (PTTs). Gyrfalcons were ringed with a standard Danish numbered lock-on ring on one leg and an alpha-numeric ring (ACRAFT, Edmonton, Canada) on the other.

At occupied Gyrfalcon nest sites, data were routinely collected on reproduction and nest site characteristics, but the emphasis was on obtaining DNA samples from nestlings for a phylogeographic study which I initiated (Johnson *et al.* 2007). At nest sites and capture and ringing sites, obtaining morphometric measurements, DNA, and attaching PTTs to adult and flying immature falcons were a priority.

All falcons were captured and released unharmed. Several capture methods were used, depending upon the time of year and the physical situation. See Appendix A for further information.

Nest site characteristics

In the Thule and Kangerlussuaq areas, physical data were collected from nests of active breeding Gyrfalcons. Data were collected in the way described by Falk *et al.* (1986) and Wightman & Fuller (2005) for Peregrine Falcon nests in South Greenland and Kangerlussuaq, respectively. Degrees were corrected to True North for both areas. Circular data were analyzed as described by Zar (2004) and Fisher (1996). Nests were included only once during analyses even if occupied in multiple years.

Morphometrics

See Chapter 2 for methods used for taking measurements and genetic confirmation of sex. If individuals were obviously molting and their centre tail feathers or their outside primaries were missing or growing, these measurements were not included in analyses. Crop weight was estimated using the methods described for Peregrines in Chapter 2; however, the number of quail eaten per day in captivity was greater for Gyrfalcons than Peregrines (C. Sandfort pers. comm.), and female and male Gyrfalcons ate on average 2.0 and 1.5 Japanese Quail per day, respectively, when provided an unlimited food. Statistical analysis was similar to that described for Peregrines in Chapter 2 and female and male

Gyrfalcons were analyzed independently. Body mass was included in all Gyrfalcon analyses.

Satellite-received telemetry

Between 2000 and 2004, 56 satellite-received transmitters (PTTs; Microwave Telemetry Inc., Columbia, MD, USA, and North Star Science and Technology, LLC, Baltimore, MD, USA) were placed on Gyrfalcons in the Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq areas. Units weighed from 18 to 30 g and were battery powered and attached as backpacks using Teflon ribbon (Fuller *et al*. 1995). Duty cycles were programmed to transmit from as frequently as 4 hours on/27 hours off to 7 hours on/106 hours off, depending upon the power source and battery life. GPS locations were taken at all nest sites or capture locations where birds were tagged. Each PTT recorded information on location, battery voltage, temperature, 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 Appendix J for summary information for individual PTTs, including year deployed, region, ID number, manufacturer, duty cycle, and weight. Satellite tracking methods for Gyrfalcons were similar to those used for Peregrines, as described in Chapter 2. Completion of outward and return migration was defined as when falcons stopped moving in a general southerly and northerly direction, respectively, and stayed in a general area, albeit large in some instances. Incomplete migrations were determined by visual inspection of the data and the location of the individual when the last PTT location was received.

RESULTS

Surveys and breeding biology

Data were collected on occupancy, reproduction, nesting chronology, and prey in Kangerlussuaq and Thule and results will be compared between study areas to identify

similarities and differences. Individual populations were analyzed to determine the extent of fluctuations in numbers and/or breeding success over time.

Surveys and occupancy

Results from surveys in Kangerlussuaq and Thule were minimal estimates, and some nests had probably failed before they were checked the first time, resulting in a bias towards successful nests. For logistical and financial reasons successful nest sites were frequently only visited a single time, 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 (Barber *et al.* 1998, Griffin *et al.* 1998). Surveys conducted in Kangerlussuaq were by helicopter and occurred in early-to-mid June when young were usually approximately 20 days old. Surveys in Thule typically occurred from late July through mid-August, when young were usually at least 30 days old and in some cases had already left the nest. Surveys in Thule were usually conducted by boat, and due to the late break-up of ocean pack-ice earlier surveys were not possible.

Surveys and occupancy: Kangerlussuaq

Occupied sites were those where one or more territorial adults and/or young were observed. If only adults were present, to be considered as occupants, they had to be observed on multiple visits to the site or to act territorially toward researchers. Approximately half of the currently known Gyrfalcon nesting locations in Kangerlussuaq have also had Peregrines nest at the same location, at times in the same nest, but more commonly at another location on the same cliff, with both species occasionally nesting on the same cliff in the same year. From 1972 to 1997 (n = 26), Mattox surveyed specifically for Peregrine Falcons and also for Gyrfalcons during 1990–1993 (n = 4). During each year, researchers visited Gyrfalcon cliffs while surveying for Peregrines (cliffs that both species had nested on) and took notes as they travelled by additional Gyrfalcon nests while looking

for Peregrines. Surveys for Peregrines were usually pre-fledging, and Gyrfalcon young had commonly already left the nest by this time, in some cases the breeding area, but more frequently were still flying about the cliff face while being tended by adults. Even though some breeding Gyrfalcons were no doubt missed, others were seen at cliffs in most years (Table 4.1). From 1998 through 2005 (n = 8), between 51% and 96% of the known Gyrfalcon nesting locations were occupied in Kangerlussuaq (Table 4.1). During this period territorial Gyrfalcons were documented on 94 occasions and an additional 19 new breeding sites were located. From 1972 to the early 2000s, the study area increased in size, which contributed to the increased number of Gyrfalcon nest sites (Table 4.1).

Table 4.1. Nest site occupancy by Gyrfalcons in Kangerlussuaq, Greenland, from 1972 to 2005 (Burnham & Mattox 1984, Mattox annual reports from 1982 to 1997).

Year	Gyrfalcon sites checked from 1972 to 2005	Known Gyrfalcon sites	Known Gyr sites checked (%)	Known Gyr sites occupied when checked (%)	Total sites occupied (new sites found)
1972	11	–	–	–	6 (6)
1973	13	6	5 (83%)	4 (80%)	7 (3)
1974	15	9	6 (67%)	3 (50%)	6 (3)
1975	8	12	4 (33%)	1 (25%)	1 (0)
1976	8	12	3 (25%)	1 (33%)	3 (2)
1977	8	14	4 (29%)	2 (50%)	2 (0)
1978	10	14	7 (50%)	4 (57%)	4 (0)
1979	14	14	6 (43%)	3 (50%)	5 (2)
1980	15	16	5 (31%)	1 (20%)	4 (3)
1981	18	19	6 (32%)	1 (17%)	5 (4)
1982	14	23	7 (30%)	2 (29%)	3 (1)
1983	15	24	7 (29%)	0 (0%)	0 (0)
1984	17	24	8 (33%)	1 (13%)	3 (2)
1985	19	26	12 (46%)	0 (0%)	1 (1)
1986	23	27	15 (56%)	3 (25%)	5 (2)
1987	23	29	14 (48%)	1 (7%)	3 (2)
1988	21	31	14 (45%)	0 (0%)	0 (0)
1989	24	31	15 (48%)	4 (27%)	5 (1)
1990[a]	42	32	25 (78%)	6 (24%)	13 (7)
1991[a]	46	39	32 (82%)	13 (41%)	22 (9)
1992[a]	48	48	38 (79%)	3 (8%)	7 (4)
1993[a]	42	52	40 (77%)	5 (13%)	6 (1)
1994	20	53	16 (30%)	3 (19%)	4 (1)
1995	31	54	25 (46%)	6 (24%)	7 (1)
1996	20	55	14 (25%)	2 (14%)	3 (1)
1997	9	56	7 (13%)	1 (14%)	2 (1)
1998[a]	46	57	43 (75%)	7 (16%)	10 (3)
1999[a]	58	60	54 (90%)	14 (26%)	18 (4)
2000[a]	61	64	55 (86%)	11 (20%)	16 (5)
2001[a]	64	69	59 (86%)	11 (17%)	15 (4)
2002[a]	37	73	37 (51%)	10 (27%)	10 (0)
2003[a]	49	73	47 (64%)	6 (13%)	6 (0)
2004[a]	60	73	59 (81%)	9 (15%)	10 (1)
2005[a]	73	74	71 (96%)	7 (10%)	9 (2)

[a]years when surveys occurred specifically for Gyrfalcons.

During 1990–93 and 1998–2005 (n = 12 years), surveys were made specifically for Gyrfalcons in Kangerlussuaq, in which 51–96% (median = 80, average = 79, sd ± 11.9) of known nest sites were checked each year to determine occupancy (Table 4.1). During these two periods between 8 (1992) and 41% (1991) of known sites that were surveyed were occupied (median = 16.5, average = 19, sd ± 9.2) (Table 4.1). A high of 22 (1991) sites

were occupied with a low of six in both 1993 and 2003 (mean = 11.8, sd ± 5, median = 10) (Table 4.1). Sites that appeared suitable but where Gyrfalcons had not previously been recorded were also checked, revealing a limited number of new occupied sites.

As mentioned above, surveys specifically for Gyrfalcons took place during 1990–1993 and 1998–2005 in Kangerlussuaq. However, between these periods the overall size of the study area increased, with a new and very productive valley to the north of the original study area included in the surveys from 1998 onward. The data from the original area in both periods are given in Table 4.2. Data in the "initial study area" encompassed all nest sites known from 1990 to 1993 in addition to other nest sites found later but within the same area/boundaries. The "total study area" includes all sites in the "initial study area" in addition to all nest sites found in the expanded area.

Table 4.2: Nest site occupancy by Gyrfalcons in Kangerlussuaq, Greenland, from 1990 to 1993 and from 1998 to 2005 in the "initial study area." (Mattox annual reports from 1990 to 1993).

Year	Occupied (% of checked occupied)	Successful	Known Gyr sites checked (%)	Known Gyrfalcon sites
1990	13 (52%)	7	25 (100%)	25
1991	22 (69%)	12	32 (100%)	32
1992	7 (18%)	3	38 (100%)	38
1993	6 (15%)	0	40 (100%)	40
1998	8 (18%)	8	45 (78%)	58
1999	14 (26%)	11	54 (92%)	59
2000	12 (22%)	11	55 (90%)	61
2001	11 (20%)	11	55 (90%)	62
2002	8 (25%)	7	32 (52%)	62
2003	6 (14%)	3	42 (68%)	62
2004	7 (13%)	6	53 (85%)	62
2005	6 (10%)	6	60 (97%)	62

Only from 1990 to 1993 and from 1998 to 2005, when surveys were conducted specifically for Gyrfalcons, were occupancy records comparable. Using occupied and successful nest sites located within the initial study area (Table 4.2), there appeared to be

two possible Gyrfalcon population peaks, in 1991 and during 1999–2001 (Figure 4.1). The high in 1991 was followed by a large and immediate drop, while the high from 1999 to 2001 was followed by a more moderate decline. The time interval between population peaks and lows appeared to be between eight and 10 years, respectively. Although the initial peak and decline from 1991–1993 was more severe than for the period 1999–2003, this may simply be a function of peak height and trough depth varying from one cycle to another, as has been observed in other species which fluctuate cyclically.

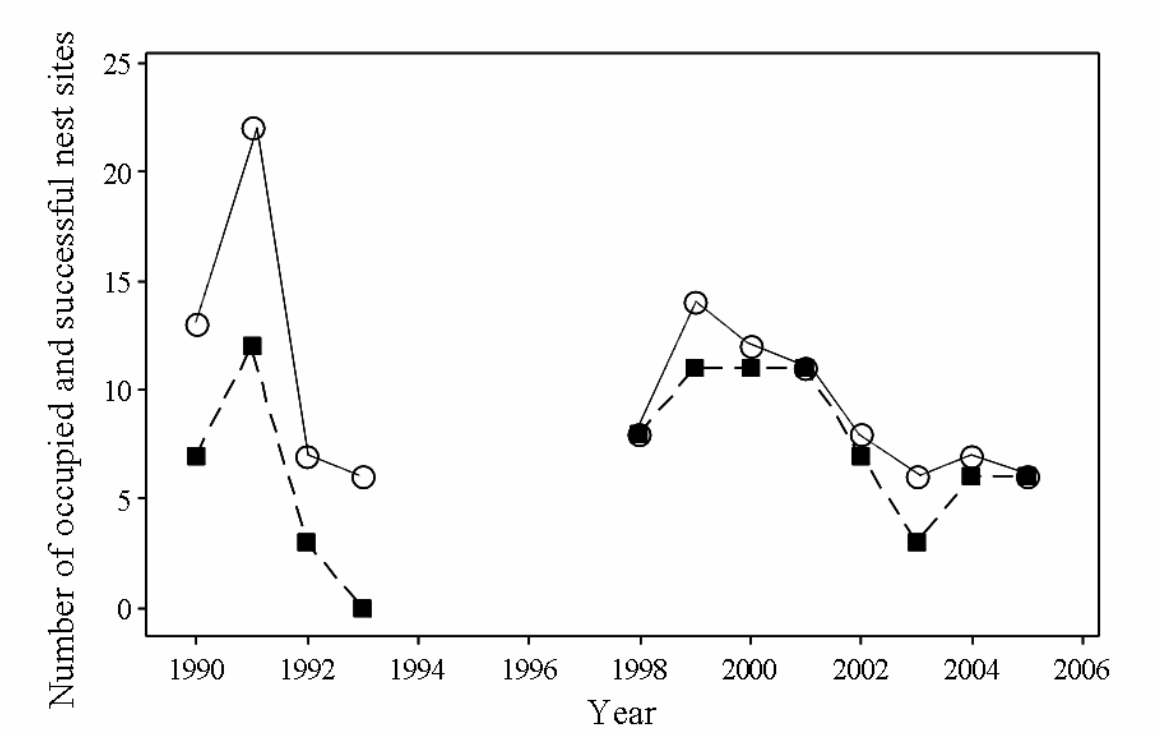

Figure 4.1. The number of occupied (circles and solid line) and successful (squares and dashed line) Gyrfalcon nest sites from 1990 to 1993 (Mattox annual reports) and from 1998 to 2005 in the "initial study area" in the Kangerlussuaq area. Population peaks occurred in 1991 and between 1999 and 2001.

Generally speaking, the number of known Gyrfalcon nest sites that were surveyed each year in the "initial study area" increased over the entire study period, with a low of 25 in 1990 and a high of 60 in 2005 (Figure 4.2). Despite more nest sites known and surveyed each year, and more thorough and improved survey techniques, the number of occupied sites found decreased, with the number of successful nests approximately the same over the

entire period (Figure 4.2). A similar pattern was observed when data for the "total study area" were used; however, the number of successful nests increased slightly more (Appendix K).

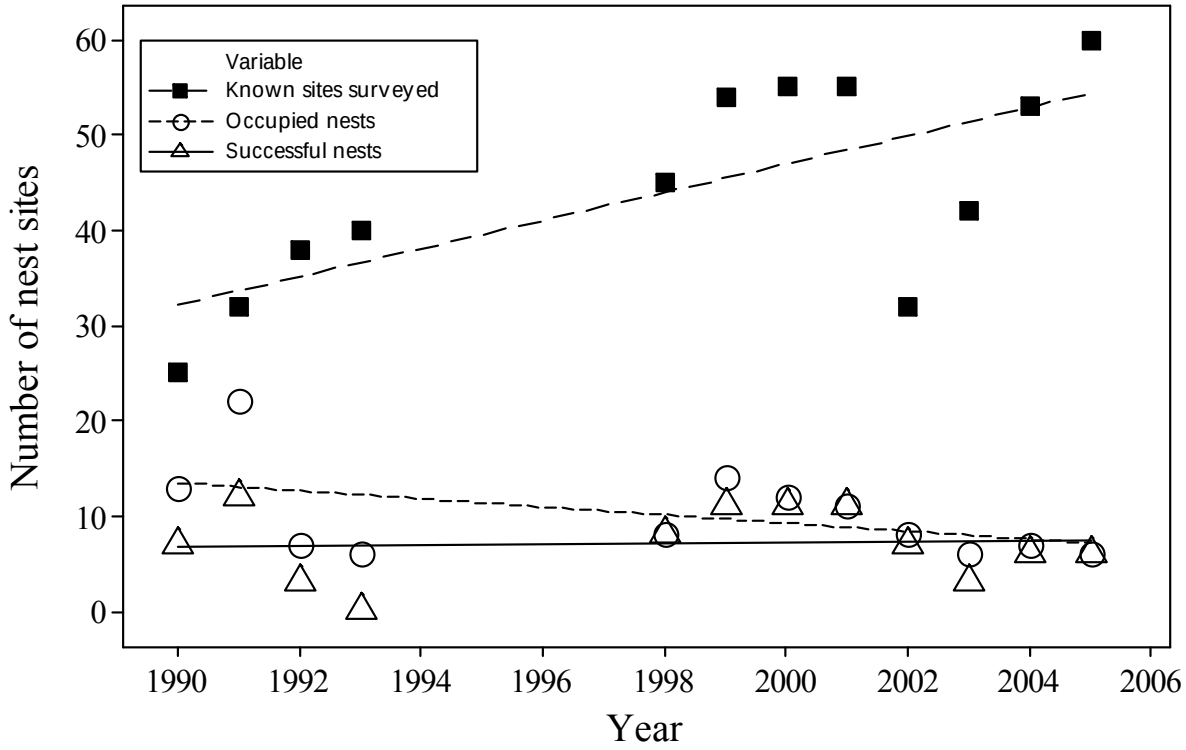

Figure 4.2. The number of known Gyrfalcon sites surveyed, occupied, and successful from 1990 to 1993 and from 1998 to 2005 in the "initial study area" in Kangerlussuaq, Greenland.

While it is possible that sites with single, non-breeding pairs, or failed pairs of Gyrfalcons were missed, most locations where reproduction occurred were probably discovered. From 1998 to 2000 a limited number of nest sites surveyed by helicopter were also surveyed by other falcon researchers on foot during the same period. In total we surveyed 51 known Gyrfalcon nests in common, with my results exactly matching theirs.

Little information is available on the failure rate of Gyrfalcon nests in Kangerlussuaq during this study. However, in 1999 and 2000 surveys of known Gyrfalcon

nest sites were conducted in the early spring (April, when egg laying occurred) in an attempt to determine proportion later failing, with eight and six nests found occupied, respectively. Of those nests found occupied in the early spring, four were no longer occupied at a repeat survey in June 1999 and one was no longer occupied at a repeat survey in June 2000. However, eggs were not observed at any of these nest sites in the early spring and, although adults appeared to be incubating in some instances, pairs may have moved to other nests in the vicinity. Further, in 1999 and 2000 four nest sites that were not occupied in April were found to be occupied by breeding pairs of Gyrfalcons when they were later re-checked in June. This would perhaps be expected from the large range of egg laying dates observed in Kangerlussuaq (>40 days in some years, see section on nesting chronology). Based on these poor and inconclusive results, and safety concerns for falcons, early spring surveys were discontinued.

During 1999–2005, locations with recent occupancy were prioritized for re-checking in subsequent years. Typically, these were locations with nest ledges or potholes, or in some cases sticks nests recently used by Northern Ravens. Northern Raven nests are typically used by Gyrfalcons for only a single breeding season before being damaged beyond re-use by the chicks. Gyrfalcons are not known to build stick-nests of their own.

In Kangerlussuaq, during 1972–1981 (n = 10), Burnham and Mattox (1984) found 65% of breeding Gyrfalcons (n = 22) nesting in old Raven nests. They reasoned that the number was probably higher than elsewhere in Greenland because of the large Raven population that fed at the local refuse dump. They located human trash (foil, plastic, glass, etc.) in raven castings at nests up to 40 km from Kangerlussuaq. I examined 66 occupied Gyrfalcon nest sites during 1998–2005 and found 36 (55%) to be on ledges or potholes and 30 (45%) to be in former Raven stick nests. Some of the non-raven nest sites had deposits of guano up to one meter thick (see Chapter 3).

It seems that some Gyrfalcon nesting territories have alternative nest sites. Seven territories in Kangerlussuaq had multiple adjacent nest sites (one to four) never discovered to have been used simultaneously during the entire study, which makes a strong case they were alternative nest sites within the same territories, although this cannot be proven with certainty as the adults were not ringed. If true, the total number of known nesting territories available for breeding would be reduced and nest sites could be grouped together by territory for analyses.

Surveys and occupancy: Thule

I surveyed for Gyrfalcon nest sites from 1993 to 2005 (n = 13) and documented territorial Gyrfalcons 52 times at 18 locations (Table 4.3). Surveys were accomplished during June (by dogsled) through July and August (boat, backpacking, and helicopter) from 75.9 to 77.6° N along the coast and islands of northwest Greenland, covering at least 984 km of coastline. Although the entire area was not surveyed every year, almost all locations were visited multiple times over the 13-year period.

Table 4.3. Nest site occupancy by Gyrfalcons in Thule, Greenland, from 1993 to 2005.

Year	Sites checked from 1993 to 2005	Known Gyrfalcon sites	Known Gyr sites checked (%)	Known Gyr sites occupied (%)	Total sites occupied (new sites found)
1993	1	–	–	–	1 (1)
1994	3	1	1 (100%)	1 (100%)	2 (1)
1995	3	2	2 (100%)	1 (50%)	2 (1)
1996	2	3	2 (66%)	1 (50%)	1 (0)
1997	3	3	3 (100%)	2 (66%)	2 (0)
1998	5	3	3 (100%)	2 (66%)	3 (1)
1999	5	4	4 (100%)	2 (50%)	3 (1)
2000	5	5	3 (60%)	3 (100%)	4 (1)
2001	8	6	5 (83%)	2 (40%)	5 (3)
2002	10	9	7 (78%)	6 (86%)	8 (2)
2003	5	11	4 (36%)	1 (25%)	2 (1)
2004	13	12	11 (92%)	7 (64%)	9 (2)
2005	18	14	13 (93%)	6 (46%)	10 (4)

During surveys for nesting Gyrfalcons in Thule, few if any occupied nests were likely to have been missed. Adults and juveniles were almost exclusively bright white in plumage and in general were obvious to the naked eye when observed on cliffs, even at long distances. From 1993 to 2003 no obvious use of alternative nest sites occurred and all breeding took place on ledges or in potholes. Beginning in 2004 and continuing in 2005, it appeared likely that pairs began using alternative nesting sites within breeding territories; however, adults were not ringed and it was not possible to determine the specific movements of individuals. During this period, the use of Northern Raven nests by Gyrfalcons in the Thule area was observed for the first time, with multiple raven nests used in 2004 and 2005. The increase of new nesting sites found in 2004 and 2005, two and four respectively, is primarily a result of these raven nests being used for nesting by Gyrfalcons and in most cases previously used ledges or potholes were within one kilometer.

Results from the Thule area provide the first information on the local Gyrfalcon population, but despite research occurring from 1993 to 2005, limited conclusions can be drawn on occupancy. Only in 2001 were surveys started on a large enough scale to provide data on a number of nests each year. It appears that the Thule population was relatively stable, apart from 2003 when only two occupied sites were found, with eight occupied in 2002 and nine in 2004. However, it does not appear that the population was peaking or crashing, and only four known Gyrfalcon nests sites were surveyed in 2003 compared to seven in 2002 and 11 in 2004.

Occupancy of nest sites is difficult to compare between Kangerlussuaq and Thule. Within the Kangerlussuaq area, the majority of Gyrfalcon nest sites were documented by others prior to this study, which provided me with significant overall knowledge of the study area. In Thule, I had no previous knowledge of nest site locations and each year required new and extended surveys.

Distance between nest sites: Kangerlussuaq

Burnham & Mattox (1984) reported 10.4 km between occupied sites and 12.3 km for successful Gyrfalcon nest sites in 1973 and 1974 (n = 12). From 1990 to 1993 the mean minimum distance between occupied and successful sites was 17.1 km (sd ± 4.1, median = 17.7, range = 11.6–21.5) and 26.1 km (sd ± 8.5, median = 29.1, range = 16.5–32.7), respectively; however, no successful nest sites were documented in 1993 (Table 4.4). For the period of my research, 1998–2005, the mean minimum distance between occupied and successful sites in the "initial study area" was 23.2 km (sd ± 5.6, median = 21.7, range = 17.3–33.9) and 25.5 km (sd ± 6.5, median = 23.5, range = 18.8–36.3), respectively (Table 4.4). The mean minimum distance of occupied and successful nest sites in the "initial study area" were plotted over time and both appear to have increased, the mean minimum distance of occupied sites significantly so ($p = 0.008$, $r^2 = 52.6$) (Figure 4.3).

Table 4.4. Mean minimum distance between occupied and successful Gyrfalcon nest sites in Kangerlussuaq, Greenland, from 1990 to 1993 and from 1998 to 2005. "Initial study area" encompasses all nest sites known from 1990 to 1993 in addition to nest sites found later but within the same geographic area. "Total study area" is all nest sites known in the Kangerlussuaq area, inside or outside of the "initial study area."

	Initial study area		Total study area	
Year	Occupied (n)	Successful (n)	Occupied (n)	Successful (n)
1990	17.50 (13)	29.09 (7)	na	na
1991	11.55 (22)	16.52 (12)	na	na
1992	21.51 (7)	32.72 (3)	na	na
1993	17.89 (6)	–	na	na
1998	21.47 (8)	21.47 (8)	22.24 (10)	22.24 (10)
1999	17.26 (14)	21.60 (11)	15.38 (18)	21.00 (15)
2000	17.82 (12)	18.75 (11)	17.67 (16)	18.29 (15)
2001	20.18 (11)	20.18 (11)	21.25 (15)	21.25 (15)
2002	21.84 (8)	26.07 (7)	19.10 (10)	19.10 (10)
2003	27.78 (6)	36.34 (3)	27.78 (6)	36.34 (3)
2004	25.05 (7)	25.44 (6)	21.09 (10)	20.84 (9)
2005	33.89 (6)	33.89 (6)	27.63 (9)	27.63 (9)

na–not applicable, survey area was smaller than from 1998 to 2005.

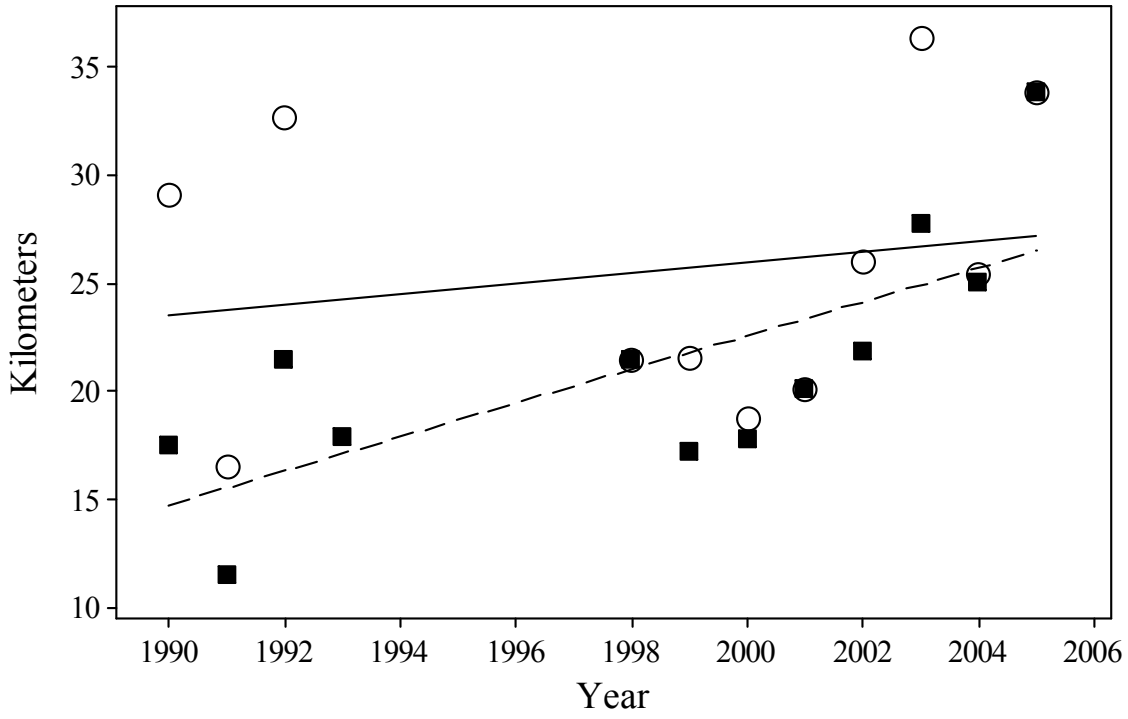

Figure 4.3. Mean minimum distance between occupied (squares, dashed line) and successful (circles, solid line) nest sites in the Kangerlussuaq area during 1990–1993 and 1998–2005. A significant positive relationship between time and mean minimum distance between occupied sites was found ($p = 0.008$, $r^2 = 52.6$).

Burnham & Mattox (1984) reported an approximately 1:1 ratio of Peregrines to Gyrfalcons in the Kangerlussuaq area from 1972 to 1981. Since 1972 over 170 separate nesting cliffs have been located for Peregrines in Kangerlussuaq while only 76 separate Gyrfalcon nest sites were located. The maximum number of Gyrfalcon sites ever known to be occupied in a single year was 22 in 1991, while over 81 Peregrine nest sites were found occupied the same year, a ratio of 1:3.7 (Mattox 1991).

Distance between nest sites: Thule

Limited numbers of occupied Gyrfalcon nest sites were found each year in Thule and were distributed linearly along the coastline. Because of this the mean minimum distance between nest sites was of limited use and was not calculated.

Reproduction: Kangerlussuaq

Information exists on reproduction for 29 years, from 1972 to 2005, with most data available for 1998–2005. The age at the time of cliff visit varied from incubation through young having already departed the nest. The numbers presented are minima as I was frequently not able to ascertain the total number of young. In some cases chicks were too young, too near fledging, or cliffs were too overhung for the nest to be entered safely. When young were small, less than one week in age, adult females frequently did not leave the nest when approached by helicopter and observations were limited to a mass of nestling down under the front of the female's breast. In these instances, reproduction was recorded as ≥1.

From 1972 to 2005 occupied Gyrfalcon nest sites were observed on 221 separate occasions in the Kangerlussuaq area. Those occupied produced at least 361 young, or ≥1.63 per occupied site (Table 4.5). Of the 221 occupied sites, young were confirmed at 131, an average of ≥2.75 young per successful nest (Table 4.5). At those sites, a single young was produced only once and five young twice, with median production being three young. In June, nests with adults incubating eggs were grouped as occupied and probably failed, as the eggs were likely dead or would have hatched too late for the young to survive and migrate. Table 4.5 compares reproduction for the time period of my research (1998–2005) with the prior period (1972–1997). While large differences are observed in reproduction between periods this is likely a result of the majority of surveys from 1972 to 1997 taking place when Gyrfalcon young had already fledged and begun to disperse, making the number of young present difficult to determine. Further, the large difference between occupied (n = 221) and successful (n = 131) sites is not solely a result of pairs failing. Instead, it is likely a case of adults being observed but reproduction being unknown.

Table 4.5. Average number of Gyrfalcon young produced near Kangerlussuaq, Greenland, from 1972 to 2005 (Burnham & Mattox 1984, Mattox annual reports from 1982 to 1997).

Years	Occupied (*n*)	Successful (*n*)
1972–1997*	≥ 1.30 (127)	≥ 2.50 (66)
1998–2005	≥ 2.09 (94)	≥ 3.02 (65)
1972–2005	≥ 1.63 (221)	≥ 2.75 (131)

*Mattox annual reports from 1972 to 1997.

Reproduction: Thule

Thirteen years of information exist for Gyrfalcons in Thule, from 1993 to 2005. Using the same criteria for sites being occupied and productive as in the Kangerlussuaq area, I located 52 occupied territories that produced an average of ≥1.88 young per nest, and a minimum of 41 successful sites which produced a minimum of ≥2.39 young per nest. Nest sites were rarely visited until after the young were too old to safely ring, or flying in many cases, and I could not be certain of the total number of young produced at most locations. A single young was recorded only once and a maximum of five young was recorded once.

During this study Gyrfalcons in Kangerlussuaq produced more young per occupied and successful nest than those in Thule, 2.09 vs. 1.88 and 3.02 vs. 2.39, respectively. However, nests in Thule were surveyed approximately 2–3 weeks later during the breeding cycle than those in Kangerlussuaq. It was not possible to determine the amount of increased mortality incurred during this 2–3 week period in Thule and the observed difference in reproduction between areas was likely recorded as greater than if surveys had occurred when young were approximately the same age in both areas.

Nesting chronology

During 2002–2005 for Kangerlussuaq and 1994–2005 for Thule, data were collected on the nesting chronology of Gyrfalcons, counting backwards from the estimated average age of nestlings or fledglings. I assumed a four-egg clutch with an egg laid every other day,

with incubation beginning on the third egg and a 35-day incubation period (C. Sandfort pers. comm., Platt 1977). Poole and Bromley (1988) reported that males fledged at 45–47 days and females at 47–50 days. I used 47 days as an average fledging age.

Gyrfalcons in Kangerlussuaq began nesting approximately 17 days later than those in Thule, with the first egg laid on 22 April (sd ± 25) and 9 May (sd ± 7.4), respectively (Table 4.6). Calculating forward, young departed the nest around 16 July in Kangerlussuaq and 2 August in Thule (Table 4.6). Based on research in Canada and Iceland (Cramp & Simmons 1980, Nielsen & Cade 1990a, respectively), which showed young Gyrfalcons became independent of adult care at an average of ≥4 weeks after they left the nest, independence would be reached in mid-August in Kangerlussuaq and early September in Thule.

Table 4.6. Nesting chronology of Gyrfalcons in the Thule and Kangerlussuaq areas, Greenland. Hatch dates were calculated from estimated age of young. Average dates for first egg laid and start of incubation were calculated by subtracting 35 and 39 days, respectively (see text). Average fledging date was calculated by adding 47 days to hatch date (see text). Calculated dates were consistent with dates observed in the field.

Date of:	Kangerlussuaq average (min–max, median, *n* = years)	Thule average (min–max, median, *n* = nesting attempts)
1st egg laid	22 April (30 March–19 May, 10 April, *n* = 22)	9 May (26 April–28 May, 9 May, *n* = 35)
Start of incubation	26 April (4–23 May, 14 April, *n* = 22)	13 May (30 April–1 June, 13 May, *n* = 35)
Hatch	30 May (7 May–26 June, 18 May, *n* = 22)	17 June (3 June–6 July, 17 June, *n* = 35)
Fledge	16 July (24 June–11 August, 4 July, *n* = 22)	2 August (19 July–21 August, 2 Aug, *n* = 35)

In general, Gyrfalcons in Kangerlussuaq had a much wider range of dates, or longer time period, during which reproduction occurred. In Kangerlussuaq, fledging took place over a 49-day period (24 June–11 August) compared to a 34-day period in the more northern Thule area (19 July–21 August, 34-day period) (Table 4.6). This was also

noticeable when nests were surveyed in Kangerlussuaq. In one instance in Kangerlussuaq, two nests were visited on the same day (within 20 km of each other) with one nest having pipped/hatching eggs and the other nest young that were almost fully feathered and ready to depart the nest.

Prey

Jenkins (1978), Burnham & Mattox (1984), and Booms & Fuller (2003) have documented prey species delivered to Gyrfalcon nest sites in Kangerlussuaq. It was determined that Gyrfalcons prey on virtually all small to medium-size birds and mammals present there. During this study, ptarmigan remains were the most common prey item in Gyrfalcon nests, e.g., one 2005 nest with four approximately 38-day-old nestling Gyrfalcons contained 55 ptarmigan and two Oldsquaw keels. Arctic Hare, Snow Bunting, and Lapland Longspur remains were also found, but much less frequently. However, from 1972 to 1981, Burnham and Mattox (1984) emphasized the apparent importance of passerines as food to supplement ptarmigan and hare when their numbers were few.

Several Gyrfalcon nests in Kangerlussuaq overlooked fjords and PTT data showed that two females that nested inland travelled 25–40 km to the ocean/fjords; however, no seabird remains were found at nests. Having personally travelled the fjord/ocean region in this area I did not observe any small seabirds (only large gulls were observed) and the most frequently encountered prey species was Oldsquaw, which also nested on lakes throughout the study area, but which I observed in large non-breeding groups along the coastline.

Although Rock Ptarmigan have been shown to have cyclic population fluctuations throughout the Arctic (Gudmundsson 1960, Weeden & Theberge 1972, Watson *et al.* 1998, Moss & Watson 2001), and specifically in Greenland (Salomonsen 1950–51), no data were available during this study. From 1998 to 2000 surveys were conducted both during the

early spring, when individuals were still in flocks, and during the mating season when cocks were on territory. In general, surveys were unsuccessful and frequently no birds were found. It appeared that ptarmigan density was much lower in Greenland than in other areas in the Arctic. Additionally, although hare and ptarmigan populations have been shown to fluctuate together in other areas in the Arctic (Boutin *et al.* 1995), I can provide no evidence for or against this possibility in Kangerlussuaq or Thule.

In Thule, prey remains were collected at 29 Gyrfalcon nest sites from 1994 to 2005. Dovekie remains were present in 79% of the nests. Fourteen nests had exclusively Dovekie remains, the only prey species for which that was the case. Rock Ptarmigan remains were found at eight nests (28%), Black Guillemot at five (17%), Arctic Hares at five (14%), Oldsquaw at three (10%), songbirds and Black-legged Kittiwakes at two (7%), and Common Eiders and Snow Geese at one (3%). Although I did not conduct prey transects, there was an obvious positive correlation between potential prey seen in the general areas of nest sites and prey species remains in nests. For example, one nest site located approximately 60 km up from the mouth of the Olrik Fjord, and an even greater-distance from any breeding seabird colonies, yielded mainly Arctic Hare leverets and songbird remains.

The principle prey species varied between areas, with ptarmigan being most frequently captured in Kangerlussuaq and Dovekies in Thule. However, both ptarmigan and Arctic Hares were important prey species in both areas. In general, Gyrfalcons in Kangerlussuaq and Thule appeared to be opportunistic feeders, and captured the majority of prey species, both avian and mammal, found in each respective area.

Nest site characteristics

Data were collected from Gyrfalcon nest sites in Kangerlussuaq and Thule to determine if differences existed between areas. Further, by comparing characteristics within an area I have attempted to determine if nest sites were limiting. However, because of time and financial restraints it was not possible to collect data on randomly selected cliffs and I was unable to determine if Gyrfalcons were selecting for specific nest sites.

Breeding pairs of Gyrfalcons were found at 76 different locations in the Kangerlussuaq area between 1972 and 2005 (Mattox reports from 1972 to 1997, Burnham & Mattox 1984, personal data recorded from 1998 to 2005). In some cases, multiple nests at the same location were occupied during the study period. These locations commonly consisted of continuous or broken cliff lines, which extended up to one km. In these instances, each individual nest at the location was included in analyses as nest site characteristics varied along a cliff face.

I found Gyrfalcons breeding at 18 different locations in the Thule study area from 1994 to 2005. As in Kangerlussuaq, some locations had multiple nests that were occupied by Gyrfalcons during the study period and each of these nests was included a single time in these analyses. However, few Gyrfalcon nests were entered and the majority of the data presented is on cliff characteristics. All Gyrfalcon nest sites in Thule were within three km of the sea.

Gyrfalcons occupied cliffs in Kangerlussuaq which had a mean height of 46 m (range = 5–152, median = 38, n = 83, sd ± 31) (Table 4.7). These were less than half as tall as those is Thule which had a mean height of 119 m (range = 23–305, n = 14, sd ± 71) (Table 4.7). However, nest ledges in both areas were located in similar areas on the cliff face, a mean of 61% (range = 13–90, n = 14, sd ± 23) below the rock crest (0% = top, 100%

= ground below cliff) in Kangerlussuaq and 62% (range = 20–90, median = 64, *n* = 40, sd ± 19) in Thule (Table 4.7). Additionally, cliffs in both areas generally faced a similar direction, with a mean cliff aspect of 172° (range = 225, median = 178, *n* = 85, sd ± 49) in Kangerlussuaq and 211° (range = 270, *n* = 17, sd ± 72) in Thule (Table 4.7).

Table 4.7. Nest sites characteristics from Kangerlussuaq and Thule, Greenland. Each individual nest site (ledge) was included only once.

	Kangerlussuaq	Thule
	Mean ± sd *n*	Mean ± sd *n*
Cliff characteristics		
Elevation of cliff asl (m)	291 ± 114 *n* = 85	171 ± 69 *n* = 14
Cliff height (m)	46 ± 31 *n* = 83	119 ± 71 *n* = 14
Cliff aspect (°)	172 ± 49 *n* = 85	211 ± 72 *n* = 17
Location on cliff (0% being top)	62 ± 19 *n* = 40	61 ± 27 *n* = 14
Height of ledge (m)	19 ± 16 *n* = 40	41 ± 27 *n* = 14
Nest ledge characteristics		
Length of nest ledge (cm)	133 ± 103 *n* = 19	86 ± 43 *n* = 6
Depth of nest ledge (cm)	90 ± 37 *n* = 19	122 ± 53 *n* = 6
Nest ledge aspect (°)	187 ± 42 *n* = 22	59 ± 116 *n* = 6
Horizontal angle of exposure (°)	133 ± 32 *n* = 22	129 ± 37 *n* = 6
Vertical angle of exposure (°)	44 ± 15 *n* = 19	52 ± 9 *n* = 5

All nest ledge characteristics were relatively similar between areas except for nest ledge aspect. Nest ledge aspect was over 100° different between areas with a mean of 187° (range = 232, *n* = 22, sd ± 42) in Kangerlussuaq and 59° (range = 270, *n* = 6, sd ± 116) in Thule (Table 4.7). However, the sample size in Thule was small and even though a mean was calculated, based on Figure 4.4, Gyrfalcon nests in Thule do not appear to face a specific direction, in contrast to those in Kangerlussuaq.

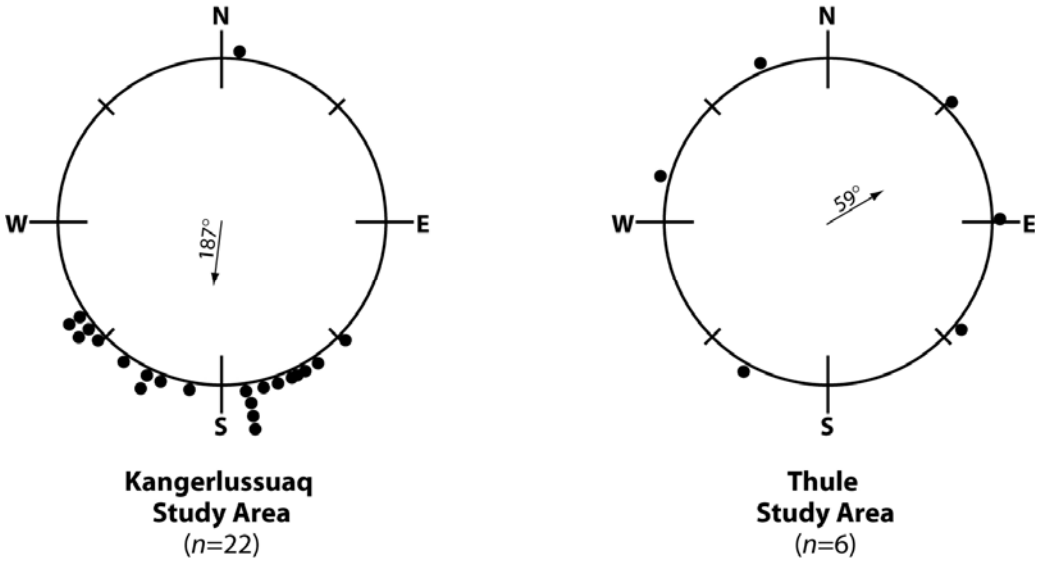

Figure 4.4. Directional aspects/exposure of Gyrfalcon nests in the Kangerlussuaq and Thule areas, Greenland. The average vectors are indicated.

Plumage colour variants

As mentioned in the introduction, discussion continues about plumage colour variation in Gyrfalcons which I contribute to only in reference to what was observed in the three study areas. In Kangerlussuaq during 1972–1977, the plumage of 29 adult Gyrfalcons was recorded as 16 (55%) "white" and 13 (45%) "grey." During 1998–2005, the plumage colour of 112 adults was recorded as 58 (52%) "white," 14 (13%) "silver," and 40 (36%) "grey." During the 1970s "silver" was included with "grey" and on this basis no difference was apparent between time periods. Combining colours observed during both time periods, 74 (52%) were "white" and 67 (48%) "silver/grey." Salomonsen (1950–51) reported a 50:50 ratio white and dark plumages near the Arctic Circle. These results are consistent, also supporting the notion of no change over time.

More than 170 juvenile and adult Gyrfalcons were observed during 1993–2005 in Thule, of which two had "grey" plumage (adult female and her daughter) and one "silver." The remainder of the Gyrfalcons had very "white" plumages and most showed no visible

dark pigmentation on their tails, even as juveniles. These are the whitest plumages I observed in the wild and in skin collections.

In Scoresbysund, East Greenland, in 2004 (n = 38) and 2005 (n = 87), 125 Gyrfalcons were captured and released. All but two had "white" plumage, the remaining two being "grey." The predominately "white" colour plumages are consistent with specimens from East Greenland in museums and the literature. Although "white" in plumage, few individuals were as white as those observed in northwest Greenland.

Although obvious from the above figures, chi-square tests confirmed a significant association between colour plumage and study area (Kangerlussuaq and Thule, $p < 0.001$/Kangerlussuaq and Scoresbysund, $p < 0.001$). As expected from past museum skins, no association was found between Thule and Scoresbysund ($p = 0.914$), with virtually all individuals in both areas being white. Repeat sightings may have occurred from one year to the next as few adults were ringed and it was not possible to tell individuals apart. Colour phase of individuals stayed consistent throughout their lives, as evident from captive birds.

Morphometrics

Measurements were taken from all captured adult and juvenile Gyrfalcons to find whether size differences were present between populations within Greenland.

Adults

Using t-tests, no significant size differences were found between adults from the four areas where data were collected, although sample sizes were small, especially for males (see Appendix L for data on measurements and Appendices M & N for t-test results). PCAs yielded two components for both females and males, which explained 62% and 73% of the total variance, respectively (Table 4.8). The first principal component (PC1) described

overall body size for females (tarsus length, wing chord, tail length, and body mass), and was highly positively correlated with all variables except bill length (Table 4.8). Bill length and tail length loaded heavily and negatively onto the second principal component (PC2) for females, with bill length having a high and negative correlation with PC2 (Table 4.8). For adult males PC1 described body mass, and to a lesser extent tail and tarsus length, with bill length being highly negative (Table 4.8). A high and positive correlation was found between PC1 and body mass, while a high and negative correlation was found between bill length and PC1. All variables on PC2 had negative loadings, with wing chord being the most negative and having a high and negative correlation with PC2 (Table 4.8).

Table 4.8. Results of two separate principal component analyses (PCA): (1) adult female Gyrfalcons from Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq and (2) adult males from Thule, Scoresbysund, and Maniitsoq, Greenland. Component loadings on each significant axis and percent of total variance explained are shown.

	Adult females (n = 22)		Adult males (n = 9)	
Variable	PC1	PC2	PC1	PC2
Bill length	-0.191	-0.760	-0.580	-0.373
Tarsus length	0.506	0.120	0.345	-0.414
Wing chord	0.607	-0.266	-0.231	-0.673
Tail length	0.344	-0.509	0.347	-0.476
Body mass	0.469	0.279	0.610	-0.104
% Variance explained	40	22	39	34

For adult females a Kruskal-Wallis test was performed on PC1 and showed a significant difference ($x^2 = 9.50$, df = 3, p = 0.023) among all areas (Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq) for overall body size, although it was not possible to identify between which specific areas. No significance between areas was found for PC2. Using PC1 adult males also showed a significant difference ($x^2 = 7.0$, df = 2, p = 0.03) between populations (Thule, Scoresbysund, and Maniitsoq) using a Kruskal-Wallis test while no

difference was found for PC2. Sample sizes for both female (n = 22) and male (n = 9) adults were small, and results should be viewed with some skepticism.

Juveniles

T-tests between juvenile males in Thule and Scoresbysund showed significant differences for tail (T = 4.13, df = 16, p = 0.001) and tarsus length (T = 4.30, df = 30, p < 0.001). No other significant differences were found between biometric data when using t-tests (see Appendix O for data on measurements and Appendices P & Q for t-test results). PCAs yielded two components for both females and males, which explained 51% and 67% of the variance, respectively (Table 4.9). For juvenile females and males, all loadings on PC1 were negative and highly correlated (negatively) with PC1 and described body size. For females, wing chord and tarsus and tail length had positive loadings on PC2 while bill length and body mass had negative loadings (Table 4.9). All five variables were highly correlated with PC2, with positive loadings correlating positively and negative loadings correlating negatively. For males, bill length and wing chord had high positive loadings and were highly and positively correlated, while body mass and tarsus length had high negative loadings, and in turn were highly and negatively correlated.

Table 4.9. Results of two separate principal component analyses (PCA): (1) juvenile female Gyrfalcons from Thule, Scoresbysund, and Maniitsoq and (2) juvenile males from the same three areas, Greenland. Component loadings on each significant axis and percent of total variance explained are shown.

	Juvenile females (n = 70)		Juvenile males (n = 63)	
Variable	PC1	PC2	PC1	PC2
Bill length	-0.477	-0.459	-0.348	0.566
Tarsus length	-0.476	0.337	-0.481	-0.322
Wing chord	-0.506	0.286	-0.475	0.332
Tail length	-0.352	0.467	-0.538	0.087
Body mass	-0.408	-0.613	-0.364	-0.677
% Variance explained	31	20	48	19

A Kruskal-Wallis test performed on PC1 showed that populations (Kangerlussuaq, Thule, and Maniitsoq) of juvenile female Gyrfalcons were significantly different in size (x^2 = 7.06, df = 2, p = 0.029), although no significant difference was found for PC2. A Mann-Whitney test performed on PC1 showed that juvenile male Gyrfalcon populations in Thule and Scoresbysund are significantly different in size (W = 1811.0, p = 0.002), while there was no significant difference between populations for PC2. Based upon these results, it appears that juveniles vary in size (PC1) but not in overall shape (PC2) between areas.

Principle component analysis indicated significant size differences within populations of both adult and juvenile male and female Gyrfalcons in Greenland. Test results do not identify between exactly which areas these differences are present. However; of the five body measurements recorded for male and female juvenile and adult Gyrfalcons, the Thule (most northern) individuals were in general the largest. Thule birds had the greatest average body mass, tarsus length, and tail length. Bill length was longest among Maniitsoq individuals for all ages and sexes. Wing chord was longest in Thule for adult females and juvenile males, longest in Maniitsoq for adult males, and equal between Thule and Maniitsoq for juvenile females. For Maniitsoq, among juvenile males only body mass had a sample size greater than one while no adult males or juveniles were measured in Kangerlussuaq.

Satellite-received telemetry

Satellite transmitters were used to address long-standing questions on the movements of Gyrfalcons nesting in both Low and High Arctic Greenland. Individuals were captured and tagged in order to find whether Gyrfalcons were complete or partial migrants, whether size and location of wintering areas used by individuals varied among geographic populations, whether size of breeding home ranges varied among populations, and the variation between individuals in speed and route of outward and return migration.

In order to minimize any potential impacts that PTTs might have had on the ability of adults to rear young, in no instance were both members of a breeding pair tagged.

Transmitters: numbers deployed, longevity, and location classes

A total of 56 PTTs were placed on Gyrfalcons in the Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq study areas between 2000 and 2004. Of those, 29 were placed on adults (one adult which was recaptured and fitted with a new unit, so true $n = 28$ adults tagged), 22 on juveniles, and four on nestlings (Table 4.10). In Kangerlussuaq, all units were placed on individuals at the nest. In Thule, all juveniles were tagged at a ringing station and three adult females were tagged at the nest and two at a ringing station, with a single adult male tagged at a ringing station. For Scoresbysund and Maniitsoq all individuals were captured at ringing stations while presumably on outward migration. Individuals in Kangerlussuaq were tagged in June-July, in Thule during July–September, in Scoresbysund during September–November, and in Maniitsoq in September–October. All PTTs weighed less than 3% of the body weight of Gyrfalcons tagged. Individual Gyrfalcons have been identified by their five-digit Argos PTT ID numbers.

Table 4.10. Number of PTTs deployed and location, sex, and age of individual Gyrfalcons tagged in Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq, Greenland, from 2000 to 2004.

	Males			Females		
	Adults	Juveniles	Nestlings	Adults	Juveniles	Nestlings
Kangerlussuaq	1	0	1	5[a]	0	1
Thule	1	8	1	5[b]	10	1
Scoresbysund	3	2	0	3	2	0
Maniitsoq	4	0	0	8	0	0

[a]includes one adult female first tagged at Maniitsoq, which later bred in the Kangerlussuaq area and was captured and had PTT replaced.
[b]includes two sub-adults, or second-year birds, that were grouped with adults.

The number of days for which PTTs on individual Gyrfalcons operated varied, from five to 392 days, with a median of 37 days (mean = 95, sd ± 108.8, $n = 49$ PTTs) (Table

4.11). For seven PTTs, no data were included in the analysis. These seven PTTs either failed to operate once attached, fell off shortly after attachment, or falcons died immediately after being tagged. In several other cases data were received, but it was clear based on activity and/or temperature readings that the unit was no longer on a living falcon. For the 49 units which operated, a total of 15,013 locations was received, with an average of 306 per individual (n = 49, median = 150, sd ± 374, range = 9–1726). Locations with LC 3–0 made up an average of 64.1% of the data (median = 64.7, sd ± 13.9). The most accurate locations, LC 3 and 2, made up an average of 6.1% of all data collected (n = 49, median = 4.0, sd ± 5.2). When locations with LC Z did not include a latitude and longitude they were excluded from all analyses. For further details on individual PTTs see Appendices R, S, T, & U.

Table 4.11. Number of days PTTs transmitted on Gyrfalcons tagged in Greenland from 2000 to 2004.

	n	Median	Mean	SD	Range
All Gyrfalcons	49	37	95	± 109	5–392
Adults	27	101	147	± 121	5–392
Juveniles	21	24	31	± 39	5–193
Nestlings[a]	1	51	na	na	na

[a]Data from a single individual, no mean or standard deviation.

Breeding home range

When adults were tagged at the nest site, breeding home ranges included all points obtained from PTT attachment, usually during young-rearing, until departure for an outward pre-migration home range or for outward migration (Ganusevich *et al.* 2004). For adult Gyrfalcons tagged with PTTs during outward migration or while already on winter home range, breeding home ranges included all points obtained the following breeding season: between the completion of return migration to the nest site and departure for outward

migration. Although in some instances it was not possible to verify that individuals bred, based on movements and dates it was possible to make likely inferences.

Breeding home range size was estimated for nine adult Gyrfalcons, seven females and two males (Table 4.12). Of those nine, five were tagged at the nest while rearing young (10095, 10112, 35245, 35252, 35253) and four were captured at ringing stations, with breeding home ranges calculated the following spring/summer. Gyrfalcon 11988 was initially captured at the Maniitsoq ringing station and using locations received from the PTT was tracked to a nest site in the Kangerlussuaq area, where the falcon had raised four approximately 40-day-old young. The female was again captured and a new PTT, 10210, was attached. Data from units 11988 and 10210 were combined to calculate breeding home range size. Additionally, Gyrfalcon 35248, captured at the Maniitsoq ringing station in the autumn, appeared to breed in the Greely Fjord, northern Ellesmere Island (80.7° N), Canada, the following spring/summer. Gyrfalcon 35249, also captured at Maniitsoq, had a breeding home range in the northern portion of the Thule area. I was unable to visit the potential nest but based upon data obtained from the PTT, the bird arrived too late to breed successfully. Although I have included breeding home range sizes for Gyrfalcon 35249 in Table 4.12, this individual is excluded from further breeding home range analysis because it did not breed. From the Thule ringing station, Gyrfalcon 35243, that was captured in the autumn, returned the following spring, and using data from the PTT, it was located breeding successfully within 10 km of the ringing station. An additional breeding adult female Gyrfalcon (41632) was captured at the nest site. However, only nine locations with LC 3–1 were received, and a breeding home range size was not calculated.

Table 4.12. Breeding home range sizes for seven female and two male adult Gyrfalcons calculated using 90% minimum convex polygons, 95% fixed kernels, and 50% fixed kernels. All range sizes are given as square kilometers.

Breeding location	Sex	PTT ID	90% MCP	95% Kernel	50% Kernel	Days of data	Total LC 3–1
Kangerlussuaq, Greenland	M	10112	516	342	35	50	129
	F	11988/10210	1035	546	73	142	81
	F	35245	192	462	57	47	23
Thule, Greenland	F	10095	1197	738	72	52	151
	F	35243	140	88	8	132	76
	F	35249	407	829	183	63	66
	F	35252	434	590	64	43	50
	F	35253	426	316	44	63	73
Ellesmere Island, Canada	M	35248	489	218	20	156	203

Based upon the results from Chapter 2, I used locations with LC 3–1 to calculate breeding home range size for Gyrfalcons. Actual breeding home range sizes varied depending upon the method used for calculation, and 90% minimum convex polygons (MCP) provided the largest estimates for six of the nine birds (Table 4.12). Fixed 95% kernels and 50% fixed kernels provided the second and third largest estimates of home range size, respectively (Table 4.12). If breeding home range estimates included areas that encompassed glaciers and/or the Greenland Ice Cap, these areas were included because prey species have been shown to cross the Greenland Ice Cap both during migration and in the breeding season (Alerstam *et al.* 1986, R. Abbott pers. comm.).

When using 90% MCP, adult female Gyrfalcons had a calculated average breeding home range size of 571 km^2 (n = 6, median = 430, sd ± 442), varying from 140 to 1,197 km^2. The two females with the largest home range sizes, 10095 and 11988/10210, both spent large amounts of time away from the nest in multiple areas, probably hunting, and travelled up to 35 km each direction. Female 35253 also frequently travelled approximately 31 km away from the nest; however, each trip was to the same location (a large seabird colony), and because of this the home range size was not increased as much as for the other

two individuals. Fixed 95% and fixed 50% kernels gave an average calculated breeding home range size of 457 km^2 (n = 6, median = 504, sd ± 228) and 53 km^2 (n = 6, median = 61, sd ± 25), respectively, for adult female Gyrfalcons. Breeding home ranges were obtained for two adult male Gyrfalcons, with an average of 503 km^2 (sd ± 19) when using 90% MCP and 280 km^2 (sd ± 88) and 28 km^2 (sd ± 11), respectively, when using 95 and 50% fixed kernels.

Data were received for two individuals for the entire breeding cycle and home range size varied by month for each falcon. An adult male, which probably bred in northwest Ellesmere Island, had a relatively small home range in May, but the size approximately doubled in June, after which it generally decreased from June through September (Figure 4.5). A female which bred in Thule had the exact reverse pattern, and home range size increased each month from May through September (Figure 4.6).

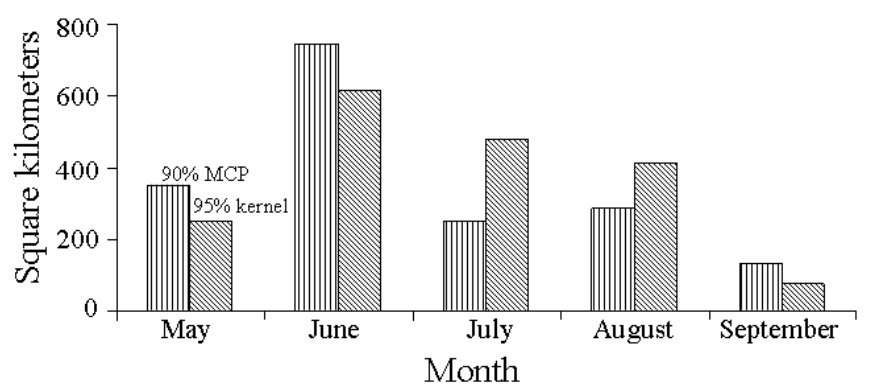

Figure 4.5. Breeding home range size by month for an adult male Gyrfalcon which nested in northeast Ellesmere Island, Canada. Home range size calculated as 90% minimum convex polygons and 95% fixed kernels, sizes given in square kilometers.

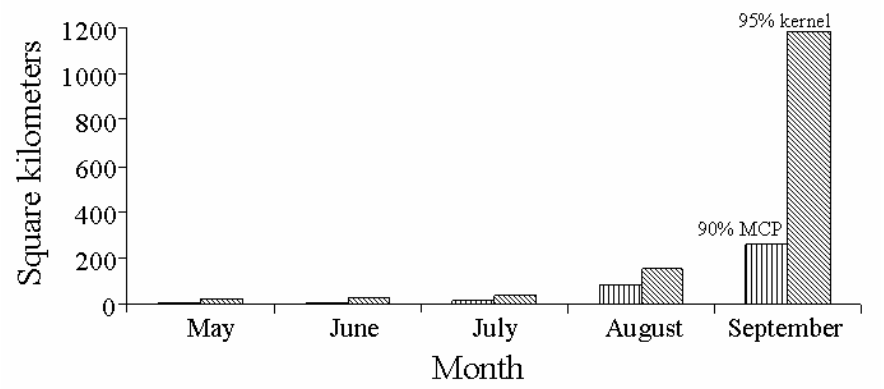

Figure 4.6. Increasing monthly breeding home range size of an adult female Gyrfalcon which nested in Thule, Greenland. Home range size calculated as 90% minimum convex polygons and 95% fixed kernels, sizes given in square kilometers.

Although home range estimates did not vary significantly between methods of calculation, the actual breeding home range size for individual Gyrfalcons probably lay somewhere between the two areas calculated using 90% MCP and 95% fixed kernels.

Outward migration: departure dates

Departure dates for Gyrfalcons could be determined accurately only for 13 of the 55 individuals tagged at the nest. All others were captured and tagged at ringing stations and were possibly from further north and already on migration. However, in several cases PTTs placed on individuals at ringing stations operated through the following breeding season and departure dates for outward migration were then recorded. Several Gyrfalcons that were tagged at ringing stations appeared to already be on winter home range, and partial outward migrations were not recorded. Additionally, two individuals tagged at ringing stations continued to have long-distance movements throughout the entire winter period, which were not included with outward migration data.

For Gyrfalcons captured and tagged at ringing stations in Maniitsoq (65.4° N) and Scoresbysund (70.4° N), it seems equally likely, based on dates and geography, that the individuals were residents or from farther north. At the Thule ringing station (76.5° N), it

seems most likely that the majority of the individuals captured were from the local population, again based on dates and geography. This is supported by one juvenile captured at the ringing station that had previously been ringed 25 km away, and by an adult female captured at the Thule ringing station which subsequently bred within 10 km of it. The place where the Thule ringing station was located appeared to be a large pre-migration/congregation area for juvenile Gyrfalcons, with large numbers of juveniles observed and captured there. The ringing station was directly next to immense seabird colonies, providing an almost unlimited food source and an excellent opportunity for young falcons to learn to hunt.

Departure dates for outward migration were obtained for two Gyrfalcons from the Kangerlussuaq area. An adult male departed the nest on 27 August and then returned to the nest vicinity on two occasions, 5 September and 11 October, with the time in-between spent up to 140 km away. The last location received for the adult male was approximately 26 km north of the nest site at which it bred. An adult female departed the nest on 12 August to the southwest. Two additional adult females continued to stay in the area around their respective nest sites until their PTTs failed, with the last signals received on 6 and 29 September.

From 2001 to 2003 six adult female Gyrfalcons tagged in Thule departed on outward migration on dates from 9 September to 4 October (mean = 25 Sept., median = 20 Sept.). Data were received from one individual for two seasons, with the departure date for both years, 28 September, being included. PTT data showed that after departing the nest site two of the individuals flew west to Ellesmere Island, at which point both individuals returned to Greenland, one to the original nest site and the other to a location south of the original nest site. Within days of arriving back in Greenland both individuals again departed to Ellesmere Island, with the trip out and back covering approximately 400 km. An adult

female which was tagged in Maniitsoq in the autumn, and tracked to Thule the following summer, departed Thule on outward migration on 19 August; however, it clearly did not fledge young and was not included in outward migration departure date calculations. A single adult male Gyrfalcon that was observed feeding young at the ringing station was captured and departed Thule on 5 October.

Average departure dates for male and female juvenile Gyrfalcons tagged at the ringing station in Thule were 19 September (n = 5, median = 19 Sept., range = 18–21 Sept.) and 24 September (n = 6, median = 21 Sept., range = 15 Sept.–16 Oct.), respectively. Only one juvenile Gyrfalcon (35241) had a departure date in October (16 Oct.), a juvenile male which departed the area around the ringing station on approximately 18 September, moving to a new area approximately 60 km northwest of the ringing station, where it stayed until departing the Thule area.

Falcon 35248, an adult male, appeared to breed in the Greely Fjord, northwest Ellesmere Island, and departed on outward migration on 7 October.

Using the average of recorded departure dates, adult female and juvenile male and female Gyrfalcons in Thule departed on outward migration at approximately the same time, with juvenile males departing approximately five days before adult and juvenile females. Median departure dates for juvenile males and females and adult females were 19, 21, and 20 September, respectively. However, both adult females and juvenile males had a wide range of departure dates, while all five juvenile females departed over a four-day period, 18–21 September. The lone adult male tagged in Thule departed on 5 October, similar to the 7 October departure of an adult male from northwest Ellesmere Island.

Outward migration: distance travelled, speed, duration, and route

The distance, speed, duration, route, and completion date of outward migration were difficult to calculate for Gyrfalcons, despite the large amount of data collected. Many individuals of known origin, i.e., tagged in their breeding area, either died or their PTTs failed/fell off before outward migration was completed. Those tagged at ringing stations were of unknown origin, and provided only limited data even if outward migration was completed. For the data that were collected, speed, duration, and route used during outward migration were wide ranging, and an overall description of movements from each area is presented below.

In total, three individuals completed outward migration from their breeding home range while seven completed outward migration from ringing stations. An additional 23 individuals had incomplete outward migrations. While cumulative results from all individuals were calculated and presented for each area, only specific "representative" or "unique" individuals have been included in maps in this chapter. Only individuals who completed greater than ten days of outward migration or that travelled over 250 km were included in these analyses.

Three individuals (11988/10210, 35248, and 35249) were initially tagged in Maniitsoq on outward migration but returned to Kangerlussuaq, Ellesmere Island, and Thule, respectively, where they departed on outward migration the following year. Outward migration data from the autumn they were tagged in Maniitsoq were included in the Maniitsoq data while outward migration data from the following year were grouped by breeding home range area. Maps for 'representative' individuals have been included in the results while data for specific individuals can be found in Appendices V, W, X, Y, & Z, for Kangerlussuaq, Thule, Scoresbysund, Maniitsoq, and Ellesmere Island, respectively.

Kangerlussuaq

Outward migrations were calculated for two individuals who were tagged at the nest site in Kangerlussuaq, an adult male and female. An incomplete outward migration was calculated for the adult male (10112), which travelled at least 805 km over a 50-day period, including several trips from the breeding home range to the coast and back and a large clockwise circle to the south. The falcon later returned to a location approximately 26 km north of its nest site, where the last signal was received from the PTT (Figure 4.7). An adult female (35245) which completed outward migration travelled approximately 391 km over a 13-day period, to southwest Greenland, at a speed of 30 km/day (Figure 4.7).

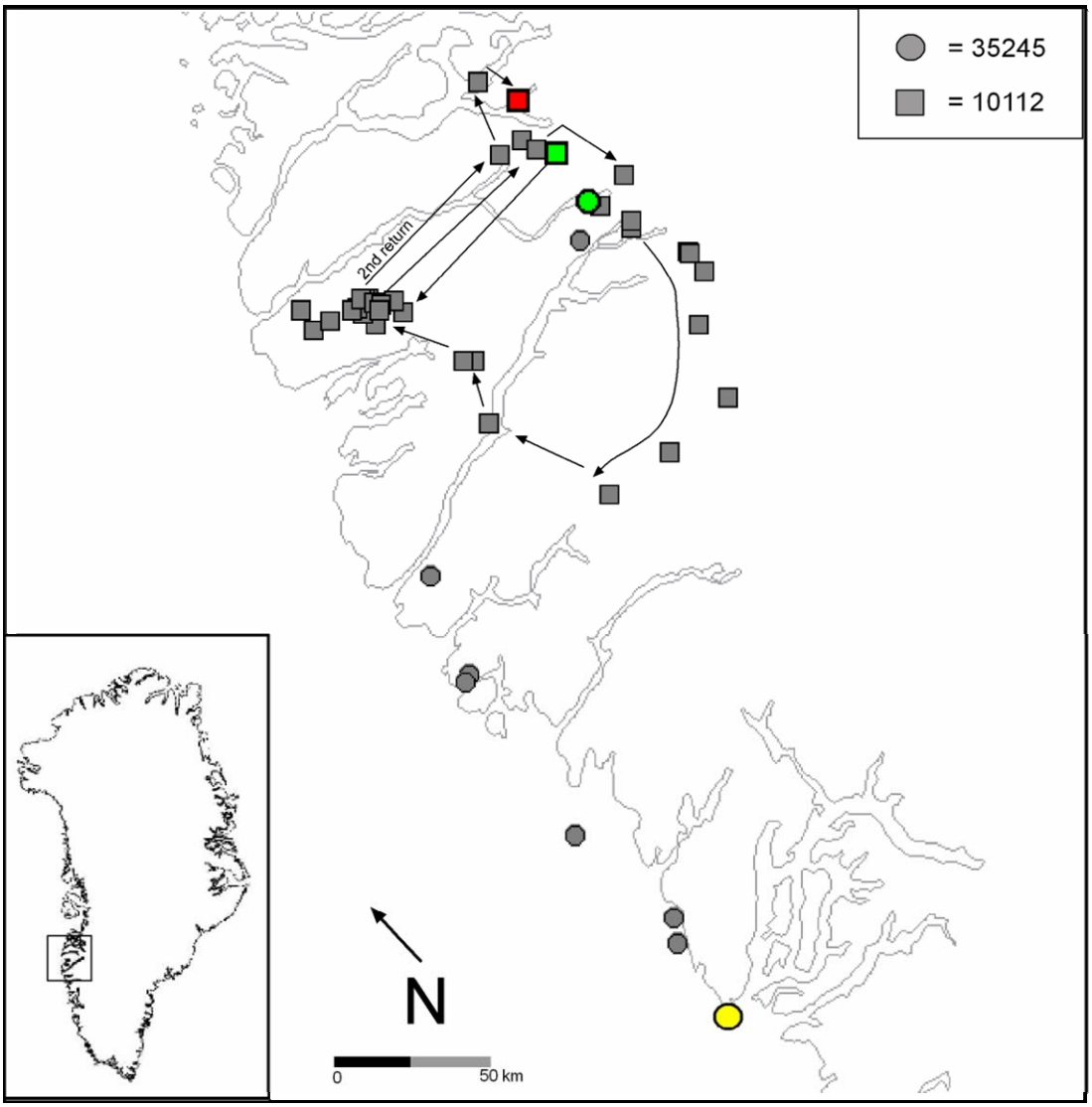

Figure 4.7. Outward migration routes for two adult Gyrfalcons tagged at the nest site in Kangerlussuaq. Green symbols are where outward migration began, the red symbol signifies the last location of an incomplete outward migration, and the yellow symbol signifies the end point of a completed outward migration. Only a single location per day has been included for each individual and only days with locations with location class 3–0 have been included.

Thule

From Thule outward migrations were calculated for 15 Gyrfalcons, six female adults and one male adult, and four female and four male juveniles. Two outward migrations were calculated for Gyrfalcon 35243, an incomplete outward migration in 2003, and in 2002 the only complete outward migration documented from the Thule area. The six incomplete outward migrations made by adult females covered an average of 1,399 km (median = 910, sd ± 1,112, range = 643–3,495) at an average speed of 37 km/day (median = 33, sd ± 16,

range = 15–58), with a mean of 46 days (median = 28, sd ± 41, range = 12–122) of data received for each bird (Table 4.13). The lone adult male travelled 647 km during the nine days data were received, a speed of 72 km/day (Table 4.13). Four juvenile females travelled an average of 690 km (median = 546, sd ± 572, range = 177–1,490) at 33 km/day (median = 35, sd ± 14, range = 14–47). Data were received for an average of 19 days for juvenile females (median = 17, sd ± 10, range = 11-32) (Table 4.13). Juvenile males flew an average of 918 km (median = 991, sd ± 459, range = 329–1,361) at 57 km/day (median = 52, sd ± 32, range = 27–99), with data received for an average of 18 days (median = 16, sd ± 11, range = 8–34) per individual (Table 4.13). The only complete outward migration documented was by 35243, which travelled 4,234 km at a speed of 60 km/day, and spent 71 days on outward migration (Table 4.13, see Figure 4.8 for map). Although 35243 was first captured and tagged at a ringing station in Thule, I considered it as a complete outward migration from the breeding home range. This was based on the fact that she was observed caring for young during the period when tagged and the following year bred within seven km of the ringing station.

Table 4.13. Distances travelled by adult and juvenile Gyrfalcons during 15 incomplete outward migrations and a single complete outward migration from Thule, Greenland, 2001–2003. Distance travelled is in kilometers and speed of travel is in kilometers/day.

	Distance travelled (mean ± sd, range, median)	Days of travel (mean ± sd, range, median)	Speed of travel (mean ± sd, range, median)
Adult females *n* = 6	1,399 ± 1,112, 643–3,495, 910	46 ± 41, 12–122, 28	37 ± 16, 15–58, 33
Adult male *n* = 1	647, na, na, na	9, na, na, na	72, na, na, na
Juvenile females *n* = 4	690 ± 572, 177–1,490, 546	19 ± 10, 11–32, 17	33 ± 14, 14–47, 35
Juvenile males *n* = 4	918 ± 459, 329–1,361, 991	18 ± 11, 8–34, 16	57 ± 32, 27–99, 52
Complete outward, *n* = 1	4,234	71	60

na–not applicable, data for only a single individual

Routes used during outward migration by Gyrfalcons from Thule were divided into the east Canada route, ocean route, and the west Greenland route. The east Canada route described a migration path where Gyrfalcons departed Greenland and travelled directly west to Canada. Once in Canada they then flew down the east coast, which included Ellesmere Island, Devon Island, Baffin Island, and in one instance as far south as the northeast coast of Labrador (Figure 4.8, examples are falcons 35252 and 35243). The one falcon which completed outward migration, 35243, used this route and crossed back into southwest Greenland at the end of the outward migration. All Gyrfalcons which used the eastern Canada route may have done similarly; however, only incomplete outward migrations were documented and I was not able to determine end locations.

Gyrfalcons which used the ocean route departed over the ocean to the south from Thule and travelled hundreds of kilometers and spent many days over open water, at times several hundred kilometers from land, before veering to the west toward central-west Baffin Island (Figure 4.8, examples 35241 and 35242). In the west Greenland route Gyrfalcons travelled down the west coast of Greenland (Figure 4.8, example 41444). While I have attempted to define and generalize routes taken by Gyrfalcons during outward migration from Thule, variation was great, and some individuals used a combination of routes.

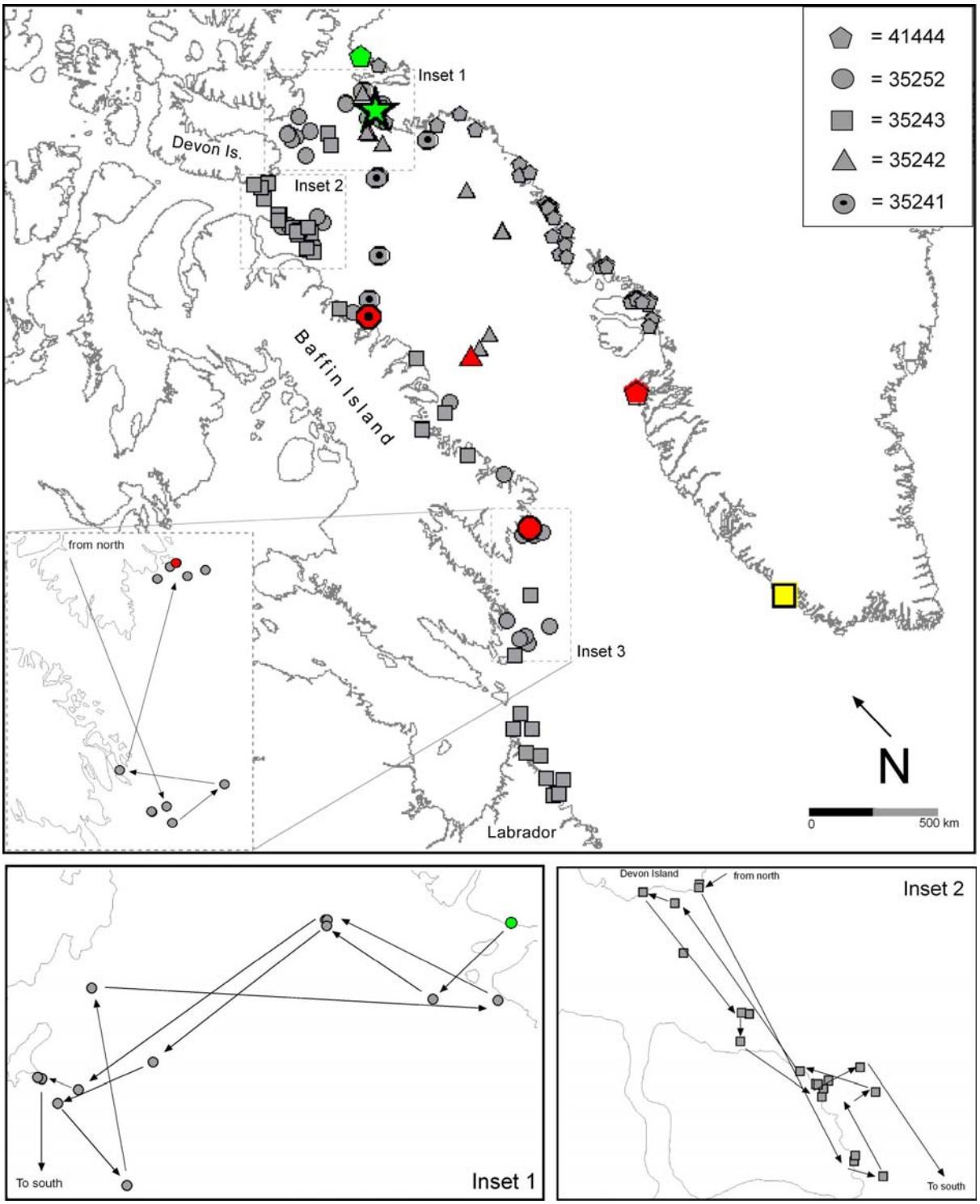

Figure 4.8. Outward migration routes used by five Gyrfalcons from the Thule area, northwest Greenland, from 2001 to 2003. The green star represents the departure point for outward migration unless a green symbol is otherwise present. Red symbols signify the last location of an incomplete outward migration and the yellow symbol signifies the end point of a completed outward migration. Only a single location was included each day for each bird and only days with locations in classes 3–0 were used.

Of the 16 outward migration routes documented for Gyrfalcons from the Thule area during 2001–2003, the east Canada route was used on eight (50%) occasions, the ocean

route six (37.5%) times, and the west Greenland route twice (12.5%) (Table 4.14). The east Canada route was used in all three years and was the most direct path to Canada. The ocean route was used in 2002 and 2003. Two individuals that used the ocean route travelled to Canada, although they flew much further south before they arrived in central-west Ellesmere Island. A third falcon that used the ocean route also appeared to be travelling to Canada, but its PTT stopped functioning shortly before it would have arrived. Data from the other three birds that used the ocean route were inconclusive as PTTs failed shortly after the start of outward migration. Two falcons used the west Greenland route, one of which was tagged in the Maniitsoq area in autumn 2002, and which used the west Greenland migration route during return migration to the Thule area in the summer of 2003. Gyrfalcon 35243, an adult female, used the eastern Canada route in 2002 and 2003, and both years were included in analysis.

Table 4.14. Outward migration paths used by 15 Gyrfalcons from the Thule area, northwest Greenland, 2001–2003.

	East Canada route	Ocean route	West Greenland route
2001	ad♀	-	-
2002[a]	3 x ad♀, 2 x ju♂	2 x ju♂	-
2003[a]	ad♀, ju♀	ad♂, 3 x ju♀	2 x ad♀

[a]female 35243 included for both 2002 and 2003, east Canada route used both years.

Although sample sizes are limited, the east Canada coast line was the most used route during outward migration from Thule. While eight birds travelled directly to Canada using the east Canada route, at a minimum, at least half of the birds that used the ocean route also travelled to Canada, albeit further south. Of the eight outward migrations of adult Gyrfalcons, six travelled to Canada, while two adult females stayed in Greenland. Canada may be of even more importance to juvenile Gyrfalcons than adults during outward migration. Five of the eight juveniles tracked on outward migration travelled to Canada

while none stayed in Greenland. Data on the other three are insufficient; however, other individuals that had similar departure locations and movements travelled to Canada.

Scoresbysund

Data on outward migration were collected from seven Gyrfalcons from the Scoresbysund ringing station, of which three completed their outward journeys. These three birds, two adult males and an adult female, continued down the east coast of Greenland and travelled an average of 1,564 km (median = 1,664, sd ± 543, range = 978–2,050) during outward migration at an average speed of 50 km/day (median = 47, sd ± 9, range = 42–60) (see Figure 4.9 for maps of two individual's movements). However, based on the continued movements of all three falcons (49762, 49764, and 49771) there was no specific end to their outward migration and no obvious winter home range. The four individuals, one adult male and two female and one male juveniles, that had incomplete outward migrations travelled an average of 603 km (median = 590, sd ± 596, range = 53–1,342) over an average of 21 days (median = 19, sd ± 10, range = 12–33), giving an average speed of 29 km/day (median = 36, sd ± 17, range = 4–41). Two of the individual's PTTs stopped working in the Scoresbysund area, while one juvenile female, 49769, continued on outward migration to the southeast and travelled 824 km before the last location was received approximately halfway between Greenland and Iceland (Figure 4.9). The juvenile male, 49761, spent almost the entire next month in the Scoresbysund area, but then travelled east, with the last signal over 425 km northeast of Iceland and approximately 475 km north of the Faroe Islands (Figure 4.9).

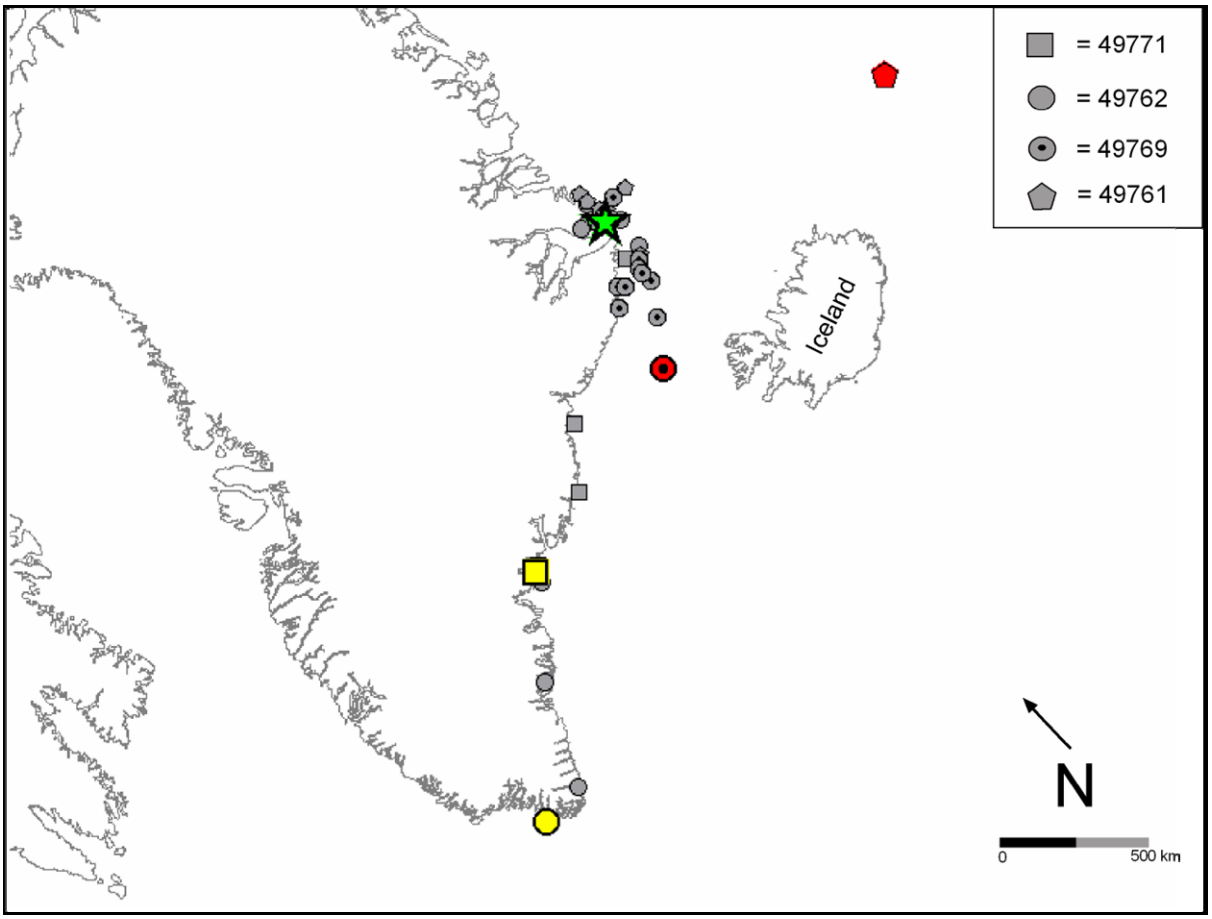

Figure 4.9. Routes of four Gyrfalcons tagged in the Scoresbysund area, east Greenland, in 2005 during outward migration. The green star represents location where falcons were initially tagged, red symbols signify the last location of an incomplete outward migration, and yellow symbols signify the end point of a completed outward migration. Only one point was included per day per individual and only days with locations with location class 3–0 are represented.

Maniitsoq

Data from outward migration were collected from seven Gyrfalcons tagged at the Maniitsoq ringing station. Of those, three adult females and an adult male completed outward migration and flew an average of 505 km (median = 551, sd ± 195, range = 254–664) over an average of 12 days (median = 14, sd ± 9, range = 6–26), giving a speed of 43 km/day (median = 45, sd ± 21, range = 17–66). All four continued to travel down the southwest coast of Greenland, each stopping in a different location; however, 35249 frequently travelled up and down the coast. Within one month of completing outward migration, the PTT on 36319 stopped functioning, leaving open the possibility that the falcon may have continued to move throughout the winter. The two female adults and one

male adult that had incomplete outward migrations travelled an average of 624 km (median = 678, sd ± 241, range = 360–833) over an average of 30 days (median = 27, sd ± 6, range = 26–36), giving a speed of 23 km/day (median = 19, sd ± 7, range = 19–31). All three individuals continued moving south along the coast, but one male and one female stopped and returned north, and both PTTs failed near the ringing station. See Figure 4.10 for general movements of falcons tagged at the Maniitsoq ringing station.

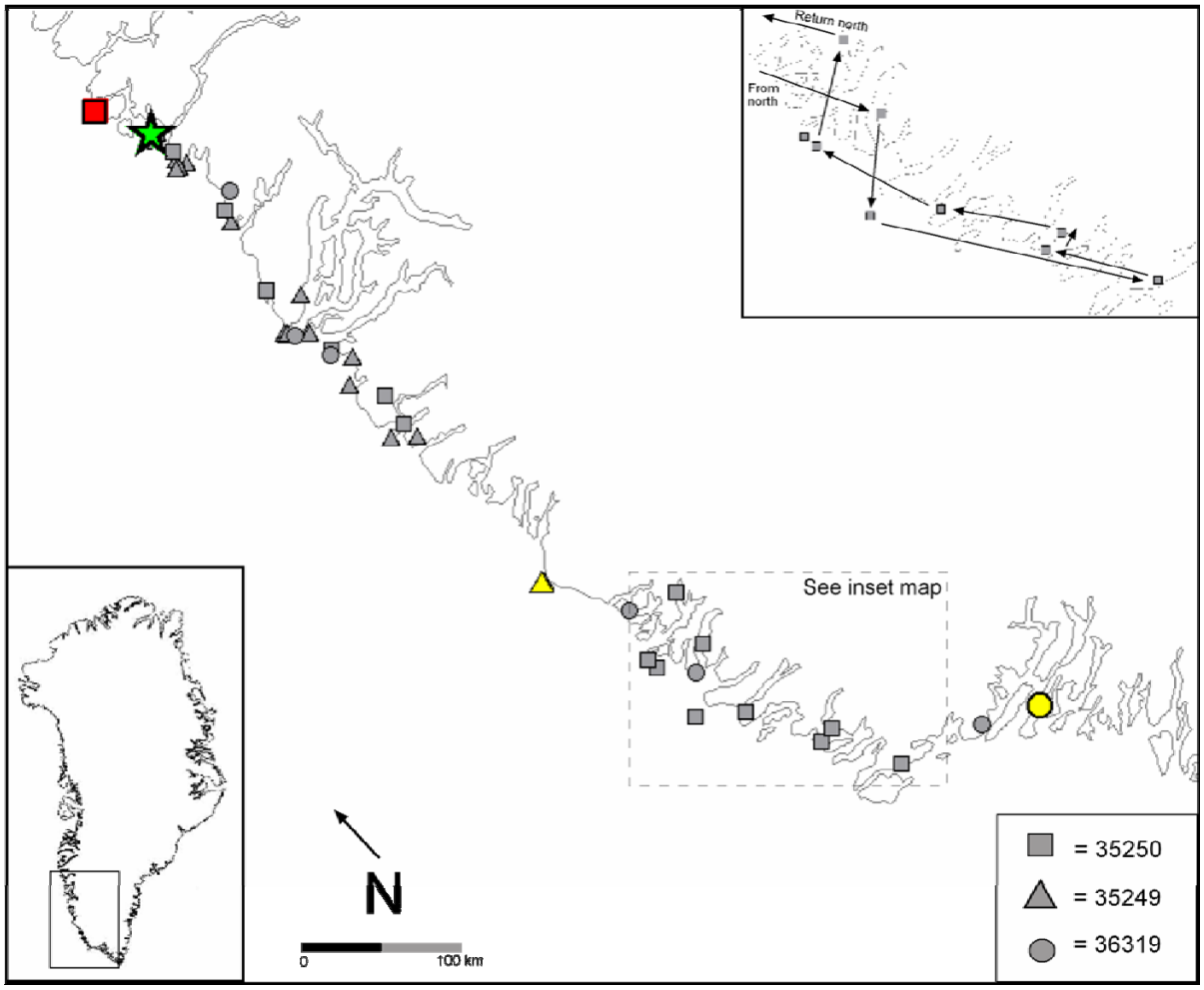

Figure 4.10. Routes of three Gyrfalcons tagged in the Maniitsoq area, central-west Greenland, during outward migration. The green star represents location where falcons were initially tagged, the red symbol signifies the last location of an incomplete outward migration, and the yellow symbols signify the end point of a completed outward migration. Only one point is used per day per individual and only days with locations of classes 3–0 were included.

An adult male Gyrfalcon, 35248, which probably bred in northwest Ellesmere Island, travelled 3,137 km on outward migration at an average speed of 83 km/day. Falcon

35248 spent 38 days on outward migration and travelled southwest once departing the nest site, and arrived at the southeast corner of Ellesmere Island where it then continued south along the coast of Baffin Island before it crossed into southwest Greenland (Figure 4.11).

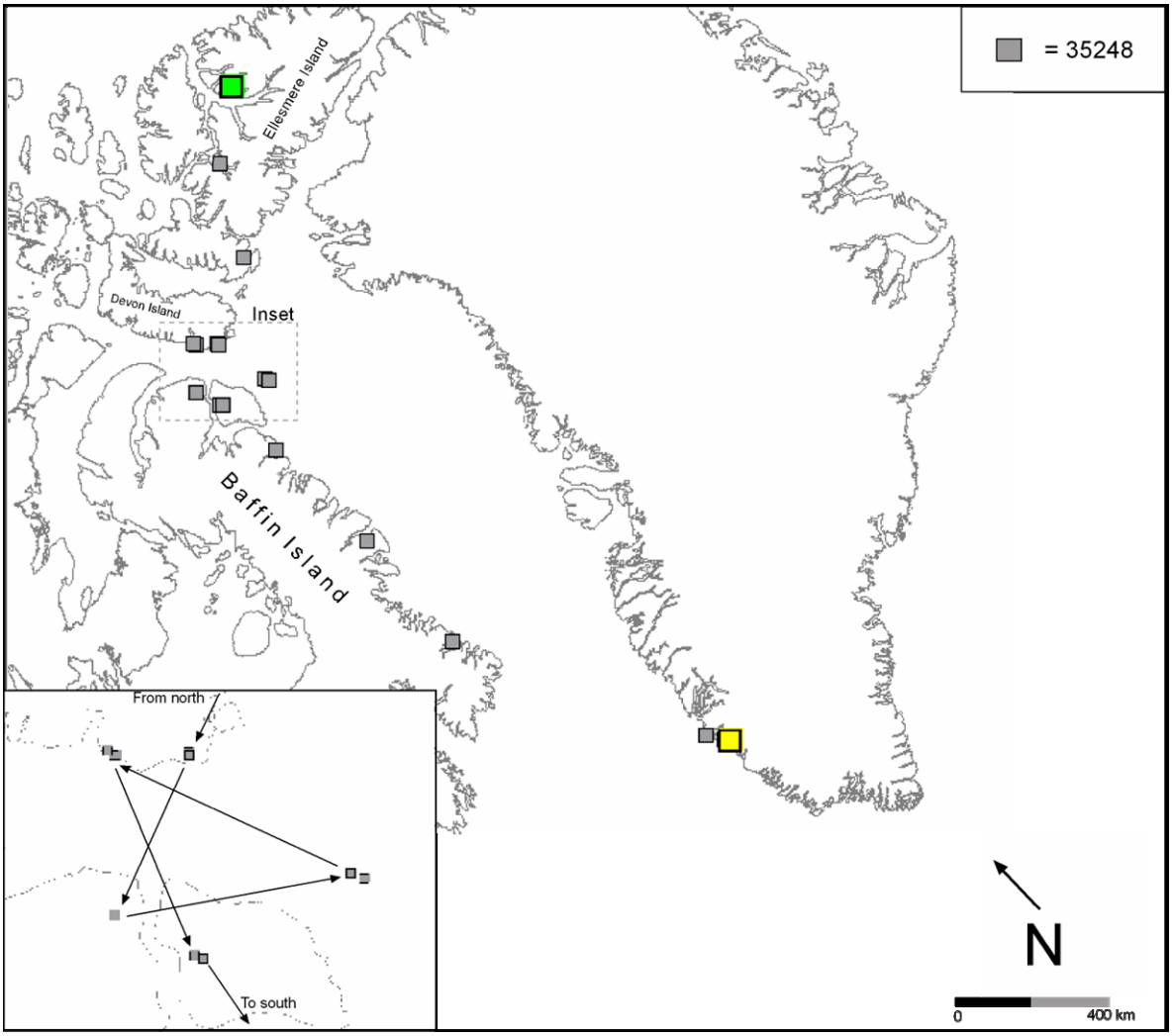

Figure 4.11. Complete outward migration of an adult male Gyrfalcon from northwest Ellesmere Island, Canada. Green square represents breeding area and the yellow square signifies the end point of the completed outward migration**.** Only one point is used per day and only days with locations classes 3–0 were used.

The individual speed of migration per day, or maximum and minimum distances travelled per day, varied greatly among Gyrfalcons. Juvenile male 49761, which was tagged in Scoresbysund, travelled the farthest in a single day, 389 km. However, adult female 35242, tagged in Thule, was on the southeast coast of Baffin Island on 5 December with the next location, on 7 December, being in southwest Greenland, a distance of 776 km.

While it is possible that the bird travelled half way each day (388 km/day), it seems equally possible that the entire distance was covered in one day. The shortest distance travelled each day, zero km, was similar among a number of Gyrfalcons, with at least 28 (85%) of the 34 documented outward migrations showing Gyrfalcons travelled less than 10 km on any given day. Taking into account the inaccuracy of the Argos tracking system (see Chapter 2, Methods, Satellite-received telemetry), daily distances should be treated with some caution; however, all data were visually inspected and locations used are in concordance with other locations received based on distance, time, and date.

Average speed of outward migration for Gyrfalcons ranged from four to 99 km per day (n = 33). However, these numbers include incomplete outward migrations and represent only small portions of longer sequences. For the three individuals that completed outward migrations from their breeding home ranges, 35248, which nested the farthest north, travelled at fastest speed during migration, at 83 km/day. Falcon 35243, which nested the second farthest north, was the second fastest at 60 km/day. The slowest speed, 30 km/day, was from falcon 35245 which nested the farthest south. With the lack of complete outward migrations it is difficult to make any general statements comparing one area to another. However, within the Thule area and based on limited samples, it appears that males, both adults and juveniles, migrate at a faster speed than adult and juvenile females, although further research is needed.

The total distances travelled by the three Gyrfalcons that completed outward migration from breeding home ranges varied from 391 to 4,234 km. Falcon 35248, which nested in northwest Ellesmere Island, over 500 km northwest of where falcon 35243 nested in Thule, travelled 3,137 km on outward migration, compared to 4,234 km for 35243, a difference of 1,097 km. While some of this distance can be explained by the approximate 125 km difference in the location of winter home ranges, it is obvious that falcon 35243

took a very indirect and at times wandering path to its winter range. Additionally, falcon 35243, despite having a much shorter distance to travel to its winter home range than 35248, spent 71 days on outward migration, compared to 38 days by 35248. Although Gyrfalcons 35243 and 35248 completed outward migration from the most northern study areas, they did not spend the most days on outward migration. Gyrfalcon 41444, an adult female which was tagged in Thule, spent 122 days on outward migration before her PTT failed while she was still travelling south.

This trend also appeared in a number of other tagged falcons, when individuals frequently had a slow speed of travel and utilized multiple areas for days, if not weeks or even months, while on outward migration. Additionally, a number of falcons also reversed their migration path, and in one case an individual travelled over 550 km northwards back to an area that it had previously migrated through. In general, Gyrfalcons appeared to have erratic outward migrations, both in relation to speed of travel and the number of days spent on outward migration. This could likely be in response to following prey, with falcons only moving when necessary and at times staying in an area until a prey species had been depleted or had moved.

Outward migration: completion dates

Outward migrations were completed on 10 occasions, with Gyrfalcon 35248 completing an outward migration in both 2002 and 2003 to the same area. Of the completed outward migrations, three individuals completed outward migration from breeding home ranges, while seven individuals completed outward migration after being tagged at ringing stations. A single adult female, 35245 from Kangerlussuaq, completed outward migration from her breeding home range and arrived at her winter range on 24 August. From Thule, a single adult female, 35243, arrived at her winter range on 7 December. Three adult Gyrfalcons completed outward migration after being tagged in Scoresbysund, two females

(49762 and 49764) and a male (49771), and finished outward migration on 22 and 19 September and 8 October, respectively. Four adult Gyrfalcons completed outward migration from the Maniitsoq ringing station, three females (11988, 35248, and 36319) and a male (35248), with an average completion date of 26 October (range = 14 Oct.–5 Nov.) for females and the lone male completed outward migration on 24 October. Outward migration completion dates were difficult to determine and several falcons had sustained movements throughout the winter period.

Winter home range

Gyrfalcons wintered on the respective coast in Greenland where they were initially tagged. Only over a section of coastline approximately 200 km long, on the southern tip of Greenland, did individuals from both coasts overlap in winter. The furthest north any individual occurred while on winter home range was approximately 67.9° N, where twilight would have been present for almost six hours. However, falcon 41444, an adult female tagged in Thule and which did not complete outward migration, was at approximately 70.6° N during the winter solstice (21 December), at which point no sunlight would have been visible and only three and a half hours of twilight were available each day.

Winter home range sizes were calculated for eight female and three male adult Gyrfalcons using locations with LC 3–1. Size of winter home ranges varied greatly, even among the same method of calculation. After winter home range sizes were log transformed, results from t-tests showed that winter home ranges were significantly larger on the east coast for all three methods of range size calculation (see Appendix AA for t-test results). Averages were categorized by west and east coast. Adult males and females and data from multiple years were grouped together because of the small sample size and no apparent differences between sexes and years. Within the range of values obtained here, the total number of locations used to calculate winter home range size did not appear to have

any effect on their size. Additionally, when arrival dates on winter home range and range size were compared, no trends were evident.

For adults on the west coast of Greenland, using 90% MCP, an average winter home range size of 2,595 km^2 was calculated (n = 8, sd ± 2,533, median = 1,054, range = 383–6,657) (Table 4.15). Fixed 95 and 50% kernels gave an average size of 5,822 km^2 (n = 8, sd ± 7,006, median = 1,630, range = 357–18,443) and 813 km^2 (n = 8, sd ± 912, median = 268, range = 53–2,067), respectively (Table 4.15). Adults on the east coast, on this basis of 90% MCP, had an average winter home range size of 48,380 km^2 (n = 3, sd ± 19,210, median = 54,683, range = 26,810–63,647), and on 95 and 50% fixed kernels, 118,351 km^2 (n = 3, sd ± 48,353, median = 104,896, range = 78,151–172,007) and 20,103 km^2 (n = 3, sd ± 9,165, median = 24,594, range = 9,559–26,157), respectively (Table 4.15).

Table 4.15. Winter home range sizes for adult Gyrfalcons calculated using 90% minimum convex polygons, 95% fixed kernels, and 50% fixed kernels. All range sizes are in square kilometers. Unless otherwise noted, days on range is the entire time period Gyrfalcons spent on winter home range. Range sizes given as square kilometers.

Location PTT was attached or breeding area, if known	Sex	PTT ID	90% MCP	95% Kernel	50% Kernel	Days on range	Total LC 3-1
Kanger., 2000/01	F	11988	945	1,566	160	139	52
Kanger., 2002/03	F	35245	383	357	59	197	100
Thule, 2002/03	F	35243	4,931	14,398	2,067	115	65
Thule, 2002/03	F	35249	6,657	18,443	1,984	168	79
Scoresby., 2004/05	M	49762	54,683	78,151	9,559	189	30
Scoresby., 2004/05	M	49764	26,810	104,896	26,157	162	16
Scoresby., 2004/05	F	49771	63,647	172,007	24,594	185	46
Maniitsoq, 2000/01	F	05707	5,160	7,675	1,647	194	68
Maniitsoq, 2002/03[a]	F	35259	708	1,694	348	86	46
Maniitsoq, 2002/03	F	36318	1,163	1,153	53	169	162
Ellesmere Is., 2002/03	M	35248	816	1,292	187	171	64

[a]PTT stopped functioning part way through the period spent on winter home range.

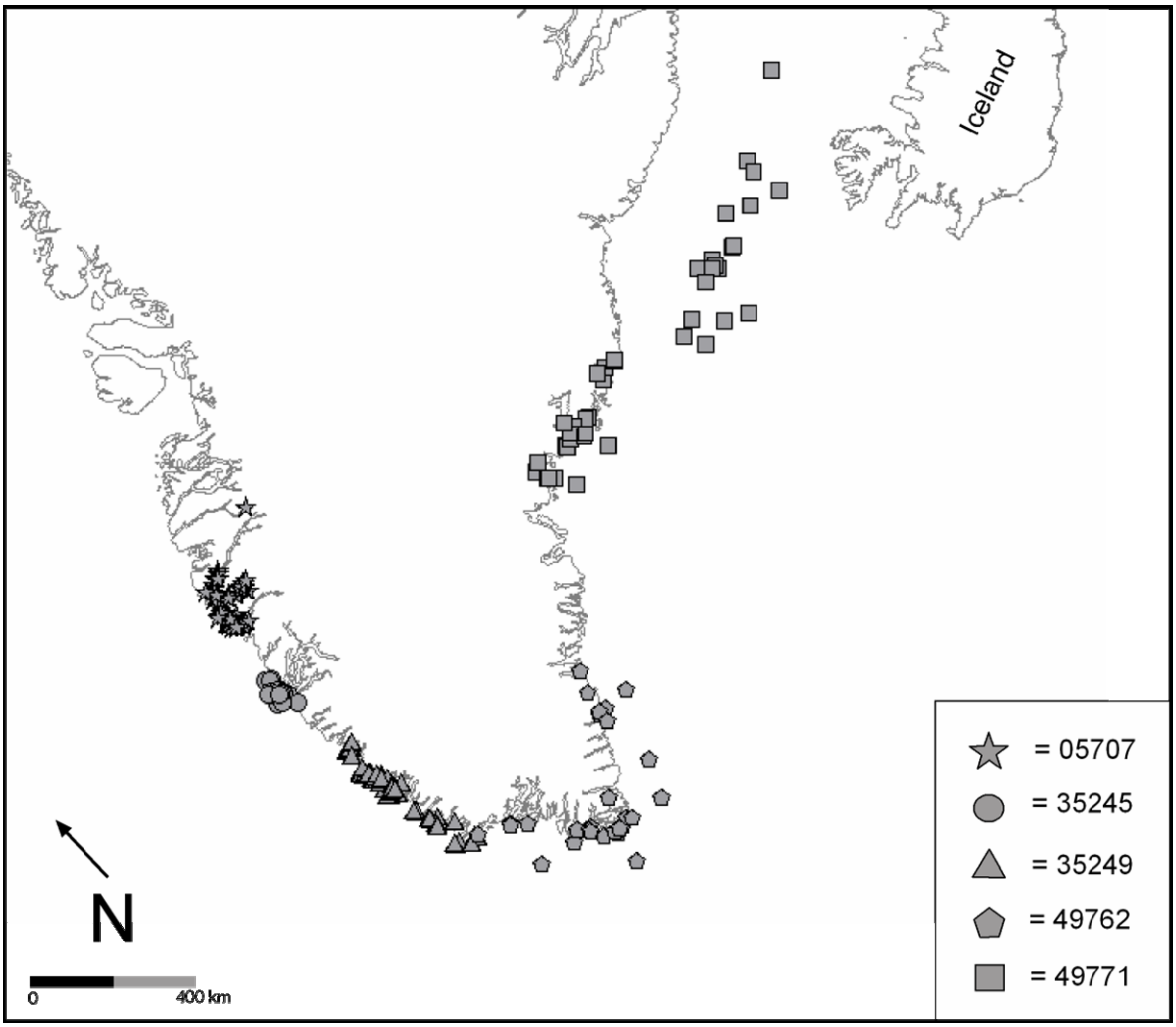

Figure 4.12. Winter home ranges for five adult Gyrfalcons tagged in Greenland during 2000–2004. Points included are locations received from PTTs with location classes 3–1 during the time period spent on winter home range by each individual. Only a single location was included for each day.

Figure 4.12 depicts the highly varied sizes and locations of Gyrfalcons' winter home ranges. While not shown, large amounts of overlap existed between individuals on both coasts, with some individuals with very large ranges completely overlapping individuals with small ranges. Some winter home ranges were obvious and easily defined, such as those of falcons 05707 and 35245, while the much larger home ranges documented for falcons such as 49762 and 49771 were more open to subjective interpretation (Figure 4.12). In the case of both falcons 49762 and 49771, while each individual did not use its entire winter home range each month, large portions were utilized in any one month. Figures 4.13 and 4.14 show the monthly usage of the winter range by both individuals, with each month

spent on winter range represented by a different symbol. Based on data from PTTs, locations over the ocean likely represent falcons that lived over the ocean for up to a month in some instances, using icebergs to rest on and from which to hunt seabirds. While individuals on both coasts used areas over the ocean, only on the east coast did falcons spend extended amounts of time over the ocean and far from land.

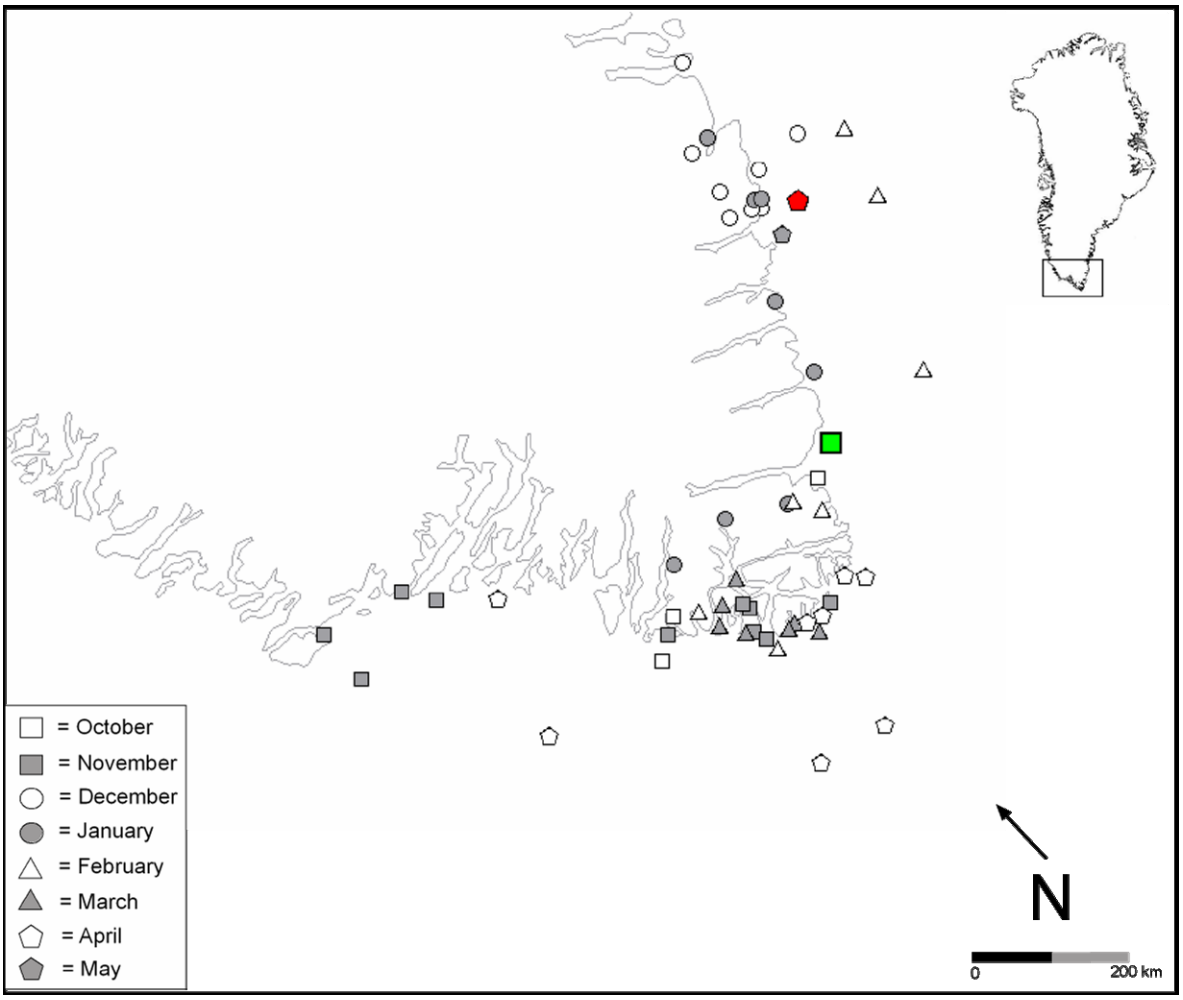

Figure 4.13. Area used by Gyrfalcon 49762 while on winter home range with each individual month represented by a different symbol. Green square represents arrival on winter home ranges and red pentagon represents last location before departure on return migration. Only one location in classes 3–0 was included per day.

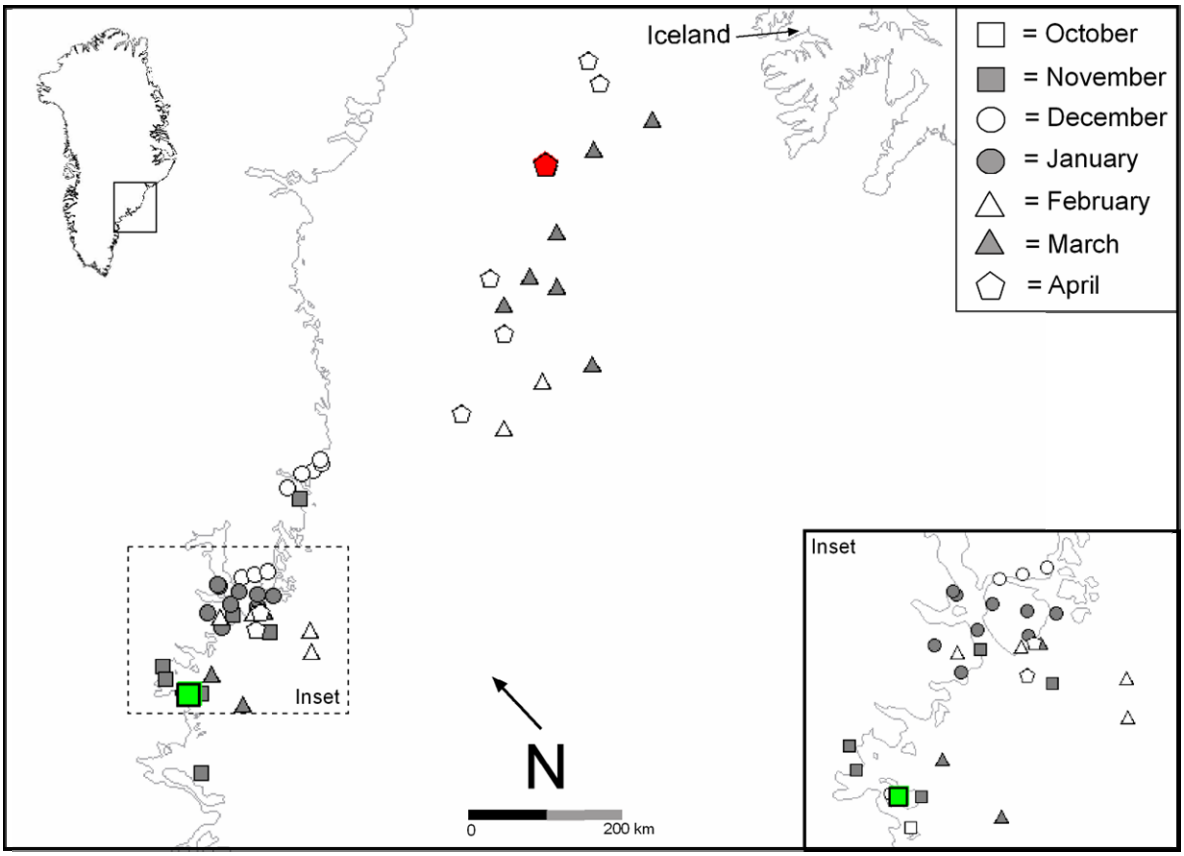

Figure 4.14. Area used by Gyrfalcon 49771 while on winter home range with locations from each individual month represented by a different symbol. Green square represents arrival on winter home ranges and red octagon represents last location before departure on return migration. Only a single location was used for any given day and only days with locations in classes 3–1 were included.

An adult male tagged at Maniitsoq (35258) continued to migrate down the southwest coast of Greenland throughout the entire winter period, and did not stop moving in a southerly direction until late April (Figure 4.15). Throughout the winter period falcon 35258 appeared to have between two and four use or stopover areas, which were each used for approximately one to three months (Figure 4.15). If this period had been classified as a winter home range, calculated ranges sizes would have been: 15,364 km^2 (90% MCP), 39,840 km^2 (95% kernel), and 9,419 km^2 (50% kernel).

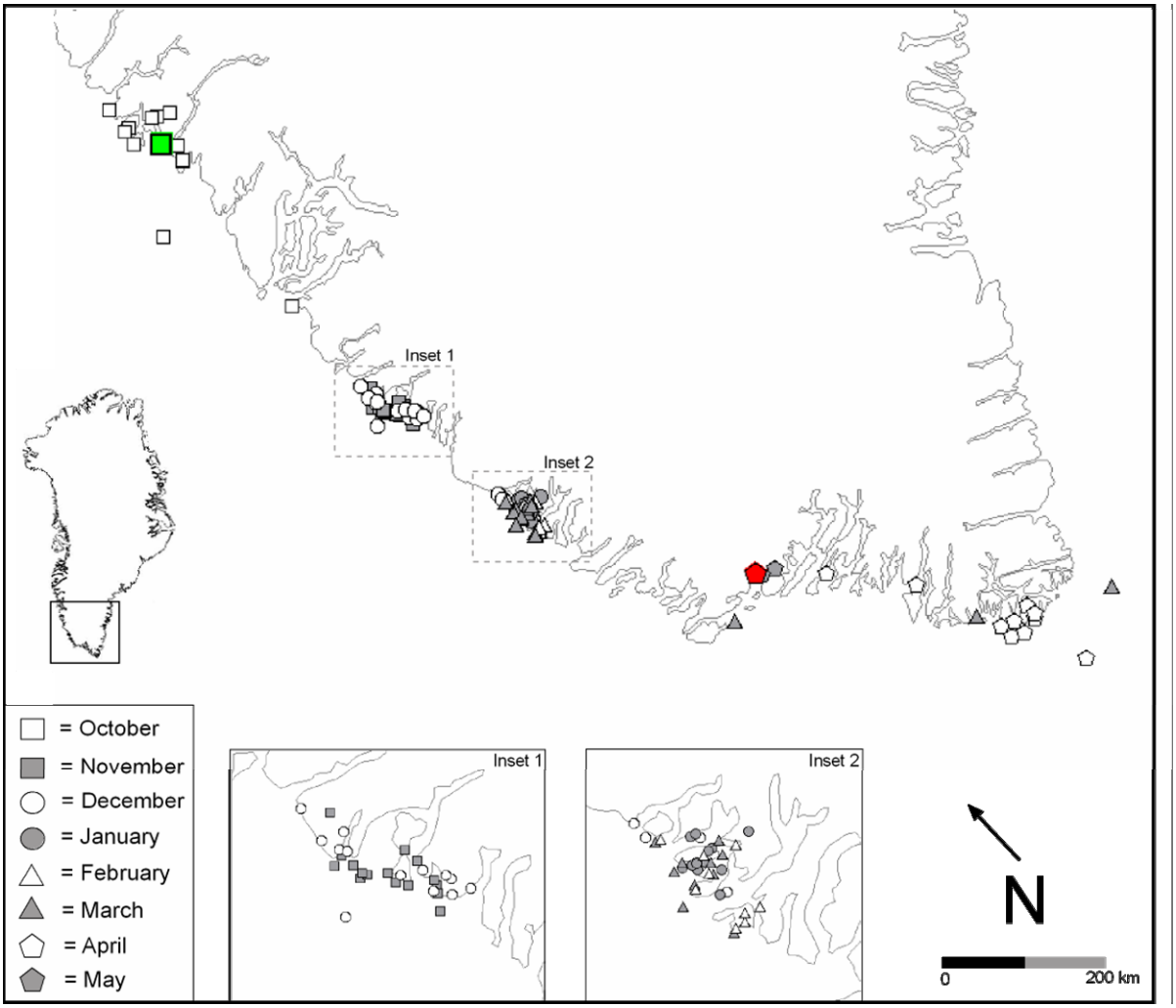

Figure 4.15. Area used by Gyrfalcon 35258 while on winter home range with locations from each individual month represented by a different symbol. Green square represents arrival on winter home ranges and red octagon represents last location before departure on return migration. Only a single location was used for any given day and only days with locations in classes 3–0 were included.

After tagged in Scoresbysund, a juvenile female Gyrfalcon (49768) moved continually and travelled over 4,548 km during a 200-day period, an area that included portions of the east coast of Greenland and northwest Iceland (Figure 4.16). During this period 49768 spent over half of its time over the ocean, likely hunting alcids or other seabirds and resting on icebergs, with the longest continuous period over the ocean approximately 40 days. Using the same methods as above to calculate winter home range size, falcon 49768 had a range size of: 160,225 km^2 90% MCP, 265,547 km^2 95% kernels, and 84,143 km^2 50% fixed kernel.

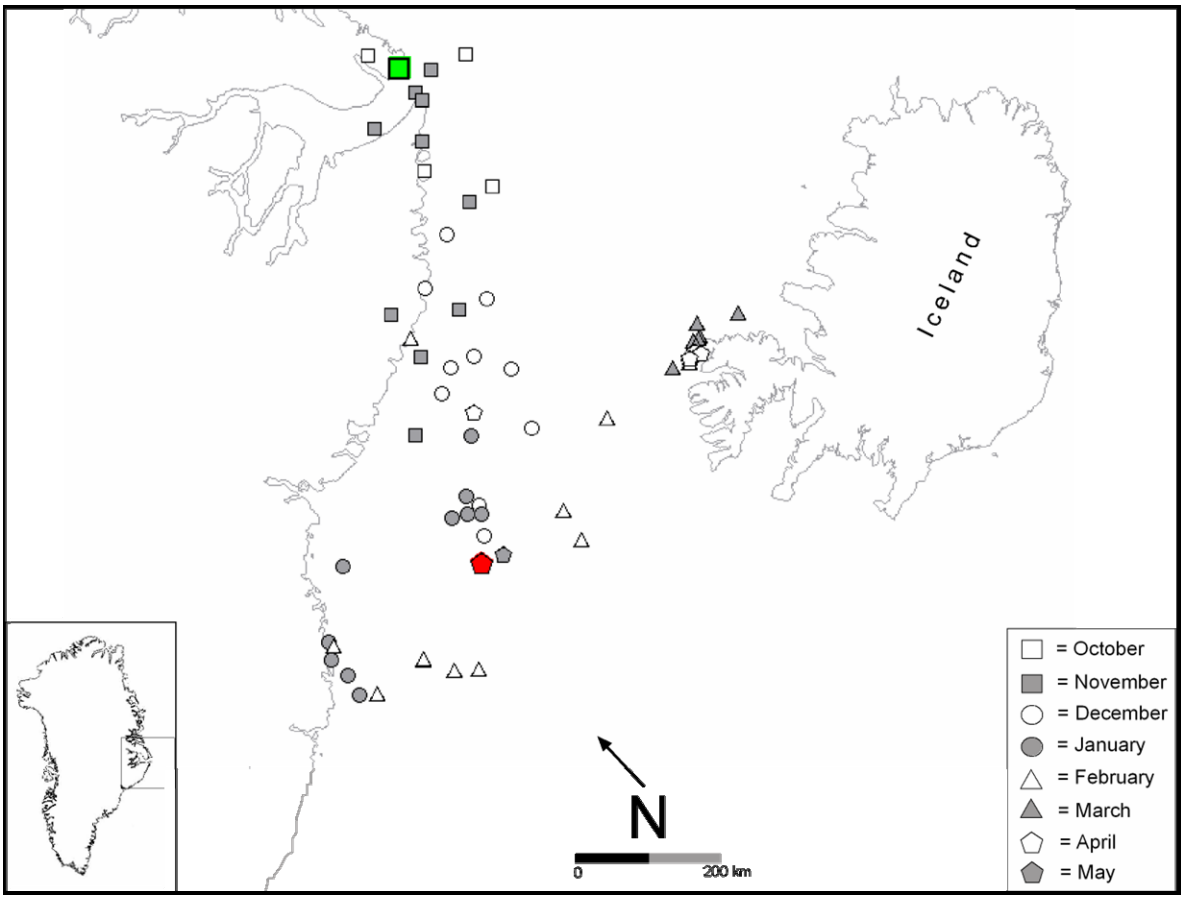

Figure 4.16. Area used by Gyrfalcon 49768 while on winter home range with locations from each individual month represented by a different symbol. Green square represents arrival on winter home ranges and red octagon represents last location before departure on return migration. Only a single location was used for any given day and only days with locations in classes 3–0 were included.

As mentioned previously, the distinction between extremely large winter home ranges or nomadic movements during winter months is difficult to determine. In addition to the two individuals above, three other Gyrfalcons, all adults tagged in the Scoresbysund area (49762, 49764, 49771), had similar long distance movements and covered large areas. However, they tended to inhabit the same areas repeatedly, albeit large. On the west coast an adult female from Thule (41444) and two adult males tagged in Maniitsoq (35250 and 35257) moved throughout the entire time their PTTs functioned. While their movements could have been considered nomadic, their PTTs failed too early for conclusive results to be determined.

The main findings to emerge from these various results are that Gyrfalcons can wander over huge areas in winter, and some individuals make long movements at any date during this period. All tagged birds moved away from their breeding areas, so could be classed as complete migrants, the first part of their migrations being obligate in nature, but later parts facultative.

Return migration: departure dates

Eight adult Gyrfalcons departed on return migration from 7 March to 3 May (mean = 4 Apr., median = 5 Apr.) from southern Greenland (Table 4.16). Of those, six were tracked until they had completed their return journey. Four probably bred while an additional two appeared to establish summer home ranges, but did not breed (based on dates). Of the other two adults which may not have completed return migration, individual 36318 travelled approximately 450 km north before it returned south to its winter home range, where the PTT then stopped. The other, adult female 35245, briefly returned to the nest site where she was originally tagged and then also returned to her winter home range, where she then continued 150 km south down the coast to where her PTT stopped. A single juvenile female began return migration on 5 May after being tagged in Scoresbysund, but her PTT failed before she established a summer home range. Of the three adults which likely bred after completing return migrations on the west coast, the further north each individual bred the later it departed on return migration. The female that bred in Kangerlussuaq departed 13 March, the female which bred in Thule departed 30 March, and the male which likely bred in northwest Ellesmere Island departed 11 April.

Table 4.16. Return migration data from adult Gyrfalcons that spent the winter non-breeding season in southern Greenland (distances given as Great Circle Distances).

Breeding home range, PTT, age, and sex	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 calculations[b] (LC 3, 2, 1, 0)
Kangerlussuaq 11988/ad♀	13 Mar–22 Mar	848	85	10	8 (80.0)	5–276	1, 0, 1, 4
Thule 35243/ad♀	30 Mar–8 May	4,502	113	40	28 (70.0)	11–536	2, 4, 12, 8
Thule 35249/ad♀	20 Apr–13 Jun	2,763	50	55	34 (61.8)	1–143	0, 9, 15, 8
Scoresby. 49762/ad♂	3 May–27 May	1,657	66	25	9 (36.0)	27–148	0, 0, 3, 4
Scoresby. 49771/ad♀	20 Apr–4 May	1,576	105	15	6 (40.0)	31–223	0, 0, 4, 0
Ellesmere 35248/ad♂	11 Apr–2 May	2,792	127	22	14 (63.6)	15–320	0, 5, 4, 3

[a]Range of distances travelled per day, see Chapter 1 methods section for further description.
[b]Location for start and end date of migration not included.

Return migration: distance travelled, speed, duration, and route

The shortest distance travelled by Gyrfalcons on return migration was for falcon 11988 which spent 10 days on return migration and travelled 848 km at a speed of 85 km/day (Table 4.16). From Thule, falcon 35243 spent 40 days on return migration and travelled over 4,502 km at a speed of 113 km/day while falcon 35249, which did not breed, travelled 2,763 km over 55 days, a speed of only 50 km/day (Table 4.16). Individuals initially tagged in Scoresbysund travelled 1,657 and 1,576 km on return migration, spending 25 (66 km/day) and 15 (105 km/day) days on return migration, respectively (Table 4.16). The adult male which travelled to northwest Ellesmere Island spent 22 days on return migration, and travelled 2,792 km at a speed of 127 km/day (Table 4.16). In general, their speeds were faster than those recorded on autumn migration.

Routes used during return migration were similar to those used during outward migration; however, falcon 35243 from Thule, which used the east Canada route during

outward migration, used the ocean route on return (Figure 4.17). Additionally, falcon 35248 which travelled down the east coast of Canada during outward migration travelled almost exclusively over the ocean during return, with the period over the ocean encompassing at least 2,370 km over a 15-day period (Figure 4.17). Individuals initially tagged in Scoresbysund which completed return migration travelled along the east coast of Greenland.

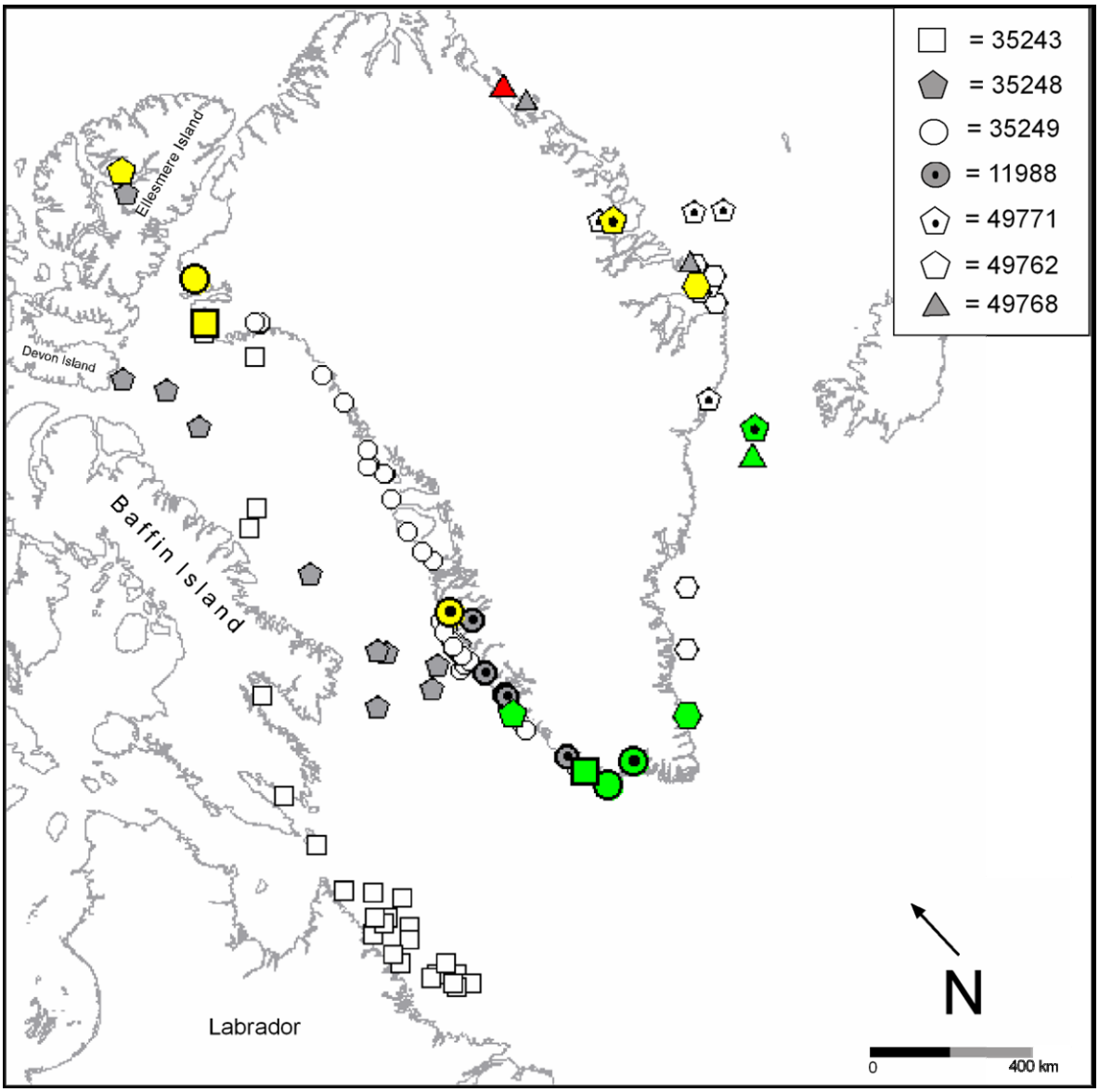

Figure 4.17. Routes used by Gyrfalcons that wintered in Greenland. Green symbols are where return migrations began, the red symbol the last location of an incomplete return migration, and yellow symbols indicate the breeding home range of individuals which completed return migrations. Only one symbol is included per day and only days with locations in classes 3-0 were used.

DISCUSSION

Surveys and populations

The world population of Gyrfalcons was estimated by Cade (1960, 1982) at 15,000–17,000 pairs. More recently Potapov & Sale (2005) estimated the world population at 7,880–10,900 pairs, totaled using country estimates. For Greenland alone, Mattox (1970) estimated 850 pairs and Cade (1982) 500–1,000 pairs, between 5 and 10% of the possible world population, although no one really knows.

One of the most important influences on the breeding density of birds is food supply (Newton 1979, 1998). Ratcliffe (1969) showed that for three inland Peregrine Falcon populations in the United Kingdom, that were not limited by nest sites, the average breeding home range per pair for each area was correlated with land-productivity and food. However, prey densities were not quantified. Additionally, numerous other raptor species have been shown to have significant relationships between prey abundance and nesting density (see Newton 1979).

Based on hunter kills, Vibe (1967) found ptarmigan populations to fluctuate in Greenland on approximately 11-year cycles from 1886 to 1954. Nielsen (1999) reported a 10-year cycle for ptarmigan in Iceland and found that Gyrfalcon populations lagged behind by three years. Mossop and Hays (1982, 1994) reported that in the Yukon Territory the Gyrfalcon population fluctuated on a 10-year cycle, probably following population fluctuations of Willow Grouse *Lagopus lagopus*. Additionally, Nyström *et al.* (2005) showed a significant relationship between the number of Gyrfalcon chicks fledged each year and ptarmigan population levels. Alternatively, Mindell *et al.* (1987) and Mindell and White (1988) found no relationship between Gyrfalcon and ptarmigan populations in Alaska, and Shank and Poole (1994) found the same for Canada's Northwest Territories. In Kangerlussuaq where the smallest mammals are the Arctic Fox *Alopex lagopus* and Arctic

Hare, and relatively few potential bird prey species exist, ptarmigan remains were found most frequently in Gyrfalcon nests from 1998 to 2005. Based on data collected from 1990 to 1993 and from 1998 to 2005 it seems likely that Gyrfalcon and ptarmigan populations were inter-related in that area.

The potential prey item differences between Kangerlussuaq and Thule varied primarily by the large numbers of songbirds in Kangerlussuaq from mid-May to mid-September and by the tens of millions of seabirds present in northwest Greenland from mid-May to August–September. In general, Gyrfalcons appeared to prey upon whatever species were available in the areas where they bred, utilizing all suitable species present locally.

As previously stated, only in east-central to northeast Greenland do lemmings and weasels occur. They are non-migratory. Throughout most of the remainder of the Gyrfalcons' circumpolar range (apart from Iceland where there are no rodents or Arctic Hares, and ptarmigan are the dominant wild herbivore, Nielsen 1999), microtone rodents and a larger variety of avian species were available than in Greenland (Cade 1982). Manniche (1910) reported that in northeast Greenland Gyrfalcon numbers appeared to be influenced by lemming numbers in 1906. Quoting Manniche (1910) and Pedersen (1934), Salomonsen (1950–51) concluded the Gyrfalcon population in northeast Greenland fluctuated with lemming numbers. Although Meltofte (1975) published locations of breeding Gyrfalcons, including several reported by Manniche, and related data collected from 76 to 78° N between 1969 and 1971, he provided limited information on Gyrfalcon prey. Cabot *et al.* (1988) reported 84 prey deliveries in 1987 at a Gyrfalcon nest in northeast Greenland (77.7° N 20.9° W). They stated that prey reflected what was available in the area at the time. While monitoring terrestrial species, Gilg *et al.* (1997) visited a Gyrfalcon nest in 1990, 1992, and 1995 in northeast Greenland (73.8° N 24.7 W°) collecting prey remains. They determined that Gyrfalcons fed most importantly upon

lemming when populations were high and much less so during low lemming years. Snow Bunting and ptarmigan remains were more abundant among prey taken during low lemming years. Although there might be a correlation between Gyrfalcon breeding numbers and lemming numbers, the data are not conclusive.

In both Kangerlussuaq and Thule, it seems probable that Gyrfalcon numbers, or density, were regulated to prey, and specifically ptarmigan. Of primary importance is likely the prey availability when the Gyrfalcons first arrived on territory in spring, with Rock Ptarmigan, Snow Buntings, and adult Arctic Hares present in Kangerlussuaq and Rock Ptarmigan and adult Arctic Hares in Thule. However, it is likely that Rock Ptarmigan are the single most important prey species early in the season, as shown by Nielsen & Cade (1990b) in Iceland.

Population changes

Has the total number of nesting pairs of Gyrfalcons in Greenland changed during the past several decades? Although there are insufficient data to state accurately whether a change has occurred throughout the island, some regional decreases may have occurred, in particular from the Uummannaq District south to the southwestern tip of Greenland. For this region, comparing the number of Gyrfalcons reported by Bertelsen (1921) in early 1900 and Burnham *et al.* (2005) in 2000, almost 100 years later, fewer pairs were located during the later survey. Additionally, further south in the Disko Bay area, no breeding Gyrfalcons were located by Burnham and Sherrod in 1974 (Burnham & Mattox 1984), despite Salomonsen's (1950–51) statement that the Gyrfalcon breeds "rather locally in S.W. Greenland but in the Disko Bay region it increases considerably in number," referencing Bertelsen (1937) and Fencker (1929). In very southwest Greenland (60.32–61.0° N), Falk and co-workers have conducted falcon surveys from 1981 to 2005, and found no Gyrfalcons nesting during their research (K. Falk pers. comm.). However, Hagerup (1891), Winge

(1898), and Muller (1906) all reported Gyrfalcons as commonly occurring and breeding throughout southern Greenland. It seems, therefore, that Gyrfalcons have disappeared as breeders from the southernmost parts of their range in Greenland. This would perhaps have been expected under climate warming.

Based on the number of successful nest sites found, the Gyrfalcon population in Kangerlussuaq has stayed approximately level from the early 1990s through 2005, with year-to-year fluctuations. For successful and occupied nest sites, however, the mean nearest neighbor distance between nests has increased from the mid-1970s (Burnham & Mattox 1984) onward, a possible sign of a declining population. Additionally, despite a doubling in the number of nest sites known and surveyed, and improved survey techniques (foot and small planes in the early 1990s versus foot and small helicopter during this study), the number of occupied nests has decreased in the Kangerlussuaq area. It appears likely that the Gyrfalcon population in the Kangerlussuaq area has at best remained stable (with year-to-year fluctuations), but more likely declined, especially from the 1970s to the early 1990s.

Using DNA material collected from this study, Johnson *et al.* (2007) showed that Gyrfalcons in Kangerlussuaq and Thule on the west coast, were genetically similar. However, individuals captured at Scoresbysund, on the east coast, were genetically dissimilar from those on the west coast. Results from carbon dating (Chapter 3) of accumulated guano at nest sites suggest that Gyrfalcons may have colonized the Kangerlussuaq area approximately 1,800 years earlier than the more northern Thule area. These genetic and carbon dating results suggest that the Thule area was colonized by immigration of individuals from further south, such as in Kangerlussuaq, and not from the east coast of Greenland.

For this northward expansion to have occurred, asymmetric gene flow would have likely existed, with most dispersal occurring from south (Kangerlussuaq area) to north (Thule area). Over time, as the populations in both areas stabilized, gene flow would have probably stabilized, and become more symmetric between areas. However, Johnson *et al.* (2007) showed that current gene flow between the two areas is not symmetric, being predominantly from north (Thule) to south (Kangerlussuaq). So why, if individuals from Kangerlussuaq colonized the Thule area as described above, is gene flow not at least symmetric between areas, but instead asymmetric from north to south?

One possible explanation is that the southern population is declining, and is being augmented with individuals from further north in order to maintain its current breeding level. Further DNA studies using historic genetic data from both areas need to be carried out in order to determine if gene flow between the populations was more symmetrical in the past and if the currently observed asymmetry is recent.

Interactions between Gyrfalcons and Peregrines

There is little doubt that the ratio of nesting Peregrines to Gyrfalcons changed in Kangerlussuaq over the years surveyed, from nearly 1:1 during 1972–1981 to approximately 4:1 in 1991 (Restani & Mattox 2000). Currently over 170 Peregrine nest sites are known in the Kangerlussuaq area. Using information on occupancy collected by Mattox (1998) during 1988–1997, the last 10 years of large scale surveys for Peregrines made in the Kangerlussuaq area, an average of 84.7% (median = 85, sd ± 6.7) of checked sites were occupied. If occupancy remained similar during my study, then approximately 144 Peregrine nests were likely occupied each season, making the ratio of Peregrines to Gyrfalcons more than 14:1.

Although perhaps ultimately driven by climate change, might the probable Gyrfalcon population decline be associated with the increase in Peregrines? Salomonsen (1950–51) states, "The number of Gyr-Falcons in the low-arctic region is probably to some extent checked by the Peregrine…" He made the statement because of overlap between the species in food and nest sites. In Kangerlussuaq territorial Peregrine Falcons and Gyrfalcons were located on the same cliff ≥25 times (Mattox annual reports and this study). Before 1982 this level of overlap was never witnessed (Burnham & Mattox 1984). At a cliff where a pair of Gyrfalcons and Peregrines nested simultaneously, the adult female Gyrfalcon was found below the cliff unable to fly, evidently because of concussion. After being held in captivity for a short time she was later released at the nest site, but disappeared within days, and the Gyrfalcon pairs' small young died shortly after. The Peregrines were very aggressive, and successfully reared their own young. Aerial encounters between the species were seen several times, and I was never convinced that Gyrfalcons were dominant over the Peregrines, but the reverse was true on several occasions with Peregrines observed driving adult Gyrfalcons away from the nest and/or fledged young, on occasion even striking the Gyrfalcon and locking feet. Similar observations were made by Fowles (1981) who commented that "The large falcon tended to look clumsy and confused as it attempted to evade the agile stoops of the…Peregrines." As a species, the Peregrine Falcon is very aggressive toward other species, including other Peregrines (Tordoff & Redig 2003).

Other than by direct aggression and displacement, how might Peregrines influence breeding Gyrfalcons? Direct displacement is probably difficult for Peregrines because the Gyrfalcons begin breeding earlier in the spring. But indirect displacement may occur through the Peregrine's influence on the ptarmigan population. As explained in Chapter 2, Peregrines prey on ptarmigan and other avian species. When Gyrfalcons arrive at nest sites, display and lay eggs, and throughout much of their incubation, the prey species available

are primarily ptarmigan, adult hare, and Snow Buntings. Of the three, ptarmigan is probably the most important. As Peregrine numbers have increased in Kangerlussuaq so has their impact on ptarmigan, reducing the number surviving the summer and autumn seasons, thus reducing the number of birds available in the spring when the Gyrfalcons arrive to breed.

A similar situation, with Peregrines and Hen Harriers *Circus cyaneus* holding Red Grouse *Lagopus l. scoticus* populations at low levels, has been described in Scotland (Redpath & Thirgood 1999). Again, both raptors were supported at high density mainly by other prey, but had their major impact on the more vulnerable grouse. No raptor in the Scottish situation was as heavily dependent on grouse as Greenland Gyrfalcons were on ptarmigan. Likewise, in Norway, Selås (1998) studied the effect of Red Fox *Vulpes vulpes* density on Goshawks *Accipter gentilis*. Through a natural experiment where Goshawk, fox, and grouse populations were monitored over several decades in a 650 km^2 area, it was determined that Red Fox influenced Goshawk breeding densities negatively by limiting the number of grouse. I suggest that this type of relationship is occurring between Peregrine, Gyrfalcon, and ptarmigan populations in Kangerlussuaq.

Reproduction

Reproduction may have varied regionally and annually, but I do not have enough information to prove that this is the case in Greenland. As mentioned in the results, in both the Kangerlussuaq and Thule areas many of the Gyrfalcon nest sites were found after the young were flying and the total number could not be confirmed. Therefore, most numbers provided are minima. Additionally, the difference in reproduction between occupied and successful nests is likely underreported, because surveys took place late in the breeding season and at nest sites that had failed, adults may have already left the area biassing the results towards successful nests. Further, although Gyrfalcon reproduction has been shown

to fluctuate between years according to prey densities (White and Cade 1971, Nyström *et al.* 2005), it was not possible to determine if this was the case in Greenland.

Potapov and Sale (2005) reported a mean brood size of 2.6 young (sd ± 0.91, n = 364) across the entire range of the Gyrfalcon. In Kangerlussuaq, from 1972 to 2005, surveys showed ≥ 1.63 (n = 221) young per occupied and ≥ 2.75 (n = 131) young per successful nest site. Thule Gyrfalcon nest sites had ≥ 1.88 (n = 52) young per occupied and ≥ 2.39 (n = 41) young per successful nest site. These were lower than for Kangerlussuaq, but many more of the sites in Thule were visited when young were flying and birds were probably more frequently missed. The data for central-east and northeast Greenland are too limited to contribute meaningfully to this discussion. Results from Greenland appear to fit within ranges of reproduction reported by others for Gyrfalcons. However, it is difficult to make direct comparison between studies since the timing of nest visits vary.

In Kangerlussuaq, on several occasions nest sites were visited that had been occupied the previous year and the remains of dead young, in some cases fully feathered, were found below the nest site. First-year survival also appears to be low. Of the 25 juveniles tagged with PTTs, only a single female was known to have survived through the winter, indicating a maximum possible mortality rate of 96%. Without knowing what effect PTTs had on juvenile Gyrfalcons, it is not possible to determine if this high mortality rate was anthropogenically (PTTs) or naturally caused. However, first-year survival is expected to vary greatly from year to year, according to prey supply.

Further examination of data from both adult and juvenile Gyrfalcons tagged with PTTs suggests that they were likely negatively affected by units. Of the 27 adults which were tagged and had PTTs function correctly only four (14.8%) operated more than 300 days (Appendices R, S, T, & U), this despite that all PTTs should have had sufficient

battery power to function for at least 350 days. While some of these PTTs likely stopped functioning as a result of the unit failing, a large but unknown percentage potentially failed because individual falcons died. While the apparent high mortality rate observed in juvenile and adult Gyrfalcons was much higher than expected and may be natural, it is highly unlikely, given that if this rate occurred for an extended period mortality would outpace reproduction and the species would likely be extirpated. Instead, it seems most likely that PTTs had a negative effect on survival.

Increased mortality associated with PTTs has been documented in another large falcon species, the Prairie Falcon *Falco mexicanus*, where adult females with PTTs had an annual survival of 49% compared to 87% for individuals who shed their units (Steenhof *et al.* 2006). Additionally, in Tawny Owls *Strix aluco*, back-mounted radio tags have been shown to have a significant negative effect on juvenile survival, with only one (1.8%) individual recruited from a sample of 55 tagged birds while 14 (16%) were recruited from 89 untagged birds (Petty *et al*. 2004). However, results in owls have varied, with Sunde (2006) finding no consistent negative effects on either juvenile or adult Tawny Owls marked with back-mounted radio tags. Tests using Homing Pigeons *Columba livia* have shown more detailed effects of back-mounted radio tags, with tagged individuals having longer flight times between locations and having a much higher rate of CO_2 production than untagged individuals (Gessaman & Nagy 1988).

Breeding chronology

The Kangerlussuaq and Thule areas are approximately 1,170 km or 8.4° of latitude apart. The average nesting chronology in Kangerlussuaq and Thule vary by approximately 17 days with Kangerlussuaq Gyrfalcons fledging on 16 July, on average, and the more northern Thule Gyrfalcons on 2 August. There is less information from the Scoresbysund area of east Greenland. In 1999 T. Cade and O. Nielsen located nest sites with five

incubating Gyrfalcons between 9 and 11 June (Burnham 1999). In 2000, Nielsen observed only a single occupied nest and it had three approximately 25-day-old young on 16 July (O. Nielsen, pers. comm.). Average fledging dates for Iceland (66º N) were 12 July from 1981 to 1985 (Nielsen & Cade 1990a). As expected, more northern Gyrfalcons bred seasonally later than do those which bred further south. Furthermore, greater synchrony was observed in the starting dates for individuals breeding in the north than in the south, as described for other raptors by Newton (1979).

Nest site characteristics

Nest site availability has been shown to limit the density of many species of birds, including raptors (Cavé 1968, Hamerstrom *et al.* 1973, Newton 1979, 1998, Steenhof *et al.* 1993). Nest site characteristics, to include attributes regarding the general area, cliff, and nest ledge have all been shown as important factors in determining the attractiveness of specific nest sites for raptors (Donazar *et al.* 1993, Gainzarain *et al.* 2000, Sergio *et al.* 2004, Wightman & Fuller 2005). In Kangerlussuaq, Wightman & Fuller (2005) concluded that specific cliff features, including height, view, nest ledge overhang, and inaccessibility to ground predators were all important factors determining if cliffs were used by Peregrines.

Meaningful comparisons between nest sites used by Gyrfalcons in Kangerlussuaq and Thule were difficult, with many more data available for Kangerlussuaq. Cliff and ledge height were over twice as high in Thule than in Kangerlussuaq, and probably could be correlated. However, despite the large difference in cliff and ledge height between areas, falcons nested in approximately the same location on cliffs in both areas, 62% of the way down the cliff face in Kangerlussuaq and 61% down the cliff face in Thule. Cliff aspect was also similar between areas, with nests sites in Thule facing to the southwest and nest sites in Kangerlussuaq facing more southward. On average, cliffs in Kangerlussuaq were at an elevation of 291 meters compared to 171 in Thule, probably a result of the majority of

the cliffs in Thule being beside the ocean and the cliffs in Kangerlussuaq being inland. In general, data on cliffs were difficult to collect and define. Many cliffs were terraced and broken up and the definition of the "top" or cliff height was somewhat arbitrary. Even nest height could be difficult to determine, with extremely steep talus or grass slopes below and above many cliffs.

While measurements were taken and presented on nest ledge characteristics they are probably not representative. In both Kangerlussuaq and Thule, only the most accessible nests were entered due to safety of falcons and researchers. Some cliffs would have required well over 400 meters of rope and had overhangs greater than 20 meters. Other nest ledges were too small for researchers to enter for the safety of falcons.

Because of possible biases, perhaps the best and most meaningful data to compare are the cliff and nest ledge aspects within areas. In Kangerlussuaq, the mean cliff aspect was 172° while the mean nest ledge aspect was 187°, a small difference of 15°. For Thule, the mean cliff aspect was 211° and the mean nest ledge aspect was 59°, a 152° difference. While the Thule sample is small, I believe this difference between study areas is correct. In the Thule area most commonly used nest ledges were located around corners from the main cliff face, and afforded significant protection from the elements. In Kangerlussuaq this was less common, and the cliff and nest ledge typically faced in the same general direction. Additionally, nest ledges in both areas almost always had extremely large overhangs which appeared to be critical for nesting success given the extreme conditions in both areas in spring. However, it was not possible to measure this cliff/nest ledge characteristic in a meaningful way.

Based on my observations of Gyrfalcon nests in Kangerlussuaq and Thule compared with my observations of approximately 45 Gyrfalcon nests in northeast Iceland in 2003,

nests in Greenland were much more overhung and significantly less accessible. All nest sites observed in Greenland required technical rock climbing equipment, while a number of nests in Iceland were walk-ins from below. Further, in Iceland I observed one nest on a rock pinnacle and others that were at ground level on the tops of cliffs. While overhangs have been suggested to protect nests against snow, in early season surveys in the Kangerlussuaq area after snow falls it was not uncommon to observe females incubating eggs with only their upper body and head visible through snow. It seems that overhangs in Greenland are more effective against rain, which typically is heavier than snowflakes and less easily blown by the wind.

In Kangerlussuaq and Thule it seems probable that Gyrfalcon densities are not limited by shortage of nesting sites. In both areas, and especially Kangerlussuaq, a large number of previously used nest sites were not used for breeding in any one year. This wide variety of nest sites may have provided pairs with flexibility when it came time to nest, and depending upon winter weather conditions, some sites were rendered unusable each year. However, with the wide range of nest sites that were available, Gyrfalcons were still able to breed successfully.

Plumage colour variants

The observed plumage colour variation in the three main study areas is comparable with findings reported elsewhere for Gyrfalcons, with a higher proportion of white falcons in the north than further south. As previously mentioned, Johnson *et al.* (2007) showed that gene flow between Kangerlussuaq and Thule is asymmetrical, with dispersal predominately from north to south. Based on this one might expect a predominately "white" colour plumage to occur in Kangerlussuaq, which is not the case. It seems most likely that gene flow has occurred in both directions at different times, with "dark" individuals surviving better in the south and "white" in the north. If, as I suggested earlier, the population in

Kangerlussuaq is declining and being augmented with individuals from Thule, a shift in the observed plumage colour frequency likely would not occur, as "dark" or "grey" individuals would continue to survive better than "white" individuals in the Kangerlussuaq area.

Morphometrics

Johnson *et al.* (2007) showed "low, yet significant, levels of population genetic differentiation based on microsatellite allele frequency differences (F_{ST})" between Gyrfalcon populations on the west coast (Kangerlussuaq and Thule) and east coast (Scoresbysund samples) of Greenland. However, gene flow was shown between these areas when using other DNA markers.

Results from this study support differences between Gyrfalcon populations on the west and east coasts, with Gyrfalcons of all ages and sexes from Thule being the largest based on average body mass, tarsus length, and tail length. In the few instances when Gyrfalcons from Thule did not have the largest average measurement, such as bill length for all ages and sexes and wing chord for adult males, individuals from Maniitsoq were the largest. Based on PTT data presented earlier, individuals captured in Maniitsoq are likely from along the entire west coast of Greenland, including Thule, along with portions of northeast Canada, and should not be viewed as entirely local to that area.

Bergman's Rule states that in general within warm blooded vertebrate species, there is a trend for larger body size in races from cooler climates than races of the same species in warmer climates (Mayr 1963, Ridley 1996, Futuyma 1998). Within Greenland, this seems to apply to Gyrfalcons, with individuals farther north and in cooler climates being larger in size than those further south, and in warmer climates. Wyllie & Newton (1995) showed a similar latitudinal variation in the body size of Sparrowhawks *Accipiter nisus* in Britain.

Similar results were also found for a number of other species of birds, including other falcons and arctic nesting species (see Meiri & Dayan 2003 for a review).

Home range size

The home range sizes of breeding Gyrfalcons in Kangerlussuaq, Thule, and Ellesmere Island appeared to be similar, with no apparent differences between areas or sexes. For six of the nine individuals, 90% MCP provided the largest calculated breeding home range, while 95% fixed kernels were the largest for the other three. The lack of an obvious difference in breeding home range size between areas was unexpected, based on the observed availability of prey in each area. In Thule, once Dovekies arrived in large numbers, they were available within kilometers of almost all nest sites, and a small breeding home range was expected as a result. For Kangerlussuaq, while limited numbers of prey items were observed close to Gyrfalcon nest sites, the overall density of prey appeared to be much lower than in Thule, and it was predicted that Gyrfalcons would have to travel generally further for food. However, as discussed earlier, ptarmigan populations have been shown to cycle and it was not known at what point in this cycle the local population was during this study. It seems likely that, if dramatic changes in ptarmigan densities do occur in the Kangerlussuaq area, that the size of Gyrfalcon breeding home ranges would be affected.

Klugman *et al.* (1993) provided the only other known breeding home range size for Gyrfalcons. In 1990 in Kangerlussuaq they tagged a breeding adult female with a PTT at the nest. Using "higher quality locations" they calculated a home range size of 589 km^2 using a minimum convex polygon.

Sizes of breeding home ranges for other large falcon species varied when compared to Gyrfalcons. Prairie Falcons tagged by Marzluff e*t al.* (1997) in Idaho, U.S.A., had an

average range size of approximately 300 km^2, one-third to almost half as small as Gyrfalcons depending upon method of calculation. However, conventional telemetry and slightly different methods were used to calculate home range size. On the Kola Peninsula, Russia, four breeding adult female Peregrines were tagged with PTTs by Ganusevich *et al.* (2004), and had an average calculated range size of 1,175 km^2 using 90% MCP. This was more than double the average size (547 km^2) calculated using 90% MCP for the seven adult female Gyrfalcons included in this study; however, Ganusevich *et al.* (2004) included locations with LC 0, which may have artificially inflated their estimated home range size.

Data were recorded for two individuals for the entire approximate five-month period they were on breeding range. The range size for adult female 35243, which bred in Thule, increased in size each month, probably as a result of the young rearing process, as described by Newton (1979, 1986) for other species of raptors. However, in an adult male which probably bred in northwest Ellesmere Island, range size decreased throughout the breeding period. Based on PTT locations it appeared the nest was located in a large fjord. It seems probable that early in the season prey was scarce in this area, with ptarmigan and adult hares the only likely source, and that as sea ice breakup occurred the number and density of prey species increased, which allowed the male to make shorter and closer foraging trips from the nest.

Winter home ranges of Gyrfalcons varied widely within Greenland, with birds tagged in Scoresbysund having significantly larger winter home ranges than those on the west coast. Gyrfalcons tagged in Scoresbysund used extensive areas over the ocean during winter months, which was not observed in west coast birds.

On the west coast, Gyrfalcon movements varied from individuals having small and stationary winter home ranges to continually moving up and down the coast over several

hundred kilometers. Additionally, some individuals had multiple wintering areas as they travelled up and down the west coast. Using 90% MCP, winter home range size varied from 357 to 6,657 km^2 (n = 8). Winter home ranges calculated using fixed 95% kernels ranged from 357 to 18,443 km^2 (n = 8).

Winter home range sizes for three Gyrfalcons on the east coast of Greenland were extremely large. Using 90% MCP and 95% fixed kernels, range sizes varied from 26,810 to 63,647 km^2 and 78,151 to 172,007 km^2, respectively. While the three falcons did not use their entire winter home range each month, I calculated the minimum distance travelled by both individuals while on winter home range (same method as used to calculate distance travelled on outward and return migration) and falcon 49762 travelled over 5,201 km and falcon 49773 over 3,864 km. These birds covered an average of 28 and 21 km/day while on winter range. Falcon 49764 had an even greater average distance travelled each day, 30 km/day. The speed of travel for all three of these birds while on winter home range was actually faster than some falcons' speed of travel while on outward migration.

Two Gyrfalcons did not have typical winter ranges and were not included in winter home range analyses. A juvenile female that was tagged in Scoresbysund spent the majority of the winter over the ocean and continually moved, occasionally utilizing the east coast of Greenland in addition to the northwest coast of Iceland. On this basis, a winter range would have covered 160,225 km^2 90% MCP, 265,547 km^2 95% kernel, and 84,143 km^2 50% fixed kernel. This bird moved at a mean speed of almost 23 km per day. An adult male tagged in Maniitsoq continued to move south along the coast throughout the entire winter, with multiple use areas. Its calculated range size was: 15,364 km^2 90% MCP, 39,840 km^2 95% kernel, and 9,419 km^2 50% kernel.

Winter home ranges calculated for Gyrfalcons in this study are some of the largest ever recorded for raptors. For an arctic nesting female Peregrine, Ganusevich *et al.* (2004) reported a winter range size of 213 km^2 using 90% MCP. For this study, using 90% MCP, the average for seven adult Gyrfalcon females on the west coast of Greenland was 1,170 km^2, and the lone female on the east coast had a range size of 63,647 km^2. Further, Ganusevich *et al.* (2004) included locations with LC 0 in calculations, which if included in this study would have increased the reported range sizes. McGrady *et al.* (2002) reported a similar winter range size for Peregrines wintering on the Gulf of Mexico, 169 km^2 90% MCP (n = 11), again much smaller than the mean for Gyrfalcons in this study. Only a Lesser Spotted Eagle *Aquila pomarina* had a reported winter home range that approached the size of estimated ranges for Gyrfalcons in this study; it covered approximately 25,000 km^2, albeit different parts were occupied at different dates throughout the winter (Meyburg *et al.* 1995, Meyburg *et al.* 2004).

While falcons tagged on the east coast had significantly larger home range sizes than those on the west coast, both coasts had individuals that moved considerably and had large home ranges. On the west coast, in some instances falcons with large winter home ranges completely overlapped those with much smaller ones, while on the east coast individuals also showed a considerable amount of overlap. Use areas on both coasts were not always in one direction, such as south, and movements could have also been described as 'pursuing' or weather-related behaviour, terms typically associated with migration (Berthold 2001).

While it would be difficult to determine exactly why some individuals on the west coast had much larger home ranges than others, one possibility is that Gyrfalcons are very territorial during the winter and those Gyrfalcons with small winter home ranges, which likely have an abundance of food, drive off other falcons. Individuals which are not able to establish small winter home ranges are left to wander, possibly being pushed from one area

to another and thereby achieving larger winter home ranges. In extreme situations when prey are difficult to find, juveniles may be forced out over the ocean for extended periods, or in the case of the east coast, to Iceland. Why Gyrfalcons on the east coast have such large home ranges, to include large expanses over the ocean, is unknown. However, it seems most likely that prey species may have a more patchy distribution than on the west coast and that falcons have to continually move, either following their prey or searching out new sources. Perhaps the only comparable species may be another arctic nester, the Snowy Owl, in which some radio-tagged individuals did not exhibit regular migration, but frequently moved long distances throughout winter months, probably facing many of the same difficulties as Gyrfalcons in this harsh environment (Fuller *et al.* 2003). The lack of consistent patterns among individuals is another feature of Gyrfalcon movements. Individual falcons probably adapt to environmental conditions, and more importantly to continually shifting prey availability, with their daily movements a reflection of this.

Timing of breeding and migration

PTT data showed that an adult female Gyrfalcon arrived in the Kangerlussuaq area on 22 March and spent 145 days on breeding home range (Table 4.14). Egg laying began approximately on 22 April. In Thule an adult female arrived at the nest on 8 May and spent 145 days on breeding range, with an average laying date of 9 May; however, the 8 May arrival is well within the recorded range (Table 4.4). In northern Ellesmere Island an adult male arrived at a likely nesting site on 2 May and spent 159 days on breeding home range, but no data are available on timing of breeding. Both adult females spent almost the exact same amount of time on breeding home range, while the adult male spent approximately two more weeks.

In Thule, on average, adult female Gyrfalcons departed on outward migration on 25 September (n = 6) while a single adult male departed on 5 October. On average, juvenile

male (n = 5) and female (n = 6) Gyrfalcons departed on outward migration on 19 and 24 September. Using a calculated average fledging date of 2 August, juveniles spent a post fledging period of between six and eight weeks in the Thule area before departure. Potapov and Sale (2005) reported that Gyrfalcon young learn to hunt slowly, and that after fledging they are fed by the parents for approximately six weeks. This seems to fit well with the data from Thule, where large numbers of juveniles were observed at the ringing station. In most cases young were still observed food begging when adults were present, and though captured using bait they were often timid and walked up to the pigeon and just stepped onto it. Rarely was the bait harmed, and in most cases it appeared that young falcons did not know how to kill their prey. In some cases up to eight individuals were observed standing around the pigeon, at times food begging to one another and apparently not sure what to do.

While it appears that adults departed within days of juveniles, there is no evidence to support adults travelling with their own young on outward migration, but it remains possible. Even though large numbers of juveniles congregated and were observed together at the ringing station in Thule, PTT data suggest that they did not travel in groups during outward migration. However, at the Scoresbysund ringing station, it was not uncommon to capture up to 6–8 juveniles on a single day, or even 2–3 individuals in a matter of one or two hours. Similar occurrences were reported by Manniche (1910) for northeast Greenland, who reported "Often 4 to 5 individuals would appear at one time either circling around the mast-heads…watching for pigeons." Whether this was a result of juveniles travelling in groups is unknown, and it is equally possible that large numbers of falcons were travelling through the area independently of one another and were attracted to the ringing station by other individuals stooping/diving at the bait.

The routes used by Gyrfalcons on outward migration varied considerably. While outward migration routes could be divided into three categories for the Thule area, in

general, Gyrfalcons from Thule simply flew south, and the flyway included the west coast of Greenland to the east coast of Canada, and all ocean areas in-between, though the majority of individuals used the east coast of Canada. Outward migrations from Thule were all ultimately in a southerly direction; however, falcons frequently made reverse migrations and/or even stopped for weeks at a time while on outward migration. In one case an individual had a reverse migration of over 550 km northwards to an area that it had previously migrated through. While reverse movements or migration have been documented and described in a number of bird species (Åkesson *et al.* 1996, Berthold 2001), these are likely the longest recorded for raptors, although it is unknown if the reverse migrations observed in this study were associated with weather, prey, or other unknown factors. For the Kangerlussuaq, Scoresbysund, and Maniitsoq areas individuals all moved in a southerly direction after being tagged. However, as in the Thule area, some falcons travelled up and down the coast for many hundreds of kilometers.

The speed of travel during outward migration ranged widely, with the most complete and perhaps most accurate data provided by the individuals from Ellesmere Island, Thule, and Kangerlussuaq that completed outward migration. Within these three individuals the speed of travel was fastest by the Ellesmere Island falcon and slowest by the Kangerlussuaq falcon. This was much as expected, with falcons that nest farther north having a faster speed of travel than those nesting further south. However, the individual from Thule spent 71 days on outward migration compared to 38 days for the Ellesmere Island falcon. Additionally, the Thule falcon travelled over 1,100 km more on outward migration, despite nesting closer to its winter home range than the Ellesmere Island bird, and clearly did not use the most direct route. This pattern was also apparent in other individuals which had incomplete outward migrations. It appears that the number of days spent on outward migration and the distance travelled were not correlated; however, there were too few complete data sets for outward migration to be certain.

Return migrations were recorded for six Gyrfalcons and generally appeared to be at faster speed than outward migrations. During return migration three individuals travelled at a speed greater than 100 km/day, while during outward migration the fastest speed was 99 km/day, which was for an incomplete journey. Two falcons which had complete outward migrations also had complete return migrations. The adult male that nested in northwest Ellesmere Island spent 22 days on return migration and travelled 2,792 km at a speed of 127 km/day (compared to 38 days, 3,137 km, and 83 km/day on outward migration). An adult female which nested in Thule travelled farther on return migration than on outward migration, 4,502 km compared to 4,234 km, but spent almost half as many days on return migration (40 days compared to 71 days) and travelled at almost double the speed (113 km/day compared to 60 km/day). Further, the adult female from Thule travelled at a speed of 165 km/day for the last 12 days of return migration while the adult male travelled at a speed of 232 km/day for the last eight days of return migration. The rapid speed of return migrations is likely a result of the narrow breeding window available for Gyrfalcons in the Arctic, with falcons that nest further north generally travelling faster and having a shorter breeding window than those that nest further south.

Migration strategies used by birds throughout the world vary considerably and species are commonly referred to as either obligate or facultative migrants (for reviews see Berthold 2001, Newton 2006). Obligate migrants are considered to be under fairly firm genetic control, with timing of migration based on length of day changes and a high degree of year-to-year consistency is observed in timing, distance, and route of migration (Berthold 2001, Newton 2006). In contrast, facultative migrants commonly respond to local conditions, such as an absence of food, and the timing, distance, and route of migration can vary from year to year in response to these conditions (Newton 2006). Some bird species probably change from obligate to facultative mode during migration, specifically during the starting phase, or obligate period, when areas where survival during the winter is not

possible are quickly crossed over, after which individuals change to a facultative mode and respond to local conditions, specifically food-supply (Newton 2006).

Gyrfalcons in this study have characteristics associated with both obligate and facultative migrants, with different latitudinal populations exhibiting different tendencies. As reported above for Thule, Gyrfalcons frequently departed the breeding area at nearly the same time, and in general travelled south at a fairly similar speed and direction, covering a large area where winter survival was not possible. Upon descending to lower latitudes reverse migration became more frequent and the speed of travel slowed, with individuals showing likely signs of pursuing movements, the general behaviour being more facultative in nature. Falcons tagged in Kangerlussuaq, Maniitsoq, and Scoresbysund appeared to be facultative migrants based on timing, speed, and direction of travel.

It appears that only Gyrfalcons that nest in the far north likely combine both obligate and facultative modes. Falcons in the north are likely forced to be obligate migrants for a short period, as the food supply almost completely disappears and remaining over winter is not possible. However, once these falcons travel further south and the climate moderates and prey numbers increase, they appear to assume a facultative mode, which allows them to adapt to local conditions.

So what determines the movements of Gyrfalcons both during migration and while on winter home range? The likely answer is prey. With limited light, at times as little as a few hours per day, and temperatures frequently as low as -20º C, falcons must have a continual food supply that can be depended upon and captured in a relatively short period of time. While during the breeding season falcons can spend numerous hours hunting in an area (24 hours of daylight), periodic long-distance flights or pursuing movements (Berthold 2001) may be necessary during migration and while on winter home range in order to find

large and abundant food sources that can be captured quickly. Although written to describe all migrants, Newton's (2003a) statement that migrants "mobile lifestyle enables them to exploit short-lived food-supplies at different places at different times, as they occur" is an excellent fit for Gyrfalcons. This "mobile lifestyle" is likely the key factor that enables Gyrfalcons to reproduce and survive the harsh winter weather during the non-breeding season in the Arctic.

CONCLUSION

My research has provided some of the first information on the ecological strategies used by Gyrfalcons throughout Greenland during the non-breeding season. Although previously studied during summer months, few data have been collected on Gyrfalcons during the fall, winter, and spring, with the majority of information to date based on speculation or conjecture. Additionally, by combining data I collected from 1998 to 2005 with data collected previously by others I have been able to analyze year-to-year and long-term trends in the Gyrfalcon population in Kangerlussuaq, central-west Greenland, and (from two widely-spaced surveys) from further south. Further, I collected the first long-term data on a High Arctic population of Gyrfalcons in Thule, northwest Greenland, from 1993 to 2005, and have been able to compare this coastal population with individuals breeding inland further south in Kangerlussuaq.

Gyrfalcons in Kangerlussuaq and Thule both nested on large overhung cliffs. In Thule, for individual nest sites the difference between the cliff and nest ledge aspect was much greater than for those in Kangerlussuaq, which provided more protection for the nest. Individuals in Thule fed primarily on Dovekies, though Rock Ptarmigan, Black Guillemots, and Arctic Hare were also important prey species. Results from Kangerlussuaq were similar to what others had already shown, with Rock Ptarmigan being by far the single most important prey species, with Old Squaw and songbirds taken in limited quantities.

Morphological differences were found between populations, with individuals from Thule in general being larger than those from Kangerlussuaq and Scoresbysund. This supports results from Johnson *et al.* (2007) that used genetic data from this study and showed a significant difference between east and west coast populations. While no genetic difference was observed between Kangerlussuaq and Thule, gene flow was apparent but asymmetric from north to south, although it was not sufficient to eliminate size differences between the Kangerlussuaq and Thule populations.

Gyrfalcons arrived at nests and began egg laying approximately three weeks earlier in Kangerlussuaq than in Thule, despite wintering in the same areas. Adult Gyrfalcons in Kangerlussuaq departed their breeding home ranges as early as the second week of August, with two individuals still on their breeding home ranges in September when their PTTs stopped functioning. Both juvenile and adult Gyrfalcons departed Thule in mid-to-late September, with juvenile males departing approximately five days before both juvenile and adult females. Data did not indicate that juveniles and adults travelled together while on outward migration.

Breeding home range size was similar among Gyrfalcons in all areas in this study. However, winter home range size varied greatly and individuals on the east coast had significantly larger range sizes than those on the west coast. The smallest winter home range sizes were comparable to breeding home ranges sizes, while the largest winter home ranges encompassed vast amounts of area, including over the ocean and northwest Iceland. In some instances, the large size of these ranges made it difficult to determine if they were actual winter home ranges or if falcons continually moved, without an actual range ever being established.

Routes used by Gyrfalcons during outward migration varied greatly by area, with falcons from Thule having the greatest range of diversity. When Gyrfalcons departed Thule they most frequently travelled to the east coast of Canada, either directly or after travelling south over the ocean for long-distances. Additionally, several individuals did not depart Greenland, and instead travelled down the west coast of Greenland. Falcons tagged in Kangerlussuaq and Maniitsoq travelled down the southwest coast of Greenland, while those tagged in Scoresbysund most commonly continued down the east coast of Greenland; however, one individual departed to the east and travelled towards Norway before its PTT stopped functioning. In general, Gyrfalcons tagged in all areas showed tremendous variation, both in speed and route, and in days spent on outward migration. Reverse movements were not uncommon, and some individuals back-tracked northwards for hundreds of kilometers during outward migration.

The Gyrfalcon population in central-west and southern Greenland may have declined based on information collected by others and data from this study. In Kangerlussuaq, population peaks were observed in both 1991 and 1999, although the number of occupied sites was one-third less in 1999, while the number of successful sites was similar. The mean minimum distance between successful and occupied nests has continually increased from the 1970s onward. Additionally, despite more previously-used nest sites known and improved survey techniques and knowledge of the study area, the number of occupied and successful nest sites have declined. Support is also garnered from the analysis of genetic data collected during this study (Johnson *et al.* 2007), with asymmetric gene flow from north to south a possible sign of a source-sink relationship. Furthermore, based on historic information and personal communications with others, it now appears that Gyrfalcons may no longer breed in south Greenland.

Having evolved to live in the harsh and at times sparse Arctic, Gyrfalcons have become highly adaptable. Their ability to feed on a wide range of prey species, varying in weight by more than 100-fold, has enabled them to survive and reproduce despite feeding primarily on cyclic prey species over most of their world range. Their variable behavior during outward migration and the non-breeding season highlights their ability to adapt to seasonal fluctuations in prey, be it by staying in a small area, living off of icebergs for months, or travelling long-distances on an almost daily basis. However, this highly specialized behavior may limit the ability of Gyrfalcons to adapt to climate change and increased competition from other species such as Peregrine Falcons.

Chapter 5: Conclusion.

Searches for Peregrines and Gyrfalcons were conducted during 1993–2005 in Thule (High Arctic, 75.9–77.6° N) and during 1998–2005 in Kangerlussuaq (Low Arctic, 66.5–67.5° N). A previously unknown breeding population of Peregrines was located around Thule, at higher latitude than any other known Peregrine population. In addition, much new information on the local Gyrfalcon population was obtained. Information on both species was also collected around Kangerlussuaq, while additional, unpublished data on Gyrfalcons, collected by Mattox in this area during 1972–97, were analyzed to determine whether substantial population change had occurred over time. Data were also collected from Gyrfalcons caught on migration in southwest (Maniitsoq, 2002 and 2004, 65.4° N) and east-central Greenland (Scoresbysund, 2004 and 2005, 70.6° N).

Based on historical information and data collected during this study, the Peregrine population in Thule appeared to be recently established and increasing. Six nest sites were found and several non-breeding adults observed, with each nest site occupied every year after its initial discovery. The Gyrfalcon population at Thule appears to be stable, with 10 nests occupied in 2005. Using data collected in this study and by Mattox (1972–1998), the Kangerlussuaq Gyrfalcon population appeared at best stable, and possibly declining, with a maximum of 22 occupied sites in 1991, and an average of 10 per year during 2001–2005. This apparent decline in Gyrfalcon numbers corresponded with a rapid increase in breeding Peregrines over the same time period, with over 170 currently known nest sites in the same area (though not all occupied in any one year). The ratio of breeding pairs of Peregrines to Gyrfalcons has changed from approximately 1:1 during 1972–1981 to 4:1 in 1991 (Burnham & Mattox 1984, Restani & Mattox 2000). While large-scale surveys for Peregrines have not occurred in Kangerlussuaq since 1997, the ratio of breeding pairs of Peregrines to Gyrfalcons would be greater than 14:1, if the average occupancy rate (84.7%)

documented by Mattox (1998) during 1988–97 was applied to the number of known nest sites today.

Gyrfalcons and Peregrine Falcons laid earlier in Kangerlussuaq than further north in Thule, with a difference of about 2.5 weeks in Gyrfalcons and about one week in Peregrines. This was equivalent to 1.8 and 0.7 days, respectively, per degree of latitude. In Kangerlussuaq, Peregrines laid, on average, nearly six weeks after Gyrfalcons, while in Thule Peregrines laid, on average, only four weeks after Gyrfalcons. Furthermore, Peregrines in Kangerlussuaq had a minimum of two weeks between arrival and egg laying, while those in Thule laid within a week of arriving on territory. The differences in pre-laying interval between areas probably result from the shorter breeding window available for reproduction in the High Arctic of Thule. The apparent short period between arrival and egg laying displayed by female Peregrines in Thule is one of the shortest 'courtship' periods documented for raptors.

Gyrfalcons in the Thule region nested on cliffs nearly twice as high as those used in this region by Peregrines, and also used shorter and deeper nest ledges, which offered more protection from weather. Cliff and nest ledge aspect were almost identical among Peregrine nests in Thule, although for Gyrfalcon nests the difference was approximately 150°, providing further protection from harsh weather. At Kangerlussuaq, where cliffs appeared to be smaller than the largely prevalent seaward cliffs in Thule, Gyrfalcons nested on cliffs nearly one-third the height of those used at Thule, and cliff and nest ledge aspects were similar to one another. Peregrines nested on cliffs twice as high as those used by Gyrfalcons, the opposite to the situation at Thule, while nest ledge and cliff aspect were nearly identical (Wightman & Fuller 2005). Observations in both areas suggest that neither Gyrfalcon nor Peregrine densities were limited by available nest sites: even in the years of highest densities, plenty of surplus, apparently suitable, cliffs were available at sufficient

distance from occupying pairs. It was also not obvious whether one species limited the other through competition for nest sites, but because Gyrfalcons arrived much earlier, they presumably had precedence over Peregrines. Sometimes both species nested on the same cliff, but this resulted in much direct aggression and harassment from Peregrines to Gyrfalcons, and at least in one instance, the concussion and likely ultimate death of an adult female Gyrfalcon from probable Peregrine attack.

Gyrfalcons produced more young per successful territory in Kangerlussuaq than in Thule, but for Peregrines the reverse held. In fact, the nest success of Peregrines at Thule was among the highest recorded anywhere. Peregrines in Thule fed primarily on Dovekies and, to a lesser extent, on Snow Buntings, while Peregrines in Kangerlussuaq fed primarily on passerines, although Rock Ptarmigan were taken in small numbers. Gyrfalcons in Thule fed primarily on Dovekies, although nests far from seabird colonies had remains only of Arctic Hare and Rock Ptarmigan. In Kangerlussuaq, Rock Ptarmigan remains were most frequently observed. In general, Gyrfalcons had a wider diet in terms of species captured: this was probably a result of being larger than Peregrines, for while Gyrfalcons took the same small species as Peregrines (e.g., passerines), they were also able to capture and carry larger prey such as Arctic Hares. Prey appeared to be abundant during young-rearing for both species. However, when Gyrfalcons first arrived on territory, late March to late April in Kangerlussuaq and late April to late May in Thule, prey were probably scarce, with Rock Ptarmigan being the main prey species present in both areas. Shortage of prey at this time of year could have provided a major limitation on the number of Gyrfalcon pairs which settled and attempted to breed.

Among Gyrfalcons, breeding home range size, as studied by radio-tracking during the chick-rearing period, varied over an estimated 140–1,197 km^2 on the basis of 90% minimum convex polygons (MCP), and over an estimated 88–829 km^2 on the basis of 95%

kernels. Breeding adult female Peregrines in Kangerlussuaq and Thule had estimated range sizes of 8–491 km^2 and 15–719 km^2, respectively. In general, Gyrfalcons had home range sizes nearly double those of Peregrines. This is probably a result of Gyrfalcons nesting over a month earlier than Peregrines, when food supplies are more limited and greater travel is required. Furthermore, Peregrines in Thule frequently had larger home ranges than those in Kangerlussuaq, possibly associated with the much higher nesting density in Kangerlussuaq.

Adult female Peregrines in Thule left on outward migration almost a week before Gyrfalcons, and several days before female Peregrines in Kangerlussuaq. Speed of migration among adult females completing outward migration from Thule ranged from 177–269 km per day, while a single female from Kangerlussuaq averaged only 98 km per day. The speed of migration for male and female adult and juvenile Gyrfalcons tagged in Thule varied from 15–99 km per day, while the speeds of two individuals tagged in Kangerlussuaq were 26 and 30 km per day, including incomplete outward migrations from birds whose radios failed. Gyrfalcons tagged in Maniitsoq and Scoresbysund, which completed outward migration, travelled 17–66 km per day and 42–60 km per day, respectively. In both species, individuals that nested further north appeared to travel more quickly during outward migration. Although limited, data from complete and incomplete outward migrations were averaged together. Peregrines from Thule (n = 7) travelled at 213 km per day and Peregrines from Kangerlussuaq (n = 3) at 119 km per day. Gyrfalcons from Thule (n = 13), which only included individuals that travelled a minimum of 500 km, had an average speed of 49 km per day compared to an average 23 km per day for Kangerlussuaq (n = 2). Although the difference was not significant, for both species, individuals from Thule travelled at almost twice the speed of those in Kangerlussuaq, the possible result of rapidly decreasing prey availability in the far north.

Peregrines and Gyrfalcons tagged in Thule travelled south during outward migration, with Peregrines generally travelling south along the Central Flyway in North America and Gyrfalcons using Baffin Bay, the Davis Strait, and both the west coast of Greenland and east coast of Canada. Both species crossed large bodies of water, such as Baffin Bay and the Davis Strait, while Peregrines also crossed the Gulf of Mexico and Caribbean Sea. Gyrfalcons tagged in Kangerlussuaq travelled west to the coast, and then south, while Gyrfalcons tagged in Maniitsoq frequently travelled south along the coast (although several appeared already to be on winter territories and did not move south). Adult Gyrfalcons in Scoresbysund continued south along the coast after being tagged, while several juveniles travelled over the Greenland Sea and Denmark Strait, including one which flew to Iceland. All tagged Peregrines were long-distance obligate migrants and travelled in a roughly southerly direction at a relatively rapid speed. Gyrfalcons were more flexible, with the majority of individuals nesting in the north being obligate migrants at the start of migration, and later becoming more variable in their movements, with some movements possibly weather- or prey-related. These outward migrations were some of the most unusual ever observed among raptors. No consistency was observed among individuals from the same area, and wide ranges existed for travel dates, speed, distance, and direction, to include return migrations back to the breeding grounds within months of initial departure and long-distance reverse migrations throughout the entire migration and winter period.

Breeding adult female Peregrines from Thule wintered in Mexico, Ecuador, Brazil, and Peru. Their outward migration distances were some of the longest ever recorded for raptors, with winter home range sizes ranging from 511 to 1,659 km^2 (90% MCP). Only two complete outward migrations were documented for Gyrfalcons in the High Arctic, one adult female from Thule and one adult male from northwest Ellesmere Island (80.7° N), Canada, wintering in southern Greenland. Gyrfalcons tagged in Kangerlussuaq and Maniitsoq wintered on the southwest coast of Greenland. In Scoresbysund, adult

Gyrfalcons wintered along the southeast coast while one juvenile spent over half the winter period over the Denmark Strait between Greenland and Iceland. Size of winter home ranges varied by coasts; the smallest was an adult female tagged in Kangerlussuaq (357 km^2, using 95% kernel). Gyrfalcons on the east coast had the largest winter home ranges ever documented for raptors (largest was 172,007 km^2, using 95% kernel), and were significantly larger than those on the west coast. Throughout the winter period a wide range of behavior was observed among individuals, with no congruent tendency. While some individuals had range sizes as mentioned above, others appeared to move relatively long distances on an almost daily basis, without specific winter home ranges, or had multiple wintering areas. Furthermore, a juvenile female apparently spent up to one continuous month over the ocean, probably resting on icebergs and feeding on wintering seabirds, with other juveniles and adults showing similar patterns, albeit for only a few weeks at a time.

Peregrines from Thule left their winter home ranges in Central-South America between 10 April and 7 May, while Gyrfalcons left winter home ranges between 7 March and 3 May. In general, falcons travelled more quickly during return migration than during outward migration, with many individuals having the greatest speed of travel shortly before arriving at the breeding areas. Routes of travel were similar during return and outward migration for individual falcons, although return migrations were frequently more direct and took fewer days. For Peregrines, there was a significant relationship between the number of days spent on complete outward migration and the distance travelled. Individuals from Thule (n = 5) spent from 28–70 days on outward migration while return migration ranged from 28–55 days (n = 2). Records of complete migrations were limited for Gyrfalcons, but an adult female from Thule spent 71 days on outward migration and 40 days on return, and an adult male from Ellesmere Island spent 38 days on outward migration and 22 days on return.

No significant genetic or morphometric differences were found between Peregrine populations in Kangerlussuaq and Thule. Hence, the recently established Thule population was probably formed from individuals in the south moving northward. Significant morphometric differences were found between all four areas in which Gyrfalcons were tagged (Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq), although the Scoresbysund and Maniitsoq populations were comprised of both local and migrant individuals. These morphometric findings compare favorably with genetic results from this study published by Johnson *et al.* (2007), although they showed significant differences only between Gyrfalcon populations on the east and west coasts of Greenland, with the Kangerlussuaq and Thule populations being genetically similar to one another.

Carbon dating of accumulated guano deposits from occupied Gyrfalcon nests in Kangerlussuaq and Thule showed the oldest nests to be at least 2,480±40 and 650±70 calendar years old, respectively. Distance from the ice margin was highly correlated with ^{14}C age, with nests farthest from the Greenland Ice Sheet being used the longest. From these dates it is possible to estimate when these areas were initially colonized, which presumably reflected patterns of post-glacial ice retreat. These appear to be the longest-used individual raptor nests ever documented.

Carbon dating indicates, therefore, that Gyrfalcons probably colonized the Kangerlussuaq area approximately 1,800 years earlier than the Thule area, and since the west and east coast populations differed genetically (Johnson *et al.* 2007), the Thule area was probably colonized by movement of individuals from areas further to the southwest, such as Kangerlussuaq. Initially, gene flow would have been asymmetric from south to north, with equilibrium between areas occurring over time as areas reached optimal breeding density. However, Johnson *et al.* (2007) showed that current gene flow is asymmetric, from north to south, the opposite of what might have been expected. One

possible explanation for this is that the southern population is declining, and a source-sink relationship is occurring with the southern population now being augmented with individuals from further north.

Analysis of weather data collected at Thule Air Base adds support to an ever expanding body of evidence showing a general warming climate in the Arctic. In Thule, this has resulted in earlier summers and later autumns, effectively lengthening the potential breeding window for Peregrines and other birds. Further south in Kangerlussuaq, the Peregrine population has also increased, possibly a result of both a warming climate and restrictions placed on the use of organochlorine pesticides in wintering areas. As Peregrine densities have continued to increase in both areas, competition with Gyrfalcons for resources has almost certainly been intensified. While it is difficult to measure the direct effects of the increase in Peregrines, they are clearly exploiting both nest sites and prey similar to those used by Gyrfalcons. Predation by Peregrines on ptarmigan in summer could be especially important if it reduces the numbers of ptarmigan available for Gyrfalcons in the following spring, when other prey are scarce or non-existent.

It is difficult to determine with certainty what effect climate change is having on Peregrines and Gyrfalcons, although it is clear that it is the driving force behind large-scale ecosystem change. Current observed climate change and future predictions suggest that Peregrine densities in Greenland will continue to increase, while at the same time their range will continue to move north into areas previously occupied only by Gyrfalcons. In contrast, adapted to live in the cold Arctic conditions, Gyrfalcons may well retreat from many areas where they now occur. Continued research is needed in order to determine what effects, if any, both a warming climate and an expanding Peregrine population will have on Gyrfalcons in Greenland and throughout the Arctic.

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APPENDICES

Appendix A. Methods used to capture Peregrine Falcons and Gyrfalcons in Greenland.

During the breeding season when falcons were on territory, I deployed a baited bow net or dho-gaza net below the nesting cliff (Bub 1978), baited noose-jacket with weighted drag line (Webster & Beebe 1964), or captured incubating adults using a noose carpet and artificial eggs in the nest scrape. For the latter technique, the falcon's eggs were placed in an insulated protective box safely away from the nest scrape, and then replaced after the falcon was caught and released. After release, falcons soon returned to their eggs, and no negative effects of trapping on reproduction were observed. During migration, at capture and ringing stations I employed a traditional Dutch method of falcon capture using a lure pole/bow net combination (Meredith 1961). Domestic Rock Doves *Columba livia* were used as decoy birds. To minimize the potential for dove-falcon disease transfer, doves were from a "disease-free" isolated flock established for this purpose. Such doves were from artificially incubated eggs and hand-raised young or their progeny and were kept in enclosed aviaries isolated from other birds.

Appendix B. Methods and statistics used for genetic analysis.

Genotyping and sequencing

Eight microsatellite loci originally developed for Peregrine Falcons (Fp13, Fp31, Fp54, Fp79-4, Fp82-2, Fp89, Fp92-1, and Fp107; Nejse *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 base pairs (bp) of cytochrome b (cytb) and tRNAthr 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^{TM} 4.2.2, and verified for accuracy.

Statistical analyses

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 corrections 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 the program GDA (Lewis & Zaykin 2001). 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 vs. 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 vs. 4.00 (Rozas *et al.* 2003).

To investigate population genetic structure with both microsatellite and mitochondrial DNA among sampling locations, pair-wise F_{ST} values were calculated following Weir and Cockerham (1984) , as implemented in Arlequin vs. 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 version 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 visualize 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.

Appendix C. Peregrine population in Greenland, number of individuals, and observed allele frequency distributions by locus and geographic population.

Locus	Allele	Thule	Kangerlussuaq	Maniitsoq	Overall
(*n*)		15	27	5	47
fp13	98	0.133	0.037	-	0.064
	100	0.233	0.241	0.300	0.245
	104	0.100	0.074	-	0.075
	106	0.233	0.222	0.100	0.213
	108	0.067	0.074	0.100	0.075
	110	0.200	0.352	0.500	0.319
	116	0.033	-	-	0.011
(*n*)		15	27	5	47
fp31	150	-	0.056	0.400	0.075
	158	0.133	0.204	0.200	0.181
	160	0.167	0.074	0.100	0.106
	162	0.467	0.556	0.200	0.489
	164	0.200	0.093	0.100	0.128
	166	0.033	0.019	-	0.021
(*n*)		15	26	5	46
fp54	108	0.767	0.865	0.700	0.815
	110	0.100	0.058	-	0.065
	112	0.133	0.077	0.300	0.120
(*n*)		15	24	5	44
fp79-4	150	-	0.021	0.100	0.023
	152	0.033	0.021	0.200	0.046
	154	0.200	0.167	0.200	0.182
	156	0.133	0.167	-	0.136
	158	0.233	0.063	-	0.114
	160	0.133	0.229	0.200	0.193
	162	0.200	0.083	0.200	0.136
	166	0.067	0.021	-	0.034
	168	-	0.042	0.100	0.034
	170	-	0.167	-	0.091
	172	-	0.021	-	0.011
(*n*)		15	27	5	47
fp82-2	143	0.867	0.963	0.900	0.926
	145	0.067	0.037	0.100	0.053
	147	0.067	-	-	0.021

Locus	Allele	Thule	Kangerlussuaq	Maniitsoq	Overall
(*n*)		15	27	5	47
fp89	124	0.167	0.093	-	0.106
	126	0.033	0.037	-	0.032
	132	0.233	0.278	0.600	0.298
	134	-	0.037	-	0.021
	136	0.200	0.167	0.200	0.181
	138	0.067	0.148	0.200	0.128
	140	0.233	0.074	-	0.117
	142	0.033	0	-	0.011
	146	0.033	0.037	-	0.032
	148	-	0.019	-	0.011
	150	-	0.111	-	0.064
(*n*)		15	27	5	47
fp92-1	113	-	0.037	-	0.021
	121	0.067	0.185	0.100	0.138
	123	0.667	0.537	0.300	0.553
	125	0.133	0.019	0.200	0.075
	127	0.100	0.019	0.100	0.053
	131	0.033	0.185	0.300	0.149
	135	-	0.019	-	0.011
(*n*)		15	27	5	47
fp107	211	0.567	0.519	0.400	0.521
	213	0.133	0.148	0.300	0.160
	215	0.200	0.296	0.200	0.255
	217	0.100	0.037	0.100	0.064

Appendix D. Longevity, amount, and location class of data for female Peregrine Falcons tagged with PTTs in Kangerlussuaq and Thule, Greenland.

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	Thule (01)	819	1,240	879 (70.9)	4 (0.32)	19 (1.53)	105 (8.47)
10217	Thule (01)	407	1,270	784 (61.7)	12 (0.95)	5 (3.94)	131 (10.3)
10292	Thule (01)	43	238	151 (63.4)	2 (0.84)	4 (1.68)	22 (9.24)
35234	Thule (02)	6	23	15 (65.2)	0	1 (4.35)	1 (4.35)
35240	Thule (02)	35	107	71 (66.4)	1 (0.94)	5 (4.67)	13 (12.1)
35255	Thule (02)	3	41	27 (65.9)	1 (2.44)	6 (14.6)	5 (12.2)
36014	Thule (03)	48	161	101 (62.7)	2 (1.24)	6 (3.73)	27 (16.8)
36015	Thule (03)	283	406	201 (49.5)	2 (0.49)	5 (1.23)	26 (6.40)
36016	Thule (03)	15	40	22 (55.0)	0	0	1 (2.50)
36017	Thule (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)

Appendix E. Breeding home range size in square kilometers for adult female Peregrine Falcons in Kangerlussuaq and Thule, Greenland, based on multiple calculation methods and location classes of locations received by satellite transmitter.

ID	Yr	Location	90% MCP LC3–0, LC3–1	95% Kernel LC3–0, LC3–1	50% Kernel LC3–0, LC3–1	Number of LC 3-0, respectively (Total 3-1, 3-0)
10212	01	Thule	3,297, 491	1,620, 719	254, 103	0, 9, 34, 156 (43, 199)
	03	Thule	403, 271	427, 224	52, 33	2, 5, 27, 24 (34, 58)
10217	01	Thule	305, 39	531, 88	108, 15	1, 5, 12, 13 (18, 31)
	02	Thule	4,296, 393	1,659, 157	257, 26	8, 14, 62, 152 (84, 236)
35240	02	Thule	3,760, 40	1,504, 64	232, 7	1, 5, 12, 47 (18, 65)
36014	03	Thule	1,272, 8	774, 15	229, 1	1, 5, 26, 60 (32, 92)
36015	03	Thule	5,386, 41	4,531, *	398, 38	2, 0, 4, 47 (6, 53)
36107	03	Thule	5,451, *	5,010, *	483, *	0, 1, 0, 40 (1, 41)
32948	03	Kanger.	2,709, 92	2,524, 255	590, 40	1, 1, 19, 59 (21, 80)
35235	02	Kanger.	1,720, 68	968, 82	200, 9	1, 5, 21, 100 (27, 127)
35236	02	Kanger.	1,931, 47	423, 78	68, 11	2, 10 ,44, 113 (56, 169)
35237	02	Kanger.	2,187, 154	838, 337	150, 72	2, 1, 14, 50 (17, 67)
35238	03	Kanger.	175, 33	158, 52	26, 7	2, 6, 11, 31 (19, 50)
41437	03	Kanger.	752, 62	643, 124	112, 15	0, 5, 26, 78 (31, 109)
41438	03	Kanger.	848, 50	629, 80	123, 7	1, 1, 16, 70 (18, 88)

*Not enough locations for calculation.

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

ID	*t* =total LC 3–0	*n* =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 included, not enough data points for calculation.

Appendix G. Trends in mean monthly temperature over time at Thule Air Base, Greenland, for May through September.

Years[a]	Months	Regression equation[b]	SE of slope (° C)	T	p[c]	r^2	T[d] (° C)
1979–2005	May–Sept.	$y = 0.041x - 80.30$	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	$y = 0.051x - 103.30$	0.043	1.20	0.243	0.056	1.377
1991–2005	May–Sept.	$y = 0.124x - 247.35$	0.054	2.29	0.039	0.288	1.860
	May	$y = 0.129x - 261.62$	0.120	1.07	0.303	0.081	1.935
	June	$y = 0.086x - 168.86$	0.073	1.17	0.263	0.095	1.290
	July	$y = 0.068x - 130.31$	0.081	0.84	0.415	0.052	1.020
	August	$y = 0.229x - 453.09$	0.072	3.17	0.007	0.435	3.435
	September	$y = 0.111x - 222.87$	0.122	0.91	0.380	0.060	1.665
1996–2005	May–Sept.	$y = 0.217x - 432.91$	0.106	2.05	0.075	0.344	2.170
	May	$y = 0.182x - 368.32$	0.232	0.78	0.457	0.071	1.820
	June	$y = -0.018x + 39.07$	0.156	-0.12	0.910	0.002	-0.180
	July	$y = 0.176x - 346.30$	0.172	1.02	0.337	0.115	1.760
	August	$y = 0.388x - 771.95$	0.143	2.70	0.027	0.477	3.880
	September	$y = 0.358x - 717.03$	0.251	1.43	0.192	0.202	3.580

[a]No data for September 1988. 1988 was also excluded when calculating the average of the mean monthly temperatures from May to September.
[b]Regression equation is in the format $y = mx + b$ where y is temperature, m is the slope of the line, x is the year, and b is the y intercept.
[c]p value tested using Holm's Sequential Bonferonni corrections and not found to be significant.
[d]Change in temperature over the period analyzed.

Appendix H. Trends in minimum monthly temperatures over time at Thule Air Base, Greenland, for May through September.

Years[a]	Months	Regression equation[b]	SE of slope (° C)	t	p[c]	r^2	T[d] (° C)
1979–2005	May–Sept.	$y = 0.020x - 47.89$	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	$y = 0.060x - 131.68$	0.060	0.99	0.333	0.039	1.62
1991–2005	May–Sept.	$y = 0.099x - 204.53$	0.079	1.27	0.227	0.110	1.485
	May	$y = 0.125x - 266.08$	0.163	0.46	0.457	0.043	1.875
	June	$y = 0.000x - 4.133$	0.096	-0.00	1.000	0.000	0.000
	July	$y = 0.154x - 308.24$	0.109	1.41	0.181	0.133	2.310
	August	$y = 0.086x - 175.06$	0.133	0.64	0.530	0.031	1.290
	September	$y = 0.129x - 269.15$	0.156	0.83	0.424	0.050	1.935
1996–2005	May–Sept.	$y = 0.130x - 266.87$	0.163	0.80	0.450	0.073	1.300
	May	$y = -0.139x + 262.96$	0.284	-0.49	0.637	0.029	-1.390
	June	$y = 0.012x - 28.448$	0.172	0.07	0.946	0.000	0.120
	July	$y = 0.158x - 316.23$	0.246	0.64	0.540	0.049	1.580
	August	$y = 0.491x - 986.16$	0.230	2.13	0.066	0.362	4.910
	September	$y = 0.127x - 266.51$	0.343	0.37	0.720	0.017	1.270

[a]No data for September 1988. 1988 was also excluded when calculating the average of the minimum monthly 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]p value tested using Holm's Sequential Bonferonni corrections and not found to be significant.
[d]Change in temperature over the period analyzed.

Appendix I. Trends in maximum monthly temperature over time at Thule Air Base, Greenland, for May through September.

Years[a]	Months	Regression equation[b]	SE of slope (° C)	T	p[c]	r^2	T[d] (° C)
1979–2005	May–Sept.	$y = 0.058x - 106.65$	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	$y = 0.043x - 80.01$	0.055	0.78	0.443	0.025	1.161
1991–2005	May–Sept.	$y = 0.157x - 304.08$	0.089	1.76	0.102	0.192	2.355
	May	$y = 0.207x - 408\text{-}27$	0.203	1.02	0.326	0.074	3.105
	June	$y = 0.175x - 337.12$	0.119	1.48	0.164	0.144	2.625
	July	$y = 0.114x - 214.81$	0.088	1.30	0.216	0.115	1.710
	August	$y = 0.189x - 366.66$	0.177	1.07	0.304	0.081	2.835
	September	$y = 0.100x - 193.53$	0.157	0.64	0.536	0.030	1.500
1996–2005	May–Sept.	$y = 0.273x - 535.53$	0.146	1.87	0.098	0.304	4.095
	May	$y = 0.315x - 624.66$	0.315	1.00	0.346	0.111	3.150
	June	$y = -0.061x + 134.44$	0.218	-0.28	0.788	0.010	-0.610
	July	$y = 0.370x - 726.08$	0.162	2.29	0.051	0.396	3.700
	August	$y = 0.85x - 558.14$	0.300	0.95	0.370	0.101	8.500
	September	$y = 0.455x - 903.22$	0.280	1.62	0.144	0.247	4.550

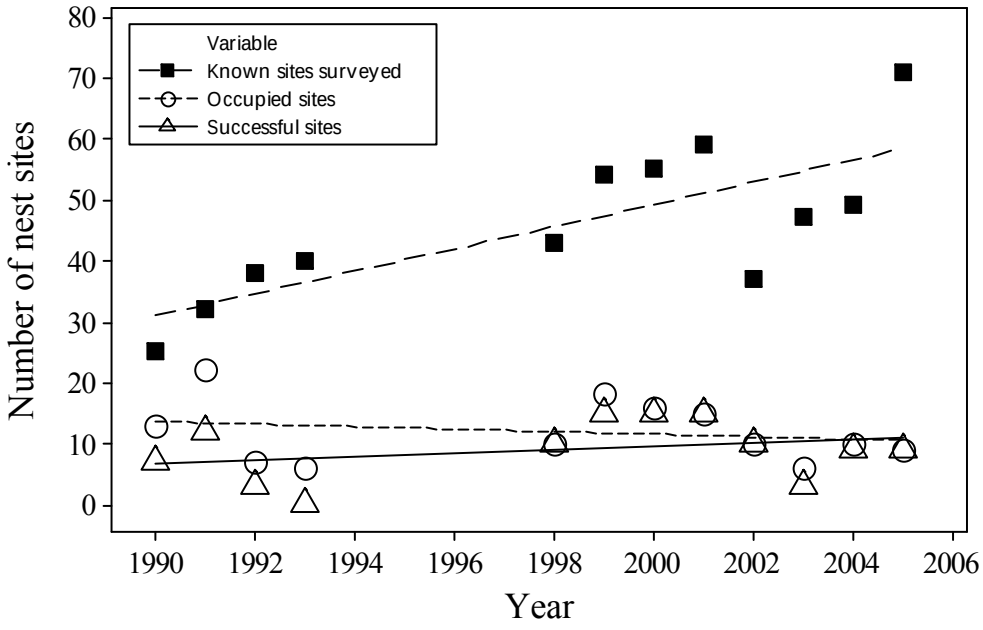
[a]No data for September 1988. 1988 was also excluded when calculating the average of the maximum monthly temperatures from May to September.
[b]Regression equation is in the format $y = mx + b$ where y is temperature, m is the slope of the line, x is the year, and b is the y intercept.
[c]p value tested using Holm's Sequential Bonferonni corrections and not found to be significant.
[d]Change in temperature over the period analyzed.

Appendix J. PTTs placed on adult and juvenile Gyrfalcons from 2000 to 2004 in Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq, Greenland.

Year	Region	ID numbers	No. Of PTTs	Brand	Duty cycle (on/off)	Weight
2000	Maniitsoq	05707	1	NS	?	30g
	Maniitsoq	11988	1	MT	?	30g
2001	Kanger.	10059, 10109, 10112, 10210	4	NS	4 h/ 27 h	30g
	Thule	10095, 10113, 10142	3	NS	4 h/ 27 h	30g
2002	Kanger.	35245, 35251	2	MT	5 h/38 h	30g
	Thule	35241–44, 35246–47, 35252–4, 35256, 36307	11	MT	5 h/38 h	30g
	Thule	35233, 36017	2	MT	10 h/24 h	30g
	Maniitsoq	35248–50, 35257–60, 36318–20	10	MT	5 h/38 h	30g
2003	Kanger.	36905, 41632	2	MT	7 h/106 h	20g
	Thule	35239, 41434–36, 41439–44	10	MT	4 h/ 61 h	20g
2004	Scoresbys.	49761–65, 49767–71	10	MT	4 h/ 61 h	20g

MT = Microwave Telemetry; NS = North Star

Appendix K. The total number of known Gyrfalcon sites surveyed, occupied, and successful from 1990 to 1993 and from 1998 to 2005 in the Kangerlussuaq area, Greenland.



Appendix L. Mean ± sd (*n*) for five measurements taken on adult and sub-adult Gyrfalcons near Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq, Greenland. Measurements are in cm except for mass which is in g.

Location Sex	Body mass	Bill length	Tarsus length	Wing chord	Tail length
Kangerlussuaq					
Female	1614 ± 121 (7)	2.64 ± 0.10 (7)	8.05 ± 0.39 (7)	404 ± 0.28 (7)	220 ± 0.80 (3)
Thule					
Female	1673 ± 94 (5)	2.69 ± 0.03 (4)	8.37 ± 0.18 (4)	411 ± 1.07 (5)	229 ± 0.73 (5)
Male	1305 ± 57 (2)	2.28 ± 0.00 (2)	7.65 ± 0.09 (2)	370 ± 1.34 (2)	197 ± 0.21 (2)
Scoresbysund					
Female	1599 ± 201 (8)	2.65 ± 0.08 (8)	7.94 ± 0.17 (7)	404 ± 0.81 (8)	225 ± 0.72 (8)
Male	1225 ± 61 (3)	2.35 ± 0.02 (3)	7.50 ± 0.25 (3)	364 ± 0.66 (3)	192 ± 0.26 (3)
Maniitsoq					
Female	1536 ± 143 (11)	2.72 ± 0.04 (7)	7.81 ± 0.42 (7)	407 ± 0.75 (7)	223 ± 0.79 (7)
Male	1181 ± 46 (6)	2.41 ± 0.06 (5)	7.44 ± 0.11 (5)	377 ± 0.71 (5)	192 ± 0.37 (5)

Appendix M: Results from t-tests performed on adult female Gyrfalcons captured in Kangerlussuaq, Thule, Scoresbysund, and Maniitsoq, Greenland. P values were tested using Holm's Sequential Bonferroni and none were found to be significant.

Study areas	Body mass	Bill length	Tarsus length	Wing length	Tail length
Kanger. x Thule	T = -0.65 p = 0.54 df = 8	T = -1.08 p = 0.30 df =12	T = -1.49 p = 0.17 df = 11	T = -0.76 p = 0.47 df = 6	T = -0.78 p = 0.46 df =9
Kanger. x Scoresbysund	T = -0.51 p = 0.63 df = 9	T = -0.20 p = 0.85 df = 15	T = -1.78 p = 0.10 df = 15	T = -0.71 p = 0.49 df = 15	T = -0.25 p = 0.80 df = 13
Kanger. x Maniitsoq	T = -1.92 p = 0.07 df = 18	T = -2.27 p = 0.04[a] df = 14	T = 1.86 p = 0.09 df = 11	T = 0.02 p = 0.98 df = 14	T = 0.68 p = 0.51 df = 12
Thule x Scoresbysund	T = -0.89 p = 0.39 df = 10	T = -1.18 p = 0.27 df = 9	T = -3.95 p = 0.01[a] df = 5	T = -1.22 p = 0.27 df = 6	T = -1.07 p = 0.32 df = 8
Thule x Maniitsoq	T = 2.27 p = 0.05[a] df = 11	T = -1.51 p = 0.18 df = 6	T = 3.11 p = 0.02[a] df = 8	T = 0.76 p = 0.48 df = 6	T = 1.43 p = 0.19 df = 9
Scoresbysund x Maniitsoq	T = 0.76 p = 0.46 df = 11	T = -2.22 p = 0.05[a] df = 9	T = 0.79 p = 0.46 df = 7	T = -0.65 p = 0.53 df = 12	T = 0.48 p = 0.64 df = 12

[a]p value tested using Holm's Sequential Bonferroni corrections and not found to be significant.

Appendix N: Results from t-tests performed on adult male Gyrfalcons captured in Thule, Scoresbysund, and Maniitsoq, Greenland.

Study areas	Body mass	Bill length	Tarsus length	Wing length	Tail length
Thule x Scoresbysund	T = 1.50 p = 0.27 df = 2	T = -4.99 p = 0.04[a] df = 2	T = 0.94 p = 0.45 df = 2	T = 0.54 p = 0.69 df = 1	T = 2.10 p = 0.17 df = 2
Thule x Maniitsoq	T = 2.69 p = 0.23 df = 1	T = -4.05 p = 0.03[a] df = 3	T = 2.39 p = 0.10 df = 3	T = -0.68 p = 0.62 df = 1	T = 1.71 p = 0.19 df = 3
Scoresbysund x Maniitsoq	T = -1.05 p = 0.37 df = 3	T = 1.72 p = 0.16 df = 4	T = -0.38 p = 0.74 df = 2	T = 2.44 p = 0.09 df = 4	T = 0.00 p = 1.00 df = 4

[a]p value tested using Holm's Sequential Bonferroni corrections and not found to be significant.

Appendix O: Mean ± sd (*n*) for five measurements taken on juvenile Gyrfalcons captured near Thule, Scoresbysund, and Maniitsoq, Greenland. Measurements are in cm except for mass which is in g.

Location Sex	Body mass	Bill length	Tarsus length	Wing chord	Tail length
Thule					
Female	1595 ± 187 (10)	2.50 ± 0.07 (10)	8.00 ± 0.17 (10)	41.6 ± 1.48 (10)	23.2 ± 1.52 (10)
Male	1217 ± 201 (9)	2.22 ± 0.09 (9)	7.60 ± 0.09 (9)	373 ± 1.38 (9)	208 ± 0.43 (9)
Scoresbysund					
Female	1521 ± 128 (54)	2.44 ± 0.07 (8)	7.86 ± 0.42 (54)	41.0 ± 0.83 (54)	22.6 ± 0.63 (54)
Male	1214 ± 105 (53)	2.20 ± 0.09 (53)	7.42 ± 0.22 (53)	371 ± 1.02 (53)	201 ± 0.71 (53)
Maniitsoq					
Female	1360 ± 186 (13)	2.54 ± 0.07 (6)	7.75 ± 0.15 (6)	41.5 ± 0.84 (6)	21.8 ± 1.75 (6)
Male	1059 ± 77 (6)	2.24 (1)	7.15 (1)	373 (1)	200 (1)

Appendix P: Results from t-tests performed on juvenile female Gyrfalcons captured in Thule, Scoresbysund, and Maniitsoq, Greenland, from 2002 to 2005.

Study areas	Body mass	Bill length	Tarsus length	Wing length	Tail length
Thule x Scoresbysund	T = 1.19 p = 0.26 df = 10	T = 2.66 p = 0.04[a] df = 13	T = 1.73 p = 0.09 df = 33	T = 1.24 p = 0.24 df = 10	T = 1.17 p = 0.27 df = 9
Thule x Maniitsoq	T = -3.00 p = 0.007[a] df = 19	T = 1.24 p = 0.24 df = 10	T = -2.98 p = 0.01[a] df = 11	T = -0.25 p = 0.80 df = 13	T = -1.68 p = 0.13 df = 9
Scoresbysund x Maniitsoq	T = -2.97 p = 0.01[a] df = 14	T = 3.16 p = 0.02[a] df = 6	T = -1.30 p = 0.21 df = 15	T = 1.25 p = 0.26 df = 6	T = -1.21 p = 0.28 df = 5

[a]p value tested using Holm's Sequential Bonferroni corrections and not found to be significant.

Appendix Q: Results from t-tests performed on juvenile male Gyrfalcons captured in Thule, Scoresbysund, and Maniitsoq, Greenland, from 2002 to 2005.

Study areas	Body mass	Bill length	Tarsus length	Wing length	Tail length
Thule x Scoresbysund	T = 0.04 p = 0.97 df = 8	T = 0.53 p = 0.61 df = 11	T = 4.30 p = 0.000 df = 30	T = 0.49 p = 0.63 df = 9	T = 4.13 p = 0.001 df = 16
Thule x Maniitsoq	T = -2.13 p = 0.06 df = 11	na	na	na	na
Scoresbysund x Maniitsoq	T = -4.43 p = 0.003 df = 7	na	na	na	na

na–not enough data, only one sample for Maniitsoq.

Appendix R: Data from PTTs attached to Gyrfalcons in Kangerlussuaq, Greenland, in 2001 and 2002.

ID	Attachment location (year)	Life of unit (days)	Total locations LC 3–Z	Total LC 3–0 (%)	Total LC 3 (%)	Total LC 2 (%)	Total LC 1 (%)
10112	Kanger. (01)	100	472	362 (76.7)	30 (6.4)	63 (13.3)	136 (28.8)
35245	Kanger. (02)	317	990	557 (56.3)	5 (0.5)	19 (1.9)	117 (11.8)
35251	Kanger. (02)	14	53	31 (58.5)	1 (1.9)	2 (3.8)	10 (18.9)
41632	Kanger. (02)	103	276	146 (52.9)	0	2 (0.7)	7 (2.5)

Appendix S: Data from PTTs attached to Gyrfalcons in Thule, Greenland, from 2001 to 2003.

ID	Attachment location (year)	Life of unit (days)	Total locations LC 3–Z	Total LC 3–0 (%)	Total LC 3 (%)	Total LC 2 (%)	Total LC 1 (%)
10095	Thule (01)	81	501	396 (79.0)	13 (2.6)	49 (9.8)	145
10142	Thule (01)	51	328	249 (75.9)	9 (2.7)	40 (12.2)	96 (29.3)
35233	Thule (02)	5	9	9 (100.0)	0	0	6 (6.7)
35239	Thule (02)	25	60	51 (0.85)	0	7 (11.7)	14 (23.3)
35241	Thule (02)	43	203	145 (71.4)	1 (0.5)	9 (4.4)	42 (20.7)
35242	Thule (02)	30	158	112 (70.9)	1 (0.6)	3 (1.9)	32 (20.3)
35243	Thule (02)	388	1,453	839 (57.7)	11 (0.8)	35 (2.4)	205 (14)
35244	Thule (02)	15	58	41 (70.7)	1 (1.7)	12 (20.7)	15 (25.9)
35246	Thule (02)	13	74	58 (78.4)	0	1 (1.6)	20 (27.0)
35247	Thule (02)	51	268	189 (70.5)	6 (2.2)	12 (4.5)	49 (18.3)
35252	Thule (02)	101	561	369 (65.8)	3 (0.5)	19 (3.4)	91 (16.2)
35253	Thule (02)	86	430	311 (72.3)	3 (0.7)	12 (2.8)	86 (20.0)
35254	Thule (02)	26	133	91 (68.4)	3 (2.3)	5 (3.8)	35 (26.3)
35256	Thule (02)	8	39	27 (69.2)	0	5 (12.8)	11 (28.2)
36317	Thule (02)	24	114	87 (76.3)	1 (0.9)	8 (7.0)	16 (14.0)
41434	Thule (03)	37	122	55 (45.1)	0	1 (0.8)	3 (2.6)
41435	Thule (03)	14	50	27 (54.0)	1 (2.0)	1 (2.0)	4 (8.0)
41436	Thule (03)	23	61	28 (45.9)	0	0	1 (1.6)
41439	Thule (03)	5	16	7 (43.8)	0	1 (1.0)	3 (2.0)
41440	Thule (03)	38	126	126 (69.0)	1 (0.8)	9 (7.1)	21 (16.7)
41441	Thule (03)	19	53	30 (56.6)	0	2 (3.8)	14 (26.4)
41442	Thule (03)	33	80	47 (58.8)	1 (1.3)	1 (1.3)	17 (21.3)
41443	Thule (03)	20	76	54 (71.1)	1 (1.3)	5 (6.6)	13 (17.1)
41444	Thule (03)	139	436	245 (56.2)	4 (0.9)	9 (2.1)	79 (18.1)

Appendix T: Data from PTTs attached to Gyrfalcons in Scoresbysund, Greenland, in 2004.

ID	Attachment location (year)	Life of unit (days)	Total locations LC 3–Z	Total LC 3–0 (%)	Total LC 3 (%)	Total LC 2 (%)	Total LC 1 (%)
49761	Scoresbysund (04)	33	49	30 (61.2)	0	2 (4.1)	8 (16.3)
49762	Scoresbysund (04)	248	323	180 (55.7)	1 (0.3)	5 (1.5)	38 (11.8)
49764	Scoresbysund (04)	190	199	113 (56.8)	1 (0.5)	5 (2.5)	16 (8.0)
48765	Scoresbysund (04)	12	21	8 (38.1)	0	1 (4.8)	0
49767	Scoresbysund (04)	12	38	29 (76.3)	1 (2.6)	3 (7.9)	11 (28.9)
49768	Scoresbysund (04)	193	369	218 (59.1)	3 (0.8)	14 (3.8)	63 (17.1)
49769	Scoresbysund (04)	25	72	49 (68.1)	1 (1.4)	3 (4.2)	15 (20.8)
49771	Scoresbysund (04)	284	352	215 (61.1)	1 (0.3)	4 (1.1)	58 (16.5)

Appendix U: Data from PTTs attached to Gyrfalcons in Maniitsoq, Greenland, in 2000 and 2002.

ID	Attachment location (year)	Life of unit (days)	Total locations LC 3–Z	Total LC 3–0 (%)	Total LC 3 (%)	Total LC 2 (%)	Total LC 1 (%)
5707	Maniitsoq (00)	194	167	116 (69.5)	9 (5.4)	20 (12.0)	39 (23.4)
10210	Replaced 11988	69	285	216 (75.8)	6 (2.1)	41 (14.4)	69 (24.2)
11988	Maniitsoq (00)	266	626	366 (58.5)	11 (1.8)	13 (2.1)	51 (8.1)
35248	Maniitsoq (02)	392	1,726	1025 (59.4)	11 (0.6)	55 (3.2)	243
35249	Maniitsoq (02)	329	1,141	603 (52.8)	7 (0.6)	36 (3.2)	178
35250	Maniitsoq (02)	30	101	50 (49.5)	1 (1.0)	3 (3.0)	8 (7.9)
35257	Maniitsoq (02)	36	150	102 (68.0)	3 (2.0)	2 (1.3)	19 (12.7)
35258	Maniitsoq (02)	212	628	356 (56.7)	8 (1.3)	12 (1.9)	77 (12.3)
35259	Maniitsoq (02)	87	347	212 (61.1)	4 (1.2)	7 (2.0)	35 (10.1)
35260	Maniitsoq (02)	26	101	41 (62.4)	1 (1.0)	5 (5.0)	20 (19.8)
36318	Maniitsoq (02)	185	929	621 (66.8)	10 (1.1)	26 (2.8)	153(16.5)
36319	Maniitsoq (02)	37	139	90 (64.7)	1 (0.7)	4 (2.9)	21 (15.1)
36320	Maniitsoq (02)	8	50	36 (72.0)	3 (6.0)	4 (8.0)	12 (24.0)

Appendix V. Date from outward migrations by Gyrfalcons tagged at the nest site with PTTs in 2001 and 2002 in Kangerlussuaq, Greenland. Only individuals encompassing ≥5 days of travel are included, individual in bold completed outward migration from their breeding home range to winter home range (distances are given as Great Circle Distances).

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 traveled per day[a] (km)	Location classes used for daily calculations[b] (LC 3, 2, 1, 0)
10112/ad♂	27 Aug 01–15 Oct 01	805	16	50	35 (70.0)	1–102	12, 10, 10, 2
35245/ad♀	12 Aug 02–24 Aug 02	391	30	13	9 (69.2)	2–74	0, 0, 3, 4

[a]Range of distances traveled per day, see Chapter 2, Methods, for further description.
[b]Locations for start date of migration not included, if individuals completed outward migration final location also was not included.

Appendix W. Data from outward migrations by Gyrfalcons tagged with PTTs from 2001 to 2003 in Thule, Greenland. Included individuals were either tagged at the nesting site or at a ringing station. Only individuals encompassing ≥5 days of travel are included, the individual in bold completed outward migration from its breeding home range to winter home range (distances are given as Great Circle Distances).

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 traveled per day (km)	Location classes used for daily locations[a] (LC 3, 2, 1, 0)
10095/ad♀	9 Sep 01–7 Oct 01	987	34	29	19 (65.5)	4–102	5, 6, 6, 1
35239/ju♀	21 Sep 03–3 Oct 03	177	14	13	4 (30.8)	3–34	0, 3, 0, 0
35241/ju♂	16 Oct 02–23 Oct 02	791	99	8	7 (87.5)	3–217	0, 3, 2, 1
35242/ju♂	22 Sep 02–10 Oct 02	1,190	63	19	14 (68.4)	0–294	0, 2, 10, 1
35243/ad♀	**28 Sep 02–7 Dec 02**	4,234	60	71	43 (60.6)	1–388	2, 12, 12, 15
	28 Sep 03–9 Oct 03	643	54	12	8 (66.7)	4–184	1, 0, 2, 4
35244/ju♂	17 Sep 02–28 Sep 02	329	27	12	7 (58.3)	3–49	1, 4, 0, 1
35247/ju♂	15 Sep 02–18 Oct 02	1,361	40	34	24 (70.6)	1–200	1, 6, 10, 6
35249/ad♀	19 Aug 03–4 Sep 03	833	31	27	9 (33.3)	2–130	1, 1, 5, 1
35252/ad♀	21 Sep 02–19 Nov 02	3,495	58	60	32 (53.3)	1–252	1, 6, 17, 7
35253/ad♀	4 Oct 02–26 Oct 02	644	28	23	17 (73.9)	2–72	0, 2, 10, 4
41434/ju♀	19 Sep 03–15 Oct 03	681	32	21	12 (57.1)	6–82	0, 1, 3, 7
41440/ju♀	20 Sep 03–21 Oct 03	1,490	47	32	15 (46.9)	13–134	1, 7, 5, 1
41442/ad♂	5 Oct 03–13 Oct 03	647	72	9	4 (44.4)	47–127	1, 1, 1, 0
41443/ju♀	18 Sep 03–28 Sep 03	410	37	11	5 (45.5)	19–62	1, 1, 2, 0
41444/ad♀	27 Sep 03–26 Jan 04	1,794	15	122	42 (34.4)	0–92	2, 4, 28, 7

[a]Range of distances traveled per day, see Chapter 2, Methods, for further description.
[b]Locations for start date of migration not included, if individuals completed outward migration final location also was not included.

Appendix X. Data from Gyrfalcons with incomplete outward migrations that were tagged with PTTs at a ringing station in Scoresbysund, Greenland, in the autumn of 2004. Only individuals with ≥5 days of travel were included, individuals in bold completed outward migration (distances are given as Great Circle Distances).

PTT ID, age, and sex	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 traveled per day[a] (km)	Location classes used for daily locations[b] (LC 3, 2, 1, 0)
49761/ju♂	13 Oct 04–14 Nov 04	1,342	41	33	12 (36.4)	6–389	0, 2, 7, 2
49762/ad♂	22 Sep 04–25 Oct 04	2,050	60	34	12 (35.3)	2–119	0, 0, 4, 6
49764/ad♂	19 Sep 04–28 Oct 04	1,664	42	40	10 (25.0)	7–195	0, 0, 6, 2
49765/ad♂	5 Oct 04–16 Oct 04	53	4	12	2 (16.7)	na	0, 1, 0, 0
49767/ju♀	17 Oct 04–28 Oct 04	193	39	12	5 (41.7)	2–35	0, 2, 1, 1
49769/ju♀	18 Oct 04–11 Nov 04	824	33	25	11 (44.0)	6–68	1, 1, 6, 2
49771/ad♀	8 Oct 04–28 Oct 04	978	47	21	6 (28.6)	7–89	0, 0, 3, 1

[a]Range of distances traveled per day, see Chapter 2, Methods, for further description.
[b]Locations for start date of migration not included, if individuals completed outward migration final location also was not included.

Appendix Y. Data from Gyrfalcons with incomplete outward migrations that were tagged with PTTs at a ringing station in Maniitsoq, Greenland, in the autumn of 2000 and 2002. Only individuals with ≥5 days of travel were included, individuals in bold completed outward migration (distances are given as Great Circle Distances).

PTT ID, age, and sex	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 traveled per day[a] (km)	Location classes used for daily locations[b] (LC 3, 2, 1, 0)
11988/ad♀	18 Oct 00–27 Oct 00	664	66	10	4 (40.0)	6–135	0, 0, 1, 1
35248/ad♂	19 Oct 02–24 Oct 02	254	42	6	4 (66.7)	34–64	0, 1, 0, 1
35249/ad♀	11 Oct 02–5 Nov 02	447	17	26	17 (65.4)	0–112	0, 2, 9, 4
35250/ad♂	13 Oct 02–11 Nov 02	1,249	42	30	17 (56.7)	6–184	1, 2, 3, 10
35257/ad♀	9 Oct 02–13 Nov 02	678	19	36	25 (69.4)	1–120	3, 1, 12, 8
35260/ad♀	19 Oct 02–13 Nov 02	360	19	26	17 (65.4)	0–69	1, 4, 7, 4
36319/ad♀	1 Oct 02–14 Oct 02	655	47	14	9 (64.3)	3–113	0, 1, 4, 2

[a]Range of distances traveled per day, see Chapter 2, Methods, for further description.
[b]Locations for start date of migration not included, if individuals completed outward migration final location also was not included.

Appendix Z. Complete outward migration data from an adult male Gyrfalcon which likely bred in northwest Ellesmere Island, Canada during 2003 (distances given as Great Circle Distances).

PTT ID, age, and sex	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 traveled per day[a] (km)	Location classes used for daily locations[b] (LC 3, 2, 1, 0)
35248/ad♂	7 Oct 03–13 Nov 03	3,137	83	38	18 (47.2)	1–342	0, 1, 7, 8

[a]Range of distances traveled per day, see Chapter 2, Methods, for further description.
[b]Locations for start and end date of migration not included.

Appendix AA. T-tests results that show a significant difference between winter home range sizes of Gyrfalcons on the west and east coast of Greenland.

	90% MCP	95% kernel	50% kernel
West coast x east coast	T = -7.18 p = 0.000 df = 8	T = -6.88 p = 0.000 df = 8	T = -6.28 p = 0.000 df = 8