Gyrfalcon *Falco rusticolus* post-glacial colonization and extreme long-term use of nest-sites in Greenland

KURT K. BURNHAM,[1,2*†] WILLIAM A. BURNHAM[2‡] & IAN NEWTON[3]
[1]*Department of Zoology, Edward Grey Institute, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*
[2]*The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709, USA*
[3]*Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon OX10 8BB, UK*

Gyrfalcons *Falco rusticolus* use the same nest-sites over long periods of time, and in the cold dry climate of Greenland, guano and other nest debris decay slowly. Nineteen guano samples and three feathers were collected from 13 Gyrfalcon nests with stratified faecal accumulation in central-west and northwest Greenland. Samples were ^{14}C dated, with the oldest guano sample dating to *c.* 2740–2360 calendar years (cal yr) before present (BP) and three others were probably > 1000 cal yr BP. Feather samples ranged from 670 to 60 cal yr BP. Although the estimated age of material was correlated with sample depth, both sample depth and guano thickness gave a much less reliable prediction of sample age than use of radiocarbon dating on which the margin of error was less. Older samples were obtained from sites farther from the current Greenland Ice Sheet and at higher elevations, while younger samples were closer to the current ice sheet and at lower elevations. Values for δ^{13}C showed that Gyrfalcons nesting farther from the Greenland Ice Sheet had a more marine diet, whereas those nesting closer to the ice sheet (= further inland) fed on a more terrestrial diet. The duration of nest-site use by Gyrfalcons is a probable indicator of both the time at which colonization occurred and the palaeoenvironmental conditions and patterns of glacial retreat. Nowhere before has such extreme long-term to present use of raptor nest-sites been documented.

Keywords: carbon dating, guano, palaeoenvironmental conditions, δ^{13}C.

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, Peregrine Falcons *Falco peregrinus* disappeared from large areas of North America and Europe during the 1960s as a result of organochlorine pesticide use. Many years later, following the restriction in the use of these chemicals, released or recolonizing Peregrines usually reoccupied former territories first, frequently re-using the same nest ledges their predecessors did (Newton 1979, Ratcliffe 1993, Oakleaf 2003).

Gyrfalcons *Falco rusticolus* 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 weather (Cade 1960). Gyrfalcons usually nest on cliff ledges overhung by rock, in potholes, or in sheltered stick-nests built by Northern Ravens *Corvus corax* (Cade 1960, Burnham & Mattox 1984). These nesting situations provide protection from falling rock and the extreme weather conditions often found 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

*Corresponding author.
Email: kburnham@higharctic.org

[†]Present address: High Arctic Institute, 603 10th Avenue, Orion, IL 61273, USA.

[‡]Deceased.

are used long-term by Gyrfalcons (Burnham & Mattox 1984). Gyrfalcons and Northern Ravens do not seem to alternate the use of the same nest-site from year to year in Greenland. At re-used sites, faecal accumulation frequently occurs where Gyrfalcons roost and nest. Deposited over periods of years, the stratified accumulation of guano can become greater than 1.5 m thick in locations protected from erosion and where dry and cold environmental conditions enhance preservation (Fig. 1). There are many such nest-sites throughout ice-free areas of Greenland.

The Greenland Ice Sheet covers 82% of the land mass of Greenland (Ohmura *et al.* 1999), and ice-free land occurs only along the periphery of the island. 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 palaeoenvironments 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, particularly valley bottoms, had the thickest covering of ice and was exposed last (Fristrup 1966). We therefore hypothesized that guano in Gyrfalcon nests at lower elevations and closer to the current ice sheet would have accumulated over shorter periods than that at nests at higher elevations and further from the current Greenland Ice Sheet. To investigate this question we sampled and radiocarbon dated guano from Gyrfalcon nest-sites in two areas, in Kangerlussuaq, central-west
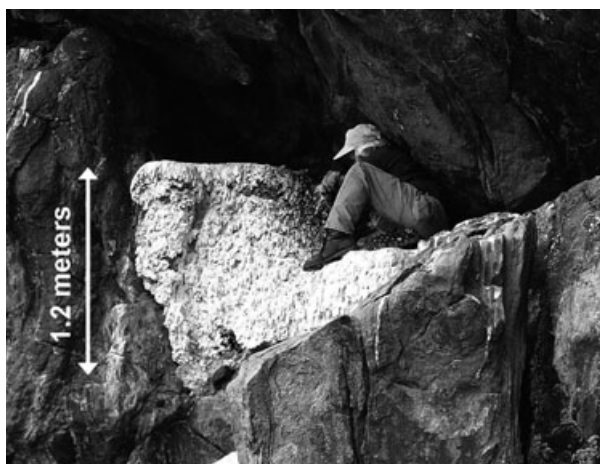
Figure 1. Gyrfalcon nest-site 123 being sampled for radiocarbon dating in Kangerlussuaq, central-west Greenland, with a ^{14}C age of 1160–920 cal yr BP.

(66.50–67.00 °N), and Thule, northwest (76.25–77.17 °N), Greenland. These study areas were separated by about 9° latitude and 1100 km.

Study areas

The Kangerlussuaq study area is located at the head of a 175-km-long fjord and about 25 km from the current ice sheet margin. The Low Arctic tundra landscape in this area was sculpted by glaciation, with rolling hills and valleys, moraines and lakes, dissected by several meltwater rivers, and dominated mainly by shrubs up to 2 m in height. Primary prey species for Gyrfalcons in Kangerlussuaq include both Rock Ptarmigan *Lagopus mutus* 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's glacial history (Ten Brink & Weidick 1974, Eisner *et al.* 1995). From projected rates of deglaciation (see below), we can estimate that some Gyrfalcon nest-sites may have been uncovered c. 6500–6000 years before the present (yr BP).

The Thule study area is centred around Pituffik/Thule Air Base and the current ice sheet margin lies up to 26 km inland from the sea, but it reaches the sea at several locations. The environment is High Arctic with an appearance of recent deglaciation, and sparsely vegetated prostrate growing herbs and shrubs. In this area, Gyrfalcons fed primarily on Little Auks *Alle alle*, Rock Ptarmigans and Arctic Hares, with seabirds, waterfowl, and passerines taken in smaller numbers (Burnham 2008). 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 consistent use of existing Gyrfalcon nest-sites may not have occurred until 1350 yr BP or more recently (see below).

METHODS

Gyrfalcon nest-sites are distributed widely and irregularly throughout the two study areas and ice-free Greenland as a whole. 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 exact 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 centimetres of stratified guano, probably representing accumulation over decades or longer. Notes were made of sample depth (cm), cliff height (m), and nest ledge elevation (meters above sea level, m asl). All nests sampled had been occupied by Gyrfalcons within the past 25 years (Table 1).

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 centimetres of faecal build-up, we 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, FL, USA, using either the conventional radiometric technique (samples > 30 g) or accelerator mass spectrometry (AMS) (samples < 30 g). Guano samples were pre-treated using an 'acid wash', and 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 Inc. 2005). AMS results were obtained by the reduction of sample carbon to graphite (100% C) along with standards and backgrounds (Beta Analytic Inc. 2005). 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 Inc. 2005). Calibrated results provide both a maximum and minimum age for each sample in calendar years (cal yr) before present (BP), with a 95% confidence that the actual age falls within this range. 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, 19 bulk guano samples and three feathers were collected from 13 Gyrfalcon nest-sites. Five guano samples and one feather were from four nests in Thule, and 14 guano samples and two feathers from nine nests in Kangerlussuaq. To test for relationships between age of guano samples and nest variables (using JMP IN, v. 4, SAS Institute Inc., Cary, NC, USA), we 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 guano sample was from nest-site 087 in Kangerlussuaq and was dated 2740–2360 cal yr BP (Table 1). Three nests in Kangerlussuaq showed evidence of occupation > 1000 cal yr BP, with the most recent nest being first occupied from 650 to 520 cal yr BP. In Thule, the oldest nest was between 690 and 530 cal yr BP, with two nests indicating use only within the past 50 years (Table 1). Sites in Kangerlussuaq seem to have been used approximately 1800–2000 years longer than those further north in Thule. Sites with multiple samples collected showed an increase in ^{14}C age with sample depth (Table 1). The three analyzed Gyrfalcon feathers were between 670 and 60 cal yr BP. Sample

Table 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. No specific nest locations are given in order to protect against possible collection of eggs and chicks.

| Nest-site	Beta Analytic sample #	Sample depth (cm)	Cliff height (m)	Nest elevation (m asl)	Distance from ice margin (km)	$\delta^{13}C$ (‰) (PDB)[c]	Last used	Conventional ^{14}C age (yr BP ± 1σ)	Calibrated age range (cal yr BP ± 2σ)
Kangerlussuaq, central-west Greenland									
019	195586	20–25	15	355	9	−22.7	1992	790 ± 60	790–650
053A	191125	30–35	15	304	11	−22.4	1991	1290 ± 50	1300–1080
053B	191126	15–20	15	304	11	−22.4	1991	1090 ± 80	1180–900, 850–810
053C[a]	191295	15	15	304	11	−22.5	1991	320 ± 30	470–300
068A	191127	15–20	152	55	14	−22.9	2000	570 ± 50	650–520
068B	195576	10–15	152	55	14	−20.7	2000	240 ± 60	450–260, 220–140, 30–0
082	195577	25–30	76	441	5	−23.2	1999	830 ± 70	920–660
087A	168839	30–35	46	365	54	−21.9	2002	2480 ± 40	2740–2360
087B	168840	25–30	46	365	54	−20.9	2002	350 ± 40	500–300
087C	168838	0–3	46	365	54	−24.2	2002	105.09 ± 0.66 pMC[b]	outside calibration range[b]
087D[a]	168837	15	46	365	54	−21.3	2002	170 ± 40	300–60, 40–0
123	195578	20–25	46	258	62	−21.1	~1985	1090 ± 60	1160–920
163	195587	100–110	152	395	72	−20.8	2003	960 ± 60	970–740
170	195579	15–20	24	103	28	−21.3	2004	690 ± 60	710–550
201A	195580	35–40	23	200	78	−17.8	2000	1430 ± 70	1480–1470, 1430–1250
201B	195581	10–15	23	200	78	−21.3	2000	820 ± 60	910–660
Thule, northwest Greenland									
500A	195583	5–8	46	152	14	−23.3	2003	113.34 ± 0.71 pMC[b]	outside calibration range[b]
500B	195582	3–6	46	152	14	−21.2	2003	122.08 ± 0.73 pMC[b]	outside calibration range[b]
501	195584	2–4	117	122	2	−23.2	2004	115.29 ± 0.66 pMC[b]	outside calibration range[b]
502	195585	15–20	23	152	9	−20.2	2004	640 ± 50	670–540
503A	191124	20–25	76	304	17	−19.1	2004	650 ± 70	690–530
503B[a]	191348	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 was used as conventional ^{14}C age, while Calibrated Age Range is outside calibration range.
[c]PD belemnite.

087D had two possible calibrated age ranges, 300–60 and 40–0 cal yr BP, and the older range was most likely accurate based on other samples from the same nest and sample depth. While the bulk samples of guano represent a number of years of site use, the feathers were from a precise moment in time.

The maximum conventional ^{14}C age for each individual nest was significantly correlated with the current distance from the ice margin ($r_s = 0.56$, $P < 0.05$, $n = 13$; Fig. 2), nest elevation ($r_s = 0.61$, $P < 0.05$, $n = 13$; Fig. 3), and sample depth ($r_s = 0.88$, $P < 0.0001$, $n = 13$; Fig. 4). While sample depth could be used as a predictor of ^{14}C age, the margin of error would be much greater than if using radiocarbon dating directly (e.g. 087A & 163, Fig. 4).
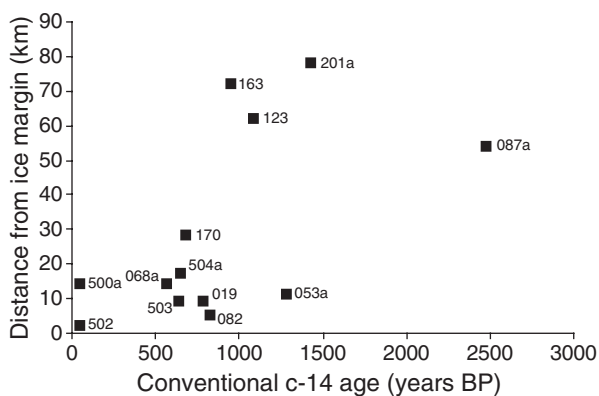
Figure 2. Relationship between maximum ^{14}C age and nest-site distance from current ice margin.
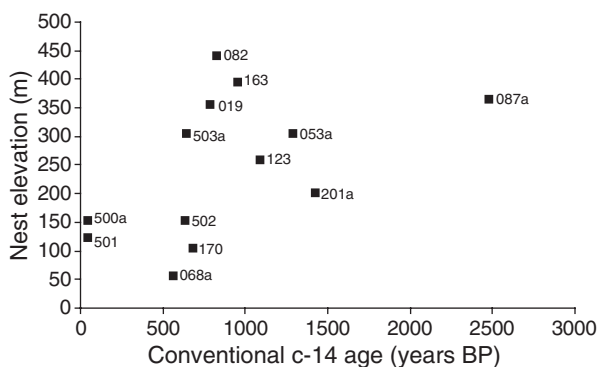
Figure 3. Relationship between maximum ^{14}C age and nest-site elevation (m above sea level).
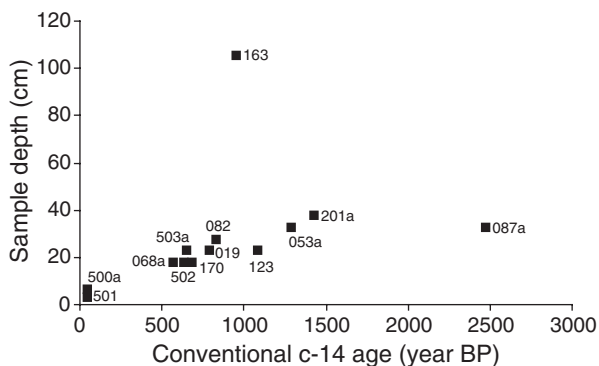
Figure 4. Relationship between maximum ^{14}C age and sample depth.

In general, organisms from marine food chains or animals that feed on them have less negative δ^{13}C values, while more negative δ^{13}C values are typically associated with terrestrial ecosystems (Rounick & Winterbourn 1986, Angerbjörn *et al.* 1994). The δ^{13}C values from the oldest guano sample from each nest varied slightly from a median of −21.9‰ ($n = 9$, $\sigma^2 = 2.7$) for Kangerlussuaq to −21.5‰ ($n = 4$, $\sigma^2 = 4.5$) for Thule, with no statistical difference between the two areas. A significant correlation exists between δ^{13}C for the oldest guano sample from each nest and current distance to the Greenland Ice Sheet ($r_s = 0.63$, $P < 0.05$, $n = 13$), with less negative values being associated with nests farther from the current ice sheet (Fig. 5).

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 1800–2000 years earlier than those further north in Thule, probably an effect of earlier deglaciation and a more stable and warmer climate 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 *Uria lomvia* (Gaston & Donaldson 1995), and Adelie Penguins *Pygoscelis adeliae* (Emslie *et al.* 2007), for which radiocarbon age has been calculated using solidified stomach oil deposits, peat moss deposits, and bone and feather samples from moulting sites, respectively, and minimum dates for the establishment or colonization of bird colonies have been given (∼ 34 000 yr BP, 1500–3800 yr BP, and > 44 000 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 found 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 *c.* 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 there (Salomonsen 1950) 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
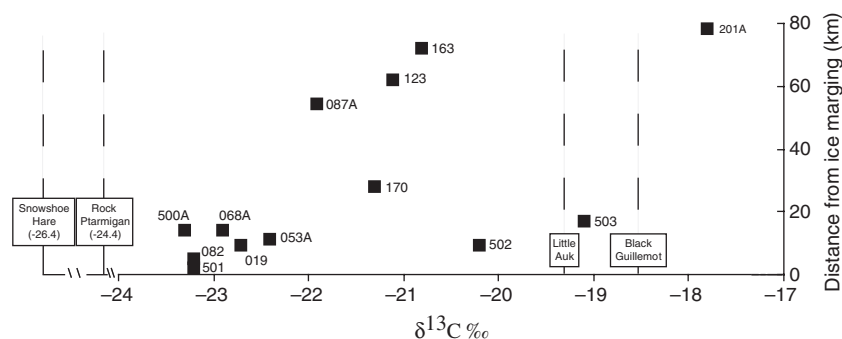
Figure 5. Relationship between δ^{13}C and distance from current ice margin. Frequent prey of Gyrfalcons shown with associated δ^{13}C value. δ^{13}C values for Snowshoe Hare *Lepus americanus* (substituted for Arctic Hare as no values were found in the literature for Arctic Hare), Rock Ptarmigan, Little Auk, and Black Guillemot are from Roth *et al.* (2007), Ricca *et al.* (2007), and Hobson *et al.* (2002).

than do falcons. Gulls nest colonially and sites cannot be confused with falcon nests. Except for Iceland Gulls *Larus glaucoides* and Glaucous Gulls *Larus 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 palaeoenvironment 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 a site offering good 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 likelihood 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 ($\sim$ 15 000 yr BP), but with fre-

quent re-expansions (Ten Brink & Weidick 1974, Funder 1989) (Fig. 6). A slow retreat of the ice sheet (1 km/100 years) occurred from *c.* 15 000 to 10 000 yr BP followed by an oscillatory but more rapid retreat (3 km/100 years) of nearly 100 km from *c.* 9500 to 6500 yr BP (Ten Brink & Weidick 1974). By 6000 yr BP the ice sheet had reached its present position, although between 5- and 10-km re-advances occurred from *c.* 4800 to 4000 and from 2500 to 2000 yr BP (Ten Brink & Weidick 1974) (Fig. 6). At that time the sea level was nearly at that of the present day. Eisner *et al.* (1995) reported that Kangerlussuaq experienced a 'climatic optimum' from *c.* 4400 to 3400 yr BP and that a climatically stable period is believed to have also encompassed the period from 2000 to 1200 yr BP (Fig. 6). Based on lichenometry, the period from *c.* 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).

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 *c.* 4800 and 4000 and from 2500 to 2000 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 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 < 50 km from the ice edge and, based on the projected rate of ice sheet retreat, these nest-sites were ice-free by 6500–6000 yr BP. That does not preclude, however, the possibility of isolated snow banks and glaciers covering nest-sites,
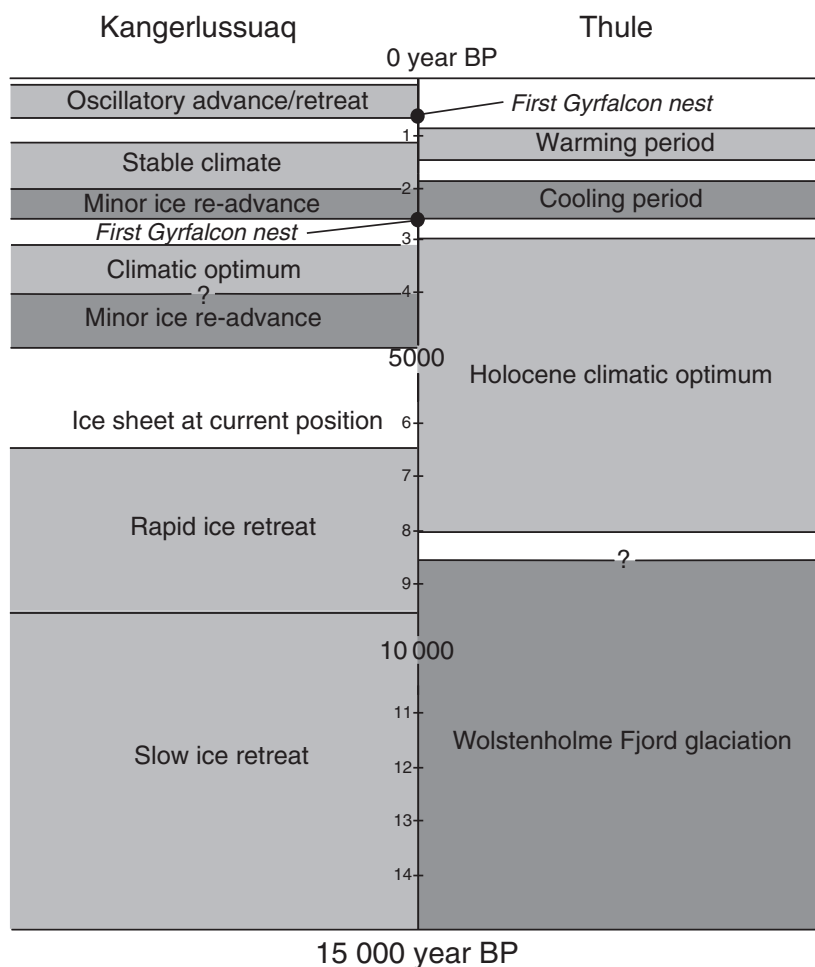
Figure 6. Glacial and climate history for the past 15 000 yr BP for the Kangerlussuaq and Thule study areas. For sources on dates used in the figure please see text.

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 4400 to 3400 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 more contentious than that from Kangerlussuaq. In Thule, Malaurie *et al.* (1972) used data from marine deposits of terraces to estimate that deglaciation began *c.* 8000 yr BP, and Kelly *et al.* (1999) postulate that much of the area has been ice-free for at least 9000 years (Fig. 6). From the period extending 8000–3000 yr BP the Thule area experienced a climatic optimum, with significant surface melting occurring (Reeh 1984) (Fig. 6). Archaeological evidence indicates unfavourable, cool condi-

tions from 2500 to 1900 yr BP followed by three centuries with a warmer climate (McGhee 1972) (Fig. 6). During the period *c.* 1350–900 yr BP a moist and probably warm climate prevailed, with conditions cooling and vegetation changing to drier heath at the end of this period (Fredskild 1973) (Fig. 6). From *c.* 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 *c.* 1900 AD (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).

In Thule, the existence of consistent long-term nest-site availability is more recent than in

Kangerlussuaq. While some nest-sites may have been ice-free as early as *c.* 9000–6000 yr BP, they may have been 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 1350 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 affected nest-sites.

The significant correlation between $\delta^{13}C$ values and distance to the current ice sheet is probably a reflection of diet, with Gyrfalcons breeding nearer the coast feeding on a mixed diet of marine and terrestrial prey items, and those breeding more inland having an almost completely terrestrial diet. Primary terrestrial prey items, such as Rock Ptarmigan and Arctic Hare, have probable $\delta^{13}C$ values in the range of −24 to −27‰ (Fig. 5) (Ricca *et al.* 2007, Roth *et al.* 2007), while marine prey items, such as Little Auks and Black Guillemots *Cepphus grylle*, have $\delta^{13}C$ values ranging from −18 to −20‰ (Fig. 5) (Hobson *et al.* 2002). Other prey species taken in more limited quantities, such as shorebirds (e.g. Red Knot *Calidris canutus* and Ruddy Turnstone *Arenaria interpres*) and waterfowl (e.g. Long-tailed Duck *Clangula hyemalis*), have $\delta^{13}C$ values with much wider ranges (−16.6 to −24.7‰, −18.1 to −24.1‰, ∼ −17 to −21‰, respectively), mainly as a result of seasonal shifts in foraging between marine and terrestrial areas (Morrison & Hobson 2004, Braune *et al.* 2005).

In Kangerlussuaq, $\delta^{13}C$ values for each of the oldest ^{14}C dated nests ranged from −23.2 to −17.8‰. Nest 082 has the most negative $\delta^{13}C$ value and is closest to the current ice sheet (5 km), and nest 201A has the least negative $\delta^{13}C$ value and is farthest from the ice sheet (78 km) (Fig 5). Of particular interest is nest 087A, which is the oldest sampled nest in Kangerlussuaq by ∼ 1000 years, and has the median $\delta^{13}C$ of the nine nests sampled in Kangerlussuaq. Although this nest is 54 km from the current ice sheet, it is approximately 1 km from a large fjord, allowing adult Gyrfalcons potential access to both a marine and terrestrial diet. The benefit of readily accessing such a large variety of prey may have allowed for earlier colonization of the nest-site. For Thule, nests 500A and 501 have very negative $\delta^{13}C$ values, with nest 500A almost 100 km from the nearest breeding seabird colonies and prey remains consisting almost solely of Arctic

Hare in recent years, and nest 501 in a large wetland area, with prey remains primarily consisting of Rock Ptarmigan. The other two Thule nest-sites, 502 and 503A, are in areas with large numbers of Little Auks and Black Guillemots. For both study areas multiple samples from the same nest-site show changes of up to −3‰ in $\delta^{13}C$ over time (e.g. site 087 in Kangerlussuaq, Table 1), which is probably the result of changes in prey composition over time.

On the basis of palaeoenvironmental investigations by others, we 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 probably occurred. Furthermore, past use of sites indicates that favourable environmental conditions existed for prey species as well. Values from $\delta^{13}C$ provide insight into likely prey species that existed at the time of colonization and possible changes in prey species over time. While results from this study are specific to Kangerlussuaq and Thule, it is possible that similar correlations exist in other regions of Greenland. These results shed further light on local, and probably regional, palaeoenvironmental conditions and glaciation in the Arctic.

REFERENCES

Angerbjörn, A., Hersteinsson, P., Lidén, K. & Nelson, E. 1994. Dietary variation in arctic foxes (*Alopex lagopus*) – an analysis of stable carbon isotopes. *Oecologia* **99**: 226–232.

Beta Analytic Inc. 2005. 4985 S. W. Court, Miami, FL, 33155, USA. http://www.radiocarbon.com.

Booms, T. & Fuller, M. 2003. Gyrfalcon diet in central west Greenland during the nesting period. *Condor* **105**: 528–537.

Bowdler, S. 1984. *Hunter Hill, Hunter Island: Archaeological Investigation of a Prehistoric Tasmanian site. Terra Australis 8*. Canberra: Australian National University Press.

Braune, B.M., Hobson, K.A. & Malone, B.J. 2005. Regional differences in collagen stable isotope and tissue trace element profiles in populations of long-tailed duck breeding in the Canadian Arctic. *Sci. Total Environ.* **346**: 156–168.

Burnham, K.K. 2008. *Inter- and Intraspecific Variation of Breeding Biology, Movements, and Genotype in Peregrine Falcon* Falco peregrinus *and Gyrfalcon* F. rusticolus *Populations in Greenland*. D.Phil. Thesis, University of Oxford.

Burnham, W.A. & Mattox, W.G. 1984. Biology of the Peregrine and Gyrfalcon in Greenland. *Meddelelser om Grønland: Bioscience* **14**: 1–25.

Cade, T.J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zool.* **63**: 151–290.

Davies, W.E., Krinsley, D.B. & Nicol, A.H. 1963. Geology of North Star Bay area, northwest Greenland. *Meddelelser om Grønland* **162**: 1–68.

Dowdeswell, J.A. 1995. Glaciers in the High Arctic and recent environmental change. *Philos. Trans. R. Soc. Lond.: Phys. Sci. Eng.* **352**: 321–334.

Eisner, W.R., Tornqvist, T.E., Koster, E.A., Bennike, O. & van Leeuwen, J.F.N. 1995. Paleoecological studies of a Holocene lacustrine record from the Kangerlussuaq (Søndre Strømfjord) region of West Greenland. *Quatern. Res.* **43**: 55–66.

Emslie, S.D., Coats, L. & Licht, K. 2007. A 45,000 yr old record of Adélie penguins and climate change in the Ross Sea, Antarctica. *Geology* **35**: 61–64.

Fredskild, B. 1973. Studies in the vegetational history of Greenland. *Meddelelser om Grønland* **198**: 1–245.

Fredskild, B. 1985. The Holocene vegetational development of Tugtuligssuaq and Qeqertat, northwest Greenland. *Meddelelser om Grønland, Geoscience* **14**: 1–20.

Fristrup, B. 1966. *The Greenland Ice Cap*. Copenhagen: Rhodos, International Science Publishers.

Funder, S. 1989. Quaternary geology of the ice-free areas and adjacent shelves of Greenland. In Fulton, R.J. (ed.) *Quaternary Geology of Canada and Greenland*: 741–792. Ottawa: Geological Society of Canada.

Gaston, A.J. & Donaldson, G. 1995. Peat deposits and Thick-billed Murre colonies in Hudson Strait and Northern Hudson Bay: clue to post-glacial colonization of the area by seabirds. *Arctic* **48**: 354–358.

Hickey, J.J. 1942. Eastern population of the Duck Hawk. *Auk* **59**: 176–204.

Hiller, A., Wand, U., Kämpf, H. & Stackebrandt, W. 1988. Occupation of the Antarctic continent by petrels during the past 35,000 years: inferences from a ^{14}C study of stomach oil deposits. *Polar Biol.* **9**: 69–77.

Hobson, K.A., Gilchrist, G. & Falk, K. 2002. Isotopic investigations of seabirds of the north water polynya: contrasting trophic relationships between the eastern and western sectors. *Condor* **104**: 1–11.

Johnsen, S.J., Dansgaard, W., Clausen, H.B. & Langway, C.C. 1970. Climatic oscillations 1200–2000 AD. *Nature* **227**: 482–483.

Kelly, M.S., Funder, M., Houmark-Nielsen, K.L., Knudsen, K.L., Kronbory, C., Landvik, J. & Sorby, L. 1999. Quaternary glacial and marine environmental history of northwest Greenland: a review and reappraisal. *Quatern. Sci. Rev.* **18**: 373–392.

Malaurie, J., Vasari, Y., Hyvarinen, H., Delibrias, G. & Labeyrie, J. 1972. Preliminary remarks on Holocene paleoclimates in the regions of Thule and Inglefield Land, above all since the beginning of our own era. *Acta Univ. Oul. A 3. Geol.* **1**: 105–133.

McGhee, R. 1972. Climatic change and the development of Canadian Arctic cultural traditions. *Acta Univ. Oul. A 3. Geol.* **1**: 39–57.

Morrison, R.I.G. & Hobson, K.A. 2004. Use of body stores in shorebirds after arrival on High-Arctic breeding grounds. *Auk* **121**: 333–334.

Newton, I. 1979. *Population Ecology of Raptors*. Berkhamsted: T. & A.D. Poyser.

Oakleaf, R. 2003. Peregrine restoration from a state biologist's perspective. In Cade, T.J. & Burnham, W. (eds) *Return of the Peregrine, a North American Saga of Tenacity and Teamwork*: 297–304. Boise, ID: The Peregrine Fund.

Ohmura, A., Calanca, P., Wild, M. & Anklin, M. 1999. Precipitation, accumulation and mass balance of the Greenland Ice Sheet. *Z. Gletsherk. Glazialgeol.* **35**: 1–20.

Ratcliffe, D. 1993. *The Peregrine Falcon*. London: T & AD Poyser.

Reeh, N. 1984. Reconstruction of the glacial ice covers of Greenland and the Canadian Arctic islands by three-dimensional, perfectly plastic ice-sheet modeling. *Ann. Glaciol.* **5**: 115–121.

Ricca, M.A., Miles, A.K., Anthony, R.G., Deng, X. & Hung, S.S.O. 2007. Effect of lipid extraction on analysis of stable carbon and stable nitrogen isotopes in coastal organisms of the Aleutian archipelago. *Can. J. Zool.* **85**: 40–48.

Roth, J.D., Marshall, J.D., Murray, D.L., Nickerson, D.M. & Steury, T.D. 2007. Geographical gradients in diet affect population dynamics of Canada Lynx. *Ecology* **88**: 2736–2743.

Rounick, J.S. & Winterbourn, M.J. 1986. Stable carbon isotopes and carbon flow in ecosystems. *Bioscience* **36**: 171–177.

Salomonsen, F. 1950. *Grønlands Fugle ⁄ Birds of Greenland*. Copenhagen: Ejnar Munksgaard.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, G., van der Plicht, J. & Spurk, M. 1998. INTCAL98 Radiocarbon Age Calibration. *Radiocarbon* **40**: 1041–1083.

Talma, A.S. & Vogel, J.C. 1993. A simplified approach to calibrating C14 Dates. *Radiocarbon* **35**: 317–322.

Ten Brink, N.W. & Weidick, A. 1974. Greenland Ice Sheet history since the last glaciation. *Quatern. Res.* **4**: 429–440.