Interplay between peat formation and animal behaviour in the Spitsbergen archipelago, recorded in peat sections

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Abstract
In the Spitsbergen archipelago, peat mires are usually closely associated with bird cliffs or the breeding territories of Arctic Skuas. This suggests that the formation of peat layers requires the additional input of nutrients. For that reason, the minimum age of the bird colonies and the breeding territories can be estimated by dating the peat layers; estimates are 5000 years for a bird colony and 4500 years for two Arctic Skua breeding territories. The discovery of peat layers between 8700 and 4200 years old of a type not associated with enhanced manuring indicates that the climate of Spitsbergen was warmer and likely also wetter in those times than today. The occurrence of reindeer faecal pellets in part of this peat up to 5700 years old indicates that reindeer immigrated into the archipelago before that time. Pollen in these faecal pellets indicate that in the past the reindeer were not feeding on bird-cliff vegetation, in contrast to their feeding habits today; either the tundra was so productive that there was no need, or no bird colony was present locally, or both.

1. Introduction
Interactions between animals and vegetation are manifold. On the high arctic archipelago of Spitsbergen, the formation of peat layers by vegetation has remarkable and (for central-Europeans) unusual relationships with animal life. We started to guess this during our field work in 1981, and further observation made this very clear to us during our second and last field work on Spitsbergen in 1984, when for our stay on Edgeøya we were the guests of Piet Oosterveld, to whom this paper is dedicated.

Peat was the focus of our field work on Spitsbergen, because it is a valuable natural archive from which we intended to extract information on the vegetation and the landscape in the past. Back in the laboratory, we studied the composition of the peat, especially the pollen and spores, but also the mosses and other plant remains that form the main bulk of the peat deposits.
The mechanisms and prerequisites for the formation of peat layers are known in broad outline for the temperate and boreal zones of the northern hemisphere. Peat-forming vegetation is generally wet, it has a low pH, it is poor in nutrients, and it is typically dominated by *Sphagnum*, the peat-moss *par excellence*. Animals have no essential role: peat can grow without them. This was our knowledge when we first came to Spitsbergen; and this mental picture was soon scattered. In this paper we will share with you some of our new insights and findings, laid down more fully in our PhD Thesis (van der Knaap 1989a; separate chapters of interest published in 1985, 1988ab, 1989b, and 1991).

2. Peat formation on Spitsbergen

Here, we will first explore how peat is formed in temperate to boreal climates, and then we contrast this with our findings on Spitsbergen. Peat is formed in mires. In mires, plants grow faster than they rot away, resulting in the accumulation of organic layers called peat. This process requires special conditions. In temperate and boreal climates, peat formation depends on conditions that prevent microbial and fungal decomposition of dead plant remains. These conditions are (a) a low pH, which implies a low nutrient status, (b) a low availability of oxygen, achieved by water-logging of the substrate, and peat formation is helped by (c) the dominance of a plant which is more resistant to decay than most: *Sphagnum*.

Mires are of two types. A bog (also called raised bog, peat-bog; Hoogveen in Dutch) is completely cut off from nutrient input from its surroundings; no water flows from outside into a bog. This is achieved by the table of the ground-water in a bog being higher than in its direct surroundings. The scarcity of nutrients and the water-logging allow only a rather slow growth of the bog plants, but decay comes nearly to a standstill. A fen is a mire into which water flows from the surroundings, carrying its nutrients with it. This allows a more rapid plant growth, and also a faster decay, but peat accumulates as long as growth prevails. But the amount of nutrients flowing into a fen is rather small. It cannot be large, because although nutrient input stimulates plant growth, it stimulates plant decomposition to a higher degree. As a result, plant decomposition will prevail over growth if the water is too rich in nutrients, in which case the site is not a mire but a different kind of wetland. Summarizing, bogs are usually extremely poor in nutrients, fens are slightly richer, and plant decay is the limiting factor that determines whether or not peat can accumulate.
On the Spitsbergen archipelago, however, decay does not seem to be limiting. We came to this conclusion on the basis of field observations and of our study of the peat deposits that we had collected (fig. 1). Due to the low temperatures of the arctic climate, plants decay slowly, whether the substrate is wet or dry, poor or rich in nutrients, and whatever the pH. But in most places in the tundra, plant growth is so terribly slow that it can’t keep up even with the very slow decay. Peat layers are formed only where plant growth is stimulated by the additional input of nutrients.

The main observation that made us think this is the close association in the field of peat layers with places where birds are breeding. Other evidence was that the peat-forming vegetation invariably contained plants indicative of a high nutrient status, and that peat layers were absent below the rare patches of *Sphagnum* that we encountered; *Sphagnum* avoids nutrient-rich conditions.

The inferred dependence of mires on animals opened new possibilities of research. If peat formation depends on animal behaviour, the peat layers
may contain information on these animals and on changes in their behaviour. Here follows what we found.

3. Skua-mounds
Skua-mounds are peaty hillocks used by Arctic Skuas (*Stercorarius parasiticum*) for surveying their breeding territory (fig. 2). The dimensions are one to ten m across and up to 70 cm high. Skua-mounds were the most widespread type of peat we saw on Spitsbergen; we saw them in nine of the eleven areas visited (Brøggerhalvøya, Hornsund, Agardhølen, and Agardhpynten on West-Spitsbergen; Meodden, Kapp Lee, Visdalen, Diskobukta, and Russebukta on Edgeøya). All the skua-mounds observed are located on coastal plains and are situated between 50 m and a few km from the sea. They are usually conspicuous from a distance owing to the bright green colour of the vegetation which results from strongly manured conditions. In a well-developed skua-mound, the permafrost level is above the level of the surrounding tundra. Stones or more often sub-fossil whale-bones protrude from the sides of most skua-mounds; these were probably
the watch-posts originally chosen by the Arctic Skuas. The skua-mounds consist mainly of peat, i.e. incompletely decomposed plant material derived from the vegetation growing on them, and further contain small stones and sand blown in from the surrounding tundra, but remains of birds and their excrements are scarce.

The following field observations indicate that the peat formation depends on manuring by the Arctic Skuas. Stones and whale-bones similar to those protruding from skua-mounds are found scattered on the coastal plains of Spitsbergen, but peat is formed around them only in the breeding territories of Arctic Skuas. Arctic Skuas occasionally perch on stones or whale-bones outside their breeding territories, and beginning peat formation was occasionally observed especially around whale-bones, stimulated both by the guano and by the limestone dissolving from the bone, but the peat layers never exceeded a few cm in thickness.

The type of peat on skua-mounds needs careful classification. According to the definition quoted in Gore (1983), "fens are mires influenced by water derived predominantly from outside their immediate limits; bogs are influenced solely by water that falls directly on to them as rain or snow". This definition focuses only on the origin of the water influencing the peat-forming vegetation. Skua-mounds which have a permafrost level above the surrounding tundra are therefore "bogs"; we call them "guanogenic bogs" because their existence depends on nutrient enrichment from bird excrements. As bogs they are quite remarkable, because of their small size and their extremely high nutrient status.

We studied two skua-mounds in detail, one from Meodden on north Edgeøya measuring 40 cm high and 3 x 5 m in surface (fig. 2) and another from Agardhdalen on the eastern side of West-Spitsbergen opposite Edgeøya measuring 40 cm high and 2 x 3 m in surface. Peat formation on the two skua-mounds started ca. 4500 calendar years ago. This is therefore the minimum age of these Arctic Skua territories. The Arctic Skuas may have installed themselves in that place soon after the emergence of the beaches on which the mounds lie.

The study of the peat sections revealed that there has been a succession of various dominant plant species on the skua-mounds, which indicates that the intensities of manuring have fluctuated. In both skua-mounds, we see an abrupt transition from a strongly to a moderately manured vegetation at a level about half-way up the peat sections. The main indicative plant belongs to the Cruciferae family according to its pollen; most
likely this was *Cochlearia officinalis* (Scurvy Herb; Lepelblad in Dutch), which is today the dominant plant on many bird-cliffs (see below). This plant was abundant on the skua-mounds in their early history, and then became rare. This indicates decreased manuring by birds. On the Edgeøya skua-mound, this event coincides with an abrupt lithological transition from strongly decomposed to weakly decomposed peat, which indicates climatic cooling.

We may relate the inferred climatic cooling directly with the decreased manuring by birds, as follows. Decreased manuring indicates the diminished use of the breeding territory by the Arctic Skuas, which is most likely to be associated with a deterioration in the conditions for breeding and/or foraging. These conditions largely depend on the length of the season that the sea is free of ice; foraging is hampered if sea-ice is present until late in spring. In short, climatic cooling causes longer sea-ice in spring, and this leads to reduced breeding activity by the Arctic Skuas, which causes a change in the vegetation growing on the skua-mounds.

4. Bird cliffs
The peat layers encountered on and at the base of bird cliffs are another example of the dependence of peat formation on manuring by birds. We studied three cases.

4.1. Søre Salatberget bird cliff
The bird cliff Søre Salatberget lies 4 km from the 17th-century Dutch whaling station of Smeerenburg (= Blubber Town) on Amsterdamøya, a small island northwest of West-Spitsbergen. It houses a colony of Little Auks (*Plotus alle* L.) and other bird species. The vegetation on the bird cliff is dominated by *Cochlearia officinalis* (Scurvy Herb), a plant occasionally collected by the Dutch whalers as a remedy against scurvy. The peat layers consist mainly of the remains of Scurvy Herb, and further contain sand and gravel, remnants of the birds such as bones and feathers, and remnants of their food such as fish-bones, shells, and crustaceans. The study of the peat layers revealed that the vegetation has been unchanging for at least five centuries. This is therefore the minimum age of the bird colony.

4.2. Bird cliff at Stuphallet
We studied the mires below the bird cliffs of Stuphallet on the northern coast of Brøggerhalvøya, a peninsula on the northwest side of West-Spitsbergen on which the village of Ny Ålesund also lies. We mapped the large mires that
stretch below the bird cliffs (fig. 3). Water coming directly from the bird cliffs seeps through the mires, thus maintaining a high level of nutrient input. The thickness of the peat layers was difficult to assess for most of the mire surface because of the permafrost; no more than 15 cm from the surface was unfrozen in August 1981. We could reach deeper peat layers only from the vertical sides of streams and gullies. The peat layers were about 1 m thick. We studied two peat sections. The results indicate that the mires were in existence for at least the last 5000 years. This is therefore the minimum age of the bird colonies on the cliffs of Stuphallet. This age is close to that of the minimum age estimated for the skua-mounds studied (see above). A special find was the pollen of *Parnassia*, a plant now absent from Spitsbergen. Either the plant was growing there in the past, or the pollen has been transported unintentionally by migrating birds coming from other arctic regions where it is found today.

4.3. *Bird cliff at Dolerittneset*

The bird cliffs of Dolerittneset lie close to the sea at the entrance of Rosenbergdalen on Edgeøya, not far from the housing at Kapp Lee where we were the guests of Piet Oosterveld in 1984. The bedrock in this valley is in part dolerite, which is a kind of basalt and resistant to erosion, but consists in part of soft rock prone to erosion. The doleritic bird cliffs had a rather scarce population of Black Guillemots (*Cepphus grylle* (L.)). The vegetation...
below the cliffs was clearly influenced by the nutrients seeping down from the cliffs. The vegetation was luxuriant, but peat formation was prevented by a steady erosional input of gravel coming down from debris slopes nearby. In one place only, 40 m from the sea and ca. 5 m above it, peat layers were developed thanks to a special geomorphologic situation (fig. 3). This mire was protected against the influx of gravel by an irregular row of low stones arranged around the site in a parabola-like shape about 4 m wide and 6 m long, with the open end of the parabola orientated down-slope towards the sea. The stones are most densely packed at the top of the parabola which is orientated up-slope towards the bird cliff, forming an irregular wall up to 1 m wide which stopped the flow of gravel but let the water pass through into the mire. The parabola-like structure is quite remarkable. It may have been caused by sea-ice pushed inland by wind or sea-currents. We collected one peat section from this mire. This section covers only the upper 32 cm of the peat deposited at the site of collection; an unknown depth of impenetrably frozen peat lay below it. The peat section is about 700 years old at its base. The age of the bird colony must therefore be much greater.

5. Other peat mires
At three places on the Spitsbergen archipelago we encountered living mires that were not directly associated with breeding birds, but nevertheless
influenced by nutrient input by animals. We studied a short peat section from each of the mires with the aim of investigating changes in vegetation during the last few hundred years, as was done for the Dolerittneset mire described above. In none of the mires could we penetrate the complete peat deposits down to their base, because the deeper peat was frozen. This was no problem with respect to the aim of our research, but the consequence is that we could not assess the time when the peat started to accumulate. Here follow some results.

5.1. Grunnlinesletta
The mire on Grunnlinesletta lies on a coastal plain along the bay of Russebukta on the west coast of Edgeøya. The sea is at a distance of 50 m, the elevation is ca. 2 m. The mire lies on a small doleritic plateau. Most vegetation on this plateau is peat-forming. An abundance of feathers and goose excrements and the condition of the vascular plants indicate that the vegetation was strongly grazed by geese and probably also by reindeer. We studied one peat section of 40 cm depth collected from a wet place in the mire. This section reached back about 600 years, so the peat formation on the plateau must have started earlier. The results indicate that the mire at

Peat mire at Anderssonbukta on Barentsøya with location of peat collection (photo: W.O. van der Knaap).
the place where the peat was collected was in the past less wet and richer in vascular plant species than it is today; it is today comparable to drier places of the same mire today.

5.2. Anderssonbukta
The mire at Anderssonbukta lies on a small peninsula on southwest Barentsøya, close to Edgeøya. The sea is at a distance of ca. 80 m and the elevation is ca. 10 m. The situation is very similar to that of the Grunnlinesletta mire. It lies on a small doleritic plateau, most of the vegetation on the plateau is peat-forming, and there are clear traces of nutrient enrichment by geese and probably reindeer. We studied one peat section of 37 cm depth collected from a wet place in the mire. This reached back more than 1250 years in time, so the mire must have begun earlier. The results are similar to Grunnlinesletta and indicate that the place of peat collection was in the past less wet and richer in vascular plant species than it is today, being comparable to drier places of the same mire today.

5.3. Rålstranda
The mire on Rålstranda borders a pond near the entrance of Revdalen, a valley north of the Hornsund fjord in the southwest of West-Spitsbergen. It lies about 500 m from sea at ca. 15 m elevations. The vegetation indicates that the water in the mire has a high pH, similar to the other mires. To our regret, our visit to the place was only long enough to collect the peat section, and no time was left to make observations on animal impact on the site. The peat section was 22 cm deep and had a stratigraphy much disturbed by frost action, and reached several hundred years back in time.

6. Mires and reindeer history

6.1. Buried peat layers in Rosenbergdalen: a surprise
The only living peat mire we could discover in Rosendalen, in the western part of Edgeøya was in the special geomorphologic setting below the Dolerittneset bird cliffs discussed above. Two buried peat layers discovered by Piet Oosterveld higher up in the valley were therefore a welcome surprise. The peat layers emerged from the eroding, vertical banks of the main stream through the valley, 1.25 km from the sea and at about 20 m elevation. One peat layer was 0.7 m thick and had grown from about 8700 to 7600 years ago; the other was 2 m thick and had grown from about 5700 to
4200 years ago. The former presence of mires in Rosenbergdalen where they are virtually absent today points to less deposition of erosional material than today. The debris slopes must therefore have been more densely vegetated than today.

Both microfossils (pollen and spores) and mosses were studied in the two peat layers. The results indicate that the vegetation on both mires was a Homalothecium nitens tundra as described by Philippi (1973), named after the dominant moss species. This type of tundra is still common in Rosenbergdalen, but it is not peat-forming today. Moreover, this type of tundra is today not associated with bird cliffs or other sources of increased manuring by animals. In addition the pollen diagrams of the two peat layers show combinations of vascular plants that grow today on unmanured tundra. We must therefore assume that the two mires grew in unmanured conditions, which contrasts strongly with all living mires we have seen on the Spitsbergen archipelago. This implies that the growing conditions in the past were different from today; the climate must have been warmer and probably also wetter.

6.2. History of reindeer
The peat layers themselves were a surprise because of their climatic implications, but they contained yet another surprise. Excrements of reindeer were discovered in the younger of the two peat layers, oval-shaped faecal pellets. We found them from the bottom to the top of the layer, which shows that reindeer were continually present during the time of growth of this mire. On the other hand, no faecal pellets could be found in the older of the two
peat layers, even though we searched through 27 litres of peat (compared to 3.3 litres of peat in the younger deposit). This implies that reindeer had immigrated into the area (and therefore into Spitsbergen as a whole) during the time gap between the two peat layers, i.e. between about 7600 and 5700 years ago.

6.3. Changed diet of reindeer
We studied pollen and spores not only in the peat, but also in the reindeer faecal pellets found in the peat. In addition, we studied pollen and spores in fresh reindeer faecal pellets collected by Piet Oosterveld between the peat layers and the sea during two summer seasons in the area of Rosenbergdalen. The difference in pollen content between the recent and the old faecal pellets is striking. Pollen in the recent faecal pellets shows clearly that the reindeer prefer to forage under the bird cliffs, where vegetation is more productive than in unmanured tundra. This behaviour of Spitsbergen reindeer is well known. Characteristic for bird cliffs are high concentrations of pollen of *Saxifraga, Cerastium, Ranunculus, Oxyria*, and *Cruciferae*, all growing more abundantly below bird cliffs than elsewhere.

Figure 4. Dolerittneset mire on Edgeøya with location of peat collection (photo: W.O. van der Knaap).
Pollen in the old reindeer faecal pellets, on the other hand, indicates that the reindeer had been feeding in unmanured tundra, not in vegetation enriched by manuring.

This finding is of great consequence. It indicates that the vegetation of Rosenbergdalen has changed since the time that the younger peat layer was formed. This leads to two possible reconstructions of the vegetation for the time of the younger peat layer:
(a) Bird-cliff vegetation was absent, which implies that the cliffs were not sufficiently colonized by birds to merit the name bird-cliff;
(b) The unmanured tundra vegetation was so much better developed in the past than today that it met the feeding requirements of the reindeer, decreasing the necessity for selective feeding on manured bird-cliff vegetation.

The analysis of the peat itself had already indicated that the tundra vegetation was better developed in the past than today, suggesting a climate more favourable for dense vegetation. Yet bird-cliff vegetation would stand out as more productive under more favourable climatic conditions too, and we may hypothesise that bird-cliff vegetation would attract reindeer even if they did not actually need it. The absence of a bird-cliff signal in the old faecal pellets indicates therefore that the bird colonies in that time, if present at all, cannot have been of great importance.

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