

Observations on nests of *Bombus polaris* curtis usurped by *B. hyperboreus* Schönherr in Greenland (Hymenoptera: Apidae).

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Ent. Meddr 50: 145-150. Copenhagen, Denmark 1983. ISSN 0013-8851.

Two nests of *Bombus polaris*, usurped by *B. hyperboreus*, are described from West Greenland and the production of progeny is calculated from the number of cocoons. Results from honey and pollen samples are given and temperature recordings from one of the nests are presented. *B. hyperboreus* is compared with other inquilines of the genera *Bombus* and *Psithyrus*.

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Introduction

The circumpolar *Bombus polaris* and *B. hyperboreus* are the only bumblebee species occurring in Greenland (Milliron, 1973; for distribution maps see Richards, 1973), and are part of the high arctic element of the insect-fauna that immigrated from Canada via Ellesmere Island (Downes, 1966).

It has long been known that workers of *B. hyperboreus* are very rare. Milliron & Oliver (1966) and Bergwall (1970) showed that *B. hyperboreus* could appear as a social inquiline (usurping *B. polaris* in Canada and *B. jonellus* in Scandinavia), and they proposed independently that the paucity of workers was a result of this behaviour. Thorough investigations by Richards (1973) confirm this, and it is a reasonable supposition that *B. hyperboreus* is an obligate inquiline.

The present paper deals with two composite nests of *B. polaris* workers and *B. hyperboreus* sexuals discovered near the Arctic Station, Godhavn, Disko Island, West Greenland. The nests were found on the southeastern shore of Avangnarput Inlet in Disko Fjord (69° 33' N, 53° 55' W) in a moist, mossy dwarf shrub heath, dominated by glaucous willow (*Salix glauca*), a few other higher plants, and bryophytes and lichens.

Descriptions of nests

Nest no. 1: This nest was located in a *Salix glauca* scrub at the upper parts of an east-facing slope bordering the bed of a dried-up

melt water course. The entrance hole was located southwest of the nest, which was in level with the surrounding surface and well camouflaged. The nest material consisted exclusively of litter, among which could be recognized twigs and withered leaves of *Salix glauca* and dry leaves of *Pyrola grandiflora*. The nest was uncovered on 29 July 1982 and as they issued from the nest all individuals were captured and killed in fumes of ethylacetate. A single specimen returned from a foraging trip and was likewise captured giving a total of 15 *polaris* workers, 3 *hyperboreus* queens, and 9 *hyperboreus* males. Two last-instar queen larvae in separate cells and five small larvae in a common brood cell were observed. 17 unhatched cocoons, 15 larger, and 2 smaller, probably containing queen and male pupae respectively, were obtained, but their contents were not examined. The nest was rather inaccessible under the *Salix* scrub, and most of the vacated cocoons were destroyed when removed, making an estimate of the total production impossible.

Nest no. 2: The entrance hole was located southeast of the nest which was built on level ground, and had a domed cover, 13 cm in diameter, arching about 3 cm above the surrounding moss surface (Fig. 1). The nest canopy consisted of the bryophyte *Drepanocladus uncinatus* and some twigs and withered leaves of *Salix glauca* and *Pyrola grandiflora*. A thin and uneven wax coating supported the canopy over the comb, and a



Fig. 1. Exterior view of nest no 2. Note the entrance hole at top and the inserted thermistor probe below. M. Sasa photo.

layer of small bits of *D. uncinatus* and some twigs of *Salix* made the demarcation below. A passage, 4 cm long, led to a small room where a thin layer of pollen covered the ground – possibly accumulated excrements.

The nest was uncovered at 30 July 1982 during a drizzle which kept all individuals inside, and all the bees were captured and killed (20 *polaris* workers, 1 *hyperboreus* male, and 15 *hyperboreus* queens). Twenty-one worker cocoons constituted the base of the comb, and with the exception of one containing a dead, mummified larva, all were vacated and more or less filled with honey. The upper layers merged into each other and were used for the production of sexuals. The cocoons could be separated into two groups: 19 male cocoons (15 vacated, 4 closed) were located mainly in the center of the comb and 34 queen cocoons (14 vacated, 20 closed) mainly at the top, giving a sex ratio of 1:1,79 (males:queens).

Practically all vacated cocoons contained honey; a few, however, were half-filled with pollen. Two accumulations of pollen were found on the ground near the worker cocoons, and a brood cell with five eggs was located on the upper side of the comb. These eggs probably would not have completed development under natural conditions.

All killed specimens were weighed after returning to the laboratory (unfortunately bad weather caused a delay of two days and possibly some ethyl acetate had accumulated in the fat bodies). Five of the queen cocoons from nest no. 2 hatched during the first 24 hours after the comb was brought to the laboratory (Fig. 2) and the emerged *B. hyperboreus* queens were weighed. The results are given in Table 1.

Honey and pollen

The sugar concentration of the honey was measured in both nests with a hand refractometer (Euromex, range 0-90%) immediately after exposing the comb. From nest no. 1 a sample from the damaged honey pots showed 64,0% sugar and two samples from vacated cocoons contained 74,5% and 70,0% sugar respectively. A single sample from a cocoon in nest no. 2 contained 74,2% sugar. The values are somewhat lower than those obtained by Richards (1973) from nests of a similar stage of development, where thick and thin honey showed concentrations of about 80% and 70% respectively.

The total amount of honey in nest no. 2 was estimated to about 15 ml which is quite a lot considering the relatively large number of sexuals produced which do not assist in collecting.

Three pollen samples were taken, two from the pollen stored beside the comb in nest no 2 and one corbicular pollen load of a returning worker from nest no 1. The results are seen in Table 2. Pollen of *Salix glauca* dominate. A few pollen of *Salix arctophila* may be included in this type. Morphologically the Ericales pollen are very similar, and a great overlap exists between species and genera. Most of the Ericales pollen originated from *Pyrola grandiflora*, which was common in the area. The corbicular sample contained some pollen of *Angelica archangelica*, a species usually growing only in boreal and protected low-

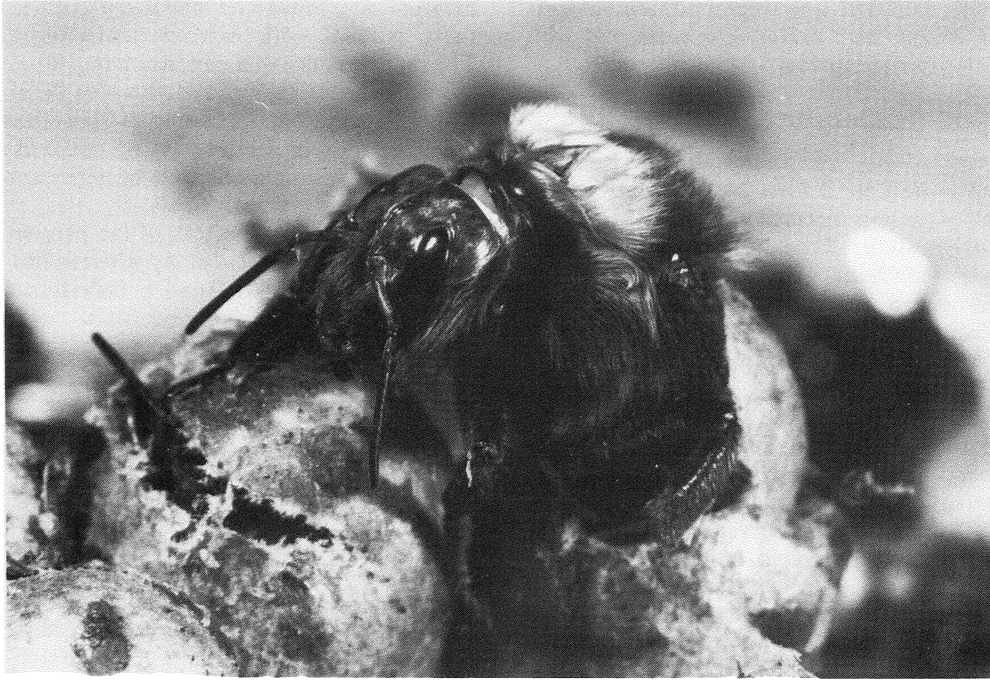


Fig 2. *B. hyperboreus* queen hatching in the laboratory. Another individual has just begun cutting the cocoon. B. Christensen photo.

Old queens from previous season	Newly emerged queens	Queens emerged in the lab	Drones	<i>polaris</i> -workers
N=2 0,84 ± 0,05	N=14 0,98 ± 0,08	N=5 0,93 ± 0,06	N=10 0,40 ± 0,02	N=35 0,15 (0,06-0,24)

Table 1. Weights (in grams) of *B. hyperboreus* sexuals and *B. polaris* workers. The queens which emerged in the laboratory were weighed alive, immediately after the intestinal evacuation. Worker-weights do not follow the normal distribution for which reason standard deviation is omitted.

	a	b	c
<i>Salix glauca</i> type	80,0	78,6	90,5
Ericales	16,9	19,7	6,7
<i>Pedicularis</i> spp.	2,1	1,5	0,2
<i>Dryas integrifolia</i>	0,9	0,2	0,2
<i>Epilobium latifolium</i>	0,1		0,2
<i>Angelica archangelica</i>			2,1
Pollen counted	812	929	475

Table 2. Percentages and total numbers of pollen counted in two pollen aggregates from nest no.2 (a-b) and in one corbicular pollen load (c) from nest no.1.

arctic sites, but with some northern outposts on Disko, here exclusively associated with homothermic springs.

Nest temperature

Temperature measurements were carried out in nest no. 2 from 24 to 29 July with a self-recording thermistor (Grants Miniature Temperature Recorder) with recordings every half-hour. One thermistor probe was introduced through the roofing material, placing the sensitive tip between the upper queen cocoons, and another probe was placed on the moss surface, about 20 cm from the nest. Exposing the surface probe results in a temperature reading of 1-2°C above the actual temperature when exposed to direct insolation.

The temperature curves obtained (Fig. 3) show a fairly constant nest temperature in the range 25-35°C, with small fluctuations reflecting the ambient microclimate. At night the bumblebees were able to maintain a temperature difference of 26-27°C above surface temperature for several hours.

Nest parasitism

Four dead queens were found in association with the two nests, either concealed in the nest material or lying on the moss surface near the entrance. One of these, found in nest no. 2, was a *B. polaris* queen, possibly the original founder of the nest. The three others were old *B. hyperboreus* queens, hatched the previous year. This was judged from worn wings and reduced thoracic pubescence. These dead queens may represent intraspecific nest parasitism in *B. hyperboreus*.

Discussion

The construction of the nests was similar to that of nests described by Milliron & Oliver (1966) and Richards (1973) except for the very few plant species used in nest building.

Richards (1973) compared the temperature in natural *B. polaris* nests and in artificial styrofoam nests. In the latter the temperature fluctuated between 27 and 35°C during the »period of equilibrium« (sensu Hasselrot, 1960) and was, at this developmental stage, independent of variations in external temperature. In natural nests, however, tem-

perature was lower and fluctuated considerably parallel with external temperature. The maintenance of a constant temperature in nest no. 2, in spite of the advanced developmental stage (the beginning of Hasselrots (1960) »period of decline«), is no doubt explained by the ample resources of honey and the high number of individuals.

A remarkable female bias of the progeny was found in the present study whereas Milliron & Oliver (1966) found a male-biased sex ratio in *B. hyperboreus* from arctic Canada. This difference may reflect difference in size, small colonies producing an excess of males (Owen et al., 1980).

Facultative nest parasitism is common in *Bombus* (Wilson, 1971) but so far evidence for obligate nest parasitism, as in *Psithyrus*, is only known in two species: *B. inexpectatus* (Yarrow, 1970) and *B. hyperboreus*. The genus *Psithyrus* is known to possess some behavioural and morphological adaptations associated with the life as a social inquiline and it would be reasonable to look for similar modifications in *B. hyperboreus*. The queen of *B. hyperboreus* is morphologically very similar to the most frequent host, *B. polaris*, and does not have any *Psithyrus*-like features (in contrast to *B. inexpectatus*). The auricles and the corbiculae seem perfectly suited for pollen gathering and are obviously functional: Ranta & Lundberg (1981) collected several corbicular pollen loads from *B. hyperboreus* queens in subarctic Scandinavia, and 8 of 14 museum specimens (from Scandinavia?) examined by Yarrow (1970) showed signs of pollen foraging in their corbiculae. The *B. hyperboreus* queen from the nest described by Bergwall (1970), however, only collected nectar, but Bergwall ascribes this to a damaged wing which made flight difficult. I have examined most of the Greenlandic specimens of *B. hyperboreus* queens at the Zoological Museum, Copenhagen, and of 50 queens 19 showed signs of pollen in their corbiculae, with the amounts varying from traces to distinct pollen loads. Of the two old queens in the nests described, the one from nest no. 2 had small amounts of pollen in the right corbicula, the left being nonfunctional because the tarsus was missing. In contrast to this, Michener (1974) mentioned that *B. hyperboreus* was not seen collecting or carrying pollen in arctic Cana-

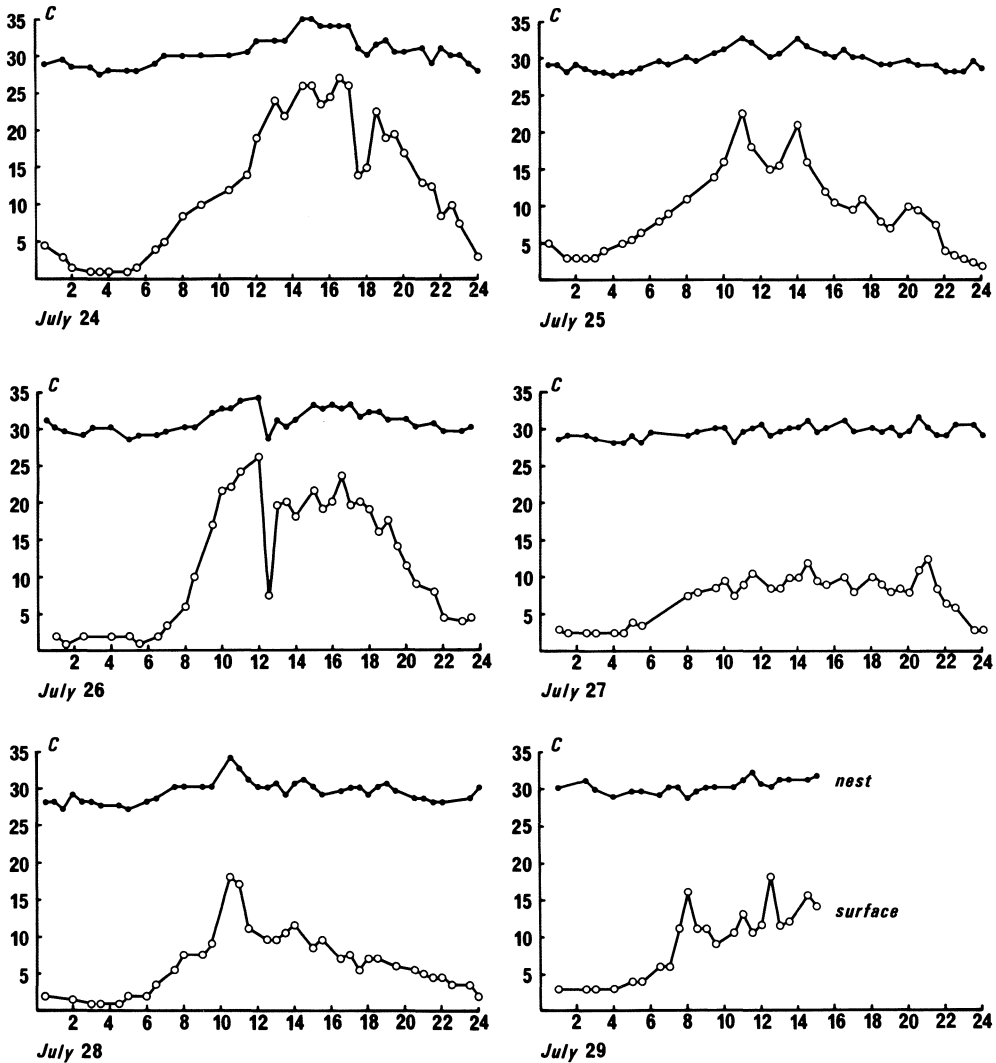


Fig. 3. Temperature curves showing nest temperature (filled circles) and temperature of ambient moss surface (open circles) in the period 24-29 July.

da. It is interesting that the possible absence of pollen collecting in the North American arctic coincides with an apparent absence of workers. Milliron (1973), however, described a single worker hypotype from Søndre Strømfjord, West Greenland. The remaining workers are from Scandinavia, the Kola peninsula, Novaya Zemlja, and Russian Lapland (Friese & Wagner, 1912; Løken, 1973). Sparre-Schneider (1906) mentioned four *B. hyperboreus* workers from Green-

land but Løken (1973) has redetermined them as *B. polaris*. Michener (1974) suggested that similar misidentifications might account for the remaining *B. hyperboreus* workers.

Apparently *B. hyperboreus* is actively collecting nectar, at least in Scandinavia. The *B. hyperboreus* queen of the nest described by Bergwall (1970) gathered more nectar than the combined efforts of the eleven workers.

Although an obligate inquiline, it seems as if *B. hyperboreus* behaves like a »normal« *Bombus* species except for the absence of the worker caste. The greater loading capacity of the queen may be of importance in the

short arctic season where only few workers are produced before sexuals. The absence of workers and lack of observations of pollen gathering in the Canadian arctic suggest, however, that the North American population may be a step ahead in the evolution of behavioural and physiological parallelism to *Psithyrus*.

Acknowledgements

I wish to thank Mikako Sasa, Susanne Bek and Torben Madsen for assistance in the field and Bent Fredskild for analysing the pollen samples. I am also grateful to Hans Dreisig, who read and commented the first draft of the manuscript.

Sammendrag

Observationer af reder af *Bombus polaris* Curtis overtaget af *B. hyperboreus* Schönherr i Grønland (Hymenoptera: Apidae).

To reder af *Bombus polaris*, begge overtaget af den obligate redeparasit *B. hyperboreus*, blev fundet ved Avangnarput på Disko, Vestgrønland. Begge reder var anbragt i jordoverfladen, og redematerialet var dels bladmosset *Drepanocladus uncinatus*, dels førne af *Salix glauca* og *Pyrola grandiflora*.

I rederne kunne skelnes to generationer af *B. hyperboreus* kønsindivider, en drone- og en dronningegeneration, med sidstnævnte i overtal.

Honningprøver fra rederne viste en sukkerkoncentration mellem 64% og 74%. Pollenprøver viste en dominans af *Salix glauca* og *Pyrola grandiflora*, der begge var hyppige på lokaliteten. Temperaturmålinger i den ene rede viste en ret konstant temperatur i intervallet 27-35°C med små udsving forårsaget af det omgivende mikroklima. Om natten kunne humlebieerne opretholde en temperaturdifference på 26-27°C i forhold til overfladetemperaturen.

En død *B. polaris* dronning og tre døde *B. hyperboreus* dronninger fundet i forbindelse med rederne tydes som resultatet af henholdsvis intra- og interspecifik redeparasitisme.

B. hyperboreus dronningen deltager, i modsætning til dronninger af *Psithyrus*, aktivt i indsamling af pollen og nektar til reden. I arktisk Canada er *B. hyperboreus* dog ikke set samle pollen.

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