MEDDELELSER OM GRØNLAND
UDGIVNE AF
KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND
Bd. **191** · Nr. **4**

FEEDING BIOLOGY OF *NYSIUS GROENLANDICUS* (ZETT.) (HETEROPTERA: LYGAEIDAE) IN GREENLAND

WITH A NOTE ON OVIPOSITION IN RELATION TO FOOD-SOURCE AND DISPERSAL OF THE SPECIES

BY

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WITH 12 FIGURES AND 9 TABLES IN THE TEXT,
AND 5 PLATES

С РУССКИМ РЕЗЮМЕ

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BIANCO LUNOS BOGTRYKKERI A/S
1972

Abstract

The habitat of *Nysius groenlandicus* (Zett.) and field observations of feeding indicated that seeds constitute the food. This was confirmed experimentally; the species is polyphagous, but some seeds are preferred to others, and some are unsuitable. In certain cases the purpose of flower visiting seems to be drinking of nectar.

Field studies on the foraging on two species of Compositae demonstrated a cyclic change in the number of bugs attending the capitula. The number was at a minimum at noon and attained its maximum late in the afternoon or in the evening. Mainly females foraged in the capitula, and the percentage of nymphs was lower than on the ground surface.

Because of a tendency for *N. groenlandicus* to oviposit on seeds and fruits, many of which are equipped with a parachute device, it is suggested that the eggs are frequently dispersed by the wind attached to airborne seeds and fruits. This might account for the ubiquity of the species in Greenland.

РЕЗЮМЕ

Вид *Nysius groenlandicus* (Zett.) практически повсеместно распространен в Гренландии. Места распространения этого вида, а также полевые наблюдения показывают, что продуктами его питания являются семена и плоды. Это было исследовано на опыте. *N. groenlandicus* являетса полифаговым насекомым, хотя некоторые семена предпочитаются другим, а некоторые являются совершенно непригодными. в некоторых случаях посещение цветов обусловлено, повидимому, сбором нектара.

Детальные полевые наблюдения по фуражировке *N. groenlandicus*, проведенные по двум видам *Compositae*, показали периодическое изменение количества насекомых на капитулах. Наименьшее число насчитывалось в полдень, а максимальное - во второй половине дня и вечером. В основном на капитулах наблюдались самки, иногда самцы практически отсутствовали, а процентное количество личинок всегда было намного ниже, чем на земле. Числовые данные были получены для среднего количества насекомых на капитулу и на квадратный метр капитул.

Так как *N. groenlandicus* откладывает яйца преимущественно на семенах и плодах, многие из которых снабжены парашютным приспособлением, то возможно, что многие яйца таким образом рассеиваются ветром. Этим, вероятно, объясняется широкая распространенность вида Гренландии.

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ISBN 87 421 0062 3

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Manuscript received September 28th, 1971.

INTRODUCTION

Until very recently the feeding biology of most members of the Lygaeidae was unknown and somewhat mysterious. Many species were considered carnivorous, but there were few observations and no investigations. On the other hand, some species were known to be phytophagous (the Blissinae), and a few, including the Artheneinae and *Oncopeltus fasciatus* (DALLAS) (Lygaeinae), were known as monophagous seed-feeders. However, in 1956, PUCHKOV published his fundamental paper on the "basic trophic groups of phytophagous hemipterous insects" in which the true nature of many genera of Lygaeidae as oligophagous or polyphagous feeders on ripe plant seeds was brought to light. SWEET (1960) independently arrived at the same conclusion, studying the Rhyparochrominae of New England. He suggested the name "the seed bugs" for the Lygaeidae. Two years earlier, ASHLOCK (1958) presented observations and experiments indicating seed-feeding in different Rhyparochrominae. Later on SWEET (1964) and EYLES (1964) made valuable and comprehensive investigations of the general biology and ecology, and the feeding habits, respectively, of this subfamily.

However, another important subfamily, the Orsillinae, that includes the large, cosmopolitan genus, *Nysius* DALLAS, remained rather unexplored biologically. The first information about feeding habits in this subfamily seems to be that of HEIDEMANN (1902), who reported that *Belonochilus numenius* (SAY) completed its life cycle on the seed balls of *Platanus occidentalis*.

Summarizing the literature on the economic status of the lygaeids, HOFFMANN (1932) mentioned nine species of *Nysius* as pests of cultivated crops in different parts of the world. In most cases the damage reported seems to be caused by the bugs sucking on succulent fruits or on the vegetative parts of the plants in question; a single species (*N. binotatus* GERM., in South Africa) was reported on sunflower seed heads. Possibly the majority of these injuries are due to drinking rather than feeding on the part of the bugs (*cf.* PUCHKOV, 1956; ASHLOCK, 1967), but *N. huttoni* WHITE from New Zealand, a pest of clover, lucerne, wheat etc. (GURR, 1957; EYLES, 1965; EYLES & ASHLOCK, 1969), undoubtedly feeds on the vegetative parts of plants, even though it sometimes sucks wheat kernels.

EYLES (1963) could rear the species successfully merely on fresh sprigs of *Coronopus didymus* (Cruciferae), and GURR kept reproducing imagines on stems of *Capsella bursa-pastoris* (Cruciferae). The same seems to be valid for *N. vinitor* BERG. that is a pest on a multitude of vegetables and other crops in Queensland (SMITH, 1927).

USINGER & ASHLOCK (1966), studying the Orsillinae of Hawaii and other oceanic islands, mentioned a number of orsilline host plants belonging to thirteen plant families, with certain composite genera (*Bidens*, *Emilia*, *Erigeron*, *Raillardia; Scalesia* on the Galapagos) predominating. Most of the Hawaiian Orsillinae were characterized as host-specific; however, only in one case was the portion of the plant fed upon stated: *Neseis (Trachynysius) nitidus* (WHITE) and *N. (T.) hiloensis* (PERKINS) both feed on the tough seeds of a *Pipturus* sp. (Urticaceae). The two species have different beak lengths, thus probably avoiding competition by sucking on different parts of the seeds.

BEARDSLEY (1966), in his investigation of migrating *Nysius* spp. at Haleakala, Maui (Hawaii), threw light on the feeding biology of the species. Of the six species studied, four (*N. communis* USINGER, *N. kinbergi* USINGER, *N. lichenicola* KIRKALDY, *N. nemorivagus* WHITE) bred host-specifically on the flower heads and fruit heads of, respectively, *Raillardia menziesii* (Compositae), *Tetramalopium* sp. (Compositae), *Trisetum glomeratum* (Graminae) and *Chenopodium oahuense* (Chenopodiaceae). The remaining two species (*N. coenosulus* STÅL and *N. terrestris* USINGER) were collected on inflorescences and infructescences of various plant species belonging to Amaranthaceae, Chenopodiaceae and Portulacaceae.

ASHLOCK (1967) reviewed the scanty literature on the feeding biology of the Orsillinae and added some original contributions. He was able to rear *Nysius tenellus* BARBER through several generations on water and dried flower heads of *Cotula coronopifolia* (Compositae). He also kept *Ortholomus arphnoides* Baker on sunflower seeds and water. In the Galapagos Islands he watched *Darwinysius marginalis* (DALLAS) feeding on the loose seeds of a *Portulaca* sp.

In conclusion, only a little work has been done on the feeding habits of the Orsillinae, and little information is available. Some species seem to feed on vegetative parts of plants; but in most cases unripe or ripe seeds, either on the plants or fallen to the ground, are suspected, strongly indicated or, in a few cases, shown to be the food. The species are monophagous, oligophagous or polyphagous.

The present investigations were carried out partly during my term 1967–1970 as scientific leader of the Arctic Station, University of Copenhagen (situated at Godhavn, Disko, West Greenland), and partly while partaking in the Danish biological expedition to the Kap Farvel area, South Greenland, in the summer of 1970.

OBSERVATIONS IN THE FIELD

Nysius groenlandicus (Zetterstedt) is very common practically everywhere in Greenland. It is univoltine and hibernates in the egg-stage. Details about distribution, habitat, frequency, life cycle, etc. are to be dealt with in future papers.

No information about the feeding biology of *N. groenlandicus* exists in the literature. However, Vanhöffen (1897, p. 148) reported the species ("besonders") on the flowers of *Dryas* and *Saxifraga tricuspidata;* Lindberg (1935) found it in Dovre, Norway, on *Rumex acetosella;* and Brændegaard (1938) mentioned a "bug", undoubtedly *N. groenlandicus*, on *Chamaenerion latifolium.*

My preliminary observations in the surroundings of Godhavn established that the species might be found in any fairly xeric site, but that slopes facing the south and covered with heath, fell field or, especially, steppe-like vegetation were favoured.

N. groenlandicus is principally found on the ground surface, more specifically in dry ground litter at the base of low, sparse vegetation and along the margins of rocks or moss cushions. Sometimes, however, mostly in late summer, the species may climb the vegetation. Observations on these occasions made it clear that feeding on the ripe and ripening seeds (fruits) on the plants was the purpose of the ascent.

The preferred micro-habitat described above always contains a considerable amount of dry fruits and seeds. A sample of ground litter from a small spot at the slope of Østerlien, Godhavn, much favoured by *Nysius* (September, 1967), contained a large fraction of seeds (fruits, bulbils) from the following species: *Alchemilla glomerulans*, *Carex* sp., *Oxyria digyna*, *Polygonum viviparum*, *Potentilla crantzii*, *Taraxacum croceum*, *Veronica alpina.*

Sweet's (1964) description and discussion of the "seed rich litter biotope" (l. c. pp. 21–29) apply well in this connection. It thus soon became natural to class *N. groenlandicus* with the "fallen seed ecological niche" (Sweet, 1964, p. 21) as was suspected from the beginning of the study.

In Table 1 is found a list containing all my observations of *N. groenlandicus* sucking seeds and fruits (bulbils in *Polygonum viviparum*) on plants in the field. Reference is also made to Plates 1–2 & 4. In the table an

Table 1. *Observations of* Nysius groenlandicus *feeding on plants in the field.*

Plant species	Portion of plant sucked	Locality
Rosaceae:		
Potentilla tridentata	flower*), fruit	Anordliuitsoq
P. hookeriana	flower*)	Ikerasak, Qarássap nunatâ
P. crantzii	fruit	Igdlorssuit
Alchemilla alpina	flower*)	do.
Crassulaceae:		
Sedum rosea	flower*)	do.
Saxifragaceae:		
Saxifraga tricuspidata	flower*)	Qarássap nunatâ
S. paniculata	flower*)	Magdlak
Oenotheraceae:		
Chamaenerion latifolium	fruit	Igdlorssuit
Cruciferae:		
Draba sp.	fruit	Qarássap nunatâ
Arabis alpina	seed	Godhavn
Umbelliferae:		
Angelica archangelica	flower*)	Anordliuitsoq
Polygonaceae:		
Polygonum viviparum	bulbil	Godhavn, Anordliuitsoq
Scrophulariaceae:		
Veronica alpina	fruit	Godhavn
Campanulaceae:		
Campanula gieseckiana	flower*), fruit	Qarássap nunatâ, Igdlorssuit
Compositae:		
Erigeron humilis	fruit	Godhavn
Antennaria canescens	fruit	Godhavn, Anordliuitsoq
Gnaphalium norvegicum	fruit	Godhavn
G. supinum	fruit	Anordliuitsoq
Arnica alpina	fruit	Ikerasak, Qarássap nunatâ
Hieracium alpinum	fruit	Anordliuitsoq
H. lividorubens	fruit	Igdlorssuit
H. rigorosum	fruit	do.
Taraxacum croceum	fruit	Godhavn, Anordliuitsoq, Igdlorssuit, Tupaussat
Graminae:		
Deschampsia flexuosa	fruit	Igdlorssuit
Calamagrostis langsdorfii	fruit	Anordliuitsoq
Elymus arenarius ssp. *mollis*	fruit	Igdlorssuit

The localities mentioned are situated as follows: Anordliuitsoq, Igdlorssuit and Tupaussat in the Kap Farvel area, Ikerasak, Magdlak and Qarássap nunatâ in the Umanak district. Regarding the meaning of the asterisks, see the text.

asterisk indicates that the exact site of sucking was not clearly observed. These instances all refer to flowers in full bloom and with copious nectar in open nectaries (Plate 1, Figs 3–4). It is believed that the bugs in these cases were drinking nectar, which may be of nutritive value to the species. In addition, however, it is suggested that imbibition of the aqueous nectar may be an important way of sustaining the water balance in the dry places where *N. groenlandicus* is generally found.

In particular, this explanation would fit the observations from *Potentilla hookeriana* and *Saxifraga tricuspidata*, which were made in the extremely dry southeastern part of the Umanak district (Ikerasak and Qarássap nunatâ; *cf.* BÖCHER, 1971, Plate 4). Many bugs sat on *S. tricuspidata*, just below the flowers, with their beaks turned upwards among the petals. On *P. hookeriana* the bugs were found inside the flowers (Plate 2, Fig. 3), and sucking on the nectaries seemed to be established in some of the cases. (Confer also with VANHÖFFEN's statement cited on p. 5).

In this context it is of great interest to note that *Nysius vinitor* BERG. causes a considerable reduction of honey in Australia by taking nectar from *Eucalyptus* and other plants (HOFFMANN, 1932).

An ample supply of water was necessary for all the species of Rhyparochrominae studied by SWEET (1960), even those from xeric habitats. According to SWEET (1964), a rhyparochromine always seeks out and imbibes free water following a feeding period. In my cultures *N. groenlandicus* drank water frequently.

EXPERIMENTS

A preliminary experiment showed that when offered hulled sunflower achenes and animal food (dead insects), *N. groenlandicus* would feed readily on the seeds*), but ignored the animal food. Next it was proved that the species thrived well for a long period on a diet of sunflower seeds and water. The only instances of predation ever observed occurred in the cultures in the form of cannibalism. Sometimes a bug that was soft-skinned and unable to move away during ecdysis was sucked out. Also, first instar nymphs would suck eggs and eventually develop to second instar on this diet if no other food was available (*cf.* EYLES, 1964).

As a consequence of the field observations of *N. groenlandicus* feeding on a great variety of plant seeds, two kinds of experiments were conducted with the following questions in mind: Does the species show preferences when offered seeds from different plant species? and is it possible for the species to complete development and eventually to reproduce, when the diet is restricted to seeds of a single plant species?

I. Food preference

Glass petri dishes of 12 cm in diameter were employed as rearing containers. The floor of the dishes was lined with filter paper, and water was supplied in small, tubular vials stoppered with cotton plugs, (*cf.* SWEET, 1960). Approximately equal amounts of different native plant seeds were mixed and scattered on the floor of the dish. In contrast to the experimental chambers used by EYLES (1964) moulds seldom occurred in the dishes, and since the seeds were provided in what was considered great surplus, they were not renewed during the experiments.

The bugs used for experiments originated from eggs laid in laboratory cultures reared on sunflower seeds and water. The diapause of the eggs was broken by exposure to low temperature (details are to be published in a following paper). A large number (60 in experiment A, 100 in B) of nymphs newly hatched from the eggs were introduced into the dishes. At irregular intervals the containers were inspected using a binocular micro-

*) For simplicity, however incorrect, the term »seed« will be used in many cases to denote the fruits of composites, grasses etc. in addition to the true seeds.

Table 2. *No. of observations of* Nysius groenlandicus *sucking different seeds etc.*

A

Plant species	Instar No. I	II	III	IV	V	Adult ♀	Adult ♂	Total
Betula nana	–	1	–	1	–	–	–	2
Empetrum nigrum ssp. *hermaphroditum*	–	–	1	7	18	7	–	33
Poa alpina	2	2	1	1	–	2	–	8
Polygonum viviparum	2	1	–	7	23	21	7	61
Potentilla crantzii	1	7	–	3	2	–	1	14
Sibbaldia procumbens	16	14	4	8	4	1	1	48
Taraxacum croceum	14	1	–	2	1	3	1	22
Veronica alpina	3	6	5	1	4	3	1	23
Saxifraga tricuspidata	9	2	1	–	–	–	–	12
Total	47	34	12	30	52	37	11	223

B

Plant species	Instar No. I	II	III	IV	V	Adult ♀	Adult ♂	Total
Betula nana	3	–	2	–	–	–	–	5
Empetrum nigrum ssp. *hermaphroditum*	–	4	22	29	25	2	–	82
Poa alpina	1	–	–	3	10	5	–	19
Polygonum viviparum	3	2	4	27	36	–	–	72
Potentilla crantzii	1	–	–	–	–	–	–	1
Sibbaldia procumbens	2	10	7	1	2	–	1	23
Taraxacum croceum	5	3	2	2	10	–	–	22
Veronica alpina	15	27	10	5	7	–	–	64
Gnaphalium norvegicum	5	4	–	1	1	–	1	12
Total	35	50	47	68	91	7	2	300

scope, and all cases of sucking the seeds were noted. Handling of the dishes did not seem to disturb the bugs much during feeding. The feeding stance and general feeding behaviour is much as described for other lygaeids (*e. g.* EYLES, 1964; SWEET, 1964).

The containers were placed in the laboratory at a temperature of about 20° C. Inside the dishes a relative humidity of about 50 % was recorded by the cobalt thiocyanate method (SOLOMON, 1958); in the laboratory it was extremely low. Since the experiments were done in winter (December 12, 1968 to February 16, 1969) daylight was at a minimum, and artificial light was only switched on at intervals during daytime and in the evening.

The results of two experiments, A and B, are presented in Table 2 and Figs 1–2. Seeds from nine plant species were used in each experiment. The only difference between the arrangement of A and B is that in B *Saxifraga tricuspidata* was replaced by *Gnaphalium norvegicum*. For some unknown

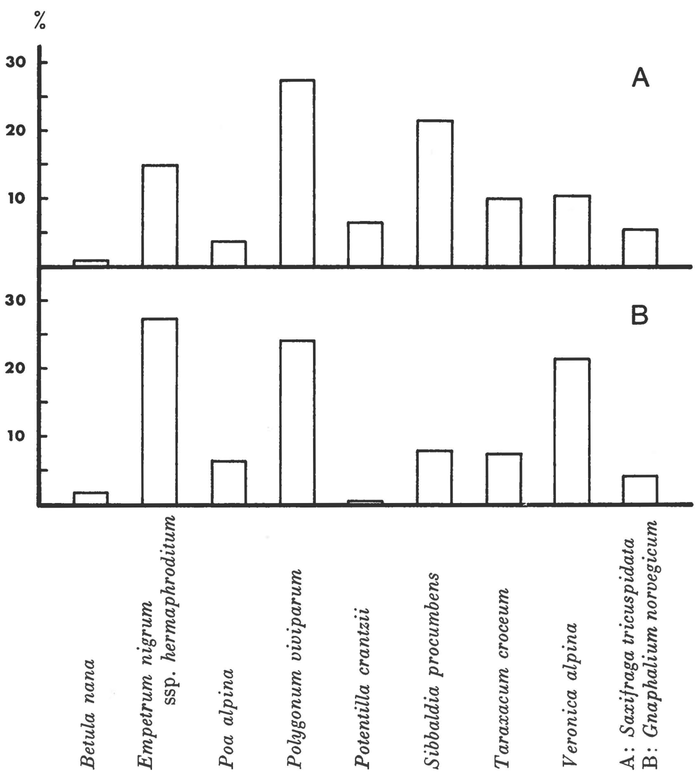

Fig. 1. Results of two food choice experiments with *Nysius groenlandicus.*

reasons a heavy mortality occurred among the adults in experiment B. This accounts for the few observations of feeding adults in this experiment.

When the total feeding is considered (Fig. 1) it is evident that *Empetrum hermaphroditum* and *Polygonum viviparum* were preferred in both experiments; in addition in A *Sibbaldia procumbens* and in B *Veronica alpina* were much favoured; *Taraxacum croceum* accounted for 9.9 $^0/_0$ and 7.3 $^0/_0$, respectively, of the observations. It must, however, be stressed that none of the seeds offered were completely neglected.

In Fig. 2 the observations of feeding on the most frequented seeds are distributed into the different nymphal instars. This makes the picture more complicated, for now it appears that the preference changed during development. This is in accordance with the observations made by PUCHKOV (1956). The young nymphs preferred *Sibbaldia*, *Veronica* and (especially in A) *Taraxacum*, but later instars changed to *Empetrum* and *Polygonum*. Not a single observation of a first instar feeding on *Empetrum* was made, but otherwise these experiments did not show an increased polyphagy during development, as stated by PUCHKOV. Females fed more

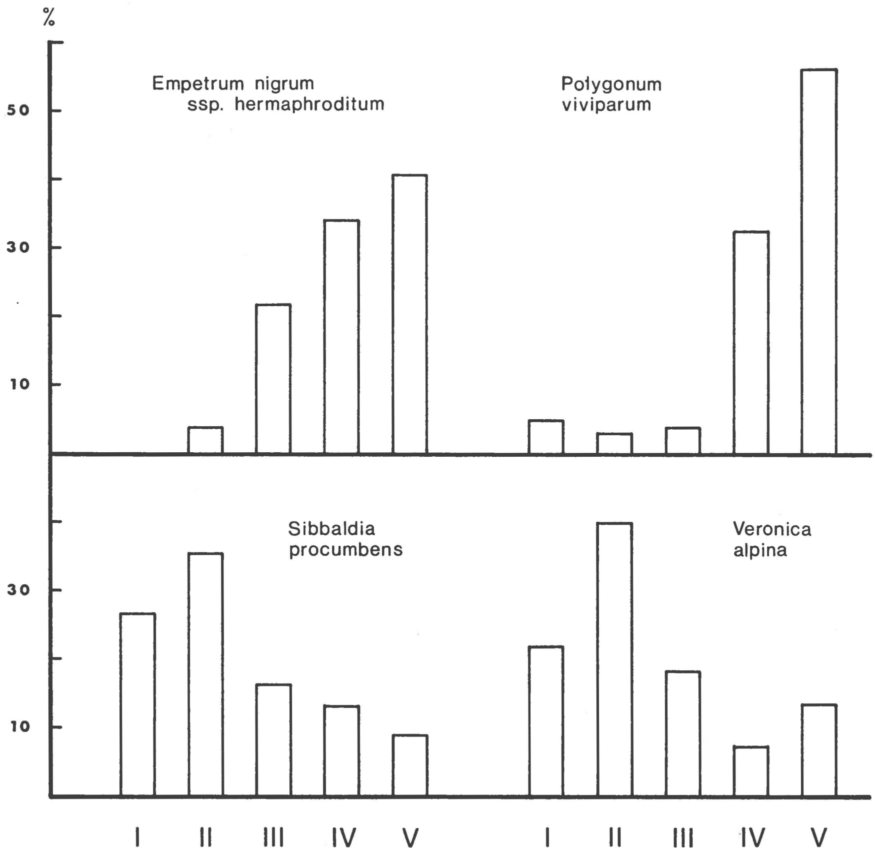

Fig. 2. Observations of sucking four of the most preferred seeds, distributed into the different nymphal instars. Data from Table 2, A and B combined.

than three times as frequently as males (44 and 13 observations, respectively; the sex ratio being about equal). This agrees with the results of field investigations (*cf.* p. 33).

II. Rearing on single-seed diets

In this experiment small colonies of newly hatched nymphs, in most cases ten, were confined in small petri dishes (of 9 cm diameter) and offered a diet of only one kind of seeds. Otherwise conditions were as described for the preference experiments.

Seeds from a total of seventeen plant species were tested, the plants belonging to those species frequently found in the habitats of *N. groenlandicus* in the Godhavn area. In addition, a single rearing dish was equipped with sunflower seeds for comparison with the natural foods, and

Table 3. *Development of* Nysius groenlandicus *on single-seed diets.*

Instar No.	I	II			III			IV			V			Adult					
Plant species	No.	No.	No. of days before appearance of the first	No. of days before maximum	No.	No. of days before appearance of the first	No. of days before maximum	No.	No. of days before appearance of the first	No. of days before maximum	No.	No. of days before appearance of the first	No. of days before maximum	No.	No. of days before appearance of the first	No. of days before maximum	Eggs laid	Maximal longevity (days)	Remarks
Dryas integrifolia..	15	5	14	16	4	20	26	4	30	32	(2)	38	–					–	Had to be interrupted after 42 days: 1 IV 2V
Potentilla crantzii..	10	6	7	11	6	13	15	6	19	23	5	27	29	1	41	–		♀:47	
Sibbaldia procumbens...........	10	6	7	9	6	13	17	6	19	23	6	25	31	4	33	35	+	♀:55 ♂:77	Great fertility
Saxifraga tricuspidata...........	10	4	6	8	3	12	16	3	20	22	3	26	32	2	34	42	+	♀:73 ♂:88	One II possibly escaped
Chamaenerion latifolium.........	17	1	8	–	1	14	–	1	20	–	1	31	–	1	41	–		–	Had to be interrupted after 42 days: 1♂
Salix glauca......	8	4	8	12	3	14	16	2	20	24								IV:30	
Betula nana......	10	5	9	11	4	13	15	4	17	21	4	23	27	2	31	35		♀:53	No oviposition in spite of introduction of males
Polygonum viviparum...........	10	9	10	10	8	14	18	6	20	24	5	26	32	5	36	42	+	♀:56 ♂:138	
Empetrum nigrum ssp. *hermaphro-* [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	

																		♂:105	the adult stage in the rearing shown
Erigeron humilis ..	**10**	**10**	4	8	**9**	10	12	**8**	14	18	**7**	20	26	**3**	28	32	+	♀:60 ♂:38	
Antennaria canescens..........	**10**	**7**	8	10	**6**	12	14	**6**	18	20	**6**	24	26	**6**	32	48	+	♀:100 ♂:96	Great fertility
Gnaphalium norvegicum........	**10**	**7**	8	16	**5**	14	18	**3**	20	24	**3**	26	32	**2**	34	40	+	♀:82 ♂:46	
Taraxacum croceum	**10**	**9**	6	8	**9**	12	16	**8**	16	20	**7**	22	28	**6**	32	42	+	♀:72 (♂:54)	Only females survived to the adult stage in the rearing shown
Helianthus sp.....	**10**	**6**	8	11	**6**	13	15	**6**	17	17	**5**	23	29	**5**	33	49	+	♀:66 ♂:66	Great fertility
Luzula confusa....	**20**	**1**	7	–	**1**	13	–											I:19 III:15	
Carex bigelowii....	**12**																	I:14	
Poa alpina.......	**10**	**7**	7	13	**5**	15	19	**4**	23	23	**3**	29	33	**2**	43	45		♀:79 ♂:77	
Mixed seeds......	**10**	**7**	9	11	**6**	13	17	**5**	19	23	**4**	25	25	**3**	33	35		♂:75	Only males survived to the adult stage
Mean values in the cases where oviposition occurred			7±2	10±3		13±1	16±2		18±2	21±2		24±2	29±3		33±2	40±5		♀:68±14 ♂:80±29	
Ranges..........			4–10	6–16		10–14	12–18		14–20	17–24		20–26	24–32		28–36	32–49		♀:55–100 ♂:38–138	

another dish contained a mixture of nearly all the seeds tested, as a sort of control.

The rearings were conducted during the winter 1968–69 and in the late autumn of 1969. The dishes were inspected once every other day. This makes the number of days elapsed before the appearance of the different instars given in Table 3 maximum values.

Rearing of small colonies instead of single individuals has some drawbacks, for instance, the bugs cannot be followed individually, as did EYLES (1964) in his impressive study of five rhyparochromine species. On the other hand, *N. groenlandicus* is pronouncedly gregarious in habits, and it was considered important to comply with this behavioural factor. On the whole, this experiment is somewhat preliminary in character, and it has, in due course, to be succeeded by more elaborate work.

The results appear from Table 3. Some of the rearings were duplicated, and only the best performances (*i. e.* greatest survival) are shown in the table. Parenthesis indicate results from a duplicate.

It will be noted that *N. groenlandicus* thrived on the seeds of all except four plants species, that is, at least one individual survived to the adult stage. In ten cases eggs were produced, but in two further cases (*Chamaenerion latifolium* and the control) only males became adults. Fecundity was especially great on the seeds of *Sibbaldia procumbens*, *Antennaria canescens* and *Helianthus* sp., thus indicating that the substitute food, sunflower seeds, used in the laboratory cultures, is as suitable as the best of the natural foods tested.

Considering separately the ten cases where oviposition occurred, the following points come out. In five cases survival to the adult stage was 50 % or more. Total mortality in the nymphal stages was 60 %, of which 32 % took place in the first instar; percentages for instars II to V were 7 %, 6 %, 6 % and 9 %, respectively. Total development from hatching of eggs to adult averaged 40 days. Mean duration of the different stages from peak to peak was as follows: I: 10 days, II: 6 days, III: 5 days, IV: 8 days, V: 11 days (standard deviations and ranges are to be found in the table). For comparison, in a rather cool summer (1967) the time of development in the field at Godhavn was estimated at about 60 days. The mean maximal longevity was a little greater for males (80 days) than for females (68 days), but the difference was not significant.

Survival was poor on seeds of *Salix glauca* and extremely poor on *Luzula confusa* and *Carex bigelowii*. The result from *Salix* ought to be tested once more, but the poor performance on seeds of *Luzula* and *Carex* strikingly seems to indicate that some seeds are completely unsuitable as food for *N. groenlandicus*. The rearing on *Dryas integrifolia* had to be interrupted, but seeds of this species did not appear to constitute a satisfactory food, since the mortality was heavy and the time of development greatly prolonged.

The mortality found in this experiment is much higher, even in the best performances, than the mortality recorded by EYLES (1964). According to EYLES most of the seeds tested should be termed "foods permitting poor survival to adults" (l. c. p. 96). Due to studies and observations in the field it is, however, unlikely that foods much more suitable than those tested are to be found in nature. It is provisionally suggested that the relatively poor survival found is caused by an inferior viability of the offspring produced by females in culture.

It is remarkable that the bulbils of *Polygonum viviparum* seem to play a significant role in the diet of *N. groenlandicus*. The same conclusion was arrived at regarding *Chlamydatus pullus* (REUT.) (*cf.* BÖCHER, 1971); and the same applies to the ptarmigan (*Lagopus mutus captus* PETERS) in Northeast Greenland (GELTING, 1937). It is interesting to note that GELTING in his extensive examinations of crop content of ptarmigans encountered only five specimens of insects, one fly (*Scatophaga furcata* SAY.) and four adult *N. groenlandicus* (l. c. p. 111). All the specimens of *Nysius* originated from the same crop, which contained a large fraction of *Polygonum*-bulbils. Undoubtedly the bugs were accidentally eaten by the ptarmigan, while both of the parties feeding on the bulbils.

FEEDING STUDIES IN THE FIELD

In the Kap Farvel area I had the opportunity of studying some very large populations of *N. groenlandicus* with respect to their foraging on the fruits of certain plant species, especially *Taraxacum croceum* and *Hieracium lividorubens* (Compositae).

I. Taraxacum

The foraging on *T. croceum* was studied during a six days' stay (July 22 to 28, 1970) at Tupaussat at the head of the fjord Kangikitsoq extending northward from Ilua.

Near the beach the vegetation consisted of a mosaic of small meadows and grassy patches, separated by dense *Salix glauca*-scrub on small, slightly elevated ridges (Plate 2). In the drier grassy areas *Nardus stricta* reigned supreme, whereas a number of species, including *T. croceum*, made up the vegetation on a little damper soil (*cf.* Table 4: Stand 1). *N. groenlandicus* was extremely abundant in the different types of grassy vegetation, and it was even taken by sweeping in the willow scrub.

In the whole area *Taraxacum* was in full fructification, and it soon became clear that *N. groenlandicus* fed on a large scale on the ripe achenes, in situ on the plants; as many as 25 bugs were counted in a single capitulum (see Plate 2). In addition, bugs were frequently observed feeding on closed, unripe fruit heads, thus (presumably) penetrating the involucre with their stylets. This action left small, brown spots on the involucre; the same happened in the case of *Hieracium* (p. 25). The nature of these spots was not established. They may either be droplets of dried up latex from the plants, or salivary sheath cones produced by the bugs (Saxena, 1963; Sweet, 1964), or possibly a combination of both.

It was noticed, moreover, that the number of bugs in the infructescences changed from time to time. On a fine, fairly clear and calm day (July 27) this was investigated in more detail (Fig. 3). The number of *Nysius* present in ten selected capitula was counted every hour, from 9 A. M. to 9 P. M. At the same time the temperature was recorded in the centre of one of the fruit heads, 20 cm above the ground, in different other places in the microenvironment, and in the air (a Grant miniature temperature

Table 4. *Plant communities.*

Stand 1. Tupaussat, Kangikitsoq. Meadow. *Alchemilla glomerulans!* *Ranunculus acris!* *Salix glauca!* *Taraxacum croceum!* *Angelica archangelica* ssp. *norvegica* *Betula glandulosa* *Carex* spp. incl. *C. bigelowii* *Deschampsia flexuosa* *Gentiana nivalis* *Nardus stricta* *Poa pratensis* *Polygonum viviparum* *Potentilla crantzii* *Thalictrum alpinum* *Vaccinium uliginosum* ssp. *microphyllum* *Stand 2.* Anordliuitsoq, Pamiagdluk. Grassy depression. *Carex bigelowii* *Cladonia* sp. *Deschampsia flexuosa* *Festuca vivipara* *Luzula* sp. mosses *Nardus stricta* *Polygonum viviparum* *Salix glauca* *Sedum rosea* *Taraxacum croceum*	*Stand 3.* Igdlorssuit, Kangersuneq qíngordleq. South facing slope. *Alchemilla alpina!* *A. glomerulans!* *Angelica archangelica* ssp. *norvegica!* *Campanula gieseckiana!* *Chamaenerion angustifolium!* *Deschampsia flexuosa!* *Hieracium lividorubens!* *Lathyrus japonicus!* *Potentilla crantzii!* *P. tridentata!* *Salix glauca!* *Thalictrum alpinum!* *Thymus drucei!* *Veronica alpina!* *Betula glandulosa* *Botrychium* (3 spp.) *Diphasium alpinum* *Draba incana* *Empetrum nigrum* ssp. *hermaphroditum* *Erigeron uniflorus* *Euphrasia frigida* *Hieracium rigorosum* *Juniperus communis* ssp. *alpina* *Leuchorchis albida* ssp. *straminea* *Luzula multiflora* *L. spicata* *Poa glauca* *Polygonum viviparum* *Polystichum lonchitis* *Rhinanthus minor* coll. *Sedum rosea* *Taraxacum croceum* *Trisetum* sp. *Woodsia ilvensis*

! Indicate dominating species.

recorder was used). The relative humidity at ground level was measured by means of a hair hygrometer (Lambrecht). On July 28, countings could, unfortunately, not be continued consistently; the few values obtained also appear in the figure.

The most interesting thing to note is that the number of bugs in the fruit heads decreased during forenoon to a rather low level at noon. After this it rose to a value three times as high at 3 P. M. and stayed about this

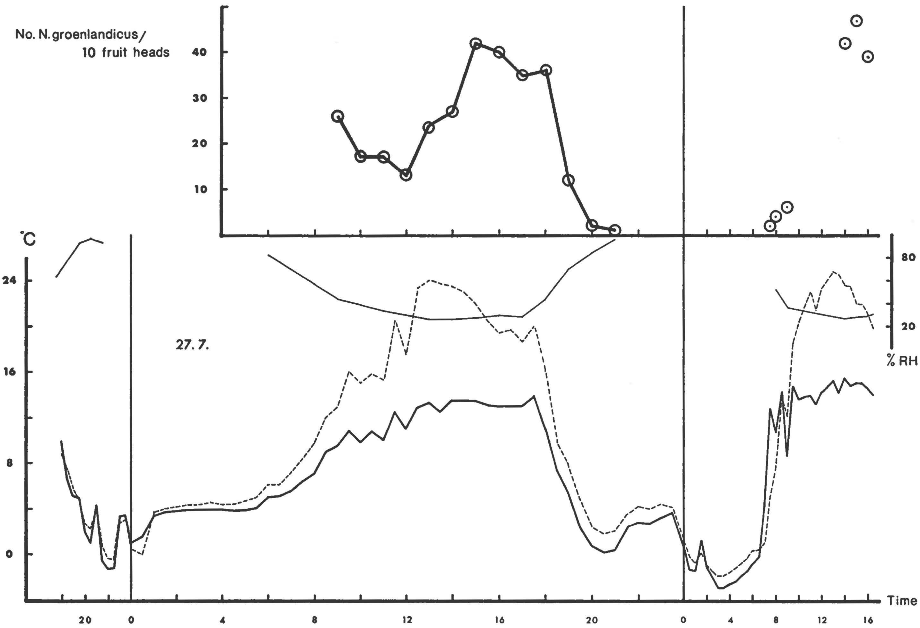

Fig. 3. Counts of *Nysius groenlandicus* in ten fruit heads of *Taraxacum croceum*, measurements of relative humidity at ground level (thin solid line), and automatic recordings (every 1/2 hour) of temperatures in a fruit head, 20 cm above ground (heavy solid line) and 1 cm above ground (thin broken line) in a grass-dominated vegetation at Tupaussat, Kangikitsoq, on July 26 to 28, 1970.

level until 6 P. M., whereupon it quickly dropped to very low values in the evening.

A rough correlation between temperature in the capitula and the number of bugs present in them is evident. However, the correlation fails in the forenoon, when the temperature rose while the number of bugs declined. The temperature on the surface of the ground reached its maximum about 1 P. M. and thereupon fell slowly during the afternoon, along with the rise in the number of bugs in the fruit heads. (Unfortunately the probe which was supposed to record the temperature on the ground surface proper was out of function; instead the temperatures from 1 cm above the ground are shown).

During the evening of July 26 the temperature dropped quickly at first to 1° C at 8.30 P. M. At this time a large number of bugs were still present in the fruit heads, but they were chilled and motionless. At 9 P. M. a light breeze moved the vegetation slightly, and many bugs fell to the ground. Later on (around 10 P. M.) the temperature fell to below zero, but the remainder of the night was fairly mild with temperatures of about 4° C, due to clouds and finally completely overcast; it did not clear up before about 9 A.M. on July 27. The overcast condition in the morning would probably exclude all activity, so the relatively high number of bugs found in the heads had most likely spent the night there.

The sun set about 6.30 P.M. and this presumably brought about the rapid decline in the number of bugs between 6 and 7 P.M. Possibly the falling temperature directly promotes an active downward movement, which was observed in some instances.

However, a number of bugs were generally trapped in the capitula by the low temperature after sunset, but this happened to only very few during the night July 27 to 28. Apart from a cloudy period before midnight, this night was clear and very cold, so that any breath of air would have shaken the chilled bugs down. In any case, extremely few bugs were found in the heads in the morning of July 28.

On July 27, from 1.45 to 2.30 P.M., the number of *N. groenlandicus* present in the fruitheads of *Taraxacum* was counted within two square metres of typical meadow vegetation. Only ripe and open infructescences which had retained at least one fourth of the achenes were included in the counting, but the fraction of heads omitted was insignificant. Each fruit head was carefully picked and immediately beaten against a white piece of cloth, from which the bugs were caught by means of an aspirator.

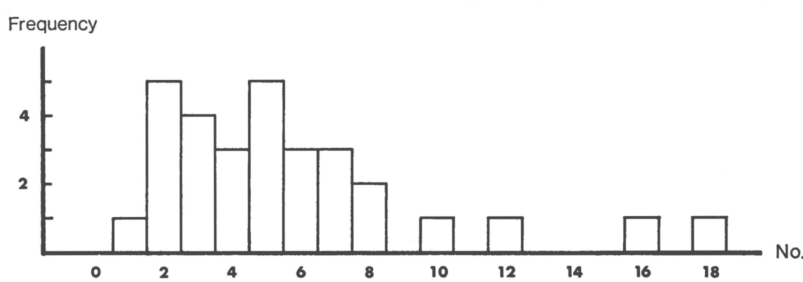

Fig. 4. Frequency distribution of the number of *Nysius groenlandicus* caught in the fruit heads of *Taraxacum croceum* from two square metres at Tupaussat, Kangikitsoq, on July 27, 1970.

The result is shown in Fig. 4. A total of 171 bugs were taken on 30 capitula, or average 5.6 ($\pm$ 5.3) per head, and 85.5 bugs in fruit heads/m^2. These values are at a minimum since the population of bugs in the heads had not yet attained its maximum (*cf.* above), and not all capitula were included. It is remarkable that no zero-values occurred.

In Fig. 5, A, the composition of the population in the infructescences is considered. Females made up 62 $^0/_0$, males 11 $^0/_0$, and nymphs (instars IV and V) accounted for 28 $^0/_0$. At the same time a sample from the ground surface (searching for 1/4 hr.) beneath the fruit heads yielded 237 *Nysius* with the composition shown in Fig. 5, B. Here the nymphs constituted 59 $^0/_0$ and the adult males outnumbered the females. It is possible to

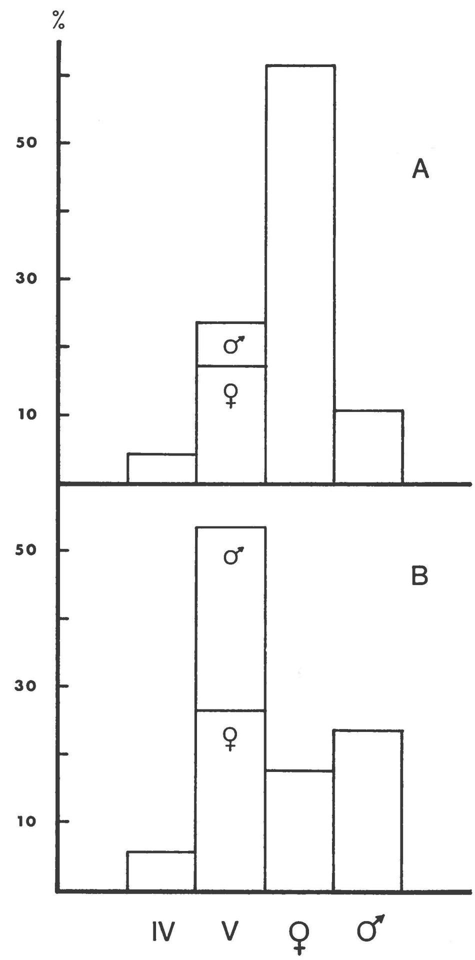

Fig. 5. The composition of the population of *Nysius groenlandicus*, A, in the fruit heads of *Taraxacum croceum* from two square metres, and, B, on the ground surface, at Tupaussat, Kangikitsoq, on July 27, 1970. (χ^2 test of sex-ratios: A, V, $P < 0.05$; A, adults, $P < 0.001$; B, V & adults, not significant).

determine the sex of the fifth instars (EYLES, 1960, 1963; JOHANSSON, 1958). In the capitula females made up 73 $^0/_0$ of this stage, whereas on the ground the sex-ratio was equal.

A similar investigation was carried out in another locality, near Anordliuitsoq on the island Pamiagdluk, on August 4. Counts were made on the infructescences of *Taraxacum*, which were found rather sparsely distributed in a grass-grown depression measuring about 2×38 m² (Table 4: Stand 2) on a slightly falling slope with a southeastern exposure. Counting was carried out from 3 to 5 P. M. in calm, clear weather with an air temperature of 13° C. All the fruit heads, whether ripe or not, were included.

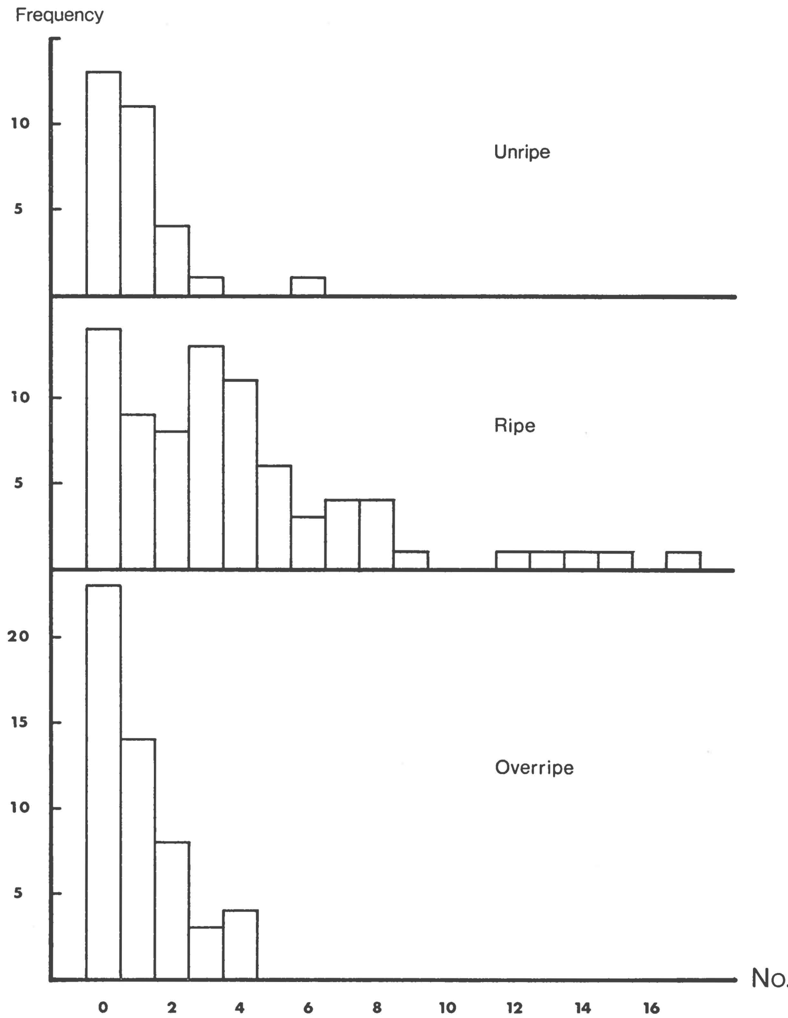

Fig. 6. Frequency distribution of the number of *Nysius groenlandicus* caught in the fruit heads of *Taraxacum* from a grass-grown depression near Anordliuitsoq, Pamiagdluk, on August 4, 1970.

The results are presented in Table 5 and Figs 6 to 7. A total of 379 *N. groenlandicus* was caught in 160 capitula, *i. e.* average 2.4 ($\pm$ 11.0) per head, and 5.0 in heads/m^2 (3.8 $\pm$ 7.9/ripe head). From Table 5 appears that though the unripe and "overripe" infructescences constituted 51 $^0/_0$ of the total, they were responsible for only 22 $^0/_0$ of the attendance of bugs. The ripe heads accounted for 3.9 bugs in heads/m^2 (compared with 85.5 in Tupaussat).

Fig. 6 shows the frequency distribution of bugs per fruit head according to the different conditions of the capitula. The largest

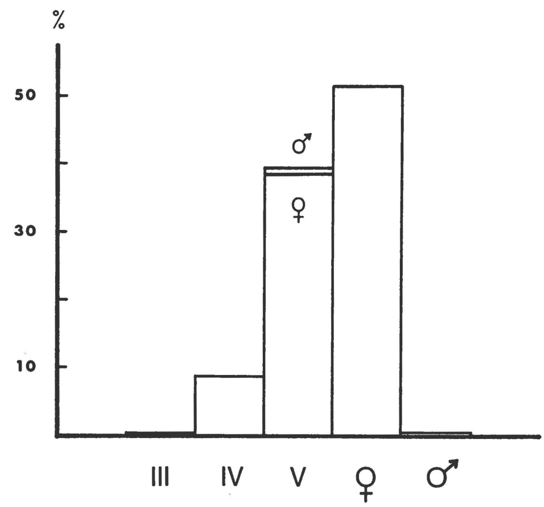

Fig. 7. The composition of the population of *Nysius groenlandicus* in the fruit heads of *Taraxacum croceum* at Anordliuitsoq, Pamiagdluk, on August 4, 1970. (χ^2 test of sex-ratios: V, $P < 0.001$; adults, $P < 0.001$).

values and the smallest fraction of zero-values were found in the ripe heads.

Fig. 7 corresponds to Fig. 5, A, and shows the composition of the population of *N. groenlandicus* in the fruit heads at Anordliuitsoq. Adult males were practically absent, only one was found, and among the fifth instar nymphs only three of the total 137 were males. In other words, the tendency met with in Tupaussat was here carried to an extreme.

Table 5. *Results of countings of* Nysius groenlandicus *in the fruit heads of* Taraxacum croceum *at Anordliuitsoq, Pamiagdluk.*

Fruit heads			Nysius		
State	No.	%	No.	%	Average/fruit head
Unripe............	30	18.8	28	7.4	0.9 ± 2.5
Ripe..............	78	48.7	296	78.1	3.8 ± 7.9
Overripe..........	52	32.5	55	14.5	1.1 ± 4.1
Total.............	160	100.0	379	100.0	2.4 ± 11.0
$2.1/m^2$			5.0 in fruit heads/m^2 3.9 in ripe fruit heads/m^2		

II. Hieracium

August 10 to 16, 1970, I was in the most inland part of the Ilua fjord-system, at Igdlorssuit in the northeastern branch, Kangersuneq qíngordleq. I have previously mentioned this magnifiscent locality (B. 1971, p. 26). A small river valley leading east-west is bordered to the north by a fairly steep slope from the mountain, Igdlorssuit qâqât (2292 m). This slope faces exactly south and is covered to a height of about 300 m by an extremely rich and luxuriant vegetation (Plate 3).

The population of *N. groenlandicus* here was the largest I have ever encountered. The species constituted 80 % of the total insects caught by a general sweep net sample from the slope. It not only occurred everywhere on the slope, but even prevailed in the scattered *Chamaenerion latifolium*-vegetation in the valley.

Hieracium lividorubens was a dominating plant on the slope, and this species, among others, was heavily infested with *N. groenlandicus.* Most *Hieracium*-plants were blooming, and buds were still present; however, the withered, yet not ripe infructescences predominated.

N. groenlandicus frequented and fed upon flower heads and fruit heads in all stages of development. In nearly all the cases when sucking was observed, it occurred on the exterior of the capitula, *i. e.* the mouthparts had to pierce the involucre before reaching the developing achenes (Plate 4).

A study area was established in a typical vegetation (Table 4: Stand 3) about 50 m above sea-level (Plate 3, Fig. 2). Here temperatures were recorded in a number of characteristic places in the micro-landscape, and measurements of the relative humidity at ground level were frequently taken. Twenty plants of *H. lividorubens*, in two groups of ten, about 10 m apart, were selected. At regular intervals of one or two hours from August

Table 6. *Results of total counts of* Nysius groenlandicus *on* Hieracium lividorubens *at Igdlorssuit, Kangersuneq qíngordleq.*

		Stems	State of capitula			Total
			In bud	Flowering	Withered	
Upper stand	No.	47	46	154	207	454
(10 plants)	%	2.5	2.4	8.2	11.0	24.1
Lower stand	No.	74	28	223	1104	1429
(10 plants).........	%	3.9	1.5	11.8	58.6	75.8
Total................	No.	121	74	377	1311	1883
	%	6.4	3.9	20.0	69.6	99.9

Table 7. *Average frequentation of* Nysius groenlandicus *per capitulum of* Hieracium lividorubens *per count.*

	Total stems	State of capitula			Total
		In bud	Flowering	Withered	
Upper stand. Capitula: 20 in bud, 13 flowering, 28 withered	1.2	0.06	0.30	0.18	0.19
Lower stand. Capitula: 4 in bud, 13 flowering, 22 withered...	1.9	0.17	0.43	1.25	0.93
Total......................	3.0	0.08	0.36	0.66	0.47

12 to 15, the number of *Nysius* attending the plants and the position of the bugs on the plants were recorded by carefully counting.

The countings are summarized in Tables 6 and 7. In both tables the two stands of *Hieracium* are compared. Withered flower heads constituted 50 % of the total number of capitula and accounted for 70 % of the visiting bugs. Flowering capitula (26 %) attracted 20 % of the bugs. The remainder was noted on flowerbuds and stems (sucking was never observed on stems or leaves).

Table 7 gives the average number of bugs per capitulum per count. It appears that the heads of the "lower" stand contributed an average of five times as much as the "upper" stand to the total attendance by *N. groenlandicus*. The difference is particularly pronounced in the withered heads; in the upper stand the blooming heads were visited more than the withered ones. The vegetation and micro-topography surrounding the two stands were practically identical, so the difference in the number of bugs ascending the *Hieracium*-plants must be attributed to local variation in the population density of *N. groenlandicus*.

Fig. 8 shows, for the whole period studied, a) the results of the single counts of *N. groenlandicus* on the *Hieracium*-plants, b) the activity level of *Nysius* on the ground surface, c) relative humidity at ground level, and d) temperatures: on the ground surface (in a small spot favoured by *Nysius*), in a *Hieracium*-flower head (40 cm above ground), and in the air (100 cm above ground).

Countings started on August 12 at 10 A.M. On August 11 the weather was variable, sun in the morning and rain in the afternoon, and cleared up at 7 P.M. Aside from a fog in the morning of the 12th and some clouds in the evening and during the night 12th to 13th, the spell of August 12 to 14 was clear and there was very little wind. Sunrise and sunset took place at 6.30 A.M. and 6.15 P.M. During the evening of the 14th the sky

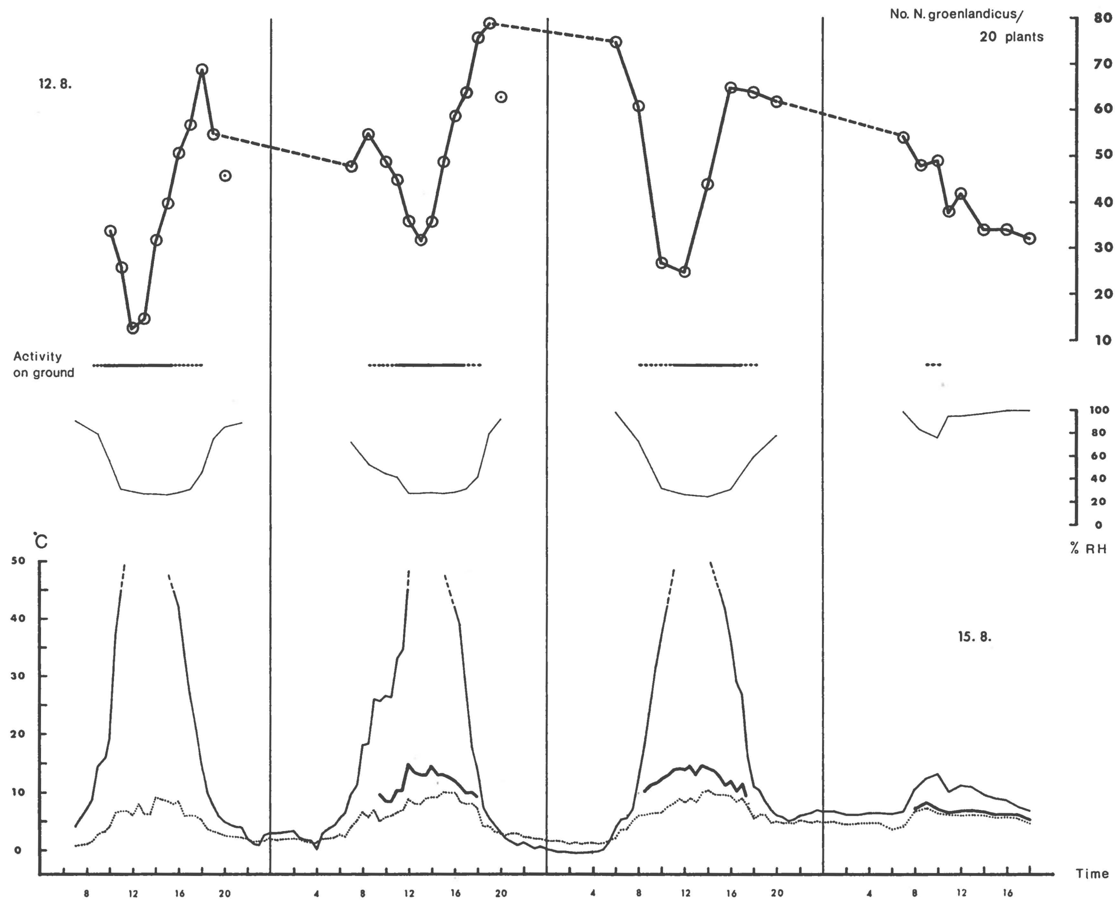

Fig. 8. Counts of *Nysius groenlandicus* on 20 plants of *Hieracium lividorubens*, observations of the species' activity on the ground surface, measurements of relative humidity at ground level, and automatic temperature recordings, from a slope at Igdlorssuit, Kangersuneq qíngordleq, on August 12 to 15, 1970. Temperature recordings taken every 1/2 hour on a) the ground surface in a small spot very much favoured by *Nysius* (solid line; the curve is incomplete because the apparatus was not prepared to measure temperatures above 45° C), b) 100 cm above ground (dotted line) and c) in a capitulum of *H. lividorubens*, 40 cm above ground (heavy solid line; recordings commensed on August 13). Only part of this curve is drawn; during night it was intermediate between the two others, although closest to the air temperature curve. Regarding the "activity on ground", the broken line indicates *N. groenlandicus* showing spontaneous activity, the solid line indicates that the species was able to fly.

clouded over, and in the morning on August 15 it began to rain. During the afternoon the rain became even heavier.

The figure convincingly shows that a cyclic change in the size of the population of *N. groenlandicus* attending the *Hieracium*-plants took place during the spell of fine weather. The number of bugs reached its maximum value about 6 to 7 P. M. and remained at approximately the same level throughout the night, however with a slight decline. (The counts at 8 P. M. on August 12 and 13 are indicated on the figure, but disregarded in the shape of the curve. The values are obviously too low, no doubt because the advancing darkness rendered the counting more difficult, and it is unlikely that the number of bugs would increase during night). During forenoon the number decreased considerably, attaining its minimum about noon, whereupon a new increase set in.

Quite another picture was seen during the rainy weather on August 15. That day there was no marked reduction about noon; the number of bugs in the capitula fell slowly and irregularly during the day.

The rain did not seem to bother *N. groenlandicus* very much; however, the accompanying lowering of the temperature hampered the activity and made the bugs nearly motionless, but they continued to feed. A characteristic retreating reaction to the rain was noted. The bugs took shelter on the underside of the flower heads, where they were found packed in clusters, most often nearly covered by water. The same reaction was observed on other plants, for instance, on the long spikes of *Elymus arenarius* ssp. *mollis* up to 16 *Nysius* were counted in a single row on the leaward side of the spikes.

The slow reduction in number during August 15 was probably due to bugs accidentally hit and driven to the ground by raindrops. On the 12th

Table 8. *Results of countings of* Nysius groenlandicus *on* Hieracium lividorubens *in two square metres at Igdlorssuit, Kangersuneq qíngordleq.*

	No.	Square metre 1	Square metre 2
Nysius	Per m^2	111	96
	Average per plant	3.1 (± 5.6) Range: 0–31	4.8 (± 3.7) Range: 0–13
	Average per capitulum	0.8 (± 1.2) Range: 0–7	1.6 (± 1.3) Range: 0–5.5
Hieracium	Per m^2	36	20
	Capitula per m^2	144	60
	Capitula average per plant	4 (± 2.5) Range: 1–12	3 (±0.9) Range: 1– 4

the number of bugs in the capitula started at a much lower level than the following two days, in fact a level similar to that during the rainy day, August 15. Accordingly, the low level on the 12th was possibly a product of the showers in the afternoon on August 11.

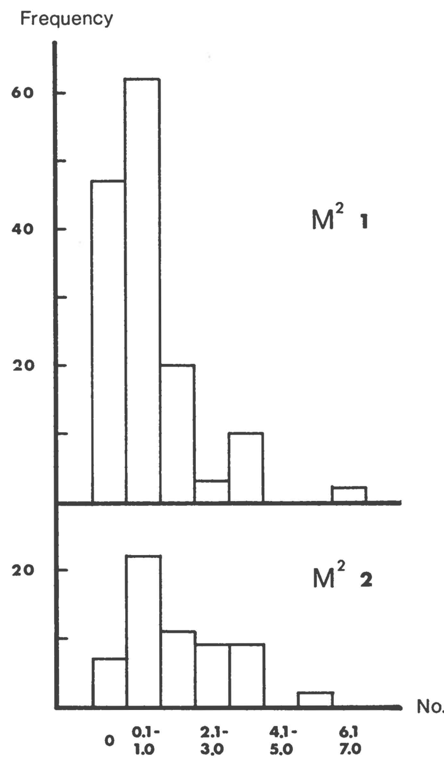

Fig. 9. Frequency distribution of *Nysius groenlandicus* caught on the plants of *Hieracium lividorubens* from two square metres at Igdlorssuit, Kangersuneq qíngord-leq, on August 12, 1970.

Table 8 and Figs 9–10 summarize the results of a collection of *N. groenlandicus* from the plants of *H. lividorubens* growing in two square metres close to the study area (August 12, 16.15 to 17.45 P. M.). It was necessary to let each plant constitute the sample unit, and the frequency distributions are based on the mean number of bugs per capitulum per plant. The two square metres were not adjoining and the results from each are treated separately.

It appears, that nearly the same number of bugs, about 100, were caught on the *Hieracium*-plants of each square meter. However, the two stands differed in density and the number of capitula per plant, so that the average number of *Nysius* per plant and per capitulum were different for the two square metres.

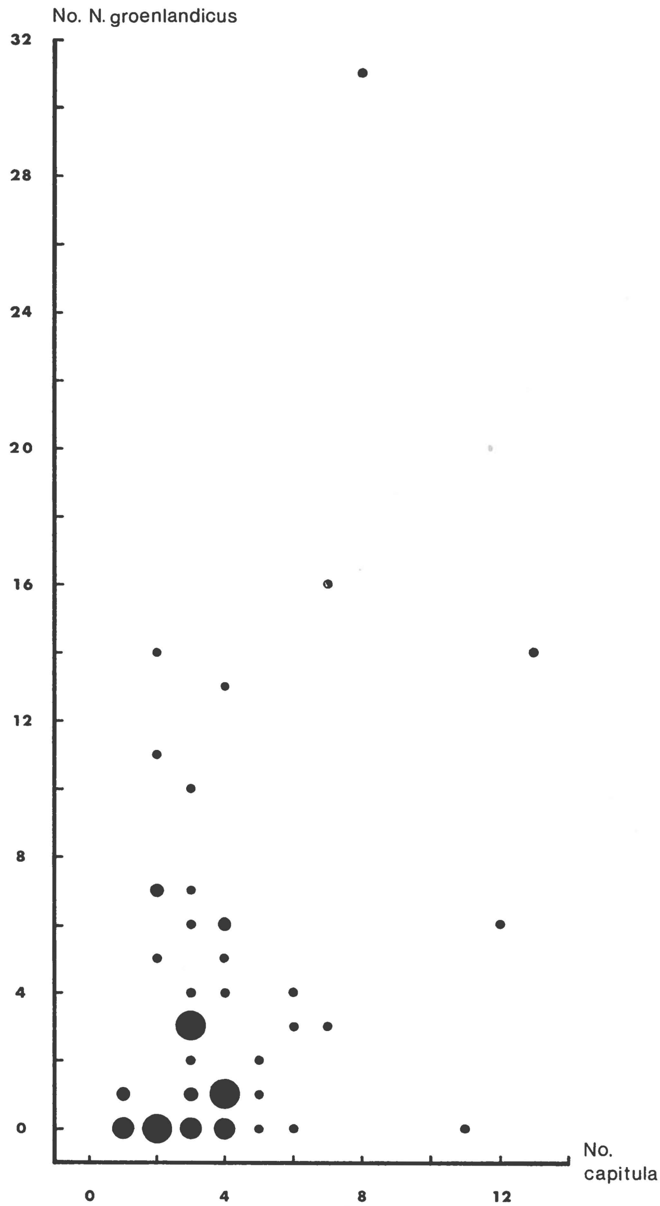

Fig. 10. The relation between the number of *Nysius groenlandicus* caught on each plant of *Hieracium lividorubens* and the number of capitula on the plants from two square metres at Igdlorssuit, Kangersuneq qíngordleq, on August 12, 1970. The four size-classes of dots represent from one to four observations.

Fig. 10 shows that there was no correlation between the number of flower heads per plant and the number of bugs per plant (results from both squares).

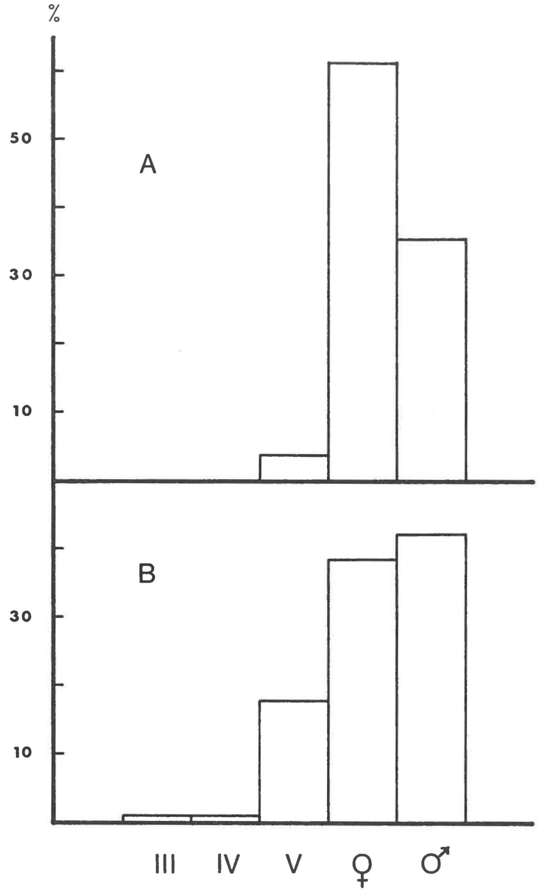

Fig. 11. The composition of the population of *Nysius groenlandicus*, A, on the plants of *Hieracium lividorubens* from two square metres, and, B, on the ground surface, at Igdlorssuit, Kangersuneq qíngordleq, on August 12, 1970. (χ^2 test of sex-ratios: A, adults, $P < 0.001$; B, adults, not significant),

The composition of the population of *N. groenlandicus* on the plants (Fig. 11, A) showed the same preponderance of females seen in the case of *Taraxacum*; and when a searching-sample (1/4 hr.) yielding 107 bugs from the ground surface among the *Hieracium*-plants is considered (Fig. 11B), it showed a more equal sex-ratio (most males) and a larger fraction of immature stages.

Discussion of the field studies

Both *N. groenlandicus* and the plants, *Taraxacum croceum* and *Hieracium lividorubens*, occur abundantly in the inland, relatively dry parts of the Kap Farvel area. From the studies on the foraging of *N. groenlandicus* on these plant species, it is evident that their fruits must be an essential part of the diet of the bug where the species are found together. The ripe achenes were clearly preferred, but feeding also took place on the developing fruits, on ovaries in blooming flowers, and even on the buds. Sucking was never observed on vegetative parts of the plants.

The cyclic changes found in the number of bugs attending the plants during the day deserve further investigation and experimental work. It is interesting to compare these changes with COULIANOS' (1961) studies on the behaviour of *Nithecus jacobaeae* (SCHILL.). Contrary to the behaviour observed in *N. groenlandicus*, this orsilline species ascended the vegetation (grasses) in the middle of hot and sunny days when the temperature on the ground surface attained maximum values. COULIANOS showed experimentally that *Nithecus* avoided temperatures above 36° C, and that it climbed the vegetation only in order to get into cooler surroundings; feeding on the grasses was never observed, whereas aggregation of bugs in the vegetation favoured copulation. COULIANOS referred to earlier observations of lygaeids and other ground-dwelling insects occasionally climbing the vegetation (for instance JORDAN'S (1933) on *Nysius* spp.) and he assumed that they were all heat-avoiding responses. MILLIKEN (1908) reported *Nysius ericae* (SCHILL.) seeking shade and feeding less during the hot part of the afternoon. On the other hand, GURR (1957) found that the main feeding period for *N. huttoni* WHITE is in the middle of the day, and that the bugs conceal themselves under clods and debris on the ground as soon as the temperature begins to fall in the evening.

N. groenlandicus is an extremely sun-loving, xerophilous and termophilous insect with a "temperature preference" well above 30° C; it does not show escape reactions until the temperature reaches above 40° C (documentation will appear in a later contribution). For the present, it is suggested that precisely this thermophily of the species accounts for the downward movement of the bugs in the middle of the day. The bugs are attracted to the hot ground-surface that permits an extreme degree of activity, allowing for dispersing to new foraging grounds, sexual activities, etc. Temperatures on the ground equalled those measured by COULIANOS (above 50°C), but the fairly dense, low vegetation and the varied microtopography made the microclimatic conditions here much less severe than in his study.

As the temperature on the ground decreases during the afternoon, an upward movement to the foraging grounds in the upper parts of the vegetation begins. The maximal number of bugs in the fruit heads is attained late in the afternoon or in the evening at 6 to 7 P. M. (*Hieracium*). In the evening *Nysius* behaved differently in the studies on *Taraxacum* and *Hieracium*: in *Taraxacum* the bugs left the infructescences after sunset, whereas in *Hieracium* the population stayed there overnight. However, it is possible that continued observations regarding the foraging on *Taraxacum* would show that the difference is not consistent, the downward movement from the infructescences on July 27 being an exception. The relatively high number of bugs in the fruit heads in the morning on July 27 might point in this direction.

In any case, it is obviously an advantage to spend the morning and evening in the capitula, because the suns' rays reach there earlier in the morning and leaves there later in the evening compared with the ground surface, thus extending the period of activity and feeding. It was observed that the bugs feeding in the capitula during morning and evening exposed their bodies to the maximal insolation (Plate 4, Figs 1–2).

A tendency to leave the exterior of the capitula and to crawl into the blooming flower heads during night was observed. At 4 P. M. on August 14 bugs were found exclusively on the outside of the capitula, whereas 13 $^0/_0$ and 23 $^0/_0$ were noted inside flower heads at 6 P. M. and 8 P. M., respectively. Possibly the bugs (reacting to the diminishing light?) seek shelter from wind, etc. during the cool hours of the night in this way. There was a slight elevation of the temperature in a flower head compared with the ambient air at the same level during the day, but this was not observed during the night.

It is evident that the only purpose of the upward movement to the capitula is to feed. Even though a few copulations have been observed on *Hieracium*, the fruit heads are the seat of sexual activity only to a minor extent, this activity generally takes place on the ground. The general excess of females in the capitula points in the same direction. Probably the greater need for nutrition on the part of the egg-producing females is responsible for this skewness, and it is interesting that it is not confined to the adult stage (Figs 5 and 7). On the whole, however, only a small fraction of the nymphs compared with the adults participate in the ascend to the capitula.

APPENDIX

Note on oviposition in relation to food-source

The results of an experiment intending to show the preferred substratum for oviposition of *N. groenlandicus* will be dealt with here because the outcome has some connection with the feeding biology of the species.

The apparatus used, a large, radially divided petri dish, was equipped with five different kinds of substrates in the radial sections, so that the two sections opposite each other contained the same material (*cf.* Böcher, 1971, p. 24). The substrates offered were 1) gravel, 2) sand, 3) ground litter, 4) moss, and 5) withered flowers, dry fruits and seeds.

A single hulled sunflower seed was put in each of the ten sections, and wet filter paper was placed in a small, central room, providing a source of water for the insects. A total of 34 females and 37 males of *N. groenlandicus* were caught in the field (the surroundings of Godhavn) in the middle of September, 1969, and introduced into the apparatus. At that time egg-laying was probably at its peak in nature, and the bugs continued deposition in captivity.

The experimental period was September 12 to 28, during which the bugs visible in each section were counted at irregular intervals using a binocular microscope; following each count the apparatus was turned to a new position. Immediately after the period, the eggs deposited in each substrate were counted.

The results are shown in Fig. 12. According to the observed position of the bugs the substrates were preferred in the following order: seeds, moss, litter, gravel and sand. According to the oviposition the substrates were preferred in the same order as above, with the exception of sand and gravel having changed places; the "seed"-sections were tremendously favoured and accounted for more than 70 % of the total deposition of eggs. The moss-sections contained nearly the remainder of the eggs, since only very few were laid in the remaining three substrates.

Table 9 specifies the oviposition in the sections containing fruits, seeds, etc. It appears that more than 90 % of the eggs were deposited on, and attached to the plant fragments. Only 10 % were found on the floor, but even this fraction may have originally been laid on the plants and

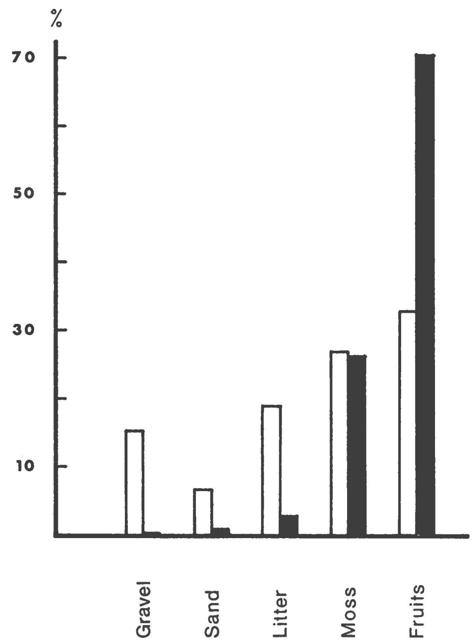

Fig. 12. Frequency distribution of *Nysius groenlandicus* counted on different substrates (white columns) and the number of eggs deposited in the substrates (black columns). Total 1634 positions were recorded by 51 countings. The total number of eggs was 2480.

Table 9. *Contents of the sections (cp. Fig. 12) equipped with fruits, seeds etc. and the position of eggs deposited by* Nysius groenlandicus.

Plant species	Part of the plant	No. of egg
Alchemilla glomerulans	1 inflorescence	17
Antennaria canescens	9 inflorescences	397
Campanula gieseckiana	1 flower	7
Cerastium alpinum	4 flowers	214
Dryas integrifolia	10 achenes	4
Empetrum nigrum ssp. *hermaphroditum*	16 berries (dry)	55
Erigeron humilis	1 inflorescence	225
Gnaphalium norvegicum	1 inflorescence	11
Polygonum viviparum	2 inflorescences	161
Potentilla crantzii	11 flowers	399
Taraxacum croceum	1 inflorescence	83
Eggs loose on the floor		173
Total		1746

later pushed off the primary site due to the intensive activity of the bugs in these sections.

It seems justified to conclude that *N. groenlandicus* prefers to oviposite on, or in the immediate vicinity of, seeds. This habit is obviously of great value for the species, since the nymphs, when hatching from the eggs, will find themselves close to a source of food. A considerable fraction of the eggs were deposited in moss. This agrees well with field observations where the small nymphs are very often found on the surface of mosses, in which they seek shelter and where extremes of the microclimate are avoided. Moreover, mosses act as "collectors of seeds". Along the margins of moss cushions a fringe of seeds is usually present.

Plate 5 shows some examples of how individual eggs were deposited in the experiment. The cases (Figs 3–4) where eggs were attached to the achenes of composites (and *Dryas*) that are equipped with a parachute device for wind dispersal are of particular interest.

In a following paper it will be documented that *N. groenlandicus*, in spite of its very stationary habits and the absence of migrational movements, is distributed throughout Greenland and occurs as good as ubiquitously. The species is present on even the smallest and most remote islands; the author has as yet not visited a single place in Greenland devoid of the species.

Egg-laying of *N. groenlandicus* has not yet been observed in nature, but oviposition in fruit heads etc. has been reported for some other orsilline species (MILLIKEN, 1918; SMITH, 1927; USINGER, 1942; CARRILLO, 1967).

SMITH noted oviposition of *Nysius vinitor* BERG. on the pappus of the mature flower heads of *Sonchus oleraceus* (Compositae) in Queensland. Bundles of eggs were attached to the lower half of the pappus. Occasionally he found eggs attached singly to the feathery awns of the seeds in the mature panicle of the grass, *Imperata arundinacea.*

If *N. groenlandicus* usually deposits its eggs on seeds and fruits equipped with parachutes, as demonstrated in the laboratory, this might imply an important means of dispersal of the species, and possibly account for its ubiquity. The bug would, so to speak, be a parasite on the dispersal mechanism of the plants. Furthermore, the small nymphs would be ensured at least some food readily available—namely the seed or fruit on which the egg was borne.

It is important to note that the fruits of the Compositae that seem to play a dominating role in the diet of *N. groenlandicus* are nearly all equipped with parachutes. Other plants which might be considered in this connection are *Dryas*, *Chamaenerion*, some grasses, and possibly *Salix.*

Of course, the eggs would increase the weight of the fruits (seeds) and thereby reduce the distance that the parachute would otherwise have been able to carry it. However, as far as the large, robust achenes of, for instance, *Taraxacum* and *Hieracium* are concerned, the augmentation in weight would be negligible; but further observations and experiments are very greatly needed.

Nonetheless, it is provisionally suggested that a tendency for *N. groenlandicus* to oviposit on fruits and seeds, many of which are dispersed by the wind, is responsible for the ubiquity of the species in Greenland. In this way the general trend for arctic insects to loose their migrative behaviour and to become stationary (*cf.* DOWNES, 1962, 1965) is combined with an effective method of dispersal that does not involve the adult insect.

Going through the literature on Orsillinae, I encountered a small note that expresses the same idea and adds to the likelihood of the hypothesis suggested above. CARRILLO (1967) observed a heavy infestation of *Nysius tenellus* BARBER on *Picris echioides* (Compositae) in California. He found that eggs were commonly fastened to the pappus bristles of the fruits, singly or in groups of up to six eggs stuck to several bristles in each fruit. He concluded as follows: "This habit of oviposition may well represent a means of dispersal of the species, since the fruits are easily blown by the wind carrying the eggs along".

SUMMARY AND CONCLUSIONS

1. Among the Lygaeidae a number of studies have recently been made on the general biology and the feeding habits of the dominant subfamily, the Rhyparochrominae. However, another important subfamily, the Orsillinae, including *Nysius* Dallas, is relatively unknown biologically.

2. *Nysius groenlandicus* (Zett.) is distributed throughout Greenland and is very common nearly everywhere. The micro-habitat of the species and observations of the species sucking seeds and fruits on plants in the field indicated seed-feeding. Occasionally *N. groenlandicus* was observed visiting flowers in full bloom and with copious nectar in open nectaries. It is suggested that the bugs in these cases were imbibing nectar, which may be of importance for sustaining the water balance in the xeric places inhabited by the species.

3. Experimentally it was confirmed that seeds and fruits constituted the food since *N. groenlandicus* was able to develop from egg to egg-producing adult not only on a mixture of different native seeds, but also when the diet was restricted to seeds of single plant species (including *Helianthus*, the achenes of which were used as a substitute food in laboratory cultures). In the first case a preference for certain seeds was established, but the preference changed during development of the bugs. Some natural seeds were found to be completely unsuitable as food for *N. groenlandicus*.

4. Investigations concerning the foraging of the species on *Taraxacum croceum* and *Hieracium lividorubens* (Compositae) were carried out in the field. In both species a cyclic change in the number of bugs attending the capitula was found during fine weather spells. The number decreased markedly about noon and attained a maximum late in the afternoon or in the evening. It is suggested that the hot ground surface at noon attracts the thermophilous bugs from the feeding places in the upper strata of the vegetation. On the other hand, it is advantagious to spend the morning and evening in the fruit heads, where the sun period is extended compared with the ground surface. Mainly females foraged in the capitula, presumably because of their greater need for nutrition; sometimes males were

rare, and nymphs made up a much lower percentage in the capitula than on the ground. Values were obtained for the average number of bugs per capitulum and in capitula per square meter.

5. An experiment regarding the preferred substratum for oviposition in the species is described. A substratum consisting of a mixture of withered flowers, dry fruits and seeds was clearly preferred to gravel, sand, ground litter and moss. The cases where eggs were attached to seeds and fruits equipped with a parachute device for wind dispersal are of special interest. It is provisionally suggested that the tendency for *N. groenlandicus* to oviposit on fruits and seeds, many of which are dispersed by the wind, may account for the ubiquity of the species in Greenland.

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Færdig fra trykkeriet den 30. maj 1972.

PLATES

Plate 1

Fig. 1. *Nysius groenlandicus* feeding on the fruits of *Calamagrostis langsdorfii* at Anordliuitsoq, Pamiagdluk, in the Kap Farvel area. The length of the bug is 4–5 mm.
J. B. phot. 21/8 1970.

Fig. 2. *Nysius groenlandicus* feeding—and nearly hidden—in a fruit head of *Erigeron humilis*. Taken at Anordliuitsoq, Pamiagdluk, in the Kap Farvel area.
J. B. phot. 31/8 1970.

Fig. 3. *Nysius groenlandicus* probably drinking nectar from a flower of *Potentilla hookeriana* at Ikerasak in the Umanak district. J. B. phot. 20/7 1969.

Fig. 4. *Nysius groenlandicus* probably drinking nectar from a flower of *Potentilla tridentata* at Anordliuitsoq, Pamiagdluk, in the Kap Farvel area.
J. B. phot. 22/8 1970.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Plate 2

Fig. 1. Meadow vegetation dominated by *Taraxacum croceum* and surrounded by willow scrub at Tupaussat, Kangikitsoq, in the Kap Farvel area, facing W. *Cf.* Table 4: Stand 1.

Figs 2–3. *Nysius groenlandicus* feeding in fruit heads of *Taraxacum croceum* at Tupaussat. In Fig. 2 the fruit head is heavily infested (at least 20 bugs are visible).
J. B. phot. 27/8 1970.

Fig. 1

Fig. 2

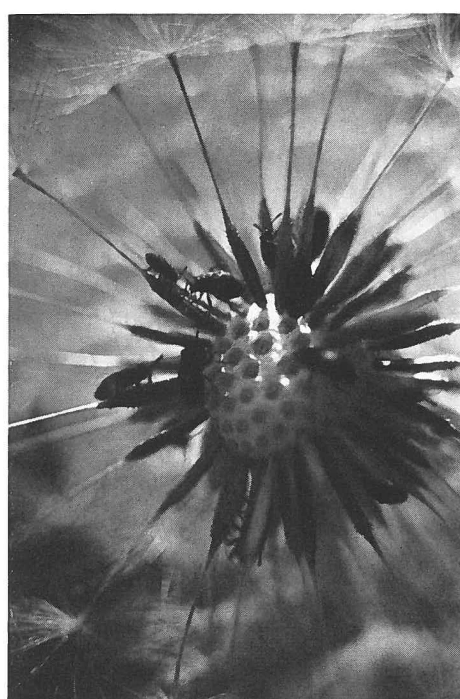


Fig. 3

Plate 3

Fig. 1. View of the slope at Igdlorssuit, Kangersuneq qíngordleq, in the Kap Farvel area, facing W.

Fig. 2. The study area on the slope at Igdlorssuit. The flowering plants are *Hieracium lividorubens* and *Chamaenerion angustifolium*. The willow branch in the middle of the picture was used to carry some of the probes from the miniature temperature recorder (in the case). *Cf.* Table 4: Stand 3. J. B. phot. 13/8 1970.

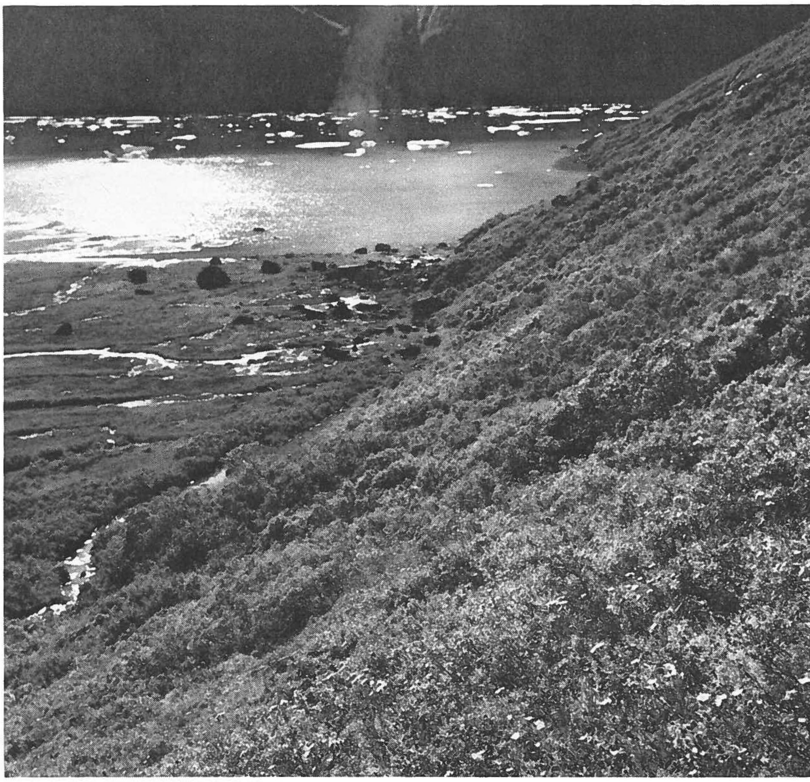


Fig. 1

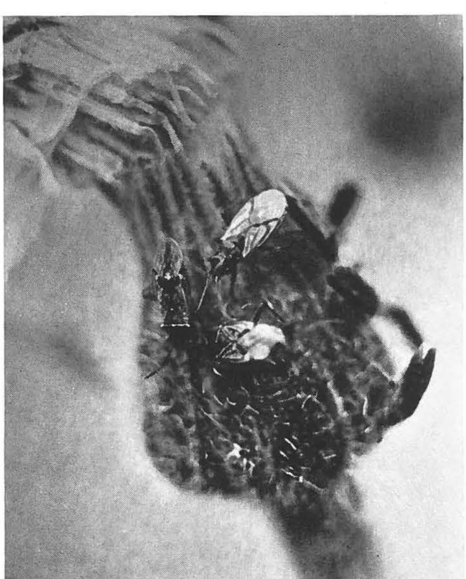
Fig. 2

Plate 4

Nysius groenlandicus feeding on unripe capitula of *Hieracium lividorubens* at Igdlorssuit, Kangersuneq qíngordleq, in the Kap Farvel area. In Figs 1–2, which are taken early in the morning and late in the evening, respectively, the bugs expose themselves to the maximal insolation. In Fig. 4, the specimen to the right has buried its mouthparts completely in the plant, presumably in order to reach the ripening achenes through the involucre. J. B. phot. 12–14/8 1970.

Fig. 1

Fig. 2



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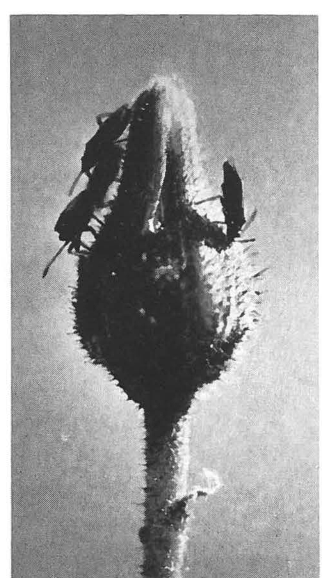


Fig. 4

Plate 5

Examples of how eggs of *Nysius groenlandicus* were deposited in a substrate choice experiment (*cf.* p. 34). The length of the egg is about 1 mm.

Fig. 1. Eggs squeezed into the crevices of a dry berry from *Empetrum nigrum* ssp. *hermaphroditum*.

Fig. 2. Eggs deposited on the achenes in a withered flower of *Potentilla crantzii*.

Figs 3–4. Eggs attached to the wind-dispersed achenes of *Erigeron humilis* (Fig. 3) and *Antennaria canescens* (Fig. 4). Small arrows point to some of the eggs.

J. B. phot. 14/11 1969.


Fig. 1

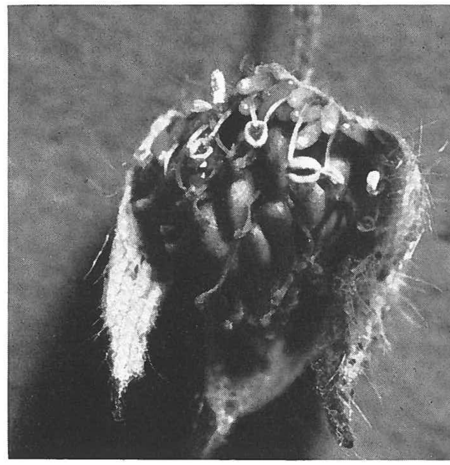
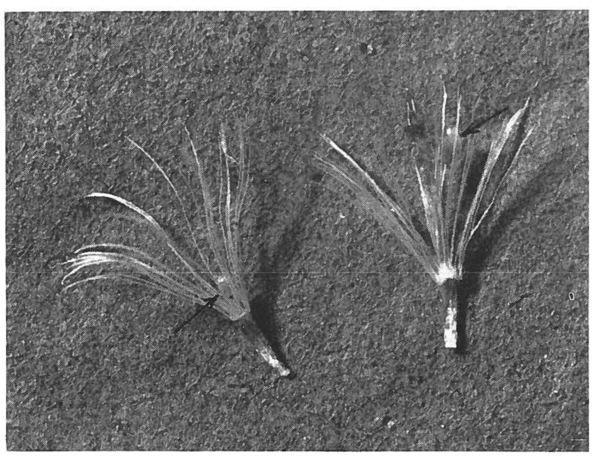


Fig. 2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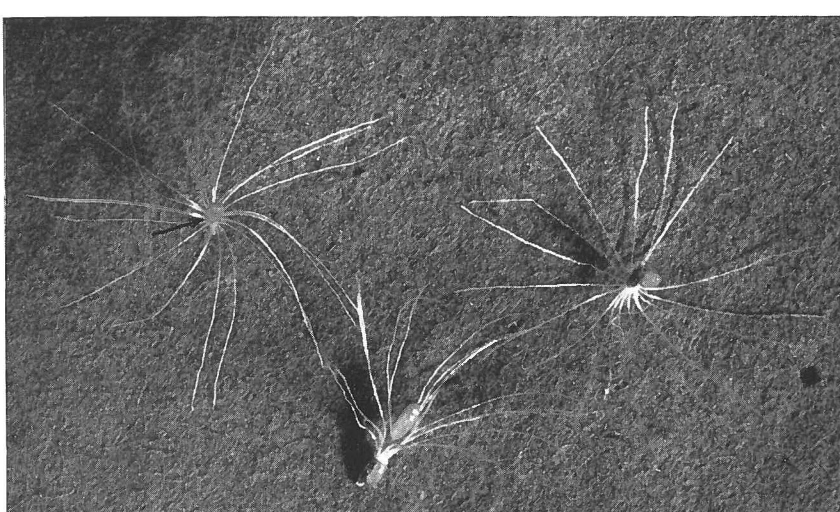
Fig. 4