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Insect-flower associations in the high Arctic with special reference to nectar[1]

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Abstract

665 measurements of nectar concentration and 983 of nectar volume per day, distributed among 37 out of 43 species of flowering plants examined, are recorded and analysed. Nectar production per unit area per season was substantially less at Lake Hazen, 82° N, than at Churchill, 58° N. Nectar yield in mg sugar/flower/day was higher at Lake Hazen than at Churchill in eight of the ten species for which data were obtained at both localities. There is competition between flowers for pollinators rather than among pollinators for nectar. Heliotropic flowers, notably *Dryas* and *Papaver*, focus sunlight falling on them in the region of the germ cells; it is shown that the thermal increments obtainable by black insects resting in these flowers can be important. 184 different plant species – insect species associations are reported, based on about 350 observations and 760 insect specimens; these associations fall into 9 activity categories (some into more than one), as follows: ambush (6), basking (4), flying over (20), hidden in (20), courtship behaviour (1), nectar feeding (23), ovipositing (2), pollen feeding or collecting (12), resting on or uncertain (96). It is concluded that flowers and floral groups are important as aggregation centres for insect populations in this environment.

Резюме

На 37 из 43 видов цветущих растений проводили определения концентрации и об"ема нектара в цветках (665 определений концентрации нектара и 983 определения об"ема нектара). Установлено, что продукция нектара на единицу площади в течение сезона в Лейк-Хазен (82° с.ш.) значительно ниже, чем в Черчхилле (58° с.ш.). Количество нектара, выраженное в мг сахар/цветок/день в Лейк-Хазон выше, чем в Черчхилле у 8 из 10 видов растений, для которых получены данные в обоих пунктах. Предполагается, что конкуренция между цветами из-за опылителей более вероятна, чем между опылителями из-за нектара. Гелиотропные цветы, например. *Dryas* и *Papaver*, фокусируют падающий на них солнечный свет на зародышевых клетках. Показано, что повышение температуры, которое способны вызывать черные насекомые, отдыхающие на цветах, может иметь значение для жизнедеятельности цветов. Установлено 184 вида связей "вид растения" – "вид насекомого", которые основаны на 350 наблюдениях за 760 видами насекомых. Выделено 9 категорий связей насекомых с цветами: засада в цветке (6), обогревание на солнце (4), полет над цветком (20), укрывание в цветке (20), брачные игры (1), питание нектаром (23), откладка яиц (2), питание пыльцой или ее сбор (12), отдых или неопределенное поведение (96). Установлено, что цветы и цветущие группы растений имеют значение как центры скопления популяций насекомых.

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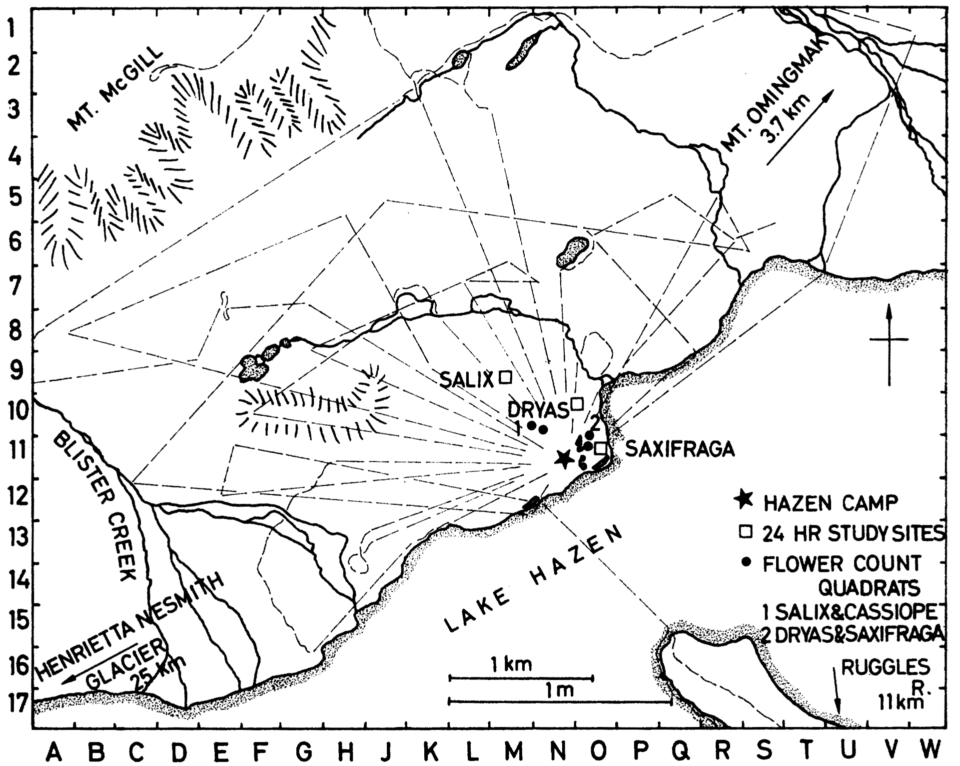

Fig. 1. The central area of the study, showing the transects walked in estimating plant abundance in 1967, the quadrat areas, and the 24 hour study sites.

1. Introduction

Both botanical and entomological interest attaches to the relationships between flowers and insects and to the changes in these with increasing latitude. Primarily, this interest is in the pollination of the flowers of most dicotyledonous plants and in the nutrition of the adults of many, if not most representatives of the higher orders of insects and of a few of the larvae of these. From this beginning, however, interest extends into gene flow and speciation in plants, into flight range and dispersal in insects, and hence into the distribution of plants and animals and the relationship between plant and animal geography, as well as into many applied fields.

A study conducted for the most part at Churchill, Manitoba, lat. 58° N, long. 94° W (Hocking 1953), confirmed Shuel's (1952) demonstration of the significance of insolation to nectar secretion and linked this to the flight range of certain groups of blood-sucking flies. Nectar production was less in the forest than on the tundra and forest species of blood-sucking flies had correspondingly less mobility. Against this background, opportunities to study nectar secretion and flower visiting insects at Hazen Camp on the northwest shore of Lake Hazen, Ellesmere Island, N.W.T. at 81°49′ N and 71°18′ W proved irresistible.

A general ecological description of this area has been given by Savile (1964), and additional information on the flora and fauna is to be found in Downes (1964), Leech (1966), Oliver (1963), Savile and Oliver (1964), and other papers in the series "Studies on Arctic Insects" of the Entomology Research Institute, Canada Department of Agriculture. Most of the observations in this paper were made in the area

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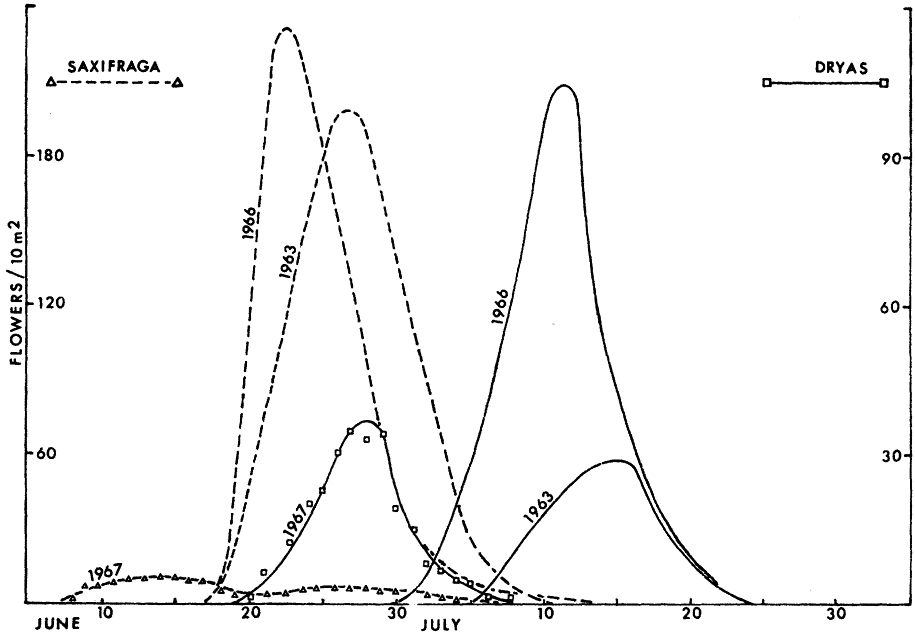

Fig. 2. The progression of flowering of *Saxifraga oppositifolia* (△) broken lines, and *Dryas integrifolia* (□) solid lines at L. Hazen 1963, 1966, and 1967.

included in Savile's (1964: 256–257) map (Fig. 1), but some were made 3.7 km to the N.E. of this area on the slopes of Mt. Omingmak (summit 1130 m by aneroid) where material was collected on sun-facing slopes throughout a 24 hour period, i.e. on all slopes; some were made 11 to 32 km to the south, along the Ruggles River, flowing from Lake Hazen to Chandler's Fiord, and some in the vicinity of the Henrietta Nesmith glacier, 25 km to the southwest.

Brief accounts of two discrete facets of this work have already been published (Hocking and Sharplin 1964, 1965) and a preliminary study of the anthophilous Diptera in 1962 by McAlpine (1965) provided a valuable starting point.

2. The plant species and their seasonal succession

Of the 115 vascular plant species occurring in the area 36 are monocotyledons and four are pteridophytes; 43 of the remaining 75 species were examined for nectar production, 37 of them yielding significant amounts. Observations were made of insects visiting 37 plant species, all except one of them (*Papaver radicatum* Rottb.) among the nectar producers. These 37 plants represent the following families: Salicaceae (1), Polygonaceae (1), Caryophyllaceae (7), Cruciferae (10), Saxifragaceae (5), Rosaceae (4), Onagraceae (1), Ericaceae (1), Primulaceae (1), Scrophulariaceae (4), Compositae (2).

The species studied are listed below (Appendix A) with the data obtained on them. Notes on their occurrence, abundance, and phenology for 1957–58 will be found in Powell (1961) and for 1962 in Savile (1964).

In mid-June 1963 six to ten quadrats, each covering about a square metre, were marked out on level ground near the camp, for each of four of the most important species: *Saxifraga oppositifolia* L., *Dryas integrifolia* M. Vahl., *Salix arctica* Pall., and *Cassiope tetra-*

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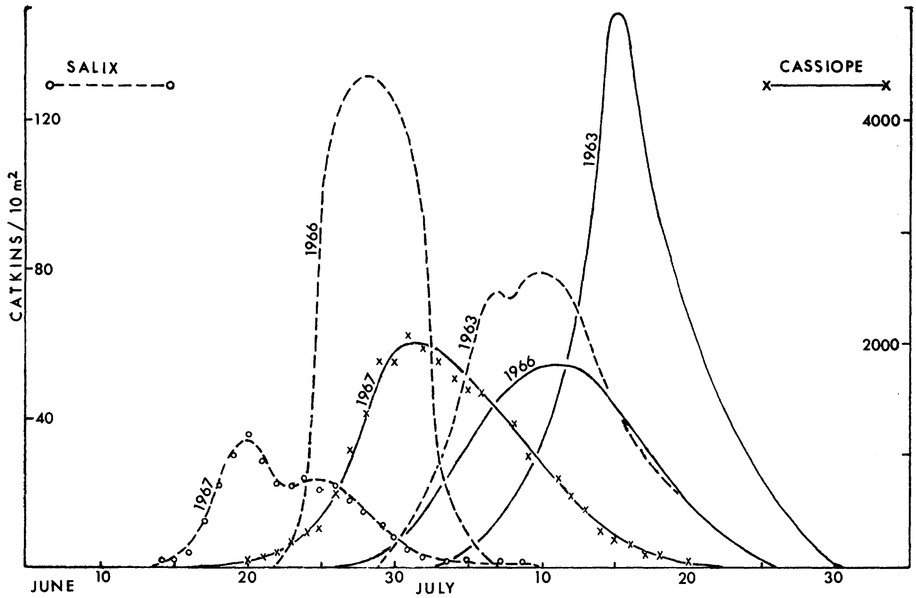

Fig. 3. The progression of flowering of *Salix arctica* (○) broken lines, and *Cassiope tetragona* (×) solid lines, at L. Hazen 1963, 1966, and 1967.

gona (L.), by P. S. Corbet and H. Rutz. The numbers of individual flowers (or catkins) in each plot carrying or receptive to pollen were counted daily or at two day intervals until flowering was over. With minor changes these observations were repeated in 1966 and 1967. The results adjusted to 10 m^2 are plotted in Figs. 2 and 3, where smoothed curves have been drawn from 5 day running means. The double peak for *Salix* in 1963 suggested that the two sexes should be recorded separately. This was done in 1966 and 1967 and the results are plotted in Fig. 4. In each year *Salix* pollen was available before receptive stigmata. It seems likely that the peak of male flowering usually precedes that of female; in 1967 the difference was five days. In 1966 the peaks of male and female flowering were almost coincident; this was probably the result of a compression of the flowering period into a shorter than usual time. A comparison of dates in these three seasons, and in 1962 as recorded by Savile shows the tremendous variation which occurs between seasons and serves as a warning against attaching too much importance to results from a single season's work. *Dryas*, for example, started flowering almost three weeks later in 1963 than in 1962 or 1967; since it only remained in flower for three weeks there was almost no overlap in flowering period between the early seasons and the late one. The variation in the numbers of flowers produced is equally striking in *Saxifraga* and *Dryas*, but somewhat less so in the woody plants, *Salix* and *Cassiope*, in which there appears to be some compensation for a short season by more prolific flowering. The *Saxifraga* plot was badly trampled by musk-ox at the beginning of the 1967 season so that the figures are unduly low; other observations confirmed, however, that it was a very poor year for *Saxifraga oppositifolia*.

3. Nectar yield and production

A. Methods

Nectar production was measured, as at Churchill (Hocking 1953: 25), by extracting it with a wax-lined micro-pipette after a flower had been protected from insects for 24 hours.

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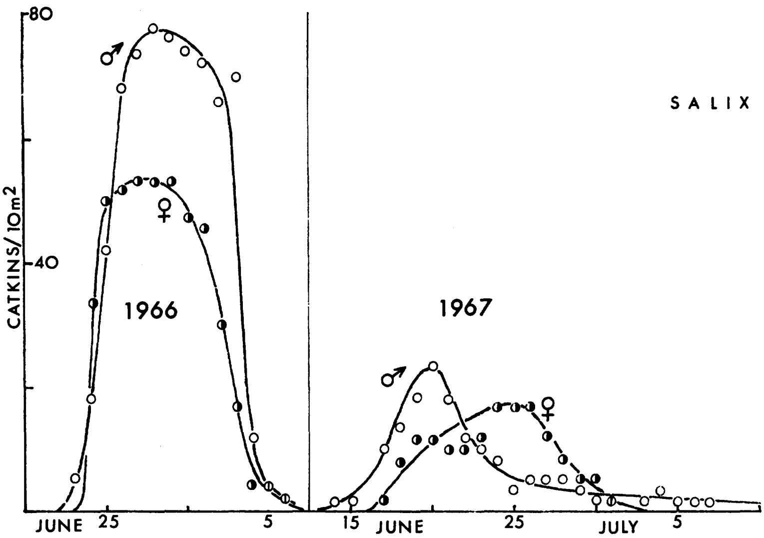

Fig. 4. The progression of flowering of *Salix arctica*, male (○) and female (◑) at L. Hazen 1966 and 1967. Divided circles (∅) are coincident points for the two sexes.

The volume was then read and the nectar transferred to a pocket refractometer for estimating the percentage of total sugars. Nesting truncated 30° cones of acetate sheet, 30 cm high, with the top and three holes (all 4 cm diameter) made low down in the sides covered with nylon marquisette were found to be lighter, more convenient for covering flowers, and less fragile than glass lamp chimneys; no Lake Hazen plants grow tall enough to require the muslin bag technique. Covered plants were marked with red fluorescent painted stakes.

It was not uncommon to find flowers at Lake Hazen which had not been covered, containing measurable amounts of nectar (see Appendix); this suggests that here, unlike at Churchill, there was competition among plants for pollinators, rather than among pollinating insects for nectar. It also means that the figures obtained for daily and for seasonal production may be too high. On the other hand this error may be offset by the fact that the secretion of nectar is stimulated by its removal (Wykes 1950, 1951) and, presumably, retarded if it is allowed to accumulate. In a test in which one half of a clump of *Saxifraga oppositifolia* was covered to exclude insects, the mean value of total sugars for 10 uncovered flowers was two-thirds of that for 10 covered flowers; this was exceptional. In most other tests the ratio was nearer 1 to 10. Nectar measurements on most of the more important species continued for most of the flowering period. The presence of reducing sugars in the nectar of most species was demonstrated with Benedict's reagent. On 9 July a series of ten boards coated with a fermenting molasses and fruit mixture was set out and checked at intervals for 24 hours; that only one insect (*Boreellus atriceps*) was caught seems to support the view that there was no competition for nectar.

Whenever possible the overall number of hours of sunshine during the 24 hour period when each batch of flowers was covered, and the magnitude and direction of ground slope measured by clinometer and compass at each site were recorded. Simultaneous measurements of nectar secretion were made on flowers of *Dryas integrifolia*, the most abundant flower which produced plenty of nectar, from North facing 30° slopes, level areas, and from South facing 30° slopes. As a check on the possible effect of soil moisture on nectar secretion, simultaneous measurements were

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Tab. 1. Milligrams sugar in nectar/flower/day at two Arctic localities for ten plant species.

Species	Churchill 1951 Lat. 58° N Mean (no. of readings)	Max.	Lake Hazen 1963 Lat. 82° N Mean (no. of readings)	Max.
*Polygonum viviparum**	0.15 (3)	0.155	0.095 (7)	0.12
Cerastium alpinum	nil		0.43 (11)	0.52
Stellaria sp.	0.41 (2)	0.82	0.53 (26)	0.65
Lesquerella arctica	traces		0.20 (29)	0.30
Saxifraga Hirculus	0.13 (2)	0.26	0.27 (4)	0.28
S. oppositifolia	0.76 (6)	0.76	1.4 (42)	3.3
S. tricuspidata	0.27 (13)	0.55	0.70 (24)	0.80
Dryas integrifolia	0.62 (18)	0.71	0.79 (64)	1.6
*Epilobium latifolium**	2.5 (8)	3.5	1.5 (32)	1.9
Androsace septentrionalis	nil		0.039 (1)	
Means of all yields measurable at both localities	0.69 (52)		0.76 (197)	
				Transmission coefficient
Approximate solstitial insolation, g cal/cm²	670		630	0.8
(from Sørensen 1941)	1010		1110	1.0

* Readings lower at Lake Hazen than at Churchill.

also made on *Cassiope* growing from waterlogged and well drained situations. In series of measurements on *Salix*, *Erysimum*, *Pedicularis arctica* and *P. capitata* the position of the flower in the inflorescence was recorded in an attempt to characterize the change in secretion with flower age.

B. Results

The full data obtained in this work are given in Appendix A. The yields of sugar per flower per day of 10 species which were included in both the Churchill and the Lake Hazen studies are compared in Tab. 1, the maximum nectar volumes of the five greatest producers and the maximum nectar concentrations (6 species) in Tab. 2, and the estimated collective nectar yield in grams of sugar per unit area over the season in Tab. 3. These estimates were made from the data in Figs. 2 and 3, Tab. I, Appendix A, and from general notes and photographs made while in the field in 1963 and specific notes made while walking the transects shown in the map in Fig. 1 in 1967. They were modified and amplified by reference to published work (Powell 1961, Savile 1964) and by discussion with colleagues and consideration of independent estimates made by them. Wide divergences of opinion were nearly always comprehensible in terms of seasonal variation. For example Savile's (personal communication) estimate of *Cassiope* abundance made in 1962, a poor flowering year, was 20 per cent of my initial estimate made in 1963, an excellent year. Brassard (1968) has reported that *Cassiope* is more common around the head of Tanquary Fiord, 100 km to the southwest. The procedures used in the Churchill study were kept in mind with the object of making valid comparisons. An initial step was the computation of mean annual flower-days for the species in Figs. 1 and 2 by measuring and averaging the areas under the curves for the three seasons for each species. The density of flowering in the quadrats was then compared with the maximum density found elsewhere in the field. For other species the figures are less precise, but carefully reasoned estimates made for me by Savile proved invaluable.

The accessibility of nectar was limited in a number of flowers; the depth of the corolla

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Tab. 2. Maximum volumes of nectar secreted in mm³/day and maximum concentrations in per cent total sugars at two Arctic localities.

Churchill 1951 Lat. 58° N		Lake Hazen 1963 Lat. 82° N	
Volumes:			
Potentilla palustris	53	*Dryas integrifolia*	13
Salix cordifolia	28	*Salix arctica* ♂	10
S. candida	18	*Salix arctica* ♀	9
S. arctophila	12	*Saxifraga oppositifolia*	9
Epilobium latifolium	10	*Lychnis triflora*	9
Concentrations:			
Epilobium angustifolium	77	*Potentilla* spp.	80
Ledum groenlandicum	77	*Dryas integrifolia*	77
Rhododendron lapponicum	76	*Pedicularis arctica*	73
Parnassia palustris	75	*P. hirsuta*	71
Rubus acaulis	74	*Epilobium latifolium*	71
Ribes oxyacanthoides	72	*Arnica alpina*	70

tube in *Lychnis triflora* is 6–7 mm, in *L. apetala* it is 9 mm and in *Pedicularis* spp. up to 1 cm. The pendent bells of *Cassiope*, with a restricted opening, presented difficulties to some insects; the depth is 3–4 mm.

C. The effect of terrain and sunshine

A summary of the data on slope and hours of sunshine in relation to nectar secretion is included in Appendix A. All readings on one day for nectar secretion by each species from each locality were converted to milligrams of sugar secreted in 24 hours and averaged for that species. Most averages represent from 5 to 10 readings. Corresponding data for slope, aspect, and hours of sunshine were used to estimate the relevant insolation in gram calories per square centimeter from data in the literature (Kimball and Hand 1922, Perl 1963, Sørensen 1941). The results of direct measurements of *Dryas* secretion in relation to slope are summarized in Tab. 4. The re-

Tab. 3. Total seasonal nectar flow, in grams of total sugars per unit area for two Arctic localities.

Churchill (tundra), 1951	g per hectare	acre	Lake Hazen, 1963 Lat. 82°	Mean flower-days per 10 m²/ season	% of area oc- cupied	g per hectare	acre
Salix arctophila	575	233	*Dryas integrifolia*	493	23	378	153
Rhododendron lapponicum	395	160	*Saxifraga oppositifolia*	1,296	3	227	92
Salix planifolia	276	112	*Salix arctica*[1]	954	6	185	75
Dryas integrifolia	106	43	*Cassiope tetragona*	32,630	6	150	61
Oxytropis campestris	57	23		Max.			
Vaccinium uliginosum	47	19		flowers/m²			
Arctostaphylos rubra	30	12	*Pedicularis arctica* (10)[2]	18	3	27	11
Senecio congestus	20	8	*Epilobium latifolium* (7)	25	3.5	25	10
Arnica attenuata	12	5	*Pedicularis capitata* (9)	6	2	12	5
Salix reticulata	12	5	*Potentilla* spp. (15)	10	4	12	5
Salix Richardsonii	10	4	*Lesquerella arctica* (15)	20	2.5	7	3
	1540	624				1020	414

[1] Catkins.
[2] Approximate mean nectar period in days.

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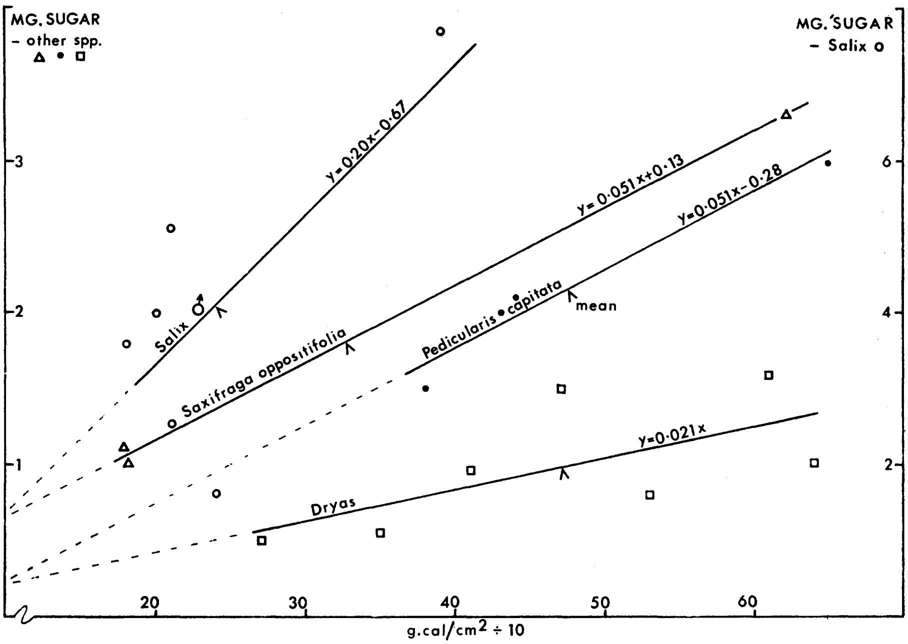

Fig. 5. The regression of nectar production in mg sugar per flower (catkin for *Salix*) on insolation for *Salix arctica* (○) male, *Saxifraga oppositifolia* (△), *Pedicularis capitata* (●), and *Dryas integrifolia* (□), L. Hazen, 1963.

Tab. 4. The effect of slope and aspect on nectar yield of *Dryas integrifolia* at Lake Hazen, 82° N.

Slope	Insolation g cal/cm²/day	Yield mg sugar/flower/day (means of 20 readings)
30° N.....	310	0.51
level......	470	0.87
30° S......	570	1.3

Difference between N and S slopes significant at the $P < 0.01$ level.

gression lines of milligrams sugar secretion on insolation have been calculated and four of these are plotted in Fig. 5. The rise of nectar secretion at the beginning of the flowering period and the decay of this towards the end (see below) tend to obscure the effect of insolation, giving a low correlation coefficient when readings extend over a long period (e.g. *Salix*, r = 0.39), or even a negative coefficient if readings are few and are similarly extended. Correlation coefficients are much higher where several readings were taken in a period of a few days (*Dryas* slope tests, r = 0.64; *Pedicularis capitata*, r = 0.98); they may be fortuitously high if only a few readings are available (*Saxifraga oppositifolia*, r = 0.99). For some species, such as *Pedicularis capitata* and *Salix arctica* (male flowers only) *c* in the regression equation has a negative value, indicating that a threshold intensity of insolation is required for nectar secretion; for most species, however, the regression line intersects the axis very close to the origin. Wide differences are found in the relationship between insolation and nectar secretion between species in the same genus (c.f. Park 1930a, b).

D. Effects of soil moisture and flower age

In *Cassiope*, no significant effect of soil moisture on either the amount or the concentration of nectar secreted could be demonstrated.

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Tab. 5. The variation in the concentration and production of nectar (maxima italicized) with the position of the flower in the catkin; *Salix*, Lake Hazen, 1963.

	Concentration – percentage of total sugars			Production – mg sugar		
	♂	♀	Mean	♂	♀	Mean
Apical	*37.3*	*38.5*	*38.2*	1.69	1.38	1.49
Mid section	36.4	34.4	35.1	*1.87*	1.88	*2.11*
Basal	28.7	29.7	29.4	1.30	*1.88*	1.82
No. of readings × no. of nectaries	9×5	17×5	26×5	10×5	18×5	28×5

Differences between base and apex in ♀ significant at the $P < 0.01$ level, in ♂ just short of significant at the $P < 0.05$ level.

In *Salix* (♂ and ♀), in *Erysimum*, and in *Pedicularis arctica* clear evidence of the expected rise and decay of nectar production, expressed as total sugars, through the life of the flower was obtained. The data also indicated that the peak of concentration occurs earlier in the life of the flower than the peak of production. The results with *Salix*, given in Tab. 5 are representative. This is of interest in relation to the observation that *Megabombus polaris* works the spikes of *Pedicularis* upwards from the bottom; adaptation to sweetness in the gustatory organs is thus offset by increasing concentration.

4. The germ cells and associated tissues

A. Pollen

Pollen constitutes an important protein supplement in the diet of many insects which obtain their primary energy requirements from nectar. Most plants produce it in superabundance, many have evolved specific adaptations to ensure its transfer by insects, and many insects have specific adaptations for collecting it and for using it as food. Because of its more precise and clearly marked location in the flower it is usually easier to observe pollen feeding than nectar feeding. Most insects visiting flowers which do not secrete nectar do so in search of pollen for food. Pollen grains collected from the hairs or body surface of an insect can usually be identified, at least to genus; pollen from the gut can sometimes be identified too. With careful collecting, superficial pollen provides good circumstantial evidence of a specific visiting association; pollen from the gut is usually proof of a feeding association. Pollen taken from the corbiculae of bumble bees, but not necessarily that from the body hairs, may be taken as proof of a larval feeding association.

B. Ovarian tissue

The ovarian tissue of plants is of interest to insects principally as a source of food for the next generation, that is, as an oviposition site. I know of no observations of adult insects feeding on ovarian tissue at Lake Hazen.

During a period of 24 hour observations on insect activity on *Dryas* flowers, 13 July, and also at other times, very small, presumed first instar, pinkish caterpillars of *Sympistris labradoris* Staud. (Noctuidae) were encountered in the flowers. Usually there was only one to a flower; the caterpillar fed rapidly, starting on the tissue between the nectaries and the ovary, but damaging both of these structures, and proceeding to eat out the whole of the ovary. Cast head capsules were found, in badly damaged flowers, until 22 July; there were never more than two to a flower. These observations are taken as evidence of oviposition by *Sympistris* in *Dryas* flowers.

5. Other factors attracting insects to flowers

A full appreciation of the relative importance of smell and vision in the attraction of insects to flowers will call for a much better understanding of the nature of these two senses in insects than we are likely to have for some time to come. The care needed in interpreting

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Tab. 6. Temperature differentials in Arctic heliotropic flowers, °C, Lake Hazen, 1963.

Plant Species	Shade	Temperatures Sun, outside flower	Sun, inside flower	Difference	No. of series of readings
Cerastium alpinum	max. 12.2	12.3	12.9	0.6	
	mean 12.2	11.8	12.5	0.7	1
Papaver radicatum	max. 14.3	15.6	19.2	3.6	
	mean 12.8	12.7	16.1	3.4	11
Dryas integrifolia	max. 14.0	23.9	28.3	4.4	
	mean 12.8	14.8	16.4	1.6	12

observations is shown by the demonstration (Lex 1954) that the familiar "honey-guides", pattern pointers to nectaries on the petals of some flowers, are also smell pointers.

It is noteworthy that some plant species at Lake Hazen (e.g. *Lychnis apetala* and *Cassiope tetragona*) capture small insects by means of sticky or hocked hairs or other devices. The significance of this seems uncertain; I have no evidence that it is either protective or nutritional, from the plant viewpoint, nor that there is a specific attractive influence. It seems to be related to the fact that the approach of many smaller insects (midges, mosquitoes, *Fucellia*) to flowers is commonly, when the wind is strong, by walking and climbing rather than by flying.

A. Odour

The odour characteristics to man of most of the flowers studied were recorded (see Appendix A) incidentally, but no observations on the role of odour in the field were possible.

B. Visual and thermal factors

Where colour pattern exists on the petals of flowers at Lake Hazen it is on a small scale (e.g. *Saxifraga tricuspidata*), unlikely to have stimulatory value for insect eyes at a distance. It is noteworthy that, except for *Erysimum Pallasii*, *Epilobium latifolium*, *Saxifraga oppositifolia*, and two species of *Pedicularis*, all the abundant plant species important to insects have yellow, creamy, or white flowers, and that white forms of the saxifrage, *Erysimum*, and the *Pedicularis* spp. occur.

It was observed that insects, initially mosquitoes, would spend time (*Aedes* spp. ♂♂ up to 13 min. 49 sec., ♀♀ up to 12 min. 3 sec.) resting in flowers, with no apparent specific activity. Females of the same species completed a blood meal (on king eider) in 2 min. 45 sec.; it may be supposed that both sexes could engorge on any but the strongest nectars in a similar time. Later it transpired that these insects were usually black, the flowers cup-shaped, and the cup rotated continuously to face towards the sun. The most strikingly heliotropic flowers were *Papaver radicatum* and *Dryas integrifolia*; species of *Potentilla* showed some turning. This led us to suppose, as reported elsewhere (Hocking and Sharplin 1965), that these phenomena had a thermal significance, both to the plant and to the insect. Accordingly, comparative temperature measurements were made with blackened copper-constantan thermocouples placed at the estimated principal foci and elsewhere within these more or less paraboloid corollas, and at equivalent positions outside the corollas. One series of measurements was made in *Cerastium alpinum* which has a corolla of very different shape. Temperature differentials were measured with a potentiometer and are recorded in Tab. 6; some typical temperature sequences are plotted in Fig. 6. Thermocouple potentials were measured with a potentiometer and galvanometer calibrated with a reference junction in melting ice and warm junction adjacent to a mercury thermometer shielded in the shade. Readings inside and outside the flowers were taken alternately with approximately one

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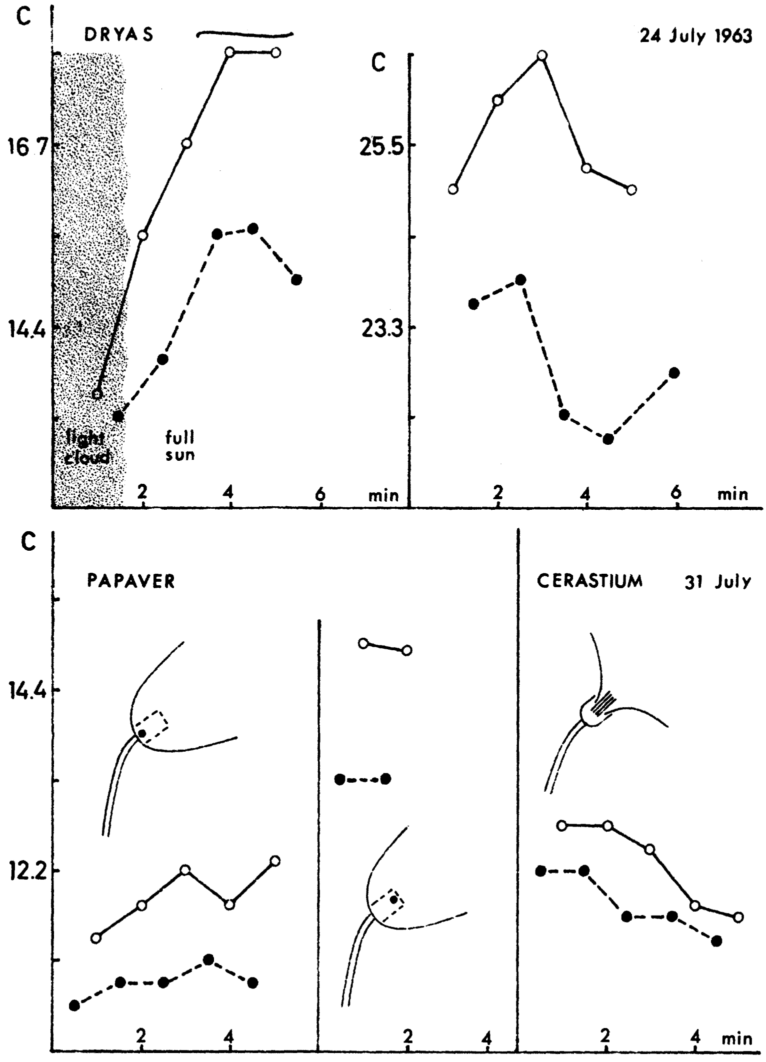

Fig. 6. Representative examples of temperatures recorded inside (○) and outside (●) heliotropic flowers (*Cerastium*, control) at L. Hazen, 1963.

minute between readings from each location. When there was wind it was helpful to anchor the flower to a stake and sometimes to shield it. Some readings were taken in flowers with the sexual organs removed to allow free searching for a temperature maximum. This could be localized quite well in *Papaver*, on the axis of the flower and just proximal to the position of the apex of the sexual organs; it could not be so well defined in *Dryas*. Temperature differentials increased with the altitude of the sun and decreased promptly with cloud cover.

6. Insect visitors to flowers

A. Methods

Evidence on flower visiting by insects was obtained in a variety of ways. Where the flora and fauna is so limited as at Lake Hazen,

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Tab. 7. The distribution of insect visitors, by major groups, among plant orders, Lake Hazen 1963.

Line 1: Number of species associations.
Line 2: Distribution of associations among activities (A. ambush; B. basking; H. hidden in; N. nectar feeding; P. pollen feeding or collecting. Resting, flying over or uncertain not designated).
Line 3: Number of: males, specimens of uncertain sex, females.

	Arachnids, Apterygotes, Exopterygotes, and Coleoptera (8 spp.)	Lepidoptera (10 spp.)	Lower Diptera (40 spp.)	Diptera-Cyclorrhapha (14 spp.)	Hymenoptera (10 spp.)	Totals (82 spp.)
Salicales	2	2	13	5	5	27
(1 sp. ♂ + ♀)	2H	2N	7H,N	N	2N	9H,6N
	0,2+,0	0,6,0	113,3+,30	3,2,4	2,0,26+	118,12+,60+
Caryophyllales	1		16	1	5	21
(7 spp.)	H				P	2 H,P
	0,12,0		22,0,17	1,0,1	0,1,7	23,13,25
Rhoedales	2	2	11	5	4	24
Papaver + *Crucif.*	A			N		A,N
(12 spp.)	0,0,1+	0,2,0	1,3,17	2,1,8	2,0,3	5,6,29+
Rosales	3	11	48	20	9	91
Potentilla, *Sax.* + Dryas	3A	5N	A,4B,10H,4N,2P	N	N,2P	4A,4B,10H,11N,4P
(8 spp.)	3,25,0	0,26,0	120+,6+,150+	18,9,18	0,2,40+	142+,68+,208+
Myrtales + Ericales		1	2	2	4	5
Epilobium, *Cassiope*					2N,3P	2N,3P
(2 spp.)		1,0,1		0,1,1	0,0,12+	1,2,14+
Tubiflorae + Campan.	1	1	5	2	3	12
Scroph. + Comp.	A		P?		3N,3P	A,3N,4P
(7 spp.)	0,0,2	0,1,0	2,1,2	0,2,0	0,0,20+	2,4,24+
Totals (37 spp.)	9	17	93	35	30	184
Activity Totals	5A,3H	7N	A,4B,17H,5N,2P?	3N	8N,9P	6A,4B,20H,23N,12P
Sex totals:						
♂, unknown, ♀	4,39+,3+	0,35,0	259+,13+,217+	24,15,32	4,3,108+	291+,105+,360+

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direct observation in the field often permits specific identification. For this purpose a pair of field glasses with either an extended focussing adjustment or supplementary lenses to permit focussing to within one meter is very helpful. When possible specimens were collected for confirmation of identification and sometimes for dissection to confirm feeding on nectar, using a pocket refractometer, tasting, and Benedict's test for reducing sugars. A difficult decision was constantly called for in the field; to continue to observe in the hope of behavioural confirmation of the nature of the relationship, or to collect and be sure of specific identification, with the hope of confirmation by dissection.

Some crop and stomach contents were examined microscopically for pollen grains. Specimens collected in circumstances other than while visiting flowers were also examined for superficial pollen grains. When pollen grains were found, slides were made of them and compared with a reference set of slides prepared from freshly collected flowers.

In a search for relationships manifest only at particular times of day and for possible diurnal periodicity in relationships, dense stands of each of three important species (*Saxifraga oppositifolia*, *Dryas*, and *Salix*) were observed continuously for 24 hours in 2 to 4 hour shifts near the peak of the flowering season.

B. Results

Tab. 7 summarizes all the observations on flower visiting. The details are given in Appendix B with an indication of the nature of the evidence in each case. Nearly all of the observations relate to Lake Hazen in 1963. A few were derived from pollen found on specimens collected earlier, e.g. *Megabombus polaris* and *M. hyperboreus* taken at Lake Hazen by Oliver in 1961. A few are from Resolute Bay, Cornwallis Island, taken on the way to or from Lake Hazen.

For convenience in presentation the activities are divided into a number of categories with arbitrary limits. The broadest, and least significant, of these are "Flying over" (F) and "Resting on" (R). The former includes observations and usually captures of many insects, usually of both sexes, hovering or flying limited circuits over a group of flowers; random flight over flowers was ignored. The latter includes all observations and captures of insects settled on flowers for which no strong evidence of the nature of the activity was obtained. Neither of these categories, because of their abundance, nor "Courtship" (M) and "Oviposition" (O), because of their rarity, are designated in Tab. 7. "Ambush" (A) includes observations of prey capture within or directly from flowers; "Basking" (B) includes resting for a minute or more in sunlit flowers, whether heliotropic or not, without other specific activity; "Feeding" (N or P) includes observations of the mouth parts working in contact with an edible part of a flower as well as finding this part in the gut; "Hidden in" (H) usually means the insect was discovered concealed within the flower when this was distorted or taken apart, as for nectar examination.

The possibility that pollen from *M. hyperboreus* was collected by *M. polaris* should be borne in mind. Many of the records of insect visitors were made or confirmed during the 24 hour watches. Some of the data obtained are presented in Tab. 8; it is hard to say whether this shows a persistent diel periodicity on the part of any or all of the plants, the insects, or the collectors.

A series of *Megabombus polaris* collected from *Saxifraga oppositifolia* on 27 July, but having no pollen on the outside of the body, was dissected. The honey stomachs contained up to 0.6 mg sugar in the form of 4–5% solution, and the stomach proper in each insect contained an orange pigment, matching the saxifrage pollen, in fatty globules. On 14 July a sample of 5 female *Aedes nigripes* from an aggregated flight which hovered over the cookhouse from about 20.30 till at least 23.30 hours was dissected. The ventral diverticula yielded an average of 0.11 mg sugar at an average concentration of 50%. This contains sufficient energy for a flight of about 5 km. Willow or *Potentilla* were likely sources for this nectar.

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Tab. 8. A summary of the activity of Diptera in the vicinity of dense growth of *Dryas integrifolia* over a 24 hour period at Lake Hazen, 13 July, 1963.

	00.00–04.00 hrs.	04.00–08.00 hrs.	08.00–12.00 hrs.	12.00–16.00 hrs.	16.00–20.00 hrs.	20.00–24.00 hrs.
Aedes impiger	3 ♂ –	3 ♂ 2 ♀	2 ♂ –	– –	– –	– 5 ♀
A. nigripes	36 ♂ 15 ♀	25 ♂ 15 ♀	19 ♂ 9 ♀	17 ♂ 8 ♀	6 ♂ –	1 ♂ 36 ♀
Rhamphomyia nigrita	– 2 ♀	– –	– 3 ♀	– –	– –	1 ♂ 2 ♀
R. filicauda	4 ♂ 5 ♀	1 ♂ 5 ♀	1 ♂ 2 ♀	– 1 ♀	3 ♂ 2 ♀	– –
R. sp. nr. *lamelliseta*	3 ♂ 9 ♀	4 ♂ 7 ♀	3 ♂ 8 ♀	1 ♂ 5 ♀	– 2 ♀	– –
Spilogona spp.*	4*	2	3	8	0	0
Other flies	*Carposcalis* 1 unidentified	*Carposcalis* Chironomid.		Mycetophil. *Boreellus*		*Tipula*
Total flies	46 ♂, 4*, 31 ♀	33 ♂, 2, 20 ♀	25 ♂, 3, 22 ♀	18 ♂, 8, 14 ♀	8 ♂, 0, 4 ♀	2 ♂, 0, 43 ♀
					Overall Total:	132 ♂, 17, 134 ♀

* Sex uncertain

7. Discussion

Although the measurements of nectar yield per flower of particular species per day at latitude 82 are greater than at latitude 58 (Tab. 1), the differences are small in comparison with, for example, seasonal differences in insolation to be expected at either locality. The total nectar production per unit area per season is lower. Maximum concentrations of nectars are comparable, but maximum volumes per day are substantially lower at the higher latitude; this may be a result of drier conditions in the soil, in the atmosphere, or both. The lower seasonal production can be attributed to the shorter season, the sparser vegetation, and perhaps in part to less prolific flowering and the drier conditions. Despite the poorer supply there appears to be a surplus, resulting in competition among plants for pollinators rather than among pollinators for nectar. This is not surprising in the light of Downes' (1964: 292) figures for the relationship between numbers of plant species and insect species in the arctic. These numbers of species, in comparable environments, probably result from, or result in, corresponding numbers of individuals; in either case a similar relationship between total populations is to be expected.

Broadly speaking, nectar yield tends to vary directly with insolation at the rate of about 0.5 mg sugar per flower for each 100 g cal/cm^2. This means that weather conditions, through their effect on the transmission coefficient of the atmosphere are of substantially greater importance than latitude, and data for Churchill and Lake Hazen exhibit about as much variation between them as can be expected between any two arctic or subarctic localities.

Eighty-two of the about 250 taxa of insects recorded for the area have been recorded in some kind of an association with flowers. These associations include pollen feeding and collecting, nectar feeding, and basking as prominent activities. The several observations of predation in or at flowers, the occasional observation of courtship behaviour at them,

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and the large number of records of associations which could not be characterized suggest that flowers also function as general centres of aggregation. It is difficult to assess the importance of this function, but it may be supposed that where both plant and insect populations are sparse and the season is short, the behavioural formation of fluctuating locally higher population densities in the neighbourhood of flowers, inflorescences, and patches of flowering plants, has survival value for many species.

Of the flower visiting insects the chironomid *Smittia extrema* and the bee *Megabombus polaris* are the most ubiquitous; each was recorded from 10 plant species, including both sexes of *Salix*. Paradoxically, *M. polaris* is also the most specific. It was the only insect recorded from any species of *Pedicularis* and fed on this whenever it was available in preference to other species. Looking at the major groups (Tab. 7), outstanding features are the abundance and variety of both the lower and higher flies on the Rosales (*Saxifraga* spp. and *Dryas*) and the few visitors of any kind, but especially the Lepidoptera and cyclorrhaphous Diptera to the Caryophyllales, *Epilobium*, and *Cassiope*.

Nectar feeding is common in all the endopterygote groups (except the beetles), and on all the flower groups except the Caryophyllales. Many of the records of insects hidden in flowers were noted when these were dissected for nectar examination; the great majority of them are small nematocerous flies and the most used flowers are willow and the Rosales.

The 24 hour observations on *Dryas*, but not those on other species, show a peak of activity around midnight, particularly on the part of the lower flies. With increasing latitude dawn and dusk twilight periods merge at midnight. The crepuscular activities of species originally adapted to lower latitudes would tend to merge similarly as their range extended northward. Further study would be useful. More careful and detailed study will also confirm many other associations and enable many of those recorded to be categorized. The best returns may be obtained from studies of Nematocera between 22.00 and 06.00 hours, and from general studies with relatively short periods devoted to each plant species at a time, to allow a fuller picture of seasonal succession to be obtained for many more plant species.

Further work on flower temperatures is clearly indicated. The significance of the temperature differentials (Tab. 5 and Fig. 6) becomes apparent if they are added to the daily means of screen temperatures for 1964 (Corbet 1967: 7–9) and the results computed for plotting on Corbet's graph (ibid.: Fig. 8, p. 15) of accumulation of growing degree-days. The resulting cumulative temperature for 1964, the coldest year he records, becomes closely comparable with that for 1962, by far the warmest year.

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Appendix A

Records of nectar secretion and hours of sunshine at Lake Hazen, Ellesmere Island, 1963. Plant species arranged according to Porsild (1957: 15).
d – dominant, a – abundant, f– frequent, o – occasional, r – rare, l – locally.

Date	No. of readings conc./vol.	Con-centration % sugars	Mean mg sugar/flower/ day	Slope °	Aspect true bearing °	Hrs. sunshine
Salicales, Salicaceae:						
f. *Salix arctica* Pall. Sweet scent, ♂ and ♀ similar. Total of 105 nectar concentration readings, 354 volume readings, eleven insolation values, correlation coefficient 0.39. Flower-days/10 m²: 1963, 1027; 1966, 1943; 1967, 343. Flowering period 29 days, 6% of ground cover.						
♀						
27.VI...........	4/4	12–21	1.8	3	37	1.17
29.VI...........	12/51	23–44	5.8	8	47	4.67
29.VI...........	12/13	21–27	3.8	6	132	4.67
30.VI...........	12/12	32–52	5.0	level	level	2.92
9.VII...........	18/87	25–58	3.1	8	219	15.33
♂						
21.VI...........	4/4	12–48	2.5	level	level	2.75
27.VI...........	2/10	22–26	3.6	3	37	1.17
28.VI...........	10/23	10–37	4.0	6	132	2.33
30.VI...........	5/5	31–51	1.6	level	level	2.92
29.VI...........	12/56	22–64	5.1	8	47	4.67
9.VII...........	18/89	23–41	7.7	5	230	15.33
Polygonales, Polygonaceae:						
l.a. *Oxyria digyna* (L.) no scent.						
26.VI..........	–	no nectar	–	29	235	24.00
12.VII..........	–	no nectar	–	level	level	
l.f. *Polygonum viviparum* L.						
19.VII..........	7/8	18–31	0.095	level	level	20.67
Caryophyllales, Caryophyllaceae:						
l.f. *Arenaria rubella* (Wahlenb.) Faint scent, 8 concentration, 22 volume readings.						
12.VII..........	2/15	51–68	0.088	level	level	24.00
20.VII..........	6/7	31–49	0.15	29	305	19.00
l.f. *Cerastium alpinum* L. Strong sweet scent. 11 concentration and volume readings.						
16.VII..........	4/4	35–44	0.52	level	level	12.50
23.VII..........	7/7	21–35	0.33	5	0	23.00
l.f. *Cerastium arcticum* Lange. Nectar measured only in flowers which had not been covered.						
26.VII..........	1/1	3	0.039			22.50
l.a. *Lychnis triflora* R. Br. Very sweet scent, nectar similarly flavoured. 31 concentration and volume readings, 5 insolation values, flowering period 27 days, 2% of ground cover.						
4.VII...........	3/3	23–33	0.93	5	352	12.00
7.VII...........	6/6	5–34	0.39	18	15	9.33
18.VII..........	6/6	34–52	0.84	level	level	11.25
18.VII..........	8/8	12–52	0.91	15	338	11.67
27.VII..........	7/7	13–46	0.91	20	122	09.20

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Date	No. of readings conc./vol.	Con-centration % sugars	Mean mg sugar/flower/day	Slope °	Aspect true bearing °	Hrs. sunshine
l.o. *Lychnis apetala*. L. 2 nectar readings from plants which had not been covered.						
18.VII..........	1/1	59	0.27	level	level	11.25
19.VII..........	1/2	40	0.17	level	level	20.67
Silene acaulis L. Sweet scent similar to *Lychnis* (also nectar flavour).						
27.VII..........	4/4	6–16	0.56	25	352	8.08
l.a. *Stellaria* spp. (see Savile 1964). Very faint scent. 26 concentration and 29 volume readings, 3 insolation values.						
16.VII..........	12/12	24–33	0.52	level	level	12.50
20.VII..........	9/11	28–52	0.65	29	305	18.67
20.VII..........	5/6	36–55	0.52	level	level	19.00
Ranales, Ranunculaceae						
l.a. *Ranunculus hyperboreus* Rottb.						
22.VII..........		no nectar				
Rhoedales, Papaveraceae:						
Papaver radicatum Rottb.						
2.VII...........	nil	no nectar		level	level	
Cruciferae:						
l.f. *Braya humilis* (C. A. Mey.) Robins. Faint sweet scent.						
26.VI...........	0/8	trace		48	56	1.17
27.VI...........	3/9	21–24	0.081	16	32	2.33
l.f. *Braya purpurascens* (R. Br.) Bunge.						
19.VII..........		trace		20	122	
l.f. *Braya Thorild-Wulffii* Ostenf. Not covered.						
19.VII..........		nectar present				
o. *Draba Bellii* Holm. Not covered.						
19.VII..........		nectar present				
o. *Draba cinerea* Adams.						
26.VII..........	"plenty"					
r. *Draba groenlandica* El. Ekman. Not covered.						
19.VII..........		nectar present				
l.f. *Draba lactea* Adams. Not covered.						
19.VII..........		nectar present				
o. *Draba oblongata* R. Br.						
26.VII..........		no nectar				
r. *Draba subcapitata* Simm. Not covered.						
19.VII..........		nectar present				

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Date	No. of readings conv./vol.	Con- centration % sugars	Mean mg sugar/flower/ day	Slope °	Aspect true bearing °	Hrs. sunshine

l.a. *Erysimum Pallasii* (Pursh) Fern. Strong sweet scent. 23 concentration and 17 volume readings, 4 insolation values, correlation coefficient −0.30. Flowering period 33 days, 1.5% of ground cover.

19.VI..........	1/1	58	0.41	40	20	20.83
21.VI..........	11/12	33–49	0.52	40	20	20.50
21.VI..........	4/4	30–32	0.24	40	20	20.50
26.VI..........	7	29–37	0.59	35	177	+ 1.10
19.VII..........		no nectar		20	45	20.50

l.a. *Lesquerella arctica* (Wormsk.) Watson. Scent sweet and quite strong. 29 concentration and 31 volume readings, 4 insolation values. Flowering period 35 days, 2.5% of ground cover.

26.VI..........	6/6	22–42	0.30	46	56	1.17
27.VI..........	4/5	22–36	0.19	16	32	2.20
16.VII..........	9/10	7–27	0.19	25	310	12.30
18.VII..........	10/10	6–14	0.11	25	22	11.30

Rosales, Saxifragaceae:

1.a. *Saxifraga caespitosa* L. Not covered.

26.VII..........		no nectar				

l.f. *Saxifraga cernua* L.

27.VII..........	6/7	6–17	0.092	level	level	8.08

o. *Saxifraga flagellaris* Willd.

12.VII..........	trace					

o. *Saxifraga Hirculus* L.

20.VII..........	4/6	23–53	0.26	level	level	18.58

l.a. *Saxifraga oppositifolia* L. 42 concentration and 49 volume readings, 4 insolation values, correlation coefficient 0.99. Flower-days/10 m^2: 1963, 1835; 1966, 1880; 1967, 172*. Flowering period 35 days, 4.5% of ground cover.

19.VI..........	10/13	24–43	1.1	5	262	7.00
19.VI..........	10/12	47–69	1.	5	262	7.00
7.VII..........	20/20	21–46	3.3	6	85	23.10
18.VII..........	2/4	45–51	0.079	level	level	11.40

* Quadrats damaged by musk-ox.

f. *Saxifraga tricuspidata* Rottb.

16.VII..........	12/12	25–50	0.59	level	level	19.00
19.VII..........	12/12	21–28	0.80	30	315	20.30

Rosaceae:

l.d. *Dryas integrifolia* Vahl. 124 concentration and 130 volume readings, 14 insolation values, correlation coefficient 0.48. Flower-days/10 m^2: 1963, 298; 1966, 913; 1967, 269. Flowering period 22 days ground cover.

1.VII..........	10/12	34–77	0.48	10	195	0.55
2.VII..........	7/7	5	0.23	12	167	0.55
2.VII..........	12/12	9–19	0.53	level	level	0.55
4.VII..........	8/9	11–25	0.52	6	357	0.05
6.VII..........	14/14	6–22	0.72	9	132	23.10

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Date	No. of readings conc./vol.	Concentration % sugars	Mean mg sugar/flower/day	Slope °	Aspect true bearing °	Hrs. sunshine
7.VII...........	9/9	9–23	0.60	10	195	23.10
8.VII...........	4/4	12–16	0.46	9	132	23.10
Slope tests.						
16.VII..........	8/8	8–22	0.54	30	0	19.00
16.VII..........	6/8	9–18	1.6	30	180	19.00
16.VII..........	10/11	11–23	0.79	level	level	19.00
18.VII..........	12/12	7–16	0.49	30	0	13.00
18.VII..........	5/5	13–25	1.5	30	180	13.00
18.VII..........	10/10	12–33	0.96	level	level	13.00
20.VII..........	9/9	16–29	1.0	30	180	14.00

l.a. *Potentilla* spp. (*chamissonis* Hult., *rubricaulis* Lehm., and *hyparctica* Malte). 13 concentration and 18 volume readings, 5 insolation values. Flowering period 23 days.

2.VII...........	0/1	trace		level	level	0.05
3.VII...........	2/2	45	0.66	23	218	9.50
9.VII...........	4/4	19–25	0.39	10	100	15.20
16.VII..........	1/4	80	0.16	25	22	19.00
20.VII..........	6/7	31–45	0.49	level	level	20.10

Myrtiflorae, Onagraceae:

l.f. *Epilobium latifolium* L. Faint scent. 32 concentration and volume readings, 3 insolation values, correlation coefficient −0.22. Flowering period 24 days, 2% of ground cover.

16.VII..........	2/2	68–71	1.9	5	332	19.00
20.VII..........	18/18	26–51	1.9	5	332	19.00
27.VII..........	12/12	11–23	0.65	20	2	06.30

Ericales, Ericaceae:

l.a. *Cassiope tetragona* (L.). Sweet aromatic scent. 25 concentration and 45 volume readings, 7 insolation values, correlation coefficient −0.18. Flower-days/10 m^2: 1963, 45,300; 1966, 26,900; 1967, 25,700. Flowering period 25 days, 6% of ground cover.

4.VII...........	trace			level	level	12.58
6.VII...........	1/4	21	0.061	11	222	23.17
12.VII..........	traces			4	335	32.00
24.VII..........	3/8	35–42	0.16	25	172	21.00
25.VII..........	10/10	17–32	0.20	25	172	06.15
27.VII..........	7/10	11–28	0.059	25	302	06.30
27.VII..........	4/13	17–34	0.034	15	182	06.30

Primulales, Primulaceae:

r. *Androsace septentrionalis* L. (not covered).

26.VII..........	1/1	3	0.039			22.50

Tubiflorae, Scrophulariaceae:

l.a. *Pedicularis arctica* R. Br. 72 concentration and 74 volume readings, 6 insolation values, correlation coefficient 0.38. Flowering period 19 days, 3% of ground cover.

5.VII...........	10/11	48–73	0.74	level	level	12.00
6.VII...........	7/7	23–34	0.78	level	level	23.10
6.VII...........	19/19	28–68	1.5	level	level	24.00
6.VII...........	16/16	22–32	0.84	level	level	24.00
7.VII...........	9/9	32–51	1.3	level	level	23.10
12.VII..........	11/12	27–34	0.74	level	level	24.00

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Date	No. of readings conc./vol.	Con-centration % sugars	Mean mg sugar/flower/ day	Slope °	Aspect true bearing °	Hrs. sunshine
f. *Pedicularis capitata* Adams. 33 concentration and 36 volume readings, 4 insolation values, correlation coefficient 0.98. Flowering period 19 days, 2% of ground cover.						
14.VII..........	2/2	42–44	3.0	level	level	25.00
16.VII..........	10/13	58–69	1.5	3	190	11.40
18.VII..........	14/14	48–63	2.0	15	232	14.40
18.VII..........	7/7	43–52	2.1	3	190	14.40
l.f. *Pedicularis hirsuta* L. Flowering period 18 days.						
4.VII...........	10/11	38–51	0.53	level	level	12.00
14.VII..........	4/7	58–71	0.77	level	level	26.00
r. *Pedicularis sudetica* Willd. Faint scent. Not covered.						
23.VII..........		nectar present				
Campanulatae, Compositae:						
o. *Arnica alpina* (L.). Olin.						
27.VII..........	10/12	27–46	0.18	35	322	6.50
22.VII (not cov.).	1/2	70	1.6			
l.a. *Erigeron compositus* Pursh. Faint scent.						
12.VII..........	nil	no nectar		12	12	87.30
16.VII..........	nil	no nectar		16	8	12.30
l.a. *Taraxacum arctogenum* Dahlst.						
7.VII...........	trace			10	9	23.17
12.VII..........	nil			30	342	87.30
16.VII.........	trace in ray florets			15	8	12.50
Totals:						
19.VII–27.VII ...	665/983	0–80	<7.7			

Appendix B

Records of flower visiting by insects at Lake Hazen; dates all in 1963 except where otherwise shown. Plant species in same sequence as in Appendix A. Collected observations on one line, separated by semi-colons; sequence consistent across the line. Location indices refer to Fig. 1.

Activity:

A. ambush; B. basking; F. flying over; H. hidden in; M. courting; N. nectar feeding; O. ovipositing; P. pollen feeding or collecting; R. resting or uncertain.

Evidence:

C. collected; G. gut contents; P. pollen (superficial); V. visual.

Plant sp.	Date	No. Sex	Activity, Evidence	Location
Arachnida				
Araneae, Thomisidae				
Xysticus deichmanni Soerensen				
Dryas....................	13.VII; 17.VII		A,C	N10; N8
	20.VII	2 ♀	A,C w. *R. filicauda*	E1

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Papaver	25.VII	♀	A,C	C9
Arnica	29.VII	2♀	A,C	K2, P11
Lycosidae				
Pardosa glacialis (Thorell)				
S. oppositifolia	29.VII		A,C	K2
Dictynidae				
Dictyna borealis Pickard-Cambridge				
Potentilla sp.	27.VII		A,C	K3
Acarina				
"mites"				
Salix ♂	21.VI		H,C	N11
Insecta				
Collembola sp.				
Cerastium arcticum	26.VII		H,C	A3
Isotoma viridis (Bourlet)				
S. Hirculus	5.VIII		R,C	Resolute Bay
Homoptera, Aphidiidae				
Brevicoryne arctica				
Lesquerella	16–22.VII	many ♀, not specifically on flowers		K7, N8, P10
Coleoptera, Curculionidae				
Rhyncaenus sp.				
Salix ♂	21.VII		H,C	N11
Lepidoptera, Olethreutidae				
Olethreutes inquietana Walk.				
Dryas	13.VII	2	R,C	N10
	24.VII	4	R,C	
Olethreutes mengelana Fern.				
Dryas	4.VII; 13.VII		R,C; F.G	N10
	15–24.VII		R,C	N10
Potentilla	2.VII		R,C	V4
Noctuidae				
Anarta richardsoni Curt.				
S. tricuspidata	31.VII		R,V	F1, 610 m
Dryas	13.VII; 17.VII		N,V	G5; N10, P10
Crymodes exulis Lef.				
Erysimum	15.VII		R,V	R16
Lasiestra leucocycla Staud.				
Lesquerella	17.VII		R,C	K2
Dryas	20.VII		R,C	C11
Sympistris labradoris Staud.				
Dryas	13.VII		O, 1st instar	N10

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Nymphalidae				
Boloria sp. (*polaris* Bdv. or *chariclea* Schneid.)				
Salix ♂	3.VI.67		N,CG	J5
	12.VII; 17.VII	;2	N,V; R,V	H7
Dryas	15.VII; 17.VII	5;	N,V; R,V	J11; O10
	18.VII		R,V	E3, 920 m
	23.VII	2	R,V	F13
Potentilla sp.	25.VII		N,V	P9
Epilobium	23.VII		R,V	F13
Pieridae				
Colias hecla Lef.				
Dryas	17.VII		N,V	Q10
Taraxacum	25.VII		R,V	P9
Lycaenidae				
Plebeius aquilo Bdv.				
Salix ♀	28.VII		N,C	H8
Dryas	23.VII; 25.VII; 28.VII		R,V; N,V; R,C	F13; P9; H8
Diptera, Tipulidae				
Tipula arctica Curt.				
Dryas	15.VII		R,V	F14
Chironomidae				
Lychnis triflora	26.VII	3 ♀	R,C	N7
S. oppositifolia	5.VII	many	N,V	P11
	6.VII	many ♂ ♀	F,C	P11
Taraxacum	25.VII	♀	R,C	V4
Arnica	29.VII	♂	P ?,V	N8
Chironomus sp. 3				
S. oppositifolia	5.VII	2 ♂, 2 ♀	H,C	N:
Chironomus sp.				
Dryas	11.VII	♂	H,C	T5
S. oppositifolia	6.VII	♀♀	F,C	P11
Corynoneura scutellata Winnertz				
Salix ♀	9.4II		H,C	L9
Lychnis triflora	28.VII	7 ♂, ♀	from stem hairs	C9
Dryas	11.VII	2 ♂	H,C	T5
Cassiope	9.VII	♂	R,C	L9
Cricotopus sp.				
Lychnis triflora	28.VII	♂, ♀	from stem hairs	C9
Cricotopus lestralis Edw.				
S. oppositifolia	5.VII	♂, 2 ♀	H,C	P11
	6.VII	11 ♂, 6 ♀	H, C	P11
Einfeldia sp. 1				
S. oppositifolia	5.VII	2 ♂	H,C	N9
Gynometriocnemus sp. ?				
Salix ♂	9.VII	♀	R,C	L9

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Heterotrissocladius subpilosus (Kieff.)				
Polygonum	21.4II	♀	R,C	L2
Lychnis triflora	20.VII	2 ♂	R,C	N7
Smittia extrema Holm.				
Salix ♂	22.VI	♂, 41 ♀	H,CG	J12, N11
	27.VI; 9.VII	♂, 4 ♀; 10 ♂, 29 ♀	FR,C	L12; L9
Salix ♀	25.VII	11 ♀	H,C	L9
	9.VII	♂	H,C	L9
Cerastium alpinum	26.VII	♀	R,C	
Lychnis triflora	20.VII; 28.VII	2 ♀; 2 ♀	R,C; from stem hairs	N7; C9
Draba Bellii	29.VII	2 ♀	R,C	
D. cinerea	26.VII	♀	R,C	D1
D. oblongata	26.VII	3 ♀	R,C	D1
Erysimum	1.VII	11 ♀	R,C	H. Nesmith Glacier
S. cernua	26.VII	♀	H,C	D1
S. oppositifolia	2.VII	♂, 10 ♀	H,C	S8
	5.VII	♂, 16 ♀	H,C gravid, no sugars midgut	P11
Smittia polaris Kieff.				
Salix ♂	9.VII	10 ♂, 10 ♀?*	H,C	L9
Dryas	11.VII	4 ♂, ♀?	R,C	M10
Smittia polymorpha Ander.				
Salix ♂	9.VII	♂, 10 ♀?*	H,C	
S. oppositifolia	30.VII	♂	R,C	Omingmak
Orthocladius consobrinus (Holmg.)				
Potentilla sp.	20.VII	♂	R,C	D9
Paraphaenocladius despectus (Kieff.)				
Salix	27.VI	♂	H,C	L12
Salix	9.VII	♀	H,C	L9
Erysimum	19.VII		dead, off leaves	R16
Procladius sp. 1				
S. oppositifolia	5.VII; 6.VII	2 ♀; ♀	R,C; F,C	N9, P11
Prosmittia nanseni Kieff.				
S. oppositifolia	6.VII	2 ♂	F,C	P11
Dryas	8.4II	♂	R,C	P11
Psectrocladius barbatimanus Kieff.				
S. oppositifolia	6.VII	3 ♂	F,C	P11
Pseudodiamesa arctica Mall.				
Dryas	15.VII	♀	R,C	S15
Smittia sp.				
Cerastium alpinum	26.VII	2 ♀	R,C	
Papaver	26.VII	4 ♀	R,C	
Draba Bellii	30.VII	2 ♀	R,C	Omingmak

* ♀♀ of *S. polaris* and *S. polymorpha* could not be separated.

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
S. oppositifolia	5.VII	2 ♀	H,C	P11
Dryas	3.VII		H,C	N12
Limnophyes sp.				
Salix ♂	29.VII	♂, 2 ♀	R,C	Omingmak
Lychnis triflora	28.VII	4 ♂, 3 ♀	from stem hairs	C9
Papaver	22.VII	♂, ♀	R,C	N8
Dryas	5.VII	3 ♀	R,C	M10
Limnophyes sp. 3				
S. oppositifolia	5.VII; 6.VII	♂; 15 ♂, 9 ♀	R,C; F,C	P11
Limnophyes globifer Lundstr.				
S. oppositifolia	5.VII	4 ♂	R,C	P11
Metriocnemus obscuripes Holmgr.				
S. oppositifolia	5.VII; 6.VII	♂; ♂	H,C; F,C	P11
Micropsectra sp.				
S. oppositifolia	6.VII	♂	F,C	P11
Orthocladiinae				
Cerastium alpinum	26.VII	♀	R,C	A6
Lychnis triflora	16.VII	6 ♀	R,C	M8
Draba Bellii	29.VII	2♀	R,C	Omingmak
Lesquerella	26.VI		R,C	L3
Orthocladius sp.				
S. oppositifolia	6.VII	♂	F,C	P11
Tanytarsus niger Ander.				
S. oppositifolia	3.VII	25 ♂, 6 ♀	R,C	N12
Culicidae				
Aedes impiger Walk.				
Salix ♂	9.VII	♀	R,C	L9
Stellaria	22.VII	♀	R,C	N8
Dryas	11.VII; 12.VII	♀; ♀	N,CG; B,C	M10; N10
	13.VII	♂, ♀	BR,C	N10
Potentilla	24.VII	♀	R,C	D9
Aedes nigripes Zett.				
Salix ♂	9.VII	♀	R,C	L9
Stellaria	22.VII	♀	R,C	N8
Dryas	13.VII; 21.VII	♂, ♀; ♀	N,CG; BR, C	N10
Potentilla	25.VII	♂	R,C	N8
Arnica	29.VII	♂	R,C	K2
Aedes sp.				
Salix ♂	5.VII	♂, ♀	N,V	P11
Dryas	12.VII	4♂, 3 ♀	B,V	N10
Potentilla	17.VII; 20.VII	♀; ♀	B,V; B,V	K8; E9
Epilobium	31.VII	♀	R,V	J3
Cecidomyiidae sp.				
Salix ♂	9.VII	2	H,C	L9

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Sciaridae				
Bradysia sp.				
Salix ♀ & ♂	6.VII	several	R,V	H9
Empididae				
Rhamphomyia sp.				
S. tricuspidata	28.VII	2	N,V	K2
Potentilla	20.VII		R,V	E9
Taraxacum	29.VII		R,V	N8
Rhamphomyia filicauda Lundb.				
Dryas	13.VII	2 ♂, 3 ♀	R,C	N10
	24.VII; 25.VII	8 ♂, 13 ♀;	R,C	N10; N8
Potentilla	25.VII	♂	R,C	C9
Rhamphomyia sp. nr. *lamelliseta*				
Cerastium alpinum	24.VII	♀	R,C	G13
S. oppositifolia	6.VII	3 ♂	RF,C	P11
Dryas	11.VII; 13.VII	2 ♀; 2 ♂, 6 ♀	R,C; M,C	T5; M10, N10
	24.VII	11 ♂, 31 ♀	FR,C	N10
Rhamphomyia nigrita Zett.				
Dryas	13.VII; 24.VII	♀; ♂, 7 ♀	R,C; A,C	N10
Potentilla	19.VII	♀	R,C	M8
Erigeron	30.VII	♀	R,C	M7
Dolichopodidae				
Dolichopus dasyops Mall.				
Stellaria	22.VII	2 ♀	R,C	N8
Syrphidae				
Carposcalis carinata Cu.				
Salix ♀	9.VII	♀	R,C	L9
Papaver	26.VII		R,V	
S. oppositifolia	6.VII	♀	R,C	P11
S. tricuspidata	31.VII	♀	R,C	F6
Dryas	3.VII; 5.VII	2 ♂; ♀	R,V; F,V	N12; P11
	8.VII; 13.VII	♀; 2 ♀	P,CG; P,C	N12; N10
	22.VII; 24.VII	♀; ♀	R,C; P,C	J3; N10
Potentilla	25.VII	♀	F,C	N8
Helophilus borealis Staeg.				
Salix ♂	12.VII	♀	R,C	L2
Dryas	12.VII; 16.VII	♀; ♀	R,V; P,V	L2; T6
Phalacrodira nigropilosa Cu.				
Dryas	29.VI; 3.VII	♀; ♂	R,C; R,V	S8; P10
Piophilidae				
Allopiophila arctica Holmgr.				
Salix ♂	28.VI	♂, ♀	H,C	T7
Dryas	13.VII	♀	R,C	N10
Muscidae				
Eupogonomyia groenlandica Lundb.				
Salix ♀	30.VI	2 ♂	F,C	R9; L9
Dryas	11.VII	♂	R,C	M10

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Fucellia pictipennis Becker				
S. oppositifolia.............	5.VII		N,V	P11
Pogonomyoides segnis Holmgr.				
Salix ♀....................	9.VII	♀	R,C	L9
Papaver....................	25.VII	2 ♀	R,CP	N8
Dryas.....................	30.VI; 13.VII	♀; ♂, 2 ♀	R,C; R,C	R9; N10
Spilogona sp.				
Erysimum.................	1.4II		R,V	H. Nesmith Glacier
S. flagellaris...............	12.VII		R,V	N10
Arnica....................	27.VII		R,V	K3
Spilogona almquisti Holmgr.				
Dryas.....................	4.VIII	♀	R,C	Resolute Bay
Spilogona deflorata Holmgr.				
Dryas.....................	13.VII	♂	R,C	N10
Spilogona dorsata Zett.				
Papaver....................	4.VIII	2 ♀	R,C	Resolute Bay
Dryas.....................	4.VIII	♀	R,C	Resolute Bay
Spilogona latilamina Collin				
S. Hirculus................	4.VIII	2 ♂, ♀	R,C	Resolute Bay
Dryas.....................	13.VII	♀	R,C	N10
Spilogona melanosoma Huck.				
S. Hirculus................	4.VIII	2 ♂	R,C	Resolute Bay
Dryas.....................	11.VII; 13.VII	♀; ♂, 3 ♀	(R,Cp( )	Q7; N10
Potentilla.................	22.VII; 31.4II	2 ♀	R,C	N10; D9
Spilogona sanctipauli Mall.				
Salix ♂....................	9.VII	♂	R,C	L9
Papaver....................	22.VII; 25.VII	2 ♀; ♀	R,C	N8; P10
	4.VIII	♀	R,C	Resolute Bay
Dryas.....................	5.VII; 11.VII	4 ♂; 2 ♂	R,C	P9, P11; M10, Q7
	13.VII; 18.VII	2 ♂, 3 ♀; ♂	R,C	N10; J3
Spilogona tundrae Schnabl.				
Dryas.....................	13.VII	♂	R,CP	N10
Pegomyia sp.				
Potentilla.................	25.VII; 31.4II		R,C	P9; J3
Taraxacum................	25.VII		R,C	P9
Tachinidae				
Peleteriopsis aenea Staeg.				
Stellaria..................	22.VII	♂, ♀	R,C	N8
Lesquerella................	22.VII	2♂	N,V	N8
Petinarctia stylata (B & B)				
Salix ♂....................	26.VII	♀ on leaf	R,C	N10
Dryas.....................	25.VII		R,C	P9
Epilobium.................	29.VII		R,C	V6

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Calliphoridae				
Boreellus atriceps Zett.				
S. oppositifolia	23.VI		R,C	P11
Dryas	13.VII; 24.VII	2 ♀	R,C	N10
Protophormia terraenovae (R. D.)				
Salix ♂	24.VI; 28.VI	; 2 ♀	N,V; N ?,V	Ruggles River; P8
Salix ♀	2.VI.67		N,V	M12
Dryas	15.VII		R,V	R6
Cassiope	22.VII	♀	R,C	J3
Scatophagidae				
Scatophaga nigripalpis Beck.				
S. oppositifolia	5.VII		F,C	P11
Hymenoptera, Tenthredinidae				
Amauronematus sp.				
Salix ♀	30.V.67	♀	O ?,C	M12
Amauronematus amentorum (Forst.)				
S. oppositifolia	6.VII	♀	R,C	P11
Dryas	13.VII	♀	R,C	N10
Ichneumonidae				
Lesquerella	8.4II	♀	?,CP	W5
S. tricuspidata	29.VII	2 ♀	F,C	Omingmak
Cryptus arcticus Schiødte				
Salix ♂	4.VII; 29.VII	♂, 2 ♀	?,P	M5; L10
Stellaria	15.VII; 31.VII	♀, 2 ♀	?,P	P12; L11
Braya sp.	3.VII; 4.VII	♂, ♀	?,P	Q9; M5
Saxifraga sp.	5.VII; 31.VII	♀	?,P	N11; L11
Hyposoter luctus (Davis)				
Salix ♂	5.VII	♂	?,P	P11
Braya sp.	5.VII	♂	?,P	P11
Braconidae				
Stellaria	25.VII	♀	R,C	N8,; P9
Potentilla	2.VII; 29.VII	2 ♀	F,C; R,V	S8; P11
Chalcidae				
Lychnis triflora	18.VII		on stem hairs	N11
Potentilla	3.VII	2	R,V	N12
Bombidae				
Megabombus polaris Curt				
Salix ♂	3.VI.67	♀	N,V	J5
	3.VII; 9.VII; 18.VII	♀	N,V	L9
	18.VII–26.VII	16 ☿	N,V	
Salix ♀	9.VII	♀	N,V	L9
Stellaria	18.VII; 4.VIII	☿	P,CP	

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Plant sp.	Date	No. Sex	Activity, Evidence	Location
Silene	26.VII	☿	R,V	
Papaver	18.VII	☿	R,C	J3; K2
S. oppositifolia	23.VI; 30.VI; 3.VII	3 ♀	R,C	P11;P12;N12
	2.VII; 4.VII	☿; ♀	R,C; P,C	S8; N10
	8.VII; 29.VII	☿; ♀	R,CP; R,C	D13; 3000 ft., Omingmak
	9.VII–3.VIII	9 ☿	N,CG	A1; S8
Dryas	16.VII; 22.VII	♀; 3 ☿	F,CP; R,CP	M9; J3
	10.VII–2.VIII	10 ☿	R,CP	2000 ft., E2; J3
Epilobium	27.VII; 31.VII	☿; ☿	P,CP; R,V	V6; J3
Cassiope	11.VII–31.4II	8 ☿	R,V; P,CP	K2; P3
Pedicularis (*arctica* + *hirsuta*)	11.VII–18.VII	6 ♀	R,C; R,V	B15; J3; L9
	13.VII; 16.VII	3 ☿	R,C; P,V	N10; T6
	18.VII; 21.VII	many ☿, ☿	N,V	J4; N10
P. capitata	20.VII	4 ☿	N,V	N10
	22.VII–27.VII	3 ☿	R,CP	K2; C9; U3
	28.VII; 29.VII	♀, ♀	P,V; R,CP	K2; C8
Megabombus hyperboreus Schönherr				
Epilobium	17.VII	♀	PN,CP	V5
Apis mellifera L. (temporary import)				
Salix ♀	18.VII; 20.VII	several ☿	N,V	N10
S. oppositifolia	4.VII	several ☿	P,V	N10
Cassiope	13.VII	several ☿	N,V	N10

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