INSECT POLLINATION OF HIGH ARCTIC FLOWERS*

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INTRODUCTION

A great deal has been said about the tendency towards autogamy and apomixis in arctic plants. Even shortly after the publication of the Darwin–Knight law of nature's abhorrence of perpetual self-fertilization, Aurivillius (1883) suggested that reproduction is regularly autogamous in *Pedicularis lanata* Cham. & Schlecht. and *P. hirsuta* L. on Svalbard. Ekstam's works (1894a, b, 1897, 1899) expanded the ideas of increased autogamy in arctic flowers and Warming (1886–1920), Jessen (1913), Mathiesen (1921) and others laid the foundations of what is generally upheld today. No authors have actually said that insect pollination does not occur in the arctic, except in certain species as mentioned above. However, a quotation from Mosquin (1966, p. 60) summarizes present ideas in general, '. . . although many arctic insects clearly depend on nectar- and pollen-producing, showy-flowered plants for survival, these plants may have little or no need for insects'. Contrary ideas have been put forward by Chernov (1966), and evidence is given by Gavrilyuk (1961, 1966), Panfilov, Shamurin & Yurtsev (1960), and Shamurin (1962, 1966a, b) who cite examples of plants (particularly legumes) dependent on bumble-bees and flies for pollination and seed-set. Such arctic plants could, of course, survive without the agency of insects. Most are perennial and would presumably persist for considerable time in the absence of insects. Furthermore, seed dispersal in the arctic is relatively unimpaired (Savile 1964b) so that plants dependent on insects for seed-set may flourish beyond the ranges of their pollinators.

An account is given in this paper of new experiments on the dependence of arctic plants on insects for seed-set, and of new observations on the insects responsible for pollination. The work was conducted near Hazen Camp (81° 49' N, 71° 18' W), Ellesmere Island, Northwest Territories, Canada, in the summers of 1966, 1967, and 1968. The general ecology of this area has been described by Savile (1964a). Powell (1961), Savile (1964a), and Kevan (1970) give lists of about seventy-five species of dicotyledons in the area. The nomenclature followed here is mainly that of Porsild (1964). Throughout the text the term inflorescence is used loosely to include individual flowers when they are normally produced singly and capitulate inflorescences such as those of Compositae and Salicaceae.

EXPERIMENTS ON INSECT-EXCLUSION AND SEED-SET
Materials and methods

Insect excluders were constructed from $\frac{1}{32}$ in. (*c.* 0·8 mm) clear acetate sheet (see

Fig. 1). The excluders were truncate cones with a base diameter of 9 in. (*c.* 23 cm), and a top diameter of 2 in. (*c.* 5 cm). They were 12 in. (*c.* 30 cm) high and left plenty of room for the growth of the plants inside. About 4 in. (*c.* 10 cm) from the base, three 2 in. (*c.* 5 cm) diameter holes were made and covered with fine marquisette mesh, as was the hole at the top of the cone. These mesh-covered holes served as vents, allowing passage of air to prevent condensation within the cone, reduce the glasshouse effect, and allow the entry of the wind-borne pollen although none of the experimental plants, except *Salix arctica* Pall., was thought likely to be anemophilous (cf. Mosquin & Martin 1967).

The insect excluders were placed over, and dug in around, the individual plants or groups of plants under study. The apparatus was considered entirely insect-proof for the
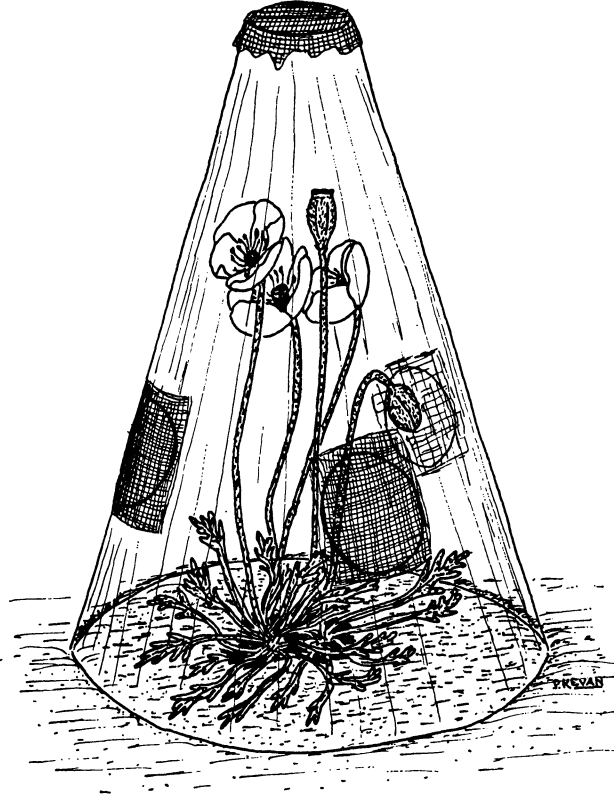

FIG. 1. Insect excluder in position over a clump of flowers of *Papaver radicatum*.

purpose of the experiments. The excluders were put into place before the plants had bloomed, and control plants were also marked at this time.

The experimental plants are listed in the results (Table 1) according to the scheme of treatments used.

Treatment 1   Untreated plants (normal flowers or inflorescences open to insect visits)
Treatment 2   Normal flowers or inflorescences enclosed under insect excluders
Treatment 3   Emasculated flowers open to insect visits
Treatment 4   Emasculated flowers enclosed under insect excluders
Treatment 5   Normal flowers enclosed under insect excluders and cross-pollinated by hand

Treatment 6   Emasculated flowers enclosed under insect excluders and cross-pollinated by hand

The experimental plants were harvested at the end of the season and taken to a laboratory for examination. The criteria used to evaluate seed production were as follows.

Dehisced seed pods or firm ripening pods on *Pedicularis* spp., *Saxifraga* spp., *Papaver radicatum*, *Cassiope tetragona*, and the Cruciferae indicated that seeds were produced. When pods were absent or withered and soft, indicating that successful fertilization had not taken place, the remains of the corollas were often evident and on some saxifrages shrivelled remains of stamens could also be seen.

Salix arctica, *Dryas integrifolia*, *Taraxacum arctogenum* and *Epilobium latifolium* with seed plumes indicated that seeds were produced. When plumes were not present in *S. arctica* and *E. latifolium* the pods were abortive and soft. In *Dryas integrifolia* seed plumes were sometimes much shorter, and the achene much smaller, than in the long plumed achene taken as the normal fruit; the smaller seeds were regarded as abortive seeds (perhaps they are haploid). Seeds were entirely absent from some flowers.

RESULTS AND DISCUSSION

The results of the pollination experiments are given in Table 1.

Species entirely dependent (or almost entirely
dependent) on insects for seed-set

Pedicularis *spp.*

Because of the lack of bumblebees on Svalbard, Aurivillius (1883) proposed auto-gamous reproduction in the species of *Pedicularis* there. Mathiesen (1921) inferred the reproductive biology of arctic *Pedicularis* spp. in Greenland from their floral structures and from information in the literature and also concluded that the plants were self-pollinating. Warming (1888), Mosquin & Martin (1967) and Savile (in Mosquin & Martin 1967) all suggest that the arctic *Pedicularis* spp. are regularly self-pollinating. However, Macior (1970) conducted pollination experiments in arctic–alpine species in Colorado and found them to be dependent on bumblebees. MacInnes' (1972) findings from the McConnel River area (60° 50′ N, 94° 25′ W) on Hudson Bay provide insight into the complexity of the pollination biology of this genus in the arctic. She has dis-covered that there are species showing independence of, partial dependence on, and complete dependence on insects for seed-set.

The present results show that *P. capitata* is entirely dependent on insects for seed-set. The only common pollinators of this species are bumblebees, particularly workers of *Bombus polaris* Curtis, although flowers are visited by queens of *B. hyperboreus* Schönherr and other (non-pollinating) insects (Kevan 1970). This finding contradicts the suggestion of Simmons (1906) that *Pedicularis capitata* rarely sets seed on Ellesmere Island and reproduces by its rhizomes, and Mathiesen's (1921) report that it is easily self-pollinated because the styles are short and hardly exserted from the flowers and, if exserted a few millimetres, have a slightly upturned stigma.

P. arctica is similarly dependent on insects for seed-set but 7% can produce capsules, and possibly seeds, autogamously. Again, pollinators are the same bumblebees. MacInnes (1972) has shown that capsules may be produced by *Pedicularis* spp. without bearing seeds. Porsild (1964) mentions forms intermediate between *P. arctica* and *P. hirsuta* L. in north-western Greenland, Ellesmere, and Baffin Island (see also Böcher, Holmen &

Insect pollination of high arctic flowers

Table 1. *Results of pollination experiments as expressed by seed-set*

Treatment	1966				1967				1968				Total				Average (all years) percent seed-set
	S	W	T	N	S	W	T	N	S	W	T	N	S	W	T	N	
Pedicularis capitata Adams. (Scrophulariaceae)																	
1									15	4	19	6	15	4	19	6	79
2									0	19	19	5	0	19	19	5	0
P. arctica R. Br. (Scrophulariaceae)																	
1					63	4	67	3	8	0	8	1	71	4	75	4	95
2					5	62	67	3	–	–	–	–*	5	62	67	3	7
Salix arctica Pall. (Salicaceae)																	
1	14	1	15	9	24	0	24	2	41	18	59	9	79	19	98	20	80
2	0	12	12	9	0	26	26	2	0	42	42	5	0	80	80	16	0
5									29	0	29	3	29	0	29	3	100
Dryas integrifolia M. Vahl (Rosaceae)†																	
1					48	15	63	6	55	12	67	8	103	27	130	14	79
2					28	57	85	6	(31)	(20)	(51)	(8)	28	57	85	6	33
3									4	1	5	1	4	1	5	1	80
4									(3)	(4)	(7)	(1)	–	–	–	–	–
5									18	1	19	3	18	1	19	1	95
Saxifraga oppositifolia L. (Saxifragaceae)																	
1	88	6	94	8	92	6	98	7	107	17	124	7	287	29	316	22	91
2	16	121	137	5	8	101	109	10	2	58	60	6	26	280	306	21	8
3	34	4	38	4	25	3	28	4	12	7	19	3	71	14	85	11	84
4					0	16	16	2	0	34	34	5	0	50	50	7	0
5									16	6	22	2	16	6	22	2	73
6									28	1	29	3	28	1	29	3	97
S. tricuspidata Rottb. (Saxifragaceae)																	
1									38	46	84	2	38	46	84	2	45
2									16	19	35	2	16	19	35	2	46
Melandrium triflorum (R. Br.) J. Vahl (Caryophyllaceae)‡																	
2									(6)	0	6	2	(6)	0	6	2	(100)
Papaver radicatum Rottb. (Papaveraceae)§																	
1	11	0	11	6	2	0	2	2	10	0	10	2	23	0	23	10	100
2	3	0	3	3	2	0	2	2	30	0	30	5	35	0	35	10	100
Lesquerella arctica (Wormskj.) Watson (Cruciferae)																	
1									93	0	93	3	93	0	93	3	100
2									135	0	135	4	135	0	135	4	100
Erysimum pallasii (Pursh) Fern. (Cruciferae)																	
1									9	0	9	1	9	0	9	1	100
2									42	0	42	1	42	0	42	1	100
Epilobium latifolium L. (Onagraceae)																	
1									6	3	9	2	6	3	9	2	67
2									15	2	17	2	15	2	17	2	88
Cassiope tetragona (L.) D. Don (Ericaceae)**																	
1									–	–	75	2	–	–	75	2	–
2									–	–	86	2	–	–	86	2	–
Taraxacum arctogenum Dahlst. (Compositae)																	
1									13	0	13	2	13	0	13	2	100
2									9	0	9	2	9	0	9	2	100

T, total number of inflorescences or flowers treated; S, number with seeds; W, number without seeds; N, number of plants or clumps treated. Treatments numbered as in the text.

* All eaten by arctic hares.

† Numbers in parentheses are the results remaining after arctic hares had upset all the excluders and eaten most of the plants within.

‡ Experiment eaten by hares before complete.

§ Treatment 4 unsuccessful; anthers dehisce before flower opens, or almost immediately after.

** Fruits developing under both treatments appeared the same, but were very variable in size.

Jacobsen 1968). This suggests insect-mediated cross-pollination and hybrid development.

  P. hirsuta and *P. sudetica* Willd. also grow around Hazen Camp, but were uncommon and not experimented upon. Warming (1888) and Mathiesen (1921) remark that *P. hirsuta* may be cross-pollinated by insects and the latter author states it 'to be *the* one of the Arctic *Pedicularis* spp., which is best fitted for self-pollination'. Mathiesen (1921) states that self-pollination could take place with ease in *P. sudetica*. MacInnes (1972) found this species to be partially dependent on insects at the McConnel River, and Macior (1970) found no evidence for selfing in the subspecies *P. s. scopulorum* in Colorado.

  In some parts of the arctic, *Helophilus* spp. (Diptera: Syrphidae) as well as *Bombus* spp. are important pollinators of *Pedicularis* spp. (MacInnes 1972).

Salix arctica

  The lack of seed-set under the cones is not an artifact as all catkins which were hand-pollinated and left under excluders developed very vigorously, growing in excess of 5 cm long. These results contradict the idea expressed by Mosquin & Martin (1967) that '. . . arctic willow may well be losing a dependence on insect pollination and evolving towards wind pollination . . .' and illustrate the generality of insect pollination prevailing in *Salix* (Hjelmquist 1948).

Species dependent on insects for maximum seed-set

Dryas integrifolia

  The greatly reduced percentage seed-set under the excluders is not an artifact caused by the excluders as flowers hand-pollinated and left under them had 95% seed-set. Emasculation of these flowers is tedious work so few were treated; still fewer survived the ravages of arctic hares. Even so, the importance of insect pollination is shown by the four of five emasculated flowers left in the open setting seed, and by three of the seven placed under excluders (which were knocked off by hares) setting seed.

  D. integrifolia is dependent on insects for maximum seed-set but can develop seeds autogamously, as was suggested might occur by Simmons (1906) and Jessen (1913). The importance of insect pollination of *D. integrifolia* may be of considerable significance in understanding the taxonomic problems of *D. octopetala* L. and *D. integrifolia* in north-eastern Greenland (Elkington 1965). If these two species are reproductively compatible, the apparently intermediate forms can be explained by insect-mediated cross-pollination. The insect fauna of Pearyland is very similar to that of northern Ellesmere Island (D. R. Oliver and J. A. Downes, personal communication).

Saxifraga oppositifolia

  Again, the greatly reduced percentage seed-set under the excluders is not an artifact caused by the excluders as the flowers hand-pollinated and left under the excluders showed a seed-set of 88%. The importance of insect pollination in this species is further emphasized by the 84% seed-set in eighty-five emasculated flowers to which insects had access. Autogamous seed production in this species is less than 10%, but does occur; emasculated flowers within excluders failed to produce any seed. Savile (1964a) briefly mentions the role of insects in the cross-pollination and maintenance of a genetically diverse population of these plants. Many workers have seen insect visitors to *S. oppositifolia* (Knuth 1906–1908; Kevan 1970). From the present results it is difficult to interpret the significance of the floral movements described by Warming (1909) and Høeg (1932)

that are said to assure self-pollination, which is generally accepted as being always possible (cf. Jones & Richards 1956). Perhaps there are physiological differences between geographically separated populations, or temperature controlled processes which operate under cold conditions to cause floral movements and selfing (cf. Lewis 1942; Hecht 1968) or genetically different races which can self-pollinate (cf. Davis 1971). Böcher (1961) discussed the interesting origin of *S. nathorsti* (Dusén) v. Hayek in Greenland and suggests that it is probably an allopolyploid of *S. oppositifolia* and the yellow-flowered *S. aizoides* L. If that explanation is correct, insect-mediated cross-pollination must be assumed.

Species independent of insects for seed-set

Saxifraga tricuspidata

Warming (1909) discussed the biology of this species and suggested that it is easily selfed by stamen and pistil movements and mutual contact. It is not clear why only about 50% of the flowers (one or two on each stem) set seed. All flowers were, as far as could be determined in the present study, hermaphroditic (cf. Warming 1909). Pollen is not produced copiously in the flowers around Hazen Camp (Kevan 1970). Perhaps the movements of floral parts are not as important for seed set as Warming (1909) implies (cf. *S. oppositifolia*). Insect visitors are uncommon (Warming 1909; Hocking 1968; Kevan 1970).

The pollination biology of the arctic species of *Saxifraga*, some of which reproduce vegetatively and have showy flowers (e.g. *S. cernua* L., *S. flagellaris* Willd.) cannot be inferred from morphology alone. Ekstam (1894a, 1897, 1899) has noted a few visitors to most of the species on Svalbard and Novaya Zemlya. Shamurin (1962) states that *S. hirculus* L. and *S. flagellaris* are autogamous and pollinated by flies. At Hazen Camp visitors to these species are rare (Hocking 1968; Kevan 1970).

Melandrium *spp.* (= Silene *spp.*)

Two plants of *Melandrium triflorum* (= *Silene sorensenis* (Boivin) Bocquet), each bearing three flowers, appeared to have had developing fruits before they were eaten by hares. The depth of the syncalyx precludes the copious nectar being removed by any but insects with long proboscides (Kevan 1970). Almost no insect visitors to flowers of this species were found and it is concluded that *Melandrium triflorum* is independent of insects for seed-set. Warming (1920) records the flowers as slightly protogynous and self-pollinating, as in *M. affine* (J. Vahl) Martin (= *Silene involucrata* (Cham. & Schlecht.) Bocquet) and *Melandrium apetalum* (L.) Fenzl (= *Silene uralensis* (Rupr.) Bocquet). Interestingly Shamurin (1962) records the last-mentioned species as autogamous and pollinated by flies, but in three seasons at Hazen Camp visitors to its flowers were never found.

Papaver radicatum

The flowers produce abundant pollen almost as soon as they open. Presumably self-fertilization occurs as it does in the alpine regions of Norway (Knaben 1959b). Fryxell (1957), however, lists four species of *Papaver* as principally cross-fertilized and self-incompatible, and includes *P. radicatum* in this category (as *P. nudicaule* L.) (cf. East 1940). *P. radicatum* is made up of at least five chromosomal races (Knaben 1959a; Mosquin & Hayley 1966); they could well show differences in their reproductive behaviour.

Cruciferae

Erysimum pallasii is probably apomictic (Mulligan 1966). Insect visitors are few and infrequent despite the floral scent and abundant but deeply hidden nectar (Kevan 1970). *Lesquerella arctica*, on the other hand, is quite commonly visited by insects. An interesting relationship exists between the flowers of this species and a collembolan *Entombrya comparata* Folsom, but this is not important in cross-pollination (Kevan & Kevan 1970). *Lesquerella arctica* is probably self-fertilized: meiosis is normal (G. A. Mulligan, personal communication). The closely related species from the northern Yukon Territory, *L. calderi* Mulligan and Porsild, is an obligate out-crosser (G. A. Mulligan, personal communication). Most of the Cruciferae around Lake Hazen are probably self-fertilized (cf. Mulligan 1964, 1965, 1966; Mulligan & Findlay 1970); insect visitors to white-flowered species are rare.

Potentilla nivea

About ten flowers from which insects were excluded appeared to have had developing fruits before they were eaten by hares. Gustaffson (1946) and Nygren (1954) record *Potentilla* species as parthenogenetic, and Fryxell (1957) records numerous apomicts in this complex genus but notes that insufficient information is available to state whether apomixis is facultative or obligate. Shamurin (1962) records that *P. nivea* is pollinated by flies and is not autogamous. Certainly insect visitors are not uncommon (Hartz 1895; Savile 1964a; Hocking 1968; Kevan 1970) but Warming (in Jessen 1913) noted that 'self-pollination must undoubtedly take place'. Dansereau & Steiner (1956) write of a hybrid of *P. chamissonis* Hult. (? = *P. nivea*) and *P. pulchella* R. Br.; this must have been insect-mediated. It appears that arctic *Potentilla* spp. in general are independent of insects for seed-set, but undergo out-crossing due to the activities of insects.

Epilobium latifolium

Bumblebees have been recorded visiting the flowers (Milliron & Oliver 1966; Hocking 1968; Richards 1970; Kevan 1970) and Small (1968) wrote, '. . . it seems clear that the plants are adapted to insect pollination and are normally out-crossed'. However, in the present study very few insects have been found on the flowers despite the abundant, but hidden nectar. Insect-mediated pollination must occur as a hybrid with *E. angustifolium* L. (as *E. ambiguum* Fries) has been recorded from Disco, Greenland (Böcher 1962; Knuth 1906–1908, II, 447) and other arctic *Epilobium* hybrids are known (Small 1968). Warming (1886) remarks that autogamy may result from the falling of pollen on to the stigma, supported by its short down-curved style, as anthers and stigmas mature almost simultaneously (cf. *E. angustifolium*, p. 841). Selfing may not happen easily because the pollen grains are bound together with threads of viscin and are difficult to dislodge from the anthers. Of the three chromosomal types ($2n = 36, 54, 72$) Small (1968) discounts the significance of the triploids as having arisen from unreduced gametes and exemplifying the occasional variant. A more critical examination of the pollen biology of this species is required.

Cassiope tetragona

Fryxell (1957) records most of the Ericaceae as autogamous. The present incomplete experiments support that generalization, as do Shamurin's (1962) data. Out-crossing undoubtedly occurs due to the activities of insects: bumblebees have been recorded on the flowers by Hocking (1968), Richards (1970), Høeg (1929) and others; Ekstam (1899)

found flies occasionally visiting the flowers. Warming (1908) writes that the flowers are first protandrous and then homogamous, and that self-pollination may easily occur, as in other Ericaceae with urceolate flowers. Fryxell's (1957) generalization, however, is open to grave doubt as obligate out-crossers are well known in *Vaccinium* spp. (cf. Free 1970). In the Faroes pollination by thrips is reported in *Calluna* (Hagerup 1950) and *Erica tetralix* L. (Hagerup & Hagerup 1953) but no analogous relationship was found for *Cassiope tetragona* at Hazen Camp. Thrips (*Frankliniella tritici* (Fitch)) were found in the flowers of *Arctostaphylos rubra* (Rehd. & Wils.) Fern. around Inuvik (68° 21′ N, 133° 43′ W), N.W.T., in early June 1970, and small flies visiting flowers of *Phyllodoce aleutica* (Spreng.) Heller on Mount Alyeska (60° 58′ N, 149° 04′ W), Alaska, on 13 September 1970. Generally, however, bees are considered to be the important pollinators in the Ericaceae.

Taraxacum arctogenum

This species produces little pollen (Kevan 1970). It is probably agamospermous (Jørgensen, Sørensen & Westergaard 1958) like other *Taraxacum* species (Nygren 1954; Jørgensen *et al.* 1958); some of them produce no pollen in the arctic (Porsild 1964). Nevertheless, inflorescences of *T. arctogenum* were found in the present study to be fairly well visited by insects so the possibility of insect-mediated out-crossing exists.

INSECTS RESPONSIBLE FOR POLLINATION

The ability to carry pollen grains is not enough to characterize a pollinating insect. Effective pollinators must visit more than one flower of the same species within the period of viability of the pollen grains they carry. They must also visit flowers in such a way as to pick up viable pollen and transfer it to the receptive stigmas of subsequently visited flowers. Insects which are constant or steadfast to particular flowers, and behave as above, are more effective pollinators than insects which visit many kinds of flowers.

Shamurin (1966a) discusses the roles of pollinators on the tundra and considers bumblebees the most effective pollinators, while Diptera are important too because of their high numbers. The primary importance of bumblebees and secondary importance of Diptera as pollinators is brought out by Chernov (1966) and Gavrilyuk (1966). Hocking (1968) considers that there is 'competition between flowers for pollinators rather than among pollinators for nectar'.

McAlpine (1965a) says that '. . . probably 85 to 90% of the netted specimens (of flies) taken from Lake Hazen area have at least a few grains of pollen caught among the hairs of their bodies'. Table 2 presents findings on the pollen-carrying ability of the insects at Hazen Camp in terms of the percentage of the population of each species collected from flowers and carrying pollen. From the species listed, the most important pollinators are probably the Empididae, Syrphidae, Phaoniinae, *Spilogona* spp. and *Bombus* spp. Of lesser importance are Tachinidae, *Boreellus atriceps*, *Aedes* spp., Lepidoptera, and *Smittia velutina*. Table 3 shows the flowers dependent, at least for maximum seed-set, on insects and the insects mostly responsible for their cross-pollination.

. From the foregoing discussion and from Table 3, it is obvious that bumblebees are not as important as Diptera as pollen vectors, which is the reverse of the situation described by Shamurin (1966a). The Diptera are especially important in the high arctic as they show obligatory flower constancy or steadfastness due to the preponderance of flowers of one species available at one time. In most temperate areas the diversity of flowers at

any one time makes available to 'polylectic' insects (e.g. many Diptera) a wide choice of blooms. If such insects visit many species their effectiveness as pollinators is reduced. In such situations insects showing flower steadfastness ('oligolectic' species, e.g. Apidae) are the more effective pollinators. To the Diptera of northern Ellesmere Island, the

Table 2. *Percentage of each anthophilous species of arthropod found on flowers that was dusted with pollen grains* (1967)

Species	% carrying pollen	Number considered
Araneida		
1 *Xysticus deichmanni* Soerensen (Thomisidae)	50	22
2 Other Araneida	25	12
Trichoptera		
3 *Apatania zonella* (Zetterstedt)	0	1
Lepidoptera		
4 *Anarta richardsoni* Curt. (Noctuidae)	63	8
5 *Crymodes exulis* Lef. (Noctuidae)	85	13
6 *Lasiestra leucocycla* Staud. (Noctuidae)	79	14
7 *Boloria polaris* Bdv. (Nymphalidae)	100	3
8 *B. chariclea* Schneid. (Nymphalidae)	88	8
9 Lycaenidae	20	5
10 Other Lepidoptera	50	2
Diptera		
11 *Tipula arctica* Curtis (Tipulidae)	100	1
12 *Smittia* spp. (Chironomidae)	85	631
13 *Limnhphyes* spp. (Chironomidae)	40	82
14 *Paraphaenocladius despectus* (Kieff.) (Chironomidae)	40	20
15 Other Chironomidae	44	25
16 *Aedes* spp. (Culicidae)	77	22
17 *Bradysia* spp. (Sciaridae)	41	27
18 *Dolichopus dasyops* Malloch (Dolichopodidae)	0	3
19 *Rhamphomyia filicauda* Henriksen & Lundbeck (Empididae)	88	215
20 *R. nigrita* Zetterstedt (Empididae)	85	44
21 *R. hoeli* Frey (Empididae)	80	37
22 *Carposcalis carinata* (Curran) (Syrphidae)	88	58
23 *Melangyna nigropilosa* (Curran) (Syrphidae)	83	18
24 *Metasyrphus chillcotti* Fluke (Syrphidae)	88	8
25 *Helophilus borealis* Staeger (Syrphidae)	100	2
26 *Phytomyza erigerontophaga* Spencer (Agromyzidae)	20	5
27 *Boreellus atriceps* (Zetterstedt) (Calliphoridae)	35	47
28 *Peleteria aenea* (Staeger) (Tachinidae)	82	17
29 *Fucellia pictipennis* Becker (Muscidae: Anthomyiinae)	40	5
30 *Pegomya* spp. (Muscidae: Anthomyiinae)	100	2
31 *Eupogonomyia groenlandica* (Lundbeck) (Muscidae: Phaoniinae)	55	11
32 *Pogonomyioides segnis* Huckett (Muscidae: Phaoniinae)	93	28
33 *Spilogona melanosoma* (Huckett) (Muscidae: Limnophorinae)	91	11
34 *S. sanctipauli* (Malloch) (Muscidae: Limnophorinae)	95	40
35 *S. tundrae* (Schnabl) (Muscidae: Limnophorinae)	83	6
36 *Spilogona*, other species (Muscidae: Limnophorinae)	90	14
Hymenoptera		
37 *Nematus* spp. (Tenthredinidae)	40	5
38 Parasitica	42	19
39 *Bombus* spp. (Bombidae)	87	22

season starts with *Saxifraga oppositifolia*, changes to *Salix arctica*, then to *Dryas integrifolia*, and at Gilman Camp (81° 34′ N, 69° 30′ W) this is followed by *Arnica alpina*. At Hazen Camp, after the finish of the *Dryas integrifolia* bloom, no single species of flower is dominant; *Stellaria longipes, Cerastium alpinum, Polygonum viviparum, Saxifraga*

hirculus, and others are all in bloom with late-flowering plants of previously mentioned species.

The Diptera listed as important pollinators all visit more than one inflorescence of each plant, as many of the present observations have shown (Kevan 1970). Certainly Mc-Alpine's (1965a) mention of the high proportion of netted specimens carrying pollen is circumstantial evidence for this argument. When visiting pleomorphic flowers (cf. Leppik (1956, 1957, 1968) and Kevan (1970) for terminology of flower types) Diptera feed on nectar in any of three positions, none of which is constant to any species. The two important positions in ducking for nectar are, first, standing on the stigma head-down

Table 3. *Flowers dependent on insects, at least for maximum seed-set, and the insects mostly responsible for pollination (numbers refer to Table 2)*

Flower species		Insect species
Pedicularis capitata	39	*Bombus* spp. (mainly *polaris*)
P. arctica	39	*Bombus* spp. (mainly *polaris*)
Salix arctica	22	*Carposcalis carinata*
	23	*Melangyna nigropilosa*
	39	*Bombus polaris*
	27	*Boreellus atriceps**
	12	*Smittia velutina* (Lundbeck)†
Dryas integrifolia	20	*Rhamphomyia nigrita*
	19	*R. filicauda*
	31	*Eupogonomyia groenlandica*
	32	*Pogonomyioides segnis*
	34	*Spilogona sanctipauli*
	33	*S. melanosoma*
	36	*Spilogona* spp.
	39	*Bombus polaris* (workers)
		Lepidoptera
	16	*Aedes* spp.
	22	*Carposcalis carinata*
Saxifraga oppositifolia	22	*Carposcalis carinata*
	23	*Melangyna nigropilosa*
	39	*Bombus polaris* (queens)
	27	*Boreellus atriceps**
	12	*Smittia velutina*†

* McAlpine (1965a) states that *Boreellus atriceps* is usually well dusted with pollen, while in the present study only 35% were recorded carrying pollen. This discrepancy is not understood.

† Individuals of *Smittia velutina* may or may not visit more than one inflorescence in their lifetime. If the latter is true they cannot be pollinators.

so that the notum rubs the anthers and, second, standing on the anthers so that the notum touches the stigmas. By feeding in these ways the insects cannot help but transfer pollen with their legs, tarsi and nota. The third position, in which the flies stand on the anthers and probe between the filaments from the outside so that only their feet touch the stamens, is only occasionally adopted and is of minor importance in pollen transfer. On secondarily actinomorphic inflorescences (e.g. Compositae) insect visitors become well dusted beneath and must transfer pollen from anthers to stigmas both within and between inflorescences. On the rhopalomorphic inflorescences (club-shaped anthia; cf. Kevan 1970) of *Salix arctica* visiting insects cannot help but become dusted with pollen from staminate catkins and transfer pollen to the stigma of pistillate catkins.

At Hazen Camp only the large zygomorphic flowers of *Pedicularis* spp. are dependent on *Bombus* spp. Hocking (1968) noticed that *B. polaris* works the spikes of *Pedicularis* upwards from the bottom, and by this behaviour the adaptation of the gustatory organs to sugar is offset by the increasing concentration of sugars in the nectar up the spike, which he measured. *Bombus* was noticed behaving as above but spiralling upwards on spikes of *Pedicularis arctica* and catkins of *Salix arctica*. This behaviour may also be significantly related to pollination. Benham (1969) demonstrated an identical pattern of visits of bumblebees to *Epilobium angustifolium* L. in Britain and postulated that strong protandry has been selected for and thus selfing from flowers of the same spike below has been eliminated. Whether or not that is applicable to insect-dependent *Pedicularis* spp. remains to be seen.

LOCAL DIFFERENCES IN SEED-SET AND POLLINATION

The experimental pollination sites were selected in regions known to have great insect activity. Because the Hazen Camp study area as a whole is far from uniform (Savile 1964a), an examination of the amount of pollination activity as determined through seed-set was needed in other parts of the study area. From counts of well-developed *versus* reduced or abortive heads of *Dryas integrifolia* in 1-m squares chosen without bias in forty-three quadrats of the study area, Table 4 was prepared. Statistical tests were applied to the results (Kevan 1970).

Table 4. *Percentage seed-set in* Dryas integrifolia *in different regions of the Hazen Camp study area (4 August* 1968)

	Region	% with well developed seed heads	Number of samples	Number of flowers
A	Along water courses with sedgy areas (E8, F8, G8, M8, J8, P9, S6, S7)	84	8	322
B	Near ponds (Q5, P10, N11, N12, L10, D9, M2, L3, T6, R5)	72	10	415
C	Near intermittent streams or at short distance from water (R8, S7, N3, M4, L8, M9, M10, N10, K10, L12, K13)	62	11	531
D	In Blister Creek delta (J14, H15, G15, F14, E13, D12)	51	6	232
E	In dry areas (M5, N2, P4, L6, L7, J9, D10, D11)	38	8	322
	Total		43	1822

The letters and numbers refer to squares in the grid system into which the Hazen Camp area was divided by Savile (1964a).

D. integrifolia generally produces significantly more seed in areas along water courses with sedgy areas and near ponds. The Blister Creek delta provides an exception but here the glacial deposits are coarse and unstable; the lack of sedge meadow vegetation and organic soil makes the area unsuitable for most insect larvae and there is a consequent paucity of adults. However, it is notable that in early summer when *Saxifraga oppositifolia* and *Salix arctica* bloom there, pollinating insects are common (and seed-set is high); at that time no flowers are available elsewhere.

Near intermittent streams and at short distances from water, *Dryas integrifolia* shows good seed-set, but significantly fewer seeds are produced than near sedgy areas. In dry regions, where *Kobresia myosuroides* (Vill.) Fiori & Paol. (Cyperaceae) is abundant, the seed-set of *Dryas integrifolia* is significantly the lowest, and almost equal to the autogamous seed production in the plants under insect excluders. It could be claimed that low seed-set resulted from lack of moisture and edaphic factors, but these cannot account for the very similar results from plants under insect excluders. No difference could be detected in the abortive seed heads which had resulted from plants being under insect excluders from those which resulted in regions of low seed-set.

The results are interpreted as reflecting the suitability of different regions for pollinators and hence the availability and abundance of them. Thus flowers of *D. integrifolia* seem to compete for pollinators (cf. Hocking 1968), at least outside regions of abundant pollinators.

GENERAL CONCLUSIONS

Kevan (1970) has shown that most of the dicotyledons around Hazen Camp display all the attributes of entomophily: they offer visual, olfactory, and other attractants, provide ample food, both solid and liquid, upon which many of the insects depend, and offer shelter and warmth. However, many of the dicotyledons of the high arctic are independent of insects for reproduction, being autogamous, apomictic, or anemophilous. As Mosquin (1966) says (cf. p. 831), many plants may have little or no need for insects. Nevertheless, insects are clearly shown to be responsible for much out-crossing in many species, increasing gene flow, heterozygosity, and population diversity in these plants (Bliss 1962; Savile 1964a).

Through pollination experiments and observations on insect visitors to flowers, the dependence of *Salix arctica* on Diptera and bumblebees, and of *Pedicularis arctica* and *P. capitata* on the latter is clearly established. *Dryas integrifolia* and *Saxifraga oppositifolia* are partially dependent on both groups of insects for maximum seed-set. The flowers of all these plants have the attributes of entomophily and are the most attractive to insects (Kevan 1970). The only highly attractive bloom which cannot be included is that of *Arnica alpina* (L.) Olin ssp. *angustifolium* (Vahl) Maguire (Compositae) for which the experiments were destroyed by hares. That is unfortunate as *A. alpina* represents an interesting problem as it has triploid (Jørgensen *et al.* 1958; Mosquin & Hayley 1966) and tetraploid (Böcher & Larsen 1950) races which could have very different modes of reproduction (cf. Afzelius 1936; Jørgensen *et al.* 1958). Around Lake Hazen it produces copious pollen which is transported by insects (Kevan 1970).

Among the hermaphroditic insect-pollinated plants, chromosome numbers are low: *Saxifraga oppositifolia*, $2n = 26$ (sometimes 39 or 52); *Dryas integrifolia*, $2n = 18$; *Pedicularis arctica*, $2n = 16$; *P. capitata*, $2n = 16$ (Böcher *et al.* 1968; Mosquin & Hayley 1966; Packer 1964; Johnson & Packer 1968), perhaps indicating that incompatibility mechanisms are still operating (cf. Mosquin 1966; Gustafsson 1948) such as is expected of plants requiring cross-pollination. The possibility is not discounted of other arctic or alpine regions having different races, genetic, chromosomal, physiological, or otherwise, of these plants which do not require cross-pollination. However, cognizance of the role of insects as pollinators may well help in the understanding of the taxonomic problems of some arctic plants, notably *Dryas* spp. and *Pedicularis* spp.

There are significant differences in the seed-set of *Dryas integrifolia* growing in different

regions of the Hazen Camp study area. Plants growing close to sedgy areas along streams and around ponds produce the most seeds, while those growing in other areas, particularly if dry or gravelly, produce fewer. These differences reflect the availability and abundance of pollinators, and the suitability of the different regions for them.

Pollination relationships are of great importance in biogeographical considerations. The paucity of flowers on the north-western Queen Elizabeth Island (Savile 1961), particularly Ellef Ringnes and adjacent Islands, would definitely prohibit the occurrence of many insects (cf. McAlpine 1964, 1965b) but the lack of insects cannot account for the lack of some plants, e.g. *D. integrifolia* with its wind-dispersed seeds. *Salix arctica* also has plumed seeds and grows on the north-western Queen Elizabeth Islands. The distribution of some *Pedicularis* spp. probably depends on the occurrence of *Bombus* spp. or Syrphidae, and *vice versa*, as is postulated for the co-distribution of legumes and bumble-bees (Panfilov *et al*. 1960), *Aconitum* (Ranunculaceae) and bumblebees (Kronfeld 1889), and other plants and bees (Cockerell 1932a, b). However, generalizations on the restriction of the distribution of arctic plants, for which the above examples are not perfect, must be made cautiously as the plants may not be restricted because of the absence of their pollinators; seed dispersal in the arctic is relatively unimpaired (Savile 1964b).

Sokolovskaya & Strelkova (1960) regard Eurasian diploids as part of the ancient arcto-alpine flora which may have resisted adverse conditions during the ice-ages while polyploids have moved into the arctic since the retreat of the ice. If this generalization is true, the refugia involved may well have included pollinating insects. Evidence for high arctic refugia in the Queen Elizabeth Islands is accumulating (Taylor 1956; Beschel 1961; Smith 1961a, b; Savile 1961, 1964a; Macpherson 1965; Leech 1966; Brassard 1971) possibly to complement that for one in Pearyland (northern Greenland) (Koch 1928; Gelting 1934). Such are the fascinating considerations on the ecological complexity of refugia.

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SUMMARY

Arctic flowers have been and are often thought of as being independent of insects for pollination and seed-set. This assumption is shown to be wrong and at Hazen Camp (81° 49′ N, 71° 18′ W) those flowers most frequently visited by insects are totally or partially dependent on them for seed-set. These plants, *Saxifraga oppositifolia*, *Dryas*

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* Most specimens are deposited in the Lyman Entomological Museum, McGill University, P. Quebec.

integrifolia, and *Salix arctica*, are among the most common in the region and are pollinated primarily by flies. Bumblebees are also important pollinators, and two species of *Pedicularis* are dependent on them for seed-set. Other species of plants, although setting seed independently, benefit from the visits of cross-pollinating insects by increased seed-set and probably by maintaining heterozygosity. Insects differ in their ability to carry and transfer pollen. Important pollen vectors imbibe nectar in ways such that they cannot help but transfer pollen. There are local differences in the seed-set of entomophilous flowers, correlated with the suitability of the region to pollinators, and there may be competition amongst the flowers for pollinators. The biogeographical and taxonomical implications of these relationships and their possible importance in proposed arctic refugia are briefly discussed.

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