Some Observations on the Pollination of Round-Leaf Orchid, *Galearis* (*Amerorchis*) *rotundifolia,* Near Jasper, Alberta

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On June 16 and 17, 2010, data were collected on pollination in a population of *Galearis rotundifolia* at the confluence of the Maligne and Athabasca Rivers north of Jasper, Alberta. The primary pollinator was the bee *Osmia proxima* and this species was also the most frequent visitor. While most flies were visitors, four species, *Eriozona* (*Megasyrphus*) *laxus, Eristalis* (*Eoseristalis*) *hirta*, *Eristalis* (*Eoseristalis*) *rupium*, and *Eupeodes* (*Lapposyrphus*) *lapponicus* also served as pollinators. It is estimated that 25-44% or more of flowers were pollinated in the previous year, a relatively high percentage that supports the "advertisement model" for evolution of food deception in orchids. The pollinating bee or fly lands on the lip and probes the spur which is approximately the same length or longer than the tongue. In the process of pushing into the flower and backing out, the sticky contents of a bursicle are either discharged by the backward movement of a flap or by forward pressure. Either of these actions may release adhesive fluid which fixes the viscidia onto the front of the insect's head. The gradual bending forward of the caudicles reduces likelihood of pollination of consecutively visited flowers with pollen from those recently visited flowers on the same plant (geitonogamous pollination) and thus promotes outcrossing.

Key Words: Round-Leaf Orchid, *Galearis rotundifolia*, pollination, bee, *Osmia proxima,* fly, *Eriozona* (*Megasyrphus*) *laxus, Eristalis* (*Eoseristalis*) *hirta*, *Eristalis* (*Eoseristalis*) *rupium*, *Eupeodes* (*Lapposyrphus*) *lapponicus,* deceptive pollination, geitonogamous pollination, fecundity, Jasper, Alberta.

The pollinators and general pollination mechanisms of many North American orchids are known (Catling & Catling 1991, van der Cingel 2001), but nothing has been recorded of the pollination of the Round-Leaf Orchid, *Galearis* (*Amerorchis*) *rotundifolia* (Banks *ex* Pursh) R. M. Bateman (Figure 1, St. Hilaire 2002; Handley and Heidel 2005). This attractive species (see Luer 1975 and Reddoch and Reddoch 1997 for illustrations and a description of the plant) has a widespread distribution in northern North America extending from Newfoundland to Alaska and south to the Great Lakes region (Sheviak and Catling 2002). It is uncommon over much of the southern and particularly the southeastern parts of this range (personal observation, St. Hilaire 2002, Handley and Heidel 2005). Here it often occurs in isolated colonies of often less than a few dozen plants in cool, calcareous swampy woods and fens (e.g., Reddoch and Reddoch 1997). In contrast, it is frequent in much of the northern boreal forest and western cordillera where substrates range from acid to alkaline and from pure organic peat to coarse sand. The largest populations occur in open conifer woodland along rivers and creeks in the Rocky Mountains (personal observation). Large and concentrated populations are often valuable for studying pollination since they attract pollinator attention and thus increase the likelihood of observing pollinations. On June 16 and 17, 2010, a large population of *Galearis rotundifolia* at the confluence of the Maligne and Athabasca Rivers north of Jasper, Alberta had reached peak flower and the weather was appropriate for observations of pollination. Here we provide information on the pollination of that population.

Methods

Study Area

The study area was located on the north side of the Maligne River at its confluence with the Athabasca River (52.9346°N, -118.0342°W). The vegetation is open White Spruce (*Picea glauca* (Moench) Voss) woodland with scattered shrubs of Bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), American Silver-Berry (*Elaeagnus commutata* Bernh. *ex* Rydb.), Shrubby Cinquefoil (*Dasiphora fruticosa* (L.) Rydb. ssp. *floribunda* (Pursh) Kartesz), Russett Buffalo-Berry (*Shepherdia canadensis* (L.) Nutt.) and birches (*Betula* spp.). Among the dominant herbaceous plants were strawberries (*Fragaria virginiana* Duchn. ssp. *glauca* (S. Wats.) Staudt) and Hair-Like Sedge (*Carex capillaris* L.). The orchids occurred in the open and among shrubs. The area was much richer in plant species, had less ground moss than surrounding woodland, and appeared to be subject to periodic short duration flooding in spring.

Pollination observations

We watched a 10 m^2 patch of 306 flowering stems of *G. rotundifolia* from 10:00 AM until 6:00 PM on 16 and 17 July 2010 and visited adjacent patches of hundreds within 20 m. The weather was mostly sunny on both days with morning temperatures of 10°C becoming 18-20°C by noon and reaching 24°C by 2-3 PM and cooling quickly after 6 PM to 15°C .

With a 40 cm diameter hoop insect net, we made an attempt to capture all insects seen to visit two or more flowers. "Pollinators" are here defined as insects consecutively visiting two or more flowers and carrying pollinia of *G. rotundifolia*. "Visitors" include (a) insects landing on two or more consecutive flowers and not carrying pollinia, (b) landing on two or more consecutive flowers but not captured and (c) landing on a flower once. Bee pollinators were identified by Dr. Cory Sheffield and Dr. Laurence Packer, both of York University using Sandhouse (1939) and Mitchell (1962) and are contained in the collection of Dr. Laurence Packer at York and also in the Canadian National Collection (CNC) in Ottawa. Flies were identified by Dr. Jeff Skevington using Stubbs & Falk (1983) and Van Veen (2004) and vouchers (35756-35763) are contained in CNC. Lepidoptera were identified by the authors using Layberry et al. (1998) with vouchers also in CNC.

Pollination success

To obtain an idea of the success of pollination in this patch of 306 flowering stems (in 2010), we counted the number of persisting dehisced capsules on dried inflorescences of the previous year. Although flowers that are not pollinated may disappear within a few to several weeks, the capsules that ripen remain intact as brown and dried material until well into the following summer. Based on the number of ripened ovaries and the number of inflorescences, we were able to calculate the % of flowers that ripened capsules assuming that the number of stems in the patch had not changed substantially since 2009.

Pollination mechanism

Based on observations of bees and manipulation of 15 fresh flowers with a needle the apparent pollination mechanism is discussed. Despite the difficulty of observation and the lack of a large sample, these suggestions may be useful in serving as a basis for future study.

Results

Pollinators

Except for flies, there was no general activity of potential pollinators until after noon when bees and some butterflies were seen. The first insects visiting the flowers were Syrphid flies but these were only resting. At 1:00 PM, the first consecutive bee and fly visitors were observed (Table 1) and these were observed on average every 10-15 minutes until 4:00 PM both days after which there was no visitation to flowers. At 4:00 PM temperatures dropped and there was no direct sun on the site.

The primary pollinator was the bee, *Osmia proxima* Cresson (Table 1), and this species was also the most frequent visitor. While most flies were visitors, four species, *Eriozona* (*Megasyrphus*) *laxus* Osten Sacken, *Eristalis* (*Eoseristalis*) *hirta* Loew, *Eristalis* (*Eoseristalis*) *rupium* Fabricius, *Eupeodes* (*Lapposyrphus*) *lapponicus* (Zetterstedt) also served as pollinators. All of these pollinators carried the pollinaria on the lower part of the front of the head between the eyes (Figures 2 and 3) and they were also frequent visitors (Table 1).

Lepidoptera, *Erynnis persius* Scudder ssp. *borealis* (Cary), *Glaucopsyche lygdamus* Doubleday, and *Papilio glaucus* Linnaeus visited the flowers rarely (Table 1) but were common in the immediate area. No scales of butterflies were present on pollinated flowers suggesting that Lepidoptera had not been the pollinators. The commonest butterfly, *G. lygdamus,* flew over orchid patches without stopping and was mostly attracted to flowers of *Hedysaum alpinum* Linnaeus, possibly for egg-laying.

Bumblebees (*Bombus melanopygus* Nylander) were frequent on an adjacent (3 m away) flowering patch of *Elaeagnus commutata* (20 captured in ½ hour and 20 others seen) but were not seen on the orchids despite their relatively high numbers on the adjacent plants. Bumblebees were also seen pollinating *Dryas drummondii* Richards. *ex* Hook. on the river gravel 50 m away. *Papilio glaucus* was also a frequent pollinator

TABLE 1. Pollinators and visitors of flowers of *Galearis rotundifolia* near Jasper, Alberta.

Species	Number
Pollinators (captured, visiting two successive flowers and carrying pollinia)	
Hymenoptera, *Osmia proxima*	8
Diptera, *Eristalis hirta*	2
Diptera, *Eristalis rupium*	1
Diptera, *Eupeodes lapponicus*	1
Visitors (captured, visiting two successive flowers, not carrying pollinia)	
Hymenoptera, *Osmia proxima*	2
Diptera, *Eristalis hirta*	2
Hymenoptera, small bee	2
Visitors (not captured, two flowers)	
Hymenoptera, cf. *Osmia proxima*	10
Diptera, cf. *Eristalis* sp.	5
Diptera, Syrphidae	5
Hymenoptera, small bee	3
Diptera, Bombylidae	2
Visitors (not captured, single flower)	
Diptera, Syrphidae	13
Hymenoptera, cf. *Osmia proxima*	6
Hymenoptera, small bee	4
Diptera, other	4
Diptera, Bombylidae	3
Diptera, cf. *Eristalis* sp.	3
Lepidoptera, *Papilio glaucus*	1
Lepidoptera, *Glaucosyche lygdamus*	1
Lepidoptera, *Erynnis persius*	1

FIGURE 1. Flower of Round-Leaf Orchid (*Galearis rotundifolia*) photographed near the confluence of the Maligne and Athabasca Rivers, on 17 June 2010. Photo by P. M. Catling.

of the adjacent patches of *Elaeagnus commutata*, but was only seen once on a flower of *G. rotundifolia*. Smaller bees (smaller than *O. proxima*) were scarce in the *Elaeagnus commutata* shrubs and among the orchids but visited *Fragaria virginiana* ssp. *glauca* frequently.

Pollination success

At least 433 fruits were produced in 2009 and at least 174 stems were involved in this production. Using the 2010 average of 5.6 flowers per spike, then the total number of flowers in 2009 was 974.4. Thus 44.44%, i.e., 433 of 974.4 of flowers produced fruit. If there had been 306 stems (the 2010 figure) in 2009, then 25.21% of the flowers would have produced fruit.

Pollination mechanism

The pollination system is apparently similar to that of related species in the genus *Orchis* (*Galearis* differing from Orchis principally in the lack of tuberoids). Pollination of species of Orchis has been extensively studied over a long period (Darwin 1888, Nilsson 1983), and is characterized by food-deceptive flowers lacking fragrance or nectar. In *G. rotundifolia*, as in many European *Orchis* species, the dorsal sepal and two lateral petals form a hood at the top of the flower (Figures 1 and 4). This restricts access to the column and spur so that an insect's head faces the stigmatic surface. The three-lobed lip (labellum) forms a sloping landing platform and the spreading lateral sepals may also assist in landing on the flower. The tubular spur is oriented in a slightly downcurved position with respect to the centre of the lip (Figure 4). The column, within the hood, is immediately above the spur. The central part of the column is surmounted by what is usually interpreted as an anther derived from a single stamen (Jacquemyn et al. 2009) with two pollinaria, one in each half of the anther (Figure 5). The club-shaped pollinarium (Figure 6), approximately 1.5 mm in length, includes an upper part with a number of masses of pollen (massulae) that are attached by threads to a central axis, thus allowing a gradual discharge of pollen to consecutive flowers (Johnson & Nilsson 1999). The massulae are attached by the caudicle to the sticky viscidium (disc). The viscidia are adjacent and contained in the fleshy and more or less purse-like bursicle which is situated on the rostellar

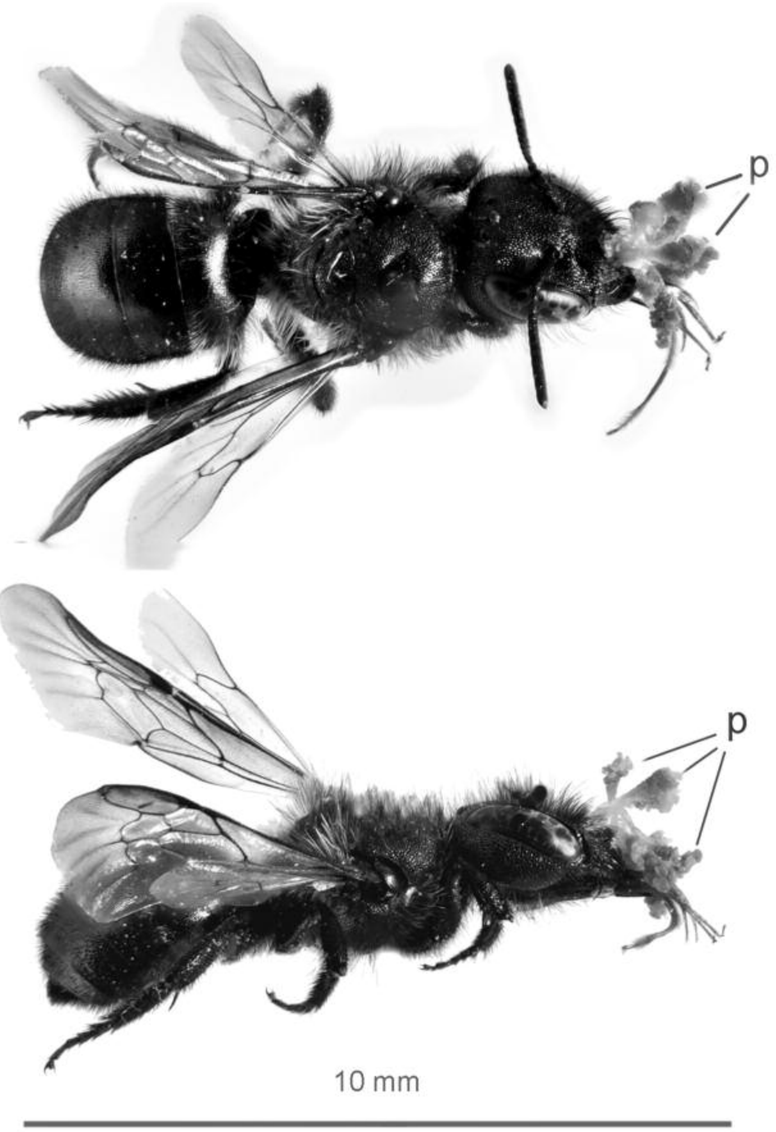

FIGURE 2. The Megachilid bee, *Osmia proxima* in lateral (below) and dorsal (above) view. The specimen was seen to visit two *G. rotundifolia* flowers consecutively and carries 9 pollinaria (p) of the orchid on the clypeus, indicating at least 5 flower visits of which at least four could have resulted in pollination. The mouthparts to 4 mm long are below the pollinaria including palps and a curled tongue (glossa) that can extend to the base of the spur when the head is fitted into the mouth of the spur. Photos by P. M. Catling.

part of the column which projects downwards into the mouth of the spur (Figures 4 and 5). The bursicle contains a sticky liquid which prevents the disc from drying out until the whole pollinium is removed by an insect visiting the flower. The bursicle may be ruptured or pushed backward as an insect, attracted by floral shape and colour at least, presses the lower front of its head, usually the clypeus, against it trying to reach the bottom of the spur. It appears that the viscidia of *Galearis rotundifolia* are often removed together but in some species of *Orchis* with similar structure one may be removed after which the flap of the bursicle returns to its original position, thus preventing the viscidium that has not been removed from drying out (Jacquemyn et al. 2009). The fluid dries out quickly (within 1 minute in a few tests), and affixes the polli-

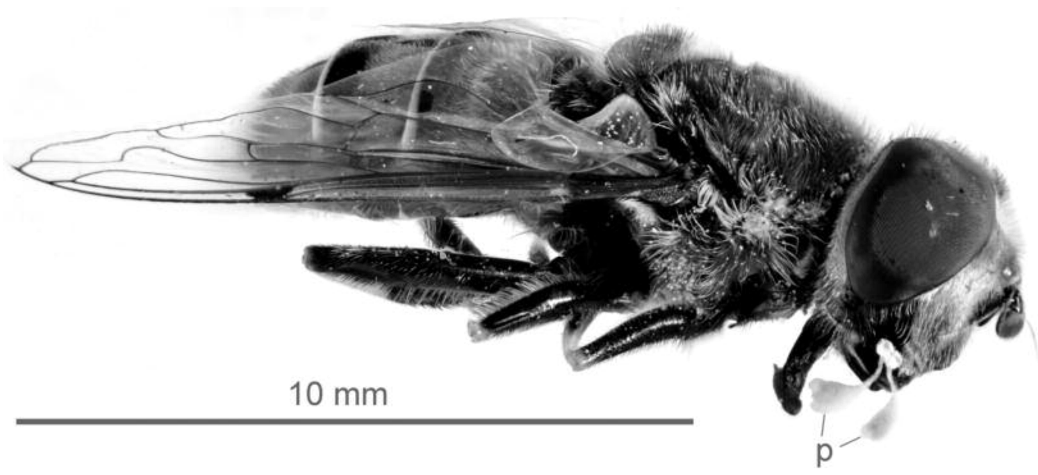

FIGURE 3. The Syrphid fly (*Eristalis* sp. with two pollinaria (p) attached to the side of the face (prefrons). The beak-like proboscis to the left of the pollinaria is less than 2 mm long and cannot reach the base of the spur. Photo by P. M. Catling.

naria to the clypeus. A forward rotation of each pollinarium resulting from a bending of the base of the caudicle was observed over the period of approx. 60 seconds, but this elapsed time was not verified with a significant sample of flowers. The rotation brings the pollinaria into a position where they contact the stigmatic surface, instead of the base of the anther sacs, of the next flower visited.

Discussion

Pollinators

It seems likely based on studies of related species of *Orchis* and *Dactylorhiza* in Europe, that *Galearis rotundifolia* would be pollinated by bees and flies. These are the pollinators of *Orchis purpurea* Huds. which has superficially similar flowers (Jacquemyn and Brys 2010). The similar *Dactylorhiza sambucina* (L.) Soó and *Orchis mascula* L. in southern Baltic island of Stora Karlsö are pollinated by a single solitary bee species and the pollinaria are similarly attached on the front of the head below and between the eyes (Pettersson and Nilsson 1983).

The principal pollinator of *G. rotundifolia, Osmia proxima* is found throughout a large area of North America (Mitchell 1962). It has been reported on a variety of flowers with differing floral morphology including *Balsamorrhiza, Houstonia, Penstemon, Rubus* and *Trifolium* (Mitchell 1962; Tepedino et al. 1999; Cane 2005). Unlike some of these plants, which have numerous pollinators, it appears that *G. rotundifolia* may be narrowly adapted to *Osmia proxima* and possibly other bees of similar size. *Osmia proxima* nests in holes in wood and hollow stems (Cane et al. 2007) and does not have extraordinary requirements making it a reliable pollinator. The tongue of *Osmia prox-*

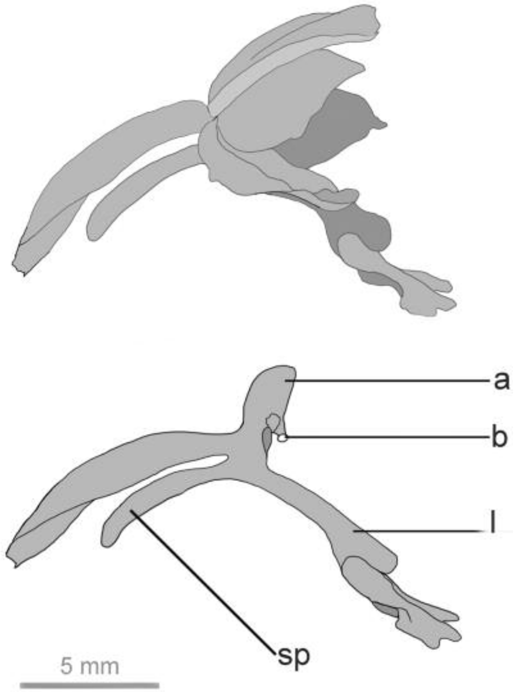

FIGURE 4. Camera lucida drawings of a flower of *Galearis rotundifolia* from Jasper, Alberta, in lateral view with all floral parts (above) and with the dorsal sepal and lateral petals (hood or galea) removed (below). In the lower drawing, the anther (a), bursicle (b), lip (l) and spur (sp) are identified. Drawings by P. M. Catling.

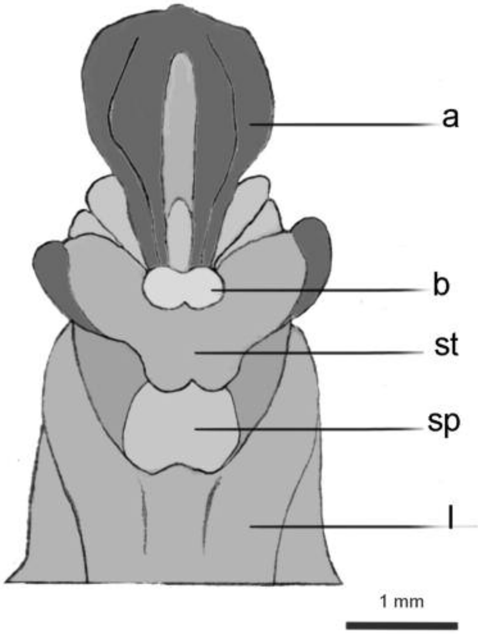

FIGURE 5. Camera lucida drawing of a column of *Galearis rotundifolia* from Jasper, Alberta, viewed from the lower front and showing the anther (a), the bursicle (b), the stigmatic surface (st), the entrance to the spur (sp), and the basal portion of the lip (l). Drawings by P. M. Catling.

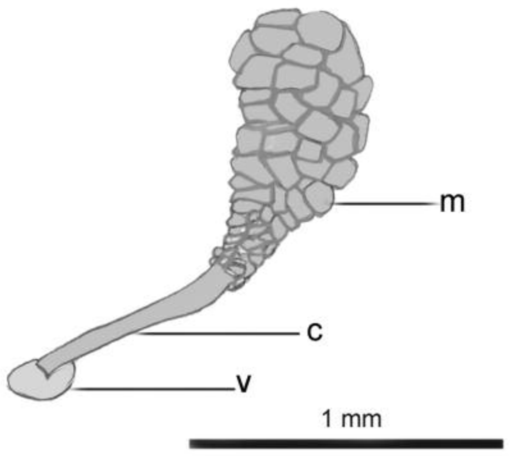

FIGURE 6. Camera lucida drawing of a pollinarium of *Galearis rotundifolia* from Jasper, Alberta, showing the packets of pollen (massulae – m), the caudicle (c) and the viscidium (v). Drawing by P. M. Catling.

ima can be extended to 5-6 mm from the head and it appears to be able to reach the base of the spur, unlike the fly pollinators. The extent to which this is relevant is unclear considering the reported lack of a reward.

The lack of visitation by *Bombus* species in this study, despite their general abundance in the area, might be attributed to the fact that these bees can quickly learn deceptive flowers and *G. rotundifolia* is a case of food deception, like most related *Orchis* species (Dafni 1987). Van der Cingel (2001) suggested, without a source, that flowers of *G. rotundifolia* are both nectar-free and scentless and Reddoch and Reddoch (1997) also suggest that there is no fragrance, but this requires more study. Our observations near Jasper are not conclusive on this point, but some flowers at least were lacking nectar, which could have been due to general lack of nectar or its removal by visiting insects.

Pollination success

In estimating the percentage of flowers developing fruit, there are assumptions such as the presence of similar numbers of plants and flowers in consecutive years, which are not reasonable for many orchid populations and for some in this group because fruit set has been shown to vary considerably between years (e.g., Jacquemyn and Brys 2010). If the population had been larger in 2009 and if stems without pollinated flowers are less likely to persist, this would have brought the percentage down, but on the other hand, the opposite seems more likely since the number of stems seems to be increasing vegetatively each year and stems with more persisting parts seem more likely to be dislodged by high wind, etc. Thus it seems appropriate to either stay with the range 25-44% of flowers or anticipate a slightly higher value.

These are relatively high numbers for a deceptive orchid. In eastern North America, *Galearis rotundifolia* and *Calypso bulbosa* often have less than 1% of plants in a population produce any seed, regardless of population size, but in some geographic regions and particularly in the western cordillera the percentage of plants setting viable seed may be much higher (personal observations, Catling & Catling 1991), likely due to generally larger population sizes in the west since a strong positive relationship exists between population size and fruit production (Jacquemyn et al. 2007).

Regardless of geographic variability, fecundity at the study site seems abnormally high considering similar and related species. For example, in a population of *Orchis purpurea*. in Belgium, 5–20% of flowers set fruit over 5 years (Jacquemyn and Brys 2010) and in parts of western Europe the fruit set for this species averaged 5.5%. In *Orchis mascula* in UK, the proportion of flowers setting fruit varied between 20.5% and 55.5% in recently coppiced woodland and between 8.8% and 13.2% in undisturbed woodland (Jacquemyn et al. 2009).

In *Orchis mascula* in Sweden, fruit production per individual was 3–20% and approx. half of the individuals in any population did not set any fruit (Nilsson 1983). In *Dactylorhiza sambucina* (L.) Soó on the southern Baltic island of Stora Karlsö, 0-8% (mostly 2%) of the flowers on an inflorescence produced fruit. The percentage is higher for *Orchis spitzelii* Sauter *ex* Koch in southern Sweden, where 8 to 60% of the flowers on a plant produced fruit (Fritz 1990).

Fruit set and lifetime fitness of orchids are usually pollen (pollinator) limited (Calvo and Horvitz 1990, Johnson and Nilsson 1999) so that the idea of lacking nectar and decreasing reward would seem to be a problem. However, the values of deception are easily underestimated. It may serve as an outcrossing advantage because lack of reward promotes visitation of fewer flowers in an inflorescence, or a clonal patch, thus favoring outbreeding at the expense of inbreeding (Dressler 1981). This explanation has limitations because inbreeding is already reduced by the amount of time required for the caudicle to bend into a position appropriate for pollination and this is generally too slow to allow pollination of consecutive flowers on the same spike. A more plausible value of deception is based on experiments with *Orchis*, where Johnson and Nilsson (1999) suggested that the selective value of food deception is that savings in nectar production are invested in advertising display which attracts increased numbers of pollinators. *Galearis rotundifolia* often forms large conspicuous patches as a result of its stoloniferous habit (personal observation) so that nectar production savings may be easily invested in number of stems in a clonal patch. Based on the extent of effective pollination in the study population, the level of advertising may have reduced the effect of pollinator limitation, thus supporting the advertisement hypothesis.

Pollination mechanism

The mass of sticky fluid in the bursicle and the fact that both pollinaria are removed at the same time may be an adaptation to attachment to the hairy surface of bees which would require more adhesive than that needed to attach to the smooth surface of a proboscis or a compound eye. The excess fluid and simultaneous removal of adjacent pollinaria is also characteristic of pollination of *Galearis spectabilis* (personal observation) unlike the situation in many species of *Platanthera* (Catling & Catling 1991). Similarities to related European species of *Orchis* and *Dactylorrhiza* are noted above.

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Much of his later work involved travels in the Canadian Arctic.

He joined Beak Consultants Limited in October 1973, where he was one of the nine principals, and became a major contributor to many Environmental Impact Statements (EISs) for large industrial projects. Many of these projects were in the north, including the Mackenzie Valley pipeline, the Dempster Highway, and many proposed mines and hydroelectric schemes.

Wilson's role initially was the terrestrial wildlife and wildlife habitat. This quickly became fused with the botanical assessments. At the same time, the issues associated with the socioeconomic impacts of development began to be included in assessments. This was a new area of investigation and Wilson developed a strong interest and expertise. He enjoyed the process of meeting with people and sharing his expertise. As much of his work was in the north, Wilson had a great deal of contact with First Nation's people. In a sense, Wilson was a pioneer in applying environmental science to mega-projects within the new environmental assessment legislation. When Geographic Information Systems (GIS) emerged as a tool, Wilson saw the value it could bring, and subsequently how it could help developing countries build a framework for the future. This meant Wilson could examine the broad scale issues and translate them into terms that would benefit individuals.

Wilson was appointed book review editor of the Canadian Field-Naturalist on 12 July 1975 and served until his untimely death on the 23 June 2003. As well as editing all reviews, he prepared a list of new titles for virtually every issue covering zoology, botany, environment and miscellaneous. In the 1980s he added a category "young naturalists" to the new titles section, and produced annual book-review editor's report. Wilson also spent many years on the Ecological and Environmental Advisory Committee (EEAC) for the Regional Municipality of Halton.

Wilson was very hard working and immensely productive, and could be relied on to get the job done on time. He would churn out well-written reports three times faster than his colleagues. Wilson had a terrific sense for new projects and business prospects – an ideal combination in a consultant. He applied this intensity to other areas of his life too. He relished finding out about other people's cultures. Without restraint he would try local foods, a perilous venture for one in his condition and something that would exasperate his colleagues.

Not surprisingly, when Wilson had the opportunity to combine his many talents to help a developing nation, he took it. In 1995, along with Drs. Greg Wickware and Festus Akindunni, he joined with some Nigerians to create a geomatics company that would employ Nigerians, working for Nigerians to better life in Nigeria. He was intrigued by Nigeria and it became his second home; a place he literally adopted. He often wore the flamboyant traditional costume. He saw a way that he could make a real difference for the people of Nigeria, but this was not without personal risk.

Wilson had been diagnosed as diabetic at 11 years old. This disease is unfortunate for someone who has chosen to wander the remote places of our planet. There was always a danger Wilson would be far out on the tundra or deep in the jungle when he needed help. Despite this risk, he persisted with his objectives in Canada and Nigeria. Indeed Nigeria was not the best place to follow the food and exercise regime required to keep this condition under control. He became ill on several occasions, but passionately continued to work in Nigeria for four to six months every year. Sadly, this strain eventually took its toll.

Wilson's work went beyond his founding of Geomatics Nigeria and building a skilled team of local people. He was involved in a variety of projects, including a GIS Space Agency conference, many forestry and park planning projects, and the African Healthcare Telematics Conference in 2000, which was in response to the HIV/AIDS problem pervading Africa. He and his wife personally supported a family with eight children, all of whom received post-secondary education.

This dynamic man will be missed by his many friends around the world.

ROY JOHN

Errata *The Canadian Field-Naturalist* 125(1): 53

In "Some Observations on the Pollination of Round-Leaf Orchid, Galearis (Amerorchis) rotundifolia, Near Jasper, Alberta", in the acknowledgements on page 53, last line "Ms. Joyce Reddoch" should be "Dr. Joyce Reddoch" and "Dr. Allen Reddoch" should be "Dr. Allan Reddoch".