

NOTES ON THE POLLINATION OF *SARRACENIA FLAVA* L. (SARRACENIACEAE) IN THE PIEDMONT PROVINCE OF NORTH CAROLINA

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ABSTRACT

Field studies were carried out on the pollination of *Sarracenia flava* L. during three flowering seasons in relict bogs of the piedmont region of North Carolina. Flowering occurs in latter April into early May, and the most systematic, common, and effective pollinators were found to be queens of *Bombus* spp. Smaller native bees and *Apis mellifera* are at best accidental or occasional secondary pollinators, mainly because of infrequency of effective flower visits and the small size of the insects relative to modes of flower entry and exit. *Sarcophaga sarraceniae* activity around flowers is very rare in this area and is not of any consequence in pollination. Various other aspects of the problem discussed in the literature over the years are reviewed critically, among them the question of protandry. The flowers were found not to be protandrous. Nectar and pollen output in these large, early spring flowers is prodigious, and nectar sugar concentration is 39%. Pollen was weighed and nectar output estimated. *Bombus* behavior while visiting a flower is described and the relative incidence of insect pollinator autogamy, geitonogamy, and xenogamy is discussed. Numbers of flowers visited in a foray, time in forays and time per flower are recorded.

Having made a few preliminary comments on the pollination of *Sarracenia flava* L. (Sarraceniaceae) in a previous paper (Schnell, 1978a), I sought to undertake more detailed observations in a different area of the plant's range. The 1978 paper commented on pollination of the species in the field in a coastal plain savanna of southeastern North Carolina and I concluded that *Bombus* spp. are probably the primary pollinators of *S. flava*. The present study was undertaken in relict seep slope sphagnum bogs of the piedmont province of the state, specifically in northern Iredell County. Here, observations could be made on an almost daily basis throughout the flowering season over several years.

The unique flower of the genus *Sarracenia* is well described in several standard references (Macfarlane, 1908; Russell, 1918; Uphof, 1936; McDaniel, 1971; Schnell & Kutt, 1973; Schnell, 1976) and will not be repeated in detail here. The flower's salient features are an essentially pendulous habit during anthesis with dehiscent pollen collected in a floral compartment bounded by an umbraculate expansion of the style as the floor of the compartment, panduri-

form petals and upward projecting points of the umbraculate style along with lower portions of the sepals forming the lateral walls, and a large tuberculate ovary with hypogynously inserted bases of stamen fascicles (usually 5–6, each with 5 stamens), petals and sepals as the roof. The petals in *S. flava* are bright yellow, but in other species of the genus vary from shades of red to cream to pale yellow. During anthesis, flowers of *S. flava* have a strong, moderately unpleasant fragrance best described as “feline” (Schnell, 1978b). Near the close of anthesis, many flowers resume a more erect position similar to the bud stage, at which time petals are shed. Seed matures over summer in the ripening ovary. The green umbraculate style and sepals are retained during the entire summer.

MATERIALS AND METHODS

Field studies were done in three relict seep slope sphagnum bogs located in the piedmont province of North Carolina, specifically Iredell County ca. 18 km NNW of Statesville. These are small, partially open bogs located in farmland, the largest being about 0.5 hectare. Two of the bogs contain *Sarracenia flava* only; the largest also has a few plants of *S. purpurea*, with rare hybrids (*S. × catesbeii*). All the bogs are in the Rocky Creek watershed, which has several more sphagnum bogs of lesser interest.

Studies were carried out during the flowering season of the years 1980–1982. Field observations were made during some part of nearly every day of anthesis for time periods ranging from two to four hours at differing times of the day. Two evening watches were carried out through dusk until complete darkness (2200 hours EDT). Observations were made in all weather from cool rain or drizzle, windy or still, to quiet, warm and sunny days. Observations for pollinator activity followed the criteria of noting systematic, purposeful, apparently learned effective working of a flower in such a way as to transfer pollen to stigmas (modified from Burr, 1979; and Faegri & van der Pijl, 1979).

Autogamy tests were carried out by gauze bagging twenty flower buds early in the season and removing covers after petals dropped. Selfing and intraspecific outcrossing had been done by me over the past twenty-five years during which I have been growing and studying the genus, and the species selfs and outcrosses freely with full seedset, there being no observed advantage of one method over the other as far as final viable seed size and quality are concerned.

Pollen output weights were done by brushing all pollen from the umbraculæ of five bagged flowers after complete anther dehiscence, and weighing the quantities on a Mettler H54AR balance (Mettler Instrument Corp., Box 100, Princeton, NJ 08540). This was done to gain some approximate idea of the range of maximum pollen output per flower.

Total nectar sugar content was estimated by collecting nectar drops in capillary glass tubes from around the bases of stamens where it aggregated. Collections were made from several dozen flowers, the nectar pooled, and then measured in an American Optical Corporation refractometer especially calibrated for sugar estimations.

Histologic sections were made and stained of the bracts, sepals, petals, ovary, and umbraculum of several flowers to determine extent and kind of gland distribution, standard histologic techniques being used. The stigma knob was examined with a dissecting microscope to clarify its gross morphology.

Insect pollen load was noted by capturing flower visitors and combing the pile of the dorsal and ventral abdomen, and scraping out corbicular contents. The pollen was then stained with lactol-phenol blue and characterized as *Sarracenia* or non-*Sarracenia*. Bee identifications are according to Mitchell (1960, 1962) and Heinrich (1979).

An attempt was made to discover the flower part source(s) of the unique flower fragrance of *S. flava* by dissecting and separating fresh flower parts (bracts, sepals, petals, style umbraculum, stamens, ovary and receptacle), placing these in sealed plastic bags or glass jars in full sunlight for an hour, and then noting the relative intensity of fragrance, if present, when uncapping.

Finally, since there is some confusion in the literature regarding possible dichogamy in the genus, I attempted to resolve the problem for this species in the study location as follows. A tight clone of several growth points having 15 flowers buds was selected in the study bog and was covered with close-mesh cage of window screen long before anthesis. The ground around the clump was thoroughly cleared of other growth to provide a tight fit of the cage bottom edge against the sphagnum and soil. Each bud was tagged and an identification number assigned. Day 1 of anthesis was defined as a completely opened flower with pendulous petals. Six flowers were hand-pollinated with their own pollen on day 1 for each flower, five

on day 2, and four on day 3, three days considered sufficient based on my experience with *Sarracenia* pollination, and since the question was one of protandry.

Ultra-violet photographic studies of flowers, a common part of pollination studies in many other genera and species in the past, were not done here in light of compelling arguments recently raised against their value, particularly regarding use of glass camera lenses, unbracketed exposures without grey scales, and apparently unwarranted assumptions on bee color vision which seems to involve the visible spectrum as well (see Kevan, 1978, 1979).

RESULTS

Gauze-bagged flowers of *Sarracenia flava* failed to set any seed in my experiments, dried and empty capsules resulting at season's end. However, in past efforts by me, flowers selfed by hand produced full seedset uniformly, as did outcrossing to flowers of the same and different clones within the species.

Pollen brushed from five bagged flowers at full dehiscence weighed as follows: 9.86, 19.17, 28.68, 47.57 and 48.55 mg. This gave an average of 30.77 mg and a median of 28.68 mg. There is little hard data in the literature on pollen output in various species and pollination syndromes; but the weights here, while variable and with relatively few samples, seem impressive for a single flower. In warm, sunny weather, all flowers had shed at least some pollen into the umbraculate cup on the first day of anthesis. In cooler, cloudy and wet weather, pollen dehiscence was often delayed a day into anthesis.

Nectar sugar content was found to be 39% by refractometer. *Sarracenia flava* nectar production was observed in undisturbed flowers growing in insect protected greenhouse as well as those caged and bagged in the field. The nectar grossly appears to be produced near the base of the ovary and collects as droplets among the stamen filament bases which act as wicks. Measuring droplet size (1.5–3.0 mm across) and calculating volumes from the five droplets among stamen fascicles at a moment of observation results in a flower volume of 4–10 μ l. This is a "point in time" quantity since more nectar is soon formed as the droplets are removed or fall. The nectar itself is clear, colorless, pale yellow, and with a definite sweet taste having no aromatic component. The only time I ever saw nectar

pooled with pollen in umbraculæ was in the case of flowers in the greenhouse, or bagged and caged in the field.

Histologic section examinations essentially confirm the results of Russell (1918). There are allurement glands over the central areas of the bracts, outside surfaces of sepals near their tips, and scattered lightly over the tips and pendulous portions of petals, but numerous near petal constrictions with no glands above that point. The complex glands in the bases of the pit canals coinciding with ovarian tubercles were most prominent over the basilar one third to half of the ovary. The glands found on other floral organs were simpler 1–3 celled surface glands. The ovarian glands are likely the source of nectar, considering the later's distribution as noted above, and the types and distribution of floral glands.

Examination of the stigma knobs located at each of the five points of the style umbraculum was of interest. The stigma knob appeared to consist of three zones, the combined structure measuring 1.5–2.0 mm in length: 1) a basilar, somewhat pyramidal tented portion of the umbraculum surface located at the point of the V-shaped cleft, the pyramidal base supporting 2) the short cylindrical column, on top of which is the 3) stigma tip or knob. The receptive stigma tip portion is villous, and this villous surface extends down the column abaxially a short distance as a V-shaped track. Adaxially, the villi occupy only a very small area at the very tip of the structure.

In the attempt to determine which parts of the flower were the source of fragrance, the odor strength was graded subjectively on a scale of 0–4+ when the containers were opened. Clearly, the strongest fragrance source resides in the petals (petal bases—3+, petal tips—4+), with the umbraculate portion of the style being 2–3+. Sepals were 2+, stamens and receptacles were 1+, with the ovary and basal style 0–1+, and bracts 0.

In the caged clone of 15 flowers pollinated by hand isogenously on specified days of anthesis, I found that 5 of 6 flowers pollinated on day one of anthesis had full seedset, 3 of 5 on day two, and 4 of 4 on day three of anthesis. Though numbers are small, these results indicate that the flowers of *Sarracenia flava* are not protandrous.

The peak flowering period for *Sarracenia flava* in the study area is a 3–4 week interval beginning the last week or two in April and extending into early May. The exact flowering peak is unpredictable

and seems to vary with weather factors, particularly temperature. The weather is capricious this time of year in piedmont North Carolina; often warm periods suddenly give way to cold, frosty nights and cool, cloudy days.

Night observations failed to disclose any insect activity from dusk into total darkness. Inspection of many flowers later in the evening failed to disclose *Sarracenia* flies resting in flowers. Dusk and nightflying moths do not appear to be pollinators. I did not notice increasing flower fragrance towards evening, but on the contrary found it stronger earlier in the day.

During daytime observation periods, various wasps were in the area often, especially mud daubers, but they did little more than work the sepals for external attractant nectar and they were never seen to enter the flower or even approach the petal or stigma. *Sarcophaga sarraceniae* were seen on and around flowers often, but seldom entered the floral chamber. On the rare occasions when they did enter a flower, the large size of the flower with its relatively open structure among *Sarracenia* flowers permitted these smaller insects to enter the opening between petals and umbrella projection without even touching the stigma knob, and they exited the same way. I would grant that occasional contact with the stigma knob might be achieved, and exiting flies were liberally dusted with pollen. But they were not sufficiently hirsute to maintain pollen loads in flight between flowers, and would at best seem to be accidental or secondary pollinators.

Small native bees identified as members of the families Megachilidae and Halictidae also occasionally visited and entered flowers, but the comments applied to the *Sarracenia* fly above would be appropriate for these insects—too few visits and easy bypass of the stigma knob.

It was interesting to observe carpenter bees (*Xylocopa* spp.) who did no more with the flowers than did wasps but which flew small circuit patterns (several meters long by 1–2 meters wide) over the flowers, vigorously attempting to drive off any other insect visitors entering their flight patterns, thus exhibiting some evidence of territoriality.

During the three years of observation for this work, *Apis mellifera* was seen working *S. flava* flowers occasionally in one season. During the other two seasons, they were not seen near *Sarracenia*

flowers in the bogs at all in this area. Honeybees could also enter and leave an *S. flava* flower by avoiding the stigma knob completely, and during the few visits they did make in the one season they were seen to do so most of the time. Due to their larger size (cf. flies, smaller native bees, etc.), they tended to brush the stigma knob somewhat more frequently and probably effect pollination. Combings of pile (dorsal and ventral) and corbicular scrapings did disclose abundant *Sarracenia* pollen. There never was a massive, organized working of flowers in the bogs as is more typical for this bee species in a favorable area, and it is likely that the few visitors were scouts.

Various moths, butterflies, small beetles, and ants were sometimes seen on flowers' surfaces, but did not engage in pollinator activity.

Clearly, the one insect genus that stands out as a systematic pollinator of *S. flava* in this location is *Bombus*. Large individuals of *Bombus* (presumably queens this time of year and considering size of individuals) were very active all three years. Their structure, behavior, and size cause them to be ideal pollinators.

During the three study years, the accumulative *Bombus* spp. list is: *B. fraternus*, *B. affinis*, *B. perplexus*, *B. pennsylvanicus pennsylvanicus*, *B. nevadensis auricomus*, *B. impatiens*, and *B. bimaculatus*. Only a few of the species were present in all three observation seasons and there was considerable year to year frequency variation among them, but the genus as a whole was constant and abundant.

The general pattern of *Bombus* activity is as follows. An individual would fly into the bog along the periphery, following a relatively straight course to the nearest flowering clones. At a distance of about one meter or so from a clone, the straight flight would change to an irregular circling approach after which the bee would land on a sepal or pendulous portion of a petal. I noticed that individuals approached gauze-bagged flowers whose color was somewhat obscured by the gauze but from which strong fragrance was emanating. Also, I observed that some bees would approach rather tightly closed buds that were still green but from which the *Sarracenia flava* fragrance was becoming apparent. This bud approach was sometimes seen in bogs with many flower buds but before anthesis had occurred at all.

After landing on the petal, or sometimes the sepal, of the initial

flower of the foray, the bee would usually circumnavigate the flower beneath the sepals but external to the petals for one or more rounds. It would then enter the flower, upside down and head first, the dorsal pile always brushing directly and firmly over the stigma knob. Even smaller *Bombus* spp. had a snug fit between the two petal edges and stigma knob, and they often struggled to enter a flower. *Bombus* activity while in the flower can easily be observed by carefully lifting a petal; the bee goes about its activities ignoring the intrusion. Still inverted, the bee works the nectar droplets enmeshed among the stamen filament bases, collecting pollen on its ventral pile and in its corbiculae, and sometimes the dorsal pile would dip into the reservoir of dehiscent pollen in the umbrella cup. While in the flower, the bee often vibrates its wings with a buzzing perceptibly different from flight or balance seeking, and a cloud of pollen might fall from incompletely dehiscent anthers. The bee would then often drop into the umbrella cup and move about in the pollen reservoir there.

If another bee approached an already occupied flower and attempted to enter, a small scuffle ensued following which it was almost always the interloper who was driven off.

Exit would be by one of three routes: 1) headfirst, inverted back over the stigma knob, thus brushing the stigma directly again; 2) lifting a petal hanging over a sway in the umbrella contour between stigma points, exiting upright and climbing the edge of the petal to the sepals; or 3) an intermediate exit in which the bee would brush the stigma knob somewhat sideways—but, due to its size, effectively depositing pollen—and partially lifting one edge of a petal which it would grasp and crawl to the sepals. Pile brushings (dorsal and ventral) and corbicular load examinations disclosed only *Sarracenia* pollen in abundance, even after flight to a second flower.

After crawling to the upper surfaces of the sepals, the bee would either stop to clean or would move promptly on to the next flower in a direct course (same clone or different), or sometimes would re-enter the flower just worked. Cleaning was never completely effective and pile and corbicular contents examinations disclosed abundant residual pollen. After cleaning, there was a liberal, irregular deposit of pollen on the sepal, and such “bee tracks” indicating a previous *Bombus* visit to that flower were distinctive and often observed on flowers while casually passing through a bog.

Flowers were open for five to ten days and each was worked many times over. I noticed a definite tendency to less bee activity on cooler, overcast, or windy days. I did not observe nectar robbing by *Bombus* puncturing sepals or by incomplete flower entry.

On different days of a season (1980), I observed how many flowers were worked (actually entered) per foray for a total of 46 forays. The fewest flowers worked was one, and the greatest 49, with an average and median of 8. This represents a marked skew and emphasizes that very large numbers of visits per foray were in the minority. These forays were counted early in anthesis and the longer ones were concurrent with shorter forays by other individuals. There appeared to be abundant nectar production during these periods.

Time per foray was noted for 45 bees, the shortest time in an area being 13 seconds, and the longest time 5432 seconds with an average of 558 seconds. Time actually in the flower was noted for 72 *Bombus* visits, the shortest being three seconds and the longest 270 seconds for an average of 53 seconds per visit.

On different days of another season (1981), 82 flower visits were tabulated for flower entrance/exit mode. There was no breakdown for size or species since I was interested in total effective pollinator activity. Stigma, intermediate and petal entrances or exits have been defined above. Sixty-three (76.8%) flower entrances were over the stigma, 18 (21.9%) were intermediate, and only one (1.2%) entrance was beneath a petal. In the exit phase, 45 (54.9%) of the exits were intermediate, 28 (34.1%) were over the stigma, and 9 exits (11.0%) were from beneath a petal with no stigma contact.

DISCUSSION

Results of my flower bagging experiments concur with those of Burr (1979) who did a thorough pollination study of another *Sarracenia* sp., *S. purpurea* ssp. *purpurea*, in Vermont bogs. She also had no seedset. However, Mandossian (1965), who made some pollination comments in a thesis concentrating on the ecology of *S. purpurea* in Michigan bogs, did get some seedset in bagged flowers, although with just a very few seeds in a few flowers. Considering Burr's results and my own, and my experience with growing some *Sarracenias* in insect-proof greenhouses over the years, I suspect that Mandossian's bagging may have been somewhat "leaky".

Nectar "sugar" content range is held to be 25-75% in flowers generally (Faegri & van der Pijl, 1979), and the 39% result in *S. flava* is within this range. As stated previously, there does not seem to be much data on total flower pollen weights, but *S. flava* clearly produces large quantities that often gather to some depth in the umbrella cup if protected from insects.

Since bagged (and greenhouse protected flowers) do not set seed, and an external pollinator is likely (as also suggested by some earlier field botanists by presumption and deduction from flower structure; e.g. James, 1883; Higley, 1909), some facets of the pollinator's activity may be predicted. The pollinator would have to pass by "choice" or compulsion directly over the stigma knob villous tip to effect pollination; a far lateral brush of the column would likely not do it, this deduced from the villous receptor surface morphology as noted above. The pollinator would therefore have to be large and strong enough to be compelled to force its way over the stigma knob between petals, rather than being smaller and entering the flower by bypassing the stigma knob. My observations of *Bombus* spp. fit this situation well.

Burr (1979) also noted that *Bombus* was the primary pollinator in her Vermont bog *Sarracenia purpurea* plants, and she noted no *Apis mellifera* activity at all. In contrast, Jones (1908, 1935), after first ruling out night pollinators which he initially suspected empirically (also ruled out by me for *S. flava* as in Jones, and by Burr in *S. purpurea*), thought that *A. mellifera* was the primary pollinator of *S. flava* in Carolinian coastal plain savannas, but in his later paper felt that many insects were equally capable of pollinating the species including beetles, something I did not find. Again, mentioning a parallel in the sister species *S. purpurea*, Mandossian (1965) also felt that *A. mellifera* was the primary pollinator in Michigan bogs, but conceded that *Bombus* spp. were also capable of accomplishing this, their activity being described as "spectacular". Since *S. purpurea* has a smaller and more closed flower with the petals often clasped over the outer surface of the umbraculum when in full anthesis in northern bogs, quite possibly honeybees and other smaller insects could achieve pollination, but Mandossian does not seem to have studied relative numbers of insects actually working the flowers and details of their activities, such as entrance and exit.

One must also recall that *Apis mellifera* is essentially an exotic introduction into North America (Faegri & van der Pijl, 1979), and

in a longterm evolutionary sense would likely not have significant effects thus far on relatively long-lived perennials, although there might be some short term effects on recent hybridization patterns in more open, disturbed bogs.

My observations on *Bombus* flower entrance and exit modes in *S. flava* are roughly similar to Jones (1908, 1935) in broad concepts although his descriptions lack detail and imply a rather constant petal exit mode. Burr (1979) described very similar detail in *Bombus* entrance into flowers of *S. purpurea*, but did not mention details of exit.

Jackson (1881) noted that on a cloudy day with a thunderstorm imminent, *flies* (italics mine, possibly *Sarcophaga sarraceniae*?) were noted in the flower cavity of *S. purpurea* where he thought they were "eating the pollen, of which scarcely a grain could be seen". Higley (1909) also thought that "dipterids" were the pollinators of *S. purpurea* in Illinois since he saw many entering and leaving the flowers with liberal dustings of pollen on their backs. Jones (1908, 1935) also thought that the *Sarracenia* fly might at least play some role in pollination of *S. flava*. However, Burr (1979), aware of these assertions and looking specifically for some *Sarcophaga* pollination activity, failed to note any in *S. purpurea* in Vermont, mentioning that the flies seemed more to be seeking refuge in the flower in inclement weather (see Jackson reference above) and did not effect pollination. She further noted, as I did, that the flies are actually not sufficiently hirsute to carry a significant pollen load from flower to flower.

Several authors have claimed that the flowers of *Sarracenia* spp. are protandrous (Macfarlane, 1893, 1908; Jones, 1908, 1935; Uphof, 1935) while Burr (1979) demonstrated that pollen readily germinated on the stigma knob surface of *S. purpurea* in Vermont the first day of anthesis (and even before in loose buds) using special staining and surface microscopic techniques. Older claims for protandry have never been supported by references or evidence and one feels that the concept "just grew" or was repeated by assumption through the years. My studies, using a different approach than Burr, indicate that in *S. flava* the flowers are not protandrous.

It is interesting to postulate whether olfactory or visual stimulus serves as the primary attractant of pollinators in *Sarracenia flava*. Faegri and van der Pijl (1979) suggest that as a general rule, a straight approach to a flower by a pollinator indicates visual

stimulus, while an irregular approach indicates olfactory stimulus, particularly if from downwind. Using this concept, the *Bombus* approach to *S. flava* that I noted seems to be one of visual for distance and olfactory for close-in confirmation. Valentine (1975) concluded that the flower color yellow is adaptively neutral and that unspecialized anthophiles were yellow, thus indicating some color attraction value, although vaguely so. However, Woodell (1978) concluded that *Bombus* tends to fly upwind to land on flowers for aerodynamic reasons and that the circling, zig-zag approach is for the purpose of seeking correct orientation to wind direction. In fact, I noticed the irregular initial close-in approach on perfectly calm days as well. I would further point out my observations that the bees would sometimes approach green, closed flower buds but from which *S. flava* flower fragrance could be detected. The latter could make a case for at least some olfactory stimulation, but Faegri and van der Pijl (1979) suggest that bees may learn to recognize the form of the whole plant as well and thus approach unopened buds for that reason.

Since I also have noticed *Bombus* approaching and landing on green, tightly closed but odoriferous buds in bogs in which *no* flowers had yet opened and in which there were no spring pitchers yet, and considering the life history of the genus (Heinrich, 1979) and the naiveté of early spring queens, this would hardly seem to be a learned activity of recognized plant form. Burr (1979) concluded in *Sarracenia purpurea* that visual and olfactory stimuli were both important, and in general Heinrich (1979) and Faegri and van der Pijl (1979) conclude that visual perception is used by *Bombus* spp. for distance orientation, and olfactory perceptions for close-in confirmation. I would, on balance, favor this combined concept in the case of *S. flava*.

There are several possibilities in the pollination results based on observing the entrance and exit modes of *Bombus* in *Sarracenia flava* flowers. Entrance would result in bringing to the stigma knob pollen from a previous flower visit, which might be the same flower since bees were occasionally observed to revisit the same flower immediately or some time later in the foray in which case selfing would occur. Or, pollen from another flower could result in either geitonogamy or xenogamy. If exit were over the stigma knob, or an effective intermediate exit, selfing would again be likely. Even

though a bee exited over a stigma knob and most certainly deposited some isogenous pollen on the stigma, one must realize that this pollen is likely mixed in the bee's pile with pollen from other flowers and that partial or mixed cross-pollination would still be possible to some extent. Further, the bee might mix exogenous pollen into the "pool" already present in the umbraculate cup.

Also, since flowers were open from five to ten days, it seems likely that pollen deposited on early days had already germinated and pollen tubes were growing and that later pollinations would be inconsequential. *Sarracenia*s produce large quantities of pollen compared to the total small stigmatic receptor surface of a flower and there may be some competition among growing pollen tubes or even those grains germinating on the villous surfaces (as with other genera in Ter-Avanesian, 1978). The comparatively huge *Bombus* pile surface again compared to the small stigma knob surface would tend to rather massive applications of pollen. Ter-Avanesian has postulated that the quantity of pollen applied to a flower stigma may influence variation patterns and evolutionary trends. Fewer grains reduce pollen tube competition and in his observations of other plant species result in more variation, while massive pollinations result in more tube competition and more uniform progeny.

Bombus syndrome flowers tend to be large with abundant hidden nectar (Faegri & van der Pijl, 1979; Heinrich, 1979) and *Sarracenia flava* flowers are certainly so. In addition, as noted above, they have a large ratio of pollen production to total stigma receptive surface. The pollen is also well concealed and protected from wind and rain (as noted by Higley in *S. purpurea*, 1909) and few casual visitors enter the flower. The abundant nectar production allows a bee to remain with a flower for a longer period of time than in smaller flowers or those otherwise producing less nectar. Heinrich (1979) has brilliantly summarized energy economics of bumblebees and indicated that the energy demands of the insects, especially early spring queens, do not permit wasted activity but that the bee is on a slim margin of reserve under the best foray circumstances. In any foray, the bee will necessarily visit more flowers that have less nectar and therefore expend more energy than in flowers with greater nectar quantities. Valuable energy is consumed flying among low nectar producers while large nectar producers allow a somewhat more leisurely approach in relative terms. This all seems to be reflected in the

time per flower observations I made above, and which Burr (1979) similarly noted in *S. purpurea*. The greater collection time per unit in a foray energy expenditure also indicates some degree of constancy and that the bees learned the flowers well (Grant, 1963). In fact, during the early days of anthesis in a bog, many of the bees (especially larger species) appeared quite clumsy in their entrance/exit activities. Later in anthesis, little difficulty was evident.

Re-entry into the same flower in sequence or later in a foray was also noted by Heinrich (1979) in other flower species, and he felt this might be related to the relative energy profitability of the flower or plant species as a whole. *Bombus* tends not to range far from good, learned nectar sources.

Macfarlane stated that mixing of nectar and pollen in the umbraculum cup was necessary for good pollen tube germination (1893, 1908) although he never documented this. I have seen nectar drops collect in the umbrella cup only in plants grown in the greenhouse or otherwise protected from insects. Furthermore, there is some question about the viability of pre-moistened pollen (Faegri, 1978; Faegri & van der Pijl, 1979).

Last to be considered is Jones' theory about the importance of the post-anthesis flower resuming an erect position (1908, 1935). Early in the growing season, the solitary bud is atop an erect scape as is the case with most flowers. As anthesis approaches, the top of the scape bends into a shepherd's crook shape so that the flower is pendulous. As anthesis ends and the petals begin to wither, the flower often—but not always—begins to resume a more erect character to varying degree. Jones felt that this was an important event in that it allowed residual pollen in the umbrella cup to fall over stigmas in case they had not been pollinated. He also felt that there was still continued pollinator activity even after petal-fall.

I do not consider this concept viable for the following reasons. In the first place, by the time the petals and stamens are shed or are in the process of doing so as the flower resumes a more erect position, the umbraculum is empty of pollen in the field, and the intense *Bombus* activity of days before has more than likely resulted in pollination with pollen tube growth well along. Also, nectar secretion ceases and the fragrance is remarkably reduced (due probably to loss of petals wherein most odor production resides, v.s.), and of course the bright yellow petals with their visual attractive value are

gone. Jones also assumes a long protandrous period of possibly three days to two weeks which has been contradicted in my study, and with *S. purpurea* (Burr, 1979). Finally, the geometry of the flower is not right for any pollen that might have been left in the umbrella cup to fall over a stigma knob when the flower is tilted back into an erect position. I stripped fresh flowers of petals and filled the cups with some red dye powder while the flower was in a pendulous position. Then by hand, I slowly turned the flower up on the scape axis to an erect position. None of the dye powder actually fell on villous stigma surfaces. The resumption of an erect position by some *Sarracenia* flowers late in anthesis is an interesting phenomenon that still awaits elucidation.

SUMMARY

In a field study, the primary pollinator of *S. flava* was found to be *Bombus* spp. At best, *Apis mellifera* and small native bees might be accidental pollinators. *Sarcophaga sarraceniae* was found not to be a pollinator. The flowers of the species are not protandrous, and a previous theory on the importance of flower erection late in anthesis for late self pollination has been contradicted. Considering pollinator activity, results can be selfing, geitonogamy, or xenogamy.

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