THE EFFECTIVENESS OF FUNGUS GNATS AS POLLINATORS[1]

Michael R. Mesler, James D. Ackerman,[2] and Karen L. Lu

Department of Biology, Humboldt State University, Arcata, California 95521; and
Department of Biological Science, Florida State University,
Tallahassee, Florida 32306

ABSTRACT

Fungus gnats (Sciaridae and Mycetophilidae) are the principal pollinators of *Listera cordata* (L.) R. Br. (Orchidaceae) and *Scoliopus bigelovii* Torr. (Liliaceae) in coastal redwood forests of northern California. Although primitive diptera have generally been regarded as relatively inefficient pollinators, fruit set for both species is high: 61–78% for *L. cordata* (1976–1978) and 94.3–98.5% for *S. bigelovii* (1978–1979). Since probability of pollination per visit is low, we attribute high fruit set to the large number of gnats present at our study sites and corresponding large number of visits to flowers. The relative frequency of geitonogamous vs. xenogamous pollen flow was estimated by emasculating flowers and subsequently comparing pollen reception or fruit set of emasculates with controls. Results for both species indicate that interplant movement of pollen is common. Thus, fungus gnats can be effective pollen vectors, both in terms of overall fruit set and potential for cross-pollination.

Small, primitive diptera such as fungus gnats are generally regarded as inefficient pollinators (Faegri and van der Pijl, 1971; Leppik, 1977; Moldenke, 1976). Compared to larger, more advanced flies (syrphids, bombyliids) and bees, they are weak, short-range fliers; their foraging behavior is not consistent, and their smooth, relatively hairless bodies are expected to carry few pollen grains. These considerations notwithstanding, the actual effectiveness of fungus gnats as pollinators has never been documented with the exception of brief remarks by van der Pijl and Dodson (1966) on the pollination of *Stelis aemula* Schltr. (Orchidaceae) by dark-winged fungus gnats (Sciaridae) and by Stebbins (1971) on the pollination of *Aristolochia californica* Torr. (Aristolochiaceae) by fungus gnats (Mycetophilidae). In this paper we report on an investigation of the pollination biology of two species, *Listera cordata* (L.) R. Br. (Orchidaceae) and *Scoliopus bigelovii* Torr. (Liliaceae), that rely on fungus gnats and dark-winged fungus gnats as principal pollen vectors in the coastal redwood forests of northern California. Specifically, we examine the hypothesis that fungus gnats deliver relatively low quality pollinator service. The dimensions of pollinator effectiveness we consider are (a) percent fruit and seed set and (b) relative levels of within-plant vs. be-tween-plant pollen movement (geitonogamy vs. xenogamy).

Scoliopus bigelovii is self-incompatible (Moldenke, 1976; Berg, 1959; Mesler, unpubl.). Each plant bears an umbel of from one to 12 foul-smelling flowers, the pedicels of which converge below ground level. The flowers depart from typical liliaceous organization in the reduction of the stamen number to three and the clear differentiation of the two perianth whorls (Berg, 1959). The petals are linear and erect. In contrast, the sepals are broad and are the primary landing platforms for pollinators. Small amounts of nectar are produced in a longitudinal channel in the center of the proximal half of each sepal (Utech, 1979). An extrorse anther is positioned above each of the nectaries and the three styles are arrayed so that a stigma lies above and extends slightly beyond each anther. Thus the flower is comprised of three "pollination units," each consisting of a sepal, stamen, and style (Berg, 1959). The anther and stigma never touch and no passive self-pollination occurs in this way (Mesler, unpubl.), but there is nothing to prevent insect-mediated selfing within or between pollination units.

The diminutive flowers of *L. cordata* are self-compatible but not autogamous (Ackerman and Mesler, 1979). They emit a foul odor reminiscent of that produced by *Scoliopus*, and nectaries are located on the surface of the lip. Pollinia are actively attached to potential pollinators. If an insect feeding at the nectary contacts the minute trigger hairs on the tip of the rostellum, the rostellum ruptures and releases a droplet of quick-drying cement onto the visitor. The pollinia then are released and fall onto the cement which secures them to the

[2] Address: Department of Biological Science, Florida State Univ., Tallahassee, FL 32306.

insect. Concurrent with this, the broad, flap-like rostellum folds over the stigma. Approximately 1 day later the rostellum retracts and the stigma is exposed. The flowers are thus protandrous but since flowers at both the male and female stage are commonly present on the same inflorescence, geitonogamy is possible.

STUDY SITES AND METHODS—Study sites for *L. cordata* are listed in Table 1. The single study site for *S. bigelovii* is on the east side of Hwy. 101 at the Seawood Dr. exit in Humboldt Co. All populations occur in second-growth redwood forests with the exception of the Lord Ellis population in a mixed evergreen forest (Munz and Keck, 1959). Both species flower in late winter and early spring and observations were made at intervals throughout the flowering season.

Percent fruit set for *L. cordata* was determined by counting flowers with expanded vs. unexpanded ovaries. Expanded ovaries invariably contained microscopically visible and presumably viable embryos. A similar analysis of fruit set for *S. bigelovii* was not possible due to rodent predation on immature fruits. However, since pedicels of pollinated flowers elongate after anthesis and eventually lie on the ground, we estimated percent fruit set by counting these elongated, prostrate pedicels vs. the shriveled, relatively shorter pedicels of unpollinated flowers. Percent seed set for *S. bigelovii* was determined for a random sample of immature fruits. To determine maximum seed set, we emasculated and cross-pollinated 56 flowers in 1979. Each flower received about 500 pollen grains from one other plant in the population.

The relative importance of geitonogamous vs. xenogamous pollen traffic for both *L. cordata* and *S. bigelovii* was estimated by emasculating selected flowers and thereby preventing insect-mediated autogamy. For *L. cordata* all pollinia were removed from experimental plants. Any fruits set by these plants were then necessarily the result of xenogamous pollinations. Since this species is self-compatible, fruit set of non-emasculated flowers (controls) is attributable to both within-plant and between-plant pollinations. If the fruit set of emasculated flowers is very low compared to controls, we can conclude that the interplant component is negligible. If, on the other hand, fruit set of the emasculates approximates that of controls, we conclude that the interplant component is more important. We used a G-test (Sokal and Rohlf, 1969) to determine whether there is a significant difference between percent fruit set of emasculates and controls. For the self-incompatible *S. bigelovii*,

TABLE 1. *Fruit set for Listeria cordata*[a]

Locality	Year	No. of flowers	No. of plants	Fruit set %
Blue Lake, Old State Hwy. 299, 1.5 km W of Korbel Rd.	1976	3,920	322	61
	1977	2,653	244	78
	1978	605	56	76
Korbel, Camp Bauer	1978	1,046	75	68
Lord Ellis Summit, State Hwy. 299	1978	665	68	66

[a] All localities in Humboldt County, Calif.

percent fruit set is itself a measure of interplant pollen flow, but does not reveal the proportion of pollen "wasted" on illegitimate intraflower and intraplant pollinations. Emasculations performed to address this issue were divided into two treatments. In treatment 1, one flower per plant was emasculated and the other flowers on the same plant left intact. In treatment 2, one flower was emasculated and all others on the same plant were removed. Pollen loads on stigmas of controls and emasculates then were compared using Dunn's distribution-free multiple comparison procedure (Hollander and Wolfe, 1973). Pollen loads were determined by collecting stigmas immediately following abscission of the perianth and mounting them in cotton blue. The three stigmas from each flower were mounted together and, therefore, the counts represent number of pollen grains received per flower.

RESULTS AND DISCUSSION—Fungus gnats in the closely related families Mycetophilidae (*Mycetophila* sp.) and Sciaridae (*Sciara* sp., *Corynoptera* sp.) were by far the most common visitors to both *L. cordata* and *S. bigelovii*. We did not detect differences in the foraging behavior of the two groups and remarks about "fungus gnats" pertain to both. We regard fungus gnats as pollinators of *S. bigelovii*, and not merely nectar thieves, because they contacted anthers and stigmas while feeding and individuals captured on the flowers carried pollen grains. Evidence that fungus gnats are pollinators of *L. cordata* has been reported elsewhere (Ackerman and Mesler, 1979). Other visitors included members of the Tipulidae (*Limnophila* sp.), Braconidae, and Ichneumonidae for *L. cordata* and Syrphidae and Muscoidea for *S. bigelovii*. Visits by these potential pollinators were sporadic and we estimate that they accounted for less then 0.1% of the total number of visits to the flowers. Fungus gnats were the predominant visitors and, therefore, we believe that most pollina-

TABLE 2. *Fruit set for some terrestrial orchids with nectar-producing, chasmogamous flowers and their major pollinators*

Species	Fruit set %	Major pollinators	Source
Platanthera ciliaris (L.) Lindl.	27.3–50	Butterflies	Smith and Snow, 1976
P. blephariglottis (Willd.) Lindl.	22.9–25.1	Moths	Smith and Snow, 1976
P. obtusata (Banks ex Pursh) Lindl.	14	Mosquitos	Thien and Utech, 1970
Goodyera oblongifolia Raf.	46.2	Bumblebees	Ackerman, 1975
	44	Bumblebees	Kallunki, 1976
G. tesselata Lodd.	79	Bumblebees	Kallunki, 1976
G. repens (L.) R. Br. var. *ophioides* Fern.	76	Bumblebees	Kallunki, 1976
Epipactis consimilis Don	15.5	Syrphids	Ivri and Dafni, 1977

tions at the study sites can be attributed to them.

Moldenke (1976) listed muscoid flies as the major pollinators of *S. bigelovii* and described it as "seldom visited" with "seed set very low." In our population, Muscoidea played only a minor role, and fruit and seed set were high. In 1978, 98.5% of 1,257 flowers on 419 plants set fruit, and in 1979, 94.3% of 267 flowers on 80 plants set fruit. The average number of ovules per ovary was 24 (n = 94). In 1978, the average seed set per capsule was 74.5% (n = 44) and in 1979, it was 69.2% (n = 50). Seed set for the experimentally cross-pollinated flowers was 79.1%. This is not significantly different from the naturally occurring seed set for 1978 ($P > .20$, t-test) and only marginally different (at the .05 level) from the seed set for 1979. We conclude that percent seed set is limited by some factor other than number of pollen grains received (e.g., allocation of photosynthates for seed production).

We believe the high fruit and seed set of *S. bigelovii* are primarily due to the abundance of fungus gnats at our locality and the corresponding large number of flower visits. We observed hundreds of foraging gnats on each of several days during the flowering season and at the peak of the season we commonly encountered five or more gnats feeding at a single flower. In addition, the gnats were active from early morning until late afternoon, foraging during the cool, foggy or rainy weather conditions which prevail in the early spring. The effectiveness of the gnats as pollinators *cannot* be attributed to a close morphological fit between them and the flowers, nor to consistent

foraging behavior. We observed that when a larger fly such as a syrphid landed at the tip of a sepal and walked in to the nectary, its back contacted the stigma and anther. A fungus gnat that followed the same path to the nectary did not pollinate the flower because the distance between the surface of the sepal and the stigma was usually greater than the height of the gnat. Furthermore, the gnats often landed at the side of the sepal and moved directly to the nectary without passing beneath the stigma. Nevertheless, fungus gnats do pollinate the flowers, although the frequency of pollinations per individual is probably very low. Pollination can occur in the following ways: (a) gnats that enter a flower that has just begun to open, following the "legitimate" path, can pollinate it because of the proximity of the surface of the sepals and corresponding stigma at this stage; (b) individuals occasionally land on the style and walk past the stigma on their way to the nectary; (c) some gnats feed standing with their bodies oriented so that the abdomen is nearly vertical and can contact the stigma if positioned appropriately. Larger gnats contact the apposing anther when feeding at the nectary and we observed several individuals with conspicuous patches of pollen on the dorsal surface of the thorax. In addition, pollen grains fall onto smaller gnats when they are feeding

TABLE 3. *Listera cordata. Fruit set of control and emasculated flowers at the Blue Lake locality. Data collected in 1977. The difference between controls and emasculates is not significant ($P > .05$, G-test)*

Treatment	No. of flowers	No. of plants	Fruit set %
Control	1,456	244	78
Emasculate	102	17	72

TABLE 4. *Scoliopus bigelovii. Pollen loads for control and emasculated flowers*[a]

Treatment	No. of flowers	Average no. of pollen grains received/ flower	Potential source(s) of pollen
1 Emasculate (>1 flower/plant)	23	153x	X, G
2 Emasculate (1 flower/plant)	25	163x	X
3 Control	20	318y	X, G, S

[a] Data collected in 1978. Potential pollen sources are S (anthers of the same flower), G (other flowers on the same plant), and X (other plants). Numbers followed by different lower case letters are significantly different at the .01 level.

beneath an anther. The muscoid flies observed by Moldenke in central California are presumably more effective pollinators of *S. bigelovii* than fungus gnats, on an individual basis, because of their larger body size. The difference in fruit set reported by us and by Moldenke probably reflects differences in pollinator abundance and visitation frequency at our respective study sites.

Fruit set for *L. cordata* ranged from 61% to 78% (Table 1). In contrast, fruit set for other allogamous terrestrial orchids for which comparable data are available is frequently lower (Table 2). Although the morphological fit between fungus gnat and flower is better for *L. cordata* than *S. bigelovii*, the ratio of number of pollinations to number of visits also was low. When feeding at the nectaries, gnats oriented their bodies in a variety of positions and did not always activate the trigger mechanism or deposit pollinia on the stigma. The low probability of pollination per flower visit was compensated by a larger number of visits. In addition, fragments of the soft, mealy pollinia rather than entire pollinia were often deposited on stigmas, so that a fungus gnat carrying pollinia from a single flower could pollinate several flowers. The specialized, active mechanism for attaching pollinia to the gnats may also increase the probability of pollination.

The difference between the percent fruit set for emasculated and control flowers of *L. cordata* was not significant (Table 3). This indicates a high potential for interplant pollination but cannot be taken to mean that all pollen flow was xenogamous. Our observations of the behavior of fungus gnats indicate that some intraplant pollination did occur. Gnats regularly visited more than one flower per inflorescence before flying to another plant. Nevertheless, if geitonogamy predominates, we would expect the percent fruit set of the emasculated plants to have been considerably lower than that of the controls.

The emasculated flowers of *S. bigelovii* in both emasculation treatment categories received about 50% fewer pollen grains than control flowers (Table 4). This suggests that about half the pollen load on stigmas of this population was derived from anthers of the same flower, not unexpected in light of the behavior of the fungus gnats. They often spent several minutes foraging at a flower, during which time they could effect repeated intraflower pollinations. The source of the other half of the pollen load can be partitioned into that contributed by other concurrently blooming flowers of the same plant and flowers on other plants. The fact that the number of grains received by the stigmas in the two experimental treatment groups (1 and 2) is not significantly

different suggests that most of this half of the pollen load came from other plants in the population. The number of pollen grains received in this way (c. 150) far exceeds the number necessary to account for the average of 20 seeds produced per capsule in 1978.

In the cool, moist redwood forest, where floral resources are widely scattered, large, efficient but energetically expensive pollinators such as bumblebees are uncommon (Moldenke, 1976). Many plants in this habitat can be expected to rely on small, relatively inefficient but presumably energetically cheaper vectors (Stebbins, 1974). We have shown that small diptera can be effective pollinators, both in terms of overall fruit set and potential for outcrossing, at least when present in large numbers.

LITERATURE CITED

ACKERMAN, J. D. 1975. Reproductive biology of *Goodyera oblongifolia* (Orchidaceae). Madroño 23: 191–198.

ACKERMAN, J. D., AND M. R. MESLER. 1979. Pollination biology of *Listera cordata* (L.) R. Br. (Orchidaceae). Amer. J. Bot. 66: 820–824.

BERG, R. Y. 1959. Seed dispersal, morphology, and taxonomic position of *Scoliopus*, Liliaceae. Norske Vidensk-Akad. Mat.-Naturvidensk. Kl. Avh. 1959. No. 4.

FAEGRI, K., AND L. VAN DER PIJL. 1971. The principles of pollination ecology. 2nd ed. Pergamon Press, New York.

HOLLANDER, M., AND D. WOLFE. 1973. Nonparamentric statistical methods. Wiley, New York.

IVRI, Y., AND A. DAFNI. 1977. The pollination ecology of *Epipactis consimilis* Don (Orchidaceae) in Israel. New Phytol. 79: 173–77.

KALLUNKI, J. A. 1976. Population studies in *Goodyera* (Orchidaceae) with emphasis on the hybrid origin of *G. tesselata*. Brittonia 28: 53–75.

LEPPIK, E. E. 1977. Floral evolution in relation to pollination ecology. Today and Tomorrow's Printers and Publishers, New Delhi.

MOLDENKE, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305–361.

MUNZ, P. A., AND D. D. KECK. 1959. A California flora. Univ. Calif. Press, Berkeley.

PIJL, L. VAN DER, AND C. H. DODSON. 1966. Orchid flowers: their pollination and evolution. Univ. Miami Press, Coral Gables, Florida.

SMITH, G. R., AND G. E. SNOW. 1976. Pollination ecology of *Platanthera (Habenaria) ciliaris* and *P. blephariglottis* (Orchidaceae). Bot. Gaz. 137: 133–140.

SOKAL, R., AND F. ROHLF. 1969. Biometry. Freeman, San Francisco.

STEBBINS, G. L. 1971. California pipe vine: a light trap for unwary flies. Calif. Native Plant Soc. Newsl. 7(3): 4–5.

———. 1974. Flowering plants: evolution above the species level. Belknap Press, Harvard University, Cambridge.

THIEN, L. B., AND F. UTECH. 1970. The mode of pollination in *Habenaria obtusata* (Orchidaceae). Amer. J. Bot. 57: 1031–1035.

UTECH, F. 1979. Floral vascular anatomy of *Scoliopus bigelovii* Torrey (Liliaceae-Parideae = Trilliaceae) and tribal note. Ann. Carneg. Mus. 48: 43–71.