ADAPTIVE SIGNIFICANCE OF RAY FLORETS IN ASTERACEAE

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ABSTRACT

It has been generally assumed that the showy ray corollas of some members of the Asteraceae are instrumental in attracting pollinators to the fertile disc florets, but actual experimental verification of this phenomenon has been limited. This relationship was studied quantitatively and experimentally in two genera, _Bidens_ and _Senecio_, which contain both radiate and naturally discoid (= rayless) species. Populations of the radiate _B. aristosa_, _S. aureus_ and _S. smallii_ were divided into three treatment groups: the control group consisted of plants with radiate heads, while the second group had the ray florets removed. The third group was bagged to prevent any insect visitation, hence measuring self-pollination. The discoid species _B. frondosa_ and _S. vulgaris_ were divided into control and bagged groups. In some experiments there were subsets within each treatment of (a) plants intermixed in the larger population ("grouped") and (b) plants that were spatially separated from the more dense population ("isolates"). Insect visitation frequency was observed in the control and, where applicable, derayed groups, and achenes were subsequently scored to determine seedset. A significantly higher number of insect visits was observed to radiate heads of _B. aristosa_ and _S. smallii_, but not to radiate heads of _S. aureus_. Seedset in _B. aristosa_ was significantly higher from radiate plants, whether grouped or isolated; this result was also found with radiate _S. smallii_

isolates, but was not consistently demonstrated with radiate *S. smallii* grouped plants.

ADAPTIVE SIGNIFICANCE OF RAY FLORETS

IN ASTERACEAE

INTRODUCTION

The assumption that ray florets, characteristic of the vast majority of composites, are significant in attracting pollinators to the fertile disc florets was supported in a study of derayed *Helianthus grosseserratus* (Stuessy, et al., 1986). While this genus lacks naturally rayless species, radiate morphs of *Senecio vulgaris* and *Bidens pilosa* in polymorphic populations also have been shown to experience a higher outcrossing frequency than non-radiate (i.e., discoid) morphs (Marshall and Abbott, 1982, 1984a, 1984b; Sun and Ganders, 1990). Nonetheless, the heads of a number of genera of Asteraceae exhibit a trend toward reduction in size of or loss of showy rays, and this is considered an "advanced" condition (Abbott and Schmitt, 1985). In *Bidens*, this trend is closely correlated with self-compatibility, perhaps reflecting the handicap which individuals without showy attractants to insects incur. One can predict, therefore, that ray loss would impose a handicap upon obligate outcrossers, decreasing cross-pollination and impairing the species' ability to produce offspring and to colonize new sites. This project was designed to test this hypothesis using both radiate and non-radiate local species of the genus *Bidens* in the fall and of *Senecio* in the spring. Both genera feature hermaphroditic disc florets and ray florets which, when present, are neuter (i.e., sterile) in *Bidens* and pistillate in *Senecio*.

In this project, significance of ray florets was assessed qualitatively and quantitatively

1) through observation of amount of insect visitation to natural populations of showy radiate and rayless species and to radiate species altered by removal of rays; and
2) through determination of the percentage of fertile achenes ultimately set by heads with and without rays.

For certain showy species such as B. aristosa, which is strongly self-incompatible, insect visitation to and seedset from artificially derayed heads were expected to be less than in the case of unaltered heads, while seedset from bagged heads was expected to approach zero. In less showy, self-compatible species, the difference in insect visits to and seedset from bagged and unbagged heads could indicate the continuing importance of such cross-pollination as these species receive.

MATERIALS AND METHODS

Populations and individual plants of five species were identified for this study with the assistance of Radford, et al. (1968) and Fernald (1950). An extensive stand of _Bidens aristosa_ (Michaux) Britton (Tickseed Sunflower), a showy annual found in low fields, was identified at Oakland Plantation in Newport News, adjacent to Ft. Eustis. This population was used for research in the fall of 1987. In addition, some plants of _B. aristosa_ were transplanted and studied in Toano to serve as a replication. Its generally non-radiate relative, the annual _B. frondosa_ L. (Black Beggar Ticks), was found in adequate numbers for this project only in one farm field in Windsor Shades, approximately three miles east of Providence Forge. Stands of the radiate perennial _Senecio aureus_ L. (Golden Ragwort) in a moist forest bottomland in Toano were studied in the spring and summer of 1988, as was the radiate perennial _S. smallii_ Britton (= _S. anonymus_ A. Wood), found along railroad tracks and in an abandoned lot near Basketville in Toano. The non-radiate annual _S. vulgaris_ L. (Common Groundsel) was located in Williamsburg adjacent to the College of William and Mary Population Lab on South Henry Street. To test the effect of distance from potential pollen sources, plants were divided into "grouped" and "isolated" plants. Isolated plants were defined as plants at least ten feet from any other conspecific plant. In addition to isolates within the above-mentioned

B. frondosa and S. smallii populations, individual plants of S. smallii were also studied along Airport Road in Williamsburg and along Diascund Road and Lake View Drive in Toano.

It should be noted that both discoid species (B. frondosa and S. vulgaris) are known to produce individuals or populations with rays. However, S. vulgaris populations locally include only the non-radiate morph, unlike the British plants studied by Marshall and Abbott (1982, 1984a, 1984b), which were radiate. Conversely, occasional rayless individuals of the normally radiate S. aureus and S. smallii have been reported (Fernald, 1950) but are apparently unknown from B. aristosa.

Treatments:

The differential effect of ray florets on seedset was determined by dividing the radiate species B. aristosa and S. smallii into three groups ("treatments"): a control group which retained the ray florets, a second group which had its rays removed as they began to emerge, and a third group in which the heads were permanently bagged prior to emergence of ray florets to preclude insect pollination. Plants in each of the first two treatments were identified by white plastic ties (control plants) or black plastic ties (derayed plants), approximately one foot long and one inch wide; these were notched to identify the habitat of the plant (i.e., whether it was part of a group of closely neighboring plants or was isolated) and were tied to the base of the plants. Heads were bagged using transparent nylon of a buff color selected to be inconspicuous to passers-by. The discoid species B. frondosa and S. vulgaris were divided into two groups: a control group which was not altered in any way and a group in which the heads were bagged prior to anthesis.

Insect visitation frequency to all five species was noted for periods of one-half hour or one hour. Sequential visits by the same insect to different heads under observation were only counted once. Spiders, predatory insects and herbivorous insects were included in the observations though they would seem less likely to facilitate cross-pollination. Typically, several heads on adjacent grouped plants could be observed at once. Prior to each period of observation, a swing psychrometer was used to determine humidity, and temperature and sun conditions were also recorded. Insects of types not previously identified were collected for later identification, which was made with the assistance of guides by Milne and Milne (1980), Borror and White (1970), and Jaques (1951).

An ultraviolet light was utilized to determine whether cryptic nectar guides which reflect UV light became perceptible on the surfaces of the ray florets. Efforts were also made to fabricate artificial ray florets of various materials, which were affixed to the base of the discoid heads of B. frondosa in an attempt to alter insect visitation.

Seedset was assessed simply by counting the "viable" versus "inviable" achenes, as judged by normal or abnormal (small, distorted, or aborted) appearance, collected at the end of the season. Statistical comparisons were made between treatments and, where applicable, between habitats within each treatment and between treatments within each habitat using tests described in Sokal and Rohlf (1981). Differential insect visitation was evaluated through similar comparisons.

RESULTS

Bidens aristosa

Ray florets of this showy species are sterile, while disc florets are perfect, producing 20 to 40 achenes per head. The rays contain yellow flavanols which fluoresce under UV light to reveal nectar guides. These appear as a differentiation of the basal area of the ray.

In the grouped Toano population (Table 1), a highly significant difference was seen in seedset between treatments. In Newport News, the addition of isolates allowed testing of a corollary hypothesis: that grouped heads, whether radiate or derayed, would experience higher seedset due to the effects of higher population density, enhancing frequency of visits from insects already attracted to the area. The higher seedset seen in radiate heads at this site (Table 2) was highly significant, as in Toano, both for isolated and grouped plants. However, a surprising result was the significantly higher seedset experienced by isolated controls as opposed to grouped controls; the slight difference found in the case of derayed heads was not significant. Bagging of grouped and isolated heads in Newport News, as expected, resulted in no seedset.

The soldier beetle (*Chauliognathus* spp.) was the major pollinator at the Newport News site (Figure 1); no observation of insect visitation was attempted in Toano. Again, the

TABLE 1: Seedset in *B. aristosa* grouped plants (Toano)

	Radiate heads	Derayed heads
Mean % seedset	60.63	46.94
Standard deviation	9.68	6.03
n	20	19

(p = 0.0004, One-Way ANOVA)

TABLE 2: Seedset in B. aristosa
grouped and isolated plants
(Newport News)

	Grouped		Isolated	
	Radiate	Derayed	Radiate	Derayed
Mean rank of % seedset	54.84	28.26	58.07	25.71
n	45	39	40	42
p (2-tailed)	0.0000		0.0000	

	Radiate		Derayed	
	Grouped	Isolated	Grouped	Isolated
Mean rank of % seedset	27.31	60.05	42.82	39.31
n	45	40	39	42
p (2-tailed)	0.0000		0.4998	

(p calculated using Mann-Whitney U-test)

(NOTE: The above analyses represent two different groupings of the same data.)

	Bagged Grouped	Bagged Isolated
Mean % seedset	0.00	0.00
n	13	4

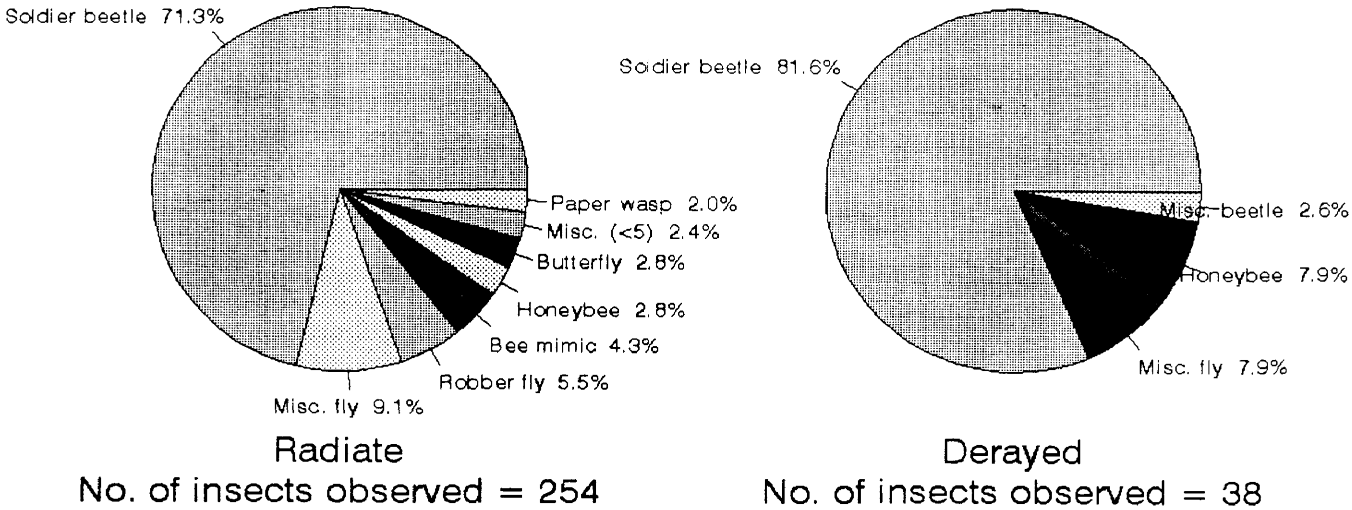


FIGURE 1: Insect visitors by type to B. aristosa (Toano and Newport News)

No. of heads observed	74
Hours observed	6.5

Insect type	No. of visits observed: Radiate	Derayed
Soldier beetle (O. Coleoptera, F. Cantharidae)	181	31
Misc. fly (O. Diptera)	23	3
Robber fly (O. Diptera, F. Asilidae)	14	0
Bee mimic	11	0
Honeybee (O. Hymenoptera, F. Apidae, Subf. Apinae)	7	3
Butterfly (O. Lepidoptera)	7	0
Paper wasp (O. Hymenoptera, F. Vespidae, Subf. Polistinae)	5	0
Spider (O. Araneae)	3	0
Bumblebee (O. Hymenoptera, F. Apidae, Subf. Apinae)	2	0
Misc. beetle (O. Coleoptera)	1	1

higher number of recorded visits to radiate as opposed to derayed plants, shown in Table 3, was significant.

Bidens frondosa

No radiate specimens of this generally discoid species were evident in the study area. Attempts to confer artificial rays on the plants met with limited success; however, in two one-half hour observations of four artificially rayed heads and four control heads, 33 insect visits were observed for the former as opposed to 8 for the latter. These limited observations do not allow a firm conclusion to be drawn that such rays serve as an attractant, but further study appears to be merited.

Insect visitation data was recorded (Figure 2), and indicates that bumblebees and soldier beetles were the major pollinators of the plants under study. Seedset results could not be reported, as the plants were found to have been mowed down prior to the time of ripening and achene collection.

Senecio smallii

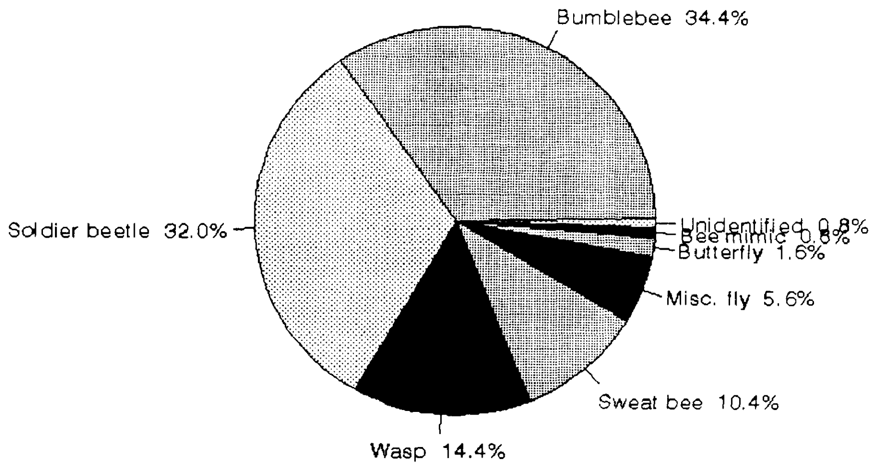
No UV reflecting nectar guides were seen on the surface of rays of this showy plant, which sets approximately 60 seeds per head.

In the Basketville population, all plants were grouped; a highly significant difference was seen in seedset between derayed heads and controls as seen in Table 4. Isolates (not part of larger populations) in Williamsburg and Toano also

TABLE 3: Insect visits to *B. aristosa*
(Newport News)

Observation period no.	Duration (hours)	No. of heads observed (each)	No. of visits Radiate	Derayed
1	0.5	5	9	4
2	1.0	5	44	14
3	1.0	4	61	16
4	0.5	12	12	0
5	1.0	8	17	0
6	1.0	8	20	1
7	0.5	8	16	3
8	0.5	12	12	0
	6.0	62	191	38

($p < .05$, Wilcoxin's signed-ranks test)



No. of insects observed = 125

FIGURE 2: Insect visitors by type to <u>B. frondosa</u>

No. of heads observed 65
Hours observed 3.5

Insect type	No. of visits observed
Bumblebee (O. Hymenoptera, F. Apidae, Subf. Apinae)	43
Soldier beetle (O. Coleoptera, F. Cantharidae)	40
Wasp (O. Hymenoptera)	18
Sweat bee (O. Hymenoptera, F. Halictidae)	13
Misc. fly (O. Diptera)	7
Butterfly (O. Lepidoptera)	2
Bee mimic	1
Unidentified	1

TABLE 4: Seedset in S. smallii grouped plants
(Basketville)

Radiate plants Viable/total	Radiate plants % seedset	Derayed plants Viable/total	Derayed plants % seedset
753/ 970	77.63	108/120	90.00
213/ 302	71.85	46/101	45.54
350/ 588	59.52	206/496	41.53
179/ 201	89.05	23/ 87	26.44
203/ 559	36.31	96/129	74.42
306/ 396	77.27	16/120	13.33
155/ 198	78.28	97/200	48.50
903/1096	82.39	13/ 42	30.95
103/ 134	76.87	52/ 82	63.41
161/ 200	80.50	177/200	88.50
128/ 137	93.43	86/189	45.50
154/ 200	77.00	128/200	64.00
126/ 200	63.00	112/200	56.00
154/ 200	77.00	17/ 78	21.79
164/ 200	82.00	79/200	39.50
116/ 200	58.00	152/200	76.00
149/ 200	74.50	148/200	74.00
173/ 200	86.50	81/200	40.50

($p < .005$, Kruskal-Wallis test)

Bagged plants

Viable/total	% seedset
2/ 200	1.00
4/ 200	2.00
0/ 200	0.00
3/ 197	1.52
0/ 200	0.00

Mean % seedset

Radiate	74.51
Derayed	52.22
Bagged	0.90

showed a significantly higher seedset for controls (Table 5). This was not the case with the grouped plants in the railroad track population (Table 6), which showed a slightly higher, if non-significant, seedset for the radiate heads. Heads from bagged plants in both populations yielded a very low seedset: 9 out of 1000 (0.9%) at the Basketville site and 12 out of 952 (1.3%) at the railroad track site.

Insect visits to grouped controls (Table 7) were significantly higher than to derayed heads observed concurrently in the same population. The major pollinators were various species of bees and flies (Figure 3).

Senecio aureus

Again, no nectar guides were associated with rays of this plant. Seedset was not determined for this population; however, insect visits are tabulated in Table 8 and fail to show a significant difference between treatments within the population, which could be due to the small sample size. Pollinator visits to these plants were low compared to S. smallii, and there was no clearly predominant pollinator (Figure 4).

Senecio vulgaris

The vast majority of achenes collected were found to be sterile, both from bagged and unbagged plants. Of 1200 achenes from bagged heads, no viable ones were scored; of 1600 from unbagged heads, only two viable achenes were scored. As

TABLE 5: Seedset in S. smallii isolated plants

Radiate plants		Derayed plants	
Viable/total	% seedset	Viable/total	% seedset
25/200	12.50	2/362	0.55
80/194	41.23	28/180	15.56
84/200	42.00	0/115	0.00
55/200	27.50	6/100	6.00
97/200	48.50	72/200	36.00
135/200	67.50	3/ 67	4.48
		0/151	0.00
		3/ 14	21.43
		181/200	90.50

($p < .05$, Kruskal-Wallis test)

Mean % seedset	
Radiate	39.87
Derayed	19.39

TABLE 6: Seedset in S. smallii grouped plants (Railroad tracks)

Radiate plants

Viable/total	% seedset
117/200	58.50
82/103	79.61
113/200	56.50
137/200	68.50
110/200	55.00
112/200	56.00
162/200	81.00
147/200	73.50
100/177	56.50
158/200	79.00
103/147	70.07
139/200	69.50
131/200	70.50
163/200	81.50

Derayed plants

Viable/total	% seedset
1/ 20	5.00
33/ 66	50.00
21/ 52	40.38
5/ 7	71.43
17/ 21	80.95
11/ 20	55.00
93/159	58.49
50/ 73	68.49
57/ 88	64.77
59/ 70	84.29
15/ 16	93.75
74/113	65.49
143/200	71.50
132/159	83.02
43/ 66	65.15
85/118	72.03
120/200	60.00

($p < .5$, Kruskal-Wallis test)

Bagged plants

Viable/total	% seedset
5/ 200	2.50
0/ 200	0.00
3/ 152	1.97
4/ 200	2.00
0/ 200	0.00

Mean % seedset

Radiate	68.26
Derayed	64.10
Bagged	1.29

TABLE 7: Insect visits to S. smallii
(Basketville and railroad tracks)

Observation period no.	Duration (hours)	No. of heads observed (each)	No. of visits Radiate	Derayed
1	0.5	11	30	9
2	0.5	14	0	0
3	0.5	14	21	4
4	0.5	18	13	2
5	0.5	10	0	0
6	0.5	18	2	4
7	0.5	20	43	0
8	0.5	20	27	0
9	0.5	15	9	6
10	0.5	15	0	0
11	0.5	23	5	1
12	0.5	12	8	4
13	0.5	9	39	2
14	0.5	9	13	2
	7.0	194	210	34

($p < .05$, Wilcoxin's signed-ranks test)

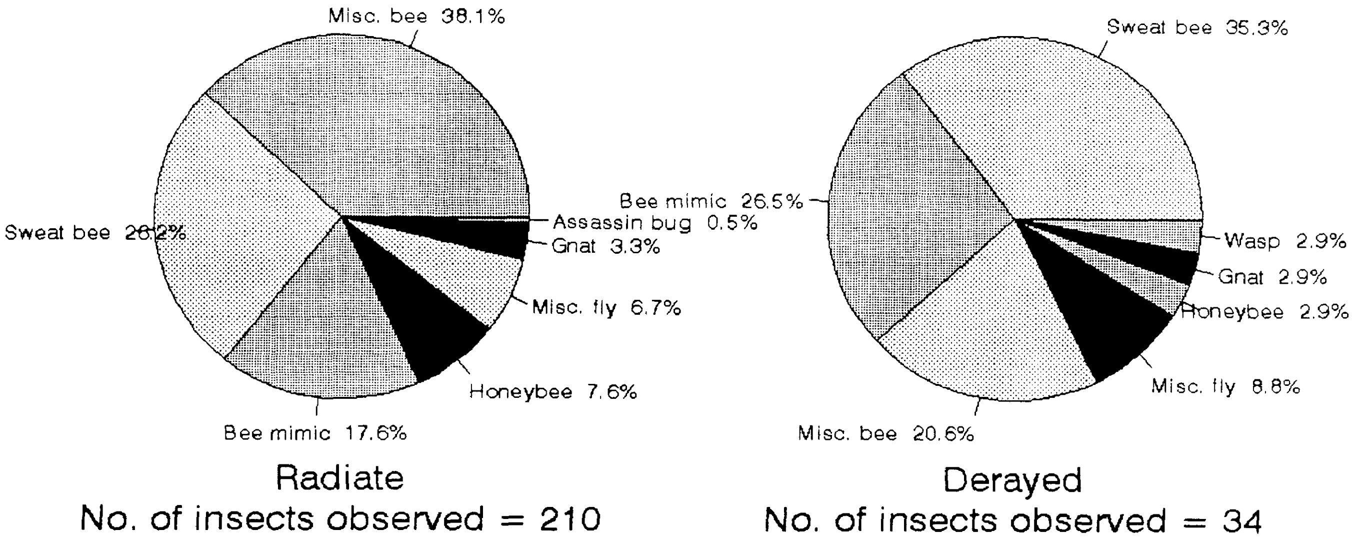


FIGURE 3: Insect visitors by type to S. smallii (Basketville and railroad tracks)

No. of heads observed 300
Hours observed 5.0

Insect type	No. of visits observed: Radiate	Derayed
Misc. bee (O. Hymenoptera)	80	7
Sweat bee (O. Hymenoptera, F. Halictidae)	55	12
Bee mimic	37	9
Honeybee (O. Hymenoptera, F. Apidae, Subf. Apinae)	16	1
Misc. fly (O. Diptera)	14	3
Gnat (O. Diptera)	7	1
Assassin bug (O. Hemiptera)	1	0
Wasp (O. Hymenoptera)	0	1

TABLE 8: Insect visits to <u>S. aureus</u>
(Toano)

Observation period no.	Duration (hours)	No. of heads observed: Radiate/derayed	No. of visits/head: Radiate	No. of visits/head: Derayed
1	1.0	5/ 27	0.40	0.33
2	1.0	18/ 8	0.11	0.00
3	0.5	4/ 11	0.00	0.00
4	0.5	12/ 7	0.08	0.00
5	0.5	12/ 9	0.42	0.22
6	1.0	17/ 12	0.12	0.08
7	0.5	14/ 15	0.00	0.00
8	0.5	8/ 14	0.00	0.00
9	1.0	22/ 14	0.05	0.21
	6.5	112/117		

($p > .05$, Wilcoxin's signed-ranks test)

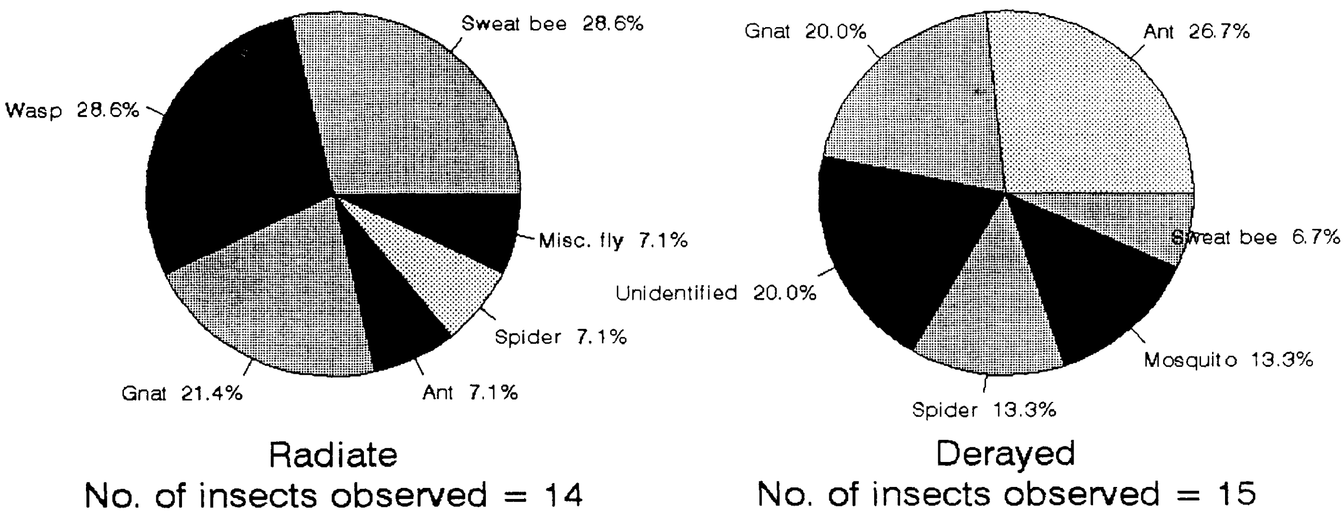


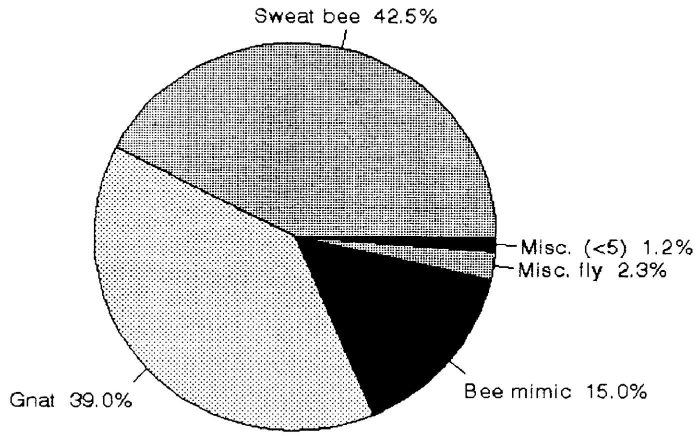
FIGURE 4: Insect visitors by type to <u>S. aureus</u>

No. of heads observed 229
Hours observed 10.0

Insect type	No. of visits observed: Radiate	No. of visits observed: Derayed
Sweat bee (O. Hymenoptera, F. Halictidae)	4	1
Wasp (O. Hymenoptera)	4	0
Gnat (O. Diptera)	3	3
Ant (O. Hymenoptera, F. Formicidae)	1	4
Spider (O. Araneae)	1	2
Misc. fly (O. Diptera)	1	0
Unidentified	0	3
Mosquito (O. Diptera, F. Culicidae)	0	2

this species is regarded as primarily self-pollinating, although frequented by insects, and as fruit collection occured at the time of fruit dispersal (when seeds are surely mature), it is difficult to understand why this result was so uniform; one possible explanation is found in the location itself, which was used as a nursery and was subjected to herbicide application, particularly as the plants under study were considered weeds in the area.

Insect visitation data seen in Figure 5 indicates that this discoid species potentially derives some benefits in pollination from insect visitors. Various species of gnats and sweat bees comprised the majority of visitors to these plants.



No. of insects observed = 433

FIGURE 5: Insect visitors by type to <u>S. vulgaris</u>

No. of heads observed 220
Hours observed 5.5

Insect type	No. of visits observed
Sweat bee (O. Hymenoptera, F. Halictidae)	184
Gnat (O. Diptera)	169
Bee mimic	65
Misc. fly (O. Diptera)	10
Harlequin bug (O. Hemiptera, F. Pentatomidae)	2
Praying mantis (O. Mantodea, F. Mantidae)	2
Misc. beetle (O. Coleoptera)	1

DISCUSSION

Results of this study support the hypothesis that ray corollas serve to attract insect pollinators to the self-incompatible heads of B. aristosa. The difference in seedset between treatments is particularly striking in light of the fact that the rays in this species are sterile; consequently, differences in seedset are attributable to pollination of the disc florets only, as in the Sun and Ganders study (1990) which yielded similar results for B. pilosa.

While the importance of nectar guides to anthophiles seeking reward has been substantiated, there has been little evidence that they enhance reproductive fitness in plants (Kevan, 1978). The presence of such guides on neuter florets, coupled with the higher frequency of insect visits shown here, suggests that they may help these plants reproduce sexually; however, such visitation may be merely attributable to the showy rays, and the role of the nectar guides was not tested in the study.

The corollary hypothesis posed with respect to B. aristosa, that grouped heads, regardless of treatment, would experience higher seedset than isolates, must be rejected. Perhaps radiate isolates receive more sequential visits from insects in the absence of other likely candidates in the vicinity (particularly as soldier beetles may maximize their energy intake and minimize their output in such a manner), while in a grouped situation such visitation may be more meaningful comparisons could be drawn between species, and conclusive results must await further study.

Despite the lack of data for B. frondosa and S. vulgaris, it appears probable that some cross-pollination occurs, as indicated by the number of insect visits in Figures 2 and 5. In asking what selective advantage may have been responsible for their discoid state, it is important to note that, according to Mayr (1983), selection favors the best genotype for a given set of constraints, not necessarily the perfect one. Consequently, self-compatibility may be the best overall strategy for these plants, facilitating establishment of new populations even by single individuals. The benefits of outcrossing with which rays are associated are perhaps outweighed by these dispersal advantages.

Hopefully studies in the future will focus on comparisons of morphs in naturally polymorphic populations, preferably species in which the ray florets do not contribute to total seedset. Seedset differences could thereby be attributed to pollinator preference rather than to pollination of the ray florets themselves. Investigations could be conducted using tetrazolium red to test seed viability, rather than relying on visual observations. Variations on this study could also be done by removing only a portion of the rays, or by retaining the rays while removing the disc florets from plants in which ray florets contribute to total seedset.

APPENDIX: Weather data during insect visit observations

B. aristosa (Newport News)

Observation period no.	Date	Time commenced	Sky conditions	Temperature (° Celsius)	Relative humidity
1	9/06/87	4:45p	-	34	-
2	9/13/87	4:00p	PC	33	57%
3	9/18/87	10:23a	S	28	58%
4	9/24/87	3:55p	S	25.5	57%
5	9/27/87	4:27p	O	27	71%
6	10/08/87	4:37p	PC	18	76%
7	10/09/87	2:13p	S	26	-
8	10/ ?/87	-	-	-	-

S. smallii (Basketville and railroad tracks)

Observation period no.	Date	Time commenced	Sky conditions	Temperature (° Celsius)	Relative humidity
1	6/01/88	4:08p	S	33	52%
2	6/01/88	5:25p	S	31	61%
3	6/01/88	5:55p	S	-	-
4	6/03/88	5:38p	PC	-	-
5	6/03/88	6:21p	PC	-	-
6	6/04/88	4:23p	PC	19	74%
7	6/05/88	12:20p	S	23	62%
8	6/05/88	12:56p	PC	25.5	62%
9	6/05/88	12:16p	S	23	62%
10	6/05/88	12:46p	PC	25.5	62%
11	6/08/88	8:50a	S	24	84%
12	6/10/88	4:12p	PC	22	68%
13	6/10/88	3:53p	PC	22	68%
14	6/10/88	4:23p	PC	-	-

S. aureus

Observation period no.	Date	Time commenced	Sky conditions	Temperature (° Celsius)	Relative humidity
1	5/01/88	2:18p	PC	22	82%
2	5/01/88	2:00p	PC	22	82%
3	5/03/88	2:07p	O	17	90%
4	5/03/88	2:13p	O	15	90%
5	5/09/88	4:54p	PC	22	61%
6	5/11/88	4:15p	PC	22.5	80%
7	5/12/88	11:39a	PC	19.5	87%
8	5/12/88	12:25p	PC	19.5	87%
9	5/13/88	1:25p	O	23	96%

Weather: S = sunny; PC = partly cloudy; O = overcast.

A dash indicates information was not collected.

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