LIFE HISTORY AND PARASITES OF *ASPHONDYLIA BORRICHIAE* (DIPTERA: CECIDOMYIIDAE), A GALL MAKER ON *BORRICHIA FRUTESCENS*

PETER STILING,[1] ANTHONY M. ROSSI, DONALD R. STRONG, AND DEREK M. JOHNSON
Department of Biological Science B-142
Florida State University
Tallahassee, Florida 32306-2043

ABSTRACT

We studied the life history, seasonal and spatial abundance, and parasites of *Asphondylia borrichiae* Rossi and Strong (Diptera: Cecidomyiidae), a newly described gall maker on sea oxeye daisy, *Borrichia frutescens* (L.) DC. Galls are located on the apical meristem of the host plant, are usually solitary, often prevent flowering, and can kill the host stem. Individual galls may contain from one to eight fly larvae, most commonly one to three. Gall size is greatest in spring. Galls can be found year round, and there are several generations, of which the largest occurs in the summer. Gall densities differ consistently between sites, but the seasonal variation of galls within sites is very similar. Fly larvae in galls are attacked by four species of Hymenoptera, *Rileya cecidomyiae* and *Tenuipetiolus teredon* (Eurytomidae), *Torymus umbilicatus* (Torymidae), and *Galeopsomyia haemon* (Eulophidae), of which *G. haemon* causes the most mortality. At least two of the parasites are facultatively hyperparasitic. Parasitism levels are low in the spring but rise quickly to reach 100% in the early summer and late fall.

RESUMEN

Se estudió la biología, la abundancia estacional y espacial y el parasitismo de *Asphondylia borrichiae* Rossi y Strong (Diptera: Cecidomyiidae), un nuevo insecto de las agallas encontrado en manzanilla loca, *Borrichia frutescens* (L.) DC. Las agallas se encuentran en el meristemo apical de la planta hospedera, y son usualmente solitarias y a menudo impiden la floración, o pueden matar el tallo. Cada agalla puede tener desde una hasta ocho larvas, pero comunmente se encuentran una o tres. Las agallas son mas grandes durante la primavera, pero pueden ser encontradas durante todo el año, contando con varias generaciones, de las cuales la mas abundante ocurre en el verano. Las densidades de las agallas difieren entre cada lugar, pero la variación estacional de las agallas entre lugares es bastante similar. Larvas de la mosca en las agallas son atacadas por cuatro especies de hymenopteros, *Rileyacecidomyiae* y *Tenuipetiolus teredon* (Eurytomidae), *Torymus umbilicatus* (Torymidae) y *Galeopsomya haemon* (Eulophidae), de los cuales *G. haemon* causa la mayor mortalidad. Al menos dos de los parasitos son facultativamente hiperparasiticos. Los niveles de parasitismo son bajos en la primavera pero aumentan rapidamente hasta 100% al comienzo del verano y al final del otoño.

Rossi & Strong (1990) recently described a new species of *Asphondylia* (*A. borrichiae* Rossi and Strong) (Diptera: Cecidomyiidae) reared from galls on oxeye daisy, *Borrichia frutescens*, in Florida. The present paper gives the first description of its life cycle, spatial and temporal distribution patterns, and rates of attack by parasites on *Borrichia*.

Borrichia frutescens (L.) DC., the oxeye daisy or sea oxeye, is a fleshy, rhizomatous herb that has yellow, sunflower-like blossoms. It is a perennial species with a life span

[1]Current address: Department of Biology, University of South Florida, Tampa, FL 33260.

of perhaps more than five years (Antlfinger 1981). Along Florida's Gulf coast it can be found in discrete, well-separated patches or clones (see photograph in Antlfinger 1981) in the salt pans behind the zones of *Spartina alterniflora* Loisel., salt-marsh cord grass, and *Juncus roemerianus* Scheele, needlerush. It is commonly found with other salt-tolerant succulents such as glasswort, *Salicornia virginica* L.; saltwort or pickleweed, *Batis maritima* L.; and the grass *Distichlis spicata* (L.) Greene. The bushes *Iva frutescens* L. and *Baccharis halimifolia* L. are commonly found on higher ground inland from *Borrichia*. Galls form on the apical regions of the stems of *Borrichia* and commonly contain between one and four chambers, maximum eight, each initiated by a fly. There is usually only one gall per stem. Galled stems normally do not flower, and they often die after a gall has senesced and rotted.

Materials and Methods

To determine the growth rates of galls and length of the life cycle of *A. borrichiae*, we marked 30 incipient galls in May 1990, at the first signs of stem swelling, at a site called Live Oak (Fig. 1), and we returned weekly to measure them until the galls senesced and rotted. To determine densities, we counted the number of galls on 500 haphazardly chosen stems at each of four sites about 1 km apart approximately every month for two years, from June 1988 to September 1990. Three of these sites, Kornegay, Rail's Nest, and Live Oak, were situated on the mainland seashore; the fourth site, Gull Island, was on an island 1 km offshore.

For estimates of parasitism levels, we collected at least 30 large galls from Rail's Nest at monthly intervals and returned these to the laboratory. Galls with no emergence holes were placed individually in 25-dram vials, together with small pieces of moist filter

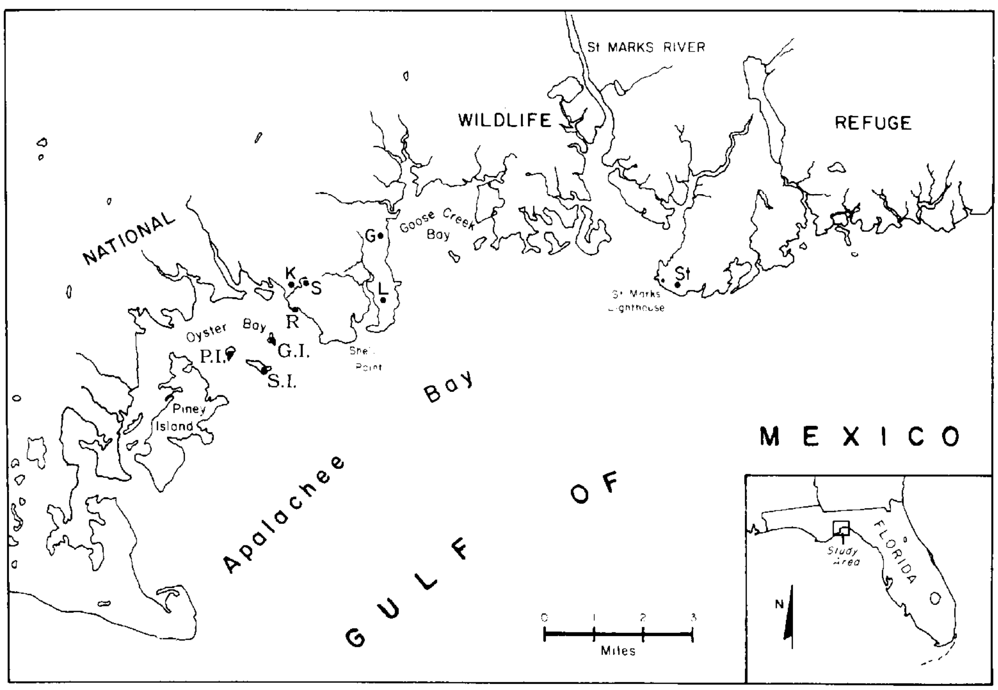

Fig. 1. The location of the study sites. P.I. = Palmetto Island, S.I. = Smith Island, G.I. = Gull Island, R = Rail's Nest, K = Kornegay, S = Southsides, L = Live Oak, G = Goose Creek, St = St. Marks.

TABLE 1. SEASONAL VARIATION IN PARASITISM LEVELS OF *ASPHONDYLIA* GALLS ON *BORRICHIA FRUTESCENS*.

Date	Number of galls successfully "cultured"	Mean number of chambers per gall ± S.D.	% of galls parasitized	% of galls completely parasitized	True parasitism: % of chambers parasitized
March 7, 1989	30	3.13 ± 1.52	10.0	3.3	7.4
March 22, 1989	19	2.58 ± 1.61	5.3	5.3	2.0
May 18, 1989	18	2.16 ± 1.45	95.0	80.0	87.2
June 8, 1989	294	1.84 ± 0.92	80.3	67.7	72.4
July 25, 1989	43	1.53 ± 0.78	65.1	53.5	57.6
September 5, 1989	218	1.34 ± 0.62	78.9	66.1	68.1
November 8, 1989	31	1.16 ± 0.45	100.0	100.0	100.0
November 27, 1989	67	1.57 ± 0.50	95.0	92.5	93.3
December 15, 1989	26	1.42 ± 0.58	100.0	100.0	100.0
February 25, 1990	34	2.56 ± 1.54	26.5	5.9	16.2
March 8, 1990	50	2.24 ± 1.22	50.0	18.0	25.9
April 25, 1990	25	2.25 ± 1.48	100.0	44.0	71.8
May 17, 1990	85	2.22 ± 1.55	90.6	44.7	69.2
June 8, 1990	42	1.81 ± 0.87	97.6	92.9	90.8
August 9, 1990	33	1.30 ± 1.12	60.6	48.5	55.8
August 17, 1990	25	1.64 ± 1.00	72.0	52.0	65.8
August 22, 1990	67	1.52 ± 0.66	59.7	37.3	54.9
September 17, 1990	64	1.28 ± 0.49	88.0	84.0	84.0

paper. Some galls rotted without issue, but most remained viable for a considerable period, and the galls were inspected daily for insect emergence. All adult insects that emerged were recorded and placed in 70% ETOH. After all insects had emerged, we dissected galls, counted the number of chambers in each gall, and recorded the presence of dead insects. Larger collections of over 200 galls were made in June and September 1989. Additional galls were periodically dissected to determine whether any contained hyperparasites or inquilines.

Results and Discussion

We normally only found one gall per stem. In 1250 galled plants examined from June 1988 through December 1989, we found only four stems with two galls. The largest galls occurred early in the year, and the number of chambers per gall decreased as the season progressed (Table 1). We could always find galled stems in the field, although their density varied greatly. Even during the cooler months of December, January, and February we found galls containing *Asphondylia*, both as larvae (first, second, and third instar) and as pupae. We found pronounced seasonal peaks of galls at all sites in all years (Fig. 2), and the largest numbers of galls were found in the summer. Synchrony of population maxima between sites was high. The absolute number of galls in any generation was always highest at Rail's Nest and lowest at Kornegay.

In the summer at Live Oak, galls reached their maximum size about five weeks after measurements began (Fig. 3). At this time many of the galls exhibited emergence holes, indicating successful emergence by flies or parasites (Fig. 4). After insects emerged, the galls quickly began to turn black and rot; seven weeks after measurements began, over 90% of the galls had disappeared (Fig. 5). If egg development, initial gall development, and the flight period of adults each take a few days (adults only live two-three days in the laboratory, as do adult midges in general [Gagné 1989]), then generation

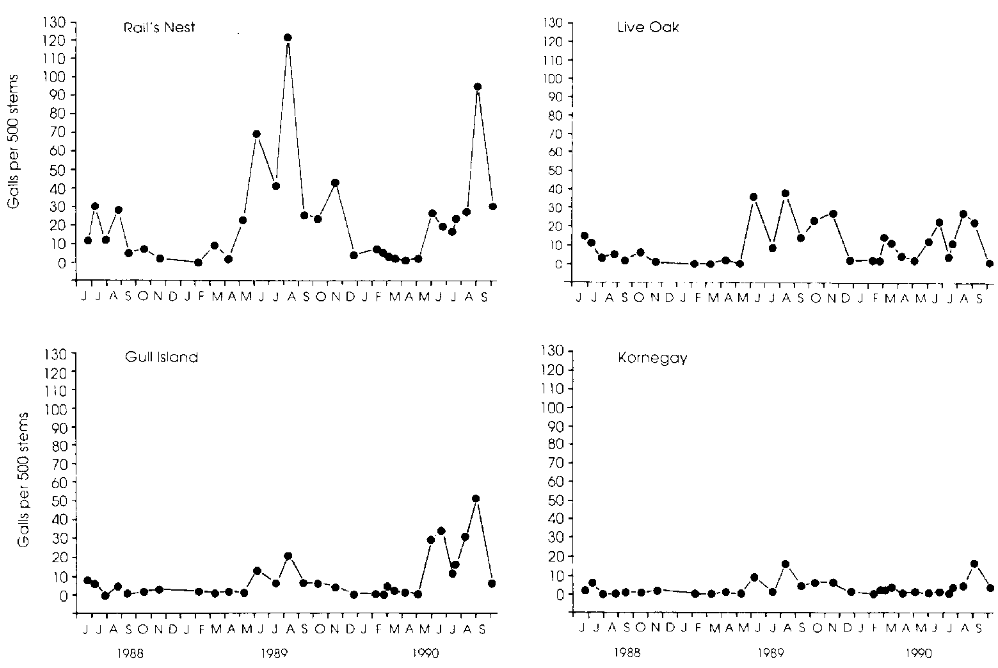

Fig. 2. Seasonal variation in the abundance of *Asphondylia* galls on *Borrichia frutescens*, 1988-1990, at four sites on Florida's Gulf Coast.

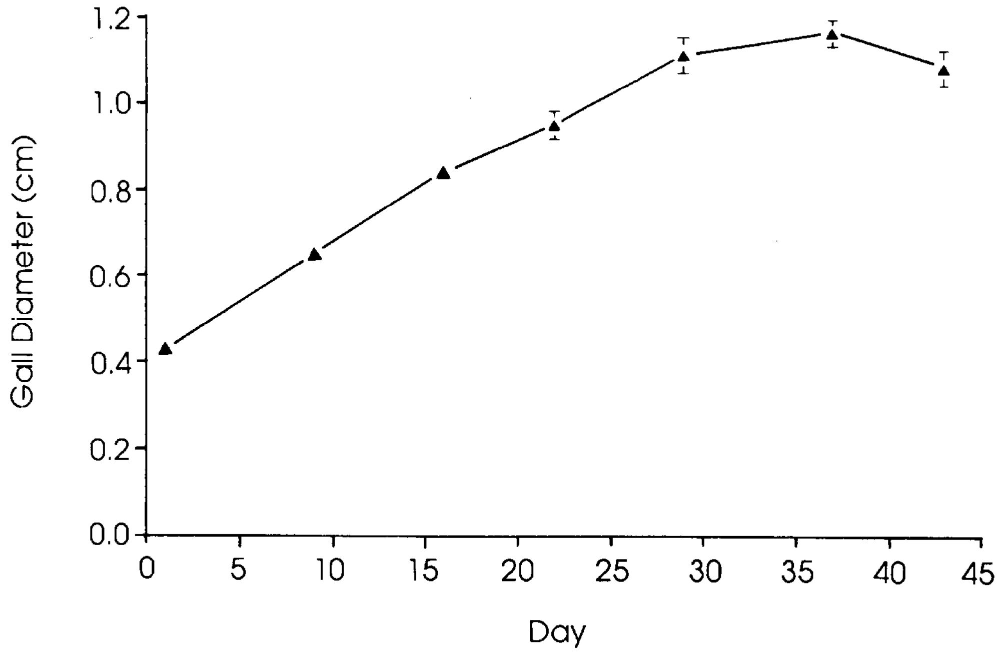

Fig. 3. Gall growth rates. The mean maximum diameter, and standard error, of 30 galls at Live Oak, May-June 1990, from time of first appearance in the field through emergence of host insects and death of galls.

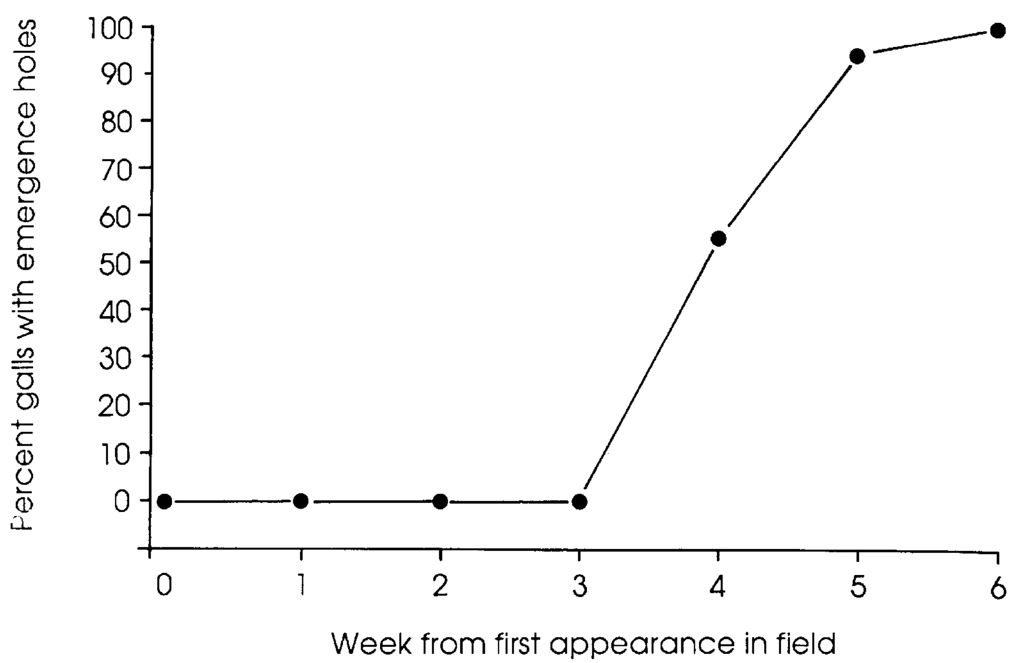

Fig. 4. Appearance of fly and parasitoid emergence holes on *A. borrichiae* galls from time of initiation of galls, week 0, through gall death, week 6. Percentage values are derived from the total number of galls that exhibited emergence holes.

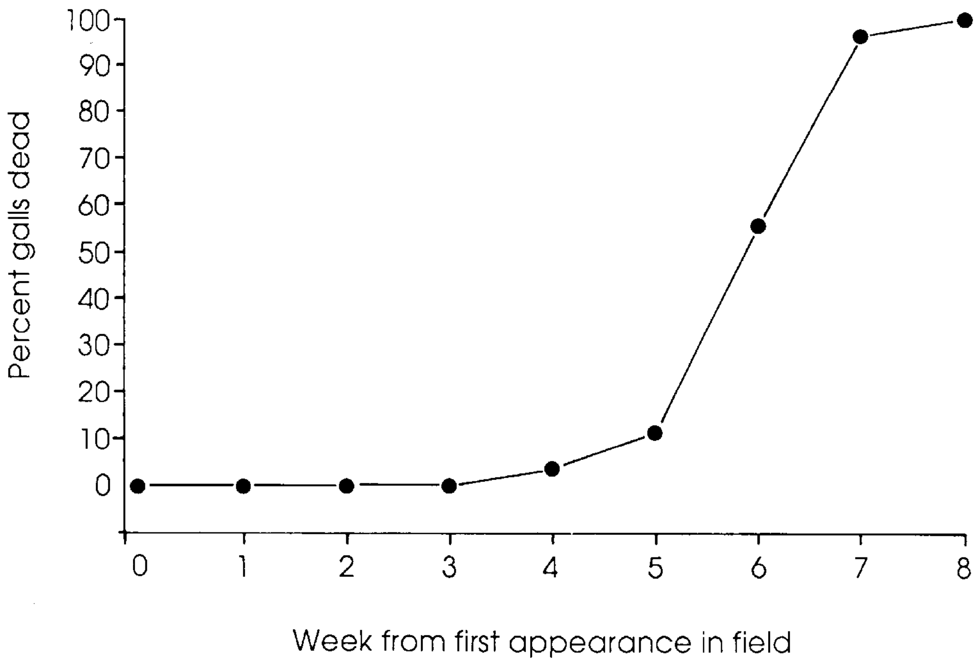

Fig. 5. Survivorship of *A. borrichiae* galls in the field from time of initiation (week 0).

time would be about 6-7 weeks. This is also the minimum length of time it took for ungalled potted plants to accrue the first galls when placed out in the field (unpublished data).

We reared out four species of parasitoids from *Borrichia* galls during 1988 and 1989: *Rileya cecidomyiae* Ashmead and *Tenuipetiolus teredon* (Walker) (Eurytomidae), *Torymus umbilicatus* (Gahan) (Torymidae), and *Galeopsomyia haemon* (Walker) (Eulophidae) (Table 2). *Galeopsomyia haemon* was consistently the most common of these, accounting for half the recorded rate of parasitism. In all species the recorded sex ratio was slightly biased in favor of females. Species of parasitoids showed no clear correlation in the time of emergence from field-collected galls. Insects emerged from day 1 after collection to day 20, but over 90% of the gall inhabitants had emerged within two weeks of the collection date. Fifty percent of galls had rotted in the laboratory 12 days after collection in the field. The longest a gall remained green after collection was 22 days.

All parasites were solitary except *G. haemon*, of which up to nine individual larvae were found to occupy a single chamber. In rearing tubes, males of this species were seen to mate with females from the same gall. The sex ratio of *G. haemon* varied little with the number of individuals per chamber (Table 3) giving little support to the theory of local mate competition, which would predict more males in larger broods (Hamilton 1967, Waage 1982, Werren 1983).

Dissections of galls proved valuable in determining the mode of action of the Hymenoptera. Parasite larvae were found feeding on fly pupae as well as fly larvae. All insects were encountered in fungus bearing chambers within galls, indicative of prior occupancy by flies (Mani 1964). *Asphondylia* fly larvae normally feed on a fungus that coats the inside of the chamber (Parnell 1964, Highland 1964). There was no evidence of inquilinism, even though *Galeopsomyia* reared from *Asphondylia* galls on *Atriplex* in southern California have been reported to be inquilines (Hawkins & Goeden 1984). Hyperparasitism was more difficult to establish. On only a few occasions was a parasite

TABLE 2. PARASITOIDS REARED FROM *BORRICHIA* GALLS.

Family	Species	Number reared	Percent males	Percent of total parasitism June	September
Eurytomidae	*Rileya cecidomyiae*	127	42.5	18.7	26.2
Torymidae	*Torymus umbilicatus*	59	39.0	11.0	7.8
Eulophidae	*Galeopsomyia haemon*	297	37.8	52.0	53.4
Eurytomidae	*Tenuipetiolus teredon*	97	34.0	18.2	12.6

TABLE 3. SEX RATIO VARIATION IN *G. HAEMON* WITH INCREASING CLUTCH SIZE.

G. haemon per chamber	% males	Galls examined
1	19.0	100
2	36.4	140
3	31.5	168
4	33.6	104
≥5	26.8	97

larva discovered feeding on another parasite larva, and because only the resultant adult parasitoids could be identified, the identity of the prey insect was never known. Further, when galls were dissected, insect larvae normally shriveled and died. In a few instances, however, we were able to rear *T. umbilicatus* adults from other parasite larvae, after "reassembling" dissected galls and surrounding them with plastic wrap. This result showed *T. umbilicatus* to be at least a facultative ectophagous hyperparasite, which is consistent with its hyperparasitic nature in other galls (Hawkins & Goeden 1984). Also, in several instances gregarious larvae were noted feeding on other parasite larvae. Because *G. haemon* is the only gregarious species, it is strongly implicated as a facultative hyperparasite also. We recorded the cooccurrences of parasites reared from the same galls. One gall from Rail's Nest, collected in June 1989, yielded a host fly and the parasites *G. haemon*, *T. umbilicatus*, and *T. teredon*. In general, however, cooccurrences were fewer than expected (Table 4), lending support to the idea that most species are facultatively hyperparasitic. The only species that cooccurred more often than expected was *G. haemon*.

TABLE 4. NUMBERS OF COOCCURRENCES OF PARASITES IN 451 *A. BORRICHIAE* GALLS, COLLECTED DURING JUNE FROM RAIL'S NEST AND CLOSELY NEIGHBORING SITES. SIGNS (+ AND −) INDICATE WHETHER PARASITE COOCCURRED IN GALLS LESS FREQUENTLY THAN EXPECTED (−) OR MORE FREQUENTLY THAN EXPECTED (+), ON THE BASIS OF χ^2 TESTS. LEVELS OF SIGNIFICANCE OF THESE TESTS ARE ALSO SHOWN.

	G. haemon n sign p level	*R. cecidomyiae* n sign p level	*T. teredon* n sign p level	*T. umbilicatus* n sign p level
G. haemon	226 + < 0.001			
R. cecidomyiae	28 − < 0.001	18 − < 0.01		
T. teredon	19 − < 0.001	13 − < 0.01	18 − < 0.90	
T. umbilicatus	8 − < 0.001	10 − < 0.20	5 − < 0.05	11 + < 0.3

We found a consistent seasonal variation in parasitism rate of *A. borrichiae* (Table 1). Parasitism was low in March, increased dramatically to nearly 90% in May, decreased to around 60% in July and August, and increased to nearly 100% by late fall. This pattern was repeated in 1989 and 1990. Most galls were parasitized to some extent, and many were completely parasitized, so no flies emerged (Table 1). The only other mortality factor we noted was predation by birds, but even when most pronounced in the field it was only 3.1%. Whether patterns of abundance of galls are linked to levels of parasitism, plant quality, or other factors will be the subject of future investigations.

ACKNOWLEDGMENTS

We thank R. J. Gagné, E. E. Grissell, and M. E. Schauff, Systematic Entomology Laboratory, Agricultural Research Service, U.S. Department of Agriculture, for identifying insects reared from *Borrichia* galls.

Financial support provided by National Science Foundation grant BSR-8703416 to Donald Strong and BSR 9007429 to Peter Stiling and Donald Strong. Current address for A.M.R and D.M.J. is Department of Biology, University of South Florida, Tampa, FL 33260; current address for D.R.S. is Bodega Marine Laboratory, University of California, Box 247, Bodega Bay, CA 94923.

REFERENCES CITED

ANTLFINGER, A. E. 1981. The genetic basis of microdifferentiation in natural and experimental populations of *Borrichia frutescens* in relation to salinity. Evolution 35: 1056-1068.

GAGNÉ, R. J. 1989. The plant feeding gall midges of North America. Cornell University Press, Ithaca, NY.

HAMILTON, W. D. 1967. Extraordinary sex ratios. Science 156: 477-488.

HAWKINS, B. A., AND R. D. GOEDEN. 1984. Organization of a parasitoid community associated with a complex of galls in *Atriplex* spp. in southern California. Ecol. Entomol. 9: 271-292.

HIGHLAND, H. A. 1964. Life history of *Asphondylia ilicicola* (Diptera: Cecidomyiidae), a pest of American holly. J. Econ. Entomol. 57: 81-83.

MANI, M. S. 1964. Ecology of plant galls. Dr. W. Junk, The Hague, Netherlands.

PARNELL, J. R. 1964. Investigations on the biology and larval morphology of the insects associated with the galls of *Asphondylia sarothamni* H. Loew (Diptera: Cecidomyiidae) on broom (*Sarothamnus scoparius* (L.) Wimmer). Trans. R. Entomol. Soc. Lond. 116: 255-273.

ROSSI, A. M., AND D. R. STRONG. 1990. A new species of *Asphondylia* (Diptera: Cecidomyiidae) on *Borrichia* (Asteraceae) from Florida. Proc. Entomol. Soc. Washington 92: 732-735.

WAAGE, J. K. 1982. Sub-mating and sex ratio strategies in scelionid wasps. Ecol. Entomol. 7: 103-112.

WERREN, J. H. 1983. Sex ratio evolution under local mate competition in a parasitic wasp. Evolution 37: 116-124.