RESOURCE UTILIZATION IN THE SIBLING SPECIES
TRUPANEA NIGRICORNIS (COQUILLETT), A POLYPHAGE,
AND THE NARROWLY OLIGOPHAGOUS *T. BISETOSA* (COQUILLETT)
(DIPTERA: TEPHRITIDAE) IN SOUTHERN CALIFORNIA

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Abstract.—The flower heads of the hosts of the sympatric, morphologically similar, probable sister species, *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett) offer an annual, stable food source in southern California. In this study, larger flower heads supported the development of more larvae per head than smaller flower heads. The size of the puparia of *T. nigricornis* was found to vary among the different hosts and with the density of larvae per flower head. The larvae of *T. nigricornis* and *T. bisetosa* exploited the flower heads in a similar way, eating their way downward from the florets first, then into the achenes. The only difference detected was in the second instars of *T. bisetosa* which continued to feed on the florets compared to the second instars of *T. nigricornis* which fed on the achenes. This variation reflected the larger achene size of the hosts of *T. bisetosa*. The percentage of damaged achenes per flower head was found to be proportional to the size of the flower head. In general, a single *T. bisetosa* larva damaged fewer achenes per head than a *T. nigricornis* larva because of the relatively larger achene size and flower head diameter of *T. bisetosa* hosts. Larvae of both tephritids did not exhaust all their food resources in a particular flower head regardless of the size of the flower head and the density of the infesting larvae. In general, the percentage of flower heads infested by *T. bisetosa* was lower than the percentage of flower heads infested by *T. nigricornis*. Plant hosts with larger flower heads did not support more insect species than hosts with smaller heads. There was little evidence of interspecific competition between the various insect species exploiting the flower heads of *T. nigricornis* and *T. bisetosa* because of the many evasion strategies adopted by those insects to minimize interspecific contact.

Key Words: Insecta, *Trupanea,* cryptic species, sympatry, resource utilization, intraspecific competion, interspecific competition

The flower-head infesting tephritids, *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett), occur in sympatry in southern California. They also are probable sister species that have morphological and genetic similarities in the immature and adult stages (Knio et al. 1996a, b), but show major ecological and behavioral differences (Knio et al. 1996a, b). For example, *Trupanea nigricornis* is a generalist, infesting plants belonging to eight tribes in the Asteraceae (Goeden 1992, unpublished data),

whereas *T. bisetosa* is narrowly oligophagous, restricted to one tribe, the Heliantheae, mainly to three *Helianthus* spp. (Cavender and Goeden 1983, Goeden 1992). Also, the eggs of *T. nigricornis* are inserted deep in the flower heads of host plants, often puncturing tissues, while those of *T. bisetosa* are deposited loosely among florets (Knio et al. 1996b). The ultrastructure of the ovipositor of these species also reflects the observed behavioral differences (Knio and Goeden, unpublished data). Further, *T. nigricornis* females lay eggs singly, with more eggs occurring per flower head later in the flowering cycle when resources are scare than earlier in the season. *T. bisetosa* females lay eggs in clusters (Knio et al. 1996b).

Because *T. nigricornis* and *T. bisetosa* are sympatric, probable sister species (Knio et al. 1996a), comparative studies, reported as a series of papers, on their biology, morphology, genetics, and ecology were undertaken to shed light on the differences that separate them. This current paper is intended to clarify the nature of polyphagy/oligophagy in *T. nigricornis* and *T. bisetosa* by addressing the question of resource utilization and interspecific interactions within the flower head guild. The objective is a comparative analysis of the strategies adopted by *T. nigricornis* and *T. bisetosa* for resource usage, resource sharing, and intraspecific and interspecific competition within the context of current evolutionary theory.

MATERIALS AND METHODS

Resource utilization by *Trupanea nigricornis* and *T. bisetosa* was studied by examining field-collected flower heads in the laboratory. Samples of flower heads of *T. nigricornis* and *T. bisetosa* host plants were collected at each of 22 desert and interior-valley locations in southern California during 1987–1992. The host plants of *T. nigricornis* sampled were *Encelia farinosa* Gray, *E. fructescens* Gray, *E. virginensis* A. Nelson, *Haplopappus acradenius* (Greene)

Hall, *Viguiera deltoidea* Gray, and *Geraea viscida* (Gray) Blake. The host plants of *T. bisetosa* sampled were *Helianthus annuus* L., *H. niveus* (Bentham), and *Geraea canescens* Torrey & Gray.

Each plant sample consisted of a 1-l plastic bag containing 100–700 mature flower heads. Flower heads sampled were taken at random from several plants at each collection site. They were transported to the laboratory in ice chests via air-conditioned vehicles and stored under refrigeration until dissection. Subsamples of 25 infested heads and 25 non-infested heads were examined with a stereomicroscope.

The total number of heads dissected to obtain both subsamples was recorded in order to calculate percent infestation. The following parameters for infested flower heads were measured: number, stage, size (diameter and length) of larvae and puparia of *T. nigricornis/T. bisetosa*; state of the larvae (healthy, feeding, parasitized, sluggish, dead); number of achenes damaged by *T.nigricornis/T. bisetosa* larvae; relative position of the larvae and puparia within the flower heads; number, stages, sizes and orientation of other insect species; number of achenes damaged by other species of insects; and number of intact achenes remaining per flower head.

The following parameters for uninfested flower heads were measured: widest diameter of individual flower heads (measured with dial calipers); length of the flower heads (from the outer base of the receptacle to the tip of the florets); widest internal diameter of the receptacle; total number of achenes per flower head; oven dry weight of all 25 flower heads as a unit.

The remaining flower heads in every sample were counted and placed in (34 × 32 × 35 cm) glass-topped, sleeve cages in the insectary at the University of California, Riverside at 60% RH and 12/12 (L D) photoperiod from 0500–1700 h. The numbers and identities of the emerging insects were recorded.

One-way ANOVA and Tukey's test were

Table 1. Summary of the flower-head characteristics of the host plants of *Trupanea nigricornis* and *T. bisetosa* in southern California.

| | Number of Heads | Diameter (mm) | Means ± SE[a], and range (in parentheses) | | | |
			Length (mm)	Receptacle Width (mm)	Number of Seeds/Head	Dry Weight of 25 Heads (gm)
T. nigricornis:						
H. acradenius	125	3.7 ± 0.2a (2.5–6)	12 ± 0.4b (9.4–15.2)	2.1 ± 0.1a (1.3–3.3)	15.3 ± 0.9a (9–22)	0.5 ± 0.1 (0.4–0.8)
E. fructescens	425	12.9 ± 0.4d (8–18.5)	15 ± 0.4c (9–24)	5.5 ± 0.2c (3–8.4)	39.9 ± 2.3b (19–75)	6.1 ± 0.5 (3.2–9.3)
V. deltoidea	150	10.4 ± 0.3b (6.7–13)	11.4 ± 0.3ab (8–13.9)	4.1 ± 0.1b (2.5–5.4)	50.4 ± 4.7c (28–93)	3.3 ± 0.5 (2.4 ± 5.5)
E. farinosa	425	11.9 ± 0.2c (8.7–16.4)	10.9 ± 0.2a (8.3–15)	4.3 ± 0.1b (2.5–6.4)	61.7 ± 2d (28–112)	3.3 ± 0.1 (2.2–4.3)
G. viscida	25	21 ± 0.3g (18.4–24.3)	23.3 ± 0.3d (20.2–25.7)	9.2 ± 0.2d (8–11)	82.6 ± 2.3e (60–102)	18.5 —
E. virginensis	225	16.5 ± 0.4e (10–22.3)	14.5 ± 0.3c (19.4–18.3)	8.6 ± 0.2d (5.6–13.4)	89.6 ± 6e (45–152)	8.4 ± 0.6 (4–10)
Hosts of T. bisetosa:						
H. niveus	50	11.8 ± 0.2c (10.5–14.7)	13.6 ± 0.2c (11.6–15.1)	9.1 ± 0.4d (6.8–11.2)	45.9 ± 1bc (28–74)	4.4 ± 0.2 (4.2–4.5)
G. canescens	175	12.1 ± 0.6c (7.7–16.8)	13.5 ± 0.2c (10–16.7)	5.7 ± 0.2c (3.8–7.5)	46.3 ± 4.6bc (22–86)	4.6 ± 0.6 (2.4–6.5)
H. annuus	200	19.2 ± 0.2f (8.5–23.5)	19.1 ± 0.9c (10–31.5)	10.8 ± 0.2e (7–16.7)	120 ± 2.5f (83–130)	21 —

[a] SE = standard error. Means followed by the same letter are not significantly different at the 95% confidence level using Tukey's test.

used to compare differences between means. Regression analysis was done using Statistica. Mean ± standard errors are provided throughout unless otherwise noted.

RESULTS

Flower-head characteristics.—Characteristics of *Trupanea nigricornis* and *T. bisetosa* flower heads are summarized in Table 1. There were significant differences in the sizes of the flower heads of *T. nigricornis* hosts, i.e., *H. acradenius* had the smallest heads (ca. 4 mm in mean width), followed by *V. deltoidea* (10 mm), *E. farinosa* (ca. 12 mm), *E. fructescens* (ca. 13 mm), *E. virginensis* (16.5 mm), and *G. viscida* (21 mm). Among *T. bisetosa* hosts, *H. niveus* and *G. canescens* had smaller heads (ca. 12 mm) than the significantly larger heads of *H. annuus* (19.2 mm).

Among the hosts of *T. nigricornis, H. acradenius* had small, ovoid flower heads,

with the smallest mean receptacle diameter and the lowest mean dry weight, followed by *V. deltoidea, E. farinosa, E. fructescens,* that are medium-sized, globose flower heads, and *E. virginensis,* and *G. viscida,* that are large, globose flower heads (Table 1). With respect to the number of achenes per flower head, *H. acradenius* had the lowest mean value of ca. 15 followed by *E. fructescens, V. deltoidea, E. farinosa, G. viscida,* and *E. virginensis* with mean values that ranged from ca. 40–90 achenes per flower head.

Among *T. bisetosa* hosts, *H. niveus* and *G. canescens* had shorter flower heads with smaller receptacle diameter and lower dry weight than *H. annuus* (Table 1) Also, *H. niveus* and *G. canescens* had only one-third the mean number of achenes per head than *H. annuus.*

As expected, there was a high correlation between the outside diameter of the flower

Table 2. Frequency distributions of larvae of *Trupanea nigricornis* in heads of different host plant species.

Hosts: Number of Larvae per Head	E. virginensis Count (%)	E. farinosa Count (%)	E. fructescens Count (%)	H. acradenius Count (%)	V. deltoidea Count (%)
1	44 (23.7)	274 (71.4)	210 (75.5)	60 (89.5)	65 (73)
2	53 (28.5)	86 (22.4)	53 (19.4)	5 (7.5)	21 (23.6)
3	36 (19.4)	22 (5.7)	13 (4.7)	1 (1.5)	2 (2.3)
4	18 (9.7)	2 (0.5)	0	1 (1.5)	1 (1.1)
5	15 (8.1)	0	1 (0.4)	0	0
6	9 (4.8)	0	0	0	0
7	4 (2.1)	0	0	0	0
8	4 (2.1)	0	0	0	0
9	3 (1.6)	0	0	0	0
Total number of heads:	186	384	278	67	89
Number of samples:	9	19	17	5	5

head and the number of achenes per flower head ($R = 0.86$) and the diameter of the receptacle and the number of achenes per flower head ($R = 0.81$). The length of the flower head had little relationship with achene number per flower head ($R = 0.38$).

Host plant phenology.—Collectively, the flower heads of *T. nigricornis* and *T. bisetosa* hosts offered continuous food resources for both tephritids. The hosts of *T. nigricornis* bloom in different seasons, such that there is a continual supply of flower heads for most of the year. They bloom mainly in two seasons, spring (e.g., *Encelia* sp.) and fall (e.g., *H. acradenius*), and for periods of 2–3 mo. depending on rainfall. The main host of *T. bisetosa*, *H. annuus*, blooms throughout the year in the absence of frost, and, thus, is a continuously available resource for this species.

Resource utilization by *T. nigricornis*.— The number of *T. nigricornis* larvae that fed and completed their development in a single head varied among different host plants. Regression analysis showed that flower head diameter ($R = 0.47$) was a moderate indicator of the number of larvae completing development per flower head; however, dry weight ($R = 0.28$) was a poor indicator of the number of larvae per flower head. The small heads of *H. acradenius* contained mainly one larva per head (89.5%); 7.5% contained two larvae and 3% had three or four larvae (Table 2). The

number of *T. nigricornis* larva(e) per flower head in the hosts with medium-sized heads (*E. farinosa*, *E. fructescens*, and *V. deltoidea*) collectively were: 71–75% of the flower heads contained one larva, 19–24% had two larvae and 3–6% had three to five larvae (Table 2). In the large heads of *E. virginensis*, the number of larva(e) per head were: ca. 24% of the flower heads had one larva, ca. 48% had two or three larvae, ca. 18% had four or five larvae, ca. 7% had six or seven larvae and ca. 4% had eight or nine larvae (Table 2). Larger flower heads supported the development of a greater number of larvae than did smaller flower heads.

Resource utilization by *T. bisetosa*.—The number of *T. bisetosa* larvae that completed their development in the large flower heads of *H. annuus* ranged from one to 12 larvae per head. Thirty percent of *H. annuus* flower heads contained only one larva, 47% contained two or three larvae, 13.2% contained four or five larvae, 6.6% contained six or seven larvae and ca. 3% contained eight to 12 larvae (Table 3). Again, flower head diameter ($R = 0.4$) and dry weight ($R = 0.38$) were moderate and poor indicators, respectively, of the number of *T. bisetosa* larvae able to complete their development within a flower head.

The relatively smaller heads of *G. canescens* contained two to four *T. bisetosa* larvae per head and those of *H. niveus* con-

Table 3. Frequency distributions of larvae of *Trupanea bisetosa* in heads of *Helianthus annuus, Geraea canescens,* and *H. niveus.*

Number of Larvae per Head	H. annuus Count (%)	G. canescens Count (%)	H. niveus Count (%)
1	41 (30.1)	0	3 (75)
2	38 (27.9)	2 (50)	1 (25)
3	26 (19.1)	0	0
4	12 (8.8)	2 (50)	0
5	6 (4.4)	0	0
6	4 (2.9)	0	0
7	5 (3.7)	0	0
8	1 (0.7)	0	0
9	1 (0.7)	0	0
10	1 (0.7)	0	0
11	0	0	0
12	1 (0.7)	0	0
Total number of heads:	136	4	4
Number of samples:	10	1	1

tained one to two larvae per head (Table 3). On the other hand, the large heads of *H. annuus* resembled those of *E. virginensis* in supporting higher number of larvae than the smaller heads of other host plants.

Puparia size.—The size of *T. nigricornis* puparia was found to vary by host plant flower head diameter (Table 4). The smallest puparia were found in the small heads of *H. acradenius*; whereas, the largest puparia were found in the medium-sized, but long heads of *E. fructescens.* All *T. nigricornis* puparia were significantly smaller

than *T. bisetosa* puparia, irrespective of host plant species (Table 4).

In some host plant species of *T. nigricornis* variation between the size of male and female puparia occurring singly in flower heads was noted (Table 5). For example, in *E. farinosa,* puparia that produced females were longer than those that yielded males. However, in *E. fructescens,* female *T. nigricornis* puparia were wider than male puparia, but not longer. In *E. virginensis,* the size of the puparia of *T. nigricornis* did not differ between males and females, although adult females of this tephritid species were generally larger than the males.

The size of *T. nigricornis* puparia varied with the density of the larvae per medium-sized flower head (Table 6). In *E. fructescens,* the puparia of *T. nigricornis* in flower heads infested by one larva were wider on average than puparia in heads infested with four or five larvae (Table 6). However, density of the larvae per head did not affect the length of the puparia dissected from *E. fructescens,* which had longer flower heads than its congeners (Table 6). No difference in the sizes of puparia was detected in *E. farinosa* flower heads with one larva and those with two to three larvae. Flower heads with four to five puparia were rare in the medium-sized heads of *E. farinosa* (Table 6). In the large flower heads of *E. vir-*

Table 4. Sizes of *Trupanea nigricornis* and *T. bisetosa* puparia in different host plants.

Host Plants	Number of Puparia Measured	Size of Puparia	
		Dᵃ ± SE (Range) mm	Lᵃ ± SE (Range) mm
T. nigricornis:			
E. farinosa	310	1.26 ± 0.002 (1–1.5) a	2.76 ± 0.01 (2.2–3.25) b
E. fructescens	270	1.28 ± 0.01 (1–1.55) c	2.84 ± 0.01 (2.16–3.25) c
E. virginensis	134	1.25 ± 0.003 (1–1.35) ab	2.73 ± 0.01 (2.2–3) b
H. acradenius	28	1.22 ± 0.01 (1–1.25) a	2.42 ± 0.03 (2.1–2.75) a
V. deltoidea	37	1.25 ± 0.01 (1.1–1.48) ab	2.72 ± 0.02 (2.5–3) b
G. viscida	4	1.25 ± 0 (1.25–1.25) ab	2.75 ± 0 (2.75–2.75) b
T. bisetosa:			
H. annuus	221	1.43 ± 0.01 (1.2–1.6) d	3.11 ± 0.01 (2.5–3.55) d

ᵃ D = diameter; L = length; SE = standard error.
Means followed by the same letter are not significant at the 95% confidence level, using Tukey's test.

Table 5. Sizes of male versus female *Trupanea nigricornis* puparia dissected from flower heads of different *Encelia* species.

Sex	Number of Puparia	Mean Diameter ± SE (range)[a] mm	Mean Length ± SE (range)[a] mm
E. farinosa:			
Females	38	1.27 a ± 0.01 (1.25–1.5)	2.85 a ± 0.02 (2.5–3.2)
Males	24	1.26 a ± 0.01 (1.2–1.45)	2.72 b ± 0.04 (2.2–3)
E. virginensis:			
Females	20	1.24 a ± 0.003 (1.2–1.25)	2.8 a ± 0.03 (2.5–3)
Males	10	1.25 a ± 0.005 (1.25–3)	2.8 a ± 0.03 (2.75–3)
E. fructescens:			
Females	7	1.43 a ± 0.04 (1.3–1.55)	2.89 a ± 0.12 (2.25–3.25)
Males	14	1.25 b ± 0.02 (1.1–1.5)	2.73 a ± 0.05 (2.5–3.1)

[a] SE = standard error. For every plant species: means followed by the same letter are not significantly different at 95% confidence level, using Tukey's test.

ginensis, the size of the puparia did not significantly differ between heads with one or two larvae and heads with four to nine larvae.

In *H. annuus,* no difference in the size of *T. bisetosa* puparia was detected between flower heads with one to three larvae and flower heads with higher larval densities (4–12) (Table 6).

Feeding behaviors by instar.—*Trupanea nigricornis* and *T. bisetosa* larvae exploited flower heads as a food source in a similar manner, except as second instars. First instars of both species tunneled and fed in the

Table 6. Sizes of *Trupanea nigricornis* and *T. bisetosa* puparia in heads infested with one to several larvae.

Sizes[a] of Puparia (mm)	Number of Larvae per Head[b]:		
	One	Two–Three	Four and More
T. nigricornis:			
E. farinosa:			
D ± SE	1.26 ± 0.01 (1–1.5)a	1.25 ± 0 (1.25–1.3)a	—
L ± SE	2.75 ± 0.01 (2.25–3.25)a	2.75 ± 0.01 (2.5–3.08)a	—
N	136	106	—
E. fructescens:			
D ± SE	1.32 ± 0.01 (1–1.55)a	1.27 ± 0.02 (1–1.3)ab	1.24 ± 0.02 (1–1.48)b
L ± SE	2.87 ± 0.03 (2.16–3.25)a	2.84 ± 0.03 (2.2–3.2)a	2.84 ± 0.05 (2.5–3.2)a
N	80	44	19
E. virginensis:			
D ± SE	1.25 ± 0 (1.25–1.25)a	1.24 ± 0.01 (1–1.35)a	1.23 ± 0 (1–1.3)a
L ± SE	2.81 ± 0.04 (2.75–3)a	2.71 ± 0.02 (2.2–3)a	2.72 ± 0.03 (2–3)a
N	8	44	54
T. bisetosa:			
D ± SE	1.46 ± 0.02 (1.25–1.55)a	1.42 ± 0.01 (1.25–1.6)a	1.44 ± 0.01 (1.2–1.6)a
L ± SE	3.08 ± 0.04 (2.55–3.5)a	3.14 ± 0.02 (2.8–3.5)	3.16 ± 0.02 (2.8–3.55)a
N	29	79	84

[a] D = Diameter; L = Length; SE = Standard error; N = Number of puparia measured.
[b] For each host, means followed by the same letter are not significantly different at the 95% confidence level using Tukey's test.

Table 7. Number of achenes damaged by *Trupanea nigricornis* and *T. bisetosa* third instar larvae in different host plants.

Host Plant	Number of Larvae	Mean of Damaged Achenes per Larva ± SE (Range)[a]:	
		Number	Achenes per Head (%)
Hosts of *T. nigricornis:*			
Encelia farinosa	225	8.8 ± 0.2 (3–16) c	18.2 ± 0 (7.1–43.5)
Viguiera deltoidea	50	8.5 ± 0.5 (4–19) bc	21.9 ± 0.01 (9.4–52)
E. virginensis	165	8 ± 0.2 (4–14) b	10.3 ± 10 (4–27.1)
E. fructescens	225	7.9 ± 0.2 (3–16) b	24.3 ± 0.01 (8–58.3)
Haplopappus acradenius	56	7.3 ± 0.3 (3–13) a	50.6 ± 0.02 (23–83)
Hosts of *T. bisetosa:*			
Helianthus annuus	225	6.4 ± 0.1 (3–11) a	6.3 ± 0 (2.4–13.8)
Geraea canescens	12	5.2 ± 0.2 (4–6) a	16.3 ± 0.02 (9–23)

[a] SE = Standard error.
Means followed by the same letter are not significantly different at the 95% confidence level according to Tukey's test.

floral tubes. Second instars of *T. nigricornis* fed in the soft achenes while second instars of *T. bisetosa* fed in the floral tubes, close to the achene-floret junction. Third instars of both species fed upon and destroyed several adjacent achenes. When more than one larva of either species were present in a flower head, they were usually located centrally, but fed on different achenes, and were separated by one or several achenes.

A single larva of *T. nigricornis* damaged from three to 19 achenes, depending on the host plant species (Table 7). During larval feeding, *T. nigricornis* consumed ca. 9 achenes in *E. farinosa*, 8 achenes in *E. virginensis* and *E. fructescens*, 8.5 achenes in *Viguiera deltoidea*, and 7 achenes in *Haplopappus acradenius* (Table 7). The number of achenes damaged by a larva in the small flower heads of *H. acradenius* was significantly less than the number of achenes damaged in the other plant species (Table 7).

The percentage of achenes consumed or damaged in a flower head by a single *T. nigricornis* larva was proportional to the size of the flower head. Damage was highly correlated with the diameter (R = 0.91) and the dry weight (R = 0.86) of the heads of *T. nigricornis* hosts. Percent achenes damaged by a single larva was highest in the

small heads of *H. acradenius* (51%), which contained the fewest achenes per head, and lowest in the large heads of *E. virginensis* (10.3%), which contained the most achenes per head (Table 7). Achene damage ranged between 18 and 24% in the medium-size heads of *E. farinosa, V. deltoidea,* and *E. fructescens* (Table 7).

The number of achenes consumed by a single *T. bisetosa* larva was less than that of *T. nigricornis*. During larval feeding *T. bisetosa* consumed a mean of 6.4 ± 0.1 achenes in *H. annuus* and a mean of 5.2 ± 0.2 achenes in *G. canescens* (Table 7). There was no significant difference in the number of achenes damaged in *H. annuus* and *G. canescens*. The number of achenes damaged by a single *T. bisetosa* larva was highly correlated with the diameter (R = 0.99) and the dry weight (R = 0.46) of the heads.

The percentage of achenes consumed or damaged per flower head by a single *T. bisetosa* larva was higher (16%) in the medium-size flower heads of *G. canescens* than the larger heads of *H. annuus* (6%) (Table 7). Also, this percentage was highly correlated with the diameter (R = 0.91) and dry weight (0.86) of the heads.

Trupanea nigricornis and *T. bisetosa* larvae did not exhaust all the achene resources

Table 8.   Number of achenes per head that remained intact in flower heads infested with one or more *Trupanea nigricornis* third instar larva.

Host Plant, N[b]	Number of Intact Achenes ± SE[a] per Head (Range) in Heads Infested with the Following Number of Larva(e):						
	1	2	3	4	5	6–7	8–9
E. fructescens	25.7 ± 0.9	23.3 ± 1.5	17.4 ± 2.1	—	7 ± 0	—	—
	(9–65)	(4–45)	(8–35)	—	—	—	—
N	157	46	14	—	1	—	—
E. farinosa	41.1 ± 0.0	32.4 ± 1.4	30.7 ± 2.2	26 ± 0	—	—	—
	(13–78)	(11–60)	(12–55)	(26–26)	—	—	—
N	201	62	23	2	—	—	—
E. virginensis	69.7 ± 3.7	73.3 ± 3.6	77.7 ± 4.5	67.8 ± 8.1	59.9 ± 6.1	53 ± 11.8	28.5 ± 12
	(34–127)	(20–121)	(42–132)	(18–132)	(15–105)	(15–93)	(5–69)
N	41	49	33	13	15	11	8
V. deltoidea	31.2 ± 0.9	38 ± 4	—	—	—	—	—
	(15–48)	(25–52)	—	—	—	—	—
N	50	6	—	—	—	—	—
H. acradenius	6.9 ± 0.3	—	—	—	—	—	—
	(2–12)	—	—	—	—	—	—
N	57	—	—	—	—	—	—

[a] SE = standard error.
[b] N = number of flower heads analyzed.

in a given flower head regardless of the size of the flower head or larval density. The mean number of intact achenes remaining in hosts infested with one to several *T. nigricornis* larvae are summarized in Table 8. The medium-sized flower heads of *E. farinosa, E. fructescens,* and *V. deltoidea* infested with one to two larvae still contained 23–41(ca. 62–68%) undamaged achenes (Table 8). However, in *H. acradenius,* ca. seven (47%) achenes remained intact after infestation with a single larva (Table 8). The large flower heads of *E. virginensis* had 28–77 (ca. 32–89%) intact achenes whether they were infested with one or several larvae. However, there was a gradual decrease in the number of undamaged achenes when more than four larvae were present in *E. virginensis* (Table 8). Similarly, in *T. bisetosa* hosts, the mean number of intact achenes in *H. annuus* remained high (63–103; 53–86%), whether they were infested with 1–12 larvae (Table 9). Again, there was a gradual decrease in the number of intact achenes as the density of *T. bisetosa* larvae increased from one to 12 per head (Table 9).

Interspecific interactions.—The mean numbers of intact achenes remaining in heads infested concurrently with *T. nigricornis* and other herbivorous insects are summarized in Table 10. The medium-sized flower heads of *E. farinosa* and *E. fructescens* with multiple infestations still contained 24–51 (ca. 40–85%) and 4–22 (10–55%) intact achenes, respectively (Table 10). *Encelia virginensis* flower heads with multiple infestations retained 22–95 (ca. 25–100%) intact achenes suggesting little interspecific competition for achenes.

The mean numbers of intact achenes in heads infested with *T. bisetosa* and other insects are summarized in Table 11. The flower heads of *H. annuus* with multiple infestations retained 56–106 (47–88%) intact achenes. The flower heads of *G. canescens* with multiple infestations retained 20–21 (ca. 43%) intact achenes (Table 11).

The percentage infestation by *T. nigricornis* was highest in *E. virginensis* (44.2 ± 5.7%) and moderate to high in *E. farinosa* (32.5 ± 2.8%), *V. deltoidea* (29.6 ± 5.3%), and *E. fructescens* (25.5 ± 4.7%). Percentage infestation was lowest in the

Table 9. Number of achenes per head that remained intact in flower heads infested with one or more *Trupanea bisetosa* third instars.

Host Plant, N[b]	Number of Intact Achenes ± SE[a] per Head (Range) in Heads Infested with the Following Number of Larva(e):						
	1	2	3	4	5–6	9–10	11–12
H. annuus:	102.8 ± 3.8	96.9 ± 5.4	84.1 ± 6.5	78.8 ± 5.8	68.3 ± 6	70.7 ± 7	62.8 ± 6
	(55–142)	(56–124)	(58–105)	(56–107)	(48–102)	(35–95)	(45–82)
N	40	13	9	10	9	10	6
G. canescens:	36	15 ± 5	—	21.5 ± 3.5	—	—	—
	—	(10–20)	—	(18–25)	—	—	—
N	1	2	—	2	—	—	—

[a] SE = standard error.
[b] N = number of flower heads analyzed.

small heads of *H. acradenius* (12.3 ± 5.9%), which unlike the other hosts, bloomed in the fall instead of the spring. The percentage of *E. virginensis* flower heads with *T. nigricornis* plus at least one other species ranged from 28.4 to 71.4% (49.3 ± 4.8%); which was higher than the range found in the medium-sized flower heads of *E. farinosa, E. fructescens*, and *V. deltoidea*; 16.0 to 71.0% (40.1 ± 3.2%), 9.6 to 83% (35.7 ± 4.4%), 14.3 to 43% (31.5 ± 6.0%), respectively. Samples of *H. acradenius* with multiple insect infestations were rare. The insects that co-occurred with *T. nigricornis* in the host plant species examined were *Melanagromyza viridis* (Frost)

Table 10. Number of achenes per head that remained intact in flower heads with multiple infestations of insects including *Trupanea nigricornis*.

Host Plant	Number of Heads Examined	Mean Number of Intact Achenes per Head ± SE[a] (Range)	Number of Insects[b] per Head					
			T.n.	M.v.	N.f.	Lep.	C.g.	C.f.
E. farinosa	22	30.1 ± 2.6 (12–58)	1	—	1	—	—	—
	3	24.3 ± 5.4 (18–35)	2	1	—	—	—	—
	2	51 ± 1 (50–52)	1	1	—	—	—	—
	3	39.3 ± 9 (22–52)	1	—	—	1	—	—
	1	26	2	—	—	1	—	—
E. fructescens	3	21.7 ± 3.8 (16–29)	1	—	—	—	—	—
	6	20.3 ± 4.2 (10–40)	1–2	1	—	—	—	—
	1	10	1	1	—	—	6	—
	2	19 ± 6.9 (13–25)	1	—	—	—	—	1
	1	4	1	—	—	—	—	11
E. virginensis	8	89.5 ± 7 (66–121)	1	1	—	—	—	—
	3	95.3 ± 18.7 (59–121)	1	2–3	—	—	—	—
	10	67 ± 6.6 (32–105)	2–4	1–2	—	—	—	—
	2	73.5 ± 18.5 (55–92)	3–5	—	1	—	—	—
	1	90	4	2	1	—	—	—
	1	22	1	—	1	1	—	—
	2	49 ± 1 (48–50)	1–4	1	—	1	—	—
	2	24.5 ± 15.5 (9–40)	2–5	—	—	1	—	—
	4	62.8 ± 7 (40–99)	1	—	—	—	1–3	—
	4	74.3 ± 5.1 (61–89)	2–3	—	—	—	1–2	—

[a] SE = standard error.
[b] T.n. = *Trupanea nigricornis*; M.v. = *Melanogromyza viridis*; N.f. = *Neotephritis finalis*; Lep. = Lepidoptera larva (Noctuidae); C.g. = Cecidomyidae galls; C.f. = Cecidomyidae free-living larvae.

Table 11. Number of achenes per head that remained intact in flower heads with multiple infestations of insects including *Trupanea bisetosa*.

Host Plant	Number of Heads	Number of Intact Achenes per Head ± SE[a] (Range)	Number of Flies[b]/Head		
			T.b.	M.v.	N.f.
Helianthus annuus	3	105.7 ± 2.3 (102–110)	1–2	1	—
	3	56.3 ± 3 (52–62)	2–4	—	1
Geraea canescens	1	20	2	1	—
	1	21	1	2	—

[a] SE = standard error.
[b] T.b. = *Trupanea bisetosa*; M.v. = *Melanagromyza viridis*; N.f. = *Neotephritis finalis*.

(Agromyzidae), *Neotephritis finalis* (Loew) (Tephritidae), an undetermined species of *Smycronix* (Curculionidae), an undetermined Noctuidae species, and undetermined Cecidomyiidae gall formers and free-living, presumably predaceous, species.

The percentage flower head infestation by *T. bisetosa* and other insects in 15 *H. annuus* samples ranged from 9.1 to 61.9% (23 ± 4.2%). These were lower than the total percentage infestation of *T. nigricornis* hosts, with the exception of *H. acradenius*. The percentage of infested flower heads of *H. annuus* with *T. bisetosa* ranged from 3.6 to 59.5% (18.6 ± 4.3%). Few heads, 0–25% (3.0 ± 1.7%), were infested with *T. bisetosa* and other insects contemporaneously. The other insects that occurred with *T. bisetosa* in *H. annuus* flower heads were *M. viridis*, *N. finalis*, *Paracantha cultaris* (Coquillett) (Tephritidae), and an undetermined species of Noctuidae.

Only one sample of *H. niveus* yielded *T. bisetosa* with 4% of heads infested solely by this species. An additional 4% had mainly *M. viridis* occuring in flower heads.

The percentages of flower heads of *G. canescens* that yielded *T. bisetosa* were low, ranging from 1.2 to 13.3% (5.5 ± 4%), and there were few heads, 0–4% (1.3 ± 1.3%), with multiple infestations. The samples of *G. canescens* mainly yielded *M. viridis*.

Trupanea nigricornis and *T. bisetosa* populations showed several differences in the manner in which they infested their hosts. 1) The percentage flower heads in-

fested by *T. bisetosa* was lower on average than the percentage of flower heads infested by *T. nigricornis*, except in *H. acradenius*. 2) The number of samples of *T. bisetosa* hosts that did not yield any *T. bisetosa* was greater than the number of samples of *T. nigricornis* hosts that did not yield any *T. nigricornis*. Among samples of *T. nigricornis* hosts, one of 10 (10%) *E. virginensis*, two of 17 (10.5%) *E. fructescens*, three of eight (37.5%) *H. acradenius* and two of eight (25%) *V. deltoidea* samples were not infested with *T. nigricornis*. All samples taken of *E. farinosa* yielded *T. nigricornis*. Among samples of *T. bisetosa* hosts, 19 of 33 (57.6%) samples of *H. annuus*, two of four (50%) *H. niveus*, and six of nine (66.7%) *G. canescens* were not infested with *T. bisetosa*. 3) Percentage infestation by *T. bisetosa* varied during the year. Infestations of *H. annuus* heads by *T. bisetosa* were highest late in the fall, when the densities of the plants in flower decreased. Percentage infestations were low to moderate in the spring, depending on the availability of soil moisture, and were low in the summer.

The total numbers and identities of other insects reared from flower heads of samples of *T. nigricornis* and *T. bisetosa* hosts are listed in Table 12. Members of other guilds including polyphagous, phytophagous insects and general predators and parasites were not listed. The agromyzid, *M. viridis*, and the tephritid, *N. finalis*, infested most plant species that host *T. nigricornis* and *T. bisetosa*. Adults of *M. viridis* were reared

Table 12. Total numbers of insects, by species, that were reared from samples of flower heads of *Trupanea nigricornis* and *T. bisetosa* hosts collected during 1987–1992.

Hosts, Number of Samples	Insect Species[a]:						Parasite Species[b]:					
	T.n.	T.b.	N.f.	M.v.	T.w.	P.c.	H	P	C	Pr	E	Others
E. farinosa:	1,379	—	934	55	1	—	517	241	46	2	8	—
N = 29	29	—	26	8	1	—	29	20	6	2	2	—
E. fructescens:	212	—	15	62	—	—	59	40	9	2	1	C, C.f.
N = 18	18	—	4	11	—	—	10	8	3	1	1	4, 1
E. virginensis:	204	—	22	40	—	—	30	31	82	—	5	C, C.f.
N = 10	10	—	4	6	—	—	6	7	7	—	2	6, 3
V. deltoidea:	26	—	—	20	—	—	2	2	—	—	—	C.f.
N = 5	5	—	—	3	—	—	2	1	—	—	—	1
H. acradenius:	63	—	—	—	1	—	1	39	—	—	—	2U.f
N = 4	4	—	—	—	1	—	1	3	—	—	—	1
G. viscida:	1	—	—	5	—	—	—	—	—	—	—	—
N = 1	1	—	—	1	—	—	—	—	—	—	—	—
G. canescens:	—	21	—	1,256	—	—	—	—	—	—	—	—
N = 7	—	3	—	7	—	—	—	—	—	—	—	—
H. annuus:	—	763	278	127	—	26	—	107	—	—	—	—
N = 34	—	34	9	9	—	7	—	18	—	—	—	—
H. niveus:	—	2	—	12	—	—	—	—	—	—	—	—
N = 2	—	1	—	2	—	—	—	—	—	—	—	—

[a] T.n. = *Trupanea nigricornis* (Tephritidae); T.b. = *Trupanea bisetosa* (Tephritidae); N.f. = *Neotephritis finalis* (Tephritidae); M.v. = *Melanogromyza viridis*; T. wheeleri = *Trupanea wheeleri* (Tephritidae); P.c. = *Paracantha cultaris* (Tephritidae).

[b] H = *Halticoptera* sp. (Pteromalidae); P = *Pteromalus* sp. (Pteromalidae); C = *Colotrechnus ignotus* Burks (Ptermalidae); Pr = Perilampidae; E = *Eurytoma* sp. (Eurytomidae); C = gall-forming Cecidomyiidae; C.f. = free-living Cecidomyiidae; U.f. = *Urophora formosa* (Tephritidae).

from all *T. nigricornis* hosts studied, except *Haplopappus acradenius*. They were also common in *T. bisetosa* hosts, and heavily infested all samples of flower heads of *G. canescens*. Adults of *N. finalis* were reared from all *Encelia* spp. studied as hosts of *T. nigricornis*, as well as from *H. annuus*. Less common species that occurred in *T. nigriconis* hosts were the tephritid *Trupanea wheeleri* Curran, found in one sample each of *H. acradenius* and *E. farinosa*, and the tephritid, *Goedenia* (formerly *Urophora*) *formosa* (Coquillett), that emerged from one sample of *H. acradenius*. Gallicolous as well as free-living, probably predaceous, cecidomyiid larvae were found in flower heads of *E. fructescens*, *E. virginensis*, and *V. deltoidea*. The tephritid *Paracantha cultaris* (Coquillett) was only reared from *H. annuus*.

Among the hosts of *T. nigricornis*, *E. farinosa*, and then *E. fructescens* and *E. vir-* *ginensis*, were richer in numbers and abundance of associated insect species, as well as their parasites, than *V. deltoidea*, *H. acradenius*, and *G. viscida* (Table 12). The flower heads of *E. farinosa* and *E. fructescens* were exploited mainly by three dipterous species, *T. nigricornis*, *N. finalis*, and *M. viridis*, and their five species of pteromalid parasites. Flower heads of *E. virginensis* were utilized by the same three species of flies, but yielded only four species of parasites. Two other hosts of *T. nigricornis* studied, *V. deltoidea* and *H. acradenius*, were infested with mainly two species of flies, *T. nigricornis* and *M. viridis* in *V. deltoidea*, and *T. nigricornis* and *T. wheeleri* in *H. acradenius*, and two species of parasites (Table 12).

Among the three *T. bisetosa* host plants studied, the flower heads of *H. annuus* had the most species infesting them (Table 12). They were utilized by four species of flies,

but only one species of parasite. The other hosts, *H. niveus* and *G. canescens*, were infested with two species of flies, and no parasites were reared from them.

Flower guild resource utilization.—The most common insects that fed within flower heads and shared space and food resources with *T. nigricornis* and *T. bisetosa* were *M. viridis*, *N. finalis* and a noctuid larva. Other insects like *P. cultaris* and larvae of the weevil, *Smicronyx* sp., infested host plants of *T. bisetosa* and *T. nigricornis*, respectively, but they did not share the same flower heads.

The agromyzid, *M. viridis*, was common in host plants of both *T. nigricornis* and *T. bisetosa*. Its larvae fed mainly in the upper part of the achenes and in the florets. The puparia were slightly smaller than those of *T. nigricornis*; averaging 1.1 ± 0.02 (0.8–1.3) mm in width and 2.5 ± 0.03 (1.5–3.1) mm in length (n = 60). They were easily recognized by their yellow color and their long posterior spiracles. The number of achenes damaged by one *M. viridis* larva ranged between 2 and 15. Among *T. nigricornis* hosts, the mean number of damaged achenes was 6.3 ± 0.6 (n = 12; range = 3–10) in *E. farinosa*, 6.6 ± 0.3 (n = 38; range 4–12) in *E. virginensis*, and 8.4 ± 0.5 (n = 27; range 4–15) in *E. fructescens*. This was less than the mean number of achenes damaged by *T. nigricornis* in these hosts (6–8 for *M. viridis* as opposed to 8–9 for *T. nigricornis*). In *T. bisetosa* hosts, the average number of achenes damaged by a single *M. viridis* larva was 5.1 ± 0.3 (n = 15; range = 4–8) in *H. niveus*, 5.4 ± 0.2 (n = 75; range = 3–9) in *G. canescens*, and 3.8 ± 0.6 (n = 10; range = 2–9) in *H. annuus*. Like *T. bisetosa*, agromyzid larvae caused less damage in *H. annuus* heads; however, a full size *T. bisetosa* larva destroyed more *H. annuus* achenes (6.5/per larva) than a full-sized *M. viridis* larva.

Like *T. nigricornis* and *T. bisetosa*, *M. viridis* did not use all of the achene resources present in a flower head. The numbers of intact achenes that remained in heads of different hosts infested with one or several *M. viridis* larvae are summarized in Table 13. The data show that *M. viridis* destroyed only a portion of the achenes in a given flower head, even when several larvae developed in the same head.

The tephritid *Neotephritis finalis* also was a common associate in both *T. nigricornis* and *T. bisetosa* hosts. Its larvae fed in the achenes, sometimes producing a little frass during their feeding. The puparia of *N. finalis* were easy to recognize; they were brown and measured 1.5 ± 0.02 (1.4–1.6) mm in diameter and 3.4 ± 0.02 (3–3.8) mm in length (n = 65). The mean number of achenes damaged by one larva of *N. finalis* was 13.3 ± 0.4 (n = 65; range = 9–22) in *E. farinosa*. This was higher than the damage caused by a single *T. nigricornis* larva. The mean number of achenes left intact in heads of *E. farinosa* infested with *N. finalis* was 33.7 ± 1.9 (n = 31; range = 13–55) in heads with one larva and 25.9 ± 1.8 (n = 23; range = 11–47) in heads with two larvae. The mean number of achenes damaged by one larva of *N. finalis* in *H. annuus* was 5.7 ± 0.4 (n = 10; range = 4–8). The mean number of undamaged achenes per head infested with one *N. finalis* larva in *H. annuus* was 94.6 ± 5.4 (n = 10; range 59–120). Thus, *N. finalis* also did not utilize all the achenes present in the flower heads of its hosts.

Noctuid larvae co-infested host plants of both *T. nigricornis* and *T. bisetosa*. Each noctuid larva fed within several flower heads over the course of its development. The average number of achenes damaged per flower head by one noctuid larva was (21.5 ± 1.7) (range = 9–40) in *E. farinosa*; and ranged from 3–20 achenes in *E. virginensis*; from 10 to all achenes, plus receptacles, in *E. fructescens*; from 10 to all achenes in *H. acradenius*, and from 7–60 achenes in *H. annuus*.

Curculionid larvae, *Smycronix* sp., infested the small flower heads of *H. acradenius*. Upon completion of its development each weevil larva had destroyed all

Table 13. Numbers of achenes remaining intact in flower heads of *Trupanea nigricornis* and *T. bisetosa* host plants infested with one or several *Melanogromyza viridis* third instars.

Host Plant	1 Larva	2 Larvae	3 Larvae	4 Larvae	5 Larvae
	Number of Intact Achenes ± SE[b] per Head (Range) in Heads Infested with:				
G. canescens:	30.9 ± 2.4	26 ± 1.9	18.4 ± 2.5	17 ± 3.3	17.3 ± 3.9
	(17–58)	(10–45)	(4–38)	(9–25)	(12–25)
N[a]	25	23	13	4	3
H. niveus:	31.6 ± 1.7	33.3 ± 3.4	—	—	—
	(20–40)	(23–40)	—	—	—
N	24	7	—	—	—
H. annuus:	99 ± 10	—	—	—	—
	(60–140)	—	—	—	—
N	10	—	—	—	—
E. virginensis:	83.7 ± 8.2	88.6 ± 10.9	71 ± 6.7	—	—
	(58–122)	(51–121)	(48–105)	—	—
N	7	7	9	—	—
E. fructescens:	25.1 ± 1.6	—	—	—	—
	(12–43)	—	—	—	—
N	27	—	—	—	—
E. farinosa:	56.3 ± 4.1	—	—	—	—
	(34–82)	—	—	—	—
N	12	—	—	—	—

[a] N = number of analyzed flower heads.
[b] SE = standard error.

the achenes in *H. acradenius.* Thus, unlike *T. nigricornis,* the weevil exhausted all the food resources present in the flower head of its hosts.

The height above the surface of the receptacle at which *T. nigricornis* and other insects associated with *T. nigricornis* hosts were found in the flower heads varied according to the plant and insect species. In the medium-size heads of *E. farinosa,* most (81%) puparia and third instars of *T. nigricornis* were found between 0.4 and 1 mm above the receptacle. A few (7%) third instars fed upon and later formed puparia atop the receptacle. In six of 15 cases (40%), these latter larvae slightly scored the receptacle after destroying the achene in which they fed before moving to adjacent achenes. In the medium-size, elongate heads of *E. fructescens,* very few (0.8%) third instars were found feeding on the receptacle and consequently no scoring of the receptacle occurred. Most larvae in *E. fructescens* were found between 0.6–2 mm above the receptacle. In the large heads of *E. virgi-*

nensis, few (1.2%) larvae fed on the receptacle and the majority were found at various levels, between 0.8 and 3.2 mm above the receptacle. Contrary to *Encelia* spp., most (90%) of the larvae and puparia in the small heads of *H. acradenius* were found at the surface of the receptacle. Consequently, the receptacle was scored 57% of the time. In the medium-size heads of *V. deltoidea,* larvae were found between 0 and 1.2 mm above the receptacle; however, no scoring of the receptacle was observed.

The heights above the receptacle at which *Trupanea bisetosa* larvae and puparia were found also varied among the host species. In *G. canescens,* the larvae fed mainly between 1 and 2 mm above the receptacle. In the large heads of *H. annuus,* 89% of the larvae and puparia were found between 0.8 and 2 mm above the receptacle and only 2% were found at the surface of the receptacle. No scoring of the receptacle by *T. bisetosa* was observed in *H. annuus* flower heads.

Third instars and puparia of *M. viridis*

were mainly found near the achene/floret junction in the flower heads of *T. nigricornis* hosts. Third instars of *M. viridis* were found at 1–2, 0.4–2 and 0.4–2.8 mm above the receptacle in heads of *G. viscida, V. deltoidea* and *E. farinosa*, respectively. There was no scoring of the receptacle by *M. viridis* larvae in any host.

The positions of *M. viridis* larvae and puparia in the flower heads of *T. bisetosa* hosts varied according to the plant species. The larvae and puparia of *M. viridis* were found at 2–3.2 mm above the receptacle in *H. annuus* heads, which was higher than in *G. canescens* heads at 0–2 mm above the receptacle. This was because the larvae fed in the florets in the large heads of *H. annuus*, but mainly fed in the soft achenes and lower parts of the florets in the medium-size heads of *G. canescens*.

The levels at which *N. finalis* larvae and puparia were found in the flower heads of *T. nigricornis* and *T. bisetosa* also varied among its hosts. In *E. farinosa* heads, most *N. finalis* third instars fed, then pupariated, atop the receptacle. Half of the time, they scored the receptacle creating a shallow cavity (0.5–1 mm deep) that was wider (1.5–1.8 mm in diameter, N = 16) than that of *T. nigricornis*. In other hosts, *N. finalis* larvae and puparia were found at various levels above the receptacle: 0.8–2 mm in *E. fructescens*, 0.8–1.6 mm in *H. annuus*, and 0.8–3.2 mm in *E. virginensis*. No scoring of the receptacle was observed in the large heads of *E. virginenis*.

In *H. acradenius* and *E. fructescens*, noctuid larvae fed on the receptacle after destroying the achenes; whereas, in *H. annuus*, they fed inside the receptacle either without damaging the achenes or damaging the achene bases. In *E. virginensis* and *E. farinosa*, noctuid larvae were found at various levels and destroyed the achenes, but without feeding in the receptacles.

DISCUSSION

Comparison of *T. nigricornis* and *T. bisetosa* resource utilization and interspecific interactions did not illuminate any major differences that could be implicated in the "why" these two probable sister species have diverged so intricately in their host associations. Hosts of *T. nigricornis*, such as *Encelia* spp., grow right next to *H. annuus*, the primary host of *T. bisetosa*, yet the two tephritid species do not interact in any way that we have observed.

How these species used their resources included subtle differences. *Trupanea nigricornis* females apparently adjusted the number of eggs laid according to the size of the flower heads in order to avoid intraspecific competition (Headrick and Goeden 1998). Zwölfer (1973) reported that ". . . the intensity of competition within an individual flower head is dependent on the size of the head, the numbers and sizes of competing individuals, and their mode of feeding." Further, Zwölfer (1988) found a significant correlation between the body size of insects exploiting thistle flower heads and the diameter of the flower heads. Similar results were observed herein as *T. nigricornis* puparia were generally larger in larger sized flower heads, but not as large as *T. bisetosa* puparia that occurred in the large flower heads of *H. annuus*.

The flower heads of *H. annuus* did not support more species of insects than the smaller heads of the other hosts studied. Regression analysis showed that the number of species was poorly correlated with the diameter (R = 0.06) and dry weight (R = 0.07) of the flower heads of *T. nigricornis* and *T. bisetosa* host plants. This phenomenon has been observed for other tephritid systems and is summarized by Headrick and Goeden (1998).

Scoring of the receptacle is a facultative mode of resource exploitation that can provide extra nutrients to allow for continued development within a flower head. In *T. nigricornis* receptacle scoring is different from what Headrick and Goeden (1990) originally reported for *Paracantha gentilis*. Third instars of *P. gentilis* scored the receptacle at the center of the flower heads

when they occurred at high densities (three or more larvae per head). These depressions provided the larvae with enough sap and nutrients to complete their development when the central achenes were depleted (Headrick and Goeden 1990). The occasional scoring of the receptacle by *T. nigricornis* produced smaller cavities than those of *P. gentilis,* and contrary to *P. gentilis,* a *T. nigricornis* larva produced three to four small cavities instead of a large one and the cavities were not located at the center of the flower head but they were found at the base of the three to four achenes in which the larva had fed. Also, occasional scoring of the receptacle by *T. nigricornis* was observed in heads with one larva as well as in heads with two to four larvae. Hence, this process in *T. nigricornis* is not related to larval density as in *P. gentilis,* but still may provide nutrients for development not otherwise obtained.

Interspecific competition among the different insect species infesting the flower heads of *T. nigricronis* and *T. bisetosa* hosts was low because few heads sampled had multiple infestations and where they occurred many achenes were left intact. Several strategies may be utilized to minimize interspecific competition. First, the timing of infestations differed among the different insect species. Noctuid larvae infested the heads of *H. annuus* early in the fall (September); whereas, *T. bisetosa* larval populations increased later in the fall. *Paracantha cultaris* infested the young heads of *H. annuus* late in the spring and in the summer when *T. bisetosa* populations were low. *Neotephitis finalis* infested the flower heads of *E. farinosa* later in the season than *T. nigricornis.* Both *T. nigricornis* and *M. viridis* attacked the flower heads of *E. farinosa* early in the season.

The second strategy may be temporal partitioning. Oviposition in different stages of flower heads may lead to exploitation of different stages of the flower heads by larvae of different species. In *H. annuus,* the eggs and first instars of *P. gentilis* devel-

oped in mature heads, whereas eggs and first instars of *T. bisetosa* developed in the closed immature heads. However, eggs of *T. bisetosa* and *N. finalis* were often found in the same stage heads. Females of both species may deposit a short term oviposition-deterring pheromone; however, there is no evidence yet of the presence of such pheromones. The larvae of unidentified noctuids infested mature heads of all *T. nigricornis* hosts. The heads infested by noctuids often contained puparia from which *T. nigricornis* adults had emerged.

The third strategy may involve spatial partitioning of the flower heads. In *Encelia* sp., most larvae of *M. viridis* fed in the florets, while *T. nigricornis* and *N. finalis* larvae fed in the achenes, closer to the receptacle. When larvae of *T. nigricornis* and *N. finalis* occurred in the same heads, they fed either at different depths in the achenes, with most *N. finalis* larvae at the base of receptacle, or at similar levels but separated by one or several achenes. In the large heads of *H. annuus,* the larvae of *T. bisetosa* and those of *N. finalis* occurred at different depths and also were separated by several achenes.

All three strategies used to minimize competition in this study fall under the "evasion strategy" described by Zwölfer (1979). He reported that insects sharing food resources have to follow one of two strategies for survival: evasion strategy or by maximizing their competitive capacity. Evasion strategies work to reduce competitive contacts between congeneric species. They involve processes like adopting a different time for oviposition, changing the time of larval development, or changing the feeding site. Such processes can create ecological character displacements. The disadvantage of these evasion strategies is that they promote specialization and narrow the food base of a species (Zwölfer 1979). If *T. nigricornis* and *T. bisetosa* are sister species, such evasion strategies could have been one of the factors accounting for the shift, i.e., adoption of a new host and spe-

cialization of *T. bisetosa* on *H. annnuus* in order to avoid competition. Evasion strategies have been observed in the tephritid *P. gentilis* feeding on thistles and other tephritid systems (Headrick and Goeden 1998).

Interspecific competition is an important factor structuring insect communities (Strong et al. 1984). It was low among insect species exploiting the flower heads of *T. nigricornis* and *T. bisetosa* host plants because of the many evasion strategies adopted by these insects that reduced interspecific contacts and because so very few heads had multiple infestations and many achenes were left intact in these heads. Interspecific competition among phytophagous insects for food and space is generally uncommon and feeble (Strong et al. 1984). It is not the most important factor that shapes phytophagous insect communities. Most insect populations exist at low densities as a result of predation and parasitism. Consequently, natural enemies reduce interspecific competion because of their impact on insect populations (Strong et al. 1984).

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