Life History and Description of Immature Stages of *Euaesta stigmatica* (Diptera: Tephritidae) on *Ambrosia* spp. (Asteraceae) in Southern California

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ABSTRACT *Euaesta stigmatica* Coquillett is bivoltine and nearly monophagous on four native ragweeds, *Ambrosia* spp. (Asteraceae), in the southwestern United States. In southern California, larvae of the spring (F_1) generation develop singly in and feed on one or both ovules of young fruiting involucre of *Ambrosia ilicifolia* (Gray) Payne, with a small proportion infesting the staminate involucre. Adults emerge after ≈ 1 mo, with their reproductive organs immature. The F_2 generation develops in the involucre of fall-blooming *Ambrosia acanthicarpa* Hooker. The egg is described and illustrated for the first time for any species of *Euaesta*. First, second, and third instars and the puparium are described and illustrated for the first time for *E. stigmatica*. The posterior spiracular plates of all three instars bear only three interspiracular processes, whereas the larvae and puparia of all other nonfrugivorous tephritids described to date bear four such processes. Adult behaviors described from field and laboratory studies include courtship, copulation, and territoriality. Male courtship displays include three behaviors previously undescribed for Tephritidae: a side-to-side dance, rapid side stepping, and a middle leg abduction. Hymenopterous parasitoids of *E. stigmatica* include two solitary, primary larval-pupal, endoparasitoids, *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae). Potential use of *E. stigmatica* as a biological control agent for ragweeds in Eurasia is discussed.

KEY WORDS *Euaesta*, biology, behavior

THE CURRENT STUDY OF *Euaesta stigmatica* Coquillett was an outgrowth of faunistic studies of the insect associates of ragweeds (*Ambrosia* spp.) and other Ambrosiinae (Asteraceae) in southern California conducted by Goeden & Ricker (1974a, b; 1975; 1976a–c; 1986), Hilgendorf & Goeden (1983), and Goeden & Teerink (1993). The genus *Euaesta* is native and widespread in North and South America (Norrbom 1993). Six of the eight Nearctic species occur in California (Foote et al. 1993), where *E. stigmatica* is common and widespread.

Little is known of the biologies of most *Euaesta* spp. Marlatt (1891) briefly described the biology of *Euaesta aequalis* (Loew) and Phillips (1946) described its larvae and their feeding behavior. Both *E. aequalis* and *Euaesta bullans* (Wiedemann) have been introduced into Australia for biological control of *Xanthium* spp. (Julien 1992). Foote (1984) summarized the host-plant associations for North American species of *Euaesta* that specialize on *Ambrosia* and *Xanthium* spp. Batra (1979) studied the biology and behavior of *E. bella* (Loew) and *Euaesta festiva* (Loew) in assessing them as potential agents for the biological control of ragweeds accidentally introduced to Eurasia from North America (Goeden & Teerink 1993). We provide

new knowledge of the biology, immature stages, and reproductive behavior of *E. stigmatica* derived from field and laboratory studies on fall- and spring-blooming, native ragweeds in southern California.

Materials and Methods

Preliminary field studies and collections of *E. stigmatica* were made in 1969–1973 on *Ambrosia ilicifolia* (Gray) Payne and *Ambrosia acanthicarpa* Hooker at many locations throughout southern California (Goeden & Ricker 1974a, 1976b). More intensive field studies were conducted in 1991 and 1992 at the Edmund C. Jaeger Nature Preserve, Desert Center, Riverside County, on *A. ilicifolia*, its spring-blooming host, and on or near the campus of the University of California, Riverside, on *A. acanthicarpa*, its fall-blooming host. Bulk samples of infested ragweed inflorescences were collected at these sites and brought to the laboratory in ice chests in an air-conditioned van and stored under refrigeration for subsequent dissection, measurement, photography, and description of all life stages.

Immature stages were described using scanning electron microscopy of two ova dissected from gravid, field-collected females, as well as four, sev-

Fig. 1. *A. ilicifolia* study plant at the E. Jaeger Preserve.

en, and nine each first, second, and third instars and four puparia dissected from fruiting involucre. All specimens for microscopy were fixed in 70% EtOH, dehydrated to absolute EtOH, sonicated for ≈ 1 min in Hexanes (Fisher, Fair Lawn, NJ) to remove accumulated debris, rehydrated to distilled water, post fixed in 2% aqueous osmium tetroxide for 24 h, then dehydrated to absolute EtOH, critical-point dried, mounted on stubs, sputter coated with a gold-palladium alloy and examined on a JEOL JSM C35 scanning electron microscope in the Department of Nematology, University of California, Riverside. Micrographs were prepared on Polaroid P/N 55 film at 15 kV accelerating voltage.

Adults were reared from puparia dissected from fruiting involucre held in individual, glass-shell vials in humidity chambers at 22–24°C and 76% RH. Newly emerged adults were isolated in clear plastic cages (850 ml) fitted with screened lids for ventilation, basal water reservoirs, and provisioned with honey and protein hydrolyzate (Headrick & Goeden 1993). Five mating trials lasting 2 wk each were conducted with virgin adults held in disposable, plastic petri dish arenas (10-cm diameter) (Headrick & Goeden 1993). Mating trials were conducted in the laboratory under artificial lighting between 0900 and 1800 hours PST.

Field observations of reproductive behaviors were made for at least 4 h each day on 25 February and 4, 11, 18, and 24 March 1992, at the Jaeger Reserve, where *A. ilicifolia* plants were located in a deep, N/S-oriented, dry, sandy wash at an elevation of 850 m. A single plant (≈ 1 by 2 m wide and 1 m tall) located between large granite boulders was the primary study location (Fig. 1). This plant's stems (0.3–0.6 m long) had shorter branches, spiny holly-like leaves, and apical spikes of staminate involucre above the separate, pistillate, fruiting involucre. This study area and this same plant had been noted by R.D.G. 20 yr earlier during a study of the insect fauna of this native ragweed to host "an abundance of *E. stigmatica*

adults" (Goeden & Ricker 1976a; R.D.G., unpublished data).

Euaresta names used in this article follow Foote et al. (1993) and Norrbom (1993); nomenclature on larval taxonomy follows Headrick & Goeden (1991); nomenclature for wing displays by adults follows Headrick & Goeden (1991), Green et al. (1993), and Goeden et al. (1994b); ragweed inflorescence morphology follows Payne (1963); and plant names follow Munz (1968, 1974). Voucher specimens of reared adults of *E. stigmatica* and its parasitoids reside in the research collections of R.D.G.; preserved specimens of *E. stigmatica* larvae and puparia are stored in separate collections maintained by J.A.T. and D.H.H. Means $\pm$ SEM are provided throughout this article.

Results and Discussion

Taxonomy. *Euaresta* has 14 recognized species (Norrbom 1993), 6 of which occur in California (Foote et al. 1993). The species occurring in America north of Mexico have recently been treated by Foote et al. (1993), and those occurring in Central and South America by Norrbom (1993); both treatments included keys to adult stages. Descriptions of the immature stages of *E. stigmatica* are provided below for the first time.

Egg. Twenty-five ova, dissected from field-collected females, were white, superficially smooth, elongate-ellipsoidal, 0.17 ± 0.004 mm wide (range, 0.14–0.20) and 0.67 ± 0.01 long (range, 0.54–0.76), with a rounded, anterior pedicel 0.02 mm long (Fig. 2 A and B), and a sharply tapered posterior end measuring 0.09 ± 0.003 mm long (range, 0.06–0.12). Examination with light microscopy showed the posterior end to be free of embryonic tissues. Sixteen eggs dissected from plant tissue averaged 0.17 ± 0.007 mm in width (range, 0.14–0.30) and 0.64 ± 0.008 mm in length (range, 0.58–0.71).

This is the first description of the egg of any species of *Euaresta*. The general size and shape of *E. stigmatica* eggs are similar to those of *Paroxyna genalis* (Thomson) (Goeden et al. 1994b). However, the eggs of *E. stigmatica* are more parallel sided than described for other nonfrugivorous tephritid species (cf. Goeden & Headrick 1991a, b; Headrick & Goeden 1993; Goeden et al. 1994b). The elongate posterior end of *E. stigmatica* eggs also differs from other nonfrugivorous tephritid eggs described thus far, and its function remains unknown.

Third Instar. Third instar superficially smooth, barrel-shaped, slightly tapered anteriorly, rounded posteriorly (Fig. 3A); integument white with the caudal segment black; thoracic segments with minute acanthae dorsally, abdominal intersegmental area circumscribed by minute acanthae; gnathocephalon conical, laterally flattened, smooth with few rugose pads dorsally, broad serrated rugose pads laterally along mouth lumen (Fig. 3B, 1 and

Fig. 2. Egg of *E. stigmatica*: (A) habitus, anterior end at left; (B) detail of pedicel, showing aeropyles.

D, 1); paired dorsal sensory organs lie mediad of anterior sensory lobes, each consisting of single dome-shaped papilla (Fig. 3B, 2 and C, 1); anterior sensory lobes bearing terminal sensory organ (Fig. 3C, 2), pit sensory organ (Fig. 3C, 3), lateral sensory organ (Fig. 3C, 4) supralateral sensory organ (Fig. 3C, 5); stomal sense organs lie ventrad of anterior sensory lobes, near mouth lumen (Fig. 3B, 3 and C, 6); mouth hooks bidentate, teeth stout, bluntly conical (Fig. 3B, 4 and D, 2); median oral lobe laterally compressed, tapers apically to a fine point; attached ventrally to labial lobe (Fig. 3D, 3); labial lobe with paired sensilla (Fig. 3B, 5); lateral and ventrolateral lobes each bearing a verrucate sensillum with a central pore (Fig. 3B, 6 and 7); anterior thoracic spiracles located dorsolaterally on posterior margin of prothorax, each bearing five, rounded papillae (Fig. 3E); lateral spiracular complex on meso- and metathorax composed of small open spiracle (Fig. 3F, 1) and two, verruciform sensilla (Fig. 3F, 2); lateral spiracular complex on abdominal segments composed of an open spiracle and single verruciform sensillum; caudal segment smooth with no acanthae, bearing nonprominent, noncontiguous posterior spiracular plates (Fig. 3G, 1); each plate with three elongate-oval rimae

≈ 0.025 mm long (Fig. 3H, 1), and three interspiracular processes with two to four branches each, the longest measuring 0.015 mm (Fig. 3H, 2); stelix sensilla (Fig. 3G, 2) surrounding margin of caudal segment in four-dorsal, six-ventral arrangement; caudal segment additionally bearing a pair of verruciform sensilla ventrad of the spiracular plates (Fig. 3G, 3).

Euaresta stigmatica belongs to the tribe Tephritini, which also includes *Dioxya*, *Neotephritis*, *Paroxya*, *Tephritis*, *Trupanea*, and many other genera (Foote et al. 1993). The general larval body shape is closer to that of *Trupanea* and *Paroxya* than to *Dioxya*, *Neotephritis*, and *Tephritis* species previously examined (Novak & Foote 1968; Goeden & Headrick 1991b; Headrick & Goeden 1991; Goeden et al. 1993, 1994b; unpublished data). *Trupanea* species can be distinguished from *E. stigmatica* by the rows of rugose pads circumscribing the prothorax (Headrick & Goeden 1991; unpublished data). In *E. stigmatica*, the mouth-hooks of the larvae appear to have been worn down considerably, perhaps caused by the toughness of the seed tissues. The number of sensilla in the lateral spiracular complex differ between the metathoracic and abdominal segments in *E. stigmatica*. One other species, *Acuirina thoracica* Curran has shown similar differences; however, the number of sensilla differed between the mesothoracic and the metathoracic and abdominal segments (Headrick & Goeden 1993).

Phillips (1946) described the mature larva of *E. aequalis*. According to her description, *E. aequalis* is very similar morphologically to *E. stigmatica* with a few minor differences: the anterior thoracic spiracles in *E. aequalis* bear 9–10 papillae (versus 5 in *stigmatica*), and the caudal segment of *E. aequalis* has four interspiracular processes with two to three branches each, whereas, as noted above, *E. stigmatica* has only three processes each with two to four branches, the only tephritid species known to have only three interspiracular processes. In *E. stigmatica* and *E. aequalis*, the sensilla ventrad of the posterior spiracular plates are composed of a single verruciform papilla with a central pore. Other tephritid species have paired compound sensory organs composed of a stelix and medusoid sensillum (cf. Goeden & Headrick 1991b; Goeden et al. 1993; 1994a, b; unpublished data).

Second Instar. Second instar elongate, cylindrical, tapered anteriorly, rounded posteriorly (Fig. 4A); integument creamy white; gnathocephalon conical, smooth with few rugose pads (Fig. 4B), two small, serrated pads laterad of stomal sense organs (Fig. 4B, 1); dorsal sensory organs lie dorsomedially of anterior sensory lobes, each consisting of a single, dome-shaped papilla (Fig. 4C, 1); anterior sensory lobes flattened, bearing terminal sensory organ (Fig. 4C, 2), pit sensory organ (Fig. 4C, 3), lateral sensory organ (Fig. 4C, 4), supralateral sensory organ (Fig. 4C, 5); stomal sense organs

Fig. 3. Third instar of *E. stigmatica*: (A) habitus, anterior to left; (B) gnathocephalon, left ventrolateral view, (1) serrated rugose pads, (2) dorsal sensory organ, (3) stomal sense organ, (4) mouth hooks, (5) labial lobe sensilla, (6) lateral sensillum, (7) ventrolateral sensillum; (C) gnathocephalon, left lateral view, (1) dorsal sensory organ, (2) terminal sensory organ, (3) pit sensory organ, (4) lateral sensory organ, (5) supralateral sensory organ, (6) stomal sense organ; (D) gnathocephalon, anterior view, (1) serrated rugose pads, (2) mouth hooks, (3) median oral lobe; (E) anterior thoracic spiracles; (F) lateral spiracular complex, metathorax, (1) spiracle, (2) verruciform sensillum; (G) caudal segment, (1) posterior spiracular plate, (2) stelex sensillum, (3) verruciform sensillum; (H) caudal segment, posterior spiracular plate, (1) rimae, (2) interspiracular process.

Fig. 4. Second instar of *E. stigmatica*: (A) habitus, anterior to left; (B) gnathocephalon, left ventrolateral view, (1) serrated rugose pads, (2) mouth hooks, (3) median oral lobe, (4) lateral sensillum, (5) ventrolateral sensillum; (C) gnathocephalon, left lateral view, (1) dorsal sensory organ, (2) terminal sensory organ, (3) pit sensory organ, (4) lateral sensory organ, (5) supralateral sensory organ, (6) stomal sense organ; (D) gnathocephalon, ventral view, (1) mouth hooks, (2) median oral lobe, (3) labial lobe sensilla; (E) anterior thoracic spiracle; (F) caudal segment, posterior spiracular plate, (1) rimae, (2) interspiracular process.

lie ventrolaterad of anterior sensory lobes (Fig. 4C, 6); mouth hooks bidentate, teeth conical, sharply pointed (Fig. 4B, 2 and D, 1); median oral lobe laterally compressed, smooth, rounded anteriorly, attached to labial lobe (Fig. 4B, 3 and D, 2); labial

lobe bearing paired sensilla (Fig. 4D, 3); lateral and ventrolateral sensilla present, each bearing verruciform sensillum (Fig. 4B, 4 and 5); anterior thoracic spiracles dorsolaterad on posterior margin of prothorax, each bearing five oval papillae (Fig.

Fig. 5. First instar of *E. stigmatica*: (A) habitus, ventral view, anterior to left; (B) gnathocephalon, left lateral view, (1) dorsal sensory organ, (2) terminal sensory organ, (3) pit sensory organ, (4) lateral sensory organ, (5) supralateral sensory organ, (6) stomal sense organ; (C) gnathocephalon, ventrolateral view, (1) mouth hooks, (2) median oral lobe, (3) labial lobe sensilla, (4) lateral sensillum, (5) ventrolateral sensillum; (D) caudal segment, posterior spiracular plates, (1) rimae, (2) interspiracular process.

4E); caudal segment bearing posterior spiracular plates (Fig. 4F); each plate with three oval rimae ≈ 0.015 mm long (Fig. 4F, 1), and three, interspiracular processes each with one to three branches, longest measuring 0.01 mm (Fig. 4F, 2).

The second instar differs from the third instar in its general body shape, being more cylindrical than barrel shaped. The gnathocephalon of the second instar has only two serrated rugose pads laterad of the stomal sense organ. The median oral lobe is not as distinctly tapered as in the third instar. Because of the wrinkled nature of the second instar prepared for scanning electron microscopy, the lateral spiracular complex was not observed, nor were the caudal sensilla.

First Instar. First instar cylindrical, rounded anteriorly and posteriorly, thoracic segments smooth, lacking the minute acanthae which circumscribe the abdominal segments (Fig. 5A); gnathocephalon conical, smooth with no rugose pads (Fig. 5C); dorsal sensory organs flattened, indistinct round papillae located dorsomedial of anterior sensory

lobes (Fig. 5B, 1); anterior sensory lobes flattened, not well defined, bearing the terminal sensory organ (Fig. 5B, 2); pit sensory organ (Fig. 5B, 3); lateral sensory organ (Fig. 5B, 4), supralateral sensory organ (Fig. 5B, 5); stomal sense organs small, not well defined, lie ventrad of anterior sensory lobes (Fig. 5B, 6); mouth hooks bidentate, conical, sharply pointed (Fig. 5C, 1); median oral lobe laterally compressed, tapered anteriorly, attached to labial lobe (Fig. 5C, 2); labial lobe bears two sensilla (Fig. 5C, 3); lateral and ventrolateral sensilla present (Fig. 5C, 4 and 5); anterior thoracic spiracles absent; caudal segment bears the posterior spiracular plates (Fig. 5D); each plate bears two oval rimae, ≈ 0.004 mm in length (Fig. 5D, 1), and three, stout, spine-like interspiracular processes, the longest measuring 0.003 mm (Fig. 5D, 2); stilet sensilla located around margin of caudal segment.

First instars are more cylindrical than second instars. There are no rugose pads on the gnathocephalon of first instars, the anterior sensory lobes are

not well defined, and the sensory organs are indistinct. The stomal sense organ is poorly defined compared with second instars. The respiratory system undergoes substantial morphogenesis between the first and second instars. First-instar *E. stigmatica* lack anterior thoracic spiracles; the lateral spiracles were not observed and the posterior spiracular plates bear two, small rimae.

Puparium. Puparia were either entirely dark or darkened only on both ends, elongate-ellipsoidal, truncated anteriorly, rounded posteriorly, superficially smooth, thoracic segments with minute acanthae dorsally, abdominal intersegmental areas circumscribed by minute acanthae (Fig. 6A); 16 intact puparia measured 2.84 ± 0.07 mm long (range, 2.03–3.12) and 1.39 ± 0.035 mm wide (range, 1.07–1.58); anterior end bearing invagination scar (Fig. 6B, 1) and raised anterior thoracic spiracles dorsolaterad of invagination scar (Fig. 6B, 2); caudal segment bears the posterior spiracular plates (Fig. 6C); each plate bears three oval rimae, ≈ 0.02 mm long (Fig. 6C, 1), and three interspiracular processes, two to five branches each, longest measuring 0.015 mm (Fig. 6C, 2); verruciform sensilla ventrad of spiracular plates are distinct (Fig. 6C, 3).

Distribution and Host Range. *E. stigmatica* is strictly Nearctic (Norrbon 1993). Its distribution north of Mexico was mapped by Foote et al. (1993). It appears to be common in the Southwest, but there are also records from Kansas and Montana. This tephritid is nearly monophagous, as known to date, reproducing solely in the involucre of four native ragweeds: *A. acanthicarpa* and *A. ilicifolia* in southern California (Goeden & Ricker 1974a, 1976b) and *A. ambrosiodes* (Cavanilles) Payne, *A. deltoidea* (Torrey) Payne, and *A. ilicifolia* in southwestern Arizona (Foote 1984).

Biology. **Egg.** The female pierces the outer seed coat with her aculeus and inserts a single egg for approximately two-thirds of its length, pedicel last into an ovule within a fruiting involucre. In laboratory cages and field-collected samples, egg placement was either near the base or apex of a fruiting involucre (Fig. 7A). Egg pedicels typically protruded from the seed coats; however, some eggs were inserted entirely beneath the seed coat and lay hidden lengthwise, alongside an ovule. Two seeds develop within each fruiting involucre in individual chambers separated by a thin septum. In *A. ilicifolia*, the larva attacked both seeds in 41 of 126 (33%) infested involucre. In contrast, in *A. acanthicarpa* the larva attacked only one seed in each of 57 infested involucre examined. Multiple ovipositions into individual involucre were rare; 2 larvae occurred in only 5 of 126 (4%) infested involucre of *A. ilicifolia* and none of *A. acanthicarpa*.

The staminate, pollen-bearing involucre of *A. acanthicarpa* and *A. ilicifolia* also are occasionally infested by *E. stigmatica*. Eggs were laid singly into the staminate florets of 3 of 137 (2%) staminate involucre of *A. ilicifolia* examined. Twelve males

Fig. 6. Puparium of *E. stigmatica*: (A) habitus, anterior to left; (B) anterior end, (1) invagination scar, (2) anterior thoracic spiracle; (C) caudal segment, posterior spiracular plate, (1) rimae, (2) interspiracular process, (3) verruciform sensillum.

and four females were reared from bulk samples of isolated staminate involucre of *A. acanthicarpa*.

Larva. First instars eclose after ≈ 3 –5 d, exit from the posterior end of the egg after first rotating 180° while still an embryo, then tunnel into and initially feed at the base of the ovule. Two involucre were dissected in which the attacked ovules

Fig. 7. Life stages of *E. stigmatica* from *A. ilicifolia* (A–C, E–G) and *A. acanthicarpa* (D): (A) Egg inserted into ovule of fruiting involucre, (B) second instar feeding in ovule, (C) third instar in feeding chamber in fruiting involucre, (D) third instar in feeding chamber, (E) view of excavated exit window from inside fruiting involucre, (F) third instar larva feeding centrally among florets of staminate involucre, (G) puparium in excavated chamber, (H) adult female, (I) pair in copula on fruiting involucre of *A. ilicifolia* taken in nature.

Table 1. Distribution, abundance, and sex ratios of *E. stigmatica* on *A. ilicifolia*, Ed. Jaeger Preserve, spring 1992

March date	No. stems	No. adults per stem	Range	No. males	No. females	Total	Sex ratio	No. males		Mated pairs
								Courting	Resting	
4	40	2.1	1-4	64	29	93	2.2:1	—	—	—
11	14	1.9	1-4	35	12	47	2.9:1	4	31	5
18	30	1.5	1-3	63	33	96	1.9:1	5	58	9
24	30	1.5	1-4	54	29	83	1.8:1	5	49	2

had aborted and the larvae within had died. In one-third of the 157 fruiting involucre of *A. ilicifolia* examined in which one ovule was infested by a first instar, the other ovule within the involucre had died and shriveled and was rendered unsuitable for continued larval feeding and development. First instars molted after ≈ 1 wk and continued to feed as second instars on the remaining ovule in involucre of *A. ilicifolia* (Fig. 7B). By the second molt, after ≈ 2 wk, much of the second ovule also was consumed. The uninfested seeds normally are white inside, but infested seeds become darkly stained, dried, and lined with frass compacted at both ends of the open ellipsoidal feeding chamber (Fig. 7C). Third instars continue to excavate the fruiting involucre, leaving intact only the dried, hard, and darkened fruit coats in both *A. ilicifolia* (Fig. 7C) and *A. acanthicarpa* (Fig. 7D). Most growth takes place during this third stadium, which lasts for ≈ 1 wk. The mature third instar is approximately half the length and about as wide as its feeding chamber. Before pupariation, the third instar scrapes away a small exit hole in the wall at the base of the involucre, leaving a translucent, circular, epidermal window (Fig. 7E). Windows averaged 0.58 ± 0.015 mm in diameter ($n = 25$; range, 0.43–0.73) and were located 0.86 ± 0.047 mm from the stalk of the involucre ($n = 25$; range, 0.51–1.47).

In staminate involucre, all larval stages feed within the pollen-bearing, staminate florets. No exit window is made and third instars orient with their heads directed outward in the hollowed-out feeding cavity before pupariation (Fig. 7F).

Puparium. Pupariation by *E. stigmatica* in a fruiting involucre is unusual in that the third instar does not face outward, but remains oriented with its head facing the base of the involucre, allowing the emerging adult direct access to the exit hole (Fig. 7G). In contrast, most, but not all (R.D.G. & J.A.T., unpublished data), tephritids that we have studied position their exit windows toward the apex of a gall, or infested branch or stem (cf. Goeden 1988, Headrick & Goeden 1990, Goeden & Headrick 1991b, Goeden et al. 1993).

Adult. The spring, F_1 generation of adults reared from *A. ilicifolia* lived an average of 76 ± 3.5 d ($n = 145$; range, 4–155) (Fig. 7H). The fall, F_2 generation of adults from *A. acanthicarpa* were longer lived, averaging 168 ± 17.7 d ($n = 46$; range, 24–312). Females always emerged reproductively im-

mature, and required 4–6 wk of feeding on protein hydrolyzate and honey to develop eggs in individual laboratory cagings. Females collected from rendezvous sites in early spring (see discussion below) were also reproductively immature, but collections of females from the same plant 1 wk later showed them to contain full-sized ova ($n = 3$).

Abundance. Field observations were made during 5 wk at the Jaeger Reserve study site beginning on 25 February 1992, when ≈ 20 adults were recorded on the main study plant, the "rendezvous site" (Zwölfer 1974), but only 3 or fewer were found on other, nearby plants of comparable size. Table 1 records the numbers of adults present on this plant during the next 4 wk beginning 4 March 1992. Males consistently outnumbered females, but the total number of adults fluctuated considerably from week to week. The number of adults per stem were distributed relatively uniformly over the entire rendezvous plant during the observation period. Generally, from one to four individuals were observed on each stem, for averages of 1.5–2.1 adults per stem during the study period (Table 1). Adults of the next generation began emerging 2–3 wk later. The daily pattern of abundance of F_2 flies of both sexes also was monitored for the next 4 wk. Both sexes were abundant and active by 0930 hours, the greatest number of mated pairs was observed at ≈ 1200 hours (maximum, 9) on each of the observation days, and the number of single males declined thereafter. The number of single females ovipositing remained high until ≈ 1500 hours daily, after which adults were rarely observed.

Wing Displays. Under field conditions, *E. stigmatica* exhibited enantion, lofting, and rarely hama-tion and asynchronous supination as defined by Headrick & Goeden (1991), Green et al. (1993), and Goeden et al. (1994b). The most common display by both sexes in field and laboratory observations was a unique form of enantion in which the wings were held flat over the dorsum and extended forward synchronously from the midline of the body through $\approx 90^\circ$ without supination. The extensions occurred in rapid bursts lasting ≈ 1 s, with short pauses of 1–2 s between each episode. Males exhibited this type of enantion most often and as a continuous part of their territorial display. Males also exhibited this enantion while in copula, especially when the females moved or otherwise were disturbed.

Fig. 8. (A) Male courtship display (drawn from field photo), male on right, arrows denote distended abdominal pleura, extended mouth parts, lofted wings, double-headed arrow denotes direction of lofting/dance display. (B) Male positioned behind female for aculeus exertion (drawn from field photo), arrow denotes male abdomen curled underneath the body.

Males displayed an exaggerated form of lofting during courtship displays with females. The wings were lofted to 90° , perpendicular to the long axis of the body and parallel to each other (Fig. 8A). They were not vibrated while lofted but rather held in this position, while the male rocked his entire body vigorously from side to side (see *Courtship* section below). Wing lofting was similar to that of *Paroxyna genalis* (Goeden et al. 1994b), but in *E. stigmatica* the wings were held lofted at 90° with respect to the substrate and parallel to each other. Only males displayed lofting in *E. stigmatica*. Males also displayed lofting in territorial bouts with other males, in which the wings were extended to only 45° above the body, parallel to the midline of the body, with the wing blades parted $\approx 45^\circ$.

Courtship. In the field, males usually were observed on sunlit leaves while walking about the adaxial surfaces, observing, and orienting to face nearby flies. Little site fidelity was shown by males, as they only remained on a particular leaf for up to 15 min, and often vacated a leaf after combat with other males whether they won or lost. However, all courtship and territorial displays by males took place on the adaxial surfaces of leaves.

In contrast, females continually moved about a plant while probing for ovipositional sites with the apices of their ovipositors in immature fruiting involucre, and much less frequently, in the staminate involucre. As they explored the plant in this manner, they encountered patrolling males perched on leaves. Males initially raised and lowered their fore legs once to any individual walking onto their leaf surface ($n = 24$). Other males answered in kind and combat usually ensued; however, females did not respond with any observable body movement and the males immediately initiated courtship ($n = 14$).

Males faced females, extended their mouthparts fully, distended their abdominal pleura, and crouched (Fig. 8A). If the females remained, males lofted their wings fully upright and began rocking their bodies from side to side rapidly for brief episodes lasting $\approx 2\text{--}3$ s (Fig. 8A). Males did not keep their mouthparts extended during their courtship displays, but while a male rocked or danced, he extended his mouthparts and tried to place them against the female's mouthparts (Fig. 8A). The female responded by extending her mouthparts toward the male and briefly touching them or by extending them and moving toward the male as he backed away. No fluids were observed to be exchanged, as reported for several other species of tephritids whose premating trophallaxis required several minutes (Stolzfus & Foote 1965, Headrick & Goeden 1990, Goeden & Headrick 1992). When a male displayed wing lofting/dancing during courtship, he stilted on his legs with his abdomen held higher than the rest of his body. During this dance, the male's tarsi did not move, only his body. This side-to-side dance was repeated often, and a male generally held his wings lofted until he moved behind a female.

Unreceptive females never permitted males to move into position behind them. The courting male moved sideways, side-stepping rapidly while facing the female, so as to position himself behind her. However, the unreceptive female held her wings flat and overlapped on her dorsum and turned in one spot, always facing the side-stepping male. Males often switched directions and side-stepped rapidly back and forth through $\approx 180^\circ$. If a female remained unreceptive, the male stopped side stepping, raised his front legs above his head, lowered his anterior end, extended his mouthparts, and either resumed side stepping in arcs around the female or began a lofting/dance display.

However, if the female was receptive, she allowed the male to get into position behind her. Once positioned behind the female, the male returned his wings to their resting position flat on his dorsum and deflated his abdominal pleura. He stood behind her, sometimes placed his fore tarsi on the tips of her wings, curled his abdomen forward beneath him, placed his epandrium at the apex of her ovipositor, and waited (Fig. 8B). If the female was unreceptive at this point, she did not

exert her aculeus, and the male returned to face her again from the front. Once in front of her again, he raised both of his middle legs once, synchronously, high above his thorax, then dropped them to the substrate. After this middle leg abduction, he again began his lofting/dance display. After a few more episodes of the lofting/dance display, he again maneuvered behind the female, lowered his wings, deflated his pleura, and curled his abdomen beneath him so his epandrium again touched the apex of her oviscapae.

Courtship displays with individual females continued for as long as a half hour or until an unreceptive female walked away. There were many distractions for courting males, such as other males moving in and initiating combat. Because of the high densities of flies on the study plant (Table 1), some males were observed to court two females simultaneously, all the while intermittently fighting with intruding males. The courting males were able to switch from their courtship displays to fighting displays (described below) and back again without pause.

Copulatory Induction Behavior. Males remained passive behind females, with their epandrium poised for the exertion of the aculeus, while they sometimes touched the wing tips of the females with their fore tarsi. Thus, unlike other tephritid males studied to date, *E. stigmatica* males do not mount females before exertion of the aculeus, and thus, do not rub their hind or middle legs on the oviscapae of the female to stimulate exertion of the aculeus.

Copulation. The male engaged the exerted aculeus with his surstyli as he mounted the female and wrapped his front legs around the middle of her abdomen. As he moved forward, her ovipositor was raised slightly. In this initial position, the male was stilted on his extended legs above the female, with his head over the middle of her abdomen, and his abdomen curled downward (Fig. 71). The aculeus remained exerted, and pushed the male's abdomen backward. At this point the male began rubbing the oviscapae with his hind legs, and intermittently displayed enantion, typical of copulatory induction behavior displays of other nonfrugivorous tephritid males such as *Aciurina thoracica* Curran (Headrick & Goeden 1993) and *Trupanea californica* Malloch (Headrick & Goeden 1991). The female sat quietly with her wings spread and mouthparts pumping during copulation. As insertion of the aedeagus proceeded, the aculeus was slowly retracted and the male moved slightly forward on the female. In his final position, the male's abdomen was bent downward only slightly, both his hind and middle legs were on the substrate, and his front legs grasped the abdomen of the female near her thorax. The final mating posture was achieved 2–3 min after initial exertion of the aculeus. The female walked around while the male continued to use his middle and hind legs to groom or drum on the female's abdomen. The

mated pair remained quiet, usually staying on or near the same leaf, and occasionally moved from sunlight into shade.

Encounters between males and mating pairs were frequent because of the high numbers of individuals on the plant (Table 1). Single males approached mating pairs and displayed toward the females. Some males attempted to mount mating pairs. These intruding males were met with aggressive lunges by the copulating females and wing displays by the copulating males. These interactions always ended with the intruding males departing ($n = 5$).

Timed copulations lasted an average of 1 h in the field ($n = 9$ observed from initiation to disengagement). Disengagement was quick. A male turned to one side, stepped down from the female's dorsum onto the substrate, and moved away from her while pulling his aedeagus from her aculeus. Once parted, they sat still apart from each other and groomed for a short time. Then, either one, and ultimately both flies moved off the leaf and onto other parts of the branch or nearby branches. In one instance, a female in copula walked away from the male while he remained stationary. She continued forward, pulling his abdomen forward underneath him. He stepped backward away from the female, and his aedeagus pulled free. This male then moved toward the female and began courtship displays, but soon stopped his displays and moved away from the female.

Oviposition. Females did not oviposit directly after disengagement from copulation, but rather usually sat grooming. Oviposition was observed most commonly in the afternoon, i.e., after ≈ 1300 hours. Females walked upon and examined fruiting involucre of certain sizes, i.e., >7 mm in diameter, or those with two stigmas exposed. They probed while facing away from the center of the involucre, where the tips of their oviscapae were directed. Oviposition followed probing and lasted ≈ 3 –5 min. Females remained on the fruit after oviposition and groomed and rested.

Feeding. Feeding by adults was readily observed in laboratory arenas and in field observations. Adults readily fed at water and protein sources provided in arenas and produced droplets as observed and described for other tephritid species (cf. Goeden & Headrick 1992; Headrick & Goeden 1991, 1993; Green et al. 1993). Adults in the field touched their mouthparts to leaves and branches, to fruiting and staminate involucre, and to the carcasses of dead arthropods.

Territoriality. A single leaf was patrolled by a male, and he displayed his front legs to any individual that moved onto this leaf. Intruding males answered in kind and ritual combat began ($n = 10$). During this combat, males faced each other with their abdominal pleura distended, wings partially lofted, and mouthparts extended. Battles began with the males drumming their raised front

legs together. The males then dropped to the substrate, lowered their wings, and pressed their extended mouthparts together. They began to move from side to side asynchronously to each other, rubbing their extended mouthparts together at each pass. Some males moved off the leaf after this initial encounter, but other battles became more involved. If both males remained, they continued the battle by raising their front legs again and engaged in mouthpart rubbing. After this behavior, each male tried to turn sideways toward the other male and bat him with an extended, supinated wing. Each male also tried to grasp the other's wings with his front legs in a *leg-lock*, i.e., trapping the wing blade between the fore tibia and femur. They continued to wrestle and batter each other until one turned and moved away. The losers were usually chased by the victors until the former were on another branch or out of sight. Combat sessions lasted up to 5 min and ended with the victor returning or not returning to their leaf. Females were not attracted to males in combat. Male combat in other tephritid species has many similar components; e.g., appendage displays, mouth part extension and touching, stilting and wrestling, but these behaviors are rarely observed in natural field settings (Boyce 1934, Dodson 1985, Headrick & Goeden 1990; unpublished data).

Batra (1979) described the courtship and mating behavior of *E. bella* and *E. festiva* from *Ambrosia artemisiifolia* L. and *A. trifida* L., respectively. *E. bella* and *E. festiva* adults were most active in the late afternoon and both tended to remain on or near their host plants (Batra 1979). *E. stigmatica* adults were active from ≈ 0900 to 1500 hours but females were generally more abundant and active after ≈ 1300 hours.

Courtship behaviors for *E. bella* and *E. festiva* appear similar to those of *E. stigmatica*, except in terms of interpretation. Batra (1979) listed 10 courtship behavior "patterns" observed for both *E. bella* and *E. festiva*, "(1) visual orientation, (2) alternate wing waving with vibration, (3) both wings extended horizontally, (4) both wings extended with proboscis extended, (5) both wings extended with head butting, (6) tapping with front feet, (7) rapid flicks of both wings simultaneously, (8) territoriality (lekking), (9) male following female, abdomen curved, (10) male following female, wings flattened against abdomen." Interpreting the courtship sequence for *E. bella* and *E. festiva* as described by Batra (1979) is difficult because other behaviors beside courtship were involved simultaneously; e.g., aggression, male-male interactions, and female-female interactions. From the data she presented, we interpret that during courtship, males approached females with a wing display other than lofting; mouthpart contact was made; males of *E. festiva* followed females for courtship with their abdomens curved, their wings flat over their dorsa, and male courtship took place while females were ovipositing; whereas, *E. bella* males

did not court ovipositing females. Also according to Batra (1979), males of both *E. bella* and *E. festiva* established territories, but of differing sizes. *E. bella* males had a territory of one or two leaves, which they occupied for a few hours; however, *E. festiva* males had a territory of 1 m², which individual males occupied for more than a few hours (Batra 1979). Copulation for *E. festiva* occurred late in the afternoon, and lasted for ≈ 1 h ($n = 2$); copulation for *E. bella* occurred throughout the day and lasted 20–60 min ($n = 15$) (Batra 1979).

The behavioral similarities of both of these species, and especially *E. festiva*, to *E. stigmatica* is an example of the many shared behavioral attributes of congeners and helps to substantiate the closeness of these three species hypothesized by Norrbom (1993). Behaviors observed in all three species include wing enantion or "rapid flicks of both wings simultaneously," asynchronous supination or "alternate wing waving with vibration" (though less common in *E. stigmatica*), mouthpart contact, and territoriality. *E. stigmatica* and *E. festiva* also share two more features: males curling their abdomens underneath them and holding their wings flat over their dorsa while sitting behind females. However, *E. stigmatica* did not court ovipositing females as did *E. festiva*, and copulations took place only on the upper surfaces of leaves patrolled or defended by males. Other behaviors reported here for *E. stigmatica* and not reported by Batra (1979) for *E. bella* and *E. festiva* include wing lofting, abdominal pleura distension, males raising their front legs as an initial greeting, male lofting/dance during courtship, a courting male's rapid side stepping to maneuver behind a female, a courting male raising his middle legs after initial rejection by an unreceptive female, and male ritual combat.

Seasonal History. *E. bella* and *E. festiva* are both monophagous and univoltine (Foote 1984, Foote et al. 1993); whereas *E. stigmatica* is bivoltine in southern California, producing a spring generation on *A. ilicifolia* and a fall generation on *A. acanthicarpa* (B. A. Foote reported rearing a spring generation of *E. stigmatica* from *A. ambrosioides* in southwest Arizona and noted that another host-plant species must be used by these adults because *A. ambrosioides* was no longer producing involucre, personal communication). *E. bella* adults are found from mid-June to late September in Ohio and Maryland, whereas *E. festiva* adults appear in July in Maryland and reach their peak abundance in mid-September (Batra 1979, Foote 1984). Both *E. bella* and *E. festiva* overwinter as diapausing larvae in fruiting involucre (Foote 1965, 1984; Batra 1979).

Adults of *E. bella* and *E. festiva* females emerged reproductively immature, but after a month mature, then oviposit for another month (Batra 1979). This compares with the similar pre-reproductive period of 4–6 wk observed in the current study with caged F₁ adults of *E. stigmatica*

reared from involucre of *A. ilicifolia* collected at the Jaeger Reserve study site. These F_1 adults in nature apparently overwinter and reproduce in the fall in southern California on the widespread, annual ragweed, *A. acanthicarpa*. *E. stigmatica* then overwinters as F_2 adults that rendezvous on *A. ilicifolia* in the Colorado Desert in the spring to reproduce and complete the cycle. Reproduction by *E. bella* and *E. festiva* was concurrent with the flowering of their sole hosts (Batra 1979, Foote 1984), as with bivoltine *E. stigmatica* on its two hosts in southern California.

Natural Enemies. The principal natural enemies of immature *E. stigmatica* in fruiting and staminate involucre of *A. acanthicarpa* and *A. ilicifolia* were the solitary, primary, larval-pupal, endoparasitic, chalcidoid Hymenoptera, *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae). Both wasp genera are commonly associated with other nonfrugivorous, florivorous Tephritidae in southern California, but additional taxonomic study is needed to determine how many and what species of these parasitoids are involved, for which our voucher specimens may someday find use. Also reared in limited numbers from *A. ilicifolia* involucre infested by *E. stigmatica* were the following chalcidoid Hymenoptera, that also presumably are solitary, primary parasitoids: *Heteroschema* sp. (Pteromalidae) and ?*Glyphomerus* sp. (Torymidae).

Biological Control. The role of *E. aequalis* as a seed predator of cocklebur, *Xanthium strumarium* L., has long been known (Marlatt 1891); accordingly, it was one of the first insects exported to Australia in 1932 from its native United States for the biological control of this annual, noxious weed (Julien 1992). Though established at low levels, it afforded no cocklebur control. Subsequent transfers of *E. aequalis* from Australia to Fiji in 1951 failed to establish this fly (Julien 1992).

The reproductive behaviors of *E. bella* and *E. festiva* were studied by Batra (1979) to help to assess their potential for use as biological control agents of adventive North American ragweeds in Eurasia. *E. bella* had been exported to the then U.S.S.R. from the United States and Canada in 1969 and 1977, but was not established on *Ambrosia artemisiifolia* (Kovalev 1980, Julien 1992). *E. bella* was introduced again in 1990 from the United States and released in the North Caucasus, but its establishment remains unconfirmed (Julien 1992).

Euaresta stigmatica from *A. acanthicarpa* in southern California, like *E. festiva* and *Ambrosia trifida* in eastern North America, remains under consideration as a biological control agent for ragweeds in Eurasia (Harris & Piper 1970, Goeden & Teerink 1993). The former species remains untested in the field as a biological control agent for *A. trifida*, to which *E. stigmatica* would have to transfer if exported and released in Eurasia. *A. acanthicarpa* is the native ragweed most closely al-

lied taxonomically to *A. artemisiifolia* and *A. trifida* (Payne 1963), but unlike them has not been accidentally exported from North America as an agricultural weed and a growing, worrisome source of aeroallergenic pollen in Eurasia. Therefore, if it can be successfully induced to attack these two ragweeds, *E. stigmatica* obtained from *A. acanthicarpa*, in comparison with *E. bella* and *E. festiva* attacking their natural host plants, may provide a good test of the so-called "new-host theory" of Hokkanen & Pimentel (1984). It was in this context that the current study of *E. stigmatica* was undertaken, as our contribution to a new cooperative research and natural enemy exchange program between Agriculture Canada and the Academy of Agricultural Sciences of the People's Republic of China involving, among other projects, the biological control of ragweeds (Goeden & Teerink 1993; R.D.G.; unpublished data).

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