LIFE HISTORY, COURTSHIP, AND MATING BEHAVIOR OF THE
GALL-FORMING ACIURINA TRIXA (DIPTERA: TEPHRITIDAE) ON
CHRYSOTHAMNUS NAUSEOSUS HOLOLEUCUS (ASTERACEAE)

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Abstract.—Life history and reproductive behavior of the Aciurina trixa Curran (Diptera:
Tephritidae) on a new host plant subspecies, Chrysothamnus nauseosus hololeucus (As-
teraceae) is described from a two-year study. Eggs are laid on axillary buds formed in the
previous year. After egg hatch, larval feeding induces a spheroid gall. The larva feeds on
the innermost gall tissue while the gall continues to grow until the third larval instar
pupates. Sex ratios were female-biased (1989—1.00:1.49; 1990—1.00:1.17). Wing move-
ments and auditory signals were observed during courtship and in agonistic encounters
with siblings. Courtship and mating averaged 104 min (1 SE ± 38 min) and 159 min (1
SE ± 7 min), respectively. Soon after emergence and mating, females started searching
for oviposition sites. Our data are compared with other A. trixa populations attacking
other subspecies of rabbitbrush in Idaho and New Mexico.

Key Words: Aciurina, Asteraceae, Chrysothamnus, courtship, insect behavior, insect
galls, life history, mating behavior, Tephritidae

Aciurina species (Diptera: Tephritidae) form galls on plants in the family Asteraceae. The primary hosts are in the genus
Chrysothamnus but hosts also include Artemisia, Baccharis, Gutierrezia, Haplopappus, Solidago, Bebbia, and Senecio (Foote
and Blanc 1963, Washbauer 1972, Steyskal 1984, Dodson and George 1986). At least 12 species of Aciurina occur throughout the
western United States and northern Mexico (Washbauer 1972, Steyskal 1984). However, the genus may be larger due to the presence
of several sibling species. For example, two morphs of A. bigeloviae were separated into two distinct species, A. bigeloviae (Cock-
rell) and A. trixa Curran, on the basis of genetic evidence, gall morphology, host plant
subspecies selection, mating behavior, and life history parameters (Dodson and George
1986).

This paper describes life history parameters, courtship, and mating behavior of A. trixa on a new host subspecies of rabbit-
brush, Chrysothamnus nauseosus hololeucus, in northern Arizona. This study is part
of a larger study on female preference and larval performance of galling insects and the
adaptive significance of gall formation (see Price et al. 1986, 1987, Fernandes and Price

Material and Methods

Field observations were carried out between 1987 and 1990 along Schultz Pass Road, 2.4 km north of Highway 1-89 (ele-
vation: 2440 m), near Flagstaff, Coconino...
County, Arizona. Galls were collected weekly during the period of gall development, and every other month for the remainder of the year. Some were used for rearing the gallers and their parasitoids, and some were opened to observe the internal gall, and the development of the inhabitants.

Adult behavior was observed during daylight hours in the field and in the laboratory. The cylindrical, nylon-mesh, field cages used (1.0 m diameter by 1.3 m height) allowed penetration of >80% of full sunlight. Adults released into the field cages were reared in the laboratory from galls collected in the field from 15 to 30 May 1988. Courtship and mating behavior were observed by placing pairs of flies in 100 × 15 mm plastic Petri dishes. A 9 mm, circular opening in the lids, covered with nylon mesh, allowed air circulation. Branches of the host plant were placed inside the dishes as a substrate. Flies were kept in the laboratory at ambient temperature, relative humidity, and photoperiod. When copulation occurred, the pair was observed until they uncoupled. Observations were carried out between 07:45 and 21:07 hours on 7 dates between 5 June and 23 June 1988. Durations of mating activities were recorded to the nearest minute.

Female fecundity was inferred in 1989 and 1990 by dissecting females and counting their egg load 72 h after emerging from galls. We tested whether female fecundity (i.e. egg load) was correlated with gall size using a simple linear regression test (Zar 1984).

RESULTS AND DISCUSSION

Host plants and galls.—Acturina trixa induces bud galls on C. n. hololeucus in Arizona. The other host subspecies for A. trixa are: C. n. latisquameus, C. n. albicaulis, C. n. consimilis and C. parryi (Wangberg 1981, Dodson 1987a, b). Despite the co-occurrence of C. n. consimilis at our study site, we did not observe A. trixa galls on this rabbitbrush subspecies. In addition, mated females caged with C. n. consimilis (n = 5) could not be induced to oviposit on this subspecies. When placed on C. n. hololeucus, these individuals immediately walked up and down the plant stem in search of oviposition sites.

Our observations support the findings of Dodson and George (1986) that A. trixa induces smooth galls on plants with tomentum (gray rabbitbrushes), whereas A. bigeloviae induces hairy galls on green rabbitbrushes. Unlike Wangberg’s (1981) findings of A. trixa galls on C. n. consimilis (a green rabbitbrush) in Idaho, we did not observe A. trixa galls on this host subspecies. Nevertheless, the association of Acturina spp. with their specific or subspecific Chrysothamnus host plants is not clear (Wangberg 1981). This may be due in part to the enormous variation in Chrysothamnus. There are at least 16 species and subspecies of rabbitbrush, and 22 subspecies of C. nauseosus (Anderson 1986a, b, McArthur and Meyer 1987), and hybridization between subspecies may occur (GWF, pers. observ.).

Feeding behavior and life history.—The life history of A. trixa populations in Arizona is similar to populations in New Mexico (Dodson 1987b) and Idaho (Wangberg 1981). Eggs are oviposited on axillary buds formed in the previous year (Fig. 1A). Only one egg is laid on each bud, so galls occur singly, and only one larva is found per gall. After hatching, the larva induces an ellipsoid growth on the opposite side of the stem from where the egg was laid (Fig. 1B). Shortly after, a spheroid gall develops from the axillary bud where the egg was deposited (Fig. 1C). First and probably second larval instars are believed to feed inside the stem (Wangberg 1981, Benbow and Foster 1982, Dodson 1987b). After further development of the gall, the larva tunnels in, perhaps because of food depletion in the stem (Wangberg 1981, Fig. 1D). The ellipsoid swelling on the stem is left filled with frass. Gall growth continues until November, as larvae
feed on the innermost gall tissue. Larvae stop feeding at this time and return to the base of the gall to overwinter. Dormancy is broken at the end of January after which larvae again resume feeding. Third instars excavate an exit tunnel reaching the external wall at the top of the gall. A thin layer of tissue separates the gall chamber from the exterior. At this time, some individuals exit the gall. No pupation occurs and all these individuals die on the ground. Tunnel excavation was also observed in December, indicating plasticity in larval development. After excavating the exit tunnel, third instars return to the base of the gall to pupate (Fig. 1D), and they subsequently emerge as adults (Fig. 1E). Shortly after emergence, reproductive behavior begins. After mating, females begin selecting sites for oviposition. Adults were observed in the field from the
beginning of April in 1990 to the beginning of June 1990. The occurrence of the various life instars in the field is shown in Fig. 2.

Galls of *A. trixa* on *C. n. hololeucus* are generally green, spheroid, glabrous, and one-chambered, with one larva per gall. Galls have three distinct tissue layers with larval feeding on the two innermost layers. The third layer is resinous and covers the external gall walls, which have an irregular pattern of tightly appressed hairs giving the appearance of sutures on the gall surface (see also Dodson 1987b). Galls averaged 6.31 mm (1 SE ± 0.74, n = 306) in 1989 and 6.35 mm (1 SE ± 0.07, n = 140) in 1990.

Wangberg (1981) described four gall morphology types, each associated with three subspecies of *C. nauseosus*. The subspecies *C. n. albicaulis* had two different gall colorations: (a) pale, white, gray, and (b) dark green, often with purple hues. We observed galls ranging from gray to dark green with purple hues, and from smooth and spherical to pear shaped with some wall protuberances. Protuberances were apparently caused by emerging leaves. Nevertheless, we never observed completely formed leaves emerging from gall tissue. Galls with wall protuberances were more common on vigorously growing plants, perhaps indicating that the gall makers had less control on plant growth and metabolism.

Sex ratios were 1.00:1.49 in 1989, and 1.00:1.17 in 1990. The *A. trixa* populations studied were protandrous, with peak male emergence occurring about 3–5 days before peak female emergence (male: 20.9 d (1 SE ± 0.7, n = 61); female: 25.0 d (1 SE ± 1.0, n = 41); t test = 3.444, *P* < 0.0005). New Mexico populations studied by Dodson and George (1986) and Dodson (1987b) were also protandrous.

Mating and oviposition were observed as adults appeared in the field. Flies were observed between 6:00 h in the morning and 0:45 min after sunset. Like many other tephritids, these flies are very alert visually. Females often terminated oviposition when bothered by other arthropods, especially ants, which were major predators on gall insect larvae. Adult flies were frequently seen probing stems of the host plant with their mouthparts, but we do not know if feeding occurred.

Female fecundity was negatively correlated with gall size in 1989 but positively correlated in 1990 (1989 regression equation: \( y = 157.304 - 8.551x \), \( F_{1,18}, r^2 = 0.17 \),
$P < 0.05$; 1990 regression equation: $y = 0.1 + 15.1x, F_{1,49}, r^2 = 0.21, P < 0.01$). Further, only 17% and 21% of the variation in female egg load was explained by gall size. This discrepancy may be the result of different sample sizes between years.

The diameter of galls in which larvae survived was not significantly larger than the diameter of those with parasitized larvae ($t$ test, $P > 0.05$ for 1989 and 1990). In 1989, non-parasitized galls averaged 6.47 mm ($1 \text{ SE} \pm 0.07, n = 102$) in diameter, whereas parasitized galls averaged 6.55 mm ($1 \text{ SE} \pm 0.13, n = 53$); and in 1990, non-parasitized galls averaged 6.33 mm ($1 \text{ SE} \pm 0.07, n = 90$) in diameter, whereas parasitized galls averaged 6.43 mm ($1 \text{ SE} \pm 0.15, n = 45$).

Many studies have shown higher parasitism and/or inquilinism rates on smaller galls compared to larger galls (e.g. Redfern and Cameron 1978, Jones 1983, Stille 1984, Weis et al. 1985, Price and Clancy 1986, Lichter et al. 1990), yet others have shown the opposite (e.g. Shorthouse 1980, Shorthouse et al. 1990). Nevertheless, parasites may interfere with the normal pattern of gall growth by killing the host larva before full development, or by feeding on gall tissue after killing the host larva. The latter makes parasitized galls larger than unparasitized galls (e.g. Shorthouse 1973, 1980, Fernandes et al. 1987, Shorthouse et al. 1990).

Male and female flies emerged from galls of different sizes. Galls from which females emerged were significantly larger than galls from which males emerged (1989: female: $6.94 \text{ mm } (1 \text{ SE} \pm 0.11, n = 41)$; male: $6.16 \text{ mm } (1 \text{ SE} \pm 0.07, n = 61); t\text{ test } = 6.0611; P < 0.0001$; 1990: female: $6.59 \text{ mm } (1 \text{ SE} \pm 0.98, n = 51)$; male: $5.97 \text{ mm } (1 \text{ SE} \pm 0.84, n = 39); t\text{ test } = 4.7611; P < 0.0001$).

Gall size was not an important factor in the fly life span. There was no relationship between life span of the insect and gall size for either sex ($r^2 = 0.00$ in both cases). Further, there were no significant differences in male and female life spans for the galls collected in the field [male: $12.6 \text{ d } (1 \text{ SE} \pm 0.7, n = 42)$; female: $10.5 \text{ d } (1 \text{ SE} \pm 0.6, n = 29); t\text{ test, } P > 0.05$].

Mating behavior.—Mating behavior in the Tephritidae has been reported for many species (e.g. Tauber and Tauber 1967, Prokopy and Bush 1973, Batra 1979, Prokopy and Hendrichs 1979, Freidberg 1981, 1982, Dodson 1982, Burk 1983, Goeden 1990a, b, Headrick and Goeden 1990, Jenkins 1990), including *A. trixa* on different host plants in Idaho and New Mexico (Wangberg 1981, Dodson 1987b).

In tephritids, courtship behavior includes prominent displays of wings, ambulatory displays, pheromone release, trophallaxis, and auditory signals (Burk 1981, Dodson 1987b). In addition to wing displays, we observed auditory signals during courtship and during some agonistic encounters with siblings. “Slow signals,” “wing fanning,” “wing flicking,” “wing thrusting,” and “wing waving” (Fig. 1–6 in Jenkins 1990) were observed for *A. trixa* during courtship. Wing thrusting was also observed during encounters between *A. trixa* and other arthropods. Wing movements in tephritids may be related to directing sex pheromone toward females, directing male odor toward intruders (Piper 1976, Jenkins 1990 and references therein), and producing sounds (Sivinsky et al. 1984).

Before and during courtship, males rubbed their hind legs against their abdominal pleura and then rubbed their wings. Jenkins (1990) argued that this activity may transfer odor from the pleura to the wings where it can then be dispersed by wing fanning (see also Nation 1972).

After spotting a male, females generally waved their wings (“advertising behavior,” Dodson 1987b). Wing movements were more frequent on windy days. Males moved slowly until reaching the female. Males never flew to females, but rather walked slowly along stems to approach females from behind. Some females left a stem or plant without being approached. Dodson (1987b) reported the same behavior for New Mexico...
populations. Frequently, males and females assumed a position perpendicular to the stem for a few seconds, then returned back to an upright position on the stem. Males climbed or leaped onto the female’s posterior and then attempted to “leglock” her legs (see Dodson 1987b). During copulation, the female’s wings stay semi-opened and the male’s head is positioned between the female’s wings. The male’s wings stayed closed during copulation. The pair generally stayed motionless on the substrate, leaving (walking) only if bothered by other arthropods. In the laboratory, courtship averaged 104 min (1 SE ± 38, n = 32), and mating averaged 159 min (1 SE ± 7 min, n = 32).

The life history of A. trixa is very similar to other gall inducing Aciurina species. However, the formation of the “stem gall” during the first, and perhaps second, larval instars, and a second bud gall where larvae terminate development is somewhat unusual among galling insects.

Aciurina trixa use a wide spectrum of displays during courtship. Courtship behavior is rich in tephritids and is a potential source for comparative data (Jenkins 1990), which may aid in the separation of the Aciurina species complex.

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