Biology and Laboratory Development of *Trirhabda geminata* (Coleoptera: Chrysomelidae) on the Composite, *Encelia farinosa*

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ABSTRACT The life history of *Trirhabda geminata* Horn was determined at 30°C in the laboratory on its host plant, *Encelia farinosa* Gray (Compositae: Asteraceae). Adult longevity averaged 35.5 d. Adult females lived longer than males (43.1 versus 27.5 d). Mean fecundity was 6.5 batches of eggs per female with an average of 19.1 eggs per batch. Mean time from oviposition to egg eclosion was 44.8 d, and the earliest egg hatch occurred 5 d after oviposition. When eggs were held under constant moist conditions (100% RH), 80% of all eggs hatched. However, eggs held dry and not moistened failed to hatch. Mean development times for first instar, second instar, third instar, prepupa, and pupa were 3.9, 3.3, 7.9, 5.2, and 6.1 d, respectively.

KEY WORDS *Trirhabda geminata, Encelia farinosa,* development

THE PHYTOPHAGOUS GENUS *Trirhabda* Leconte contains 24 North American species (Hogue 1970). Most occur in relatively xeric areas of continent, although several are found in the more mesic areas of eastern North America (Blake 1931, Hogue 1970, Reid & Harmsen 1976, Sholes 1981, Kraft & Denno 1982, Messina 1982a). *Trirhabda* spp. all tend to specialize on host plants in the families Asteraceae or Hydrophyllaceae (Hogue 1970, O'Brien 1980, Messina 1982a). Despite their relative ubiquity, little is known about the biologies of most *Trirhabda* species except for three eastern species that feed on goldenrod (*Solidago* spp.) and a few species investigated as candidate agents for the biological control of rangeland weeds (Massey & Pierce 1960, Pringle 1960, Capek 1971).

Trirhabda geminata Horn occurs commonly throughout the xeric chaparral and coastal sage scrub in Arizona and California (Hogue 1970; Wisdom 1985, 1988) and has been collected as far east as northern Texas (Hogue 1970). This species specializes on and is the dominant herbivore of the coastal sage-scrub plant *Encelia farinosa* Gray, but also feeds on *E. virginensis* A. Nels. and *E. californica* Nutt. (Hogue 1970, O'Brien 1980). Populations of *T. geminata* can increase to such high densities that *E. farinosa* plants are entirely defoliated. Larvae and adult *T. geminata* are active from late winter to early summer and their phenology is tightly associated with host-plant development (Wisdom 1985). We have observed three overlapping larval stadia; pupation and oviposition are in the soil (R.A.R. & J.A.B., unpublished data). *T. geminata* appears to be univoltine (Paine et al. 1993), apparently aestivating in the egg stage through summer. We report here our studies on the development, fecundity, and adult longevity of *T. geminata* feeding on *E. farinosa* under laboratory conditions at a constant temperature.

Material and Methods

We collected *T. geminata* larvae from areas of interior coastal sage-scrub habitat on the Box Springs Mountains adjacent to and southeast of the University of California at Riverside. Larvae were brought into the laboratory and placed on *E. farinosa* cuttings taken from the sampling areas. Cuttings were kept alive for ≈1 wk in plastic vials (50 ml) containing water and were replaced as needed. Cuttings infested with larvae were placed in the greenhouse (26.7°C, 65% RH). We allowed larvae to feed and grow until pupation. As the larvae naturally pupate in the soil, pupating larvae were collected in plastic lunch trays containing peat moss placed below the infested cuttings and were held individually in glass vials until adult emergence. Emerging adults were used in experiments.

We obtained *E. farinosa* study plants as seedlings (Tree of Life Nursery, San Juan Capistrano, CA). Plants were transplanted into potting soil (U.C. Mix #3; Matkin & Chandler 1957) in 15-cm diameter pots. Plants were maintained until needed on raised benches in a greenhouse (conditions as above), where they were watered and fertilized with Osmocote (N:P:K, 14:14:14 at 2.5 g per pot, Sierra Chemical, Milpitas, CA) as needed. These plants were used as host material for all experiments.

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All of the following studies were conducted in an environmental chamber (model Environator, Calumet Scientific, Elk Grove Village, IL) held at 30°C and 60% RH. This temperature was chosen to simulate natural environmental conditions; daytime temperatures in interior coastal sage-scrub communities routinely reach and exceed 30°C during the developmental and reproductive periods of this insect (during spring). A photoperiod of 14:10 (L:D) h was provided with fluorescent growth lights (model F20T12/GRO, GTE, St. Marys, PA).

Adult Longevity and Fecundity. A newly emerged pair of adult beetles (one male and one female) was placed in a cylindrical clear plastic cage 11-cm diameter by 18-cm height). Cages were open at one end and sealed at the other with 100-mesh brass strainer cloth. The open end of the cage was placed over a potted *E. farinosa* plant. To collect egg masses, we placed aluminum foil along the entire soil surface of the pot and around the stem of each plant. Cheese cloth was then draped over the aluminum foil as a medium for oviposition (after Hill 1975). Adults were allowed to mate, oviposit, and feed until death. Adult mortality and fecundity were monitored every 48 h throughout the life of the female. Plants were changed every 7 d to replenish the food supply. Adult males that died were replaced during the course of the trial. There was a total of 23 replicate trials. Data were checked for normality and equivalence of variances and differences in longevity between the sexes were determined by a *t*-test (Zar 1984).

Egg Eclosion. To obtain cohorts of eggs of the same age, five male–female pairs were caged together (10 insects per cage) as described above. After 24 h, all egg masses were collected. A mixture of 31 replicate eggs from these egg masses were transferred to moistened filter paper in the bottom of a plastic petri dish (100 by 20 mm) such that each egg was in direct contact with the wet paper. Dishes were sealed with Parafilm M (American National Can, Greenwich, CT). Condensation formed on the side and upper surfaces of the dish, thus humidity in these dishes was 100%. A second mixture of 22 replicate eggs was transferred to dry filter paper and held in sealed petri dishes in a similar manner. A final mixture of 17 replicate eggs was transferred to dry filter paper and held in sealed petri dishes as above. After 30 d, these eggs were then transferred to moistened filter paper such that each egg was in direct contact with wet paper, and held sealed in petri dishes as above. All dishes containing eggs were placed in an environmental chamber at 30°C and all eggs were monitored daily for eclosion. From these data, we calculated percentage of eclosion, minimal, maximal, and mean time to first hatch for the three groups of replicate eggs. Differences in mean time to eclosion among the three groups was analyzed using the Kruskal–Wallis test (Zar 1984).

Table 1. Longevity (d) of adult *T. geminata* at 30°C on *E. farinosa*

Sex	*n*	Mean ± SEM	Min.	Max	Median
Female	18	43.1 ± 5.2[a]	9	83	42
Male	17	27.5 ± 4.0	4	59	28
Female and male	35	35.5 ± 3.6	4	83	36

[a] Females live significantly longer than males ($t = 2.33$; df = 2, 17; $P = 0.026$).

Larval and Pupal Development. The duration of each stadium was estimated by placing a single, newly emerged, first instar (<24 h old) on the apical terminal of a potted *E. farinosa* plant. Larvae were then allowed to feed and grow to pupation. During this time, larval head capsule size (to nearest 0.01 mm) was measured daily and the instar determined.

To measure the developmental time of the prepupal stage, five, late third instars were placed on three, freshly clipped, young *E. farinosa* leaves. The leaves and larvae were placed on top of a layer of moistened peat moss within a 178-ml paper cup (model #5306, Sweethart Cup, Chicago, IL). Eight replicate cups (40 larvae) were tested. Larvae were held in an environmental chamber at 30°C and observed daily. Upon entering the prepupal stage, larvae burrowed into the peat moss, assumed a characteristic C-shape, and formed a pupation cell (Hogue 1970, O'Brien 1980). Prepupae were collected within 24 h and held individually in glass vials until pupation. The duration of time between initial burrowing and pupation was recorded as the development time required for the prepupal stage.

To determine the developmental time of the pupal stage, a similar methodology was used; however, instead of removing the prepupae from the peat moss, the insects were examined at 24-h intervals to detect if pupation had occurred. Upon pupation, the insects were removed and individually placed in glass vials. Pupae then were monitored daily for ecdysis.

Results

The mean adult longevity of *T. geminata* at 30°C was ≈5 wk (Table 1). Females lived ≈2 wk longer than males; however, both sexes showed considerable variation in longevity (Table 1). Of the original 23 females paired with males, a total of 14 females (61%) produced eggs (nine females died before oviposition). On average an individual female produces 6.5 ± 0.90 (mean ± SEM) egg masses each containing an average of 19.1 ± 1.28 (mean ± SEM) eggs. Each female waited an average of 24.5 ± 3.2 (mean ± SEM) d to initiate oviposition and produced a average total of 121.5 ± 17.34 (mean ± SEM) eggs. For the first 6 d of the experiment, no eggs were laid by any females, indicating that a preovipositional period is likely (Fig. 1 B and C). Fecundity peaked when females

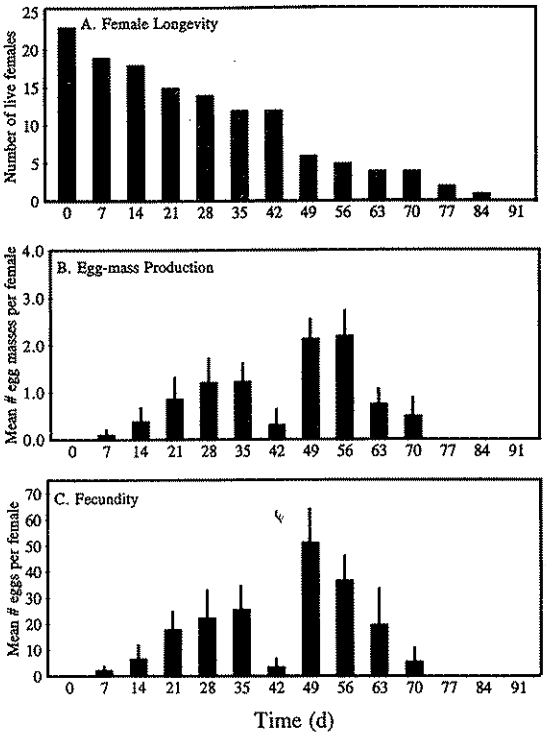

Fig. 1. Relationship between time and (A) adult female longevity, (B) egg mass production, and (C) average female fecundity (number of eggs per female per week) for *T. geminata* under laboratory conditions. For B and C vertical lines above bars denote 1 SEM.

were ≈7 wk old and declined rapidly thereafter (Fig. 1C). Fecundity peaking at week 7 could also be explained by egg production being depressed the preceding week (Fig. 1B). Female mortality was relatively constant over time with ≈1–2 females dying every week (Fig. 1A).

When eggs were provided with a constant source of moisture on which to develop (i.e., in direct contact with moisture at 30°C), 80% hatched. Average time to eclosion for these eggs occurred 5 wk after oviposition (Table 2). When eggs were held dry for 30 d and subsequently provided with a constant source of moisture, 29% hatched. The mean time to eclosion for eggs initially placed in a dry environment and then moistened 30 d later was 21.5 wk (Table 2). When eggs were not provided with a moisture source, they did not hatch (no eclosion as long as 10 mo after oviposition, Table 2).

Both first and second instars developed rapidly, with little variance in development times (a range of only 2 d for either instar [Table 3]). Third instars required an average of 7.9 d to develop and displayed considerably more variation in developmental time). Only the egg stage showed greater variation in developmental time (compare Tables 2 and 3). Third instars took an average of an additional 5.2 d to develop fully from the prepupal C-stage to the pupal stage. Pupae developed rapidly to the adult stage in just under 1 wk with little variation.

Table 2. Percentage of eclosion and egg development time (d) for *T. geminata* at 30°C on *E. farinosa*

Developmental conditions	% eclosion	Min. time to eclosion	Max time to eclosion	Mean ± SEM time to eclosion	Median time to eclosion
Wet	80.1	5	75	44.8 (5.3)a	41
Dry[a]	0.0	NA	NA	NA	NA
Dry_{30d} - Wet	29	58	189	150.9 (19.7)b	189

Mean values followed by different letters are significantly different from one another (Kruskal–Wallis test = 13.132, df = 1, $P = 0.003$).

[a] Eggs held under dry conditions were observed for 322 d without eclosion, and consequently the minimum, maximum, mean, and median are not available (NA).

Discussion

To our knowledge, the life histories of very few of the North American species of *Trirhabda* have been studied. The exceptions are relatively common species feeding on goldenrod, *T. virgata* Leconte, *T. borealis* Blake, and *T. canadensis* Kirby (Balduf 1929; Blake 1931; Hogue 1970; Sholes 1981; Messina 1982a, b). Studies of other species of *Trirhabda* have investigated theories concerning the interactions between phytophagous insects and their host plants (e.g., *T. bacharidis* Weber [Kraft & Denno 1982], *T. diducta* Leconte [Johnson et al. 1985]) or evaluated these beetles as plant biocontrol agents (Massey & Pierce 1960, Pringle 1960, Capek 1971). Our study of *T. geminata* provides standardized developmental times and fecundities for a species that is more representative of the genus (i.e., species occurring within xeric North American environments).

The life-history characteristics of *T. geminata* differed somewhat from those reported for other species of *Trirhabda*. For example, the preoviposition period of *T. virgata* and *T. borealis* lasts ≈2 wk under field conditions (Messina 1982a) but is <1 wk for *T. geminata* at 30°C. In the laboratory, *T. geminata* lays more eggs per eggmass (mean = 19.1) than either *T. virgata* or *T. borealis* in the field (mean = 12 and 8, respectively [Messina 1982a]). The percentage of egg eclosion is similar

Table 3. Developmental times (d) for larvae, prepupae, and pupae of *T. geminata* at 30°C on *E. farinosa*

Life stage	*n*	Duration of stage			
		Mean ± SEM	Min.	Max	Median
First instar	28	3.9 ± 0.1	3	5	4
Second instar	25	3.3 ± 0.1	2	4	3
Third instar	21	7.9 ± 0.6	5	16	6
Prepupa	29	5.2 ± 0.2	3	7	5
Pupa	51	6.0 ± 0.1	4	7	6

among the three species (Messina 1982a). The development times of first- and second-instar *T. geminata* are shorter than those reported for *T. sericotrachyla* Blake (O'Brien 1980). The discrepancies in various life-history characteristics among these studies (including the one presented here) are probably caused by species' differences in reproductive characteristics as well as differences in environmental conditions (such conditions were not reported by O'Brien [1980]).

Hogue (1970) suggested that *Trirhabda* species have four instars. However, we observed only three instars in *T. geminata,* which is also true for other *Trirhabda* species (e.g., *T. virgata* and *T. borealis* [Messina 1982a], *T. sericotrachyla* [O'Brien 1980], and *T. nitidicollis* [Eckberg & Cranshaw 1994]). We are confident in our assessment of the number of instars and suspect that Hogue (1970) may have made this generalization based on the limited information available at the time.

Hogue (1970) also suggested that *Trirhabda* require a cold period to stimulate egg hatch. However, this conclusion was based on studies of *Trirhabda* species occurring in northern and eastern North America (Balduf 1929, Blake 1931, Hogue 1970, Messina 1982a). *T. geminata* appears unusual in not requiring a winter chilling period for successful eclosion (i.e., a breakage of diapause). At 30°C constant temperature, *T. geminata* eggs hatch within an average of 6–7 wk (a minimum of 5 d) as long as they are provided with a moisture source (Table 2). This behavior seems adaptive, because temperatures often exceed 30°C but rarely drop below freezing in the xeric native habitats of this insect.

The requirement for a moisture source for successful egg eclosion (Table 2) seems to be an adaptation of the insect to ensure that development does not occur until its host plant has initiated new growth in the winter. The seasonal period of precipitation throughout the majority of *T. geminata* range (southern California, western Arizona) occurs during the late fall and winter months. *E. farinosa* generates new foliage each year, growth beginning ≈4–6 wk after the first heavy winter storm of the growing season and continuing to generate new foliage until drought conditions occur in late spring to early summer (Ehleringer & Clark 1988). At this time, the plant becomes drought-deciduous and drops most of its leaves (Ehleringer & Clark 1988). By using the presence of moisture (winter rains) as a proximal cue for eclosion of eggs, *T. geminata* ensures that emerging larvae will find adequate host-plant material on which to feed.

The only other species of *Trirhabda* occurring in a relatively xeric environment that has been studied to any extent is *T. sericotrachyla* (O'Brien 1980). *T. sericotrachyla* feeds almost exclusively on the host plant *Artemesia californica* Less. in the same general type of coastal sage-scrub plant community that supports *T. geminata* (Hogue 1970). Not surprisingly, O'Brien (1980) also showed that *T. sericotrachyla* does not require a winter chilling but does require a moisture source for its eggs to hatch. *T. geminata* also appears to have a similar egg development time requirement as *T. sericotrachyla* (≈45 d at 30°C for *T. geminata* versus 55 d at room temperature for *T. sericotrachyla* [O'Brien 1980, pp. 7–10]). Because most of the North American species of *Trirhabda* occur in relatively xeric habitats (Hogue 1970), we suspect that the requirement for moisture for successful egg eclosion is more widespread than reported. We feel that further studies investigating the requirements of egg eclosion are warranted in this genus.

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