

Seasonal dynamics and overwintering strategy of the tachinid fly (Diptera: Tachinidae), *Ormia ochracea* (Bigot) in southern California

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Summary

We present the first data on the seasonal abundance of an acoustically orienting parasitoid fly, *Ormia ochracea* (Bigot), in southern California. Peak population abundance of the parasitoid lags peak population abundance of its primary local host species the field cricket *Gryllus lineaticeps* Stål, by about six weeks. We also examined pupal diapause as a potential overwintering mechanism. Taken together our results suggest (1) that *O. ochracea* lacks a highly effective pupal diapause, (2) that spring adult field cricket species are safe from the fly, and (3) that most of the late fall flies die without reproducing.

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Keywords

Ormia; *Gryllus*; host-parasitoid dynamics

Introduction

Ormia ochracea (Bigot) (Figure 1) is a parasitoid fly in the Tachinidae, a diverse family of true flies (Diptera) with over 9000 named species, all of which are parasitoids (O'Hara and Wood 2004; Stireman et al. 2006). Members of the tribe Ormiini are crepuscular parasitoids of acoustically communicating orthopteran insects. There are 67 described ormiine species in eight genera worldwide, with the greatest diversity in the tropics, suggesting a tropical origin (Lehmann 2003; O'Hara and Wood 2004). Gravid female flies exhibit phonotaxis toward host calling song, and so parasitize predominantly adult calling males (Cade 1975; Allen 1995; Lehmann and Heller 1998; Allen et al. 1999; Lehmann et al. 2001). Phonotaxis is accomplished via highly specialized paired tympana on their prosternum (Robert et al. 1994; Robert and Willi 2000; Mason et al. 2001). In *O. ochracea*, the hearing organs are tuned to sound waves in the range of 4 to 6 kHz, a frequency that corresponds to the song of their field cricket hosts



Figure 1. Adult *Ormia ochracea* (Bigot).

(Robert et al. 1992). Due to this highly specialized host-location morphology, *O. ochracea* have relatively high host specificity, limited almost exclusively to field crickets in the genus *Gryllus*. *Ormia ochracea* activity peaks shortly after sunset (Cade et al. 1996), a schedule that coincides with host calling activity. Female flies larviposit on and around the calling cricket (Adamo et al. 1995a; Adamo et al. 1995b). First instar larvae burrow into the cricket, spending 7–10 days consuming the host before emerging, pupating, and spending another 10–12 days in the puparium, then metamorphosing into an adult (Cade 1975; Wineriter and Walker 1990; Adamo et al. 1995a; Adamo et al. 1995b). The complete cycle from larviposition to larviposition takes a minimum of 4 weeks under ideal temperature, humidity, and population density (Wineriter and Walker 1990; Vincent and Bertram 2009).

The confirmed geographic range of *O. ochracea* extends from Central America (and perhaps further south) through Mexico and across the southern United States. Specimens verified by mtDNA genotype are known from Guanacaste, Costa Rica, Sonora, Mexico, and within the USA from Florida, Texas, Arizona, California, and Hawaii (Gray et al. 2007; Sakaguchi and Gray 2011). *Ormia ochracea* has also been reported from Louisiana (Henne and Johnson 2001), and some older taxonomic literature reports additional specimens from Arkansas, Colorado, Kansas, Missouri, Oklahoma and even Michigan (Sabrosky 1953; O'Hara and Wood 2004). The Michigan record in particular seems anomalous, and may be in error. In the southern portions of temperate North America the flies are not active year-round (Walker 1986); seasonality in the tropics has not been examined and could require extensive new field-work as cursory inspection of various museum materials suggests that many Neotropical specimens may be misidentified. In the Santa Monica Mountains, Los Angeles County, California, repeated attempts to attract and trap flies during the winter and spring months have yielded no flies (19 Feb. 2003, 13 Mar. 2003, 22 Mar. 2003, 25–26 Mar. 2003, 30 – 31 Mar. 2003, 6 Apr. 2003, 11 Apr. 2003, 25 Apr. 2003, D. A. Gray, unpublished data), though notably, an *O. ochracea* larva emerged from a *Gryllus*

lineaticeps field cricket caught in the Santa Monica Mountains June 26, 2003 [D. A. Gray specimen, Las Virgenes View Park, Santa Monica Mountains, Los Angeles County, California (34.108° N 118.708° W), 26-vi-2003]. Some tachinids overwinter as first instar larvae within their hosts, and others overwinter as pupae (O'Hara 2008); the overwintering strategy of *O. ochracea* has not been described. Lehmann (2008) suggests that ormiines may overwinter as pupae, but this has not been tested.

Although *O. ochracea* has been studied in southern California with respect to host song selection (Wagner 1996; Wagner and Basolo 2007), there are no published data on the local ecology of this fly in southern California. The goals of this review were (1) to generate census data on the parasitoid-host population dynamics of *O. ochracea* in the Santa Monica Mountains of southern California and (2) to test the likelihood of an effective pupal overwintering strategy.

Methods

Experiment 1: Census of fly and field cricket populations

All fieldwork was performed in an abandoned agricultural field at the King Gillette Ranch near Malibu Creek State Park in the Santa Monica Mountains, Los Angeles County, California (34.104° N, 118.706° W). The surrounding area is a historically agricultural semi-natural open space jointly owned and administered by the Santa Monica Mountains Conservancy, the Mountains Recreation and Conservation Authority, the National Park Service, and California State Parks. The field itself is approximately 45,500 m² with two large Coast Live Oak trees (*Quercus agrifolia*, Fagaceae) and is bordered by roads lined with *Eucalyptus* spp. trees (Myrtaceae) on two sides, and with a strip of riparian vegetation (e.g., *Salix* Salicaceae) on a third side. Fly and calling cricket censuses were performed every 2–3 weeks from 1 August to 19 December 2008.

Fly abundance was estimated using attraction of gravid females to a speaker broadcasting synthetic cricket song (Figure 2). A slit trap designed to catch *Ormia* (Walker 1989) was placed over a portable CD player and speaker (Emerson, HD8197; Radio Shack, model 40–1441) broadcasting a synthesized *Gryllus lineaticeps* song created with CoolEdit 2000 (Syntrillium software, Scottsdale, Arizona). For details on synthetic song construction, see Gray et al. (2007). The trap was positioned approximately 5 meters outside the canopy of the oak trees on dirt. Song broadcast began at sunset and continued for 2 hours or until the ambient temperature fell below 12° C. After 2 hours, trapped flies were removed with a vial, counted and released. One to four flies were retained alive per week for related laboratory experiments. Start and end temperatures as well as moon phase were noted.

Relative abundance of field cricket hosts was estimated by systematic survey of calling male crickets. Beginning approximately 40 minutes after sunset, we acoustically censused calling crickets in the field by walking the entire field on roughly parallel paths approximately 30 m apart. The entire field was surveyed each night of the census, taking 1.5–2 hours. We recorded the approximate location of each calling male to avoid double counting. Only calling male *Gryllus* crickets were counted. In our study



Figure 2. The acoustic trap system used in this study. The left panel shows one of us (J. Paur) removing flies from the trap for counting. The right panel shows a close-up of the trap with a fly (white arrow) about to enter.

area *G. lineaticeps* is the only commonly utilized host cricket species. Although the sympatric summer and fall cricket species *G. integer* Scudder and *G. multipulsator* Weissman are also known hosts of *O. ochracea* (D. A. Gray, unpublished), they are both very uncommon (probably two or three orders of magnitude less abundant than *G. lineaticeps*) within the Santa Monica Mountains. An acoustic census such as ours underestimates actual total abundance of crickets, but can give meaningful relative abundances of potential hosts over time when applied systematically. Because *O. ochracea* is not known to have any means of locating cricket hosts other than via host calling song, only calling male crickets (such as were likely to be included in our census) are ecologically relevant from the flies' perspective. Although they have limitations, such acoustic censuses are frequently used to estimate abundance, diversity, and structure of orthopteran species assemblages (Fischer et al. 1997; Diwakar et al. 2007; Sueur et al. 2008).

Experiment 2: Pupal overwintering

Wild flies removed from the field were used to propagate a lab colony of *O. ochracea*. The house cricket, *Acheta domesticus* (Linnaeus), was used as a host. Crickets were parasitized by hand using larvae dissected from freshly killed gravid female flies; an insect pin was used to place two to three larvae onto a cricket at the non-sclerotized junction between the pronotum and the head. Crickets were housed in individual 500 ml tubs with water in a cotton-plugged vial, monkey chow for food, and a section of egg carton for substrate until the larvae emerged and pupated. To reduce pupal mortality due to molding of small particles of cricket food or feces that had adhered to the pupal case, puparia were cleaned of debris by swirling in water; fly puparia were observed to float in water (Figure 3). Three to four puparia were then placed with a small amount of vermiculite in 500 ml polyurethane tubs that had aluminum window screen mesh tops and bottoms to allow for water penetration and drainage. Tub were loosely buried in

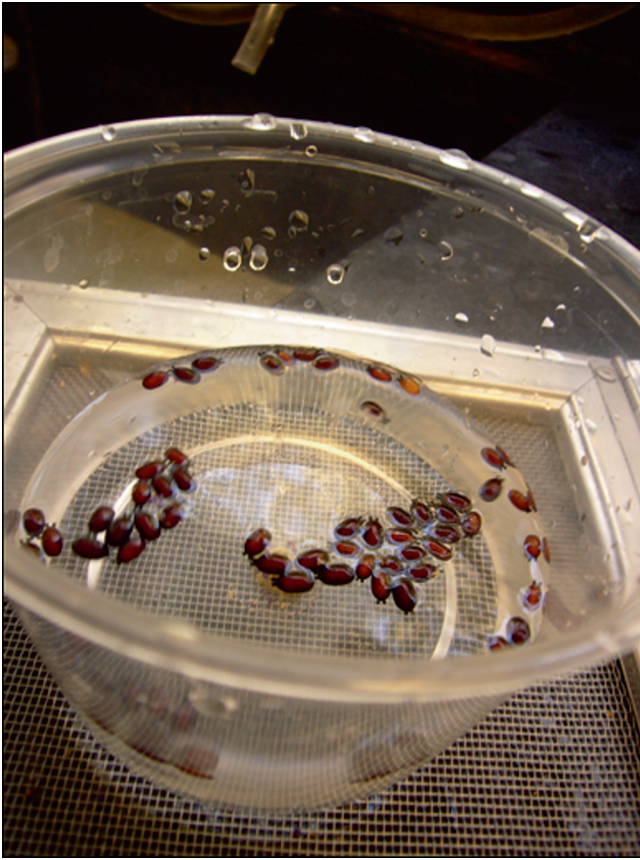


Figure 3. *Ormia ochracea* puparia floating in water.

the field flush with ground level, covered loosely with dirt clods, and marked by flagging. New puparia were buried every one to two weeks from 28 October 2008 to 4 January 2009 for a total of 43 puparia buried in 15 tubs. Tub contents were examined every one to two weeks from the beginning of burials through August 2009. Any changes in the pupal cases were noted and then the tubs were reburied.

Results

Ormia ochracea adults were active from late summer through late fall. The earliest responding flies were trapped on 11 August 2008, exhibited a seasonal abundance peak in mid-September, and continued to respond until 30 November (Figure 4). The beginning of the field cricket season occurred prior to initiation of the census. The parasitoid peak lagged behind the singing cricket host population peak by approximately 6 weeks. No calling crickets were heard in the evenings after 12 September. Censuses continued until 19 December with zero additional flies being trapped after 30 November. Temperature strongly affected fly response: sunset temperatures were

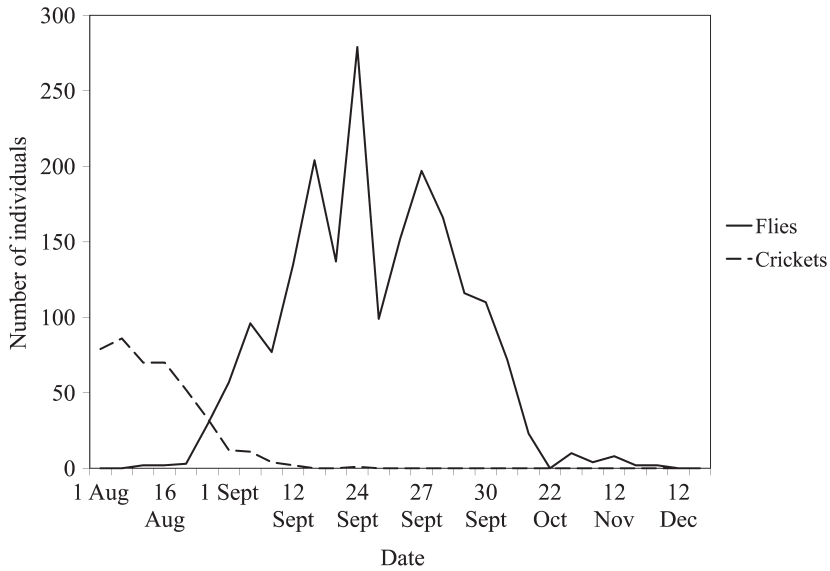


Figure 4. Seasonal abundance of *Ormia ochracea* and *Gryllus lineaticeps* field cricket hosts in the Santa Monica Mountains, Los Angeles County, California in summer and fall 2008.

Table 1. Field overwintering observations.

Date buried	Number of puparia	Results	Date of results
28 October 2008	3	No change	August 2009
12 November 2008	3	Puparia open, adults desiccated	3 May 2009
12 November 2008	3	No change	August 2009
19 December 2008	2	Emerged, no sign	21 February 2009
19 December 2008	8	No change	August 2009
4 January 2009	1	Puparia open, adult desiccated	21 February 2009
4 January 2009	8	No change	August 2009

near 12 °C after 2 December, the first date of the season to attract no flies. At temperatures above about 12 °C we noticed that trapped flies moved in synchrony with the chirps of the broadcast song, but below 12 °C trapped flies were motionless.

Experimental overwintering of flies as pupae within buried tubs produced mixed results (Table 1). Of the 43 puparia buried, only six showed any indication of successful overwintering and continued development. Of the rest, 15 developed mold, emerged before winter set in, or were not recovered; 22 were recovered intact but not viable and showing no signs of continued development. Of the six puparia that showed some indication of successful overwintering and continued development, two were open and empty pupal cases, and four were open pupal cases with a desiccated but adult appearing fly inside. In the case of the empty puparia, the vermiculite was

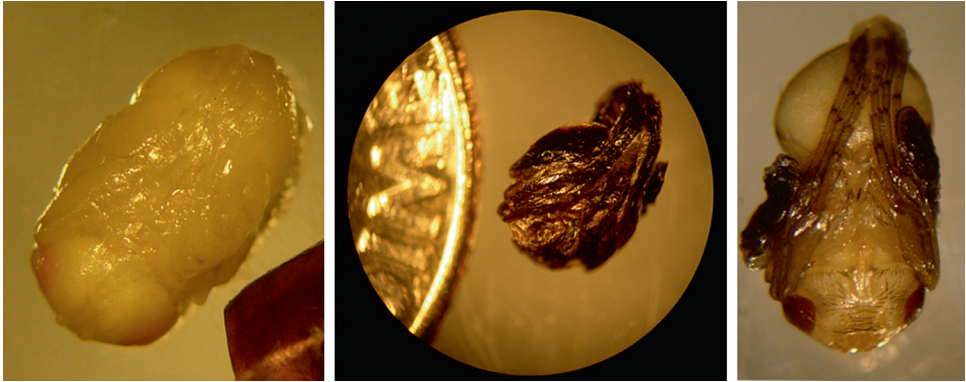


Figure 5. A comparison of developing pupae: the left panel shows a fly dissected from the puparium after 4 days of development in the laboratory (head toward bottom left); the middle panel shows one of our dried out pupae recovered from the field (same body orientation as first panel); the right panel shows a fly dissected from the puparium after 7 days of development in the laboratory (head toward bottom). Clearly developed features of the head, legs, and wings were visible in our field recovered specimens, suggesting continued development.



Figure 6. Three pupal cases, one with an emerging adult fly. Natural fly emergence leaves a characteristic opening in the puparium.

thoroughly searched but no sign of adult flies were found, with the exception of one wing. The desiccated adult flies were examined under a dissecting scope and compared to lab-reared pupae that had been dissected at different stages. The desiccated flies were in at least the very late stages of development, if not fully developed (Figure 5). The open pupal cases resembled cases opened by naturally emerging adult flies and showed no damage indicating contact by predators (puparia opened by emerging flies have a characteristic circular opening opposite the anal spiracles, see Figure 6).

Discussion

The adult *Ormia ochracea* population peaked about four weeks after the first responding flies were captured, nearly the same amount of time required for a complete life cycle in the lab. Therefore, the peak of parasitism occurred during a time when few flies were being trapped at the song broadcasts, suggesting that very few flies were the parents of the majority of the subsequent population. Further, during the population peak of adult flies, no calling crickets were heard in the field, suggesting that most adult flies in this population are alive when there are few to no hosts remaining. The European ormiine *Therobia leonidei* Mesnil also appears to progress from pupae to adults even after known suitable hosts (*Poecilimon* katydid, Tettigoniidae) have declined to near zero (Lehmann 2006). Under the assumption that the vast majority of these adult flies cannot survive several months until the next host season, this population seems to undergo an annual bottleneck, with many adult flies from late in the peak leaving no offspring. We do not know if a few of these flies can overwinter as adults or not, however during spring and early summer months it is clear that the many hundreds of fall adult flies are no longer present and active despite temperatures well above 12 °C.

Two alternate explanations of our demographic results are worth exploring. First, it is possible that many more *O. ochracea* were present in the environment in August than our data suggest, but were not attracted to our synthetic song because there were numerous calling male crickets available to ‘compete’ with our song broadcast. We cannot entirely exclude this possibility, and we are confident that there must have been some flies around even on nights when we caught none. However it seems unreasonable to us to think that there were hundreds of flies in August. This is based in large part on our experience catching flies elsewhere: even when calling male crickets are abundant, if flies are present they are caught at song traps (Gray and Cade 1999; Gray et al. 2007; Sakaguchi and Gray 2011). This is at least partly due to the fact that our broadcast song trap provides continuous stimulus, whereas real crickets call intermittently and for variable duration per night (Cade 1991; Bertram et al. 2004). The second alternative relates to the initiation date of our census. Because of permitting delays, we were unable to start our census on this property until August, after the field cricket season was underway. Therefore it is conceivable that both crickets and flies are multi-voltine and our census missed a peak of fly abundance sometime around July. Because we know that there are at least some active *O. ochracea* in July (note our single observation of a June 26, 2003 emergence) we do not dismiss this possibility entirely, but we are strongly skeptical that there is a July peak in abundance even remotely demographically equivalent to the September peak. This is because a July peak of flies would require a June peak of hosts, which has not been observed, and because similar studies of the fly in Florida also indicate a strongly univoltine major peak of fly abundance in late fall (Walker 1986) and parasitism rates of zero from December – August (Walker and Wineriter 1991).

The late-August decline in numbers of available calling male cricket hosts may be due to mortality caused by flies. The many hundreds of gravid female flies attracted to

our sound traps had all emerged from field crickets, killing them in the process. Assuming a 50:50 sex ratio of flies (Adamo et al. 1995b), and typically one but sometimes two fly pupae per cricket (Adamo et al. 1995b) this means that for every 100 female flies we caught, approximately 150 or more male crickets had died about four weeks previously (ca. 12 days for the flies to emerge from pupae, and 2-3 weeks to become sexually mature, mated, and gravid) – that is, the time lag between the crash of the cricket population and the peak of the fly population is nearly exactly the time lag one would predict if the decline in crickets was caused by mortality from flies. This idea suggests very high levels of parasitism of calling male crickets by flies. Rates of parasitism in this population have not been directly estimated, however in other species of field crickets parasitism rates by *O. ochracea* have been estimated in the wild several times. Adamo et al. (1995b) give an estimate of 8.1% parasitism of *G. texensis* Cade and Otte from Austin, Texas (studied under the previous name *G. integer*) and note that even at the end of the peak fly season perhaps 85% of male crickets are not parasitized. *Gryllus rubens* Scudder in Florida had low rates of parasitism, ca. 3% (Walker and Wineriter 1991). Rates of parasitism of male *Teleogryllus oceanicus* (Le Guillou) in Hawaii was estimated at 27% (Zuk et al. 1993); a separate later estimate (Kolluru 1999) was very similar (28%, 11 of 39 males). Parasitism rate of male *G. integer* in Aguila, Arizona was estimated at 10.3% and in Davis, California at less than 1% (Hedrick and Kortet 2006). These data might seem to suggest that flies are unlikely to have caused the dramatic decline in the calling adult male cricket population. However, all of the estimates for field crickets come from catching wild males, and determining parasitism rates from emergence and/or dissection of larvae. If parasitized males are systematically less likely to be caught and included in the test sample, then this basic approach systematically underestimates parasitism rate. There are two reasons to think that the capture of adult males biases the sample toward unparasitized crickets: (1) many crickets are located by researchers by using the male calling song, but we know that parasitized crickets dramatically reduce their calling activity once parasitized (Cade 1984; Kolluru et al. 2002; Orozco and Bertram 2004), and (2) these non-calling late stage infected crickets are likely to be deep within refugia (cracks, burrows, etc.) where they are inaccessible to predators and researchers alike. Rates of ormiine parasitism of large conspicuous katydids that do not hide underground in refugia are much higher than those reported above for the field crickets. For example, parasitism of *Neoconocephalus triops* (Linnaeus) by *O. lineifrons* Sabrosky approached 100% (Burk 1982); parasitism of *Poecilimon* katydids by *Therobia leonidei* approached 50% (Lehmann 2008); parasitism of *Sciarasaga quadrata* Rentz by *Homotrixa alleni* Barraclough approached 87% (Allen 1995). Some of these katydids continue calling once parasitized (Allen 1995), whereas others show a sharp decline in calling activity a few days after parasitism (Lehmann and Lehmann 2006). The extent to which fly parasitism contributes to the crash of the calling male cricket population is unknown, but we think the data and argument presented above suggest a significant role for flies in the mortality of these crickets; other sources of mortality are also of course likely, but are not as likely to be sex-biased. The fact that female *G. lineaticeps* can be found in the field weeks after no calling males are heard (several female crickets were

attracted to our song playbacks in late September and early October) suggests strong male-biased mortality.

The results of the overwintering study suggest that it may be possible for a few flies to overwinter as pupae and emerge as adults in spring, though success may be limited. Some pupae clearly continued development for a prolonged period of time and at least attempted to emerge from the puparium. Extended pupal development is not typical of most other ormiines studied to date (Lehmann 2008), but does occur in *Homotrixa alleni* (Allen 1995). Allen manipulated pupal temperature of developing *H. alleni* in the laboratory and also attempted a field diapause experiment. At temperatures ranging from 15–25 °C in the laboratory, development time was prolonged at cooler temperatures; field experiments with overwintering pupae failed due to predation by ants, however. In our field experiment some instances of predation are possible, but desiccation appeared to be the primary cause of failed development and/or mortality. Our pupae were buried very near the surface of the soil, and covered only with a thin layer of soil. Under natural conditions, it is likely that pupae would be buried deeper in the soil than they were in this experiment, as the larvae will have emerged from a dying cricket that is itself within a system of cracks in the soil. *Gryllus lineaticeps* routinely use the extensive crack systems that develop within the dried out clay-heavy soils of late summer as refuges (J. Paur and D. A. Gray personal observation), although it is not known how deep within these crack systems infested male crickets are likely to die and have larvae emerge to pupate. The fact that pupae were observed to float in water may allow pupae to float during the rains and avoid burial, increasing pupal survivorship.

Considering (1) the minimal success of overwintering pupae, (2) the inactivity of adult flies below about 12 °C, (3) the Neotropical origin of this genus, and (4) that the current geographic distribution of flies within North America is mostly restricted to localities with fairly mild winters, we think it is likely that *O. ochracea* lacks a true diapause overwintering strategy. Instead, we think it is more likely that both some pupae and very few adult flies survive the winter via cold-induced quiescence. It is worth noting that *G. lineaticeps* are often heard calling during late-morning hours on sunny warm days in January and February; whether some of these individuals could become parasitized and bridge the demographic gap from fall to late spring is unknown.

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