

BIOLOGY, IMMATURE STAGES, AND REDESCRIPTIONS OF *HYDRELLIA PERSONATA* DEONIER (DIPTERA: EPHYDRIDAE), A *LEMNA* MINER

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Abstract.—*Hydrellia personata* Deonier (Diptera: Ephydriidae) is a rarely collected shore fly found in the western and midwestern United States. We encountered a population in a constructed wetlands in southern California where the larvae were miners of duckweed (*Lemna minor* L.). Eggs were inserted between the upper and lower layers of epithelial tissue. Newly hatched larvae either bored into a duckweed thallus or separated the upper and lower epithelial layers to gain access to the photosynthetic tissue. Each instar mined several plants prior to molting inside of a plant thallus, and pupariation occurred inside a hollowed-out thallus. Several pupae were parasitized by the braconid *Cyrtogaster clavicornis* Walker. Overall, the biology and morphology of the immature stages were very similar to that of the closely related genus *Lemnaphila*. We describe all immature stages and redescribe the adult (male and female) based upon the newly collected materials. The unusual adult morphology of this species prevents its placement into any of the existing species groups of *Hydrellia*.

Key Words: shore flies, *Hydrellia*, aquatic insects, leaf miner, herbivory, duckweed, *Lemna*, wetlands

Shore flies (Diptera: Ephydriidae) represent a species-rich family of acalyprate Diptera with a world-wide distribution (Mathis and Zatwarnicki 1995). Most species are intimately linked to aquatic and semi-aquatic habitats, and this family displays vast adaptive radiation in larval feeding habits. Shore flies exploit detritus, bacteria, cyanobacteria, diatoms, green algae, plants, decaying animal carcasses, and prey on heterospecific invertebrates (Foote 1995). Although many shore flies are associated with aquatic macrophytes as secondary stem borers (e.g., Deonier 1999, Keiper et al. 2001) or use plant stands as

refugia (Todd and Foote 1987, Keiper et al. 1998, Keiper and Walton 2000), the genera *Hydrellia* Robineau-Desvoidy, *Lemnaphila* Cresson, and *Cavatorella* Deonier represent the only known ephydrid leaf miners from aquatic habitats (Deonier 1998).

Duckweed (*Lemna minor* L.: Lemnaceae) is a characteristically minute plant whose mature individuals are 1–3 mm long and 0.5–1 mm wide (Mason 1957). Despite its small size, certain species of *Hydrellia* (Deonier 1998) and all *Lemnaphila* spp. (Scotland 1934, 1939; Mathis and Edmiston 2000) exploit duckweed as a host plant. The best studied examples of ephydrids associated with *Lemna* are *Lemnaphila scotlandae* Cresson and *Hydrellia williamsi* Cres-

son (Williams 1938, Scotland 1939, Mathis and Edmiston 2000). Larvae mine the photosynthetic tissues of multiple plants prior to pupariation, and puparia are formed within the last larval host plant. Mansor and Buckingham (1989) discussed the possible use of *L. scotlandae* in biocontrol efforts of large populations of duckweed and demonstrated its restricted host range using ovipositional and larval development studies.

During investigations of the distribution and abundance of Diptera in the Prado Constructed Wetlands (CA, Riverside Co.), we encountered mined duckweed plants containing puparia. *Lemnaphila scotlandae* and *H. griseola* (Fallén) (Grigarick 1959) were the only two previously known Nearctic miners of duckweed. The distribution of *L. scotlandae* is restricted to areas east of the Mississippi River (Mathis and Zatwarnicki 1995, Mathis and Edmiston 2000) and *H. griseola* is highly polyphagous (Deonier 1998). Adults reared from the duckweed plants proved to be *Hydrellia personata* Deonier (1971), a relatively rare species for which few specimens are available. We provide a redescription of the male and female based on the new material obtained, and describe the immature stages and general biology.

MATERIALS AND METHODS

The Prado Constructed Wetlands are a series of freshwater marshes interconnected by water control structures, encompass more than 125 ha, and are supplied with water from the Santa Ana River. The wetlands support a mosaic of emergent and submerged vegetation, most notably California bulrush (*Schoenoplectus californicus* [Meyer] Sojak), cattails (*Typha* spp.), lesser duckweed (*Lemna minor* L.), emergent and submerged species of buttercups (*Ranunculus* spp.), and pennywort (*Hydrocotyle ranunculoides* L.). Nearby aquatic habitats include periodically flooded duck club ponds and low gradient intermittent streams.

Immature specimens were collected by

scooping up duckweed clusters with mosquito dippers. Samples were scanned with a dissecting microscope at 6–12× to find plants with eggs, larvae, or puparia. Specimens were reared in petri dishes, and active larvae were given undamaged plants to observe feeding. Plants with puparia were placed in petri dishes, kept at laboratory temperatures (18–20° C), and a 16:8 light:dark photoperiod maintained with incandescent lights. Representatives of all immature stages were fixed in KAA solution and preserved in 70% ethanol.

Field-collected adults were placed in breeding cages with marsh water and duckweed for observations of mating behavior, oviposition, and adult feeding. Small cages manufactured from plastic cups inverted on petri dishes were ineffective, as adults spent most of their time resting at the screened openings. Larger, 2 liter plastic boxes with screened lids seemed to provide a better adult habitat as the flies spent considerable time among the floating duckweed placed within. Breeding cages were exposed to the same photoperiod and temperature regime as larvae.

RESULTS AND DISCUSSION

The following adult description is based upon the original type series and 31 specimens collected by JBK, MS, JJ, and WEW at the Prado Constructed Wetlands, Riverside County, CA. For methods, indices, and other terminology see Deonier (1998).

Hydrellia personata Deonier (Figs. 1–13)

Hydrellia personata Deonier 1971: 86.—
Mathis and Zatwarnicki 1995: 85.—
Deonier 1998: 35, 42.

Diagnosis.—Maxillary palp dark brown, smoothly angular and slightly spatulate with 3–4 apical setae about 0.3+ of palpal length; 5–8 (usually 5–6) dorsal aristal rays; antenna dark brown (velvety in dorsal view); antennomere 3 with sparse (occasionally dense) light golden-brown micro-

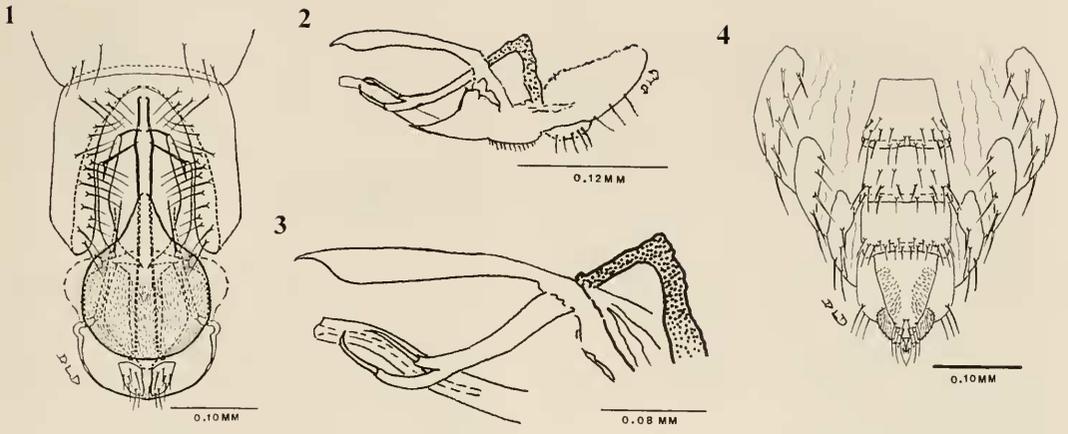
pubescence visible in dorsomedial view; frontal vitta and parafrontalia velvety dark-brown pruinose in dorsal view; antennomere 2 with usually 2 prominent spinoid apicodorsal setae; face, in profile with lower 0.5 slightly convex (not bulging) and with a slight median carina; face sericeous silvery or light-gray pruinose, contrasting with dark brown, narrow, unilinear parafacialia; 3–4 primary facial setae, with usually 1 minute upper secondary facial setula; ocular index 4.0–5.0; head width/head height 1.3–1.7; 1 postsutural (nearly sutural) dorsocentral macrochaeta present; pleuron densely olive- or reddish-brown pruinose; legs, except yellowish orange trochanters, tibial apices, and tarsal venters, dark brown; tibiae not dilated or expanded; mesonotal disc and abdomen semiglossy or glossy brown in dorsolateral view. Male length 1.28–1.80 mm; female 1.45–2.20 mm. Male postabdomen as in Figs. 1–3 and 5; female postabdomen as in Figs. 4 and 6.

Description.—*Head:* Face, in profile, with lower 0.5 slightly convex (not bulging) and with a slight, but noticeable median carina; face sericeous silvery or light-gray pruinose, contrasting with dark-brown, narrow, unilinear parafacialia; antennal foveae indistinct; epistoma squarely recessed (sometimes slightly concave with median indentation) and congruent with dark brown anteclypeus; 3–4 primary facial setae in 1 row, with 1–3 (usually 1) minute, porrect or declinate secondary facial setulae; antenna dark brown (velvety in dorsal view); antennomere 2 with usually 2 prominent, spinoid apicodorsal setae; antennomere 3 with sparse (occasionally dense) light golden-brown micropubescence visible in dorsomedial view; 5–8 (usually 5–6) dorsal arisal rays; frontal vitta and parafrontale often scarcely differentiated, both appearing velvety dark-brown pruinose in dorsal view (except ocellar triangle sometimes light-brown pruinose); fronto-orbital area concolorous with parafrontale; anterior fronto-orbital seta 0.3–0.5 length of posterior seta; frons moderately sloping; 12–16 postocular

setae in fairly regular row nearest posterior orbit; maxillary palpus dark brown, smoothly angular and slightly spathulate with 3–4 apical setae about 0.3+ of palpal length. Epistomal index 1.0–1.4; mesofacial index 1.5–2.0; vertex index 5.5–7.0; ocular index 4.0–5.0; subcranial index 1.3–2.0; head width/head height 1.3–1.7.

Thorax: Postpronotum and notopleuron usually densely olive-brown pruinose, but sometimes dark-brown or light yellowish-brown pruinose; mesonotal disc, in dorsolateral view, glossy dark brown with sparse to moderately dense olive-brown pruinosity; 3–4 antesutural (1–2 × macrochaetous) and 1 postsutural (macrochaetous) dorsocentral setae [Riverside Co. CA population with only postsutural (nearly sutural) dorsocentral seta macrochaetous]; minute, paired auxiliary apical scutellar setulae usually present between apical scutellar macrochaetae; pleuron usually concolorous with notopleuron, but sometimes moderate reddish-brown pruinose; 1 mesokatepisternal seta (macrochaetous); legs, except yellowish orange trochanters, apical 0.2 of tibiae, and tarsal venters, dark brown with sparse to moderately dense olive-brown pruinosity; meso- and metatibiae not dilated or expanded. Wing length 1.25–2.04 mm; veins dark brown; 6–8 setae on basal end of costa; 3–6 dorsal and 6–9 anterior interfractural costal setae; costal-section ratios: II: I 1.8–2.2; III: IV 3.5–4.0; V: IV 3.0–3.6; M_{1+2} index 1.2–1.5.

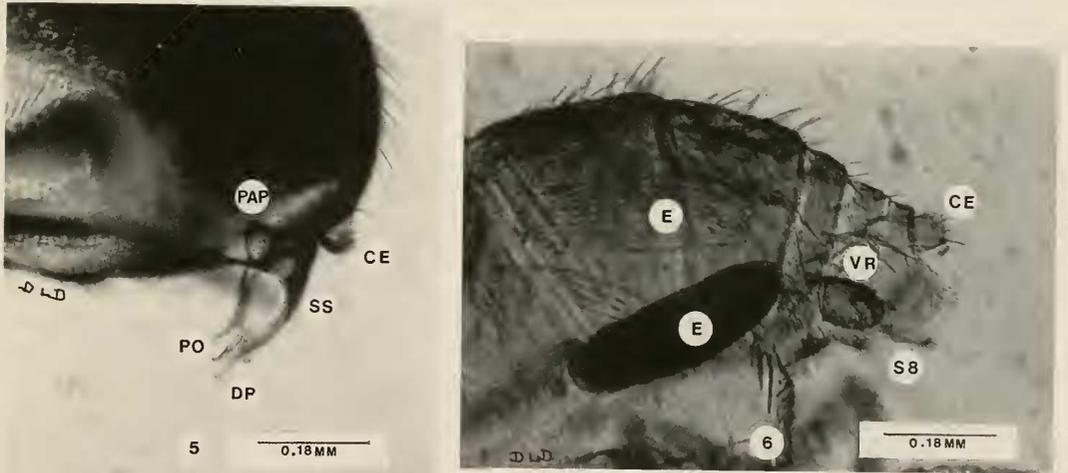
Abdomen: Terga dark brown with sparse to moderately dense light-brown pruinosity in lateral view, but glossy or semiglossy in dorsolateral and posterodorsal views. Male postabdomen: median 0.3 of sternum 5 broadly concave; anterolateral margin of sternum 5 rounded through 95°–100° angle; copulobus truncate to diagonally truncate posteriorly and somewhat irregularly setose. Postgonite bifurcate and paralleling distiphallus for over 0.5 latter's length; median branch 2.0–2.5× length of lateral branch of postgonite and with slightly curved postgonite uncus about 0.5 length of



Figs. 1-4. *Hydrellia personata*. 1, Male genitalia, ventral view. 2, Male genitalia, left lateral view. 3, Male genitalia emphasizing phallapodeme, bifurcate postgonite, and distiphallus, left lateral view. 4, Female postabdomen, ventral view.

more nearly straight uncus of lateral branch; both postgonite unci directed mediad toward distiphallus; pregonite much smaller, straight, and covered by fused surstyli; distiphallus long, digitiform, and often slightly expanded at midlength, upcurved and slightly tapering to nearly blunt apex in lateral view; basiphallus concealed in ventral view by fused surstyli (in cleared specimens appearing as slightly wider continu-

ation of distiphallus); phallapodeme, in lateral view, darkly sclerotized and forming right angle above basiphallus, but showing no distinct condylar scar or process. Fused surstyli with nonpubescent, acute, anteromedial papilliform projection and with single (paired) anteriorly projecting macrochaeta inserted anterolaterally; fused surstyli length:cercus length (ventral view) about 4.8:1.0. Epandrium (syntergum 9+10)



Figs. 5-6. *Hydrellia personata*. 5, Photomicrograph of male postabdomen with exerted genitalia, left lateral view. 6, Photomicrograph of female postabdomen (partly cleared), left lateral view. Abbreviations: CE, cercus; DP, distiphallus; E, egg; PAP, phallapodeme; PO, postgonite; SS, surstyli; S8, sternum 8; VR, ventral receptacle.

evenly rounded (semicircular) posteriorly. Female postabdomen: sternum 8 slightly narrower basally than 7, about 1.5× longer than wide, and tapering conically posteriorly; tip of sternum 8 with 6–8 long, slightly incurved setae arranged in a semirosette in ventral view; sterna 6 and 7 nearly quadrangular, 5 noticeable wider distally than basally; cercus, in lateral view, diagonally to roundly truncate distally, 1.2–1.4× as long as wide, and directed straight posteriorly. Ventral receptacle cupuliform, about 1.5× deeper than wide.

Types.—*Hydrellia personata* Deonier 1971: 86 [USA. Washington. Grand: O'Sullivan Dam; HT ♂, Washington State University (322)]; 1998: 35, 42 [revision].—Mathis and Zatwarnicki 1995: 85 [world catalog].

Additional specimens examined.—California: Riverside County, Prado Wetlands, pan trap (VII-2-1999, coll: J. B. Keiper), 3 ♂, 2 ♀; (VII-10-1999, collector: J. B. Keiper), 1 ♂, 3 ♀; (V-4-2000, collector: J. B. Keiper) 4 ♂, 18 ♀ (1 ♂ in Deonier Collection, remainder in collection of Cleveland Museum of Natural History).

Distribution.—Found from Washington to southern California, east to Iowa and Texas.

Remarks.—The identification of pregonite and postgonite was erroneously reversed in the original description. DLD has still not been able to place this species in a species-group. It differs from the *H. prudens* and *H. tibialis* species-groups noticeably by its wide head, and its normal, unexpanded male mesotibia. For the original type-series, the only habitats recorded were sedge meadow and margin of Mono Lake, California.

Immature stages.—*Egg* (n = 5): Length, 0.36–0.38 mm (\bar{x} = 0.37). White, ends bluntly rounded, with longitudinal ridges along entire length; ridges interconnected with narrow cross ridges. Micropyle small and inconspicuous (Fig. 7).

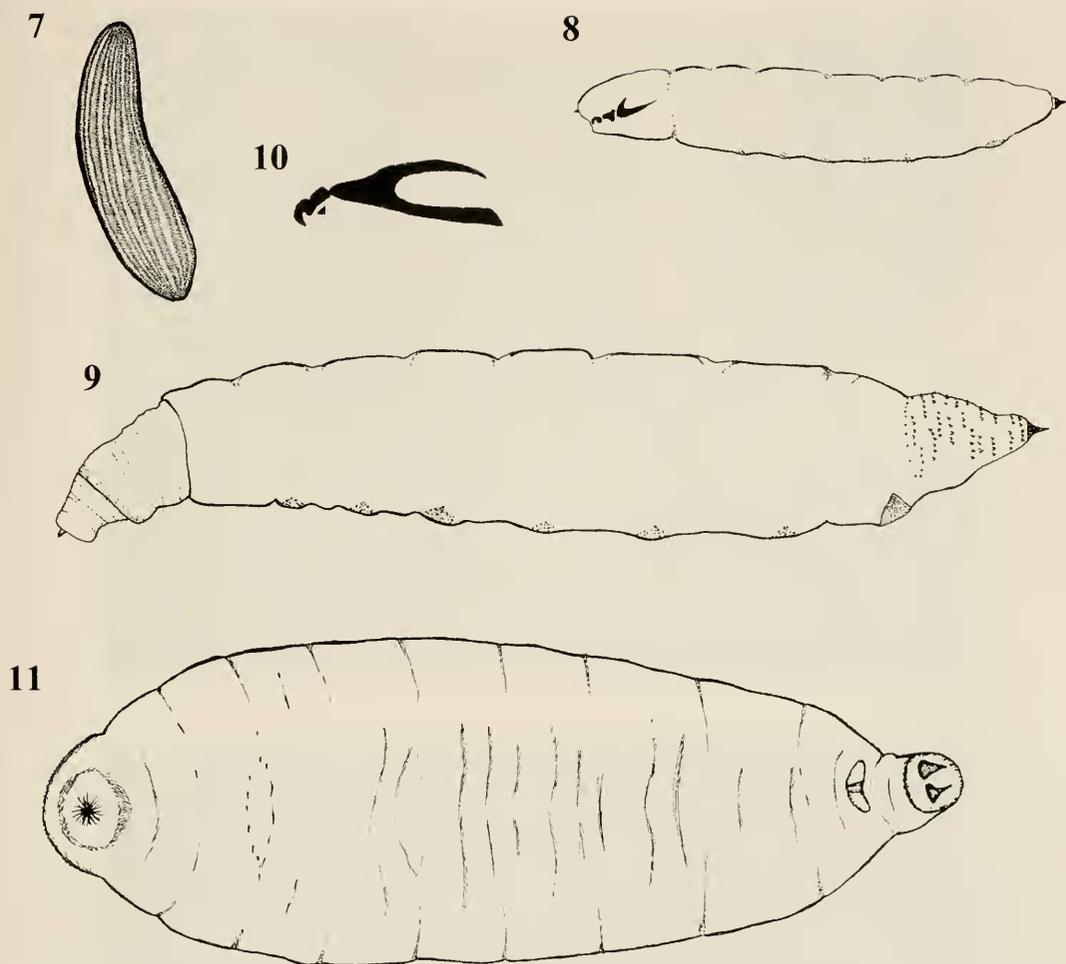
First instar (n = 2): Similar to third instar except in the following: Length, 0.87–

0.89 mm (\bar{x} = 0.88); maximum width, 0.14–0.15 mm (\bar{x} = 0.15). Body white, somewhat transparent; little distinction among abdominal and cephalic segments. Cephalopharyngeal skeleton reduced, especially dorsal cornu. Breathing tube lacking spines (Fig. 8).

Second instar (n = 6): Similar to third instar except in the following: Length, 1.13–1.65 mm (\bar{x} = 1.40); maximum width, 0.20–0.32 mm (\bar{x} = 0.26). Body nearly opaque yellowish; little distinction among abdominal and cephalic segments. Cephalopharyngeal skeleton somewhat reduced. Breathing tube with minute brown spines only.

Third instar (n = 7): Elongate, muscoid (Fig. 9). Maximum length, 2.24–2.77 mm (\bar{x} = 2.47); maximum width, 0.43–0.53 mm (\bar{x} = 0.47); widest at approximately posterior 2/3; yellow in life, fading to opaque white in preservative. Short antennae anteriorly, dark brown; facial mask generally triangular, with median carina (Fig. 12). Pseudocephalic segment lined with rows of narrow, minute spines that increase in length posteriorly; anterior spines approximately 0.2× length of longest posterior spines. Anterior spiracles absent. Abdominal segments well-defined; anterior abdominal segments not strongly adorned, posterior segments adorned with 9–10 rows of short brown spines dorsally; breathing tube short, representing <1/10 of total body length, lacking spines; posterior spiracles tipped with brown conical spines ~0.04 mm long, each spine bordered by 4 palmate groups of hydrofuge hairs (Fig. 13); abdominal segments 2–7 with fleshy ventral creeping welts adorned with fine spinules; perianal pad oblate, tapering laterad, ~0.15 mm wide. Cephalopharyngeal skeleton typical of *Hydrellia*; mouthhook strongly curved, no accessory teeth; dental sclerite small and triangular; dorsal cornu tapering posteriorly, posterior cornu truncate posteriorly, both lacking windows (Fig. 10).

Puparium (n = 17): Length, 1.52–2.16 mm (\bar{x} = 1.91); maximum width, 0.63–0.94



Figs. 7–11. *Hydrellia personata*. 7, Egg, dorsal view. 8, First instar, lateral view. 9, Third instar, lateral view. 10, Same, cephalopharyngeal skeleton. 11, Puparium, ventral view.

mm ($\bar{x} = 0.74$). Amber; segmentation conspicuous, margin of puparium smooth; broadly rounded anteriorly, tapering posteriorly, widest anteromedially. Posterior spiracles dark, curved ventrad (Fig. 11). Third instar cephalopharyngeal skeleton pressed flat, visible through puparium.

Remarks.—The eggs of *H. personata* are easily distinguished from those of *L. scotlandae* (Mathis and Edmiston 2000). Those of *L. scotlandae* are flattened ventrally, have only four longitudinal ridges, and have a light brown chorion, whereas those of *H. personata* are not flattened, have more than 4 longitudinal ridges, and the chorion

is white. In contrast, the mature larvae are very similar in these two *Lemma*-consuming species, including the general shape, ventral creeping welts, conical posterior spiracles, and morphology of the mouth-hooks of the cephalopharyngeal skeleton. A slight difference exists in the puparia, as *L. scotlandae* are widest posteromedially and *H. personata* are widest anteromedially.

Biology and larval feeding habits.—Adults of *H. personata*, some of the smallest in the genus, have been collected in five states from the Pacific coast to the Mississippi River. This distribution is entirely within the distributional range of the now



Figs. 12–13. *Hydrellia personata*. 12. Scanning electron micrograph of third instar facial mask. 13. Same, posterior spiracles.

known single larval host-plant species, *Lemna minor* L. Although this host-plant species has now been confirmed through rearings, much remains unknown about the natural history of this rare little *Hydrellia*. Despite records of populations in Iowa and Texas, prolonged surveys with floating adhesive traps or floating detergent traps by DLD on the many year-round *Lemna* pools in southeastern Kansas have failed to discover its presence there. Many *L. scotlandae* (over 100) and a few *H. griseola* and *H. bilobifera* Cresson along with four *Setacera* sp. and one *Discocerina obscurella* (Fallén) were the only ephydriids trapped.

Adult populations of the Prado Constructed Wetlands were located only in areas of dense duckweed growth (at least three plants cm^{-2}), where they were observed walking or resting on duckweed plants. Some areas of the wetlands with dense growths harbored no adults (or evidence of immatures), whereas other areas supported flies in abundance. Their small size and habit of walking on duckweed plants allowed us to observe adults or capture them with vials easily. Although adults exhibited the capacity to skate on the water surface, they did so only rarely and appeared to prefer the solid substrate offered by the floating plants. Adults fed by sponging the dorsal surface of duckweed plants with their mouthparts and sometimes touched their probosci to the water surface. Unlike *L. scotlandae* adults (Scotland 1934, Mathis and Edmiston 2000), *H. personata* did not appear to damage the plants.

Flies moved slowly over the surface of thick growths of duckweed, and flew short distances if disturbed. Intraspecific aggression was apparent when conspecifics wandered closely (approximately 1–1.5 cm) to a stationary female. The female would rapidly approach the intruder causing it to retreat. Males did not display aggressive behavior during our observations.

Eggs were infrequently collected in nature, and only one egg was laid during laboratory observations. All eggs were insert-

ed about half way into the peripheral margin of duckweed plants and positioned so the micropylar end protruded freely from the plant. Three to four eggs, situated adjacent to each other, were inserted into each of five field-collected plants; the single egg laid in the laboratory was placed similarly.

The small size of the immatures made it impossible to locate them in nature. However, population sizes were large enough that scooping duckweed from between stems of emergent plants produced ample specimens for study and rearing. Newly hatched larvae burrowed into the host plant or stretched their bodies and probed the surrounding area until a neighboring plant was located. Larvae latched onto the nearby plant with their mouthhooks and pulled themselves onto the new host. Older larvae used their mouthparts to separate the dorsal and ventral halves of plant fronds and fed on the exposed photosynthetic tissues. Larvae crawled into the hollowed area of the plant as tissue was removed. The posterior spiracles remained outside of the plant and in contact with the atmosphere. Two first instars did not separate the dorsal and ventral halves of the host frond, but moved to the underside of the plant where they burrowed through the epithelial tissue to gain access to the photosynthetic tissues. Young larvae did not hollow plants completely, but created U-shaped mines prior to exiting and moving to another host plant. Conversely, second and third instars always attacked plants by separating the two halves of the frond and consuming all the photosynthetic tissues or nearly so.

Molting occurred inside duckweed plants and exuviae remained within the hosts. Puparia were formed within hollowed-out duckweed fronds, but the posterior spiracles did not extend to the atmosphere. Damaged duckweed plants remained floating on the water surface, and atmospheric air probably diffused into the damaged plant through the epithelial break formed by third instars. Adults exited plants through the epithelial break. Five adult *Cyrtogaster clavicornis*

Walker (Hymenoptera: Braconidae) (2f, 7 Oct 1998; 3f, 9–15 Jan 2000) emerged from field-collected puparia situated within duckweed plants. This parasitoid has also been reared from puparia of *H. griseola* (Fulmek 1962).

Because of difficulty with laboratory rearings and the intimate trophic association of *H. personata* with duckweed in nature, the precopulation period, fecundity, and seasonal distribution remain unknown. The first specimens collected were puparia taken 22 September 1998, and further larvae and puparia were collected 26 September 1998 and 29 June 1999 for rearing. Adults were observed during January 2000, and puparia within plants were collected among a senescing population of duckweed at that time. No larvae or eggs were found during the winter months. Sporadic collections of adults and all immature stages indicate that *H. personata* is multivoltine and exhibits many overlapping generations in the latitude of southern California. The first, second, and third larval stadia were 2–3, 2–3, and 4–5 days, respectively, with a pupal duration of 8 days.

The control certain of pestiferous aquatic plants using dipterans has been successful (Center et al. 1997), and has been tested for *Lemna* (Mansor and Buckingham 1989). Although biocontrol programs against large blooms of duckweed have not been implemented rigorously, *Hydrellia personata* represents such an opportunity. Biocontrol efforts with this shore fly in the western United States may allow for use of a local species rather than having to import an exotic one from a geographically distant area.

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LITERATURE CITED

- Center, T. D., M. J. Grodowitz, A. F. Cofrancesco, G. Jubinsky, E. Snoddy, and J. E. Freedman. 1997. Establishment of *Hydrellia pakistanae* (Diptera: Ephydriidae) for the biological control of the submersed aquatic plant *Hydrilla verticillata* (Hydrocharitaceae) in the southwestern United States. *Biological Control* 8: 65–73.
- Deonier, D. L. 1971. A systematic and ecological study of Nearctic *Hydrellia* (Diptera: Ephydriidae). *Smithsonian Contributions to Zoology* 68: 1–147.
- . 1998. A Manual of the Common North American Species of the Aquatic Leafmining Genus *Hydrellia* (Diptera: Ephydriidae). *Memoirs on Entomology*, International 12. Associated Publishers, Gainesville. 354 pp.
- . 1999. *Rhysophora laffooni*, new species (Diptera: Ephydriidae), a saprophage on water lettuce (*Pistia stratiotes* L.) in Florida. *Proceedings of the Entomological Society of Washington* 100: 775–791.
- Foote, B. A. 1995. Biology of shore flies. *Annual Review of Entomology* 40: 417–442.
- Fulmek, L. 1962. Parasiten der Blattminierer Europas. W. Junk, The Hague. 203 pp.
- Grigarick, A. A. 1959. Bionomics of the rice leaf miner, *Hydrellia griseola* (Fallén), in California (Diptera: Ephydriidae). *Hilgardia* 29: 1–80.
- Keiper, J. B. and W. E. Walton. 2000. Biology and immature stages of *Brachydeutera sturtevanti* (Diptera: Ephydriidae), a hyponeustic generalist. *Annals of the Entomological Society of America* 93: 468–475.
- Keiper, J. B., P. L. Brutsche, and B. A. Foote. 1998. Acalyprate Diptera associated with water willow,

- Justicia americana* (Acanthaceae). Proceedings of the Entomological Society of Washington 100: 576–587.
- Keiper, J. B., J. Giannino, M. Sanford, and W. E. Walton. 2001. Biology and immature stages of *Tylopsilopa nigra* (Williston) (Diptera: Ephydriidae), a secondary consumer of damaged stems of wetland monocots. Proceedings of the Entomological Society of Washington 103: 89–97.
- Mansor, M. and G. R. Buckingham. 1989. Laboratory host range studies with a leaf-mining duckweed shore fly. Journal of Aquatic Plant Management 27: 115–118.
- Mason, H. L. 1957. A Flora of the Marshes of California. University of California Press, Los Angeles. 878 pp.
- Mathis, W. N. and J. F. Edmiston. 2000. A revision of the shore-fly genus *Lemnaphila* Cresson (Diptera: Ephydriidae). Proceedings of the Entomological Society of Washington 102: 652–677.
- Mathis, W. N. and T. Zatwarnicki. 1995. World Catalog of Shore Flies (Diptera: Ephydriidae). Memoirs on Entomology, International 4. Associated Publishers, Gainesville. 423 pp.
- Scotland, M. B. 1934. The animals of the *Lemma* association. Ecology 15: 290–294.
- . 1939. The lemma fly and some of its parasites. Annals of the Entomological Society of America 32: 713–718.
- Todd, J. L. and B. A. Foote. 1987. Spatial and temporal distribution of shore flies in a freshwater marsh (Diptera: Ephydriidae). Proceedings of the Entomological Society of Washington 89: 448–457.
- Williams, F. X. 1938. Biological studies in Hawaiian water-loving insects, Part III, Diptera or flies. A. Ephydriidae and Anthomyiidae. Proceedings of the Hawaiian Entomological Society 10: 85–119.