Biology and Immature Stages of *Brachydeutera sturtevanti* (Diptera: Ephydridae), a Hyponeustic Generalist

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ABSTRACT *Brachydeutera sturtevanti* Wirth is a shore fly found commonly in a variety of lentic habitats, including ephemeral pools, in the American Southwest and northern Mexico. We conducted field studies and laboratory rearings to elucidate the morphology and trophic ecology of this colonizer species important to newly flooded habitats such as constructed wetlands. The larvae are generally hyponeustic, suspended from the water surface by hydrofuge hairs on the posterior spiracles. All instars exhibit extremely versatile feeding strategies by collecting or scraping algae and detritus from solid substrates, or by bringing their mouthparts to the water surface and creating a vortex to initiate filter feeding. The mouthhooks are modified to form dorsoventrally-flattened plates lined with stout projections that facilitate the versatile larval feeding. The incubation period under laboratory conditions (20–22°C) was 1–4 d; the three stadia lasted 3–5 d each while the pupal period was 6–8 d. The results of a colonization experiment with 15 liter tubs containing distilled water (controls, C), oligotrophic lake water (L), lake water with a tule extract (T), lake water supplemented with the green alga *Chlamydomonas* (A), or lake water with both a tule extract and algae (TA) illustrated the ability of *B. sturtevanti* to colonize and complete larval development in habitats varying broadly in food quality. Adults were equally attracted to all treatments and each treatment produced equivalent numbers of puparia. The mean dry weight per puparium formed in each treatment showed an increasing trend of tule extract and algae > A > T > L > C, but dry weights among treatments were statistically equal. These data illustrate the generalist and opportunist nature of *B. sturtevanti*. The egg, three instars, and puparium are described and illustrated, and a preliminary key to *Brachydeutera* third instars from North America north of Mexico is given.

KEY WORDS *Brachydeutera sturtevanti*, shore flies, larval feeding habits, r-strategist, wetlands, keys

THE BIOLOGY OF shore flies (Diptera: Ephydridae) has received considerable attention by entomologists and ecologists; however, the immatures of most species remain unknown. These small flies exploit many trophic and spatial niches in aquatic ecosystems, and although some exhibit specialized feeding or microhabitat preferences, larvae of many genera use a broad spectrum of resources (Foote 1995, Courtney et al. 1996). The genus *Brachydeutera* Loew contains 15 species worldwide (Mathis and Zatwarnicki 1995) and is represented by five species in North America and Hawaii (Williams 1938, Mathis and Steiner 1986). Larvae are present in a variety of lentic habitats and appear to be trophic generalists. Adults and larvae are found at the water surface, usually among emergent vegetation. Williams (1938) reared *B. hebes* Cresson in Hawaii and reported that larvae scraped materials from dead and living leaves, consumed algal filaments, and scavenged dead animal tissues. *Brachydeutera argentata* (Walker) (Johannsen 1935) and *B. neotropica* Wirth (Lizarralde de Grosso 1972) also exhibit scavenging habits. Scheiring and Foote (1973) reared *B. sturtevanti* Wirth on decaying lettuce; the larvae probably obtained most of their nutriment from associated microorganisms. *Brachydeutera longipes* Hendel is an adventive species from the Oriental region and remains unreared; no biological observations have been published for this species (Mathis and Steiner 1986).

The third instars of *B. hebes* (Williams 1938), *B. argentata* (Johannsen 1935), and *B. neotropica* (Lizarralde de Grosso 1972) have been described, whereas those of *B. longipes* and *B. sturtevanti* have not. No published information on the morphology of early instars of *Brachydeutera* is available. Herein, we give information on the biology and morphology of all immature stages of *B. sturtevanti* from southern California. We also present the results of an experiment that addressed the hypotheses that adults are not selective in their use of water containing different potential larval food sources as breeding sites, and that the mean time until formation of the puparium and pupal mass are equal regardless of the food source provided to larvae. Species of *Brachydeutera* appear to be important colonizers, and frequently we have observed *B. sturtevanti* adults and immatures in large numbers in newly flooded habitats. Constructed wetlands are becoming common in the arid southwestern United States (Walton and Workman 1998), and knowledge of the natural history and feeding ecology of early colonists is important to understanding the

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community structure and ecosystem processes of these anthropogenic environments. A preliminary key to species of *Brachydeutera* larvae from North America north of Mexico is given to provide ecologists a means to identify field-collected larvae, and to provide morphological comparisons among species to shed light on the systematics of the genus.

Materials and Methods

Adults were taken in several areas of Riverside County, CA, during this study. Several hundred were collected at the Hemet/San Jacinto Multipurpose Treatment Wetlands, an assemblage of constructed wetlands supplied with secondary effluent from a nearby sewage treatment plant (Walton and Workman 1998). Flies were pan trapped (Southwood 1978) and swept with an aerial net from around the periphery of stands of tules [*Schoenoplectus californicus* (Meyer) Soják]. Approximately 200 were collected from the Prado Constructed Wetlands near the city of Corona; these wetlands were supplied with water diverted from the Santa Ana River. Adults were taken from stands of tules and cattails (*Typha* spp.). The University of California-Riverside Agricultural Experiment Station is the location of a diverse array of shallow mesocosms designed for the study of aquatic entomology; adults were taken while resting on the water surface or positioned on floating algal mats. The last, and the most ephemeral habitat studied, was shallow pools at the margins of the Colorado River Aqueduct near the city of Whitewater. These pools were formed when the level of the aqueduct receded, and water puddled in concavities of the rocky shore.

Immatures were usually located by hand at the water surface near vertical structures such as emergent vegetation and along the edges of mesocosms; larvae and pupae were collected with small mesh scoops, whereas some specimens were collected with standard 300-ml dippers during routine sampling for mosquitoes. Eggs were sometimes taken from floating algal mats where adults were observed to congregate. Field-collected immatures were saved for rearing, preserved in the field with 50% ethanol (dips), or killed in near boiling water, fixed in Kahle's solution, and preserved in 70% ethanol. Larvae saved for rearing were placed in small petri dishes with 3–5 ml of sieved lake water and a potential food source. Rearing dishes were placed near a window to maintain a natural photoperiod and kept at room temperature (20–22°C).

Field-collected adults were placed in small breeding jars consisting of a plastic cup with its bottom replaced with fine mesh screen inverted on a petri dish containing water, algae, and detrital material. Because only one egg was obtained from 12 females, another 12 females were placed in two larger transparent containers (30 by 15 by 10 cm) with screened lids containing the same substrates as the breeding jars. These females oviposited liberally, and adult feeding, mating, and oviposition were observed. Eggs were removed and distributed to petri dishes as described above. Dishes were examined daily for larval hatch and subsequent larval development. Larvae were observed with a dissecting microscope at 6–50× with a fiberoptics light source at the lowest setting needed for observation to avoid altering larval behavior. Duration of the incubation period and each stadium was determined by direct observation of eclosion and molts, respectively.

Only specimens killed in near boiling water and fixed in Kahle's solution were used for description and illustration. Immature stages were placed in petri dishes of 70% ethanol, and tagged image format computer files were obtained using a low-light camera (Optronics Engineering DEI-470; Goleta, CA) attached to a Wild MZ8 dissecting microscope and Image Pro Plus software for an IBM personal computer. Tagged image format files were printed and then traced on a light table or used as a reference to facilitate illustration. The cephalopharyngeal skeleton and spiracles were dissected from specimens cut in half longitudinally from the breathing tube to the metathoracic segment and placed in 10% KOH overnight. Dissected materials were neutralized with a drop of glacial acetic acid, and slide mounted with Canada balsam. Tagged image format files of dissections were obtained using the low light camera attached to a compound microscope at 100–400×.

To determine if adults were differentially attracted to newly inundated habitats with different potential larval food sources, 25 black plastic tubs (15 liter), each containing 8 liters of water, were arranged randomly in five rows of five at the University of California-Riverside Agricultural Experiment Station on 30 April 1999. Each tub was separated by 2 m. Treatments were lake water only (L), lake water with a tule extract (T), lake water spiked with a culture of the unicellular green alga *Chlamydomonas* spp. (Chlorophyta) (A), tule extract coupled with the *Chlamydomonas* inocula, and control tubs (C) containing distilled water. Lake water obtained from holding ponds on the premises that supported low densities of planktonic algae (≈700 cells per milliliter) and was sieved through a 1-mm mesh to remove large particles. The tule extract was prepared by adding 90 g of dried *S. californicus* to 20 liters of lake water and left to incubate at room temperature for 10 d to create a dense population of bacteria that has been shown to be attractive to hyponeustic insects such as mosquitoes (Diptera: Culicidae) (Walton and Workman 1998). Tule extract was sieved through 1-mm mesh before addition to tubs. *Chlamydomonas* cultures were obtained from the University of Texas algal collection and incubated with soil media (Harris 1989) to produce a dense population of ≈19,000 cells per milliliter. Each T tub received 2 liters of infusion and 6 liters of lake water; each A tub received 0.25 liters of culture and 7.75 liters of lake water; and each tule extract and algae tub received 2 liters of infusion, 0.25 liters of algal inocula, and 5.75 liters of lake water. The experiment ran 5 wk, and tubs were periodically topped off with lake water (L, T, A, and tule extract and algae) or distilled water (C) to counter evaporative loss.

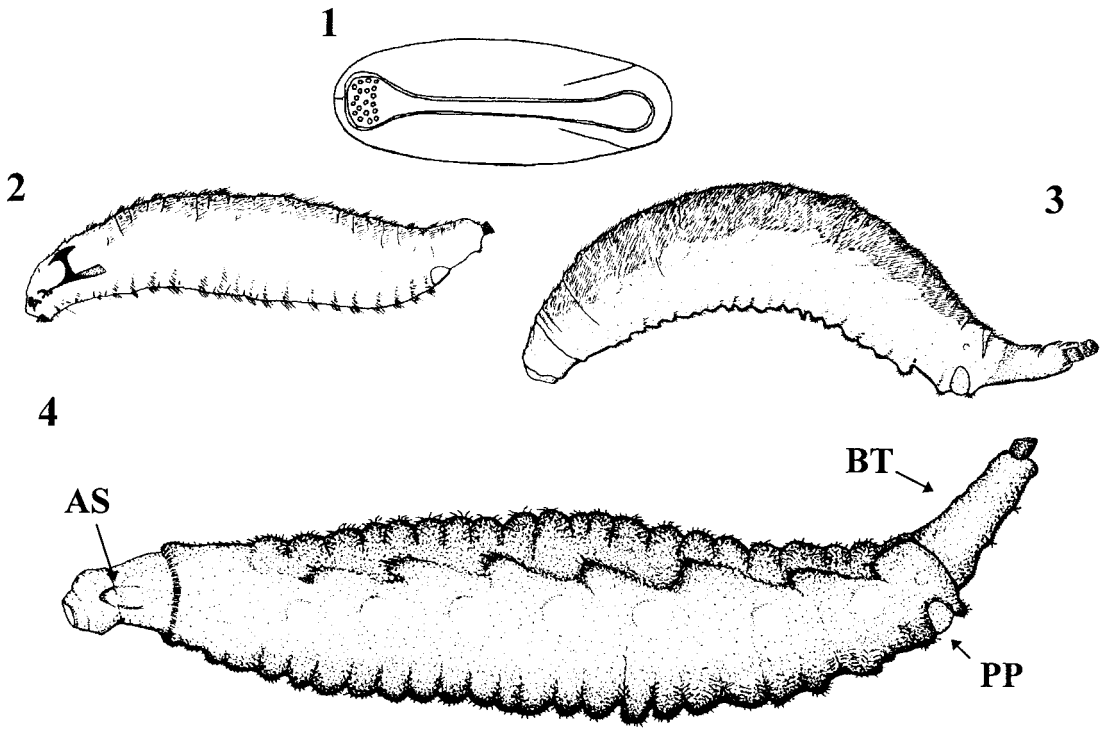


Fig. 1–4. *B. sturtevanti.* (1) Egg, dorsal view. (2) First instar, lateral view. (3) Second instar, lateral view. (4) Third instar, lateral view (AS, anterior spiracle; BT, breathing tube; PP, perianal pad).

The number of adult flies visiting each tub was recorded every 1–3 d and the daily mean calculated. Approaching the tubs to count adults rarely caused *B. sturtevanti* to fly away. The successional mean occurrence was calculated for each treatment to determine if adult visitation varied over time among the five treatments (Hanski 1980, Hirschberger 1998). The successional mean occurrence value (in days) represents the mean of the colonization curve generated by the daily mean number of adults visiting the five tubs of each treatment, and was calculated as

$$\mathrm{SMO} = \sum_{i=1}^{n} p_i(t_i - t_{i-1})t_i \Big/ \sum_{i=1}^{n} p_i(t_i - t_{i-1}),$$

where p_i is the mean cumulative number of adults recorded for each treatment, t_i is the number of days from the beginning of the experiment, and n is the number of sampling days along the succession. A chi-square test was used to detect significant differences in the successional mean occurrence (Hirschberger 1998). A one-way analysis of variance (ANOVA) was calculated to compare the total mean adult visitation for each treatment.

All puparia produced in each treatment were collected before adult emergence, and the number of puparia collected on each date was recorded for each tub. These data were compared among treatments with a one-way ANOVA to test the null hypotheses that treatments are equal in the mean duration from the start of the experiment until formation of the first puparium and mean number of puparia formed. Puparia collected from tubs were placed in glass shell vials and frozen until analysis when they were dried in an oven at 45°C for 24 h and weighed on a microbalance to the nearest 0.0001 g. The mean dry weight per puparium for each treatment was compared with a one-way ANOVA to test the null hypothesis that pupal mass was equal among treatments.

Results and Discussion

Description of Immature Stages. *Eggs* (n = 8). Length 0.15–0.16 mm (mean = 0.15); greatest width 0.05–0.06 mm (mean = 0.06). Oblate in dorsal view (Fig. 1), slightly arcuate in lateral view; micropylar end rounded with 18–20 pits, opposite end lacking pits. Chorion with grainy surface and faint reticulate hexagonal pattern, visible only at high magnification. Countershaded brown dorsally, gradually grading to white ventrally. Single mid-dorsal furrow spanning most of length, narrowing medially. Line of weakness apparent on end opposite of micropyle.

First Instar (n = 4). Similar to third instar except for the following: length 1.42–1.84 mm (mean = 1.53); greatest width 0.28–0.32 mm (mean = 0.30); body not flattened dorsoventrally; translucent and colorless, with annulations indistinct (Fig. 2). Body covered

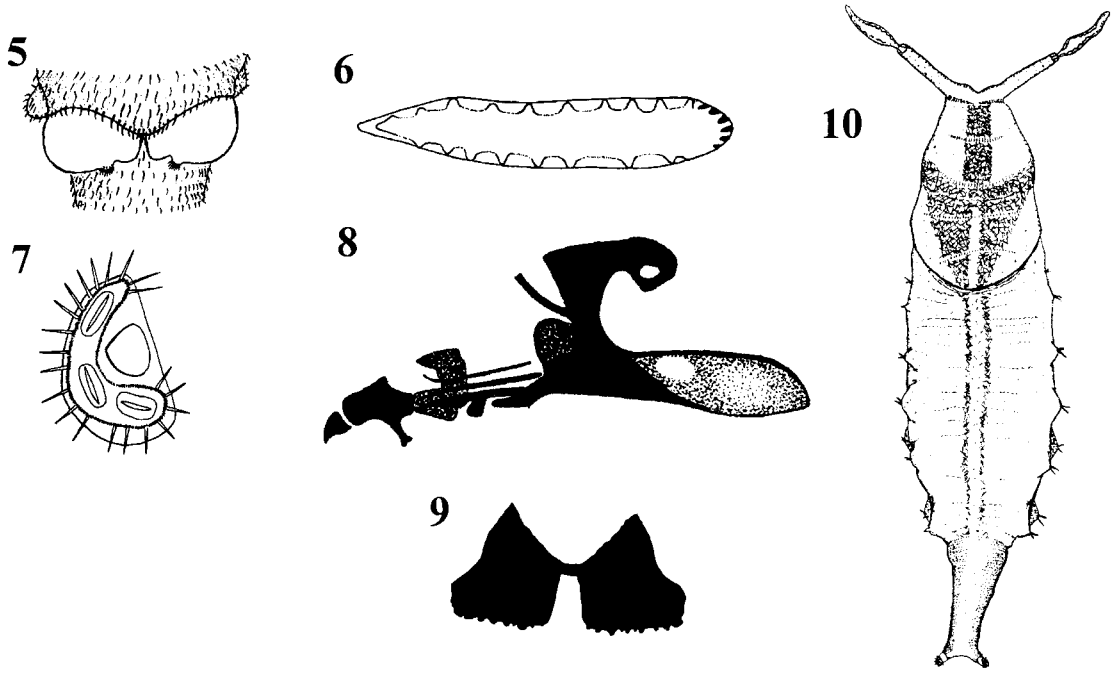


Fig. 5–10. *B. sturtevanti.* (5) Perianal pad, third instar, ventral view. (6) Anterior spiracle, third instar. (7) Posterior spiracle, third instar. (8) Cephalopharyngeal skeleton, third instar. (9) Same, mouthhooks, dorsal view. (10) Puparium, dorsal view.

with short setulae; no dorsal spots. Anterior spiracles absent; posterior spiracles pigmented dark brown to black, hydrofuge hairs inconspicuous. Breathing tube relatively short, approximately one-eighth total body length. Strong spines lining oral margin ventrally; cephalopharyngeal skeleton with reduced dorsal bridge and dorsal cornu, mouthhooks small, no windows.

Second Instar ($n = 5$). Similar to third instar except for the following: length 2.86–4.60 mm (mean = 3.95); greatest width 0.42–0.98 mm (mean = 0.80); body not flattened dorsoventrally; nearly transparent, colorless, annulations indistinct (Fig. 3). Spines absent, dorsum with dense black pile; spinules present in rows on venter of each abdominal segment. Few pigmented spots dorsally, no broken line present. Anterior spiracles similar to third instar but reduced; posterior spiracles with hydrofuge hairs less conspicuous. Cephalopharyngeal skeleton similar, but dorsal cornu shorter.

Third Instar ($n = 9$). Total length 5.10–7.44 mm (mean = 6.25); greatest width 1.08–1.72 mm (mean = 1.33). Shape elongate muscoid (Fig. 4), somewhat flattened dorsoventrally; anterior half tapering to head; posterior half tapering to short breathing tube representing approximately one-sixth of total body length; body yellowish brown, slightly darker dorsally than ventrally; dorsum of thoracic and abdominal segments with series of closely set dark brown spots forming two broken longitudinal lines in mature specimens, each spot covered densely by minute spinules; body with small, dark brown spines throughout (visible at high magnification only). Segments one and two retractile, segment one bearing minute rod-shaped antennae anteriorly; segments 4–11 annulated, each annulus bearing heavy spines mostly directed posteriad; segments 5–10 bearing two lateral protuberances with one or two stout setae. Perianal pad white, bulbous, each half bordered by small posterior evagination bearing stout setae (Fig. 5); integument anterior to pad bearing relatively large spines. Anterior spiracles elongate, retractile, bearing usually six dark digits apically (Fig. 6). Posterior breathing tube bifurcate distally, covered with minute spines, bearing two patches of relatively long setae ventrally; posterior spiracles dark brown, glabrous; central spiracular scar roughly round; spiracular plate with three oblate spiracles, bordered outwardly by approximately 20 short unbranched float hairs (Fig. 7). Cephalopharyngeal skeleton darkly pigmented (Fig. 8); mouthhooks paired and connected, modified to form dorsoventrally flattened plates bordered by stout projections (Fig. 9); ventral sclerite with two lobes distally; hypopharynx narrow in lateral view; parastomal bar narrow, curving upward apically; epipharyngeal sclerite polygonal in lateral view; lateral pharyngeal bridge rounded; dorsal bridge narrow and strap like; dorsal cornu somewhat rounded posteriorly with one posterior window; ventral cornu darkly pigmented along dorsal edge, grading to central lightly pigmented area and with one window, strongly tapered distally.

Puparium ($n = 11$). Length 5.40–6.94 mm (mean = 6.29); greatest width 1.32–1.86 mm (mean = 1.62). Darkly pigmented amber to brown, darkening with

age, with dorsal spots forming line similar to that of third instar (Fig. 10). Body uniformly arcuate in lateral view; with strong tubercles laterally, segments annulated. Anterior spiracles at distal end of elongate respiratory arms; breathing tube (1.02–1.48 mm) and posterior spiracles identical to third instar. Dorsal cephalic cap flattened, boldly patterned in older specimens, with peripheral carina; line of weakness following carina, "hinged" posteriorly. Area of perianal pad atrophied, wrinkled, grayish. Cephalopharyngeal skeleton of third instar visible through puparium, pressed flat against venter anteriorly.

***Brachydeutera sturtevanti* Life History.** Adults are active year round in southern California, although they were infrequently observed from November through February. Periods of cool weather undoubtedly slow or halt the development of immature stages, and may inhibit mating. During periods of successive warm days, newly inundated artificial and natural habitats were visited by adults within 2–3 d. Adults were collected from freshwater marshes, ponds, and pools formed by receding water levels at the margins of streams; no specimens were taken at inland or coastal saline habitats. Other ephydrid adults commonly found in the habitat of *B. sturtevanti* included *Scatella stagnalis* (Fallén), *S. palludum* (Meigen), *Notiphila aenigma* Cresson, *N. decoris* Williston, *N. macrochaeta* Loew, *N. olivacea* Cresson, *Hydrellia* spp., *Ephydra* spp., and *Parydra* spp.; other species were encountered, but they were either taken rarely, or their larvae are known to exploit strictly semiaquatic or terrestrial niches. Mosquito larvae of the genera *Culex* and *Culiseta* were probably the most common and abundant dipteran co-occurring with *B. sturtevanti.*

Adults were found almost exclusively on the water surface where they remained with the distal four tarsal segments of each leg flat against the surface tension. This behavior appears to distribute their weight equitably and avoid compromising the surface film. Adults were rarely encountered sitting on vertical structures such as emergent vegetation or the sides of tubs; however, they occasionally rested one leg on a relatively stable substrate such as an algal mat or floating leaf to prevent their drift across the water. Movement across the surface was accomplished with a stroking motion of the legs that propelled them forward short distances, albeit somewhat slowly and awkwardly. Adult flies were not wary but would halt feeding and fly near the water surface short distances if approached too closely; flight normally occurred ≈5–20 cm above the water. Much of an adult's time was spent feeding at the water surface by rapidly extending and retracting its proboscis ≈4–6 times per second. Particles floating on the surface near a feeding adult were drawn to the proboscis by this action. Adults often aggregated on floating algal mats, leaves, or debris where they rested, fed, and mated. No apparent territorial behavior was exhibited.

In permanent habitats containing established vegetation, adults were taken frequently from the water surface within stands of plants with simple, rod like physical structure (e.g., cattails and bulrush). In contrast, plants with complex physical structure such as emergent buttercups (Ranunculaceae: *Ranunculus* spp.) and smart weeds (Polygonaceae: *Polygonum* spp.) that have highly branched stems and broad lateral leaves supported few adults. Structurally complex emergent vegetation has been shown to harbor species-rich communities of Ephydridae, and although not all species use plants as a larval food or respiratory source, it has been suggested that these flies find protection from predators and weather as well as an adult food source (e.g., nectar) here (Todd and Foote 1985, Keiper et al. 1998). The adult habit of resting exclusively on the water surface is probably hindered by a tangled mesh of vegetation, therefore, adults mate, oviposit, and feed in areas where plants are separated by areas of open water.

Although courtship behavior is common among ephydrids (Deonier 1972, Simpson 1975), no recognizable courtship behavior was exhibited by *B. sturtevanti.* Mating behavior was similar to that described for another wetland-inhabiting shore fly, *Paracoenia bisetosa* Coquillett (Zack 1983). Males appeared to stalk females, gradually moving closer to them while exhibiting feeding behavior. When a female was ≈1–2 cm away, the male would quickly leap onto the dorsum of the fly it was stalking. Receptive females spread their wings and tilted them forward ≈45°; copulation lasted up to ≈30 s. Unreceptive females brought their hind legs forward and slid them across their dorsum, kicking and ultimately dislodging the male within a few seconds. More than 20 successful copulation events were recorded in the laboratory and field, and easily three times as many unsuccessful attempts were recorded.

Females oviposited on the water surface, partially submerged leaves, and floating algal mats such as *Ulothrix* (Chlorophyta). Each of these surfaces offered a moist substrate, and laboratory observations showed that eggs are not desiccation resistant. Those laid in an area of open water drifted until they came in contact with another larger object such as an algal mat, emergent vegetation, floating debris, or the sides of a rearing container. Eggs floated dorsal side up keeping the micropyle in contact with the atmosphere for gas exchange. The dorsal furrow maintained an air pocket that prevented the egg from becoming overturned; submerging an egg with a fine probe invariably resulted in the egg returning upright to the water surface. The difficulty associated with attempting to obtain eggs from field-collected females in small breeding jars illustrated that the larger plastic containers (≈2 liters) may have simulated natural conditions for oviposition better than breeding jars.

The incubation period lasted 1–4 d. Upon eclosion, first instars floated beneath the water surface suspended by their posterior spiracles, which are lined peripherally with hydrofuge hairs. Larvae frequently gulped air at the water surface to enhance their buoyancy. In rearing dishes or tubs, larvae frequently floated to the meniscus formed at vertical structures protruding above the water surface. Early instars moved across these substrates while their posterior

spiracles were in contact with the atmosphere, although larvae sometimes drew their spiracles below the water surface while retaining an attached air bubble. This latter behavior allowed individuals to feed up to several centimeters below the water for up to ≈10 min before surfacing. Larvae occasionally burrowed into algal mats and used air bubbles for gas exchange. While completely submerged, all instars exhibited the ability to swim by simultaneously thrusting their anterior segments ventrally and bringing their posterior segments anteriorly; this was followed by larvae bringing their anterior segments to the same plane of the body while thrusting their posterior segments to the same plane. These behaviors were exhibited by all instars.

Whereas most dipteran larvae are anatomically suited for exhibiting a particular feeding strategy such as scraping (e.g., Blepharoceridae), shredding (e.g., Tipulidae), collecting/gathering (e.g., Chironomidae), or predation (e.g., Tabanidae), larval *B. sturtevanti* are notably versatile. *Brachydeutera* larvae are categorized as collector-gatherers (Courtney et al. 1996) consuming decaying materials (Williams 1938, Scheiring and Foote 1973). The mouthhooks of *B. sturtevanti* are modified as flat disks with stout lateral spines that facilitate grasping masses of detritus and algae. However, larvae also moved across algae-encrusted leaves and wood fragments scraping the algal cells such as diatoms from the submerged substrates. All instars also demonstrated the remarkable ability to filter feed. Larvae suspended from the surface film by their posterior spiracles frequently arched their bodies dorsad bringing the pseudocephalic segment perpendicular to the water surface. Larvae rapidly rasped their modified mouthhooks to create a vortex bringing water and suspended materials into their oral opening. Materials ingested included detrital particles, unicellular algae, protozoans, and undoubtedly microorganisms such as bacteria and fungi. The vortex created by a first instar drew materials positioned up to approximately half the maggot's length away, whereas third instars pulled materials up to twice the larva's length away. If a particle was too large for passive ingestion, larvae halted the filter feeding process to manipulate the particle (usually a small detrital mass) for consumption. Bouts of filter feeding usually lasted 1–3 min, and was estimated to represent ≈25% of a larva's feeding efforts.

Although larvae spent much of their time among the hyponeuston, solid substrates projecting above the water such as the walls of tubs and emergent vegetation that remained moist because of capillary action were exploited. Periphyton (mostly *Ulothrix*, *Oscillatoria*, and diatoms) and detritus frequently covered these areas, providing a food source that larvae scraped. Most individuals were found within 1 cm of the water surface. Each stadium lasted ≈3–5 d under laboratory conditions.

Formation of the puparium usually took place while a larva floated against emergent substrata. The strongly arcuate puparium floated by the posterior spiracles in a manner similar to larvae. The laterally

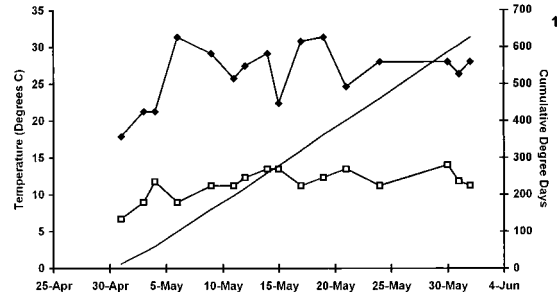


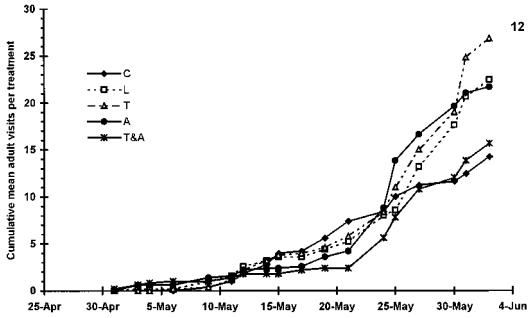
Fig. 11. High (◆) and low (□) temperatures during colonization experiment, with cumulative degree-days (—).

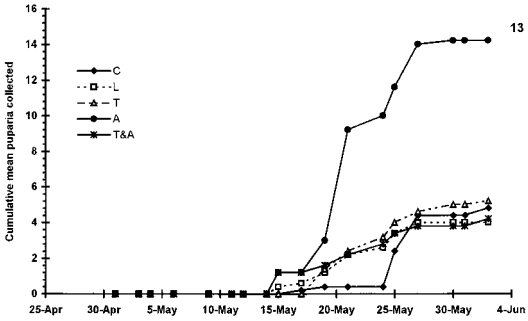
flattened anterior spiracles are also hydrophobic and further supported the body. Adults were liberated by breaking through at the cephalic cap, leaving behind the empty puparium still floating on the water surface. The pupal period lasted 6–8 d.

As hyponeustic insects, *B. sturtevanti* larvae are frequently susceptible to aquatic predators, whereas adults are exposed to predators while resting at the water surface. Vertebrate predators present in the larval habitat include fish and shorebirds (Aves: Charadriiformes). Zack (1983) stated that birds may constitute a significant predation pressure on *P. bisetosa* adult populations, and the same may be true for *B. sturtevanti.* Predacious Coleoptera (Dytiscidae and larval Hydrophilidae) and Odonata were observed frequently in the larval habitat. In the laboratory, first instars were stung and paralyzed by *Hydra* spp. (Cnidaria: Hydrozoa: Hydroida) placed in the petri dishes. *Hydra* maneuvered maggots for ingestion head first; after engulfing half of a first instar, the cnidarian rejected it probably because the girth of the larva was too great (similar-sized *Hydra* consumed chironomid midge larvae of the same length that were substantially narrower). These paralyzed and rejected larvae never recovered. Perhaps the ability of *B. sturtevanti* to exploit newly created ephemeral habitats allows this species to escape predation pressure from heterospecific invertebrates that colonize these areas more slowly.

Based on adult visitation and pupal formation data (see below), ≈2 wk is required for larval development in southern California during May; this represented ≈300 DD (Fig. 11). Adults and immatures faced moderate temperatures ≈7–31°C during the colonization experiment (Fig. 11). Considering pupal duration data from laboratory rearings, field observations of adult activity from March to October, and a mean annual temperature of 16.8°C, ≈7 nonoverlapping generations can be produced per year in southern California.

Colonization Experiment. The mean number of adult visits to the experimental tubs were equal statistically among treatments ($F = 0.86$; df = 4, 80; $P = 0.49$) (Fig. 12). The successional mean occurrence calculations for all treatments were nearly identical, ranging from 27.6 to 29.2 d (C, 27.6; L, 28.8; T, 29.2; A, 28.6; tule extract and algae, 27.9), illustrating that vis-





Figs. 12–13. (12) Cumulative mean adult visits during colonization experiment (C, controls; L, lake water; T, tule extract; A, algal inocula; T&A, tule extract plus algal inocula). (13) Cumulative mean puparia collected during colonization experiment; abbreviations as in Fig. 12.

itation patterns among treatments were indistinguishable statistically ($\chi^2 = 0.06$, df = 4; $P > 0.05$). Although A tubs produced comparatively more puparia, a Kruskal–Wallis one-way ANOVA on ranks detected no statistically significant difference ($H = 5.93$; df = 4, 1; $P = 0.20$) (Fig. 13). There was no correlation between the number of adult visits and the number of puparia formed in each tub ($R^2 = 0.03$), illustrating that increased numbers of puparia formed were not a result simply of greater numbers of adults visiting these tubs.

The mean dry weight per puparium exhibited the trend of tule extract and algae > A > T > L > C; however, these values were statistically equal among treatments (Fig. 14; $F = 2.49$; df = 4, 17; $P = 0.08$). The trend of algae-spiked treatments producing heavier puparia and the fact that A tubs produced more puparia than other treatments suggest that the algae-spiked treatments were a more beneficial food source than the others. *Chlamydomonas* is both a motile nektonic and biofilm-forming alga (Harris 1989), which the versatile food acquisition strategies of *B. sturtevanti* are well-suited for exploiting. It was unexpected that A treatments produced comparatively more puparia than the tule extract and algae treatments. Algae and bacteria are known to compete for nutrients (Currie and Kalff 1984), and perhaps this phenomenon reduced the quality or quantity of either food source. Alternatively, large populations of planktonic bacteria and algae that exist both planktonically

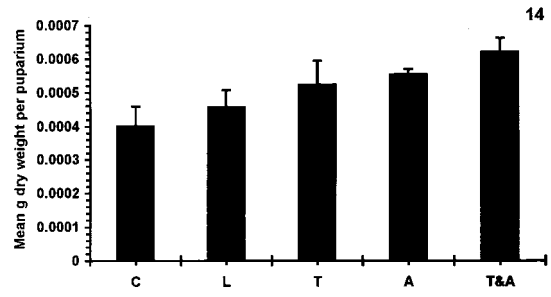


Fig. 14. Mean ± 1 SE grams dry weight per puparium for each treatment collected during colonization experiment; abbreviations as in Fig. 12.

and as biofilm might have influenced the feeding strategies exhibited by larvae (i.e., frequent switching between filter feeding and scraping thus reducing feeding efficiency). These concerns were beyond the scope of this investigation, and future efforts exploring these observations are warranted.

It is remarkable that in just >2 wk of natural conditioning, distilled water (i.e., C treatments) produced puparia that were equal statistically in mass compared with all other treatments. These tubs probably contained a diverse assemblage of pollen, bacteria, fungi, and algae that became introduced by wind, arthropod carriers (including *B. sturtevanti* adults) visiting the tubs, and other allochthonous input. The experimental and life history data gathered during this investigation strongly support the perception that *B. sturtevanti* immatures are versatile in their feeding strategies, generalized in their food requirements, and opportunistically colonize and complete larval development in novel and unexploited habitats. These traits are characteristic of r-strategists and account for the ability to successfully make use of ephemeral environments. Newly inundated habitats that harbor *Brachydeutera* populations often suddenly stop producing adults, suggesting that this genus is an important colonizer taxon (B. A. Foote, Kent State University, personal communication).

Conclusions

The genus *Brachydeutera* is placed in the subfamily Ephydrinae and the tribe Dagini (Mathis and Zatwarnicki 1995). This subfamily includes genera (e.g., *Ephydra, Paracoenia, Setacera,* and *Scatella*) whose larvae are strict algivores that can use a variety of algal taxa (Foote 1995, Courtney et al. 1996). The feeding habits exhibited by *B. sturtevanti* support the inclusion of this genus into the Ephydrinae. However, *B. sturtevanti* larvae use such a variety of feeding strategies that placing *Brachydeutera* in a tribe separate from the algivores listed above is supported by its unique opportunistic nature. Larvae successfully develop in a wide range of habitats (temporary pools and permanent lentic environments) with a wide range of feeding strategies (i.e., collecting/gathering, scraping, and

filter feeding). No other ephydrid genus exhibits this spectrum of feeding habits.

Herein, we provide a preliminary key to third instars, and include *B. hebes* because it is possible that it could be introduced to the mainland United States from Hawaii. No information is available on the immature stages of the introduced species *B. longipes,* but Mathis and Steiner (1986) reported that it is established only along the southeastern coast of the United States from Maryland to Georgia. Any *Brachydeutera* larvae collected in that area should be determined with caution; rearings to associate the immature stages with the adventive adult are recommended.

Key to Third-Instar *Brachydeutera* from North America North of Mexico

1. Posterior spiracles with bifurcated float hairs; perianal pad small, indistinct . . . . . *B. hebes* Cresson
1'. Posterior spiracles with float hairs single, not divided (Fig. 5); perianal pad large, conspicuous 2
2. Cephalopharyngeal skeleton lacking window on ventral cornu; dorsal abdominal maculations uniformly round, never forming a broken line. . . . . *B. argentata* (Walker)
2'. Cephalopharyngeal skeleton with window on ventral cornu (Fig. 6); dorsal abdominal maculations round to amorphous, may or may not form a broken line 3
3. Anterior spiracles with distal spiracular digits darkened (Fig. 4); dorsum of abdomen with maculations forming a broken but distinct line in some specimens . . . . . *B. sturtevanti* Wirth
3'. Anterior spiracles with distal spiracular digits not darkened; dorsum of abdomen with maculations not forming a line . . . . . *B. neotropica* Wirth

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