

BIOLOGY AND ECOLOGY OF HIGHER DIPTERA FROM FRESHWATER WETLANDS

Joe B. Keiper,¹ William E. Walton,² and
Benjamin A. Foote³

¹*Department of Invertebrate Zoology, Cleveland Museum of Natural History, Cleveland, Ohio 44106; e-mail: jkeiper@cmnh.org*

²*Department of Entomology, University of California, Riverside, California 92521; e-mail: walton@mail.ucr.edu*

³*Department of Biological Sciences, Kent State University, Kent, Ohio 44242; e-mail: bfoote@kent.edu*

Key Words Cyclorrhapha: Schizophora, life history, feeding habits, niche partitioning, aquatic insects

■ **Abstract** Although studies of freshwater entomofauna frequently do not include the biodiversity and ecological roles of higher Diptera, cyclorrhaphous flies are often numerous and species rich in wetlands. Seventeen families are commonly found in freshwater wetlands, with Ephydriidae, Chloropidae, Sciomyzidae, Sphaeroceridae, and Scathophagidae being among the most important in terms of population size and species richness. Difficulty with sampling cryptic larval habitats and species identification challenges may account for the exclusion of acalyptrate and other dipterans from wetlands ecology studies. Large populations are facilitated by the high productivity of freshwater wetlands and the high intrinsic rate of increase characteristic of many species. Higher dipterans exist in all freshwater wetland types, are microhabitat selective, and play significant roles in food webs. The varied strategies for food acquisition and patterns of spatial and temporal distribution limit ecological overlap among the higher Diptera.

CONTENTS

INTRODUCTION	208
DIVERSITY AND IMPORTANCE OF WETLANDS	208
Classification of Freshwater Wetlands	208
Importance of Wetland Ecosystems	210
SAMPLING HIGHER DIPTERA	211
Wetland Taxa	211
Higher Dipteran Habitat	211
Sampling Techniques	212
POPULATION AND COMMUNITY ECOLOGY	213
Habitat Distribution	213
Microhabitat Specificity	215

Demography	215
Colonization Ecology	216
TROPHIC ECOLOGY AND FEEDING HABITS	216
Larval Feeding Habits	216
Importance to Other Organisms	220
EVOLUTIONARY CONSIDERATIONS	222
Adaptive Radiation	222
Selection for Particular Wetlands	222
CONCLUDING REMARKS	222

INTRODUCTION

Our knowledge of the ecology of wetland invertebrates has been reviewed and enhanced by recent syntheses (13, 15). Invertebrates play significant roles as nutrient recyclers, primary and secondary consumers, food for wildlife, and indicators of ecosystem function (7, 13, 53, 56). The increased interest in wetlands fauna is timely because many of the world's wetlands have been lost to draining, construction, agriculture, and pollution (124, 129). However, with the exceptions of Culicidae and Chironomidae, studies of wetlands invertebrates often ignore the roles of adult and larval dipterans. Higher Diptera produce large populations (108), are species rich (118, 170, 171), and exhibit diverse trophic ecology (18, 57, 72, 119, 136) in freshwater wetlands.

Relatively few studies of the life history, biology, and larval morphology are available for most higher dipteran families (Diptera: Cyclorrhapha: Schizophora) occurring in wetlands despite their abundance and ubiquitous nature. More interest in dipteran ecology has been shown for populations from unusual habitats such as hot springs and alkaline environments (24, 31–34). Shore flies (Ephydriidae) and snail-killing flies (Sciomyzidae) are probably the most-well-studied wetland-inhabiting families because of their diverse and fascinating habits (18, 72), but our understanding of the basic biology and ecology exhibits gaps even in these two thoroughly studied groups (45, 46, 78). This review summarizes our knowledge of the life history, larval feeding habits, and ecology of higher Diptera from freshwater wetlands in hopes of stimulating future research on this often neglected group of insects. We limit our review to freshwater systems because of concern for inland wetlands such as marshes, swamps, bogs, and fens, and because of the increasing use of human-made wetlands for restoration, replacement of lost habitat, and wastewater treatment (96, 124).

DIVERSITY AND IMPORTANCE OF WETLANDS

Classification of Freshwater Wetlands

There is no universally applicable and accepted general classification scheme for wetlands; they are difficult to define precisely, and the diversity of classification schemes reflects the variety of interests and issues associated with wetlands.

Delineation of wetlands is often difficult, particularly for legal issues, because hydrologic boundaries of wetlands can vary temporally. Wetland classification is made difficult by the great geographical extent, variable hydrologic conditions in which wetlands are found, diversity in sizes and locations, and degree of human influence on wetlands (124, 156). There are few studies that incorporate invertebrates into classification methods (e.g., 82).

Wetlands have been historically classified and inventoried according to their vegetation physiognomic type, geomorphic and hydrologic regime, water chemistry, plant and/or animal species, wetland function and value, conditions of boundary delineation, and other characteristics (38, 124, 187). Nontidal wetlands were classified by hydroperiod or vegetation in recent reviews of the ecology of wetland invertebrates (13, 15). Aselmann and Crutzen (8, 9) used five categories: bogs, fens, swamps, marshes, and floodplains. These are similar to the categories of the Canadian Wetland Classification System (187), except that shallow-water marsh replaces floodplains as a class at the top of the hierarchy of more than 70 wetland categories.

Although a variety of classification schemes exist (e.g., 38), we follow Mitsch & Gosselink (124), who divided North American wetlands into two major groups: (a) coastal wetlands—tidal salt marshes, tidal freshwater marshes, and mangrove wetlands; and (b) inland wetlands—freshwater marshes, peatlands, freshwater swamps, and riparian wetlands. Eighty percent of the estimated 42 million hectares of wetlands in the conterminous United States (40) are inland wetlands (80). Freshwater marshes are characterized by (a) emergent soft-stemmed plants such as cattails, bulrush, pickerelweed, grasses, and sedges; (b) a shallow water regime; and (c) generally shallow peat deposits (124). These wetlands occur in isolated basins, as well as in littoral zones of lakes and riparian wetlands along sluggish streams and rivers. Although man-made and restored wetlands are seldom functionally equivalent to natural wetlands (42, 129), most restoration projects and wetlands constructed for wastewater and stormwater processing are marshes (96).

Peatlands (i.e., bogs and fens) occur where plant production exceeds decomposition (15) and include the deep peat deposits of the boreal regions of the world (124). These wetlands are commonly found in cold-temperate climates of high humidity where precipitation exceeds evapotranspiration and the soil is saturated (156), or anywhere drainage is restricted and anoxia is prevalent. High elevation mountain ranges and poorly drained areas in southern regions of North America may also be rich with peatlands (156). Bogs and fens are differentiated by nutrients, water supply, and subtle floristic variations (127, 192). Bogs (ombrotrophic peatlands) receive water and nutrients primarily from precipitation and are characterized by their nutrient deficiency, waterlogged conditions, and pH; their buffering capacity and salinity are lower than in fens. Fens (minerotrophic peatlands) are supplied water and nutrients by groundwater, surface sources, and precipitation. Depending on the climate, fens exhibit varying degrees of emergent aquatic vegetation (sedges and other monocots) and terrestrial flora such as graminoids (127, 183, 192). The flora of bogs is dominated by mosses such as *Sphagnum*. A third type of peatland,

transitional or mesotrophic peatland (poor fens), is chemically intermediate between the previous two (124).

Freshwater swamps are forested wetlands that have standing water for most of the growing season (124), occur in regions of extensive rainfall, and have restricted overland flow or drainage (156). Swamps occur most often in floodplains and are dominated by bottomland hardwoods. Depressional wetlands supporting trees (e.g., cypress domes, Carolina bays, and limestone sinks), ephemeral woodland ponds and pools, and flooded forests created by beavers are also examples of swamps (156).

Riparian wetlands occur along rivers and streams and are often flooded for only a portion of the year (124). There is some overlap in classification of riparian wetlands and freshwater swamps, particularly in the southeastern United States. Mitsch & Gosselink (124) classified wetlands dominated by cypress (*Taxodium*), tupelo (*Nyssa*), and red maple (*Acer rubrum*) as freshwater swamps and bottomland hardwood forests of the southeastern United States as riparian ecosystems, whereas Sharitz & Batzer (156) classify the latter systems as freshwater swamps. Together, the two wetland types are the most extensive class of wetlands in the United States, covering 22–25 million ha in the United States (40). Riparian wetlands also occur in arid and semiarid regions. Because riparian wetlands are found in a variety of climates, they support diverse vegetation that varies along gradients of flooding frequency (124).

Importance of Wetland Ecosystems

The world's wetlands are thought to encompass 7–9 million km², or about 4–6% of Earth's land surface (124). Wetlands provide habitat and nurseries for fish and wildlife, improve water quality, protect shorelines, stabilize water supplies, moderate the effects of floods, recharge groundwater aquifers, and have aesthetic and heritage values. Wetlands also contribute to the stability of global levels of available nitrogen, atmospheric sulfur, carbon dioxide, and methane. Riverine and lacustrine wetlands are estimated to be 160 times greater in economic value to society than an equal area of cropland (24).

Wetland ecosystems form a transition between terrestrial upland habitats and deepwater aquatic habitats such as lakes, rivers, and estuaries. They share characteristics and flora and fauna from both terrestrial and deepwater habitats (124), but they exhibit emergent properties not found in either upland or deepwater systems. Nonequilibrium conditions created by disturbance and spatial heterogeneity in many streams promote higher insect biodiversity (3, 88) compared with deepwater habitats such as ponds (140). The physical structure provided by macrophytes and position of wetlands between upland and deepwater habitats promotes the diversity of fauna. For wetland insects, rate of flow and water depth on environmental conditions has a marked influence on life histories and habitat preferences.

In shallow wetlands, biota can encounter periodic, at times unpredictable, drying. Rooted emergent and submergent vegetation form the base of primary

production in wetlands instead of phytoplankton in the deepwater systems. Wetlands typically have higher rates of primary production and slower rates of decomposition than do deepwater systems and tend to be organic exporters or inorganic nutrient sinks (124, 192). Terrestrial, wetland, and littoral biota can profoundly influence the quality and quantity of inorganic and organic loading to the pelagial zone of most lakes (192).

SAMPLING HIGHER DIPTERA

Wetland Taxa

Seventeen families of higher Diptera are commonly encountered in freshwater wetlands. Shore flies (Ephydriidae) represent the most speciose family (118) and are ubiquitous components of the freshwater wetland entomofauna. Sphaeroceridae, Sciomyzidae, and Chloropidae sometimes rival the ephydriids in numbers. Agromyzidae, Anthomyzidae, Chamaemyiidae, Drosophilidae, Lauxaniidae, Micropezidae, Muscidae, Opomyzidae, Otitidae, Psilidae, Sarcophagidae, Scathophagidae, and Sepsidae frequently contribute to wetlands community structure. Whereas some families appear to reach their greatest abundance and species richness in wetlands environments, no dipteran family is restricted solely to wetlands (57).

Higher Dipteran Habitat

Maximum biodiversity occurs at the interface of wetland and littoral areas with pelagic regions of lakes or channels of rivers. Maximum functional stability of aquatic ecosystems occurs where the terrestrial-wetland-littoral interface regions are strongly coupled to the open water of lakes and rivers. Most higher Diptera reside in the interface between wetlands and other ecosystems. Mudflats, sand shores, emergent vegetation, and rotting masses of organic matter are prime locations for adult and larval activity (43, 109, 115, 151, 163, 169).

Relatively few higher dipterans use habitats traditionally associated with benthic macroinvertebrates. Some species make use of submerged anoxic sediments (Ephydriidae) or neustic (i.e., water surface) areas (Ephydriidae, Sciomyzidae), and some are periphytic (Sciomyzidae). However, most species are specialized for semi-aquatic areas such as mud shores, detritus deposits, floating algal mats, macrophytes, and other surfaces that are somewhat exposed (21, 43, 57, 119, 151). Herbivores (Anthomyzidae, Agromyzidae, Chloropidae, Ephydriidae, Opomyzidae, Scathophagidae) and secondary stem borers (Chloropidae, Otitidae, Ephydriidae) are intimately tied to wetland host plants. Many Ephydriidae are specialists of floating algal mats rather than periphytic algal resources (63, 64). Detritivores (Sphaeroceridae, Otitidae, Ephydriidae, Muscidae, Sepsidae) are numerous in areas supporting masses of decaying vegetation or exposed sediments (57). Predatory ephydriid adults hunt smaller insects in complex wetland environments, whereas

their larvae live in exposed wet sediments. Larvae of some taxa burrow into animal hosts (Sciomyzidae). Few exceptions exist where nondipteran aquatic macroinvertebrates make use of habitats that support large dipteran populations, such as the interior of damaged plants (100).

Sampling Techniques

The approach used to sample insects of aquatic environments is usually based upon the habitat (e.g., lotic versus lentic) and the ecological community (e.g., open water, drift, vegetation, benthos) being studied (120, 161). In addition to the two aforementioned considerations, the decision to use a particular sampling method and design depends on the objectives of the study and characteristics of the habitat being sampled [e.g., substrate composition (120)]. There is a great variety of samplers and sampling methods for aquatic insects. Comprehensive reviews of sampling considerations and approaches are numerous. A recent detailed discussion of the efficacy of particular methods was given by Turner & Trexler (176).

Standard methods used to sample aquatic insects in wetlands (119), such as aquatic nets, corers, hand dippers, emergence traps, grabs, and artificial substrates, may inadequately sample immature stages and adults of higher Diptera. Qualitative samples for seasonal and spatial population trends can be obtained passively using detergent pan traps (33, 108) or by active sampling using pull-up samplers (19) and aerial nets (150, 195). Pan traps, sticky traps, emergence traps, and sweep netting capture ample specimens for study (102, 108, 170, 171, 186). Standard collection methods have been used for quantitative samples of ephydrid larvae found in the sediments of large saline lakes (Ekman grabs) and emerging adults (submerged or floating emergence traps), but sediment traps and quadrat samples using SCUBA were needed to quantitatively sample eggs and pupae, respectively (33). Sampling larvae associated with hard substrates (126) also requires special consideration.

Dipteran adults have feeding habits that are in many cases dramatically different from the habits of their immature stages. Many aquatic insect adults do not feed, and their ecological roles are restricted to reproduction, dispersal, and providing food for higher trophic levels (119). Certain higher dipteran taxa (e.g., Ephydriidae, Muscidae) have adults that are detritivores, filter feeders, algivores, or predators (20, 44, 57). Adult sampling therefore provides data for a more terrestrial component of wetland insects and can be used to monitor colonization events.

Quadrat samplers in which vegetation is cut/clipped provide a quantitative sample of vegetation. However, subsequent laboratory processing using flotation and other techniques for separating insects from vegetation/debris is unlikely to provide an adequate sample of leaf-mining, stem-boring, and other cryptic higher dipteran larvae. Direct counts made by scanning vegetation, dissection, bleaching, selective staining, and other methods typically applied to plant and plant product pests (161) are needed.

POPULATION AND COMMUNITY ECOLOGY

Most work on the seasonal occurrence, spatial distribution, and community structure of higher Diptera from wetlands has focused on the family Ephydriidae owing to its abundance and species richness (e.g., 36, 48, 108, 151, 171). However, some work on Chloropidae from marshes has provided insights into dipteran ecology (e.g., 10, 144, 170, 188). Few other taxa from freshwater wetlands have been examined at the population or community level.

Habitat Distribution

Intensive work on habitat specificity over relatively large spatial scales in the Ephydriidae shows that species within a family are habitat selective across a region (i.e., found most commonly in marshes, riparian wetlands, rain pools, salt pools, wet woodlands, roadside ditches, etc.) and microhabitat selective within particular environments (43, 150, 151, 163, 164, 196, 198). Freshwater wetlands have been subdivided by dipteran habitat types, including muddy-shore, marsh-reed, sedge-meadow, floating-vegetation, floating-algal-mat, and Hudsonian-moist-meadow. Scheiring & Deonier (150) compared the habitat distribution of Ephydriidae from Iowa and Ohio and demonstrated that, although those states contain similar ephydrid habitats, they supported different ephydrid communities. Similarity in the ephydrid fauna from each habitat category ranged from 0 to approximately 50%. It was suggested that although the species composition in similar habitats may differ geographically, the community structure is probably comparable because trophic and spatial niches are filled by ecological equivalents.

Habitat selectivity is driven by specialization for the consumption of distinctive food resources among herbivores, parasitoids, and certain predators. Agromyzidae, Anthomyzidae, Chloropidae, Ephydriidae, Scathophagidae, and Sciomyzidae contain species that have intimate associations with wetland plants or animals (18, 57, 72, 136, 152, 153, 173). Sciomyzid larvae prey on mollusks with varying degrees of specificity; therefore, their habitat distribution is often narrow (18, 78). Many chloropid, ephydrid, and scathophagid larvae are herbivorous, thus restricting their occurrence in nature to habitats that support appropriate host plants (47, 117, 182, 188). Among dipteran families with species considered to be general scavengers, Marshall (115) found that 15 of 73 species of Sphaeroceridae recorded from peatlands in Canada were found only in bogs (i.e., tyrophilous) and were not taken from other wetland habitats. However, it appears that much of the biology of the adult and immature Diptera found in these acidic wetlands is unstudied, thus the reason for their limited habitat distribution is unknown. Relatively little is known of higher Diptera from fens and swamps, and these habitats require further study.

Using data on the habitat distribution of Ephydriidae from Iowa (43) and Ohio (151), we categorized the larval feeding habits of species collected from wetland habitat types (e.g., marsh-reed, floating algal mat, sand shore, and others) into

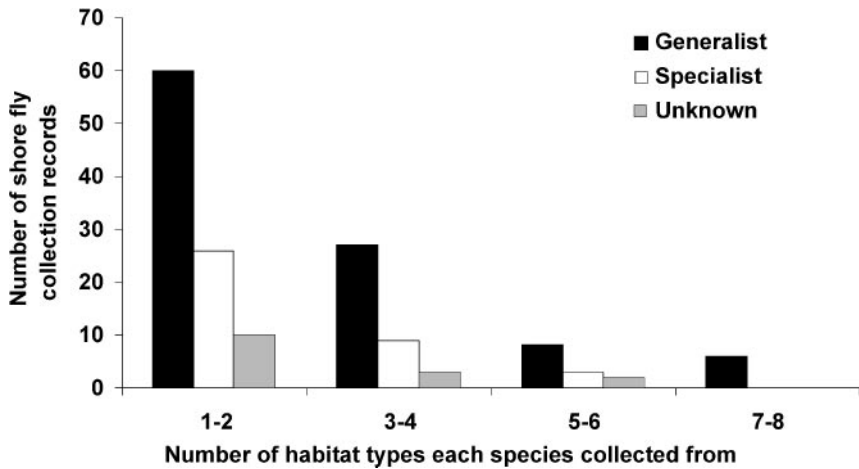


Figure 1 Number of habitat types occupied by ephydrid species encountered during surveys of habitat distribution (43, 151). Species were categorized as trophic generalists, specialists, or having unknown feeding habits.

generalists (i.e., nonselective in their food sources), specialists (i.e., narrow range of food sources), and those of unknown trophic habits. The number of species collection records was plotted against the number of habitat types in which each species was collected (Figure 1). Roughly twice as many species with known feeding habits (or feeding habits inferred from knowledge of closely related species) are generalists, and most wetland-inhabiting ephydrids are found in only one or two wetland habitat types. Only a few species were taken from ≥ 7 habitat types, and all of those species were generalists. These data show that many wetland Ephydridae are habitat selective regardless of the extent of trophic specialization.

Relatively little study has been conducted on the impacts of pollution on habitat distribution and species richness of higher Diptera. Anthropogenic eutrophication can alter fly community composition (102) or cause densities of certain taxa to increase or decrease (200), thus complicating analyses of microhabitat specificity and resource partitioning within wetlands. The use of higher dipteran taxa as indicators of environmental health is presently unexplored and deserves attention (but see 102).

Lotic systems are well known for their high species richness of invertebrates (119). Few studies of higher Diptera from flowing water habitats (such as riparian wetlands) are available, but it is apparent that stream systems do not support the higher dipteran species richness that wetlands do. Studies of the acalyprate Diptera from lotic habitats (91, 98) recorded species richness lower than in a variety of freshwater wetlands (108, 170, 171; J.B. Keiper & W.E. Walton, unpublished observations). Steinly (163) found that disturbances caused by violent wave action reduce the number of species of Ephydridae present on the Lake Erie shoreline.

These data suggest that higher Diptera are much better suited to lentic habitats such as wetlands than to lotic systems that experience frequent disturbances such as floods and scouring.

Microhabitat Specificity

Microhabitat specialists are common among the higher Diptera. In general, aquatic insects are categorized trophically into the functional feeding groups (FFGs) of predator, grazer/scrapper, piercer/herbivore, shredder, and collector gatherer. Aquatic insects can also be grouped by mode of existence, such as skater, planktonic, diver, swimmer, clinger, sprawler, climber, and burrower (119). These trophic and mode of locomotion categories have been an effective means of grouping taxa ecologically. Dipteran microhabitat specialists include the Agromyzidae, Chloropidae, Ephydriidae, Otitidae, Platystomatidae, and Sciomyzidae (5, 18, 57, 72, 152, 181); their specific habits frequently preclude using trophic categories normally applied to benthic macroinvertebrates. Most specialists are herbivores of algae and vascular plants (47, 64, 98, 113, 152, 182), secondary invaders of vascular plants (5, 99, 182), and parasites and parasitoids of aquatic fauna (18). Some specialists live within anoxic sediments and pierce roots of specific plants with their spiracles to obtain oxygen for respiration (26, 108, 116).

Spatial, temporal, and trophic partitioning limit niche overlap among higher Diptera from wetlands. Spatial distribution is one of the most important factors limiting niche overlap among sympatric taxa (138). The spatial distribution of wetland Agromyzidae, Chloropidae, and Ephydriidae appears largely restricted to particular plant species (52, 109, 170, 171; J.B. Keiper & W.E. Walton, unpublished observations), plant density (10, 54), or substrate type (20, 149). Temporal partitioning appears to limit the number of species using wetland habitats at any one time (20, 108, 170, 171). The specificity of food sources exhibited by higher dipterans further limits their niche overlap (see below). The combination of the high productivity of wetlands with the coexistence of generalist and specialist taxa appears to explain why higher Diptera from freshwater wetlands are notably species rich.

Demography

The only demographic study of a higher dipteran from wetlands examined *Scatella picea*, a common and widespread ephydrid (36). This species is a grazer of algae in ephemeral, semi-aquatic habitats and has ovipositional preferences for mud shores or algal mats (35). Compared with other insect species, *S. picea* has a high intrinsic rate of increase, and populations grew more quickly than those species that utilize comparatively stable, long-lasting habitats. High intrinsic rates of growth were characteristic of species using oviposition sites that are unpredictable through space or time (36). Although life tables have not been calculated for other higher dipteran species from freshwater wetlands, many species appear to exploit unpredictable oviposition sites and other variable resources (20, 44, 169).

Colonization Ecology

In the vicinity of naturally occurring or human-made lentic habitats, colonization of a new wetland by higher Diptera can be rapid. The shore fly *Brachydeutera sturtevanti* is a neustic insect both in the larval and adult stages that employs generalist feeding strategies (i.e., filtering particles and collecting detrital or algal deposits); it is one of the more common dipterans in southern California marshes. Artificial pools attracted adults within 2 days, and puparia were produced within 2 weeks (101). Collections from newly flooded constructed wastewater treatment wetlands at 2 days postflooding produced adult Sphaeroceridae, Chloropidae, Ephydriidae, Agromyzidae, and Muscidae. Further study showed that these and other populations became established within the wetlands; thus, the individuals captured were not simply incidentals (J.B. Keiper & W.E. Walton, unpublished observations). Ephydrid larvae were found on floating mammalian carcasses placed in the field for less than 3 weeks during experiments of carrion colonization (172), further illustrating the rapidity with which new aquatic habitats may be colonized by higher Diptera.

TROPHIC ECOLOGY AND FEEDING HABITS

Much work has been done on the trophic ecology of wetlands Diptera (57, 72), yet we have information on the feeding habits for only a small fraction of species from North America and other parts of the world. Insects from aquatic habitats are frequently generalized trophically by FFGs (119), yet the diverse, and oftentimes specific, feeding habits of higher Diptera necessitates that more precise trophic categories be used. For instance, herbivory of vascular plants is considered rare in aquatic systems (192); thus the term “herbivore” applied to aquatic insects denotes a nonselective feeder of algae. Herbivory among higher dipterans can take the form of a primary herbivore of vascular plants, secondary herbivore of damaged vascular plant tissue, algal herbivore, or cyanobacterial herbivore (57). Primary herbivores may specifically mine leaves (e.g., 47) or bore stems (e.g., 98, 138), and cyanobacterial and algal herbivores may feed on a limited array of algal flora (63, 64). The varied nature of dipteran herbivory illustrates the difficulty of applying the FFG concept to those taxa.

Larval Feeding Habits

We summarize here what is known about the basic biology of selected Diptera families that commonly occur in wetlands, with particular reference to the larval feeding habits. Families are taken up alphabetically, not phylogenetically. Coverage is restricted largely to North America.

AGROMYZIDAE This is a large and widely distributed family having phytophagous larvae that are leaf miners, stem borers, or seed predators (162). Numerous species

can be found in wetlands where their larvae attack a great variety of monocots and dicots. Genera and their host plants that are particularly common in wetland habitats include *Agromyza* (*Celtis*, *Echinochloa*, *Phalaris*, *Populus*, *Salix*, *Ulmus*), *Amauromyza* (*Bidens*, *Eupatorium*), *Calycomyza* (*Ambrosia*, *Eupatorium*), *Cerodontha* (*Carex*, *Echinochloa*, *Glyceria*, *Phalaris*, *Typha*), *Chromatomyia* (*Carex*), *Hexomyza* (*Salix*), *Liriomyza* (*Asclepias*, *Triglochin*, *Vernonia*), *Melanagromyza* (*Ambrosia*, *Bidens*, *Desmodium*, *Eupatorium*, *Verbesina*, *Vernonia*), and *Phytomyza* (*Cicuta*, *Cornus*).

ANTHOMYZIDAE Larvae of *Anthomyza* and *Mumetopia* are known to feed within the culms of wetland sedges, although there is some question as to whether the larvae are phytophagous or feed as secondary invaders of damaged stems (177).

CHAMAEMYIIDAE The only genus of this family regularly collected in freshwater marshes is *Plunomia*, which has been found in association with sedges belonging to the genus *Carex* (76). Nothing is known of the larval feeding habits, but it is suspected that the larvae prey on scale insects infesting sedge leaves. Species of *Chamaemyia* and *Leucopsis* also are occasionally encountered in wetlands where their larvae prey on aphids and scale insects (159, 160).

CHLOROPIDAE This family is well represented in aquatic and semi-aquatic habitats and is particularly abundant in marshes. Species of *Elliponeura* and *Pseudopachychaeta* are seed predators of sedges and rushes (182, 188), and larvae of *Dicraeus* attack inflorescences of grasses (1). Larvae of several species of *Cetema*, *Chlorops*, *Epichlorops*, *Meromyza*, *Oscinella*, *Pachylophus*, and *Parectecephala* are phytophagous stem borers of monocots (6, 144, 182, 191). A number of genera (*Apallates*, *Aphanotrigonum*, *Conioscinella*, *Diplotoxa*, *Elachiptera*, *Eribolus*, *Eugaurax*, *Incertella*, *Olcella*, *Rhopalopterum*, *Stenoscinis*, *Lasiosina*, *Tricimba*) have stem-inhabiting larvae but are generally secondary saprophagous invaders of tissue previously damaged by more phytophagous larvae (148, 168, 180, 182, 191). Larvae of *Thaumatomyia* are thought to prey on aphids (57, 191).

DIASTATIDAE The only genus of this family regularly encountered in wetland habitats is *Diastata*, which occurs in marshes dominated by sedges and grasses. No information on the larval feeding habits has been published, but recently larvae of *Diastata repleta* were reared to adults on feces of small rodents (B.A. Foote, unpublished observations).

DROSOPHILIDAE Only a handful of species of this large and widely distributed family are regularly collected in wetlands, and little is known of their biology. *Drosophila quinaria* and *Drosophila tripunctata* have been reared from larvae feeding on decaying skunk cabbage (*Symplocarpus foetidus*) (86); larvae of *Drosophila deflecta* are scavengers of decaying yellow water lilies (*Nuphar*); and those of *Drosophila palustris* and *Drosophila subpalustris* have recently been

found to feed on decaying leaves and stems of wetland grasses and sedges (B.A. Foote, unpublished observations). In contrast to those taxa associated with wetlands flora, larvae of *Cladochaeta inversa* have the interesting habit of feeding within the spittle masses of spittlebugs (Cercopidae) occurring on branches of alders (*Alnus* spp.) (87).

EPHYDRIDAE This large family of flies is abundant in wetlands and has a wide diversity of feeding habits (72). Many genera, such as *Athyroglossa* (86), *Coenia* (70), *Discocerina* (77), *Leptopsilopa* (165), *Paracoenia* (34, 151, 197), *Paralimna* (151), and *Typopsilopa* (99, 151), have saprophagous larvae that feed on a variety of decaying plant material, whereas other genera, including *Allotrichoma* (169), *Platygympnopa* (194), and *Pseudohecamede* (146), feed on decaying animal flesh or dung on the surface of marshes. Larvae of the detritivorous genus *Notiphila* are unusual in that they possess long spiracular spines that allow them to tap the intercellular air spaces of plants growing in anaerobic soils (17, 26, 48, 98, 108). Larval *Brachydeutera* are highly polyphagous on microbial, algal, and detrital materials (101). Larvae of *Ochthera* are predators of other insect larvae, whereas adults feed on smaller winged insects (157). *Trimerina* larvae prey on spider eggs (69).

Herbivory on vascular plants, algae, and cyanobacteria is common in the Ephydridae. Some genera are specific in their trophic ecology and limit their feeding to cyanophytes [*Axysta* (63), *Hyadina* (63, 71), *Lytogaster* (65), *Nostima* (68), *Pelina* (66)], diatoms [*Ilythea* (72), *Parydra* (49, 169), *Zeros* (72)], or a mixture of algae [*Ephydra* (195), *Scatella* (35, 64, 199), *Setacera* (67)]. Species of *Hydrellia*, a large and widely distributed genus, have larvae that feed as leaf-miners on many hydrophilic plants (17, 47, 85). Some genera are more specific in their host plant preference. Larvae of *Rhysophora* feed within the flower heads of pickerelweed (139), those of *Lemnaphila* mine the thalli of duckweeds (117, 154, 155), and those of *Psilopa* mine leaves of species of Chenopodiaceae (107).

LAUXANIIDAE This family is typically found in wooded habitats where its larvae feed on decaying mesophyll of fallen leaves of deciduous trees, or feed as scavengers on accumulations of rotting plant material (122, 123). *Minettia lupulina* occurs regularly in marshy wetlands, and several species of *Homoneura* are commonly encountered in swamps.

MICROPEZIDAE Only *Compsobata pallipes* and *Compsobata univittata* are regularly encountered in marshy habitats. The larvae are scavengers of decaying plant material (167). Adults of *Rainieria antennaepe*s were reared from larvae found in the crotch of an old American elm tree (147), and larvae of *Taeniaaptera lasciva* were found to feed on decaying sugar cane cuttings (39).

MUSCIDAE An excellent reference on the basic biology of this large and widely distributed family is Skidmore (158). Relatively few species are regularly encountered in freshwater wetlands. The stem-boring larvae of *Atherigona* and

Dichaetomyia can be economically important pests of rice and other cereals (158). Species of *Graphomyia* are aquatic or semi-aquatic and have larvae that are saprophagous in decaying plant material. Some species of *Coenosia*, *Lispe*, *Lispoides*, and *Spilogona* have aquatic larvae that prey on a wide variety of small invertebrates in wetland habitats (95, 111, 158). Larvae of species of *Schoenomyza* are stem borers of sedges (158).

OPOMYZIDAE *Opomyza petrei* and a few species of *Geomyza* are common in marshy habitats. The larvae are known to be stem borers of grasses (135).

OTITIDAE Species of *Chaetopsis* are frequently common in marshes where their larvae act as secondary invaders of the stems of herbaceous monocots damaged by other insect larvae (5, 100). Larvae of *Eumetopiella rufipes* attack the developing inflorescences of barnyard grass, *Echinochloa crusgalli* (181). Adults of *Seioptera vibrans* are occasionally found in marshes where its larvae feed on decaying plant material (4). Adults of *Ceroxys*, *Herina*, *Meliera*, and *Otites* occur regularly in marshes, but nothing is known of their larval feeding habits.

PSILIDAE Several species in two genera of this relatively small family occur in wetland habitats in North America. Larvae of *Psila* have been found feeding on the roots of *Carex* (Cyperaceae) (23) and several genera of mustards (Cruciferae) (23, 184). Adults of *Loxocera cylindrica* (Say) have been reared from larvae mining the culms of rushes and sedges (182).

SARCOPHAGIDAE Most species of flesh flies are normally not found in wetlands. However, some species are associated with bog-inhabiting plants, such as pitcher plants (*Sarracenia*) and skunk cabbage (*Symplocarpus*), where they consume dead insects trapped within the cups of the plants (2, 41). *Fletcherimyia* and *Sarcophaga* have larvae that feed on the soupy mixture of insects and liquid that accumulates at the bottoms of the plant cups in the southeastern United States (G.A. Dahlem, personal communication).

SCATHOPHAGIDAE This large, widely distributed family is well represented in wetland habitats where larvae of several species feed as stem borers of herbaceous monocots as well as a few dicots. Species of *Cordilura* mine the stems of a variety of wetland graminoid species belonging to the genera *Carex*, *Scirpus*, *Juncus*, and *Glyceria* (134, 185). Larvae of *Hydromyza* mine the submerged petioles of water lilies belonging to the genera *Nuphar* and *Nymphaea* (25, 93, 177, 189, 190). A few species of Scathophagidae have leaf-mining larvae, including *Delina* and *Neochiroso* that attack *Veratrum* (130). Detritivorous larvae of several species of *Scathophaga* can be found feeding on dung in wetland areas (29). Larvae of *Spaziphora* prey on small invertebrates occurring in lakeside muds (84, 94), whereas *Orthacheta hirtipes* is a predator of stem-boring *Cordilura* larvae (133).

SCIOMYZIDAE This is a sizeable family of over 600 species distributed throughout most regions of the world. Larvae of most species prey on a great variety of Mollusca, with many species feeding on aquatic snails, although other species show more specialized habits (18). Larvae of *Dictya*, *Elgiva*, *Hedria*, *Hoplodictya*, *Hydromya*, *Pherbina*, *Sepedon*, *Sepedonea*, and *Tetanocera* are unselective predators of pulmonate aquatic snails (11, 58, 60, 75, 104, 105, 131, 132, 179). In contrast, larvae of *Atrichomelina*, *Colobaea*, *Pherbellia*, *Pteromicra*, *Sciomyza*, and some species of *Tetanocera* frequently are predators or parasitoids of stranded aquatic or shoreline snails (22, 59, 61, 73, 74, 77, 145). Interesting trophic offshoots are demonstrated by larvae of *Antichaeta* that prey on eggs of aquatic and semi-aquatic snails (58, 103, 143), by larvae of *Renocera* that attack fingernail clams of the family Sphaeriidae (62), and by those of certain species of *Tetanocera* that consume slugs (174, 175). The only known trophic deviation from consumption of molluscan prey is *Sepedonella nana* from Africa, whose larvae developed successfully preying on aquatic oligochaetes in the laboratory (178).

SEPSIDAE Larvae of *Enicomira*, *Sepsis*, and *Themira* are commonly encountered in wetland habitats where their larvae are scavengers of dung or decaying vegetation (89, 90, 125).

SPHAEROCERIDAE This is a large family of worldwide distribution, with larvae that are basically saprophagous in feeding habits. Many species of *Leptocera*, *Lotophila*, *Rachispoda*, and *Spelobia* occur in wetland habitats where they feed on dung (29, 89, 90, 110), decaying plant material (21, 114, 142), and decomposing carcasses (16, 81, 141). Although successful in all wetland types, sphaerocerids are one of the most species-rich higher dipteran taxa from peatlands (115), where they may play significant roles in energy flow and nutrient cycling. We have observed muddy areas of constructed wetlands blackened by sphaerocerid adults after marshes were drained (J.B. Keiper & W.E. Walton, unpublished observations).

Importance to Other Organisms

The higher Diptera can be an important component of waterfowl diets (51, 55, 126), and wetland birds may exhibit significant top-down ecological effects on higher dipterans (197). Production of higher Diptera accounted for a significant portion of adult insect biomass in Lake Michigan coastal wetlands (102), with Scathophagidae, Ephydriidae, Calliphoridae, and Sciomyzidae being ranked the most abundant taxa in terms of biomass in sticky traps. Although certain taxa were obviously produced in areas outside of the wetlands (i.e., Calliphoridae), these data show clearly that higher dipterans are a potentially important food source for higher trophic levels. Management of seasonal and constructed wetlands may alter the population sizes of higher dipterans (14, 50, 52; J.B. Keiper & W.E. Walton, unpublished observations), thus influencing the breeding potential of migratory waterfowl.

Wetlands and wetland invertebrates are especially important resources for waterfowl and shorebirds, as well as for passerines that utilize emergent adults of aquatic insects and terrestrial insects associated with wetlands (28, 30, 137). Approximately 80% of America's breeding bird populations and more than 50% of the 800 species of protected migratory birds depend on wetlands (193). Because diets and primary foraging habitats differ appreciably among waterbirds, and can vary seasonally within a species, a broad diversity of wetland habitat types is important for waterbird success. Juvenile shorebirds (92) and ducks (166) feed primarily on aquatic insects. Adult dabbling ducks feed mostly on plants throughout the year, but protein and other nutrients provided by wetland invertebrates are necessary for reproduction and during feather molting (56, 106, 166). Several studies have documented that the distribution of waterfowl among wetland habitats is associated with invertebrate abundance (97, 112, 128), and the proportion of invertebrates in waterfowl diets increases from spring through autumn (12, 37, 56, 121).

In addition to serving as breeding sites, wetlands along major migratory flyways are both critical stopping-off sites and overwintering sites for many waterbirds. For example, about 60% of waterfowl migrating along the Pacific flyway utilize wetlands in a region of intensive agriculture in central California (83) for resting and foraging. Wetland invertebrates are important components in the diets of overwintering waterfowl and shorebirds (92). Brine fly (*Ephydra millbrae*) larvae established large populations soon after late summer flooding of pickleweed-dominated (*Salicornia virginica*) wetlands, but populations disappeared from ponds after November and did not reestablish large populations the following spring (14). Brine flies occurring in saline lakes (e.g., Mono Lake and the Great Salt Lake (32, 33, 126) of the western United States are a critical component of food webs and are an important food for waterfowl and shorebirds (126). Some bird species (red-necked phalaropes and Wilson's phalaropes at Mono Lake) (126) specialize on brine flies, whereas many waterfowl are opportunistic and forage extensively on brine fly pupae concentrated along the shore by the wind (56). Leaf-mining and stem-boring Diptera may be consumed more frequently than previously thought owing to inadvertent consumption by herbivorous waterfowl. Further investigation of the roles of higher Diptera in wetland avian diets is needed.

The impact of higher dipteran populations on prey, host plant, or algal food sources has not been explored, and thus represents a potentially fruitful avenue of research. Collins (32) documented high algal productivity in hot springs coupled with low chlorophyll values. The discrepancy was caused by grazing ephydriids that slowed the proliferation of algal populations. Wetlands are also known for high productivity and strong algal populations (124); therefore similar patterns of algal use may be found (64). Predators (Ephydriidae, Muscidae), primary herbivores (Agromyzidae, Chloropidae, Ephydriidae), parasitoids (Sciomyzidae), and other trophic levels should also be explored in terms of how their presence affects the production of other members of wetland communities.

EVOLUTIONARY CONSIDERATIONS

Adaptive Radiation

It has been suggested that the ancestors of modern higher Diptera were adapted for life as saprophages in rotting vegetation, which is an abundant resource in all wetland types (57, 136). Today, we see all trophic levels occupied by higher flies in wetlands. Adaptive radiation onto nondetritus resources probably occurred during selection for more specific ovipositional behaviors and feeding habits. For instance, it was hypothesized by Keiper et al. (99) that secondary invaders of wetland vascular plants were derived from species that were general scavengers but whose adults became specific in their ovipositional preferences; this shift from general scavenger to specialized secondary invader may then have given rise to primary herbivores such as stem borers. Ultimately some ecological equivalents were segregated temporally (e.g., 108, 170, 171). The combination of evolutionary radiation to different spatial and trophic resources coupled with temporal partitioning illustrates some reasons for the ample widespread success of higher dipterans in freshwater wetlands.

Selection for Particular Wetlands

Marshall's (115) work on peatland Sphaeroceridae is perhaps the clearest example of higher dipteran species being wetland selective, as he showed that more than 20% of species taken from Canadian bogs and fens were peatland specific. Much of the wetlands-specific selection may be driven by adaptations for host plants and physicochemical characteristics, but the latter has not been tested for higher Diptera. Overall, marshes appear to support the most species-rich higher fly communities as compared to peatlands, riparian wetlands, and swamps (43, 76, 108, 151, 170, 171, 198). Keiper & Walton (unpublished observations) recorded more than 50 species of higher dipteran adults inhabiting constructed wetlands flooded with secondary-treated wastewater and vegetated with bulrush monocultures in southern California. Twelve species of *Notiphila* alone were taken from a 0.5 ha marsh in northeastern Ohio (171). Although intensive work on marshes has been conducted, similar work has not been done on bogs, fens, riparian wetlands, or swamps.

CONCLUDING REMARKS

The ecological roles of higher dipterans from freshwater wetlands are diverse, as are the feeding habits of individual species. Adaptive radiation in certain taxa from wetlands has been extensive and is exemplified by the Ephydriidae and Sciomyzidae. Many of the taxa considered in this review are not economically important pests, therefore relatively little effort has been put forth to study the biology and immature stages of wetlands-inhabiting dipterans. This problem is compounded

by the fact that most species do not reside in areas of a wetlands typically sampled by benthologists, and therefore they are virtually excluded from ecological studies. When we consider the economic and aesthetic values of wetlands, their importance to biodiversity, and their overall importance to our biosphere, it becomes apparent that all biotic components of freshwater wetlands deserve our attention.

ACKNOWLEDGMENTS

We thank Ruth Chase and Marianne Stanczak (Cleveland Museum of Natural History) for proofreading and improving the manuscript. The authors thank those organizations that have funded them during their study of wetlands entomofauna: American Philosophical Society, National Science Foundation, Ohio Biological Survey, Ohio Department of Natural Resources, and the University-wide Mosquito Research Program of the Division of Agriculture and Natural Resources of the University of California.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

1. Agafonova ZY. 1962. New brome pests—flies of the genus *Dicraeus* (Diptera, Chloropidae). *Entomol. Rev. Wash.* 41: 304–9
2. Aldrich JM. 1915. The economic relations of the Sarcophagidae. *J. Econ. Entomol.* 8:242–46
3. Allan JD. 1995. *Stream Ecology: Structure and Function of Running Waters*. London: Chapman & Hall
4. Allen EJ, Foote BA. 1967. Biology and immature stages of three species of Otitidae (Diptera) which have saprophagous larvae. *Ann. Entomol. Soc. Am.* 60:826–36
5. Allen EJ, Foote BA. 1992. Biology and immature stages of *Chaetopsis massyla* (Diptera: Otitidae), a secondary invader of herbaceous stems of wetland monocots. *Proc. Entomol. Soc. Wash.* 94:320–28
6. Allen MW, Painter RH. 1937. Observations on the biology of the wheat-stem maggot in Kansas. *J. Agric. Res.* 55:215–38
7. Anderson DJ, Vondracek B. 1999. Insects as indicators of land use in three ecoregions in the prairie pothole region. *Wetlands* 19:648–64
8. Aselmann I, Crutzen PJ. 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *J. Atmos. Chem.* 8:307–58
9. Aselman I, Crutzen PJ. 1990. A global inventory of wetland distribution and seasonality, net primary productivity, and estimated methane emissions. In *Soils and the Greenhouse Effect*, ed. AF Bouwman, pp. 441–49. New York: Wiley
10. Athen O, Tschardt T. 1999. Insect communities of *Phragmites* habitats used for sewage purification: effects of age and area of habitats on species richness and herbivore-parasitoid interactions. *Limnologia* 29:71–74
11. Barraclough DA. 1983. The biology and immature stages of some *Sepedon* snail-killing flies in Natal (Diptera: Sciomyzidae). *Ann. Natal Mus.* 25:293–317
12. Batzer DP, McGee M, Resh VH, Smith RR. 1993. Characteristics of invertebrates consumed by mallards and prey response

- to wetland flooding schedules. *Wetlands* 13:41–49
13. Batzer DP, Rader RB, Wissinger SA, eds. 1999. *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. New York: Wiley
 14. Batzer DP, Resh VH. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. *Wetlands* 12:1–7
 15. Batzer DP, Wissinger SA. 1996. Ecology of insect communities in nontidal wetlands. *Annu. Rev. Entomol.* 41:75–100
 16. Beaver RA. 1972. Ecological studies on Diptera breeding in dead snails. 1. Biology of the species found in *Cepaea nemoralis* (L.). *Entomologist* 105:41–52
 17. Berg CO. 1950. *Hydrellia* (Ephydriidae) and some other acalyptrate Diptera reared from *Potamogeton*. *Ann. Entomol. Soc. Am.* 23:374–98
 18. Berg CO, Knutson LV. 1978. Biology and systematics of the Sciomyzidae. *Annu. Rev. Entomol.* 23:239–58
 19. Bergey EA, Balling SF, Collins JN, Lambert GA, Resh VH. 1992. Bionomics of invertebrates within an extensive *Potamogeton pectinatus* bed of a California marsh. *Hydrobiologia* 234:15–24
 20. Blair JM, Foote BA. 1984. Resource partitioning in five sympatric species of *Scatella* (Diptera: Ephydriidae). *Environ. Entomol.* 13:1336–39
 21. Bohart GE, Gressitt JL. 1951. Filth-inhabiting flies of Guam. *Bull. Bernice P. Bishop Mus.* 204:1–152
 22. Bratt AD, Knutson LV, Foote BA, Berg CO. 1969. Biology of *Pherbellia* (Diptera: Sciomyzidae). *Mem. Cornell Univ. Exp. Stn.* 404:1–246
 23. Brindle A. 1965. Taxonomic notes on the larvae of British Diptera. No. 22. Psilidae. *Entomologist* 98:169–73
 24. Brock ML, Wiegert RG, Brock TD. 1969. Feeding by *Paracoenia* and *Ephydra* (Diptera: Ephydriidae) on the microorgan-
 - isms of hot springs. *Ecology* 50:192–200
 25. Brock TCM, van de Velde G. 1983. An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*. *Tijdschr. Entomol.* 126:59–90
 26. Busacca JD, Foote BA. 1978. Biology and immature stages of two species of *Notiphila*, with notes on other shore flies occurring in cattail marshes (Diptera: Ephydriidae). *Ann. Entomol. Soc. Am.* 71:457–66
 27. Castanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–60
 28. Chura NJ. 1961. Food availability and preferences of juvenile mallards. *Trans. N. Am. Wildl. Conf.* 26:121–34
 29. Coffey MD. 1966. Studies on the association of flies (Diptera) with dung in southeastern Washington. *Ann. Entomol. Soc. Am.* 59:207–18
 30. Collias NE, Collias EC. 1963. Selective feeding by wild ducklings of different species. *Wilson Bull.* 75:6–14
 31. Collins NC. 1975. Population biology of a brine fly (Diptera: Ephydriidae) in the presence of abundant algal food. *Ecology* 56:1139–48
 32. Collins NC. 1980. Developmental responses to food limitation as indicators of environmental conditions for *Ephydra cinerea* Jones (Diptera). *Ecology* 61:650–61
 33. Collins N. 1980. Population ecology of *Ephydra cinerea* (Diptera: Ephydriidae), the only benthic metazoan of the Great Salt Lake, USA. *Hydrobiologia* 68:99–112
 34. Collins NC, Mitchell R, Wiegert RG. 1976. Functional analysis of a thermal spring ecosystem, with an evaluation of the role of consumers. *Ecology* 57:1221–32
 35. Connell TD, Scheiring JF. 1981. The feeding ecology of the fly *Scatella picea*

- (Walker) (Diptera: Ephydriidae). *Can. J. Zool.* 59:1831–35
36. Connell TD, Scheiring JF. 1982. Demography of the shore fly, *Scatella picea* (Walker) (Diptera: Ephydriidae). *Environ. Entomol.* 3:611–17
 37. Connelly DP, Chesemore DL. 1980. Food habits of pintails, *Anas acuta*, wintering on seasonally flooded wetlands in the northern San Joaquin Valley, California. *Calif. Fish Game* 66:233–37
 38. Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. *Classification of Wetlands and Deepwater Habitats of the United States*, FWS/OBS–79/31, Washington, DC: US Fish Wildl. Serv.
 39. Cresson ET. 1938. The Neriidae and Micropezidae of America north of Mexico (Diptera). *Trans. Am. Entomol. Soc.* 64:293–366
 40. Dahl TE, Johnson CE. 1991. *Wetlands Status and Trends in the Conterminous United States, Mid-1970s to Mid-1980s*. Washington, DC: US Dept. Inter., Fish Wildl. Serv.
 41. Dahlem GA. 1991. Sarcophagidae. In *Immature Insects*, ed. FW Stehr, 2:871–73. Dubuque, IA: Kendall/Hunt
 42. Daily GC, ed. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington, DC: Island Press
 43. Deonier DL. 1965. Ecological observations on Iowa shore flies (Diptera, Ephydriidae). *Proc. Iowa Acad. Sci.* 71:496–510
 44. Deonier DL. 1972. Observations on mating, oviposition, and food habits of certain shore flies (Diptera: Ephydriidae). *Ohio J. Sci.* 72:22–29
 45. Deonier DL, ed. 1979. *First Symposium on the Systematics and Ecology of Ephydriidae (Diptera)*. Erie, PA: N. Am. Benthol. Soc. 147 pp.
 46. Deonier DL. 1979. Introduction—a prospectus of research in Ephydriidae. See Ref. 45, pp. 1–19
 47. Deonier DL. 1998. A manual of the common North American species of the aquatic leafmining genus *Hydrellia* (Diptera: Ephydriidae). *Mem. Entomol. Int.* 12:1–354
 48. Deonier DL, Mathis WN, Regensburg JT. 1979. Natural history and life-cycle stages of *Notiphila carinata* (Diptera: Ephydriidae). *Proc. Biol. Soc. Wash.* 91:798–814
 49. Deonier DL, Regensburg JT. 1978. Biology and immature stages of *Parydra quadrituberculata* (Diptera: Ephydriidae). *Ann. Entomol. Soc. Am.* 71:341–53
 50. de Szalay FA, Batzer DP, Resh VH. 1996. Mesocosm and macrocosm experiments to examine effects of mowing emergent vegetation on wetland invertebrates. *Environ. Entomol.* 25:303–9
 51. de Szalay FA, Euliss NH Jr, Batzer DP. 1999. Seasonal and semipermanent wetlands of California. See Ref. 13, pp. 829–55
 52. de Szalay FA, Resh VH. 1996. Spatial and temporal variability of trophic relationships among aquatic macroinvertebrates in a seasonal marsh. *Wetlands* 16:458–66
 53. de Szalay FA, Resh VH. 1997. Responses of wetland invertebrates and plants important in waterfowl diets to burning and mowing of emergent vegetation. *Wetlands* 17:149–56
 54. de Szalay FA, Resh VH. 2000. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. *Freshw. Biol.* 45:295–308
 55. Euliss NH, Harris SW. 1987. Feeding ecology of northern pintails and green-winged teal wintering in California. *J. Wildl. Manage.* 51:724–32
 56. Euliss NH, Jarvis RL, Gilmer DS. 1991. Feeding ecology of waterfowl wintering on evaporation ponds in California. *Condor* 93:582–90
 57. Ferrar P. 1987. *A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha, Part 1: Text*, pp. 1–478. Leiden, The Netherlands: EJ Brill/Scandinavian
 58. Fisher TW, Orth RE. 1964. Biology and

- immature stages of *Antichaeta testacea* Melander (Diptera: Sciomyzidae). *Hilgardia* 36:1–29
59. Foote BA. 1959. Biology and life history of the snail-killing flies belonging to the genus *Sciomyza* Fallén (Diptera, Sciomyzidae). *Ann. Entomol. Soc. Am.* 52:31–43
 60. Foote BA. 1971. Biology of *Hedria mixta* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 69:931–41
 61. Foote BA. 1973. Biology of *Pherbellia prefixa* (Diptera: Sciomyzidae), a parasitoid-predator of the operculate snail *Valvata sincera* (Gastropoda: Valvatidae). *Proc. Entomol. Soc. Wash.* 75:141–49
 62. Foote BA. 1976. Biology and larval feeding habits of three species of *Renocera* (Diptera: Sciomyzidae) that prey on fingernail clams (Mollusca: Sphaeriidae). *Ann. Entomol. Soc. Am.* 69:121–33
 63. Foote BA. 1977. Utilization of blue-green algae by larvae of shore flies. *Environ. Entomol.* 6:812–14
 64. Foote BA. 1979. Utilization of algae by larvae of shore flies. See Ref. 45, pp. 61–72
 65. Foote BA. 1981. Biology and immature stages of *Lytogaster excavata*, a grazer of blue-green algae (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 83:304–15
 66. Foote BA. 1981. Biology and immature stages of *Pelina truncatula*, a consumer of blue-green algae (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 83:607–19
 67. Foote BA. 1982. Biology and immature stages of *Setacera atrovirens*, a grazer of floating algal mats (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 84:828–44
 68. Foote BA. 1983. Biology and immature stages of *Nostima approximata* (Diptera: Ephydriidae), a grazer of the blue-green algal genus *Oscillatoria*. *Proc. Entomol. Soc. Wash.* 85:472–84
 69. Foote BA. 1984. Biology of *Trimerina madizans*, a predator of spider eggs (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 86:486–92
 70. Foote BA. 1990. Biology and immature stages of *Coenia curvicauda* (Diptera: Ephydriidae). *J. NY Entomol. Soc.* 98:93–102
 71. Foote BA. 1993. Biology of *Hyadina albovenosa* (Diptera: Ephydriidae), a consumer of Cyanobacteria. *Proc. Entomol. Soc. Wash.* 95:377–82
 72. Foote BA. 1995. Biology of shore flies. *Annu. Rev. Entomol.* 40:417–42
 73. Foote BA. 1996. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Diptera: Sciomyzidae). I. Introduction and life histories of predators of shoreline snails. *Ann. Carnegie Mus.* 65:1–12
 74. Foote BA. 1996. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Diptera: Sciomyzidae). II. Life histories of predators of succineid snails. *Ann. Carnegie Mus.* 65:153–66
 75. Foote BA. 1999. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Diptera: Sciomyzidae). III. Life histories of predators of aquatic snails. *Ann. Carnegie Mus.* 68:151–74
 76. Foote BA. 2002. Acalyptrate Diptera associated with stands of *Carex lacustris* and *C. stricta* (Cyperaceae) in northeastern Ohio. *Proc. Entomol. Soc. Wash.* In press
 77. Foote BA, Eastin WC. 1974. Biology and immature stages of *Discocerina obscurella* (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 76:401–8
 78. Foote BA, Knutson LV, Keiper JB. 1999. The snail-killing flies of Alaska (Diptera: Sciomyzidae). *Insecta Mundi* 13:45–71
 79. Foote BA, Neff SE, Berg CO. 1960. Biology and immature stages of *Atrichomelina pubera* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 53:192–99
 80. Frayer WE, Monahan TJ, Bowden DC, Graybill FA. 1983. *Status and Trends of Wetlands and Deepwater Habitats in the Conterminous United States, 1950s to*

- 1970s. Fort Collins, CO: Dept. For. Wood Sci., Colorado State Univ.
81. Fuller ME. 1934. The insect inhabitants of carrion: a study in animal ecology. *Bull. Coun. Sci. Ind. Res. Melb.* 82:1–62
82. Garono RJ, Kooser JG. 1994. Ordination of wetland insect populations: evaluation of a potential mitigation monitoring tool. In *Global Wetlands: Old World and New*, ed. WJ Mitsch, pp. 509–16. New York: Elsevier Science
83. Gilmer DS, Miller MR, Bauer RD, LeDonne JR. 1982. California's Central Valley wintering waterfowl: concerns and challenges. *Trans. N. Am. Wildl. Nat. Res. Conf.* 47:441–52
84. Graham JE. 1939. The external features of the early stages of *Spathiophora hydromyzina* (Fall.) (Dipt., Cordyluridae). *Proc. R. Entomol. Soc. London B* 8:157–62
85. Grigarick AA. 1959. Bionomics of the rice leaf miner, *Hydrellia griseola* (Fallén) in California (Diptera: Ephydriidae). *Hilgardia* 29:1–80
86. Grimaldi D, Jaenike J. 1983. The Diptera breeding on skunk cabbage, *Symplocarpus foetidus* (Araceae). *J. NY Entomol. Soc.* 91:83–89
87. Grimaldi D, Nguyen T. 1999. Monograph of the spittlebug flies, genus *Cladochaeta* (Diptera: Drosophilidae: Cladochaetini). *Bull. Am. Mus. Nat. Hist.* 241:1–326
88. Grimm NB, Fisher SG. 1992. Responses of arid-land streams to changing climate. In *Global Climate Change and Freshwater Ecosystems*, ed. P Firth, SG Fisher, pp. 211–33. New York: Springer Verlag
89. Hafez M. 1939. Some ecological observations on the insect fauna of dung. *Bull. Soc. Fouad. I Entomol.* 23:241–87
90. Hammer O. 1942. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Vidensk. Medd. Dan. Naturhist. Foren.* 105:141–393
91. Harris SC, Deonier DL. 1979. Ecological observations of immature Ephydriidae in North Dakota springbrooks. See Ref. 45, pp. 111–21
92. Helmers DL. 1992. *Shorebird Management Manual*. Manomet, MA: West. Hemisphere Shorebird Reserv. Netw.
93. Hickman CP. 1935. External features of the larva of *Hydromyza confluens*. *Proc. Indiana Acad. Sci.* 44:212–16
94. Irwin AG. 1978. Some micro-habitats. Mud. In *A Dipterist's Handbook*, ed. A Stubbs, P Chandler, 15:83–86. Hanworth, UK: Amat. Entomol.
95. Johannsen OA. 1935. Aquatic Diptera. Part II. Orthorrhapha-Brachycera and Cyclorrhapha. *Mem. Cornell Univ. Agr. Exp. Stn.* 177:1–62
96. Kadlec RH, Knight RL. 1996. *Treatment Wetlands*. Boca Raton: CRC. 893 pp.
97. Kaminski RM, Prince HH. 1981. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. *Auk* 98:115–26
98. Keiper JB, Brutsche PL, Foote BA. 1998. Acalyprate Diptera associated with water willow, *Justicia americana* (Acanthaceae). *Proc. Entomol. Soc. Wash.* 100: 576–87
99. Keiper JB, Jiannino J, Sanford M, Walton WE. 2001. Biology and immature stages of *Typopsilopa nigra* (Wirth) (Diptera: Ephydriidae), a secondary consumer of damaged stems of wetlands monocots. *Proc. Entomol. Soc. Wash.* 103:89–97
100. Keiper JB, Sanford M, Jiannino J, Walton WE. 2000. Invertebrates inhabiting wetland monocots damaged by Lepidoptera. *Entomol. News* 111:348–54
101. Keiper JB, Walton WE. 2000. Biology and immature stages of *Brachydeutera sturtevantii* (Diptera: Ephydriidae), a hyponeustic generalist. *Ann. Entomol. Soc. Am.* 93:468–75
102. King RS, Brazner JC. 1999. Coastal wetland insect communities along a trophic gradient in Green Bay, Lake Michigan. *Wetlands* 19:426–37
103. Knutson LV, Abercrombie J. 1977. Biology of *Antichaeta melanosoma* (Diptera:

- Sciomyzidae), with notes on parasitoid Ichneumonidae (Hymenoptera). *Proc. Entomol. Soc. Wash.* 79:111–25
104. Knutson LV, Berg CO. 1964. Biology and immature stages of snail-killing flies: the genus *Elgiva* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 57:173–92
 105. Knutson LV, Neff SE, Berg CO. 1967. Biology of snail-killing flies from Africa and southern Spain (Sciomyzidae: *Sepeidon*). *Parasitology* 57:487–505
 106. Krapu GL. 1981. The role of nutrient reserves in mallard reproduction. *Auk* 98:29–38
 107. Landis BJ, Wallis RL, Redmond RD. 1967. *Psilopa leucostoma*, a new leaf miner of sugar beets in the United States. *J. Econ. Entomol.* 60:115–18
 108. Larson L, Foote BA. 1997. Biology of four species of *Notiphila* Fallen (Diptera: Ephydriidae) associated with the yellow water lily, *Nuphar luteum* (Nymphaeaceae). *Proc. Entomol. Soc. Wash.* 99: 541–59
 109. LaSalle MW, Rozas LP. 1991. Comparing the benthic macrofaunal assemblages of creekbank beds of the spikerush *Eleocharis parvula* (R&S) link and adjacent unvegetated areas in a Mississippi brackish marsh. *Wetlands* 11:229–44
 110. Laurence BR. 1955. The ecology of some British Sphaeroceridae (Borboridae, Diptera). *J. Anim. Ecol.* 24:187–99
 111. Le Roux EJ, Perron JP. 1960. Descriptions of immature stages of *Coenosia tigrina* (F.) (Diptera: Anthomyiidae), with notes on hibernation of larvae and predation by adults. *Can. Entomol.* 92:284–96
 112. Lillie RA, Evrard JO. 1994. Influence of macroinvertebrates and macrophytes on waterfowl utilization of wetlands in the Prairie Pothole region of northwestern Wisconsin. *Hydrobiologia* 279/280:235–46
 113. Mansor M, Buckingham GR. 1989. Laboratory host range studies with a leaf-mining duckweed shore fly. *J. Aquat. Plant Manage.* 27:115–18
 114. Marshall SA. 1982. A revision of the Nearctic *Leptocera* (*Thoracochaeta* Duda) (Diptera; Sphaeroceridae). *Can. Entomol.* 114:63–78
 115. Marshall SA. 1994. Peatland Sphaeroceridae (Diptera) of Canada. *Mem. Entomol. Soc. Can.* 169:173–79
 116. Mathis WN. 1979. Studies of Notiphilinae (Diptera: Ephydriidae). I. Revision of the Nearctic species of *Notiphila* Fallen, excluding the *caudata* group. *Smithson. Contrib. Zool.* 287:1–111
 117. Mathis WN, Edmiston JF. 2000. A revision of the shore-fly genus *Lemnaphila* Cresson (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 102:652–77
 118. Mathis WN, Zatwarnicki T. 1995. World catalog of shore flies (Diptera: Ephydriidae). *Mem. Entomol. Int.* 4:1–423
 119. Merritt RW, Cummins KW, eds. 1996. *An Introduction to the Aquatic Insects of North America*. Dubuque, IA: Kendall/Hunt. 862 pp.
 120. Merritt RW, Resh VH, Cummins KW. 1996. Design of aquatic insect studies: collecting, sampling and rearing procedures. See Ref. 119, pp. 12–28
 121. Miller MR. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *J. Wildl. Manage.* 51:405–14
 122. Miller RM. 1977. Ecology of Lauxaniidae (Diptera: Acalyptratae). I. Old and new rearing records with biological notes and discussion. *Ann. Natal Mus.* 23:215–38
 123. Miller RM, Foote BA. 1975. Biology and immature stages of eight species of Lauxaniidae (Diptera). I. Biological observations. *Proc. Entomol. Soc. Wash.* 77:308–28
 124. Mitsch WJ, Gosselink JG. 2000. *Wetlands*. New York: Wiley. 920 pp.
 125. Mohr CO. 1943. Cattle droppings as ecological units. *Ecol. Monogr.* 13:275–98
 126. Mono Basin Ecosystem Study Committee (MBESC). 1987. *The Mono Basin Ecosystem: Effects of Changing Lake*

- Level. Board on Environ. Studies Toxicol., Comm. Phys. Sci. Math. Res., Natl. Res. Council. Washington, DC: Natl. Acad. Press
127. Moore PD, Bellamy DJ. 1974. *Peatlands*. London: Elek Science. 221 pp.
128. Murkin HR, Batt BDJ. 1987. The interactions of vertebrates and invertebrates in peatlands and marshes. In *Aquatic Insects of Peatlands and Marshes of Canada*, ed. DM Rosenberg, HV Danks, 140:15–30. Ottawa: Entomol. Soc. Can.
129. National Research Council (NRC). 1992. *Restoration of Aquatic Ecosystems*. Washington, DC: National Academy Press
130. Neff SE. 1970. Observations on the life cycle and immature stages of *Neochirosa atrifrons* (Diptera; Scatophagidae). *Can. Entomol.* 102:1088–93
131. Neff SE, Berg CO. 1962. Biology and immature stages of *Hoplodictya spinicornis* and *H. setosa* (Diptera; Sciomyzidae). *Trans. Am. Entomol. Soc.* 88:77–93
132. Neff SE, Berg CO. 1966. Biology and immature stages of malacophagous Diptera of the genus *Sepedon*. *Bull. Va. Agric. Exp. Stn.* 566:1–113
133. Neff SE, Wallace JB. 1969. Biology and descriptions of immature stages of *Orthacheta hirtipes*, a predator of *Cordilura* spp. *Ann. Entomol. Soc. Am.* 62:785–90
134. Neff SE, Wallace JB. 1969. Observations on the immature stages of *Cordilura (Achaetella) deceptiva* and *A. (A.) varipes*. *Ann. Entomol. Soc. Am.* 62:775–85
135. Nye IWB. 1958. The external morphology of some of the dipterous larvae living in the Gramineae of Britain. *Trans. R. Entomol. Soc. London* 110:411–87
136. Oldroyd H. 1964. *The Natural History of Flies*. London: Weidenfeld & Nicolson. 324 pp.
137. Pehrsson O. 1979. Feeding behavior, feeding habitat utilization, and feeding efficiency of juvenile mallards (*Anas platyrhynchos* L.) as guided by a domestic duck. *Viltrevy* 10:193–218
138. Price PW. 1997. *Insect Ecology*. New York: Wiley. 3rd ed. 874 pp.
139. Rao N, Mathis WN. 1995. A revision of the shore-fly genus *Rhysophora* Cresson (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 97:666–88
140. Reice SR. 1994. Nonequilibrium determinants of biological community structure. *Am. Sci.* 82:424–35
141. Richards OW. 1930. The British species of Sphaeroceridae (Borboridae, Diptera). *Proc. Zool. Soc. London* 1930:261–345
142. Richards OW. 1973. The Sphaeroceridae (Borboridae or Cypselidae; Diptera, Cyclorrhapha) of the Australian region. *Aust. J. Zool. Suppl. Ser.* 22:297–401
143. Robinson WH, Foote BA. 1979. Biology and immature stages of *Antichaeta borealis* (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 80:388–96
144. Rogers TP, Foote BA, Todd JL. 1991. Biology and immature stages of *Chlorops certimus* and *Epichlorops exilis* (Diptera: Chloropidae), stem-borers of wetland sedges. *J. NY Entomol. Soc.* 99:664–83
145. Roskošný R, Knutson LV. 1970. Taxonomy, biology, and immature stages of Palaearctic *Pteromicra*, snail-killing Diptera (Sciomyzidae). *Ann. Entomol. Soc. Am.* 63:1434–59
146. Runyan JT, Deonier DL. 1979. A comparative study of *Pseudohecamede* and *Allotrichoma* (Diptera: Ephydriidae). See Ref. 45, pp. 123–37
147. Sabrosky CW. 1942. An unusual rearing of *Rainieria brunneipes* (Cresson) (Diptera: Micropezidae). *Entomol. News* 53:283–85
148. Sabrosky CW. 1974. *Eugaurax setigena* (Diptera: Chloropidae), a new stem miner in water hyacinth. *Fla. Entomol.* 57:347–48
149. Scheiring JF, Connell TD. 1988. Ecological observations on two co-existing species of shore flies (Diptera: Ephydriidae). *J. Kans. Entomol. Soc.* 61:134–37
150. Scheiring JF, Deonier DL. 1979. Spatial

- patterns in shore-fly community structure. See Ref. 45, pp. 73–80
151. Scheiring JF, Foote BA. 1973. Habitat distribution of the shore flies of northeastern Ohio (Diptera: Ephydriidae). *Ohio J. Sci.* 73:152–66
 152. Scheirs J, De Bruyn L. 1993. Leafminers (Diptera: Agromyzidae) of *Phragmites australis* in Belgium. *Bull. Ann. Soc. R. Belge d'Entomol.* 128:310–15
 153. Scheirs J, Vandevyuer I, De Bruyn L. 1997. Influence of monocotyl leaf anatomy on the feeding pattern of a grass-mining agromyzid (Diptera). *Ann. Entomol. Soc. Am.* 90:646–54
 154. Scotland MB. 1934. The animals of the *Lemna* association. *Ecology* 15:290–94
 155. Scotland MB. 1939. The *Lemna* fly and some of its parasites. *Ann. Entomol. Soc. Am.* 290–94
 156. Sharitz R, Batzer DP. 1999. An introduction to freshwater wetlands in North America and their invertebrates. See Ref. 13, pp. 1–22
 157. Simpson KW. 1975. Biology and immature stages of three species of Nearctic *Ochthera* (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 77:129–55
 158. Skidmore P. 1985. The biology of the Muscidae of the world. *Ser. Entomol.* 9:1–550
 159. Sluss TP, Foote BA. 1971. Biology and immature stages of *Leucopis verticalis* (Diptera: Chamaemyiidae). *Can. Entomol.* 103:1427–34
 160. Sluss TP, Foote BA. 1973. Biology and immature stages of *Leucopis pinicola* and *Chamaemyia polystigma* (Diptera: Chamaemyiidae). *Can. Entomol.* 105:1443–52
 161. Southwood TRE. 1978. *Ecological Methods, with Particular Reference to the Study of Insect Populations*. London: Chapman & Hall. 524 pp.
 162. Spencer KA, Steyskal GC. 1986. Manual of the Agromyzidae of the United States. *USDA Agric. Handb.* 638:1–478
 163. Steinly BA. 1986. Violent wave action and the exclusion of Ephydriidae (Diptera) from marine intertidal and freshwater beach habitats. *Proc. Entomol. Soc. Wash.* 88:427–37
 164. Steinly BA. 1987. The distribution of shore flies (Diptera: Ephydriidae) in Illinois. *Entomol. News* 98:165–70
 165. Steinly BA, Runyan JT. 1979. The life history of *Leptopsilopa atrimana* (Diptera: Ephydriidae). See Ref. 45, pp. 139–47
 166. Sugden LG. 1974. *Feeding Ecology of Pintail, Gadwall, American Widgeon and Lesser Scaup Ducklings*. Can. Wildl. Serv. Rep. Ser. No. 24, Ottawa: Inform. Can.
 167. Teskey HJ. 1972. The mature larva and pupa of *Compsobata univitta* (Diptera: Micropezidae). *Can. Entomol.* 104:295–98
 168. Teskey HJ, Clarke JM, Elliott CR. 1976. *Hylemya extremitata* (Diptera: Anthomyiidae) and species of Chloropidae associated with injury to bromegrass, with descriptions of larvae. *Can. Entomol.* 108:185–92
 169. Thier RW, Foote BA. 1980. Biology of mud-shore Ephydriidae (Diptera). *Proc. Entomol. Soc. Wash.* 82:517–35
 170. Todd JL, Foote BA. 1987. Resource partitioning in Chloropidae (Diptera) of a freshwater marsh. *Proc. Entomol. Soc. Wash.* 89:803–10
 171. Todd JL, Foote BA. 1987. Spatial and temporal distribution of shore flies in a freshwater marsh (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 89:448–57
 172. Tomberlin JK, Adler PH. 1998. Seasonal colonization and decomposition of rat carrion in water and on land in an open field in South Carolina. *J. Med. Entomol.* 35:704–9
 173. Torp E. 1990. Some insects visiting water-hemlock (*Cicuta virosa*). *Flora og Fauna* 96:47–50
 174. Trelka DG, Berg CO. 1977. Behavioural studies of the slug-killing larvae of two

- species of *Tetanocera* (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 79:475–86
175. Trelka DG, Foote BA. 1970. Biology of slug-killing *Tetanocera* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 63:877–95
176. Turner AM, Trexler JC. 1997. Sampling aquatic invertebrates from marshes: evaluating the options. *J. N. Am. Benthol. Soc.* 16:694–709
177. Uffen R, Chandler P. 1978. Associations with plants. Higher Plants. See Ref. 94, 15:213–28
178. Vala JC, Gbedjissi G, Knutson L, Dossou C. 2000. Extraordinary feeding behaviour in Diptera (Sciomyzidae), snail-killing flies. *Comptes Rendus l'Acad. Sci. Ser. III Sci. Vie* 323:299–304
179. Valley K, Berg CO. 1977. Biology, immature stages, and new species of snail-killing Diptera of the genus *Dictya* (Sciomyzidae). *Search Ithaca* 7:1–44
180. Valley K, Foote BA. 1996. Biology and immature stages of *Eriobolus longulus* with notes on *E. nanus* (Diptera: Chloropidae), secondary invaders of herbaceous wetland plants. *Mem. Entomol. Soc. Wash.* 18:273–79
181. Valley K, Novak JA, Foote BA. 1969. Biology and immature stages of *Eumetopiella rufipes*. *Ann. Entomol. Soc. Am.* 62:227–34
182. Valley KR, Wearsch RT, Foote BA. 1969. Larval feeding habits of certain Chloropidae (Diptera). *Proc. Entomol. Soc. Wash.* 71:29–34
183. Vitt D. 1994. An overview of factors that influence the development of Canadian peatlands. *Mem. Entomol. Soc. Can.* 169:7–20
184. Vos-de-Wilde B. 1935. *Contribution à l'étude des larves de Diptères Cyclorrhaphes, plus spécialement des larve d Anthomyides*. Amsterdam: Proefschrift. 125 pp.
185. Wallace JB, Neff SE. 1971. Biology and immature stages of the genus *Cordilura* (Diptera: Scatophagidae) in the eastern United States. *Ann. Entomol. Soc. Am.* 64:1310–30
186. Walton WE, Workman PD, Keiper JB. 1999. An inexpensive collapsible pyramidal emergence trap for the assessment of wetland insect populations. *Proc. Mosq. Vector Control Assoc. Calif.* 67:15–17
187. Warner BG, Rubec CDA, eds. 1997. *The Canadian Wetland Classification System*. Univ. Waterloo, Ontario: Natl. Wetl. Work. Group, Wetl. Res. Cent.
188. Wearsch TK, Foote BA. 1994. Biology and immature stages of Chloropidae (Insecta: Diptera) associated with spike-rushes (Cyperaceae: *Eleocharis*) I. Stem borers. *Ann. Carnegie Mus.* 63:193–213
189. Welch PS. 1914. Observations on the life history and habits of *Hydromyza confluens* Loew (Diptera). *Ann. Entomol. Soc. Am.* 7:135–47
190. Welch PS. 1917. Further studies on *Hydromyza confluens* Loew (Diptera). *Ann. Entomol. Soc. Am.* 10:35–46
191. Wendt H. 1968. Faunistisch-ökologische Untersuchungen an Halmfliegen der Berliner Umgebung. *Dt. Entomol. ZNF* 15: 49–105
192. Wetzel RG. 1983. *Limnology*. Philadelphia: Saunders. 767 pp. 2nd ed.
193. Wharton CH, Kitchens WM, Pendleton EC, Sipe TW. 1982. *The Ecology of Bottomland Hardwood Swamps of the Southeast: A Community Profile*, FWS / OBS–81/37. Washington, DC: US Fish Wildl. Serv.
194. Wirth WW. 1971. *Platygympnopa*, a new genus of Ephydriidae reared from decaying snails in North America (Diptera). *Can. Entomol.* 103:266–77
195. Wirth WW. 1971. The brine flies of the genus *Ephydra* in North America (Diptera: Ephydriidae). *Ann. Entomol. Soc. Amer.* 64:357–77
196. Zack RS. 1979. Habitat distribution of the

- Ephydriidae (Diptera) of Mount Rainier National Park (Washington State). See Ref. 45, pp. 81–98
197. Zack RS. 1983. Biology and immature stages of *Paracoenia bisetosa* (Coquillett) (Diptera: Ephydriidae). *Ann. Entomol. Soc. Am.* 76:487–97
198. Zack RS. 1998. Shore flies (Diptera: Ephydriidae) of the Hanford Site, Washington. *Northwest Sci.* 72:127–41
199. Zack RS, Foote BA. 1978. Utilization of algal monocultures by *Scatella stagnalis*. *Environ. Entomol.* 7:509–11
200. Zvereva YE. 1994. Effect of industrial pollution on fly communities (Diptera, Brachycera). *Entomol. Rev.* 73:45–57



CONTENTS

ROSS RIVER VIRUS: ECOLOGY AND DISTRIBUTION, <i>Richard C. Russell</i>	1
BIOLOGY AND MANAGEMENT OF THE SMOKYBROWN COCKROACH, <i>Arthur G. Appel and Lane M. Smith II</i>	33
SEQUESTRATION OF DEFENSIVE SUBSTANCES FROM PLANTS BY LEPIDOPTERA, <i>Ritsuo Nishida</i>	57
REGULATION OF DIAPAUSE, <i>David L. Denlinger</i>	93
BACTERIAL SYMBIONTS OF THE TRIATOMINAE AND THEIR POTENTIAL USE IN CONTROL OF CHAGAS DISEASE TRANSMISSION, <i>C. Ben Beard,</i> <i>Celia Cordon-Rosales, and Ravi V. Durvasula</i>	123
STRATEGIES AND STATISTICS OF SAMPLING FOR RARE INDIVIDUALS, <i>Robert C. Venette, Roger D. Moon, and William D. Hutchison</i>	143
BIOLOGY AND MANAGEMENT OF THE JAPANESE BEETLE, <i>Daniel A.</i> <i>Potter and David W. Held</i>	175
BIOLOGY AND ECOLOGY OF HIGHER DIPTERA FROM FRESHWATER WETLANDS, <i>Joe B. Keiper, William E. Walton, and Benjamin A. Foote</i>	207
INVASIONS BY INSECT VECTORS OF HUMAN DISEASE, <i>L. Philip Lounibos</i>	233
OMNIVORY IN TERRESTRIAL ARTHROPODS: MIXING PLANT AND PREY DIETS, <i>Moshe Coll and Moshe Guershon</i>	267
HOW TO BE A FIG WASP, <i>George D. Weiblen</i>	299
ALTERNATIVES TO METHYL BROMIDE TREATMENTS FOR STORED-PRODUCT AND QUARANTINE INSECTS, <i>Paul G. Fields</i> <i>and Noel D. G. White</i>	331
ECOLOGY AND BEHAVIOR OF FIRST INSTAR LARVAL LEPIDOPTERA, <i>Myron P. Zalucki, Anthony R. Clarke, and Stephen B. Malcolm</i>	361
ARTHROPOD ALLERGENS AND HUMAN HEALTH, <i>Larry G. Arlian</i>	395
COMPETITIVE DISPLACEMENT AMONG INSECTS AND ARACHNIDS, <i>Stuart R. Reitz and John T. Trumble</i>	435
ENDOCRINE INSIGHTS INTO THE EVOLUTION OF METAMORPHOSIS IN INSECTS, <i>James W. Truman and Lynn M. Riddiford</i>	467
BIOCHEMISTRY AND GENETICS OF INSECT RESISTANCE TO <i>BACILLUS THURINGIENSIS</i> , <i>Juan Ferré and Jeroen Van Rie</i>	501

IRON METABOLISM IN INSECTS, <i>Helen Nichol, John H. Law, and Joy J. Winzerling</i>	535
CAN GENERALIST PREDATORS BE EFFECTIVE BIOCONTROL AGENTS?, <i>W. O. C. Symondson, K. D. Sunderland, and M. H. Greenstone</i>	561
ARTHROPODS ON ISLANDS: COLONIZATION, SPECIATION, AND CONSERVATION, <i>Rosemary G. Gillespie and George K. Roderick</i>	595
THE POPULATION BIOLOGY OF OAK GALL WASPS (HYMENOPTERA: CYNIPIDAE), <i>Graham N. Stone, Karsten Schönrogge, Rachel J. Atkinson, David Bellido, and Juli Pujade-Villar</i>	633
SHORT, LONG, AND BEYOND: MOLECULAR AND EMBRYOLOGICAL APPROACHES TO INSECT SEGMENTATION, <i>Gregory K. Davis and Nipam H. Patel</i>	669
BIOLOGY AND MANAGEMENT OF ECONOMICALLY IMPORTANT LEPIDOPTERAN CEREAL STEM BORERS IN AFRICA, <i>Rami Kfir, W. A. Overholt, Z. R. Khan, and A. Polaszek</i>	701
THE ECOLOGY AND EVOLUTION OF ANT ASSOCIATION IN THE LYCAENIDAE (LEPIDOPTERA), <i>Naomi E. Pierce, Michael F. Braby, Alan Heath, David J. Lohman, John Mathew, Douglas B. Rand, and Mark A. Travassos</i>	733
SYMPATRIC SPECIATION IN PHYTOPHAGOUS INSECTS: MOVING BEYOND CONTROVERSY?, <i>Stewart H. Berlocher and Jeffrey L. Feder</i>	773
HOST PLANT QUALITY AND FECUNDITY IN HERBIVOROUS INSECTS, <i>Caroline S. Awmack and Simon R. Leather</i>	817
ECONOMIC, ECOLOGICAL, FOOD SAFETY, AND SOCIAL CONSEQUENCES OF THE DEPLOYMENT OF BT TRANSGENIC PLANTS, <i>A. M. Shelton, J.-Z. Zhao, and R. T. Roush</i>	845
CONTROL AND BIOCHEMICAL NATURE OF THE ECDYSTEROIDOGENIC PATHWAY, <i>Lawrence I. Gilbert, Robert Rybczynski, and James T. Warren</i>	883
THE BIOLOGY OF THE DANCE LANGUAGE, <i>Fred C. Dyer</i>	917
INDEXES	
Subject Index	951
Cumulative Index of Contributing Authors, Volumes 38–47	987
Cumulative Index of Chapter Titles, Volumes 38–47	991

ERRATA

An online log of corrections to *Annual Review of Entomology* chapters may be found at <http://ento.AnnualReviews.org/errata.shtml>