

SHORE FLY (DIPTERA: EPHYDRIDAE) COMMUNITY STRUCTURE IN A XERIC GRASS HABITAT

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Abstract.—Analysis of a xeric terrestrial grass shore fly population found the community composed of 17 species. In addition to the 14 species previously listed from southern Ohio terrestrial grass, *Parydra breviceps* Loew, *Hyadina binotata* (Cresson), and *H. pruinosa* (Cresson) were collected. *Leptopsilopa atrimana* (Loew) was dominant during the collection period. The consistent presence of *L. atrimana* adults and gravid females suggested the species has encountered physical and biological conditions satisfying minimum reproductive requirements. Quantitative parameters including species diversity (H'), evenness (J'), richness (s), and relative abundance (RA) were calculated for xeric terrestrial grass. A comparison of terrestrial quantitative parameters with aquatic grass shore and limnic wrack suggests fundamental differences in species composition. Also, low indices of similarity in addition to physical and biological observations substantiate the designation of xeric terrestrial grass as a new shore fly habitat.

The Ephydridae are considered one of the most diverse families of cyclorrhaphous Diptera. Of the 404 Nearctic species (Deonier, 1979), most are semi-aquatic as adults and aquatic in the immature instars. Adults are frequently found in wetland habitats, and many species survive the rigors of thermal springs (Brues, 1932; Tuxen, 1944; Wirth and Mathis, 1979), alkaline springs (Brock and Brock, 1968; Lindroth, 1931; Wirth and Mathis, 1979), inland saline pools and lakes (Aldrich, 1912; Ping, 1921; Scheiring and Foote, 1973), coastal salt marshes (Dahl, 1959; Simpson, 1976a), crude oil pools (Crawford, 1912; Thorpe, 1930), and urine-soaked wood (Oldroyd, 1964). Additionally, several unusual larval microhabitats have been reported. Larvae have been collected under a human cadaver and pig droppings (Bohart and Gressitt, 1951), reared from decaying crayfish (Runyan and Deonier, 1979), and marine mussels (Steinly and Runyan, 1979), associated with decaying land snails (Berganstamm, 1864), reared from aquatic snails (Wirth, 1971), preying on the developing eggs of a marsh-inhabiting spider (Becker, 1926; Scheiring and Foote, 1973), developing frog eggs (Bokermann, 1957), and mining leaves (Meijere, 1947). Although these microhabitats were unusual, the shore flies were located in close proximity to aquatic or marine habitats.

The first comprehensive ecological, distributional, and behavioral investigation of the Ephydridae was accomplished in Scandinavia (Dahl, 1959). Later, Deonier (1965) reported the results of his studies on the ecology and distribution of the Iowa fauna. Deonier (1965) collected more than 100 shore fly species from 12

aquatic habitats. Scheiring and Foote (1973) reported 68 species found in 12 aquatic habitat types located in northeastern Ohio. The Iowa and northeastern Ohio populations were later analyzed for spatial and temporal patterns in shore fly diversity (Scheiring, 1974; Scheiring and Deonier, 1979a). In southern Ohio, Regensburg (1976) investigated 12 wetland habitats from which were recorded 65 shore fly species (Deonier and Regensburg, 1978). The final phase of the Ohio study yielded 104 species of Ephydriidae from 13 northern Ohio aquatic habitats (Steinly, 1979; Steinly and Deonier, 1980). Also, Zack (1979) reported 45 species from aquatic habitats in Mount Rainier National Park. The Nearctic investigations have focused extensively on the ecology and distribution of the ephydrids within aquatic habitats. These habitats in Iowa, Ohio, and Washington were characterized by vegetation types and/or substrate constitution in various physiographic regions.

Several recent publications have focused on shore fly life cycle requirements and natural history. These studies have confirmed the aquatic or semi-aquatic nature of most ephydrid species (Eastin and Foote, 1971; Foote and Eastin, 1974; Simpson, 1975, 1976b; Busacca and Foote, 1978; Deonier and Regensburg, 1978; Zack and Foote, 1978; Runyan and Deonier, 1979; Deonier, Mathis and Regensburg, 1979; Thier and Foote, 1980; Foote, 1981a, b; Mathis and Simpson, 1981; Foote, 1982; Zack, 1983a, b).

Although ephydrid association with aquatic habitats has been extensively documented, only a few species have been reported from dry (xeric) habitats. One early reference to a distinctly xeric species described the dependence of *Mosillus subsultans* Fabricius on dry sand substrate into which the organism digs rapidly when shaded (Latreille, 1805; Schiner, 1863). Rapp (1942) identified three Palearctic shore fly species in dry habitats (biotopes). In a recent ecological investigation of moist, half dry, and dry grassland habitats, Bahrmann (1978) reported the largest numbers of 8 Palearctic ephydrid species from half dry to dry habitats dominated by grasses. These species were rarely collected in moist grassland habitats.

In the Nearctic region, Sturtevant and Wheeler (1954) reported the collection of *Nostima scutellaris* Cresson, *Hydrellia griseola* (Fallén), *Psilopa varipes* Coquillett, *P. compta* (Meigen), and *Philygria (Hydrina) debilis* (Loew) from a city lawn and garden. Additionally, *H. griseola*, a leaf miner, has been recorded from the leaves of oats, strawberries, sagebrush (Deonier, 1971) and late-sown barley (Lilljeborg, 1861; Grimshaw, 1925). In a discussion of the life history of *Leptopsilopa atrimana*, Steinly and Runyan (1979) reported 14 shore fly species over a grass lawn located some distance from any typical freshwater habitat. Furthermore, the authors suggested that terrestrial habitats may contain aquatic microhabitats utilized by some ephydrids. During laboratory rearing, *L. atrimana* appeared to be consuming saprophytic microorganisms trapped in the surface film on decaying grass blades (Steinly and Runyan, 1979). Similarly, Scheiring and Foote (1973) suggested the abundant decaying organic matter of the limnic wrack habitat provided a suitable substrate for the proliferation of bacteria, yeast, and unicellular algae.

Selection by shore flies of low humidity regions was experimentally verified by Dahl (1959). Also, Dahl maintained a few species at low humidity, and these species withstood desiccation. These xerophilists reached greatest predominance within the dry Hockenye and dune heath biotopes (Dahl, 1959). The dry Hockenye

and dune heath biotopes are transitional beach areas with distinctive vegetation communities and are not inundated by tides or storms. Drought and temperature resistance may enable certain Ephydriidae to colonize terrestrial habitats having aquatic microhabitats.

In this paper, I compare shore fly species diversity, evenness, and richness of selected aquatic and terrestrial habitats. Shore fly species temporal and abundance patterns are described for the Nearctic terrestrial habitat.

DESCRIPTION OF STUDY AREA

On July 4, 1978, a shore fly community was discovered over a grass lawn and garden area. These collecting localities were located 4 km north of Oxford, Ohio. The habitats were not in close proximity to surface water and not subject to irrigation. The nearest permanent surface water, an abandoned gravel pit, was located 0.5 km to the west. No shore flies were associated with ephemeral woodland seepage areas 150 m to the west.

The grass lawn collecting site included substantial accumulations of mowed grass clippings in various stages of decomposition. The lawn was mowed infrequently depending upon the growth rates of the vascular plant cover. Plant species commonly encountered in the lawn included: *Festuca elatior* Linnaeus (meadow fescue), *Cyperus esculentis* Linnaeus, *Digitaria sanguinalis* (Linnaeus) Scopoli (crabgrass), *Setaria faberi* Herrman (nodding foxtail), *S. lutescens* (Weigel) Hubbard, *Medicago lupulina* Linnaeus (hop or black medick), *Muhlenbergia schreberi* J. Gmelin and *Oxalis* sp. Linnaeus (wood sorrel).

I located a garden area 100 m south of the grass lawn with a path, approximately 50 m long on the west side. The path was in frequent use and was characterized by intermittent hard packed barren soil areas and patches of *Digitaria sanguinalis*. Although the garden path was devoid of extensive vascular plant growth, the soil areas retained moisture during periods of low and high precipitation. Soil moisture was renewed by the heavy morning dew. The garden vegetation to the east and trees in close proximity to the west shaded the exposed soil during the major portion of the day. These areas of exposed soil were covered sparsely with dried plant debris. Adjacent vegetation included *Setaria faberi*, and cultivated garden varieties of *Lycopersicon esculentum* P. Miller (tomato), and *Capsicum* sp. Linnaeus (bell pepper).

These sites were situated on a ridge sheltered by a dense tree line to the west. The ridge area was well drained, since the slope prohibited surface accumulation of precipitation.

METHODS AND MATERIALS

Shore flies were collected with a modified aerial sweep net (Regensburg, 1977) from July 4 through November, 1978. Additional sampling was continued in February, 1979 through June, 1979 over the grass lawn. Although begun in February, 1979, collecting had to be terminated over the garden area in April, because the area was brought into cultivation. Sampling was done weekly over the mowed lawn and garden path.

Adult Ephydriidae were selectively aspirated from samples collected over both localities. These adults were isolated in 7 dram vials in the field. The remaining insects in the collecting bags, including specimens of *Leptopsilopa atrimana*, were

immediately killed with ethyl acetate at the site. Dead specimens of *Leptopsilopa atrimana*, *Paralimna punctipennis* Wiedemann, *Philygria debilis*, *Nostima scutellaris*, *Hydrellia formosa* Loew, and *Hyadina albovenosa* Coquillett were examined to ascertain reproductive condition.

The percent relative abundance of each species was calculated within the terrestrial localities. The percentage ranges (Scheiring and Foote, 1973; Regensburg, 1976; Deonier and Regensburg, 1978; Steinly, 1979) were characterized as follows: 1–2% rare (r); 3–8% occasional (occ); 9–14% common (c); 15–25% abundant (a); and 26–100% very abundant (va).

The Shannon-Wiener diversity index (H') (Scheiring, 1974) was calculated because it incorporates species richness (s) and evenness (J'). Diversity was calculated by: $H' = -\sum p_i \log_{10} p_i$ where p_i is n_i/N , n_i is the number of individuals of the i th species of the habitat being considered, and N is the total number of individuals per habitat. Although Wilhm and Dorris (1968) and Olive and Dambach (1973) have stated that H' is essentially dimensionless and not affected by sample size (N), Sanders (1968), Pielou (1969), Fager (1972), and Simberloff (1972) have shown that this index is sensitive to sample size in many instances. However, no mathematically or conceptually acceptable alternative has been proposed (Scheiring, 1974). Habitats were sampled for the same approximate amount of time and differences in sample size reflect biological differences among the habitats. Evenness (J') (Scheiring, 1974) was calculated by: $J' = H'/\log_{10} s$ where s is the species richness (species number) per habitat. H' , J' , and s values for the aquatic grass shore and limnic wrack habitats (Scheiring and Foote, 1973; Scheiring, 1974; Scheiring and Deonier, 1979b) were compared with calculated values for the terrestrial grass lawn and garden localities.

The community composition of the infrequently mowed grass lawn was compared by means of the Sorenson index of similarity (I) with aquatic grass shore and limnic wrack data compiled by Regensburg (1976), Steinly (1979), and data reported by Scheiring and Foote (1973), Scheiring (1974), and Scheiring and Deonier (1979b). The similarity index was calculated with the formula $I = 2C/A + B$ where I is the index of similarity, C is the number of species shared, A is the number of species in habitat A, and B is the number of species in habitat B (Scheiring and Deonier, 1979b). The aquatic grass shore was compared with the terrestrial habitats, because these habitats were dominated by similar vascular vegetation. The limnic wrack was compared with terrestrial sites because these ephydrid populations appear to have similar larval food resources. Shore fly larvae seem to be feeding on microorganisms in terrestrial and limnic wrack habitats. The value of the Sorenson index ranges from 0 when there is no similarity (no species shared) between habitats to 1 when there is complete similarity (all species shared).

RESULTS

Relative abundance and community structure.—The dominant species of Ephydridae on the grass lawn were *Leptopsilopa atrimana* (va) and *Hydrellia formosa* (occ) (Table 1). *L. atrimana* was very abundant (Table 2) during all months of the investigation. *L. atrimana* accounted for 87.7% of the total population (Table 3) over the grass lawn. Scheiring and Foote (1973) did not report *L. atrimana* from the grass shore habitat in northeastern Ohio, but found the

Table 1. Ephyridae (Diptera) found in xeric terrestrial habitats in southeastern Ohio.

Species	Grass		Garden	
	Number N	Relative Abundance R.A.	Number N	Relative Abundance R.A.
<i>Allotrichoma simplex</i>	6	r	—	—
<i>Discocerina obscurella</i>	14	r	11	occ
<i>Ditrichophora exigua</i>	3	r	3	r
<i>Hyadina albovenosa</i>	11	r	—	—
<i>H. binotata</i>	2	r	1	r
<i>H. pruinosa</i>	2	r	1	r
<i>Hydrellia formosa</i>	153	occ	18	occ
<i>H. griseola</i>	7	r	1	r
<i>H. ischiaca</i>	4	r	1	r
<i>H. tibialis</i>	4	r	—	—
<i>Leptopsilopa atrimana</i>	1870	va	64	a
<i>Limnellia anna</i>	—	—	1	r
<i>Nostima scutellaris</i>	16	r	14	occ
<i>Ochthera mantis</i>	—	—	1	r
<i>Paralimna punctipennis</i>	15	r	217	va
<i>Parydra breviceps</i>	1	r	—	—
<i>Philygria debilis</i>	17	r	6	r
<i>Psilopa dupla</i>	3	r	—	—
<i>Trimerina madizans</i>	—	—	1	r
<i>Typopsilopa atra</i>	4	r	—	—
Total =			Total =	
2132			340	

species common (c) in the limnic wrack. Steinly (1979) and Regensburg (1976) did not encounter *L. atrimana* in the limnic wrack of northern and southern Ohio, but found the species rare (r) in the grass shore, marsh reeds, mud shore, sand shore, sedge meadow, and stagnant woodland pool habitats. Scheiring and Deonier (1979b) reported *Hydrellia griseola* and *H. tibialis* Cresson the dominant species from Iowa grass shore habitat while *Discocerina obscurella* (Fallén), *H. griseola*, and *Notiphila scalaris* Loew were dominant in northeastern Ohio.

The most numerous species over the garden area included *Paralimna punctipennis* (va), *Nostima scutellaris* (occ), *Discocerina obscurella* (occ), and *Hydrellia formosa* (occ). *P. punctipennis* accounted for 63.8% of the total specimens collected at the garden locality. The remaining species at both terrestrial localities were rare (r) (Table 1). *P. punctipennis* specimens were rarely collected in southern Ohio floating algal mat, floating vegetation, freshet seep, periphytose stream rocks, sedge meadow, terrestrial shoreline vegetation, and occasionally (occ) in limnic wrack and mud shore habitats (Regensburg, 1976). A single specimen was collected in northern Ohio from floating vegetation habitat (Steinly, 1979). Previously, *Parydra appendiculata* Loew was reported from Iowa, and *D. obscurella* and *Dichaeta caudata* (Fallén) were reported from northeastern Ohio as the dominant shore flies in the limnic wrack (Scheiring and Deonier, 1979b).

The limnic wrack, grass shore, and garden area shore fly populations were compared with the terrestrial grass species assemblage by means of the Sorenson

Table 2. Temporal patterns of shore fly species in terrestrial grass and garden habitats. Species collected from both habitats (B), collected from grass lawn only (L), and collected from garden area only (P).

Species	Month—1978					Month—1979			
	July	Aug.	Sept.	Oct.	Nov.	Mar.	Apr.	May	June
<i>Allotrichoma simplex</i>			L	L		II			
<i>Discocerina obscurella</i>	L	L	B	B		II			
<i>Ditrichophora exigua</i>			L	B		II			
<i>Hyadina albovenosa</i>	L	L				II			
<i>H. binotata</i>					P	II	L		
<i>H. pruinosa</i>	L		B			II			
<i>Hydrellia formosa</i>	L	L	B	B	L	II		L	
<i>H. griseola</i>			L	B		II			
<i>H. ischiaca</i>		L	B			II			
<i>H. tibialis</i>	L		L	L		II			
<i>Leptopsilopa atrimana</i>	L	L	B	B	L	II	L	L	L
<i>Limnellianna anna</i>	P					II			
<i>Nostima scutellaris</i>	B	L	B		P	II	B		
<i>Ochthera mantis</i>						II	P		
<i>Paralimna punctipennis</i>	P	P	B	B	P	II		L	
<i>Parydra breviceps</i>	L					II			
<i>Philygria debilis</i>	B	L	B		B	II	B	L	
<i>Psilopa dupla</i>	L					II			
<i>Trimerina madizans</i>		P				II			
<i>Typopsilopa atra</i>	L		L			II			

index of similarity (Table 4). The garden path and grass lawn had the greatest index of similarity. The similarity values for northeastern, northern, and southern Ohio grass shore and limnic wrack habitats were low. The index values for the limnic wrack were generally lower than the values calculated for the aquatic grass shore. These values suggest a fundamental difference in the composition of the ephydrid communities, particularly in the limnic wrack habitat.

Diversity.—The overall values for habitat diversity (H'), evenness (J'), and richness (s) are given in Table 5. The H' and J' were lowest for the terrestrial grass lawn due to the predominance of *Leptopsilopa atrimana* in the population. The aquatic habitats, including grass shore and limnic wrack, have relatively high H' , J' , and s values (Scheiring and Deonier, 1979b). The only exceptions were the values for H' in the Iowa grass shore and for s in the limnic wrack of northeastern Ohio (Scheiring and Deonier, 1979b). The consistent disparity between the aquatic and terrestrial H' , J' , and s values suggests a fundamental difference in shore fly community structures. In addition, the lack of J' , low s and % relative abundance for the grass lawn suggests that *L. atrimana* is the only species in the population adapted to the terrestrial habitat.

Seasonal distribution.—*Leptopsilopa atrimana* was collected consistently in large numbers during warmer months from the grass lawn. During November of 1978 and March and April of 1979, *L. atrimana* was not encountered in large numbers, but the species comprised the largest percentage of the shore flies collected (Table 3). The consistent abundance of *L. atrimana* suggests that the species was a relatively permanent inhabitant of the grass lawn. The examination and dissection

Table 3. Monthly percent relative abundance (R.A.) of *Leptopsilopa atrimana* on the grass lawn habitat.

Month	R.A.	Total Number of <i>L. atrimana</i>	Total Number of Shore Flies
July, 1978	0.910	546	600
August	0.913	306	335
September	0.821	418	509
October	0.869	345	397
November	0.625	10	16
March, 1979	0.600	9	15
April	1.000	11	11
May	0.875	168	192
June	1.000	57	57
Total = 0.877		Total = 1870	Total = 2132

of *L. atrimana*, *Philygria debilis*, *Nostima scutellaris*, *Paralimna punctipennis*, *Hyadina albovenosa*, and *Hydrellia formosa* revealed gravid females. Gravid *L. atrimana* were encountered from April to mid September. All gravid species, except *P. punctipennis*, were associated with the grass lawn. The presence of gravid females suggests that the minimum reproductive requirements for the species were being satisfied in the terrestrial habitat. One *L. atrimana* larva was collected from grass clippings on the grass lawn.

The presence of *Leptopsilopa atrimana*, *Paralimna punctipennis*, and *Disco-cerina obscurella* during September and October in lawn and garden may be attributed to immigration. *Philygria debilis* and *Nostima scutellaris* were collected often in both localities, suggesting that these species were residents and/or moved between habitats. *Typospilopa atra* Loew, *Psilopa dupla*, *Parydra breviceps*, *Hydrellia tibialis*, *Hyadina albovenosa*, and *Allotrichoma simplex* (Loew) were collected only in the grass lawn habitat, while *Trimerina madizans* (Fallén), *Ochthera mantis* (De Geer), and *Limnellia anna* Cresson were found exclusively associated with the garden path. Previously, *Hyadina binotata*, *H. pruinosa*, and *Parydra breviceps* were not reported from terrestrial grass habitat.

DISCUSSION

The seasonal persistence of ephydriids in large numbers in dry terrestrial grass, the dissimilarity of the comparative parameters, and the observed physical, biological, and population differences all support the contention that grassland is a hitherto unreported habitat for ephydriids. Moreover, the collection of Palearctic shore fly species in xeric grassland biotopes (Bahrmann, 1978) suggests the presence of the Ephydriidae in a Nearctic dry terrestrial habitat is not a biological anomaly. Preliminary experimental evidence concerning drought and temperature resistance (Dahl, 1959) has substantiated the capacity of certain Ephydriidae to withstand the physiological stresses associated with desiccation.

The presence of a reproductive shore fly population over a dry terrestrial grass habitat has been confirmed in the Nearctic region. *Leptopsilopa atrimana* was the dominant ephydriid species and very abundant during all months. Although *L. atrimana* was collected on March 3, 1979, adult overwintering was not confirmed.

Table 4. Similarity of shore-fly habitats to terrestrial grass.

Habitat	Index of Similarity (I)		
Garden area, Present Study	0.7097		
Grass shore NE Ohio ¹ (Scheiring and Foote, 1973)	0.3333	Limnic wrack ¹	0.3750
Grass shore northern Ohio ² (Steinly, 1979)	0.4615	Limnic wrack ²	0.2500
Grass shore southern Ohio ³ (Regensburg, 1976)	0.5581	Limnic wrack ³	0.2632

Comparison of the quantitative parameters H' , J' , s , and I strongly indicate fundamental differences in the ephydrid populations associated with aquatic and terrestrial grass habitats. Low H' , J' , and s values for the grass lawn, low indices of similarity, and high monthly relative abundance of *Leptopsilopa atrimana* supports the designation of a new terrestrial habitat for the Ephydridae. The low H' and J' for terrestrial grass suggests that *L. atrimana* has adapted to the intrinsic physical and biological conditions in the habitat. Even though the garden area quantitative parameters were not similar to the aquatic grass shore and limnic wrack, the designation of a new habitat (terrestrial soil) is not warranted. Although *Paralimna punctipennis* was dominant over the garden path, a relatively high similarity value suggests that the ephydrid community structure was comparable to the population within the terrestrial grass.

The gross similarities in dominant vascular vegetation are not indicative of subtle biological and physical differences encountered in the aquatic grass shore and terrestrial grass habitats. In particular, vegetation growth rate and condition on the grass shore are often regulated and/or altered by one or more of the following: the length and number of times the habitat is submerged; the intensity of flushing and scouring; the amount of habitat area flooded and subjected to flushing; and the amount and type of sediment deposition.

During laboratory rearing, *Leptopsilopa atrimana* larvae were unable to escape or survive entrapment in large areas of condensation on the vial walls (Steinly, unpubl.). Although larvae continually probed the internal condensation surface, individuals were not able to break the surface tension and expired in 4–6 hours. *L. atrimana* larval entrapment suggests the species is not well adapted to submersion.

Feeding observations suggested that *Leptopsilopa atrimana* larvae consume microorganisms on decaying vegetation surfaces (Steinly and Runyan, 1979). During flood, grass shore decaying vegetation was removed or coated with sediment (Steinly, unpubl.). The terrestrial grass habitat was not subjected to flood. The terrestrial availability of microorganisms and ephydrid oviposition sites may facilitate habitat colonization by *L. atrimana*.

Limnic wrack, composed of decaying organic matter, provides ample substrate for microorganism proliferation (Scheiring and Foote, 1973). The transient limnic wrack is subjected to physical stresses that include rapid desiccation (thermal and wind), periodic inundations, and severe wave action. These physical stresses and bird predation, in all probability, precluded the colonization and development of many ephydrid species. *Leptopsilopa atrimana* was reported common (c) from northeastern Ohio limnic wrack (Scheiring and Foote, 1973), but was encountered rarely (r) by Regensburg (1976) and Steinly (1979). Limnic wrack habitat disrupt-

Table 5. Diversity, evenness, and richness values for Ephydridae in Nearctic habitats.

Ephydrid Habitats	Diversity (H')	Evenness (J')	Richness (s)
Terrestrial grass ¹ (Present Study)	0.252	0.205	17
Garden area ¹	0.535	0.467	14
Grass shore NE Ohio ² (Scheiring and Deonier, 1979b)	0.9	0.70	19
Grass shore, Iowa ²	0.42	0.31	24
Limnic wrack, Ohio ²	0.817	0.76	12
Limnic wrack, Iowa ²	1.36	0.82	45

tion may interrupt the relatively long life cycle (17–27 days) of *L. atrimana* (Steinly and Runyan, 1979).

Leptopsilopa atrimana utilization, colonization and oviposition of terrestrial habitats may depend on the stability of decaying vegetation. The stable terrestrial grass microhabitat (decaying vegetation) provides a substrate for microorganism proliferation (Steinly and Runyan, 1979). In terrestrial grass, *L. atrimana* is not subjected to the disruptive forces common in aquatic habitats. Although adults remain in the same general area of pupation, Scheiring (1974) was convinced that the species in a habitat were determined by larval adaptation. Deonier (1965) and Scheiring (1974) have suggested that most ephydrid larvae have more specialized habitat and food requirements than the adults.

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LITERATURE CITED

Aldrich, J. M. 1912. The biology of some western species of the dipterous genus *Ephydra*. J. N.Y. Entomol. Soc. 20: 77–99.

Bahrmann, R. 1978. Ökofaunistische Untersuchungen an Ephydriden verschiedener Rasenbiotope in Thüringen (DDR) (Diptera). Dtsch. Entomol. Z. 25: 337–348.

Becker, T. 1926. Ephydridae. Family 56, pp. 1–115. In Lindner, E., ed., Die Fliegen der palaearktischen Region. Vol. 6, pt. 1. Stuttgart.

Bergenstamm, J. E. von. 1864. Die Metamorphose von *Discomyza incurva* Fall.-Verh. Zool.-Bot. Ges. Wien. 14: 713–716.

Bohart, G. E. and J. E. Gressitt. 1951. Filth-inhabiting flies of Guam. Bull. Bishop Mus. 204, 152 pp., 17 pls.

Bokermann, W. C. A. 1957. Frog eggs parasitized by dipterous larvae. Herpetologica 13: 231–232.

Brock, T. D. and M. L. Brock. 1968. Life in a hot-water basin. Nat. Hist. 77: 46–53.

Brues, C. T. 1932. Further studies on the fauna of North American hot springs. Proc. Am. Acad. Arts and Sci. 67: 185–303.

Busacca, J. D. and B. A. Foote. 1978. Biology and immature stages of two species of *Notiphila*, with notes on other shore flies occurring in cattail marshes (Diptera:Ephydridae). Ann. Entomol. Soc. Am. 71: 457–466.

Crawford, D. L. 1912. The petroleum fly in California, *Psilopa petrolei* Coq. Pomona Coll. J. Entomol. 4: 687–697.

Dahl, R. G. 1959. Studies on Scandinavian Ephydridae (Diptera Brachycera). Opusc. Entomol. Suppl. 15: 1–224.

Deonier, D. L. 1965. Ecological observations on Iowa shore flies (Diptera:Ephydridae). Proc. Iowa Acad. Sci. 71: 496–510.

- . 1971. A systematic and ecological study of Nearctic *Hydrellia* (Diptera:Ephydriidae). *Smithson. Contr. Zool.* 68: 1–147.
- . 1979. Introduction—a prospectus on research in Ephydriidae, pp. 1–19. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydriidae (Diptera). North Am. Benthol. Soc.
- Deonier, D. L. and J. T. Regensburg. 1978. Biology and immature stages of *Parydra quadrituberculata* (Diptera:Ephydriidae). *Ann. Entomol. Soc. Am.* 71: 341–353.
- Deonier, D. L., W. N. Mathis, and J. T. Regensburg. 1979. Natural history and life-cycle stages of *Notiphila carinata* (Diptera:Ephydriidae). *Proc. Biol. Soc. Wash.* 91: 798–814.
- Eastin, W. C. and B. A. Foote. 1971. Biology and immature stages of *Dichaeta caudata* (Diptera:Ephydriidae). *Ann. Entomol. Soc. Am.* 64: 271–279.
- Fager, E. W. 1972. Diversity: a sampling study. *Am. Nat.* 106: 293–310.
- Foote, B. A. 1981a. Biology and immature stages of *Lytogaster excavata*, a grazer of blue-green algae (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 83: 304–315.
- . 1981b. Biology and immature stages of *Pelina truncatula*, a consumer of blue-green algae (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 83: 607–619.
- . 1982. Biology and immature stages of *Setacera atrovirens*, a grazer of floating algal mats (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 84: 828–844.
- Foote, B. A. and W. C. Eastin. 1974. Biology and immature stages of *Discocerina obscurella* (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 76: 401–408.
- Grimshaw, P. H. 1925. The study of flies (Diptera). *Naturalist* 816: 5–20.
- Latreille, P. A. 1805. Histoire naturelle, générale et particulière des crustacés et des insectes, Tome 14, Vol. 106. *In* Sonnini, C. S., ed., Histoire naturelle par Buffon. Paris.
- Lilljeborg, W. 1861. En Flugas Harjningar å Kornfåltén i Östra Skåne, Blekinge och Södra Delarna af Kalmar län under Sommaren 1860. *Tidskrift för Landtmanna och Kommunalekonomien* (Upsala), 1861: 205–215.
- Lindroth, C. H. 1931. Die Insektenfauna Islands und ihre Probleme.—*Zool. Bidr.* 13. Upsala.
- Mathis, W. N. and K. W. Simpson. 1981. Studies of Ephydriinae (Diptera:Ephydriidae). V: The genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America. *Smithson. Contrib. Zool.* 329: 1–51.
- Meijere, J. C. H. de. 1947. Over eenige Dipterenlarven warrander een galmug, die mijngangen maakt, en twee Dipteren, die gallen op paddenstoelen veroorzaken. *Tijdschr. Entomol.* 88: 49–62.
- Olive, J. H. and C. A. Dambach. 1973. Benthic macro-invertebrates as indexes of water quality in Whetstone Creek, Morrow County, Ohio (Sciota River Basin). *Ohio J. Sci.* 73: 129–149.
- Oldroyd, H. 1964. The natural history of flies. W. W. Norton and Co., Inc., N.Y. 324 pp.
- Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, N.Y. 286 pp.
- Ping, C. 1921. The biology of *Ephydra subopaca* Loew. *New York Mem. Cornell Univ. Agr. Exp. Stn.* 49: 557–616.
- Rapp, O. 1942. Die Fliegen Thüringens unter besonderer Berücksichtigung der faunistisch-oekologischen Geographie.—Erfurt.
- Regensburg, J. T. 1976. The shore flies of southern Ohio (Diptera:Ephydriidae). Unpubl. M.S. Thesis. Miami University, Oxford, Ohio. 192 pp.
- . 1977. A modified sweep net for quantitative sampling. *Entomol. News* 88: 141–142.
- Runyan, J. T. and D. L. Deonier. 1979. A comparative study of *Pseudohecamele* and *Allotrichoma* (Diptera:Ephydriidae), pp. 123–137. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydriidae (Diptera). North Am. Benthol. Soc.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243–282.
- Scheiring, J. F. 1974. Diversity of shore flies (Diptera:Ephydriidae) in inland freshwater habitats. *J. Kan. Entomol. Soc.* 47: 485–491.
- Scheiring, J. F. and B. A. Foote. 1973. Habitat distribution of the shore flies of northeastern Ohio (Diptera:Ephydriidae). *Ohio J. Sci.* 73: 152–166.
- Scheiring, J. F. and D. L. Deonier. 1979a. Spatial and temporal patterns in Iowa shore fly diversity. *Environ. Entomol.* 8: 879–882.
- . 1979b. Spatial patterns in shorefly community structure, pp. 73–80. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydriidae (Diptera). North Am. Benthol. Soc.
- Schiner, J. R. 1862–1864. Fauna Austriaca. Die Fliegen (Diptera). II. Theil.—Wien.

- Simberloff, D. 1972. Properties of the rarefaction diversity measurement. *Am. Nat.* 106: 353-357.
- Simpson, K. W. 1975. Biology and immature stages of three species of Nearctic *Ochthera* (Diptera: Ephydriidae). *Proc. Entomol. Soc. Wash.* 77: 129-155.
- . 1976a. Shore and brine flies (Diptera:Ephydriidae). Chapter 17, pp. 465-495. *In* Cheng, L., ed., *Marine Insects*. Am. Elsevier Publ. Co., New York.
- . 1976b. The mature larvae and puparia of *Ephydra* (*Halephya*) *cinerea* Jones and *Ephydra* (*Hydropyrus*) *hians* Say (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 78: 263-269.
- Steinly, B. A. 1979. The shore flies of northern Ohio (Diptera:Ephydriidae). Unpubl. M.S. Thesis. Miami University, Oxford, Ohio. 249 pp.
- Steinly, B. A. and D. L. Deonier. 1980. New records of Ohio shore flies (Diptera:Ephydriidae). *Ohio J. Sci.* 80: 41-42.
- Steinly, B. A. and J. T. Runyan. 1979. The life history of *Leptopsilopa atrimana* (Diptera:Ephydriidae), pp. 139-147. *In* Deonier, D. L., ed., *First Symposium on the Systematics and Ecology of Ephydriidae* (Diptera). North Am. Benthol. Soc.
- Sturtevant, A. H. and M. R. Wheeler. 1954. Synopsis of Nearctic Ephydriidae (Diptera). *Trans. Am. Entomol. Soc.* 79: 151-257.
- Thier, R. W. and B. A. Foote. 1980. Biology of mud-shore Ephydriidae (Diptera). *Proc. Entomol. Soc. Wash.* 82: 517-535.
- Thorpe, W. H. 1930. The biology of the petroleum fly (*Psilopa petrolii* Coq.). *Trans. Entomol. Soc. London* 78: 331-344.
- Tuxen, S. L. 1944. The hot springs of Iceland. Their animal communities and their zoogeographical significance. *Zoology of Iceland* 1: 1-206, 7 pls. Munksgaard. Copenhagen.
- Wilhm, J. L. and T. C. Dorris. 1968. Biological parameters for water quality criteria. *BioScience* 18: 447-481.
- Wirth, W. W. 1971. *Platygymnopa*, a new genus of Ephydriidae reared from decaying snails in North America (Diptera). *Can. Entomol.* 103: 266-270.
- Wirth, W. W. and W. N. Mathis. 1979. A review of the Ephydriidae living in thermal springs, pp. 21-45. *In* Deonier, D. L., ed., *First Symposium on the Systematics and Ecology of Ephydriidae* (Diptera). North Am. Benthol. Soc.
- Zack, R. S. 1979. Habitat distribution of the Ephydriidae (Diptera) of Mount Rainier National Park (Washington State), pp. 81-98. *In* Deonier, D. L., ed., *First Symposium on the Systematics and Ecology of Ephydriidae* (Diptera). North Am. Benthol. Soc.
- . 1983a. Biology and immature stages of *Paracoenia bisetosa* (Coquillett) (Diptera:Ephydriidae). *Ann. Entomol. Soc. Amer.* 76: 487-497.
- . 1983b. Biology and immature stages of *Setacera needhami* Johannsen (Diptera:Ephydriidae). *Proc. Entomol. Soc. Wash.* 85: 10-25.
- Zack, R. S. and B. A. Foote. 1978. Utilization of algal monocultures by larvae of *Scatella stagnalis*. *Environ. Entomol.* 7: 509-511.



Steinly, B A. 1984. "Shore fly (Diptera: Ephydriidae) community structure in a xeric grass habitat." *Proceedings of the Entomological Society of Washington* 86, 749–759.

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