THE IMPORTANCE OF TEMPORARY WATERS FOR DIPTERA
(TURE-FLIES)

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Introduction

Flies are the largest order of wetland insects in Britain. Of our 6668 known species, larvae of at least 1138 are considered to be aquatic (Maitland 1977; Chandler 1998) while a large number, perhaps as many again, are associated with wetlands. Despite this abundance of species they have been neglected in nearly all studies of temporary ponds.

Wissinger (1999) made an important distinction between aquatic, wetland and terrestrial faunas. By replacing the terms semi-aquatic and semi-terrestrial with "wetland", and by giving wetland the status of a habitat distinct from a mere ecotone or hydroseral stage, he removed a conceptual constraint that has contributed to the restricted view of our wetland fauna. The role of Diptera then becomes considerably greater than nearly all studies suggest so far as a much wider range of families is involved. Chironomids are most often quoted as the dominant family in temporary pools, followed by ceratopogonids, chaoborids, culicids, and sometimes tipulids, sciomyzids and stratiomyids (e.g. Williams 1997; many papers in Batzer et al. 1999). These predominantly are truly aquatic species but the exposed shores of ponds support many other families. For instance, Wissinger's (1999) summary of the fauna of North American wetlands added ptychopterids, dixids, psychodids, tabanids, rhagionids, empids, dolichopodids, syrphids, ephydrids, sarcophagids, anthomyiids and scathophagids, and Williams & Feltmate (1992) included sepsids. Few of these are mentioned in studies by "aquatic" biologists.

The prerequisites that are usually quoted for surviving in temporary pools are an ability to reach maturity before the system dries out, physiological or behavioural mechanisms to survive the dry period, and an ability to recolonise. Larvae of many British wetland Diptera have these features, which should enable them to develop and survive in temporary ponds. Some examples are considered in this article, with brief comments on adaptations in insects from other geographical regions.

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Physiological mechanisms and behaviour to avoid drying-out

Several subtropical chironomids (non-biting midges) and ceratopogonids (biting midges) that are near-obligate inhabitants of seasonal pools and rain hollows can withstand dehydration and resume growth when wetted; *Polypedillum vanderplanckii* is the archetypal example (Hinton 1953). Chironomids of several genera form cocoons within the substratum of vernal pools before these dry up, where they remain dormant for many months, even if re-wetted, until cold temperatures break an obligatory diapause (Grodhaus 1980). Similarly, larvae of some African tabanids (horseflies) construct mud cylinders before the pools dry out (Parsons 1971). Such extreme physiological tolerance appears to be scarce in British Diptera, but larvae of the ceratopogonid *Dasyhelea saxicola* live in small solution hollows on limestone pavement where they survive repeated drying-out and wetting (Disney 1975). Those of *D. dufouri* live, among other places, in pools in the leaf axils of teasel *Dipsacus fulonum* and have been reported as living on a concrete floor subjected alternately to rain and drying out (Hinton 1953).

Complex drought-avoidance behaviour is unknown in British flies and burrowing into damp sediments is the only recorded means of avoiding drying-out. For instance, *Chironomus pseudothummi* and *Psectrotanypus varius* survived in the damp mud of a Cheshire marl pit during an October drought (Smith & Young 1973). *Chironomus plumosus* burrowed to a depth of 8 cm in the sediment of a North American reservoir when exposed as the water level dropped, but other individuals showed no response when the shoreline retreated and died in situ (Kaster & Jacobi 1978). Dipteran larvae normally confined to the margin may be better equipped behaviourally and probably migrate with moving shorelines.

The larvae of some African and American stratiomyids (soldier flies) have the ability to withstand dehydration and re-wetting (Hinton 1953). British "aquatic" species are not so adapted but survive by seeking damp refuges. For instance, *Oxycera trilineata*, *O. rara* and *O. morrisii* are frequently found on damp mud at water margins, and the first two may be found in hoof prints that clearly dry out (even though remaining damp). The larvae of *Odontomyia argentata* is probably also amphibious, as it has been found in winter-flooded grassland by a pingo pool at Thompson Common, Norfolk (Falk 1991). These aquatic stratiomyids may survive in temporary pools if the margins remain moist.

Dipteran larvae are able to survive freezing in pond-margin sediments. Wiggins et al. (1980) recorded the larvae of the ceratopogonids *Palpomyia* and *Bezzia* overwintering in frozen mud of American vernal pools. Crisp & Lloyd (1954) recorded many more dipteran larvae within the surface layer of
frozen mud in a northern English woodland compared to the abundances at a depth of 2-3 inches (5-8 cm); apparently they made no attempt to move to greater depths where they would have avoided freezing.

**Adaptations to fluctuating water levels**

Whereas adults and larvae can take action to avoid the dangers of drowning and dehydration, the usually immobile egg and pupa need suitable morphological adaptations or to be put in a suitable place by the ovipositing female or pre-pupal larva. Mosquitoes show the clearest adaptations to predictable rising water levels. *Aedes* and many *Culiseta* lay their eggs in dry places where they will be submerged later. The eggs hatch only after exposure to near-freezing conditions followed by submergence (Fallis & Snow 1983a, b). *Aedes cinereus* and *Culiseta mossi*, are typical annual freshwater species that emerge by May before their pools dry out, whereas the coastal *Aedes detritus* and *A. caspius*, unusually for mosquitoes, complete several generations each year, as the eggs hatch with each re-filling episode (Cranston et al. 1987). Several ephydrids (shore flies) place their eggs where they will avoid being flooded. For instance, the common North American species *Paracoenia bisetosa* oviposits in the drier parts of algal mats (on which the larvae will feed) where rising water levels are less likely to drown them; the egg has a respiratory horn that probably acts as an anchor to prevent it being washed away from the surface (Zack 1983).

To avoid rising water levels, the prepupal larvae of several British *Eristalis* hoverflies move from shallow water to drier ground before pupating (Hartley 1961), as do the North American ephydrids *Parydra breviceps* (a shore-dwelling species) and *Nostima approximata* (a species of wet grasslands) (Foote 1983; Bishoff & Deonier 1985). *Parydra aquila* puparia float as water levels rise (Krivosheina 1987).

**Colonisation ability**

Diptera are clearly among the most able flying insects, especially when compared with water beetles and bugs, so are well suited to colonising new sites. Several studies of colonisation of new ponds suggest that Tanytarsini chironomids are particularly abundant compared to other subfamilies (e.g. Friday 1983), and species of *Tanytarsus* are among the first to colonise and then to disappear as the pond ages. They may represent fugitive species that do better in temporary ponds before predators become numerous.

**Short life-cycles**

Many small Diptera have long flight periods and short life-cycles, in contrast to most water beetles and bugs which are mainly univoltine (Williams &
TEMPORARY PONDS AND DIPTERA

Feltmate 1992) and are therefore able to take advantage of the opportunities offered by temporary ponds. This is illustrated by the life-cycle duration of wetland ephrydids (Table 1). The adults are relatively long-lived so can survive temporary summer drought or at least have an opportunity to disperse to alternative breeding sites. Such life-cycles are probably typical of many wetland flies.

Table 1. Life-cycles of Ephyridae. Values are in days unless stated otherwise. A question mark indicates that I think this is estimate is low. * Value for some stage missing. N.Am. = North American.

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg to adult</th>
<th>Generation per year</th>
<th>Adult life span</th>
<th>British?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coenia curvicauda</td>
<td>14-20</td>
<td>9-12</td>
<td>10-27</td>
<td>Yes</td>
<td>Foote 1990</td>
</tr>
<tr>
<td>Discocera obsolecra</td>
<td>1-2 months</td>
<td>2-5</td>
<td></td>
<td>Yes</td>
<td>Foote &amp; Eastin 1974</td>
</tr>
<tr>
<td>Hyalina gutata</td>
<td>c. 2</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Dahl 1959</td>
</tr>
<tr>
<td>H. nitida</td>
<td>2</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Dahl 1959</td>
</tr>
<tr>
<td>Hydrellia albidaebris</td>
<td>c. 2 (?)</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Karnecke 1985</td>
</tr>
<tr>
<td>H. griseola</td>
<td>Several</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Karnecke 1985</td>
</tr>
<tr>
<td>H. maura</td>
<td>1-2 (?)</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Learner &amp; Potter 1974</td>
</tr>
<tr>
<td>Nostima approximata</td>
<td>20-29</td>
<td>&gt;=5</td>
<td>20-36</td>
<td>N.Am.</td>
<td>Foote 1983</td>
</tr>
<tr>
<td>Ochthora montis</td>
<td>16-21</td>
<td></td>
<td>6-48</td>
<td>Yes</td>
<td>Simpson 1975</td>
</tr>
<tr>
<td>Paracera obvosa</td>
<td>15-26</td>
<td>5-6</td>
<td>24-28</td>
<td>N.Am.</td>
<td>Zack 1983</td>
</tr>
<tr>
<td>Parytra breviceps</td>
<td>14-17</td>
<td></td>
<td></td>
<td>N.Am.</td>
<td>Bishop &amp; Deonier 1985</td>
</tr>
<tr>
<td>P. quadriruberculata</td>
<td>&gt;12-26 a</td>
<td></td>
<td>30</td>
<td>N.Am.</td>
<td>Deonier &amp; Regensberg 1978</td>
</tr>
<tr>
<td>P. aquila</td>
<td>&gt;13</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Krivosheina 1987</td>
</tr>
<tr>
<td>Petina truncatula</td>
<td>c. 30</td>
<td>5</td>
<td>21</td>
<td>N.Am.</td>
<td>Foote 1981</td>
</tr>
<tr>
<td>Scatella subguttata</td>
<td></td>
<td></td>
<td>29</td>
<td>Yes</td>
<td>Dahl 1959</td>
</tr>
<tr>
<td>S. silacea</td>
<td>20-29</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Terry 1952</td>
</tr>
<tr>
<td>S. stagnalis</td>
<td></td>
<td>Multivolitine</td>
<td></td>
<td>Yes</td>
<td>Bussacca &amp; Foote 1978</td>
</tr>
<tr>
<td>Setacea arrowlens</td>
<td>c. 25</td>
<td>4</td>
<td></td>
<td>N.Am.</td>
<td>Foote 1982</td>
</tr>
</tbody>
</table>

Even species that have only two generations each year can use most British temporary ponds which remain wet during the cooler months. When the summer generation coincides with a dry phase, the larvae will need to seek refuge in permanent ponds. This is likely to happen in several common eristaline hoverflies such as Eristalinus sepulchralis, Eristalis pertinax, E. intricarius and Helophilus pendulus, which overwinter as larvae and have a
second summer brood (Hartley 1961). However, flies, at least in temperate climates, do not seem to fall into the class of "cyclic colonisers" (Wissinger 1997) since there is no evidence that they move predictably from temporary to permanent waterbodies in order to avoid the dry period, but rather colonise temporary ponds fortuitously. Only a small proportion of British Diptera, such as the *Aedes* mosquitoes, are annual species showing strong adaptation to temporary pools.

**Range of larval habitats**

The larvae of flies may be divided into those that respire through the skin and those that need access to air. The former includes rather few families, such as chironomids, ceratopogonids and chaoborids (phantom midge larve), which dominate truly aquatic situations. Larvae of most other families are mainly or entirely air-breathers which, with the exception of mosquitoes, are necessarily restricted to very shallow water or a wet shore. Most flies are therefore animals of water margins. Broad, shallow-sloping margins of most temporary ponds inevitably provide abundant habitat for them.

**Larvae that live in shallow water**

Larvae of a few groups can occupy water that is deeper than their own body length. Of the air-breathers, mosquito larvae, having developed the ability to swim well, can feed at depths far greater than their body length but have traded this advantage for exposure to pelagic predators, so that even mosquitoes are more often found in shallow or temporary water where predators are infrequent. Ptychopterid craneflies and eristaline hoverflies have "rat-tailed" larvae whose posterior spiracles are placed at the end of a telescopic extension to the abdomen, allowing access to sediments under several centimetres of water. Hartley (1961) found *Eristalis arbustorum* in a temporary pool containing cow droppings but larvae of other species of *Eristalis, Eristalinus* and *Helophilus* can be found in sites that dry out in summer. Most of the British sciomyzids (marsh flies) are predators of aquatic or hygrophilous snails. They are able to eat snails that are normally completely submerged, by raising their own buoyancy sufficient to keep the snails afloat, thus keeping the larvae within reach of the air (Berg & Knutson 1978). They do this by swallowing air and by trapping air in hydrofuge processes or hairs surrounding the posterior spiracles.

Falk (1991) listed twenty nationally scarce or rare British sciomyzids for which fluctuating water levels are likely to be important since such fluctuations leave snails stranded and exposed to ovipositing adults. The larva of at least thirteen British species attack snails that tolerate drying-out or are
Table 2. Sciomyzids and their molluscan prey, including only species of snails that tolerate seasonal pools or are hygrophilic (grow in or prefer moist habitats). T = recorded at vernal or temporary pools or pool margins (derived from Rozkošný 1984).

<table>
<thead>
<tr>
<th>Species of sciomyzid</th>
<th>Succinea sp(t)</th>
<th>Lymnaea</th>
<th>Anisus leucostoma</th>
<th>Apelxa hypnorum</th>
<th>Hygronyia sp(t)</th>
<th>Segmentina nuda</th>
<th>truncatula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colobaea bifasciella</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Colobaea distincta</td>
<td>T</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Pherbellia nana</td>
<td>T</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pherbellia schoenherri</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Pherbellia ventralis</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Steronicra angustipennis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sciomyza simplex</td>
<td>T</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Antichaeta analis</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Antichaeta brevipes</td>
<td>T</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Hydromyia dorsiata</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Limnia unguicornis</td>
<td>T</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Psacadinia zernyi</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetanocera silvatica</td>
<td>T</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>
hygrophilous (Table 2, based on data in Rozkošný 1984). These records do not include common sciomyzids feeding on a wide range of snails which were not named by Rozkošný and suggest that at least 20% of the British fauna in this family is capable of surviving in temporary pools. This is highly likely for Colobaea bifasciella, C. distincta, Pherbellia nana, P. schoenherri, Pteromicra angustipennis and Tetanocera silvatica, whose adults can be found in midsummer next to rather shallow waterbodies which are likely to become dry later in the year.

**Larvae that live in and above water margins**

Most of the remaining Diptera are restricted to very shallow water at pool margins and habitats immediately above water level, as their spiracles are placed on short posterior siphons and so they must live within a few millimetres of the air interface. Flies can be exceptionally abundant at water margins; for instance, at a broad patch of woodland mud, Crisp & Lloyd (1954) found that fly larvae comprised 99.4% of all insects. While the habitat they studied was more akin to a seepage, a similar result is likely from the mud around ponds.

There are several reasons why exposed muddy shorelines provide a particularly suitable medium for fly larvae. The water content of a mud shore can remain moderately constant from the water's edge to fringing emergent vegetation; Thier & Foote (1980) recorded 0.67 grams of water per gram of soil next to a drainage ditch in North America, and Dahl (1959) cited water contents from 35% to 75% for Scandinavian mud shores. The temperature of a dark mud surface exposed to sunlight in summer can be higher than air temperature, thus favouring many organisms. Nutrients are generally readily available so that algal growth can be prolific and diverse; for example, Thier & Foote (1980) listed a number of genera within the euglenoids, green algae, diatoms and blue-green algae (Cyanophyta) on a mud shore. Benthic algae are likely to be far more important to insects in temporary wetlands than was previously suspected (Wissinger 1999).

Ephydrids illustrate the use made of different food sources available to mud-dwelling larvae. Parydra and Scatella, often the most abundant flies on muddy pond shores, plough slowly through the surface layer of mud, filtering green algae and diatoms from detritus (e.g. Thier & Foote, 1980). A few genera (Hyadina, Axysta) are specialists on blue-green algae on mud or in seasonally inundated grasslands (Foote 1993). Setacera feeds on floating mats of filamentous or colonial green algae (Foote, 1982), but perhaps also when it becomes stranded on receding shorelines. Ephydrids are thus well adapted to exposed shores where algae thrive.
A feature of temporary ponds on mineral soils is their limited accumulations of plant litter, as it is mineralised during the dry phase. This militates against many detritivorous fly larvae which feed on the microfungi and bacteria filtered from decaying vegetation. For this reason, the archetypal temporary pond where fairy shrimps (*Chirocephalus*) abound is likely to be a poor fly habitat, but litter-rich temporary ponds within fens, bogs, swamps and woods do not suffer this limitation and are particularly rich in flies. Birds and mammals introduce dung as an additional food resource used by eristaline hoverflies which need nutrient-enriched water, and *Themira* sepsids which need dung-enriched mud (Pont 1979); these flies can be particularly abundant at temporary field ponds trampled by cattle.

Both adults and larvae in several genera of predatory muscids are associated with bare, wet substratum beside ponds and pools (Falk & Pont 2001). Flooding is a prerequisite for several species of *Lispe*, as flooding produces bare, organically rich mud, which is presumably important in increasing the numbers of prey.

**Dipterans associated with marginal plants**

Flies may be found at temporary pools by virtue of their association with particular plants. One large and ill-defined group comprises flies whose larvae live on wetland plants that tolerate occasional drying-out, and their occurrence at temporary ponds is fortuitous. A second group consists of flies living on plants that are most abundant on the draw-down zone and these are more likely to be frequent at temporary waters.

Common reed *Phragmites australis* supports several species that are likely to be found in seasonally inundated reedbeds. The large chloropid (grass fly) *Lipara lucens* preferentially selects reed with narrow stems, which tends to be found where it is stressed by a limited water supply, such as winter-flooded ground (Mook 1967). Associated with its cigar-shaped galls are a number of inquilines (commensals using the galls), including other chloropids such as *Calamoncrosis minima* and several species of *Cryptonevra*, and the anthomyzid *Anthomyza collini*. The uncommon chloropid *Oscinella angularis* has been reared from the reed grass *Phalaris arundinacea* and collected on a number of occasions from dry ponds (Falk & Ismay 2001), and *Oscinella trochanterata* mined the leaves (Uffen & Chandler 1978). *Oscinosoma gilvipes* probably lives within *Glyceria* in similar situations. Large scathophagids (dung flies) in the genus *Cordilura* mine the stem bases of *Car ex, Scirpus* and *J uncus* (Wallace & Neff 1971), and common species such as *C. impudica* and *C. ciliata* can be associated with temporary ponds where these plants grow. Soft rush *Juncus effusus*, common in seasonally inundated
places, supports the large stem-mining psilids *Loxocera ichneumonea* and *L. albiseta*, and the uliid *Palloptera scutellata*.

Several annual and flood-tolerant perennial plants are frequent invaders of the draw-down zone of ponds. *Rumex* and *Polygonum*, including such colonists of bare wet mud as the bistorts *P. persicaria* and *P. amphibium*, are mined by the anthomyids *Pegomyia bicolor* and *P. nigrirtasis* and unspecifed species of the ephydrid *Hydrellia* (Uffen & Chandler 1978; Mathis & Zatwarnicki 1995). Water-plantain *Alisma plantago-aquatica* frequently survives in this situation too, and is the host plant of *Hydrellia flavicornis*, *H. fulviceps* and *H. mutata*. Water mint *Mentha aquatica* grows prolifically on draw-down zones and is the host of the agromyzid (leaf-miner) *Phytomyza tetristicha*. Another common agromyzid, *Phytomyza plantarginis*, mines the leaves of great plantain *Plantago major*, which can be frequent on draw-down zones (e.g. Preston 1989), and *Agromyza spiraea* mines silverweed *Potentilla anserina* which survives seasonal inundation well.

Tussocks, especially of greater tussock sedge *Carex paniculata*, purple moor-grass *Molinia caerulea* and tufted hair-grass *Deschampsia caespitosa*, are often particularly well developed where water levels fluctuate. A diverse fly fauna lives in these large tussocks and often includes species with poor flight abilities. Temporary ponds with such tussocks are therefore probably of particular interest.

**Adult flies at temporary waterbodies**

Water surfaces and the wet expanse of draw-down zones are used by many flies for courtship and feeding. In many cases the permanence of the waterbody is probably immaterial for these activities. In a number of instances it appears that pools are essential for adults of flies whose larvae develop in drier surroundings, mirroring the requirement of adult dragonflies for terrestrial hunting grounds.

The predatory empid (dance fly) *Hilara* is often seen swarming and mating over water, yet the larvae of most species probably develop in damp soil; for example, the common *H. maura* will be found swarming over puddles that are clearly of no value to the larvae. Dolichopodids (long-headed flies) are among the more conspicuous flies courting on wet mud but such shores are also well populated with sphaerocerids (lesser dung flies) and ephydrids, which show little overt courtship. Mating pairs can be found even at ponds that dry out completely and are an unsatisfactory habitat for their larvae.

Several other species of predatory flies hunt alongside mud shores. An uninterrupted vista is probably important since they hunt actively using sight, even though the range at which they recognise prey may be only a few
centimetres. Among the largest predators are the muscid \textit{Lispe tentaculata} and the ephydrid \textit{Ochthera}. The two British species of \textit{Ochthera} can be found next to pools that dry out in midsummer (e.g. McLean 1993). Their prey includes small flies commonly found on muddy margins but they also haul chironomid larvae from wet mud (Simpson 1975), and \textit{Ochthera mantis} has been reported "fishing" for mosquito larvae (Bohart & Gressit 1951). Catching organisms, especially chironomid larvae, submerged within wet mud is probably the most common method of feeding by shore-dwelling dolichopodids, although several "fish" from the water surface for microcrustaceans and mosquito larvae (Van de Velde et al. 1985). Other surface hunters are the dolichopodids \textit{Hydrophorus} and many species of \textit{Campsicnemus}, and the empid \textit{Clinocera}. The ubiquitous ephydrid \textit{Hydrellia griseola} mines a wide range of aquatic, wetland and terrestrial plants but adults will hunt on puddles and pools where they and other \textit{Hydrellia}, even though sluggish and apparently unspecialised as predators, manage to catch their prey by tumbling it over so that it becomes trapped in the surface film (Lawrence 1952; Cranston & Disney 1978; Mathis & Zatwarnicki 1995). Since the prey of these flies is frequently abundant in shallow temporary pools, this habitat is probably as valuable as permanent ponds are to the predators.

\textbf{Temporary ponds of particular value to Diptera}

While most temporary ponds will support a variety of Diptera, there is no reason to" suppose that these species are necessarily dependent upon them. However, it is clear that a number of nationally scarce and rare species are restricted to seasonal ponds in particular habitats, or are most often found there.

On wet dune slacks, characteristic species are the sciomyzids \textit{Antichaeta analis}, \textit{Pherbellia brunnipes}, \textit{P. griseola}, \textit{Psacadina verbekei}, \textit{Pteromicra glabricula} and \textit{P. pectorosa}, and muscids include \textit{Coenosia vibrissata}, \textit{C. verralli}, \textit{C. pygmaea}, \textit{C. flavimana}, \textit{Lispe caesia}, \textit{Neolimnophila virgo}, \textit{N. maritima} and \textit{Orchisia costata}. Shallow brackish pools around estuaries, at the tops of saltmarshes and in coastal grazing marshes, can support the craneflies \textit{Erioptera bivittata}, \textit{Limonia danica} and \textit{L. ventralis}, the muscids \textit{Lispe caesia} and \textit{Spilogona scutulata}, and the mosquitoes \textit{Aedes dorsalis} and \textit{A. flavescens}.

Inland on wet heaths, shallow drying muddy and sandy pools support the ephydrid \textit{Scatella crassicosta}, the cranefly \textit{Tipula yerburyi} where there is sallow carr, and the muscid \textit{Lispe uliginosa}. Pinos in Norfolk, which undergo fluctuations in water levels and sometimes dry out, support rare flies. For instance, at Thompson Common, 25 of the 65 British species of
sciomyzids occur, despite the presence of an unremarkable mollusc fauna upon which larval sciomyzids feed; these include *Psacadina zernyi*, *Pherbellia argyra*, *P. griseola*, *P. grisescens* and *P. nana*. The very rare soldierfly *Odontomyia angulata* also occurs here (Irwin 1987).

**Conclusion**

A rich fly fauna is found at and above fluctuating water margins of ponds, and its presence is dependent upon the pond, not merely fortuitous. The terrestrial aspect of temporary ponds is a necessary part of the "life-cycle" of the pond itself and fulfills a particularly important function in the life-cycle of the associated fauna. The distinction between aquatic and terrestrial components may be a useful ecological distinction but it is an artificial barrier that impedes a complete understanding of the conservation importance of temporary ponds.

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**References**


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