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Life History Analysis of Dytiscids in Selected Habitats

by E. H. Barman

Abstract: Two central New York sites provided material for the evaluation of life cycles, and preferred reproductive habitats for nineteen species of Dytiscidae.

Key words: Coleoptera Dytiscidae – New – Habitats.

A stream, a permanent pond, temporary pond and a marsh yielded specimens of *Laccophilus maculosus*, *Hygrotus sayi*, *H. nubilus*, *Hydroporus undulatus*, *H. clypealis*, *H. niger*, *Deronectes griseostriatus*, *Agabus disintegratus*, *A. phaeopterus*, *A. ambiguus*, *Rhantus consimilis*, *Colymbetes sculptilis*, *Acilius fraternus*, *Dytiscus hybridus*, and a *Coptotomus* species. Based on collections of immatures, *Agabus phaeopterus* reproduced only in the marsh. Immatures of *L. maculosus* were found in or near all sites and those of *H. sayi* in the permanent pond only. The remaining species reproduced only in the temporary pond. No immatures were collected from the stream within the study site.

Seven species, *Laccophilus maculosus*, *L. biguttatus*, *Desmopachria convexa*, *Hygrotus sayi*, *H. laccophilinus*, *Agabus erichsoni*, and *Acilius fraternus*, were obtained from an undeveloped wooded preserve with two permanent and two temporary habitats. Larvae of *L. maculosus*, *L. biguttatus*, *D. convexa*, and *H. sayi* were found only in the permanent sites and those of *A. fraternus* and *A. erichsoni* were restricted to the temporary pools.

Introduction

Availability and subsequent exploitation of suitable habitats by dytiscid populations are critical to the maintenance of established populations and/or the successful colonization of new areas or regions. NILSSON (1986) reviewed literature and his own work regarding European Agabini habitats and concluded that productivity related to seasonality is important in determining suitability. *Hydroporus* species may have different pH requirements (CUPPEN, 1986) and acidity effected coleopteran assemblage composition and distribution in ponds (FRIDAY, 1987) and drains (EYRE et al., 1990). However, JULIANO (1991) found that pH alone did not account for distribution

of *Hydroporus* species. Vegetation has also been related to distribution of water beetle assemblages (EYRE et al., 1986; FOSTER et al., 1990; EYRE et al., 1990). Varying site-water duration may be a factor determining distribution (EYRE et al., 1992) with some species adapted specifically to exploit temporary conditions (JACKSON, 1958; CARR and NILSSON, 1988). However, it is often difficult to determine if a species is actively selecting a habitat because of specific biological or physical characteristics or if behavioral and/or physiological tolerances permit exploitation of a variety of habitats (EYRE et al., 1992).

Two sites in New York State (USA), each with proximal but different habitats, including both temporary and permanent systems, provided the opportunity of evaluating habitat selection by nineteen species of Dytiscidae. Life cycle data and descriptive information of the immature stages for each of these species permitted an evaluation of habitat utilization for reproduction.

Materials and Methods

A triangular aquatic net was used to collect most of adults and larvae, although some material was taken with a plankton net and, fortuitously, in various containers while collecting water and/or food items to support laboratory cultures. Recently emerged adults and/or pupae in pupal cells, with cast sclerites, were collected by searching the gravel or soil near habitat areas where mature larvae had been collected.

Pupal cells and laboratory cultures of adults and immature material permitted a definitive association of adults with immature components of the life cycle of each species considered. Cultures were at room temperature with a variety of invertebrates (primarily dipteran larvae) of an appropriate size provided as prey. Mature larvae were provided with moistened soil for pupation.

Jaccard coefficients (KREBS, 1989) were computed to evaluate habitat similarities.

Results and Discussion

Four urban sites located on the flood plain of Cayuga Lake Inlet Creek near the junction of State Route 13 and State Route 34A (Floral Avenue) approximately 3.2 km south of Ithaca, Tompkins County, New York were collected extensively in 1969, 1970, and 1971. In addition to the creek, the area contained three lentic habi-

tats, a permanent pond and a temporary pond and marsh. The two ponds represented site-water variation extremes at this locale with one (CIP-1) demonstrating relative permanence. The second (CIP-2) had a surface area of approximately 0.4 ha in early spring but was completely dry by mid-summer. A *Typha* marsh (CIM) tended to be flooded to its maximum surface area of about 3 ha and depth of about 30 cm in the spring. However, by mid – summer this system was characterized by small disjunct stagnant pools separated by muddy areas. These lentic sites were in an area of about 18 ha transected by a creek (Figure 1) with distance between sites no

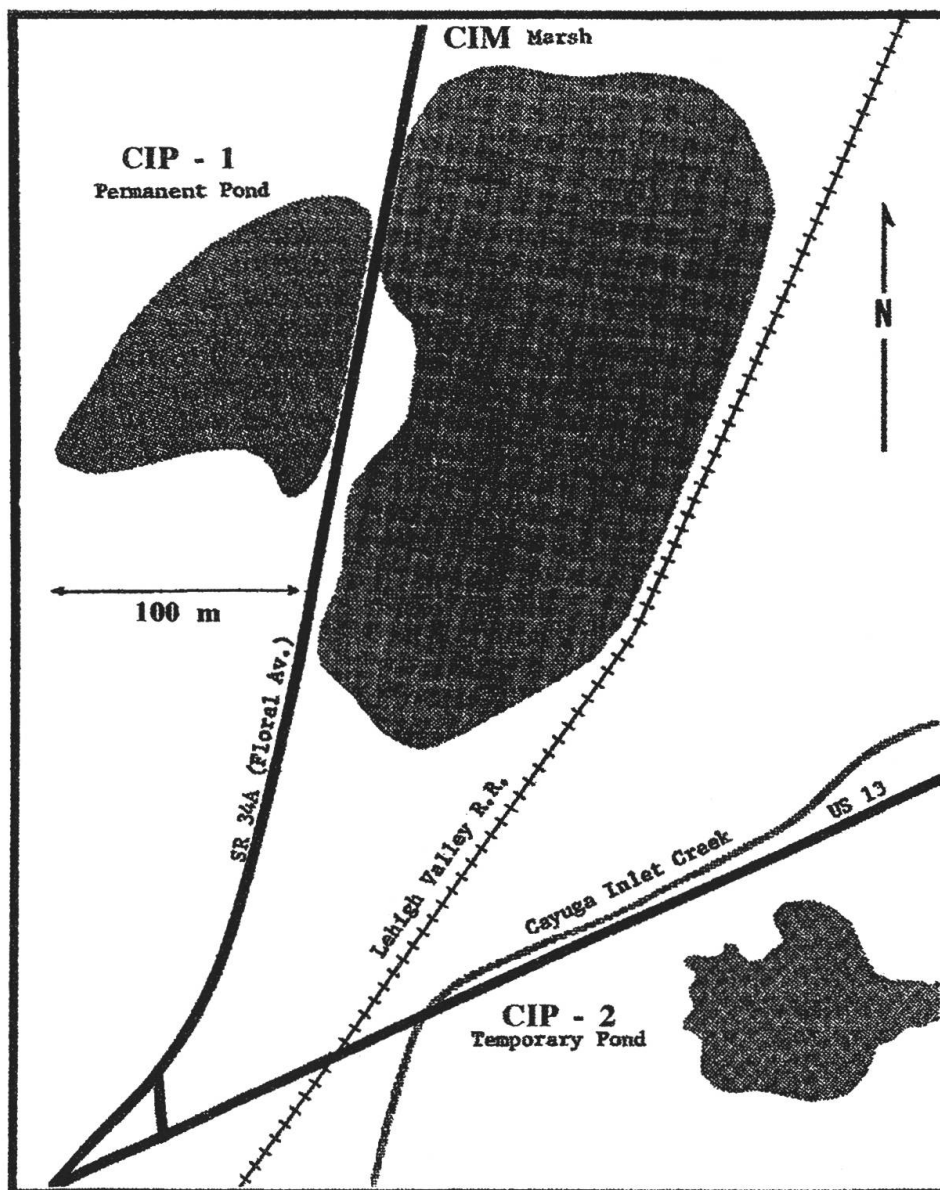


FIGURE 1. Cayuga Lake Inlet Creek Site.

greater than 300 m. In addition to proximity, the sites were separated by no significant natural or artificial barriers likely to impede movement into the area or between the habitats. Fifteen species, represented by adults and immatures, were collected from the lentic habitats within this site.

The permanent habitat, CIP-1, was shaded along its western and eastern sides and partially along its southern shore. The southeastern part of the pond was open, with various species of sedge (*Carex*) growing in the area and encroaching into the water. The northern margin was open, supporting stands of emergent vegetation including sedge and cattail (*Typha latifolia*). Dense growths of duckweed (*Lemna minor*) and watermeal (*Wolffia columbiana*) were also present particularly in the southern end. This was a eutrophic system with large quantities of organic material suspended in the water column, resulting in negligible transparency. The dytiscid fauna consisted of large populations of *Laccophilus maculosus*, *Hygrotus sayi*, *Hydroporus undulatus*, *H. niger*, *Agabus disintegratus* and a *Cototomus* species, particularly in the southern end. Occasionally taken were specimens of *Hygrotus nubilus*, *A. ambiguus*, *Rhantus consimilis*, and *Acilius fraternus*. It was possible that larvae of smaller species (i.e., *Desmopachria convexa*) were undetected because of size and the amount of detrital material involved, and adults of some of the larger beetles (i.e., *Dytiscus hybridus*) may have avoided collection (HILSENHOFF, 1987, 1991; BARMAN and WHITE, 1995).

The only larvae collected from CIP-1 were those of *Hygrotus sayi* and *Laccophilus maculosus*. *Hygrotus sayi* was observed breeding exclusively in this habitat, suggesting a reproductive preference for permanent eutrophic systems. This is reinforced by concurrent collections at Ringwood and other central New York sites and is consistent with observations by SPANGLER and GELLESPIE (1973) who cultured larvae from a habitat similar to this permanent pond. *Laccophilus maculosus* larvae were also collected here, but they were collected from each of the lentic habitats at this site and from a variety of other lentic systems. Reproductive ubiquity for this species has also been observed by HILSENHOFF (1992).

The temporary pond (CIP-2) was artificial, excavated only a few years before observations began. Only along the western end was there a well-defined, steep bank, and it is at that end that the maximum depth of about 1.0 m was found. Here there was a bed of stonewort (*Chara* sp.) and a few scattered wild celery plants (*Vallis-*

neria americana). Grass (*Glyceria* sp.) and sedge encroached into the water along the north and south margins and most of the eastern end. The extreme northeastern end extended into a wooded area where the water contained large quantities of leaves, stems, and branches in various stages of decomposition. The adults and larvae of *Laccophilus maculosus*, *Hygrotus nubilus*, *Hydroporus undulatus*, *H. clypealis*, *H. niger*, *Deronectes griseostriatus*, *Agabus disintegratus*, *A. ambiguus*, *Rhantus consimilis*, *Colymbetes sculptilis*, *Acilius frater-nus*, and the *Coptotomus* sp. were present at this site. Larvae of *Dytiscus hybridus* were numerous and adults of *H. sayi* were collected occasionally.

Laccophilus maculosus adults and larvae and *Coptotomus* adults were collected sporadically throughout CIM located directly across from CIP-1. A nearly pure stand of cattail grew near the center of this habitat, and mature larvae of *Agabus phaeopterus* were collected from the detritus originating from these plants. LARSON (1975) observed that this species was associated with *Typha* marshes in western Canada. These larvae were collected very early (9 April 1971) indicating that *A. phaeopterus* may over winter in the larval stage. No adults of this species were collected although adults of *A. disintegratus* and *A. ambiguus* were present in very low numbers. The creek transecting the area adjacent to the lentic sites yielded no dytiscids. However, adults of *Dytiscus hybridus* and both adults and larvae of *L. maculosus* were collected from back-pool areas of the creek about a kilometer south.

Table 1. Distribution of Dytiscidae at Three Habitats in the Cayuga Inlet Creek Flood Plain.

Species	CIP-1		CIP-2		CIM	
	Adults	Larvae	Adults	Larvae	Adults	Larvae
<i>Laccophilus maculosus</i>	+	+	+	+	+	+
<i>Hygrotus sayi</i>	+	+	+	—	—	—
<i>Hygrotus nubilus</i>	+	—	+	+	—	—
<i>Hydroporus undulatus</i>	+	—	+	+	—	—
<i>Hydroporus clypealis</i>	—	—	+	+	—	—
<i>Hydroporus niger</i>	+	—	+	+	—	—
<i>Deronectes griseostriatus</i>	—	—	+	+	—	—
<i>Agabus disintegratus</i>	+	—	+	+	+	—
<i>Agabus phaeopterus</i>	—	—	—	—	—	+

Table 1. Contiue

Species	CIP-1		CIP-2		CIM	
	Adults	Larvae	Adults	Larvae	Adults	Larvae
<i>Agabus ambiguus</i>	+	—	+	+	+	—
<i>Coptotomus</i> sp.	+	—	+	+	+	—
<i>Rhantus consimilis</i>	+	—	+	+	—	—
<i>Colymbetes sculptilis</i>	—	—	+	+	—	—
<i>Acilius fraternus</i>	+	—	+	+	—	—
<i>Dytiscus hybridus</i>	—	—	—	+	—	—

Table 2. Jaccard Similarity Coefficients for Three Habitats in the Cayuga Inlet Creek Flood Plain.

Stage	Habitat	CIP-1	CIP-2	CIM
Adult	CIP-1	1.00	0.77	0.40
Larval	CIP-1	1.00	0.07	0.33
Adult	CIP-2		1.00	0.31
Larval	CIP-2		1.00	0.07
Adult	CIM			1.00
Larval	CIM			1.00

If only adult dytiscids collected by netting are considered, the permanent (CIP-1) and temporary (CIP-2) ponds had comparable faunas (Table 2) with a Jaccard Coefficient of 0.77 (Table 3). However, the systems are very different if the focus is on larval distributions ($S_J = 0.07$) with the temporary pond playing a much more important role in supporting reproduction by the Dytiscidae of this site. Thirteen species either selected the variable water habitats for oviposition in preference to the other available systems or those habitats provided the complex of environmental conditions that permitted larval development and subsequent completion of each life-cycle. Larvae of *Hygrotus sayi* were the only immatures exclusive to the permanent pond, and the only generalist was *Laccophilus maculosus*, with larvae observed in each of the available systems. Thus, all but *L. maculosus* exhibited a high degree of habitat selectivity for reproduction or responded positively only to those conditions provided by either the permanent or temporary sites.

As temporary habitats dry, residents must undergo either physiological-behavioral adjustments to meet these new and very different

conditions or they must disperse to available permanent aquatic systems. Western populations of *Agabus disintegratus* employ the former strategy, with adults diapausing during dry periods (GARCIA and HAGEN, 1987; GARCIA et al., 1990). However, the populations of *A. disintegratus* considered here were represented by what appeared to be teneral adults in the water column of the temporary habitat until mid-May and at adjacent systems until at least mid-June. A reproductive cycle similar to that of the Cayuga Inlet Creek population has been observed for a southeastern population of *A. disintegratus* (BARMAN, 1994 unpublished data). Similar observations were made for most of the other dytiscids represented by larvae in the temporary sites. No adults were found in the dry sediments or on the former shore of CIP-2. Thus, it appeared that most of the species in this study with larvae restricted to temporary sites were characterized by a habitat duality, utilizing temporary systems for larval development and the permanent habitats during dry periods.

The pond, CIP-1, while supporting directly the reproductive activities of only *Hygrotus sayi* and *Laccophilus maculosus*, may have been critical to the diversity observed within the Cayuga Lake Inlet Creek site. When adults of *Hydroporus undulatus* from this and other lentic habitats began to oviposit in the laboratory, subsequent attempts to collect adults revealed that the populations had undergone significant reductions in size. This species was apparently dispersing to other habitats for oviposition, including the temporary pond (CIP – 2) where the appearance of larvae coincided with dispersal from CIP-1. Similar patterns were observed at the Inlet Creek site for *Agabus disintegratus* and the *Coptotomus* sp. HILSENHOFF (1992, 1993) observed that among Wisconsin Dytiscidae over wintering habitats often differ from breeding sites. Thus, it appeared that permanent systems provide sanctuary during dry periods and winter for those species that relied on variable-water habitats as reproduction sites.

Four habitats at the Lloyd-Cornell Ringwood Wildlife Preserve, a relatively undisturbed wooded area located on County Road 164 (Ringwood Road) 3.2 km northeast of Ellis Hollow in the town of Dryden, were collected intensively. The vegetative features of the preserve were presented by ROSS (1933) and the designations for the aquatic habitats are those of MULLEN (1971). The four sites were: Ringwood Pond (RWP-1), Overflow Swamp (RWP-2), Holly Pool (RWP-3), and Back Pond (RWP-4). Site RWP-1, a kettle hole, was

in many respects comparable to site CIP-1 in terms of depth, trophic status, water transparency, and relative permanence. RWP-2, located southwest of and adjacent to RWP-1, exhibited depths of 0.7 to 1.0 m in early spring when it was confluent with RWP-1 but consisted of only a few pools during the summer and remained in this state until snowfall. Habitats RWP-3 and RWP-4 were the most ephemeral of the variable water systems within the two areas. Patterns of distribution and specificity for reproductive habitats (Table 3) were similar to those observed for the Cayuga Lake Inlet Creek site.

Table 3. Distribution of Dytiscidae at the Ringwood Wildlife Preserve.

Species	RWP-1		RWP-2		RWP-3		RWP-4	
	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
<i>Laccophilus maculosus</i>	+	+	+	+	+	—	—	—
<i>Laccophilus biguttatus</i>	+	+	+	+	—	—	—	—
<i>Demopachria convexa</i>	+	+	+	+	+	—	—	—
<i>Hygrotus sayi</i>	+	+	+	+	+	—	—	—
<i>Hygrotus laccophilinus</i>	+	—	+	—	+	—	+	—
<i>Agabus erichsoni</i>	+	—	+	—	—	—	—	+
<i>Agabus</i> sp.	—	+	—	+	—	—	—	—
<i>Acilius fraternus</i>	+	—	+	—	+	+	—	+
<i>Dytiscus</i> sp.	—	—	—	—	—	—	—	+

Larvae of two species, *Acilius fraternus* and *Agabus erichsoni*, bred only in the temporary habitats (RWP-3 and RWP-4) at this site. Both habitats, located northeast of RWP-1, were flooded with water from melting snow beginning in early spring when maximum volume was achieved. Later water levels tended to fluctuate and both systems were dry by mid- summer. These two ponds were characterized by large amounts of benthic detrital material and very transparent water somewhat discolored by organic acids. Both systems supported large populations of mosquito larvae (*Aedes* sp.) and fairy shrimp (*Chirocephalopsis bundyi*). The larvae of *A. fraternus* were abundant in RWP-3 although the adults of this species were collected only occasionally. Adults of *Hygrotus laccophilinus* were common in this pond for a short period, and the adults of *Laccophilus maculosus*, *H. sayi*, and *Desmopachria convexa* were present sporadically. RWP-4 contained large numbers of larvae but relatively few adults of *A. erichsoni* along with a few larvae of *A. fraternus* and an undetermined species of *Dytiscus*.

Both subspecies of *Acilius fraternus* have been observed reproducing in temporary habitats (WOLFE, 1980; MATTA and PETERSON, 1987). JAMES (1970) reported that in eastern Canada *Agabus erichsoni* overwintered in the egg stage after exposure to low temperatures followed by flooding of vernal woodland pools. The early spring presence of a few adults and synchronous appearance of larvae of this species in RWP-3 and RWP-4 was indicative that *A. erichsoni* was overwintering in both the adult and egg stage. LARSON (1975) concluded that western Canadian populations of *A. erichsoni* overwintered in the adult stage. However, HILSENHOFF (1986) reported that it passed the winter in both the egg and adult stages which is consistent with a type III Agabini life cycle (NILSSON, 1986).

RWP-1 was covered with duckweed and watermeal and supported a stand of cattail in its the northeastern corner. Some marginal *Sphagnum* occurred in RWP-2 along with generally distributed duckweed and watermeal. In each the water column was laden with detrital material. The dytiscid communities of these habitats were identical (Tables 3, 4) with adults and larvae of *Laccophilus maculosus*, *L. biguttatus*, *Desmopachria convexa*, *Hygrotus sayi*, and larvae of an undetermined species of *Agabus* occurring in both. The adults of *H. laccophilinus*, *Agabus erichsoni*, and *Acilius fraternus* were also collected occasionally at both of these sites.

Table 4. Jaccard Similarity Coefficients for Four Habitats at the Ringwood Wildlife Preserv

Stage	Habitat	RWP-1	RWP-2	RWP-3	RWP-4
Adult	RWP-1	1.00	1.00	0.71	0.14
Larval	RWP-1	1.00	1.00	0	0
Adult	RWP-2		1.00	0.71	0.14
Larval	RWP-2		1.00	0	0
Adult	RWP-3			1.00	0.20
Larval	RWP-3			1.00	0.33
Adult	RWP-4				1.00
Larval	RWP-4				1.00

Life-cycle information (Table 5) was assembled for *Laccophilus maculosus*, *Desmopachria convexa*, *Hygrotus sayi*, *H. laccophilinus*, *Hydroporus undulatus*, *Deronectes griseostriatus*, *Agabus disintegratus* and a *Coptotomus* species. These data, based on cultured and

Table 5. Duration of Immature Stages

Species	Preferred Reproductive Habitat	Incubation Period (1)	Stadium I	Stadium II	Stadium III(2)	Stadia I-III	Pupal Period	Total Developmental Period
<i>Laccophilus maculosus</i>	Gen.	4-5	3-5	3-6	12-19	18-30	4-6	26-41
<i>Desmopachria convexa</i> (3)	Temp.	4-5	3-4	3-5	7-11	13-20	3-4	20-29
<i>Hygrotus sayi</i>	Perm.	5-6	...	3-4	7-10	...	2-4	...
<i>Hygrotus laccophilinus</i>	?	4-6	4-5	3-7
<i>Hydroporus undulatus</i>	Temp.	6-9	3-5	5-7	10-16	18-28	5-7	30-44
<i>Deronectes griseostriatus</i>	Temp.	5-7	10-16
<i>Agabus disintegratus</i>	Temp.	6-8	4-5	7-8	13	24-26	5-7	35-41
<i>Coptotomus</i> sp.	Temp.	5-7	4-6	5-6	11-15	20-27	4-5	29-39

1. All periods in days.

2. Stadium III includes time spent as prepupae.

3. Barman, 1973.

collected specimens and verified by *in situ* observations revealed nothing extraordinary about these life-cycles. All but *L. maculosus* appeared to be univoltine spring breeders with but a single generation produced by overwintering adults. Early spring oviposition and larval development for *A. disintegratus* is in contrast with observations (HILSENHOFF, 1986) that midwestern populations of this species overwinter in the larval stage. *Laccophilus maculosus* differed only in that it produced multiple generations. Larvae of this species were collected more or less continuously from late April to mid-August, although they were more frequently encountered in late spring and early summer. The amount of time elapsing between oviposition and emergence of adults for those species for which complete life history data were obtained ranged from 20 to 44 days. Incubation periods observed in this study, however, ranged from 3 to 9 days. Larval stages, including the terrestrial prepupal period, ranged from 18 to 30 days. The first and second stadia are about equal in length, but the third stadium is about as long as or somewhat longer than the first two combined. The amount of time spent as pupae ranged from 2 to 7 days for the species of *Laccophilus*, *Hydroporinae*, and *Colymbetinae*. That of the *Dytiscinae* was somewhat longer, ranging from 7 to 20 days. Thus, for the species reproducing in the temporary habitats, nothing comparable to either the remarkably accelerated development or synchrony reported for *Eretes sticticus* in a temporary desert pond was observed (KINGSLEY, 1985).

Fifteen of nineteen species at these two sites were observed reproducing only in temporary habitats although permanent sites were concurrently and apparently readily available. However, for all but one species, no reproductive adaptations specific for these habitats was apparent other than early spring oviposition and incubation and larval developmental periods that permitted exploitation of these transitory systems as reproductive habitats. With fall oviposition, winter dormancy, and spring hatching to correspond with habitat flooding, *Agabus erichsoni* was the only species specifically and evidently adapted to the most ephemeral of the temporary habitats within the two study sites. Teneral adults responded to habitat desiccation by migrating to other sites rather than aestivating during dry periods. Thus, those species in this study with larvae restricted to temporary sites exhibited a habitat duality, utilizing temporary habitats for larval development and the permanent systems during dry periods.

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