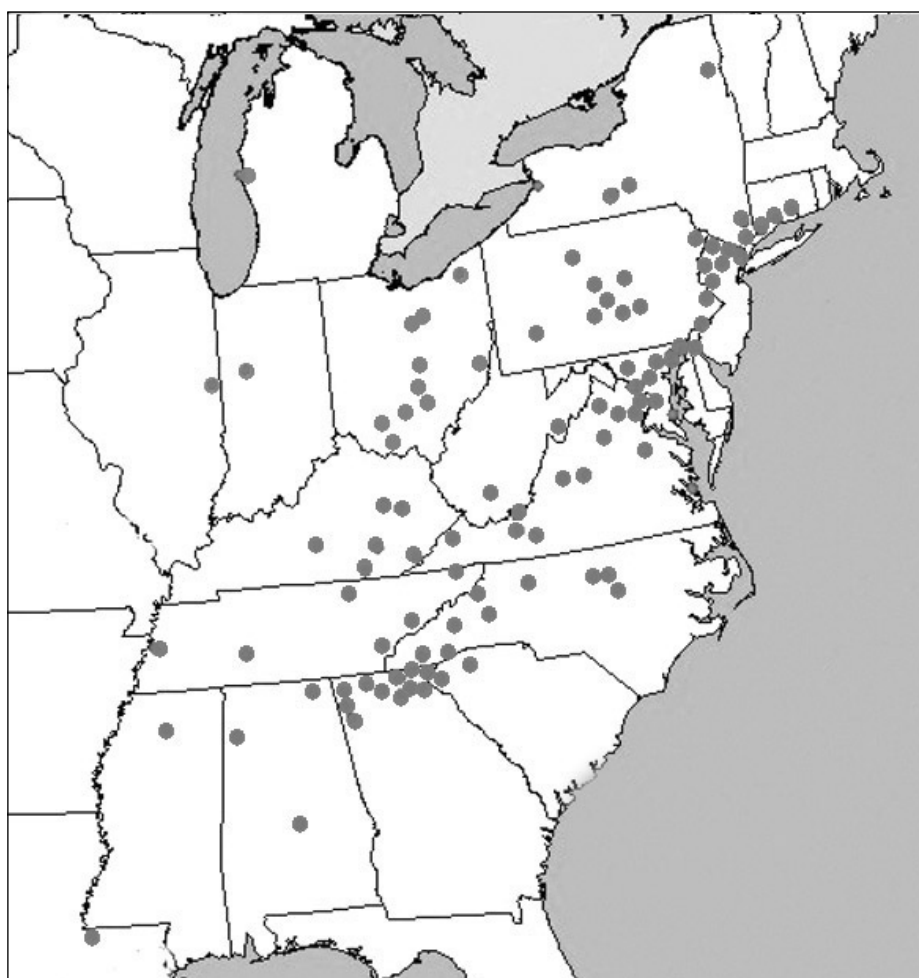


BULLETIN OF AMERICAN ODONATOLOGY



Cordulegaster erronea

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The Dragonfly Society Of The Americas

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Life History Studies of *Cordulegaster erronea* Hagen (Odonata: Cordulegastridae) in the Laboratory and the Field

Robert C. Glotzhober, Ohio Historical Society

Abstract

The life history of *Cordulegaster erronea* was studied for ten years utilizing field observations of adults and both field and laboratory studies of larvae. The documented adult flight period in Ohio is from 1 June to 3 September. Adult patrolling and larval habitat utilized consists of persistent but very narrow and shallow headwater streams, fed by seeps or springs in densely forested areas. Stream areas utilized have no fish and almost no other Odonata. The only aquatic predators observed were salamander larvae and an occasional very small crayfish. Adult males patrol regular beats during the heat of mid-day, flying low over the streamlets. Multiple males patrol the same streamlets. Adult females are uncommonly seen on the streams. Oviposition was observed between 18 June and 2 August and females made up to 370 oviposition thrusts in a single event. The author was able to establish criteria to recognize larval instars between F0 and F4 with a 92% confidence level. The larval period appears to be typically three to four years long. Some discussion and tentative hypothesis are made concerning egg development, but there is a need for direct study of the timing of hatching.

Introduction

Cordulegaster erronea Hagen (Tiger Spiketail) is a moderate to large dragonfly of the family Cordulegastridae. They have an adult total length of 65–76 mm and hind wing measurements of 42–51 mm (Riggs, 2002). Mature adults are black in color, with bright green eyes, two yellow thoracic stripes, and yellow rings encircling each abdominal segment. Mature larvae in the F0 instar have a head width between 7.0 to 8.2 mm and total length of 28 to 39 mm (this study). They are limited in distribution to 20 states within the eastern half of the United States, from Michigan and Illinois south to Louisiana, east to Georgia and north to New York (Figure 1). They tend to be quite rare near the northern, southern and western edges of their range. At least one author from a southern state considers this a northern species (Louisiana, Mauffray, 1997), while others in northern states consider it a southern species (Connecticut, Wagner et al., 1999; New York, Donnelly 1992; and Michigan, Bright and O'Brien 1999). There is only one record each from Illinois and Indiana (Donnelly, 2004).

In Ohio, when we started the statewide survey in the early 1990s it was known from only three specimens from two sites (Glotzhober, 1995), and in 1997 it was listed by Ohio as a State Endangered Species. Shortly after that time, we vastly increased our understanding of the very restricted habitat the species occupies, which is atypical of other Odonata habitat, and began to discover numerous populations. In

2002, the Ohio Division of Wildlife down listed it to a species of Special Concern. It is currently known in Ohio from multiple populations in 12 counties, and I expect that with more fieldwork additional county records will be added.

Very little information has been previously published about the details of the life history of *Cordulegaster erronea*. Kellcott (1899) indicated that all of the Cordulegastridae were uncommon, not taken often, and said that he had “seen so few specimens on the wing that I do not feel justified in giving anything of their habits in the field.” Needham (1905) echoed this note, and reported that it took him five years of work before he could capture his first *Cordulegaster obliqua*. Walker (1958) indicates that even in the more common *C. maculata*, the females are remarkably secretive. Of all the Cordulegastridae in Ohio, *C. erronea* is the least commonly observed. Barlow (1995) discussed its status in New Jersey and included some basic comments about habitat use, flight season, and behavior.

Glotzhober and Riggs (1998) discussed the beginning steps of this current project and described the use of a new method for capturing numbers of living specimens for mark/recapture studies. The only other references are notes in state publications that concentrate on distribution. This study has utilized fieldwork on the adults and larvae and laboratory rearing of larvae in an attempt to understand the life cycle and natural history of this interesting dragonfly. This report breaks down the information into discussions of habitat,

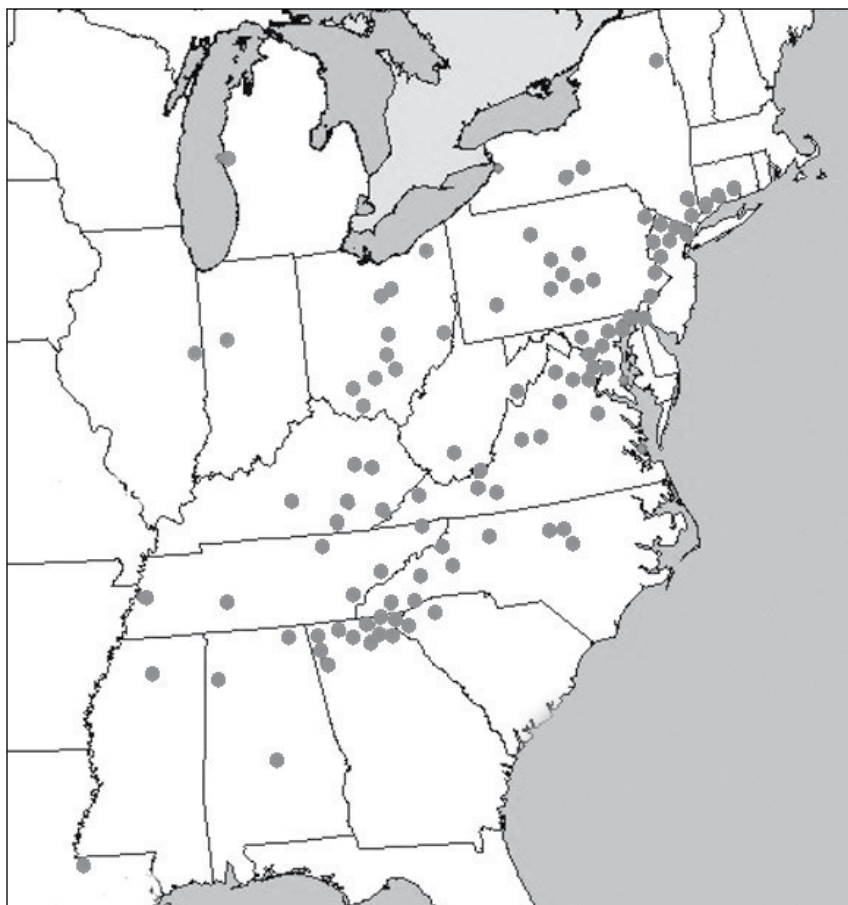


Figure 1. Distribution of *Cordulegaster erronea* in the eastern United States. Map copyrighted and used by permission of OdonataCentral, 2005. See Abbott (2005). (www.odonatacentral.com Accessed 25 November 2005).

adult behavior, and the larval life cycle based upon both laboratory and field examinations.

A. HABITAT UTILIZATION

Methods

The author and others have searched for appropriate habitat in Ohio between 1996 and the present. Once a good idea of the restrictive habitat requirements was obtained, that searching image was applied to the searches. Initially an intensive systematic effort concentrated on the area known as the Hocking Hills (parts of Hocking and Fairfield Counties, Ohio) where the earliest discoveries had been made. Later, efforts expanded to other areas of the state that were known by the author. A variety of educational programs to various natural history interest groups resulted in suggestions of additional places to search. One such program contact resulted in a participant discovering a new county record in northern Ohio several years after having seen a program that included discussion of this species and its habitat.

Results

The habitat for *C. erronea* is atypical of Odonata habitats and therefore is a habitat not often visited by Odonatologists. While working on the Ohio Odonata Survey we had targeted this species as one reported but not recently seen. In July 1996, Dan Riggs and the author finally established what type of streams to examine. During 1996 to 1998, we explored 89 primary headwater streams in seven southern Ohio counties (Glotzhofer, 1999). Sixty streams had either adults or larvae of *C. erronea*, while 29 had neither adults nor larvae (Glotzhofer, 1999). In Ohio, *Cordulegaster erronea* typically utilizes small, spring-fed streams or seeps with a sandy substrate under a heavy canopy of trees (Riggs in: Glotzhofer & McShaffrey, 2002).

In Ohio, these are most typically in regions of sandstone bedrock. These streams typically range from only 10 to 30 cm wide (4 to 12 inches) and 1 to 8 cm deep ($\frac{1}{2}$ to 3 inches). In two cases there were very large springs with the stream flowing from them initially 2 to 3 meters wide (6 to 10 feet) and (like the typical stream) only 1 to 8 cm deep. The shallow depth appears to be more important than the width of the stream. It appears that these primary headwater streams must be spring-fed and continuous or near-continuous flowing.

I examined two different streams at Ohio University's Dysart Woods Laboratory in Belmont County, Ohio that were about one-half kilometer apart. One had persistent flow and contained larvae and adults of *C. erronea*, the other was intermittent and contained no adults or larvae of *C. erronea*, but did have a population of *C. obliqua* present. Similar results were also seen in other streams, though perhaps less dramatic in their proximity (this study). Two streamlets at the Chestnut Ridge Metro Park in Fairfield County are within less than one-half kilometer apart, are at the base of the same ridge line, and have nearly identical hydrology, substrates, and flow sizes. However, one is forested and one has been cleared. The streamlet with forest cover maintains a population of *C. erronea*, while the open stream does not.

In late December of 2004, a severe ice storm created significant clearing of tree shade on the forested streamlet at Chest-

nut Ridge. A brief survey in August of 2005 of that streamlet revealed no adults present and no larvae found—again emphasizing the importance of forest cover. Other workers have also noted that the species occurred only in well-forested areas (Barlow, 1995; Tennessen et al., 1995). Barlow (2001) reported that out of nine known populations in New Jersey, one was extirpated and another was rapidly declining due to removal of the forest canopy. Several streamlets inhabited by *C. erronea* in Hocking County ravines have such a dense cover of *Tsuga canadensis* (Eastern Hemlock) that visibility along the stream is very limited due to low light levels. Throughout Ohio, streamlets containing *C. erronea* have a variety of species of trees in the forest, but some type of forest cover is consistent.

While the forested cover type appears to be a requirement, the sandy substrate seems less restrictive. Barlow (1995) and Tennessen et al. (1995) both indicate that the species is found in sandy streams and Barlow emphasizes that the substrate has little or no organic matter. While a sandy to sand/small pebble substrate is certainly the predominate case in Ohio, *C. erronea* also inhabits mucky seeps at the head of sandy-bottomed streamlets and these seeps may even serve as a refugia for the species during severe drought (personal observation). Furthermore, one population found in Adams County in southern Ohio was in a small stream sitting above dolomitic bedrock that had a substrate mixture of sand, silt, and muck. I have never found specimens along streamlets that do not contain some sort of soft substrate that permits burrowing. Ovipositing females (this study) preferred segments of the larval streamlets that had more sand and less pebbles. In several instances, females were seen to make a few ovipositing thrusts in areas of mixed sand and pebble, then move a short distance away and make numerous thrusts in a sandier location. Pfuhl (1994) reported that *C. boltoni* in Germany tested areas for suitable oviposition sites with only a few seconds of thrusting before moving to more suitable substrate.

While not experimentally tested, another habitat requirement for *C. erronea* larvae appears to be the absence of fish. Ferreras-Romero & Corbet (1999) noted that the stream in southern Spain where they found larvae of *C. boltoni* was also fish-free. In Ohio, following numerous streamlets upstream, larvae of *C. erronea* are not found until a small waterfall eliminates fish from the stream above that point (Glötzhofer, 1999). We found only two isolated exceptions to this rule: both cases were immediately below the point of fish-exclusion, and one of the larvae was concealed in sand beneath a small rock. Many of the sites where we found *C. erronea* were also occupied by *Pseudotriton ruber* (Northern Red Salamanders). These are uncommon salamanders in Ohio, and use approximately the same habitat. Pfingsten (1989) summarizes their habitat as springs that are found in

continuous shade. He further mentions that *P. ruber* spend three years as larvae, the first year they are 13–25 mm long, the second 20–40 mm, and the third 40–54. Hence, for about half of this time they are equal to or smaller than larvae of *C. erronea*, and half the time larger. Depending upon size, *P. ruber* and *C. erronea* probably alternate the role as dominant predators in their habitat when both are present, but this has not been studied. The predator/prey relationship between *P. ruber* and *C. erronea* is unknown. Small immature crayfish were also found occasionally in sites occupied by *C. erronea*. Lang et al. (2001) describe the stream habitat in Austria of *C. heros* and *C. bidentata* as the “salamander region . . . where fish are lacking and *Salmandra s. salamandra* larvae . . . and *Cordulegaster* species act as top predators.” Pfuhl (1994) found no crayfish in his sites, and the only vertebrate found was *Salmandra salamandra*.

In contrast to the fish-free habitat of *C. erronea*, *C. boltoni*, *C. heros*, and *C. bidentata*, this does not appear to be a trait for other North American members of the genus. Needham (1905) writing about *C. obliqua*, noted that competitors for food for these larvae were “red-bellied minnow and black-nosed dace” (no scientific name given, but presumed to be Southern Redbelly Dace, *Phoxinus erythrogaster* and *Rhinichthys atrarulus*). The author generally has found *C. obliqua* in Ohio along intermittent streams, which contain no fish. Needham and Heywood (1929) discussing the family Cordulegastridae indicate that captive larvae (no species given) will capture and eat young brook trout and “seem to have a decided preference for big game.” The same authors note that *C. dorsalis* in captivity is cannibalistic of smaller members of the same species. In Ohio, *C. maculata* inhabits forested streams up to the size of small rivers (Riggs, 2002) that contain numerous fish. Clearly, there are species differences within the genus and perhaps from region to region regarding their relationship to waters with or without fish. At least in Ohio, *C. erronea* are usually found in fish-free headwater streams.

In all locations where I have observed *C. erronea*, other Odonates are very uncommon to nonexistent. During the summers of 1996 and 1997, we maintained one to four malaise traps on streamlets for various periods. At one point, we operated malaise traps for 21 consecutive days with a major part of each day at the streams (Glötzhofer and Riggs, 1998). During this period, we observed and marked 142 individual *C. erronea*. The only other Odonates seen or collected were four *Somatochlora tenebrosa* (all females), two *Cordulegaster obliqua*, and two *Tachopteryx thoreyi* (Glötzhofer and Riggs, 1998). Along the main stream of Crane Hollow, a short distance downstream from the *C. erronea* habitat, we recorded 40 other species of Odonata—one of the higher concentrations of Odonata in Ohio for an area of equal size.

As mentioned above, during our search for appropriate habitat in 1996 through 1998, we examined 89 primary headwater streams and found adults or larvae in 60, or 67%. This percentage of occupation may give an inaccurate impression of occupation of habitat by *C. erronea* as we were specifically searching for favorable habitat. Using topographic maps, I prepared an analysis of the immediate region of Crane Hollow—the best and most heavily occupied habitat we have seen in Ohio. My analysis enclosed a rectangular area that includes all but the lower stretches of Crane Hollow, and included half of each section 21 and 22 plus all of sections 27, 28, 33, and 34 in Laurel Township, Hocking County, Ohio. This area enclosed roughly 1271 hectares (3141 acres) of forested land, with three known seeps and 51 primary headwater ravines identified on the map. All three seeps had larvae or adults, and 29 (57%) of the primary headwater streams had adults or larvae (Dan Riggs pers. comm., August 1996).

Measuring the potential stream/ravine habitat on the maps yielded a total of 0.30 hectares (0.74 acres) of stream or seeps, but with only 0.17 hectares (0.42 acres) of aquatic habitat occupied—or 64.4% of the aquatic habitat and only 0.013% of the total land area. Hence, despite a large percentage of primary streams within this area occupied the habitat compared to the total land area is quite small. With only casual observations, the 51 headwater streams appear very similar. Despite their uniform forest cover, close proximity, and the same basic bedrock formations, those streams not occupied had rockier substrate and/or intermittent flow. In other nearby areas, we found *C. erronea* in five of 13 ravines (38%) in Little Rocky Hollow and Big Rocky Hollow. Streams that we have explored outside of the Hocking/Fairfield County area seldom have an equal concentration of total primary headwater streams, and have significantly less concentrations of habitat occupied.

At Northwest Seep in Crane Hollow, I collected larvae on nine different dates along a stretch of primary headwater stream that measured only 26.5 meters (87 feet) long. Here I collected larvae within a range from 18 to 60 individuals per visit, with an average of 38.5 individuals per visit. Hence, larvae were quite concentrated within this habitat. Lang, Müller, and Waringer (2001) studying *Cordulegaster bidentata* and *C. heros* in Austria found concentrations of 4.13 larvae per 10 meters of shoreline (*C. bidentata*) and 7.84 larvae per 10 meters of shoreline (*C. heros*). The concentration of *C. erronea* at Northwest Seep is from 12.45 to 14.53 larvae per 10 meters of stream—a much higher figure. While these species are closely related, and all use first order streams that are forested, the two Austrian species use larger, deeper stretches of streams than the usage by *C. erronea*, so the concentrations cannot be directly compared. Lang et al. (2001) report water depths typical for both species of 1 to 16

or 20 cm, and average depths 4.4 cm for *C. bidentata* and 5.6 cm for *C. heros*—compared to typical depths for *C. erronea* of 2–3 cm. Lang et al. (2001) provide larval concentration data from other authors working with *Cordulegaster boltoni* in various parts of Europe that vary from 1.5 to 20 larvae per 10 meters of shore length. Dan Riggs, working on Silex Seep in Crane Hollow in 1997 located 53 larvae in a single visit of about 85 feet of streamlet—or very comparable to the numbers in Northwest Seep (Riggs pers. comm.) Hence, even though prime larval habitat may be very limited in size, concentration of larvae of *C. erronea* within that habitat is high compared to other species reported.

B. ADULT BEHAVIOR

Methods

Observations on adult behavior, including flight period, were made during the process of other fieldwork. While maintaining the malaise traps (Glotzhofer and Riggs, 1998) opportunity was taken to sit and observe occupied streams and record notes on male patrolling, female ovipositing, and other activities. On occupied streamlets, a period of a half-hour to an hour frequently is required to observe adults during good weather. On occasion observation periods were much longer. No systematic attempt was made to quantify any specific behavior, although some comments will be made based upon field notes. Flight season is based upon the database of the Ohio Odonata Society, which currently holds more than 27,500 total records of Odonata in Ohio, with 46 records of adult *C. erronea*, and is maintained by the author.

Results

One of the remaining mysteries is the location and timing of ecdysis in the field. Despite days of running malaise traps, searching for habitat utilization, and collecting and measuring larvae, I have never seen an exuvia, or what I could determine to be a teneral *C. erronea* in the field. In my laboratory rearing studies, options for ecdysis are limited to a fiberglass window screening attached to the side of each rearing chamber. In these cases, larvae completing ecdysis were 10 to 15 cm (4 to 6 inches) above the water, hanging vertically from the exuvia. In several cases, larvae did not climb high enough out of the water before ecdysis, and ended up with the adult dying in the water while hanging backwards off the exuvia. Several times, I have searched in the field for exuvia without avail. Correspondence with other individuals working with the genus *Cordulegaster* in North America and a literature search (see Table 1) suggest that exuvia could be quite some distance from the water and/or could be very difficult to find due to detritus attached to their hairy exoskeleton (Needham, 1905).

Table 1. Field locations of exuvia for other species of the genus *Cordulegaster* in the North America. All information comes from personal communications, or publications as noted in references.

Species	Locale	Locations	Source
<i>C. bilineata</i>	Tennessee	On trees in seepage swamps; some above head level.	Ken Tennessen, 1998
<i>C. diastatops</i>	Pennsylvania	On fern near sphagnum pool just a little above ground.	Clark Shiffer, 1999
<i>C. dorsalis</i>	California	One to five feet up the trunk of the nearest alder tree to the stream.	Kennedy, 1917
<i>C. erronea</i>	New Jersey	Exuvia found on underside of Interrupted Fern, about knee high.	Alan Barlow, 2002
<i>C. maculata</i>	Pennsylvania	Low in vegetation ten feet from a diversion ditch around a lake	Clark Shiffer, 1999
<i>C. maculata</i>	Wisconsin	Found numerous less than 1 ft. above water	Bill Smith, 1997
<i>C. maculata</i>	Michigan	On grass 1–2 ft. above water	Ken Tennessen, 1998
<i>C. maculata</i>	—	On tree trunks just above small stream	Sid Dunkle, 1997
<i>C. maculata</i>	Ontario	In “dark groins of trees whose roots have been eroded by the stream.” Less frequently on emergent plants at water’s edge, or 1 m high and up to 4–5 m laterally from water.	Paul Brunelle, 1997
<i>C. maculata</i>	Ohio	Female photographed sitting on exuvia 21–22 inches above ground on shrub, 11–12 yards from a small stream	Jerry & Barbara Jividen, 2005
<i>C. obliqua</i>	Illinois	Within one foot of water’s edge on flat ground. Hard to find because of silt on exuvial hairs conceals it well on the ground.	Needham, 1905
<i>C. obliqua</i>	Wisconsin	On dead tree adjacent to water, 3–4 feet up	Bill Smith, 1997
<i>C. obliqua</i>	Ohio	In lab, 5 inches above water (could have climbed ten or more)	Eric Chapman & Joe Keiper, 1997
<i>C. sp.</i>	Quebec	On roots just above small stream; also up to 20 feet up on tree trunks	Benoit Menard, 1998

Adult males make patrol flights over the forested streams and seeps that constitute larval habitat. These flights are low over the water, estimated to range from 8 to 15 cm high. While patrolling, their flight is purposeful and generally straightforward with the stream, halting for 1 to 3 seconds every 3 to 5 meters before continuing forward. Pfuhl (1994) recorded patrolling flights for *C. boltoni* as similar, but flying higher (20–50 cm above the stream) and pausing every 2 meters. I seldom observed any foraging in patrolling males. The one notable case was on 16 July 2004 when over a period of 80 minutes I observed an unknown number of individuals on patrol flights 25 times. During this period, three times I observed a male to briefly fly up and presumably grab some small dipteran or other insect. Certainly, in my experience they were not adding much nutrition during these patrolling flights.

On six different occasions, I tried to quantify direction of patrolling flights. Out of 78 patrolling flights, males patrolled upstream about 62.8% of the time and downstream only 37.2% of the time. Sometimes I could observe males turning around at the top of the streamlet and flying back down, other times I could see them fly into the tree canopy and disappear. Either I was often too far from the top of the streamlet, or it was too dimly lit to be able to maintain my observation of the insect.

Information and observation on foraging by adult *C. erronea* is very limited. As mentioned above, patrolling males do not seem to forage in any ratio that would adequately supply their need for nourishment. Clark Shiffer (pers. comm.) observed an adult foraging in a “small swale-like clearing near a stream along a forested road” in Pennsylvania. On 22 July 1999 Dan Riggs and I observed a male flying (and perhaps foraging) in the shade at the edge of a woodlands in a cedar-prairie glade in Adams County, Ohio. This was at about 10:30 ^{am} on a day when temperatures reached 35°C (95°F). This could suggest that foraging takes place in woodland clearings. On the other hand, whenever a captured *C. erronea* is released, its first flight is always upward toward the brightest opening in the forest canopy. Females typically drop down out of the treetops to begin ovipositing behavior. Hence, it is possible that foraging takes place in the tree canopy. Sid Dunkle (pers. comm.) indicated that *C. maculata* forages among the treetops. On 9 July 1998, Dan Riggs and I spent 5.5 hours sitting on “Airplane Rock”—a prominent cliff overhanging the tree canopy of prime *C. erronea* habitat at Crane Hollow, Hocking County, Ohio. Not once were we able to observe *C. erronea* foraging. Further work is needed in this area.

On a number of occasions, I saw a second male patrolling within 30 to 60 seconds of a first male—patrolling just out of sight around bends in the stream. Rate of patrols varied

highly, and usually took place during the heat of the day, between roughly 10:00 ^{am} and 5:00 ^{pm} with most between 11:00 ^{am} and 3:00 ^{pm}. Checking of malaise traps early and late showed no specimens captured between 5:00 ^{pm} and 8:00 ^{am} the next day, and no adults were observed the few times I was in the field earlier than 9:00 ^{am} or later than 5:00 ^{pm}. My six periods of measured observations covered 555 minutes of time, with a patrolling male seen on average one every 7.1 minutes. On a per day scale, the average varied from one every 3.2 minutes to one every 30 minutes. On an individual scale, even with high rates of patrolling, I might go 20 or 30 minutes without seeing any males, then see several over the next five or ten minutes. In good habitat on a good hot day in the middle of the flight season, it was rare to not spot a patrolling male with 30 minutes of watching.

On several occasions, Dan Riggs or the author observed obstacle avoidance by patrolling male *C. erronea*. Even though we caught 142 individuals in modified malaise traps (Glotzhober & Riggs, 1998), with 281 recaptures, each of us observed several occurrences of avoiding malaise traps and other obstructions. In 1997, Riggs (pers. comm.) observed trap avoidance three times in 20 minutes on one day, and seven times in 30 minutes on another day. In most cases, the dragonfly would approach the net (which blocked the stream), hover in front of it, then back up and fly up and over the net. Occasionally the dragonfly would simply turn around. On one occasion, Riggs observed a dragonfly actually wiggle underneath the trap, in a space less than 3 cm high between the netting and the stream. Considering the habitat used by these animals, trap avoidance is not too surprising. On at least five occasions recorded in my notes, I observed *C. erronea* approach a fallen rock or tree that blocked the flight space over the stream and exhibit the same behavior. In much of Ohio they frequent headwater streams that are in steep-sided ravines where tree or rock falls are commonplace. Therefore, obstacle avoidance is a natural adaptation to their habitat. The surprising part is that despite this behavior, we were still able to collect so many individuals within the malaise traps.

Mark/recapture efforts (Glotzhober & Riggs, 1998) were concentrated within Crane Hollow Nature Preserve, Hocking County, Ohio. At Crane Hollow, there are well over a dozen small side ravines that are habitat centers for *C. erronea*. These streamlets are separated by steep-sided ravines and uplands, and by larger, fish-inhabited streams in lower elevations. In 1997, we operated four malaise traps simultaneously for three weeks straight, often in adjacent side ravines (Glotzhober & Riggs, 1998).

Seventy-two individuals were marked and recaptured multiple times, up to seven times per individual. In only two cases did we recapture an individual in a different side hollow

than where it was first collected. These individuals relocated 0.58 km and 0.4 km in a direct line of flight, or up to 1.66 km if they followed the stream level. It is not clear if these recaptures represented a complete relocation, or merely a temporary shift within their normal home range. However, none of the other 70 individuals (97%) were caught outside of their "home" ravine, suggesting a strong tendency to remain within a single ravine.

In July of 1996, a female *C. erronea* was found dead in Ross County, Ohio and submitted to our survey. It died near a small stream near but not in a wooded area. The stream was highly intermittent and when Riggs and the author visited it we found no adults or larvae on that stream, nor could we find any other likely habitat within several kilometers. While we may have missed the habitat that originally supported this specimen, it is possible it was on an immigration flight when it died. Walker (1958) indicates that between emergence and sexual maturity, adults of *C. diastatops* may wander up to a mile (1.6 km) from their stream habitat. We have yet to identify any habitat within Ross County. Clearly, more work is required on the home range and/or immigration behavior in *C. erronea*.

Based upon 46 specimens in our collections, known flight season in Ohio for *C. erronea* ranges from 1 June to 3 September, with 83% of those falling between 28 June and 11 August, and the peak during the last two weeks of July. I am aware of one unconfirmed report by a reliable witness of an adult *C. erronea* flying on 11 September (see discussion). Field studies of larvae completed in April or May and in mid-September or October never resulted in observations of adults. It is reasonable to assume some adults may be present both before 1 June and after 3 September in limited numbers when weather is appropriate. Based upon our mark/recapture work (Glotzhober and Riggs, 1998) adult *C. erronea* may survive at least 34 days.

I never observed what could be clearly identified as male/female interaction during these patrols. In fact, I never observed any tandem or wheel flights. Several times, I did see what I presume to be males flying 30 to 60 seconds apart up a stream to its seepage head, where they met, and a wing crashing "fight" took place. I presume this to be agonistic behavior between two males, but could never positively confirm the sexes during these observations.

On sixteen occasions from 1997 through 2004, I was able to observe females ovipositing. Their behavior is the classical "pogo-stick" up and down described for Cordulegastridae. The female hovers a few centimeters above the water, with her abdomen pointing downward. At a rate estimated at 90 times per minute, she thrusts downward, pushing her spike-like ovipositor into the sand. Water levels where this is

performed are typically only 1–2 cm deep, sometimes even less. On a few occasions, I was close enough to hear sand grains being pushed aside by the female's thrusts.

On 15 of the 16 occurrences, I was able to count ovipositing thrusts. They ranged from six to 370 thrusts for a single female (sometimes included starts, stops, short move, and re-starts) averaging 120.3 thrusts, and with a mean of 78 thrusts. Actual numbers of thrusts were probably higher, as it was common that the female had already arrived and begun ovipositing before I spotted her. On at least two occasions (six thrusts and 18 thrusts), I had the impression that the female quit early due to unsatisfactory substrate, and the gravel/pebble to sand ratio was high in these two spots on the stream.

As noted above under habitat selection, Pfuhl (1994) noted that *C. boltoni* females would test areas for ovipositing by thrusting for a few seconds. If the site was unsatisfactory, she would relocate and try another spot. Several times my motion nearby disturbed the female and she quickly left, heading into the treetops. On 31 July 1997, I observed a single female oviposit 340 times, followed by a brief untimed break, followed by 30 additional thrusts. These final 30 thrusts ended when a patrolling male chased her off into the treetops. Kennedy (1917) reports *C. dorsalis* in California making only from four to ten ovipositing thrusts at each of several stops followed by moving several yards and repeating the process. Walker (1958) observed *C. maculata* in Canada making about 100 ovipositing thrusts.

Pfuhl (1994) observed one female *C. boltoni* making "around 100" thrusts within 7 minutes with an area along 30 cm of shoreline. From that spot, he was able to locate only seven fresh eggs—from which he presumed that not every oviposition thrust results in deposition of an egg. He does not discuss the degree of difficulty in finding eggs that are only 0.6 to 0.8 mm in diameter mixed in with a sandy substrate that is often about the same size as the egg. It would appear to this author that his assumption is premature, and that we do not really have a good idea how the number of thrusts and the number of eggs deposited really relate.

Most of the times that I was able to observe the female arriving; she would drop unexpectedly out of the sky and begin ovipositing almost immediately. A couple of times I observed a female working upstream, in a fashion similar to male patrols, and then begin ovipositing. I would hypothesize that females are very wary when ovipositing to avoid contact with males before they could deposit their eggs. Needham and Heywood (1929) discussing *C. diastatops* and Kennedy (1917) discussing *C. dorsalis* both indicate that females are seldom seen at the water unless they are ovipositing. The earliest date I observed ovipositing was 18 June 2004 and the latest was 2 August 1997, with a median date of 10 July with

81% of the observations on or after 16 July. Similar to the male patrolling behavior, all my observations of ovipositing took place between 10:00 ^{am} and 2:38 ^{pm} generally during the heat of the day, despite the fact that I was often in the field prior to 9:00 ^{am} and until 4:00 or 5:00 ^{pm} (especially when doing larval sampling). One female oviposited 314 times during a light rain with air temperatures between 85°–90°F.

C. LARVAL LIFE CYCLE—LABORATORY REARING

Methods

Larvae collected in the field between May of 1998 and July of 2004 were reared in the laboratory from May of 1998 beyond December of 2005. Several of the early attempts were unsuccessful. Larvae placed in the same large container quickly disappeared (presumed from intraspecific predation). In three cases, larvae not ready for ecdysis climbed out of the aquaria and died from dehydration. At one point mid-project, I tried to devise a cooling system for the water. My modified drinking fountain chiller, even though set at the warmest possible setting and buffered with an extra 200-liter (50-gallon) chamber, had temperature swings that were highly erratic and proved lethal. Field studies showed that while streamlets used by larvae were spring fed, they were shallow and water temperatures were quickly modified by the ambient temperatures (excepting that they rarely if ever froze in winter). Non-systematic temperature measures of field streamlets taken 18 times between early April and early October showed water temperatures ranging between 6.7°C and 18.9°C (44°F and 66°F), with highest temperatures as expected in July (Table 2).

After my earlier experiments with refrigerated water, I therefore allowed my rearing aquaria to be maintained at room temperature from April or May through early November. From November through March, I kept larvae at about 7°–9°C (45°–48°F) inside a refrigerator to mimic winter dormancy. Pfuhl (1994) found that larval development of *C. boltoni* is interrupted and a semi-dormant stage entered when water temperature dropped below 7°C (44.6°F). The relatively constant temperatures I eventually adopted in my lab appeared to work well in regards to both larval longevity and numbers of successful molts. Water for the aquaria was obtained from several different wells or streams within larval habitat areas to maintain consistent dissolved mineral contents.

After my first attempt ended with apparent predation, I built aquaria with Plexiglas dividers into which I cut openings covered with fiberglass window screening (Figure 2). This also enabled me to track individual larvae as they grew and molted. A recirculating pump extracted water from one end, and pumped it into another end, creating a constant flow

Table 2. Water temperature and pH variation for Northwest Seep, Crane Hollow, with additional data from other sites at Crane Hollow and Chestnut Ridge. Temperature was recorded in field in degrees Fahrenheit and converted for the table.

Date	Site	Water Temp (°F/°C)	pH
27 Jul 2001	Northwest Seep	66/18.9	6.3
15 Oct 2001	Northwest Seep	53/11.7	7.6
11 Apr 2002	Northwest Seep	56/13.3	5.6
24 May 2002	Northwest Seep	50/10.0	6.6
22 Jul 2002	Northwest Seep	66/18.9	6.1
17 Sep 2002	Northwest Seep	59/15.0	5.9
14 May 2003	Northwest Seep	52/11.1	5.6
30 May 2003	Northwest Seep	54/12.2	6.1
15 Jul 2003	Northwest Seep	59/15.0	5.7
23 Sept 2003	Northwest Seep	58/14.4	6.4
19 May 2001	Silex, C.H.	54/12.2	6.2
27 Jul 2001	Silex, C.H.	62/16.7	6.8
11 Apr 2002	Silex, C.H.	45/7.2	5.4
19 May 2001	Sub-Silex, C.H.	57/13.8	5.6
27 Jul 2001	Sub-Silex, C.H.	64/17.8	5.8
11 Apr 2002	Sub-Silex, C.H.	44/6.7	4.7
5 Jun 2001	Chestnut Ridge	56/13.3	7.6
19 Apr 2002	Chestnut Ridge	57/13.3	7.2

through the chambers and somewhat simulating the lotic environment. Initially I used a 38-liter (10-gallon) aquarium and as I expanded my work, I used a 190-liter (50-gallon) aquarium divided into 16 chambers. In each case, they were filled only about $\frac{1}{3}$ of depth capacity. Each chamber contained a very thin layer of sand taken from occupied field habitats to allow limited burrowing stimulus, but not so deep as to conceal the larvae.

In a separate aquarium I reared *Chironomus riparius* (Diptera: Chironomidae) and supplied a minimum of five of

these larvae to each *Cordulegaster* larva three times each week. *Cordulegaster* larvae in instars F2 and earlier consumed these eagerly. Larvae at F1 seemed somewhat less ravenous, and although they apparently continued to eat, they never did so while I watched. Working under the assumption that larger larvae (especially with the impressive looking labium these animals have) might require larger food, I tried a wide variety of other aquatic invertebrates, earthworms, and even small toad tadpoles—with no apparent acceptance by the F0 larvae. I did succeed in getting one F0 larvae to consume a small *Anax junius* larva.

While my earliest aquaria lost larvae (presumed from predation), I never had F0 larvae eat larvae of F2 size or earlier when I combined them in an attempt to find appropriate food for larger larvae. The F0 larvae probably consumed chironomid larvae overnight, but since the chironomids could move through the window screening, I could never be certain. The fact that I maintained at least six F0 larvae for periods between 330 days to 518 days (see Table 3) suggests either this stage

does not require much food, or they were eating chironomids that I did not observe. To test this after most of my rearing was completed; I repeatedly fed ten chironomid larvae to a single F0 larva in isolation in a watchglass, kept covered and dark for one to two hours. Typically during that time four to six of the chironomids were consumed.

Between 1998 and 2005, I attempted to rear 74 larvae of *C. erronea* in aquaria in the laboratory. Forty-eight of these died either very quickly or without any molts (see rearing discussion above) and were not used in my data analysis of instar

sizes and longevity. Five others were eliminated from analysis for various reasons—mostly due to unclear dates of molts or other operational complications. Twenty-one larvae were successfully reared for extended periods with multiple molts (Tables 3 and 4). These 21 larvae actually represent 87 total instars, or an average of 4.1 instars per individual larvae. Two larvae survived through seven molts or parts of eight instars while in captivity.

Measurements of reared larvae were made at regular intervals, and always within a day after any molt. Measure-

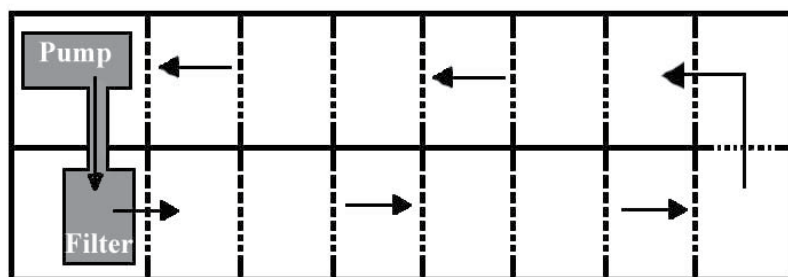


Figure 2. Rearing aquarium layout, overhead view. A fifty-gallon aquarium: length 92 cm, width 32 cm. Each of 14 rearing chambers measures roughly 10 cm × 15 cm and were created with Plexiglas dividers, broken in the centers with a screened opening to allow flow of water. Water depth in each chamber maintained at roughly 6 to 10 cm. The recirculating pump capacity is 1000 liters/hour.

ments included maximum head width (HW), total body length (L) and rear wing sheath length (WS) after Ferreras-Romero & Corbet (1999) (see Figure 3). Measurements were made under a low-power dissecting scope, and estimated to the nearest tenth of a millimeter.

Within the 21 instars used to assign age classes, not all successfully completed ecdysis from F0 to the adult. Several died after lengthy periods while still in the F0 larval stage, and several more died during ecdysis or from falling back into the water during ecdysis. The author is uncertain if failure in ecdysis was due to some weakness in the environment and food given to the larvae, or if it merely reflects high larval mortality.

Since one of the main objectives of laboratory rearing was to establish parameters of size ranges for larval instars, it was important to establish accurately which instars I was rearing. Since I started with field-collected larvae of unknown instar size, this could be assured by rearing them to a F1 or F0 instar and then counting backwards through all the earlier instars while in captivity. The stage of a larvae at F1 or F0 could be clearly established by a combination of head width and wing sheath length. Since with earlier instars there can be some overlap, this was an important criteria in assigning age classes (instars). Hence, I had a high assurance that the size ranges of instars in Table 4 and 5 represents accurate ranges for the instars they represent and yields the summary of instar sizes listed in Table 6. These size ranges and the instars they represent (Table 6) were then applied to larvae counted and measured in the field portion of this study.

Results

The 21 larvae used in my age class analysis survived quite long periods in the laboratory. Their lab longevity ranged from 105 to 622 days, with an average of 382.1 days. During this period they molted an average of 3.19 times (representing 4.14 instars), with a range of from one to seven molts, representing two to eight instars. Two larvae survived 621 days from F3 or F4 to the F0 instar or ecdysis. Tables 3 through 5 and Table 7 show summary data for these 21 larvae.

Using the measurements from the 21 larvae provides very clear size class distinctions for instars of *C. erronea* at F0, F1, and F2 and slightly less distinct size classes for F3 and F4 (see Table 5 and 6). Head width is the most reliable single character. The length of the rear wing sheath is useful for F2 through F0. Larvae in F3 generally had very little or no visible wing sheaths, however four larvae of 13 at this instar had visible wing pads that measured from 1.0 to 1.5 mm. Total length is generally useful only for a rough estimate of size class, as individual larvae can stretch or compress their abdomen, resulting in multiple total length measurements

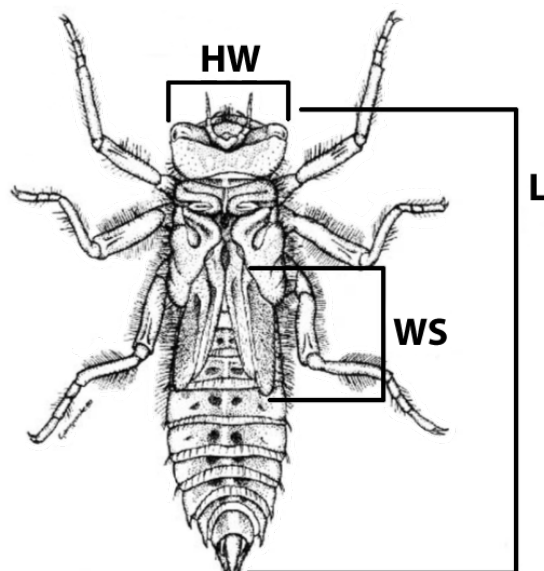


Figure 3. Measurements for *Cordulegaster* larvae. Illustration of *C. boltonii* with measurement guidelines from Ferreras-Romero (1999). HW = Maximum head width at eyes. L = Total body length. WS = Length of rear wing sheath.

on the same larva on the same day (see Figure 5). Despite the problems with total length measurements, most larvae in the instars F3 and F4 can be distinguished using a combination of measurements of head width and body length. I have not been able to determine confidently instar size classes earlier than F4 from my data. However, data for instars F7 through F5 in the Table 5 are based upon larvae that were reared to later instars that could be confidently determined by size.

D. LARVAL LIFE CYCLE—FIELD STUDIES

Methods

Field studies of larvae were all made at Crane Hollow Nature Preserve, in Laurel and Benton Townships, Hocking County, Ohio and centered at roughly N 39.474° and W 82.576°. This is a 607-hectare (1500-acre) preserve centered on Crane Hollow that extends somewhat SSE for 4.3 kilometers (2.7 miles) and has six named side hollows plus about 18 smaller side hollows. Elevation varies from 230 meters (760 feet) at the mouth of the hollow to about 333 meters (1100 feet) in some of the highlands. The area has numerous cliffs and waterfalls, with half a dozen waterfalls higher than 15 meters (50 feet), and the highest waterfall at 34 meters (112 feet). The bedrock is Mississippian sandstone composed of several types, of which Black Hand Sandstone is the most massive and best known. The preserve is almost entirely forested and lies within the mixed mesophytic region, with ten recognized plant communities, the most notable of which for this study is the hemlock gorges.

Table 3. Survival of individual reared larvae

Lab Number	Sex	Total Instars	Instar Range	Days in Each Instar							Total Days	Comments
				F7	F6	F5	F4	F3	F2	F1	F0	
7	M	3	F2 – F0						C 7+	45	53 D	*F0
8	M	2	F1 – F0							C 45+	W 281 D	
11	F	2	F1 – F0							C 25+	W 252 D	
12	F	2	F2 – F1						C 45+	121 W	*	Died w/labium extended & rigid
13	F	4	F3 – F0					C 47+	9	50	W 219 D	
14	M	4	F4 – F1				C 22+	38	23	53		
31	M	8	F7 – F0	C 18+	42	11	28	130 W	37	73	50 D	*F0
50	F	4	F3 – F0					C 29+	29	47	W 272 D/E	Died partly emerged
54	M	5	F4 – F0				C 42+	28	11	42	W 225	
55	F	5	F4 – F0			C in molt	42	27	40	UC	Dead in Molt	Dead in refrigerator unknown date
56	F	4	F3 – F0					C 23+	39	190 W	W 350 D	Near emergence
57	M	3	F2 – F0						C 31+	45	W 2 518	
58	M	4	F3 – F0					C 28+	34	207 W	W 2 335	
59	M	3	F2 – F0						C 11+	42	W 219	
62	F	5	F4 – F0				C 12+	54	168 W	32	W 2 353	
63	F	4	F3 – F0					C 47+	159 W	12	W 2 403 D	Near emergence
65	M	8	F7 – F0	C 12+	[40]		156 W	67	43	39	W 2 264	
66	F	7	F6 – F0		C 36+	W[172]		27	24	33	W 2 330	
71	M	4	F4 – F1				C 23+	43	56	Dead = W UC		Dead in refrigerator unknown date
73	F	3	F2 – F0						C 51+	50	W 197	
74	M	3	F3 – F1					C 79+	44	UC		Dead in refrigerator unknown date

C: Collected in this instar; not used for average instar length; **D:** Dead at or before molt; **W:** Overwinter during this instar; **UC:** Underterminable time of death; ***F_i**: Deleted from Table 4 for this instar due to death early in instar.

Two combined instar cells = intermediate molt date unknown; number in brackets = total span in these two instars

Total time reared in lab (n = 21) Range = 105 – 622 days, Average = 382.1 days. Average number of instars = 4.14.

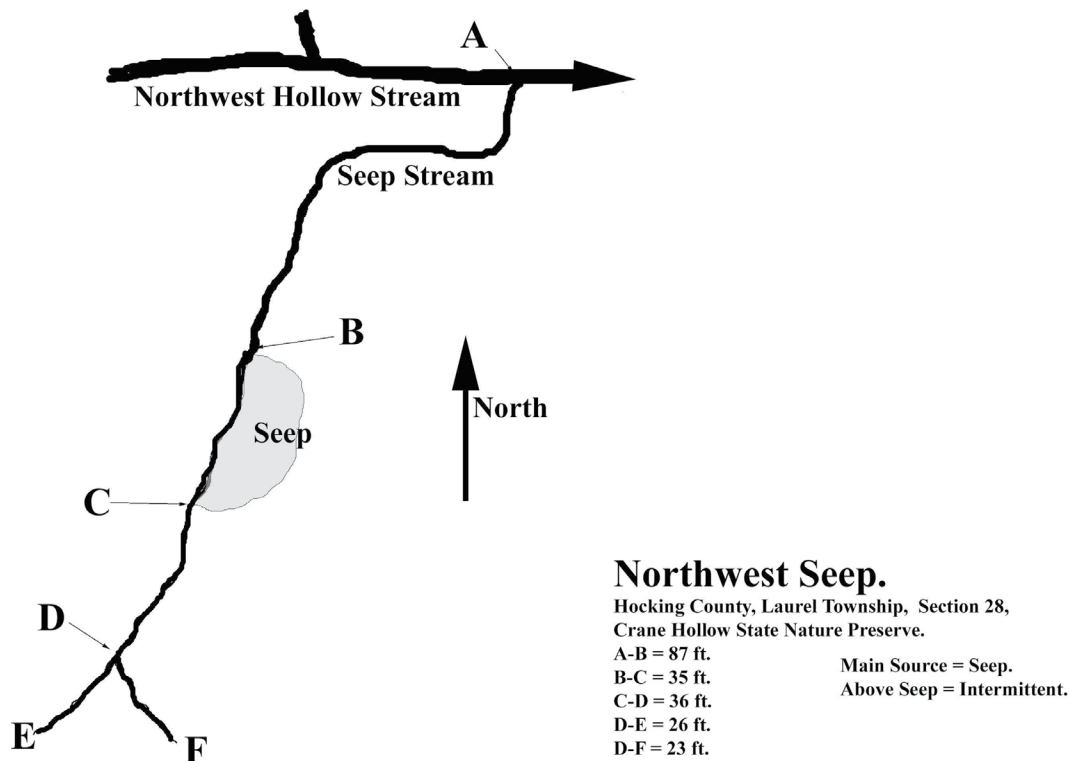


Figure 4. Map of Northwest Seep at Crane Hollow Nature Preserve.

Larval fieldwork involved making twelve trips between May of 2001 through September of 2003 (ten trips to Northwest Seep). While other duties prevented me from making trips every month of the year, as did Ferreras-Romero & Corbet (1999), trips were scheduled to cover key time periods: spring (well before ecdysis), mid-summer; and fall (after the adult flight season). In all, 550 larvae were temporarily collected, measured in the field, and returned to the streamlet or seep from which they were taken. Of the 550 larvae, only 435 will be used in my analysis, as the other 117 larvae came from three different seeps or streams. The 435 larvae were all from the location I refer to as Northwest Seep in Crane Hollow (Figure 4). The distribution was 162 larvae measured during spring; 134 larvae measured during summer; and 139 larvae measured during fall (Table 8). Measurements included maximum head width (HW), total body length (L), and, in later instars, the length of the rear wing sheath (Figure 3). Measurements in the field were made with a 3.5× magnifier mounted on a headband (to allow use of both hands) and a millimeter ruler, estimating measurements to the nearest tenth millimeter.

My prime research site, Northwest Seep, actually consists of both a seep proper and the headwater stream that drains the seep (Figure 4). Most of my larval sampling took place within the stream due to difficulty of finding larvae within the thick muck of the seep. The water surface of the North-

west Seep stream is generally 20 to 50 cm below the general land level, and 15 to 30 cm wide and generally no more than 2 to 6 cm deep. The seep proper is a semicircular area of about 40 square meters and the headwater stream travels only 26.5 meters (87 feet) below the seep before entering one of the major side channels of Crane Hollow.

Samples of substrate sand and muck were grasped by hand and dumped into a modified polypropylene box, which had the bottom replaced with aluminum window screening having a mesh size of 0.7 mm. This rectangular sieve would fit into the stream channel, so it could be agitated in the water to remove silt and sand. Larvae were then removed from the sieve and stored in individually divided containers until measurement, after which they were returned to the stream.

On each trip, water temperature and pH were recorded. Temperature was measured with a standard field thermometer, manufactured by Taylor, USA. A "Waterproof pHTestr 2" from Oakton Instruments was used to measure pH and calibrated before each field trip. Temperature and pH recordings are shown in Table 2.

Results

Water temperatures and pH at Northwest Seep were relatively consistent. On dates between early April and mid-

Table 4. Instar longevity from 21 reared larvae of *Cordulegaster erronea*.

Instar	N	Days in Instar/Range	Average Days
F0 (W)	14	197–518	301
F1 (S)	13	12–73	43.3
F1 (W)	3	121–207	172.7
F2 (S)	12	9–56	32.4
F2 (W)	2	159–168	163.5
F3 (S)	7	27–67	40.6
F3 (W)	1	130	[130]
F4 (S)	2	28–42	35
F4 (W)	1	156	156
F5	1	11	[11]
F6	1	42	[42]
F7	*2	*13+–18+	—

S: Completed instar within a single activity season.

W: Instar period included a winter dormancy.

Ad: Completed or began ecdysis to adult before death

***:** Both larvae collected at this instar, total length unknown.

Figure shown is minimum.

October, (see Table 2) temperatures ranged from 11°–19°C (52°–66°F). In spring, water temperature averaged 11.6°C (53°F). In summer, it averaged 17.8°C (64°F), and in fall, it averaged 13.8°C (57°F). Variation in pH ranged from an average in spring of 6.0, in summer 6.0, and in fall 6.6. While no formal attempt was made to correlate these variations with ambient weather, anecdotal observations suggest that most swings beyond the averages were related to unusual rainfall events such as recent heavy rains or

extended drought. Pfuhl (1994) reported that larvae enter winter dormancy at water temperatures below 7°C (44.6°F). Based upon that temperature, larvae in streams I studied were probably active and growing from early to mid-April until mid- to late October.

Of 550 larvae measured in the field at various sites, 92% readily fit the criteria developed from laboratory rearing (Table 6) and could confidently be placed into specific instars. Of the remainder, 1.3% (n = 7) fell into the overlaps between F4/F3 and F3/F2. Another 6.5% (n = 36) appeared to fit according to head width, but had a body length that was either too short (n = 3) or too long (n = 33) based upon the lab measurement criteria. The overlapping specimens were assigned instars based upon combining all measurements, and those whose total body length did not fit the criteria were assigned instars based solely upon head width.

Distribution of size classes shows some interesting data. I recognized ten size classes. The smallest five size classes were based upon head width using arbitrary size ranges, with no knowledge of what instar they represented. The largest five instars (F4–F0) were based upon the lab criteria. The curve for total specimens (Figure 6) very roughly represents a bell curve, with peaks at class 4 (HW = 2.0–2.4 mm) and class 6 (F4). The three curves of combined specimens for each season (spring, summer, fall) each has their own unique characteristics. Spring individual numbers peak at class 6 (F4 = 28.4%), summer at class 4 (HW = 2.0–2.4 mm; 17.9%), and fall individuals peak at class 3 (HW = 1.5–1.9 mm; 27.3%). Hence, fall numbers peak at smaller age/size classes than either spring or summer.

Table 5. Analysis of instar sizes from 21 reared larvae of *Cordulegaster erronea*.

Instar*	N	HW Range	HW Av.	TL Range	TL Av.	WS Range	WS Av.	# ♂	# ♀	Comment
F0	18	7.2–8.5	7.79	28.0–39	30.79	7.9–9.6	8.64	6	8	All included winter dormancy. 8 = ecdysis completed.
F1	18	5.8–6.8	6.22	21–32	24.58	3.5–5.2	4.2	8	8	1 season instar = 11/instar includes winter = 2
F2	19	4.5–5.7	5.09	16.9–24.0	20.07	1.0–2.3	1.83	8	8	
F3	13	3.6–4.5	4.12	14.3–19.1	16.22	1.0–1.5	1.18	5	6	Perhaps 11–22 days.
F4	7	3.0–3.8	3.29	10.1–14.5	12.62	—	—	2	3	
F5	4	2.3–3.0	2.6	9.0–12.2	10.63	—	—	1	2	
F6	3	1.9–2.4	2.1	7.3–10.2	8.4	—	—	?	?	Both field collected as F7.
F7	2	1.7–2.0	—	6.5–9.0	—	—	—	?	?	

* Instar number determined only after rearing to at least F1 or F0 stage.

N = number of individuals reared in this class. **HW** = Maximum head width measured in mm at compound eye.

TL = Total body length in mm. **WS** = Rear wing sheath in mm. See Figure 2.

Table 6. Identification of instar classes for larval *Cordulegaster erronea*. Based upon 21 reared individuals, 15 reared to F0 or adult.

Instar	Head Width	Length	Rear Wing Sheath
F0	7.2–8.5	28.0–39	7.9–9.6
F1	5.8–6.8	21–32	3.5–5.2
F2	4.5–5.7	16.9–24.0	1.0–2.3
F3	3.6–4.5	14.3–19.1	0 (1.0–1.5)
F4	3.0–3.8	10.1–14.5	—
<F4	≤3.0	<10.0 (12.2)	—

E. SUMMARY AND DISCUSSION

Habitat Utilization

C. erronea in Ohio utilize small, headwater streams with persistent flow and good forest cover. The stretches of streams used by larvae are upstream of fish-inhabited areas, suggesting they do not compete efficiently with predatory fish. The substrate is typically sandy, or sandy with some pebbles, or (significantly less frequent) sand-silt-muck. Barlow (1995) found siltation detrimental to survival of larvae of *C. erronea*. Streams utilized are often in steep-sided ravines where tree falls or rock falls block part of the area above the water surface. In some cases, mucky seeps (known as “Turkey Seeps” in Pennsylvania, Clark Shiffer pers. comm.), provided habitat for larvae and ovipositing females. Habitats with mostly intermittent streams, or without forest shade, were never found to be occupied by larvae of *C. erronea*.

Adult Behavior

The flight season for *C. erronea* in Ohio is from 1 June to 3 September. In New Jersey, it is listed as 20 June to 7 August (May and Carle, 1996) and 10 July to 17 August (Barlow, 1995). In Alabama, the flight season is recorded as 8 June to 4 September (Tennesen et al., 1995) and in Connecticut from 8–20 June (Wagner, 1999). Since *C. erronea* has been poorly known in most states, it is expected that the dates would be extended as more work is done in each of these states. Even in Ohio the flight season may well extend both earlier and later than recorded at present. I am aware of a single observation (unconfirmed by specimen or photograph but by a reliable field biologist) of an adult at Cantwell Cliffs in Hocking County, Ohio on 11 September 2005 (Jim McCormac, personal communication).

An individual *C. erronea* may survive as an adult for up to 34 days, based upon lim-

ited records of mark/recapture data (Glötzhofer & Riggs, 1998). Males patrol low over streamlets with regular flight for 3 to 5 meters, interrupted by a hovering pause for 1 to 3 seconds before continuing the flight and repeating this pattern. Patrolling male flights were slightly more frequently upstream (62.8%) than downstream (37.2%). Upstream flights sometimes involved an immediate turn around at the head of the stream, followed by a downstream patrol.

Based upon this study, it is unclear if foraging takes place in woodland openings, within or above the canopy, or a combination of those and/or other areas.

In good habitat and with optimum weather during the flight season, an observer posted along a streamlet should be able to observe one or more patrolling males within a 30 to 60 minute period. Such observation-bouts would be best between 10:00 ^{am} and 4:00 ^{pm} (Glötzhofer & Riggs, 1998).

Ovipositing females have been observed 16 times between 18 June and 2 August, with vertical thrusts into the substrate below shallow water averaging 120 times, with a maximum of 370 thrusts in one incident. It is not known how many eggs might be delivered per thrust.

Larval Life Cycle

From rearing studies in the lab, I was able to set criteria for placing larvae in their last five instars with a 92% confidence (Table 6). Although there was significant overlap in earlier instars, I did rear individuals from as early as F7 (Table 5).

I have split the groupings in Table 4 for instars F4 through F1: those that passed entirely through the instar within a single season and those who spent part of the instar in a winter dormancy. Clearly, larvae of *C. erronea* can enter winter dormancy at any one of these instars (and perhaps earlier instars as well). Since longevity for any three of these instars without

Table 7. Reared larvae that spent two winter dormancy periods between F7 and F0. F0+ = died while preparing to emerge but did not emerge; Ecd = Either completed ecdysis to adult, or died in ecdysis.

Lab #	Initial F	Ending F	1st Winter	2nd Winter	Total Days Reared
56	F3	F0+	F1	F0	602
57	F2	F0+	F0	F0	594
58	F3	F0+	F1	F0	604
62	F4	Ecd	F2	F0	619
63	F3	F0	F2	F0	621
65	F7	Ecd	F4	F0	621
66	F6	Ecd	F4	F0	622

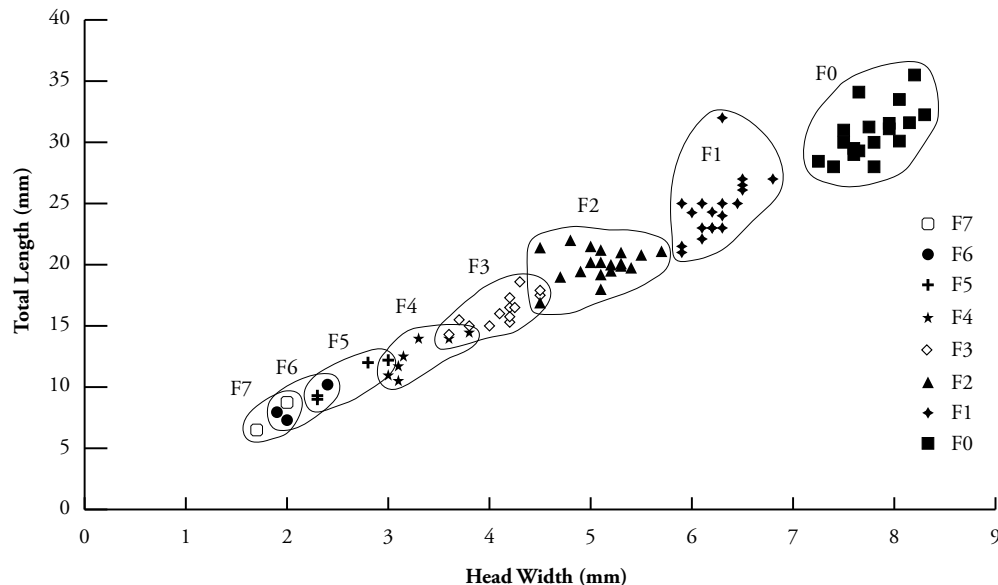


Figure 5. Size distribution of reared larvae of known instar, comparing head width against total body length.

dormancy could be completed within a single warm season period, most larvae could pass through instars F4 through F1 with only a single winter dormancy. However, seven reared larvae spent two winter dormancy periods between F4 and F0 (Table 7). This indicates that larval development during these instars is flexible and can be lengthened in some individuals. The lengthening may result under conditions of environmental stress, or as an adaptation to split cohorts (Ferrerias-Romero & Corbet, 1999). Larvae from eggs laid during the same year may therefore emerge in two different years. Ferreras-Romero & Corbet (1999) suggest that such a strategy enables long-lived species of odonates to intermix their genetics over multiple years, rather than producing single genotype year groups. In such a way, sudden environmental stress in a single year is impacted on the widest possible genetic mix and no single year's production becomes genetically stagnant.

A study of Tables 3 and 4 offers some initial insight into the length of the larval period for *C. erronea* under laboratory conditions. While individual longevity ranged from 105 to 622 days, only one individual was reared for the entire last seven instars. Even so, individuals reared for 619 days or longer ($n = 4$) clearly indicate a minimum of a two-year larval period—not counting earlier instars before F7. Corbet (1999, p. 208) indicates a range from 9 to 17 instars for Odonata in general, with 12 instars being both a median and mode. Robert (1958, reported in Verschuren 1991) estimated the number of instars for *C. boltoni* at 12. Pfuhl (1994) reports 13 instars for *C. boltoni*, not counting the prolarva. Verschuren (1991) reported 14 instars for *C. insignis* from Greece and Bulgaria, not counting the prolarva. Verschuren adds that larvae retarded in early development could add molts

and require 15 or 16 instars before ecdysis. Schütte (1997) notes that metamorphosis appears to be size-dependant rather than instar-dependant, requiring additional instars if the size-requirement has not been met. Reduced food intake or colder than normal temperatures would slow growth within any instar.

Given the above references, we could reasonably expect *C. erronea* to have 12 to

14 instars. Schütte (1997) successfully reared 14 of 26 eggs of *C. boltoni* in southern France for 11 months in a protective cage within the natural environment. After the end of 11 months, eight were in their fifth instar, and only two had reached their ninth instar. At the seventh instar ($n = 2$) head width mean was 1.31 mm—substantially smaller than the minimum of 1.7 mm that I obtained for F7 larvae ($n = 2$). It is therefore reasonable to say that from hatching to F7 could be expected to take one year in *C. erronea*.

Schütte (1997) found a growth rate of 1.27 times per instar for the first nine instars and Pfuhl (1994) found a growth rate of 1.28 (body sizes multiplied 1.27 or 1.28 between each instar). If that rate held true in later instars, and for *C. erronea* (two assumptions) Schütte's 10th instar would be equivalent to my F7 size class. The ranges in Table 5 fit this growth rate from F7 through F2, although the averages gradually move into the higher size range of my table, and then exceed my measurements for *C. erronea* for F1 and F0 instars. That could be a result of approximations using small number of larvae, or it could reflect the fact that F0 larvae of *C. boltoni* are about 10% larger than those I obtained for *C. erronea* (Ferrerias-Romero & Corbet, 1999).

Using the above assumptions of 12 to 14 instars for *C. erronea* and a development period of one year from hatching to F7, we can make some estimations of the total larval period. Table 9 gives estimated egg-hatching dates and from that, estimated total larval time for 21 reared larvae. While some lab-reared larvae may have completed their larval period within two years (2 years, $n = 1$; 2–3 years, $n = 3$), it appears much more likely that 3 years is a norm ($n = 9$), with 4 years being common (3–4 years, $n = 8$; 4 years, $n = 1$). This devel-

Table 8. Larval development of *Cordulegaster erronea*. Instars sampled in field surveys at Northwest Hollow Seep, Crane Hollow Nature Preserve. Seasonal combination for three years.

		Total Spring	Total Summer	Total Fall
Instar	F0	1	2	1
	F1	1	1	7
	F2	7	12	11
	F3	34	21	12
	F4	46	29	28
Head Width	2.5–2.9	27	19	15
	2.0–2.4	29	30	17
	1.5–1.9	16	5	38
	1.0–1.4	1	13	10
	<1.0	0	2	0
	N	162	134	139

opment speed is very similar to those summarized in Table 10 for *C. boltoni* in Europe.

Egg Hatching

The smallest larvae I collected in the field were predominately found in July (Table 8 and Figure 6). Only two smaller than HW = <1.0 mm were collected—both in July. For HW of 1.0–1.4 mm only one was collected in spring, 13 in summer, and ten in the fall. Ferreras-Romero & Corbet (1999) work-

ing with *Cordulegaster boltoni* in Spain found their smallest larvae (<0.7 mm HW) collected in July to December and interpreted this as an indication that eggs hatched promptly after being laid. However, *C. boltoni* in Spain is an earlier species than *C. erronea* in Ohio. Flight dates reported for *C. boltoni* in Spain are 5 May to 8 August, while *C. erronea* in Ohio are 1 June to 3 September. Sixteen bouts of oviposition in *C. erronea* were observed between 18 June and 2 August.

Ferreras-Romero & Corbet (1999) suggested hatching time of 17 to 43 days for *C. boltoni* and Schütte (1997) listed hatching time from 24–43 days. Pfuhl (1994) reports a hatching time for *C. boltoni* at 57 days if at 15°C (59°F) and at 120 days if at 10°C (50°F). In the field, Pfuhl found hatching in the same year as oviposition, with most larvae overwintering as the second larval instar. If hatching time were similar for *C. erronea*, the smallest larvae would not be expected until at least 5 July to 14 August, with many not hatching until mid-August to late September. With my fall field dates varying from 17 September to 15 October, a greater number of the smallest larvae would be expected in the fall rather than in the summer.

Working with *Boyeria irene* (Aeshnidae), Ferreras-Romero (1997) found the smallest larvae in May and June, concluding that this confirms the eggs of that species overwinter. Schütte (1997) reared *Cordulegaster boltoni* from eggs and measured first instar as having head width of 0.40 mm and a growth between instars of 1.23 to 1.38 times per instar. Lar-

vae reached 0.85 mm in the fourth instar, at the earliest 77 days after ovipositing.

If *C. erronea* has similar sized early larvae, my sampling screen mesh size of 0.7 mm would not have captured larvae comparable in size to the first three instars reported by Schütte (1997). Hence, if eggs overwintered and hatched in mid-spring as the waters warmed, I would not have sampled them for at least 77 days—or not until July. Table 8 shows that my mid-summer sampling indeed had the greatest number of small larvae. By September, I found no larvae smaller than 1.0 mm, a slightly reduced number of larvae with HW = 1.0–1.4 mm, but a greatly increased number of larvae with HW of 1.5–1.9 mm (increased from 5 to 38). These patterns suggest eggs overwintering, hatching in mid-spring and progressing to a

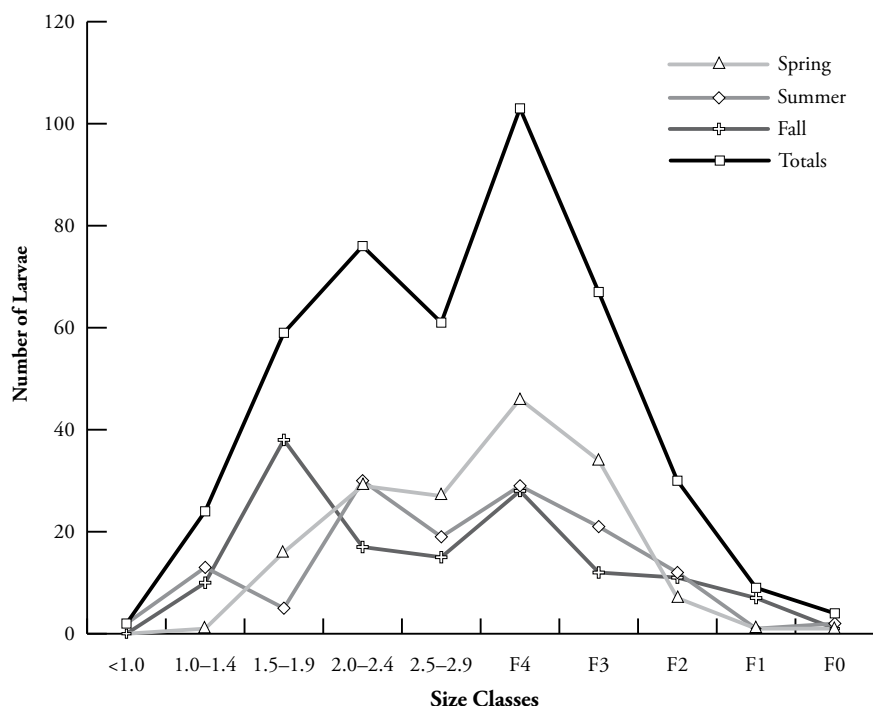


Figure 6. Numbers of larvae of *C. erronea* collected in the field. Chart based upon Table 9.

Table 9. Estimated total larva time period for selected reared larvae of *Cordulegaster erronea*.

Code #	Date Collected	Instar	# Molts	Total Days	End Date	End Instar	Sex	Days as F0	Est. Egg Hatching Date ¹	Estimated Total Years
07	20 May 1990	F2	2	103	31 Aug 1998	F0	♂	(53)	Aug 1996	2–3
08	20 May 1998	F1	1	331	16 Apr 1999	F0	?	280	Aug 1996	3
11	6 Aug 1998	F1	1	277	10 May 1999	F0	♀	(252)	Aug 1996	3
12	17 Aug 1998	F2	1	224	29 Mar 1999	F1	♀	—	Aug 1996	3–4
13	24 May 1999	F3	3	440	7 Aug 2000	F0	♀	327	Aug 1997	3
14	24 May 1999	F4	3	176	16 Nov 1999	F1	♂	—	Aug 1997	3–4
31 ²	21 Jul 2001	F7	7	(392)	23 Aug 2002	F0	?	(51)	Aug 2000	2–3
50	11 Apr 2002	F3	3	383	29 Apr 2003	F0	♀	272	Aug 2000	3
54	24 May 2002	F4	4 + E	347	6 May 2003	A	♂	225	Aug 2000	3
55 ²	24 May 2002	F5	5	(299)	(19 Mar 2003)	F0	♀	(78?)	Aug 2001	2–3
56	22 Jul 2002	F3	3	617	30 Mar 2004	F0	♀	206	Aug 2000	3–4
57	22 Jul 2002	F2	2	596	9 Mar 2004	F0	♂	518	Aug 2000	3–4
58	22 Jul 2002	F3	3 + E	604	17 Mar 2004	A	♂	335	Aug 2000	4
59	22 Jul 2002	F2	2 + E	289	7 May 2003	A	♂	219	Aug 2000	3
62	7 Aug 2003	F4	4 + E	620	18 Apr 2005	A	♀	354	Aug 2001/2002	3–4
63	7 Aug 2003	F3	3	620	18 Apr 2005	F0	♂	403	Aug 2001/2002	3–4
65	7 Aug 2003	F7	7 + E	621	19 Apr 2005	A	♂	264	Aug 2002	3
66	7 Aug 2003	F6	6 + E	620	18 Apr 2005	A	♀	328	Aug 2002	3
71	2 Jul 2004	F4	3	251	21 Mar 2005	F1	♂	—	Aug 2002	3–4
73	2 Jul 2004	F2	2 + E	276	26 Apr 2005	A	♀	197	Aug 2002	3
74	2 Jul 2004	F3	2	172	21 Feb 2005	F1	♂	—	Aug 2002	3–4

E = ecdysis to adult form. A = Adult.

¹ Based on 11 to 12 months from egg hatching to F7, and the time from F7 to collected instar using average length of instar time for a single season instar from Table 3. If a winter instar figure were added, some of the total estimated years could be expanded by one year. See discussion.

² Numbers 31 and 55 are not included in later summaries of longevity. Number 31 died unexpected early in F0. Number 55 died while in refrigeration to simulate winter dormancy, after having molted to F0.

F0 Summary: All except #7, #11, #12, #31 & #55 (died while still in F0), N = 13, Range = 197–518, Average = 302 days

Only those that went through ecdysis: N = 7, Range = 197–354, Average = 275 days

head width of 1.5–1.9 mm by early fall. If eggs overwinter, it would require the addition of one more year to the 3–4 year egg/larval period discussed earlier. My analysis of size classes (with limited numbers) as it relates to egg hatching is very tentative and somewhat debatable. No clear analysis of the timing of egg hatching can be made, and a direct study of egg development is required to confirm or refute the hypothesis I suggest above.

Field sampling of larvae supports the hypothesis of development time of larvae based upon rearing.

Both Table 8 and Figure 6 show a wide range of size classes at all seasons that were sampled, suggesting that the larvae

survive multiple years, or are semivoltine (Ferreras-Romero & Corbet, 1999). While no exuviae were found in the field, adult longevity of 34 days (Glötzhofer & Riggs, 1998) and the long flight season (Riggs in: Glötzhofer & McShaffrey, 2002) suggest that adult *C. erronea* have a protracted emergence period.

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Table 10. Published developmental periods of *Cordulegaster boltoni* in Europe and *C. dorsalis* in California.

Species	Country	Latitude	Larval Period in Years	Source
<i>C. boltoni</i>	Spain (southern)	N 38°	2–3	Ferreras-Romero/Corbet, 1999
<i>C. boltoni</i>	France (southern)	N 45°	2–3	Schütte, 1997
<i>C. boltoni</i>	Europe (mid-lat.)	N 50°	3–4	Robert, 1958 in Ferreras-Romero/Corbet, 1999
<i>C. boltoni</i>	Yugoslavia (uplands)	N 42–46°	4–5	Kiauta, 1964
<i>C. boltoni</i>	Switzerland (Alps)	N 45°	5+	Robert, 1958 in Ferreras-Romero/Corbet, 1999
<i>C. boltoni</i>	Germany (NE)	N 52°	4–5	Donath, 1987 in Ferreras-Romero/Corbet, 1999
<i>C. boltoni</i>	Germany, Lower Saxony	N 51° 30'	4–5	Pfuhl, 1994
<i>C. boltoni</i>	United Kingdom	N 54°	5+	Corbet, et al., 1960 in Ferreras-Romero/Corbet, 1999
<i>C. dorsalis</i>	California (mountains to 4,000 feet in south)	N 34–39°	4	Kennedy, 1917

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Preliminary Observations of Reproductive Behavior in *Arigomphus villosipes* (Selys) (Anisoptera: Gomphidae)

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Abstract

I studied the behavior of the *Arigomphus villosipes* (Unicorn Clubtail) at a small artificial pond in New York State from 6 June–8 July 2002. Throughout the day males adopted perch sites along the shoreline, typically 3 m or farther apart. Most of their time was spent perching, interrupted by brief patrols or chases of other males. Marking records showed that most males (79%) returned to the pond on one or more subsequent days. Individual males displayed only weak attachment to perch sites, often occupying two or more different areas along the shoreline over several hours on a given day. Female visits to the pond were brief and infrequent; pair formation occurred at the water, whereupon the pair left the pond to mate. Females oviposited by flying slowly over shallow water, dipping the abdomen once or twice at multiple sites; mate-guarding was never observed. Suggestions are given for future studies of this species.

Introduction

Detailed accounts of reproductive behavior are lacking for most North American gomphids (Gomphidae). Here I record preliminary observations on the *Arigomphus villosipes* (Unicorn Clubtail) as background for future work on this species. *A. villosipes* occurs at ponds and sluggish streams mainly in the northeastern United States, typically in habitats with muddy bottoms and scant submerged vegetation (Walker, 1958).

Methods

The study site was an artificial pond ca 78 m in circumference, 4 km east of Hamilton, Madison County, New York State. The pond was surrounded on all sides by open fields. Few floating or emergent plants were present, and the muddy, rocky shoreline supported sparse vegetation. Using markers, I divided the shoreline into 52 numbered contiguous areas, each 1.5 m long.

Data were collected during 49 h of observation from 7 June–8 July 2002, the main flight period. Most observations were made between 0930–1630, when *A. villosipes* was most active at the pond. I marked 33 males uniquely with enamel paint; females, rarely seen, were not marked. On three days I conducted 11–13 censuses at 30–60 min intervals, recording male density (total no. males at the pond), as well as the identity and location of marked individuals. On 21 other days, I made additional counts of males 2–10 times during observation periods. On three days, censuses were taken between 0645–0830, and on six days between 1700–1900.

I also conducted focal observations of 18 different males, each of which was observed continuously for 10 min to record behavior at perch sites. Also recorded during the study were data on female arrivals at the pond and any ensuing reproductive acts.

Results and Discussion

Male behavior

Males began arriving at the water in early morning. The earliest male was seen at 0655, performing wing-whirring while perched on the ground in the shade (temperature = 21.6°C). The number of males increased throughout the day and was highest from late morning to mid-afternoon (Fig. 1); the maximum density recorded was 20 males, on 18 June. On some warm days, males were present into the early evening; e.g., two males still occupied perch sites at 1910 on 1 July, when virtually all of the pond was shaded and the temperature was 28°C.

Males usually perched 3 m or farther apart on rocks, wet ground, or moss clumps within 15 cm of the water's edge.

Table 1. Data from focal observations of 18 different males at perch sites.

Activity	Mean	SD	Range
per cent time spent perching	98.0	0.95	97.2–100
number of patrols	0.4	0.86	0–3
number of chases of conspecific males	0.3	0.59	0–2
number of chases of other odonates	1.1	1.66	0–7
number of changes of perch site	0.5	0.86	0–3

Rarely, some males perched briefly on the stems of emergent vegetation, though such perch sites were scarce. Focal observations indicated that the vast majority of a male's time was spent perching (Table 1). This finding was confirmed by general field observations of male behavior at the pond.

Interspecific aggressive interactions involved chases of *Plathemis lydia* and *Ladona julia* males flying near the shoreline. I did not regularly record densities of *P. lydia* and *L. julia* during this study, but these odonates were less abundant at the pond than *A. villosipes* (typical male density for each = 1–5). However, males of both these species spent much time in flight, in contrast to *A. villosipes* males; this difference may account for the higher number of interspecific, as opposed to conspecific, chases I observed.

Chases of conspecific males were sometimes preceded by brief aerial circling, and once one male *A. villosipes* knocked another into the water. Occasionally conspecific interactions resulted in one male shifting to a different position along the shoreline or leaving the pond. However, perched males sometimes failed to react to other odonates flying within 1 m of them, and occasionally two male *A. villosipes* perched within 8–10 cm of each other with no apparent interaction (Fig. 2). Males ceased perching to make occasional patrols (Table 1), flying low over the water surface and within 1 m of the shoreline.

Most marked males (79%) returned to the pond on one or more subsequent days (= 3.8 days, SD = 2.7, range = 1–12). Over the course of a single day, individual males tended to shift to various locations along the shoreline, and might make several visits to the pond, interspersed with absences of 30 min or longer (Fig. 2). Some males, however, showed weak, transient attachments to particular locations. For example, of 13 marked males present on 18 June between 1000–1600, five were recorded perching in the same 3-m stretch of shoreline on two consecutive 30-min censuses (Fig. 2). On subsequent days, however, males showed little if any tendency to return to areas used previously; thus, a given male might perch in a variety of locations during his overall tenure at the water. Male no. 7, for example, was recorded at 26 of the 52 numbered sites along the shoreline during 41 censuses on 12 different days.

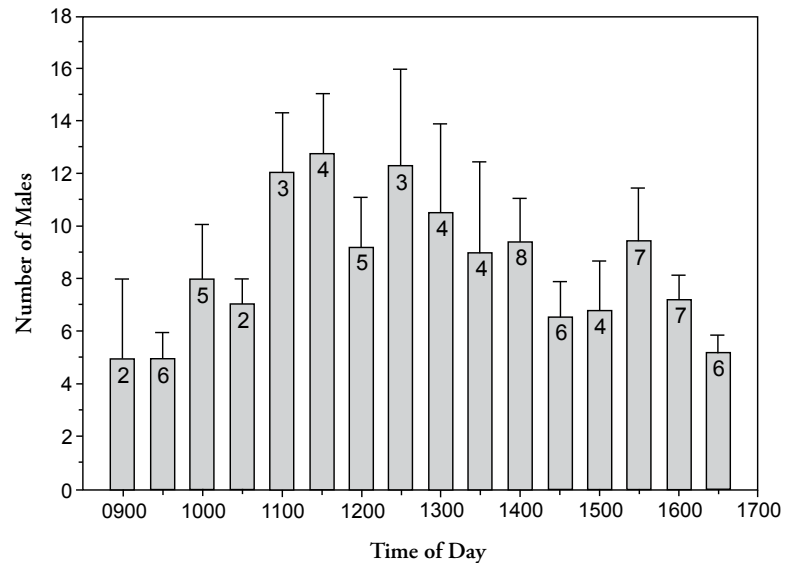


Figure 1. Number of male *A. villosipes* at the pond over the course of the day. Data are from a total of 76 censuses on seven days between 12 June–3 July; the number of censuses at each time is shown at the top of each bar. Plotted are means + SD.

Progressive shading of the pond was not a factor accounting for perch site selection during the main activity period, since the entire shoreline of the pond remained in full sun from early morning (approximately 0830) until late afternoon. By 1830–1900, virtually all of the pond was in full shade, at which time few males were present.

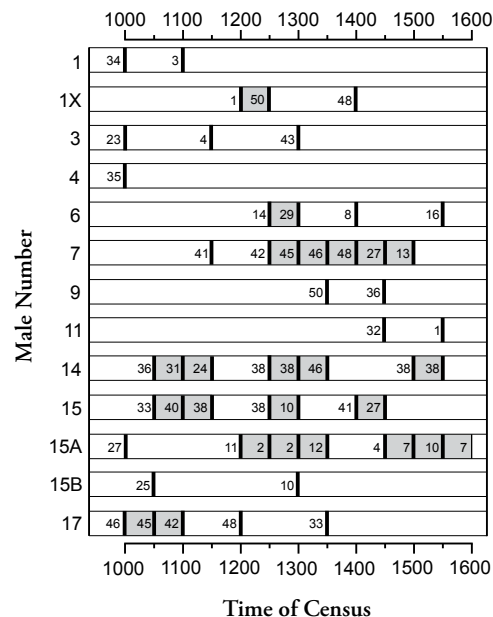


Figure 2. Data on marked males based on censuses at 30-minute intervals on 18 June 2002. The presence of a male at a particular time is indicated by a solid bar; bars are connected by shading if the male was present during two or more successive censuses. Numbers indicate the location of the male at one of 52 numbered areas around the shoreline. At 1230, male no. 14 and male no. 15 were perched 8–10 cm apart on adjacent rocks.

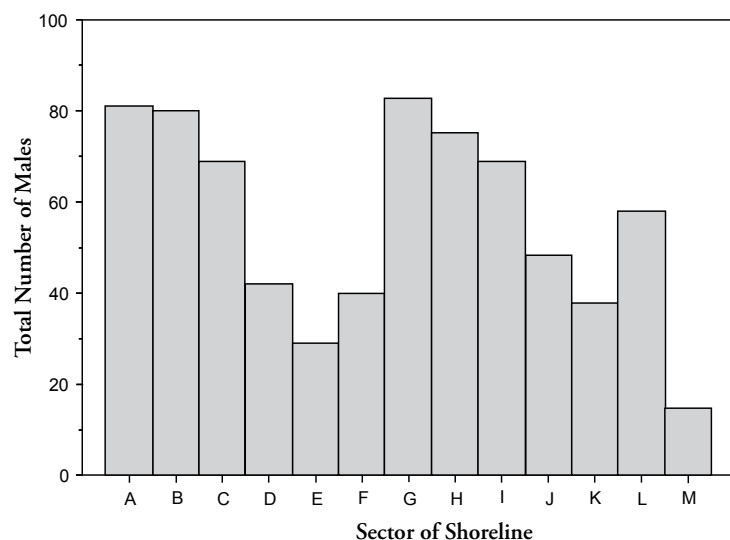


Figure 3. Number of males recorded in contiguous 6-m sectors of the shoreline. Data are from 82 censuses between 0930–1730, 12 June–18 July.

Censuses revealed that contiguous sectors of the shoreline differed with respect to the total number of male *A. villosipes* recorded in them (Fig. 3; $G = 116.6$, $df = 12$, $P < 0.001$). These differences may be related to habitat structure, since the six sectors having the fewest males either had emergent vegetation (*Phragmites*; sector M) or sprawling willow bushes (*Salix*; sectors D, E, F, J, K) growing close to the water's edge. These portions of the shoreline thus afforded fewer perch sites on the ground. When these sectors were removed from this analysis, the remaining sectors did not differ significantly in the total number of males ($G = 6.6$, $df = 6$, $P = 0.36$).

Aggressive behavior combined with some degree of site attachment has also been reported for *Onychogomphus uncatius* (Rehfeldt, 2004), and territoriality has been attributed to a few other gomphids, such as *Cacoides latro*, (Moore & Machado, 1992) and *Ictinogomphus ferox* (Miller, 1964). Moore and Machado (1992) note that territorial behavior, though rare in gomphids generally, appears to be associated with lacustrine rather than riverine habitats. In *A. villosipes*, agonistic interactions between males and site attachment, though relatively weak, serve to space out males at vantage points for intercepting females.

Pair Formation and Mating

Perched males adopted, in effect, a “sit-and-wait” strategy, flying out at and attempting to clasp females flying near their perch sites. However, female appearances at the pond were infrequent: I recorded only 16 reproductive events over the course of the study (Fig. 4).

I observed one incidence of successful pair formation: a male left his perch to clasp an ovipositing female, whereupon the tandem pair flew rapidly from the pond. Two other mating attempts (unmarked males, different dates) were unsuccessful (Fig. 4). I also recorded three pairs, already in the wheel position, flying rapidly into the surrounding field (Fig. 4). Details of copulation, which apparently occurred away from the water, could not be observed since pairs were quickly lost from sight. The possibility that some pair formation may have also occurred away from the water cannot be ruled out; in this study I did not monitor the field for reproductive behavior.

Oviposition

To oviposit, a female flew slowly over shallow water, dipping her abdomen once or twice at a series of sites within 2 m of the shore, moving 3–13 m or farther around the perimeter of the pond. I observed 13 ovipositions, all by lone females. Thus, *A. villosipes* appears to follow the common (though not universal; see Miller, 1964) gomphid pattern of unguarded oviposition.

Ovipositions occurred over the course of the day, though mostly in the afternoon, during the typical period of male residency at the pond (Fig. 4). It was not possible to obtain total oviposition durations, since all ovipositions I observed were already in progress. The longest of these lasted at least 2 min.

When approached by males, ovipositing females flew quickly from the pond. However, in most cases (10 out of 13), females completed egg-laying without male interference (Fig. 4). On two of these occasions, no males were present

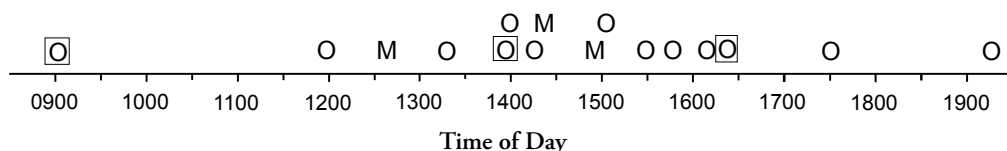


Figure 4. Times of the 16 reproductive events observed during the study. M = mating; O = Oviposition terminated by female; \square = oviposition terminated by male harassment.

at the pond; on eight occasions, male density at the water was 1–7, but females used sites where there were no males within 3 m. It remains to be seen whether females avoid moving into areas occupied by males; a more likely possibility is that, since males patrol so infrequently, some may not see or react to females at the water. Thus, perching for long periods, while energetically less expensive than patrolling, may carry the potential cost, for an individual male, of lost mating opportunities. From the female's perspective, infrequent patrolling by males may confer some protection from harassment during oviposition.

The mating system of *A. villosipes* appears to illustrate several features of the “postponed oviposition” type described by Corbet (1999), e.g., pair formation at oviposition areas, copulation away from the water, and unguarded oviposition by returning females. Detailed data are still lacking on the complete reproductive sequence in this species. Also needed are studies of other populations, particularly at higher densities, to clarify the possible effects of population density and/or habitat structure on male behavior at rendezvous sites.

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