EMERGENCE PATTERNS OF THE SUBALPINE DRAGONFLY *SOMATOCHLORA SEMICIRCULARIS* (ODONATA: CORDULIIDAE)

By Ruth L. Willey*
University of Illinois at Chicago Circle

Introduction

The genus *Somatochlora* is circumpolar and many of its species reach high into the subarctic and subalpine regions. *S. semicircularis* occurs in the Canadian and Hudsonian zones of the North American Western Cordillera from Alaska to Colorado. Towards the southern part of its range, this species is found at high altitudes in Colorado where adults have been recorded at 3000 to 3700 m (Gloyd, 1939; Walker, 1925; Carpenter, 1873). Larval habitats range from 2700 to 3600 m in shallow ponds and water meadows. These may well be the highest breeding localities for any odonate known.

The alpine and subalpine habitats offer extremes in temperature and insolation during the short growing season which follows the late snow melt (Mani, 1968). The subalpine regions, particularly, present relatively the highest day and lowest night temperatures (Billings and Mooney, 1968). Coupled with these factors, the frequent periods of drought and general unpredictability of climate contribute to the rigor of the high altitude habitat. Studies of life history strategies of insects which have adapted to high altitudes have revealed cold resistance and lowered temperature thresholds, a predominance of diurnal activity, a seasonal delay and shortening of the flight period, and a general increase in the length of the life cycle coupled with overwinter hibernation or diapause (Mani, 1968). In the dragonflies, the increased life cycle is accomplished by elongating the larval period to as much as three or four years (Paulson and Jenner, 1971; Robert, 1958). *Somatochlora semicircularis* larvae are also resistant to dessication when their ponds and water meadows dry up annually (Willey and Eiler, 1972). An ecologically sensitive part of the life history for a dragonfly is the emergence period during which the "aquatic" larva leaves the water, transforms into the

*Department of Biological Sciences, University of Illinois at Chicago Circle, Chicago, Illinois 60680; and The Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224.

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Figure 1. Pond Nine (3416 m) on Galena Mtn. in the Mexican Cut Research Area owned by The Nature Conservancy. 7 September 1970.

winged adult, and flies away as a reproductively immature (teneral) adult. The observations reported here are intended to correlate a late emergence season, a possible lowered temperature threshold, a complete shift to diurnal behavior, and an abbreviated, synchronized emergence period with the rigors of the high altitude habitat in Colorado.

Habitat

Two subalpine ponds were selected for study areas. They represent the typical habitat where larvae of *Somatochlora semicircularis* are found. The emergence areas of both ponds are restricted to the shallow, sedge-filled margins.

Pond Nine (3416 m) is one of a group of small ponds in the Mexican Cut Research Area on Galena Mountain (Gunnison Co., Colorado) owned by The Nature Conservancy and administered by the Rocky Mountain Biological Laboratory. It is 10 m in diameter and 1 m deep in the center. About 50% of its shoreline is lined with *Carex rostrata* and *C. aquatilis* in the shallow bays which make up the emergence areas for the dragonflies. The center of the pond is lined with *Isoetes bolanderi* on the bottom. The pond is surrounded by a belt of forb-sedge meadow which is surrounded by an open association of spruce-fir (*Picea engelmanni* and *Abies lasiocarpa*) (Fig. 1). In the past eleven years of observation, Pond Nine has never totally dried up.

Irwin Pond South (3141 m) lies near the edge of Lake Irwin (Lake Brennan) near Kebler Pass in Gunnison Co., Colorado. Its basin is 45 m in diameter, 1.2 m deep in June and dries up in late August and early September (observed 1968-1973). The shoreline and shallow areas where emergence takes place are lined with *C. rostrata* and *C. aquatilis*. The deeper areas support *Potamogeton foliosus* and *P. illinoisensis* and thin mats of *Drepanocladus uncinatus*. This pond has been described further by Willey and Eiler (1972).

Materials and Methods

The emergence of *Somatochlora semicircularis* was studied from 1968 to 1972. At first, the transforming larvae were marked by surveyor's flags so that the transformation of each individual could be accurately timed. Considerable trampling of the habitat was unavoidable so that the studies were repeated in 1971 by making daily collections of the cast skins left behind by the teneral adults. Fewer larvae were damaged during their transformation by this method. However, more larvae were lost through bird predation so that their cast skins could not be recorded. In order to verify the diurnal pattern of the teneral flight in an undisturbed habitat, continual observations by binoculars of the ponds were conducted from 100 feet away from the shoreline in 1972 during the peak of the emergence period.

Water temperatures were measured 3 cm below the water surface in areas of highest emergence activity. Solar radiation was measured by a recording Belfort pyrheliograph with a 12-hour gear. Environmental air temperatures were measured with a YSI telethermometer shielded from radiation by thin, flat, double-layered shields, 46 cm square, which were set horizontally 8 cm above and below the temperature probe. The inner surface of each was painted flat black and the outer surface was glossy white (Platt and Griffiths, 1964).

Observations

About one month after the ice leaves the ponds, the first larvae of *S. semicircularis* leave the water, undergo transformation, and fly

Table 1. The annual emergence periods for *S. semicircularis*

Location	Year	1st day of emergence	Total adults	Emergence Total days	Days until 50% emergence
Pond Nine	1968	15 July	543	14	3
	1969	7 July	166	15	3
Irwin Pond S.	1971	3 July	1528	21	6

away from the ponds as teneral adults (maiden flight). At Pond Nine, emergence began on 15 July 1968, 7 July 1969, and 6 July 1970. At Irwin Pond South, slightly lower in altitude and more sheltered by spruce-fir, emergence began slightly earlier — 30 June 1970, 3 July 1971, and 27 June 1972.

The total period during which emergence occurs each year is short (Table 1). The total annual production of adults occurs over an average of 16 days during which 50% of the adults emerge within the first three to six days. The 1969 emergence curve (Fig. 2) demonstrates a typical, highly synchronized pattern. The 1968 curve (Fig. 3) shows the effect of stormy weather and low temperatures on 17 and 18 July which delayed the emergence of some of the larvae and extended the emergence period. No secondary peak of emergence was ever observed later in either season.

The distance flown during the initial flight of the teneral adults is unknown. However, they remain away from the ponds, presumably in the forest near the ponds or at lower altitudes, for one to two weeks. In 1968, the first tenerals left Pond Nine on 15 July and the first mature males were observed patrolling the edges of the pond on 22 July — 7 days later. By this time, 95% of the adults had emerged and flown away (Fig. 3). In 1969, the first tenerals left on 7 July and the first patrolling male was sighted on 22 July — 2 days after the last teneral adult had flown (Fig. 2). These mature adults are individuals which emerged at the beginning of the emergence period, have matured, and returned to the pond for mating. Teneral adults and reproductively mature adults are considered here to be all part of the same emerging population. They are just temporally separated. On two occasions mature males were observed patrolling a pond when a newly emerged teneral flew up from the sedges on its maiden flight. On both occasions, the mature male harassed and tried to couple with the soft teneral before the latter could leave the pond. One of the tenerals was probably injured by

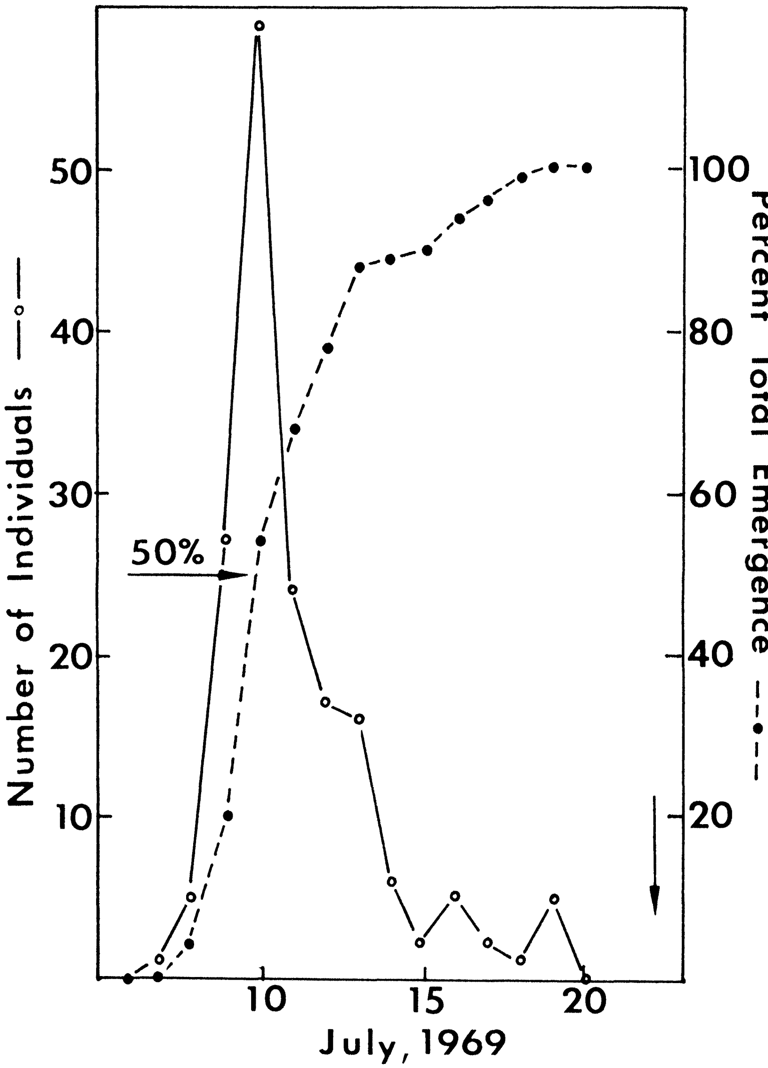

Figure 2. Seasonal emergence pattern of *S. semicircularis* at Pond Nine, 1969. Vertical arrow marks day on which first reproductive male was observed patrolling the pond.

the encounter because its subsequent flight was very erratic. The *Somatochlora* males are very aggressive and will try to grasp any other dragonfly — its own species, *Cordulia shurtleffi*,[1] or even the much larger *Aeschna interrupta*.

Water and air temperatures are relatively low in ponds at high altitudes although the diurnal water temperatures are not as low as might be expected due to the heat absorbing qualities of the pond bottoms and the shallowness of the water. The water temperature averages 12°C. (varies from 9° to 14°C.) when the larvae first emerge in the morning, whereas the air temperatures, which rise very rapidly once the sun is up, average 9°C. (vary from 4° to 12°C.). The night air temperatures drop below freezing and, on many mornings, frost still lay on the ground when the first larvae appeared. The larvae climb up the sedges in areas where the water is seldom more than 30 cm deep and usually 3 to 8 cm deep. The larvae start to leave the water after sunrise (0700 to 0800 MDT).

The maximum number of larvae leave the water between 0800 and 1100 hours (Fig. 4). By 1000 to 1700, they are ready to fly. In 1972, observations of undisturbed ponds indicate that 75% or more of the tenerals actually leave the ponds between 1100 tnd 1230 if the weather is fair and the air temperature varies between 16° and 18°C. The initiation of the flights appears to be temperature-dependent. On 1 July 1972, flights began at 1100 with an air temperature of 18°C. The flights stopped abruptly at 1230 when clouds covered the sun and the air temperature dropped to 14°C. Flights did not resume until 1430 when the sunshine returned and the air temperature rose to 16°C. All flights ended for the day at 1500 when a thunderstorm started and the air temperature dropped to 14°C. and below. Any adults which had not flown by this time had to remain on the sedges until the following morning.

Birds are the main predators of *Somatochlora* during the actual transformation process. Spiders and ants will attack larvae near the shore but generally account for a very small proportion of the loss. Specific data are being assembled for a separate report on bird predation and will not be presented here. However, a general summary is essential for the present argument. In general, bird predation does not begin until the second or third day of emergence. Under normal weather conditions, daily loss does not exceed 30 to 50% of the

[1]In the studies on drought resistance in *Somatochlora* larvae, Willey and Eiler (1972) misidentified *Cordulia shurtleffi* larvae for those of *Libellula quadrimaculata*.

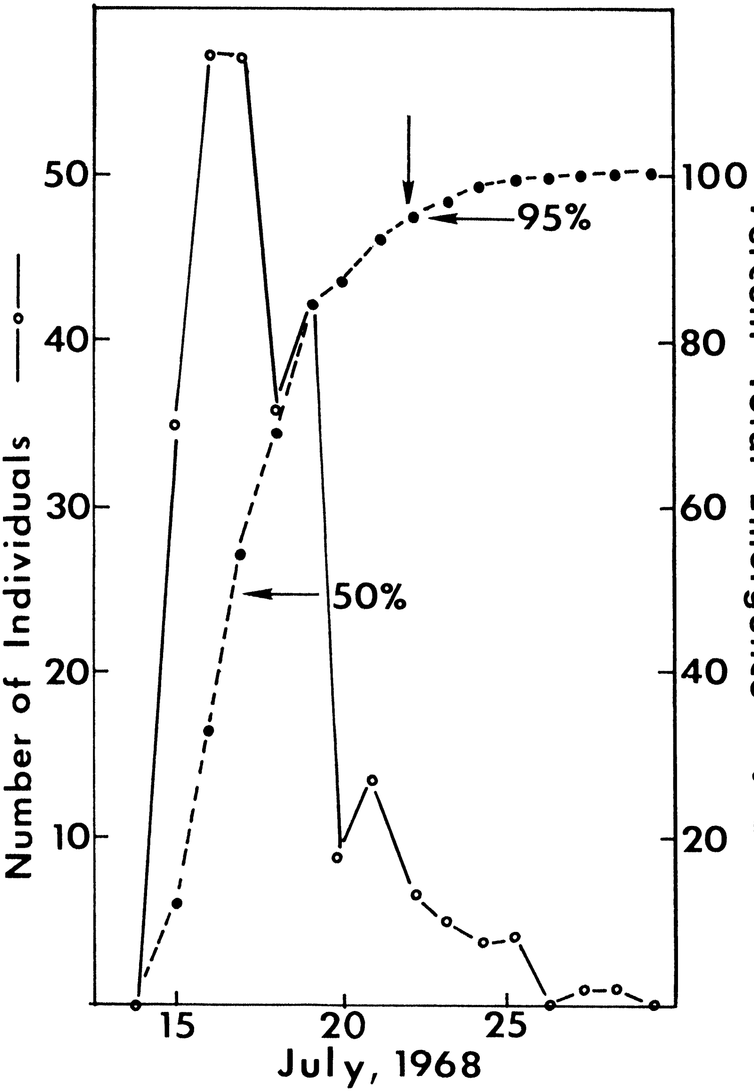

Figure 3. Seasonal emergence pattern of *S. semicircularis* at Pond Nine, 1968. Vertical arrow marks day on which first reproductive male was observed patrolling the pond.

dragonflies until the second week of emergence. On cold and stormy days, loss may approach 100% at any time during emergence. Adults which have transformed but have been prevented from flying by low temperatures or rainy weather may remain clinging to the sedges for a day or more. Most of these adults fall prey to birds. Once the tenerals fly, they are reasonably free from bird predation. Only one teneral has been observed to be caught by a bird (Western flycatcher) during its maiden flight.

Discussion

Somatochlora semicircularis is a western cordilleran dragonfly whose adults normally appear between the middle of June and the middle of July (Walker, 1925). The Colorado ponds under investigation occur at the southern limit of the species and yet the adults emerge in early July and appear as reproductives in mid-July near the end of the general emergence season. Such a relatively late season is probably correlated with the late snow melt and low temperatures of its high altitude habitat. Schiemenz (1952) has reported a similar delay of season correlated with altitude for *Libellula quadrimaculata.*

Dragonfly emergence has been shown to be temperature-dependent with the initiation of emergence primarily dependent on water temperature (Trottier, 1973; Corbet, 1963). The larvae of *S. semicircularis* in Colorado first leave the water when the water temperatures average 12°C. and the air temperatures average 9°C. Comparative data for other corduliid dragonflies are not available. The only data available come from the studies of the aeschnid dragonfly *Anax*. Corbet (1957) found that *A. imperator* in England normally left the water when the temperature reached 19° to 22°C. (air temperature, 12° to 15°C.). Trottier (1973) found that *A. junius* in Ontario, Canada, normally initiated emergence when the water temperature reached 24°C. (air temperature, 15° to 20°C.). At water temperatures below 17°C., the *Anax* larvae which had left the water would return to the water and delay emergence until the following day. The *Somatochlora* larvae were able to leave the water and undergo transformation at average temperatures 5°C. below the minimum for *Anax* larvae. Whether this difference is a specialization to high altitudes or is only a general family difference must be further investigated.

In general, teneral corduliid dragonflies at lower altitudes and/or latitudes are ready to fly early in the morning. However, the emer-

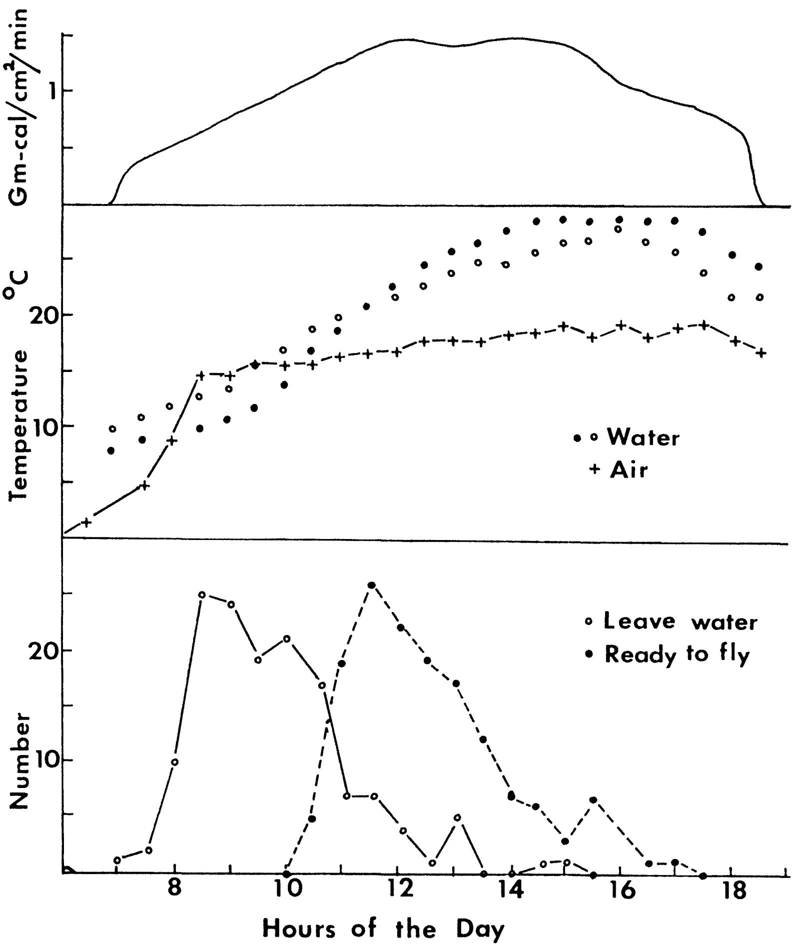

Figure 4. Daily emergence pattern of *S. semicircularis* on 2 July 1970 at Irwin Pond South. Lower curve shows the number of nymphs leaving the water (solid line) and transformed teneral adults ready to fly (dashed line) at successive hours during the day. Middle curve shows water temperature 3 cm below the surface at two separate stations, 1 m apart, and air temperature 45 cm above the surface of the water in the emergence area. Top curve shows solar radiation. Nymphs recorded here completed the entire transformation process successfully.

gence pattern is variable and freshly emerged adults have been collected throughout the day and even in early evening on cold, cloudy, or rainy days (Lutz and McMahan, 1973; Corbet, 1963; Lutz, 1961; Taketo, 1960; Kormondy, 1959; Robert, 1958; Lieftinck, 1932). The larvae of *S. semicircularis*, under normal conditions, do not leave the water until after sunrise and the tenerals generally fly at noon. A similar shift of the emergence pattern to the middle of the day has been described for *Aeschna interrupta* at high altitudes in California (Kennedy, 1925) and for *Aeschna subarctica* on the moors near Kiel, Germany (Schmidt, 1968).

The emergence curve of *Somatochlora* in Colorado is characterized by brevity (16 days) and a high degree of synchrony (Fig. 2, Table 1). Similar synchrony has been described for other dragonfly species which have been categorized by Corbet (1963) as "spring" species. Only one of these species, *Oplonaeschna armata,* exhibits a shorter time for the total period (10 days) and for the 50% emergence time (2 days). *Oplonaeschna* inhabits the water-pocket streams of New Mexico and Arizona and is subject to flash floods and severe dessication (Johnson, 1968). The lower altitude corduliid, *Tetragoneuria cynosura,* averages a 23-25 day emergence period with 50% of the adults emerging by the 6th or 7th day in Michigan (Kormondy, 1959) and North Carolina (Lutz and McMahan, 1973; Lutz, 1961 and 1962). *Tetragoneuria* in Michigan also exhibits a bimodal curve in which a second peak of emergence occurs 10 days after the end of the first peak. This bimodality has been described for other dragonfly species (see Corbet, 1963) but is missing in the *Somatochlora* curve (Figs. 2 and 3).

Selective pressures contributing to the synchrony of the single peak of the *Somatochlora* emergence curve may well involve the brevity of the season. Both in 1968 and 1969, 10 days after the end of the initial emergence peak at a time when *T. cynosura* (Kormondy, 1959) and *Anax imperator* (Corbet, 1957) normally exhibit a small second peak of emergence, the shallow areas at Irwin Pond South and Pond Nine had largely dried up. *Somatochlora* larvae leave the water by climbing up the emergent sedges. They do not crawl out on the land. Lack of emergence sites or competition for the few remaining sites can be expected to be a factor in selecting for a temporal shift toward early emergence.

Another contributing factor may involve intraspecific interference. The diurnal emergence pattern which is necessitated by the climatic character of the habitat creates problems which normally do not affect nocturnal or early morning emerging populations. Teneral adults which fly up during the middle of the day are subject to harassment and possible damage from the reproductive males. However, by the time the first *Somatochlora* reproductives return to the Colorado ponds, 95 to 100% of the annual production of tenerals have already left the pond (Figs. 2 and 3). The diurnally temporal separation of the reproductives and the nocturnal or early morning tenerals of the lower altitudes has been replaced by the seasonal separation of a 1 to 2 week teneral maturation period during which time the dragonflies fly in the forest away from the ponds while the remainder of the population is emerging. The high altitude ponds of Colorado seem to be sufficiently isolated from each other to keep recruitment of reproductives from lower, and therefore earlier, ponds to a minimum.

The diurnally transforming dragonflies are also exposed to predation by birds. The highly synchronized emergence of *Somatochlora,* however, provides that the relatively large number of larvae which emerge during the first few days ensure that many tenerals get away from the pond. To what extent a synchrony of emergence provides selective advantage to the dragonfly population by (1) partially forestalling the results of a revised predator searching image and/or shift in prey preference or (2) saturating the environment with prey with a resulting early satiation of the predators is as yet undetermined. It is likely that both predation tactics are involved and thwarted by this mechanism.

Summary

Somatochlora semicircularis has been able to adapt to the rigors of the subalpine and lower alpine habitats of Colorado. The corduliid tendency toward a flexible, early morning emergence pattern has contributed to its shift to a full diurnal emergence pattern. In addition, it may be able to initiate emergence at relatively low water and air temperatures. The emergence pattern has been strongly synchronized, shortened and restricted to a single seasonal peak, possibly as a result of ponds drying up early in the season at high altitudes, predation pressure, which may be the same or worse than that at lower altitudes, and the effects of potential interference between the aggressive reproductive males and the soft-cuticled teneral adults.

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