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Nocturnal Flight Periodicity of the Caddisflies (Trichoptera) in Forest and Meadow Habitats of a First Order Michigan Stream

Kiralyn Brakel¹, Lydia R. Wassink¹, and David C. Houghton¹*

Abstract

Using ultraviolet light traps, over 5000 caddisfly specimens were collected from a forest and a meadow habitat of Fairbanks Creek in northern Lower Michigan. Samples were collected every 15 minutes, interspersed with 15 minutes of no sampling, from sunset to sunrise during 5 nights from late June to mid-July 2014. Despite having fundamentally different caddisfly assemblages dominated by different species, mean specimen abundance and mean species richness in both habitats exhibited similar trends: peaking between 22:30 and 23:00, decreasing until 02:00 or 02:30, increasing again slightly during the later morning periods, and then decreasing to near zero by 06:00. On average, >90% of species from the forest site were caught by 00:00 and 100% by 02:00, whereas meadow site richness didn’t reach 90% until 01:00 and 100% until 05:00. Species richness per night correlated strongly with dew point for both sites, reflecting consistently warm temperatures throughout the sampling period. Our results suggest that caddisfly flight is controlled by both innate behavior and environmental factors like temperature, and that sampling should continue late into the night to maximize capture, especially in open-canopied areas.

Due to the importance of caddisflies in aquatic ecosystems (Mackay and Wiggins 1979) and their utility in biological water quality monitoring (Barbour et al. 1999, Dohet 2002, Houghton et al. 2011a, Houghton and Wasson 2013), it is imperative that field samples accurately represent caddisfly populations. Studies of adult caddisflies typically rely on ultraviolet light traps to obtain such samples. In this method, a portable light is set over a white pan filled with ethanal, placed near a sampling site at dusk, and retrieved a few hours later. While light traps are not assumed to be exhaustive collecting devices, standardizing the time of collection, wattage of the light source, and size of the collecting pan yields quantitative samples of nocturnally active caddisfly adults and allows for comparisons between sites (Nakano and Tanida 1999, Houghton 2004).

As adult caddisflies become increasingly important in biological monitoring, the importance of sampling them representatively and efficiently has also increased—for example, how long should traps be deployed and under what weather conditions in order for samples to be comparable to each other? There have been several studies addressing the effects of air temperature, wind speed, precipitation, humidity, and vegetation density on caddisfly abundance and composition in light trap samples (Resh et al. 1975; Anderson 1978; Usis and MacLean 1986; Waringer 1989, 1991; Collier and Smith 1998; Houghton and Stewart 1998; Anderson and Vondracek 1999). Seasonal flight periodicity of caddisflies has also been addressed in various climates (Moulton and Stewart 1996, Houghton and Stewart 1998, Smith et al. 2002, Houghton 2012).

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In contrast, only Wright et al.’s (2013) study of the Manistee River, a 40m wide river in northern Lower Michigan, explored the specific nocturnal flight periodicity of an assemblage of caddisflies. The authors found that specimen abundance peaked 1 h after sunset and decreased precipitously afterward. Species richness, however, continued to increase for 0.5 h after specimen abundance decreased, before decreasing gradually over 1 h.

Since Wright et al.’s study was done on a large river, we were curious if specimens from a small stream would exhibit similar or different flight patterns. The question is an important one, since small Michigan streams have fundamentally different caddisfly species assemblages than do large rivers (Houghton et al. 2011b). Thus, the primary objective of our study was to test the nocturnal adult caddisfly flight periodicity of a small stream. Further, we looked at both a meadow habitat and a forest habitat of this small stream to test potential differences in canopy cover on flight periodicity.

Materials and Methods

Fairbanks Creek is a first-order stream (Strahler 1964) located in the northwestern portion of the Lower Peninsula of Michigan. A detailed description of this site can be found in Houghton and Wasson (2013). The stream has both forested and meadow habitats within 0.5 km of length (Fig. 1), offering a unique opportunity to test different habitats within an otherwise undisturbed watershed. In our case, the meadow site (N 44.04715°, W 85.67290°) was ~100m upstream of the forest site (N 44.04615°, W 85.67383°).

Caddisflies were collected using 8-watt portable ultraviolet lights (www.bioquip.com) placed over 24 x 30 cm white plastic pans filled with ~80% ethanol. The device was placed ~1 m from the stream edge. Samples were collected every half hour from 21:30 to 06:00. Lights at both sites were turned on simultaneously and left on for 15 minutes, followed by 15 minutes with the lights off to allow dispersal. Sampling occurred during 5 nights from late June to mid-July 2014, the peak period for adult caddisfly flight in northern Lower Michigan (Houghton et al. 2011b). Sampling only occurred on evenings with daytime temperature >22°C, dusk temperature >15°C, and night time low temperature >10°C (Table 1) (Houghton 2004). Sampling did not occur if there was any noticeable wind or precipitation, or precipitation 2 h prior to sampling. Sampling ended after the 02:00 and 04:00 samples respectively on 2 nights due to the onset of precipitation (Table 1).

Collected specimens were all identified to the species level except for females of Hydroptila (n = 2), Orthotrichia (n = 3), and Oxyethira (n = 1) which lack reliable species-level characteristics. In all 3 cases, multiple congeners are known from these sites, precluding any confidence in identification. Such specimens were counted in our specimen tally but not in the species tally. All identified specimens are maintained in the Hillsdale College Insect Collection.

Mean species richness and mean specimen abundance were determined from specimen data at both sites and analyzed with 1-way Analysis of Variance with post-hoc Tukey test to determine the peak emergence periods at each site. Mean species accumulation curves were also computed for each site from these data. The total number of species caught per date by the 2:00 sample (the last sample common to all sampling dates) was correlated with daily high temperature and dew point determined for the nearby town of Luther (www.wunderground.com), and also with dusk temperature and nightly low temperature measured at a single point equidistant from both sampling sites. Sites and time periods were examined for patterns in their caddisfly assemblages with detrended correspondence analysis (DCA) using the program PC-ORD v. 5 for Windows® (McCune and Medford 2006). The analysis was performed on a two-dimensional data matrix of each individual time period for each site by mean specimen abundance for each species caught.
Figure 1. Photographs of the forest site (A) and meadow site (B) of Fairbanks Creek sampled during this study.
Results

Peak specimen abundance occurred at 22:30 in the meadow habitat, and at 22:30 and 23:00 in the forest habitat. Peak species richness occurred at 22:30 and 23:00 in both habitats. Both species richness and specimen abundance decreased from their peaks until either 02:00 or 02:30, increased slightly during the later morning periods, and then decreased to near zero by 06:00 (Fig. 2). Both species richness and specimen abundance were higher in the meadow habitat than the forest habitat for every time period except 21:30 and 22:00.

Mean species accumulation curves appeared similar for both habitats except that the forest site had a steeper curve, reaching 90% of its total nightly capture by 00:00 and 100% by 02:00. The meadow site, in contrast, didn’t reach 90% until 01:00 and 100% until 05:00 (Fig. 3). Overall species richness through completion of the 02:00 sample correlated strongly with dew point for both the meadow ($R^2 = 0.87, P < 0.01$) and forest ($R^2 = 0.79, P < 0.01$) sites, but not with high temperature, low temperature, or dusk temperature ($R^2 < 0.50$ for all). A total of 5230 specimens were collected, representing 71 species from the meadow habitat and 60 from the forest habitat.

DCA ordination of the mean specimen abundance for each species caught at each site and time period suggested that the meadow and forest habitats constituted two distinct assemblages. Except at 21:30, there was virtually no overlap between the samples from the two sites (Fig. 4). Likewise, the 5 most abundant species at the meadow site were completely different than those of the forest site (Fig. 5).

Discussion

Caddisfly flight periodicity is likely controlled by a combination of innate behavior and environmental factors, most notably temperature. That is, species will be active for a predetermined period of time if temperature is appropriate. Low dusk temperature in particular has previously been determined to be a significant factor affecting specimen abundance, species richness, and sex ratios in light trap samples (Resh et al. 1975, Anderson 1978, Usis and MacLean 1986, Waringer 1989, Anderson and Vondracek 1999, Wright et al. 2013). Specifically, dusk temperatures $<10$ °C (Anderson 1978) or $<8$ °C (Waringer 1991) lowered caddisfly specimen abundance and species richness. Temperature, however, likely only modifies an existing behavior. Jackson and Resh (1991) determined circadian rhythms in the attraction to pheromones of three caddisfly species, and found that environmental factors influenced the amount of flight activity.

Table 1. Summary data for the 5 sampling nights. HT: high temperature, DP: dew point (www.wunderground.com), DT: dusk temperature, LT: low temperature (measured at single point equidistant between sampling sites). #sppFS and #sppMS: number of species caught at the forest site and meadow site respectively through the 2:00 sample. Sampling was stopped after the 2:00 sample on 29–30 June and after the 4:00 sample on 6–7 July due to precipitation. Thus, no low temperature was recorded on those dates.

<table>
<thead>
<tr>
<th>Date</th>
<th>Sunset</th>
<th>HT(°C)</th>
<th>DT(°C)</th>
<th>LT(°C)</th>
<th>DP(°C)</th>
<th>#sppFS</th>
<th>#sppMS</th>
</tr>
</thead>
<tbody>
<tr>
<td>28–29 Jun</td>
<td>21:30</td>
<td>29</td>
<td>21</td>
<td>20</td>
<td>18</td>
<td>36</td>
<td>45</td>
</tr>
<tr>
<td>29–30 Jun</td>
<td>21:30</td>
<td>26</td>
<td>23</td>
<td>N/A</td>
<td>20</td>
<td>39</td>
<td>52</td>
</tr>
<tr>
<td>05–06 Jul</td>
<td>21:29</td>
<td>24</td>
<td>18</td>
<td>13</td>
<td>10</td>
<td>25</td>
<td>31</td>
</tr>
<tr>
<td>06–07 Jul</td>
<td>21:28</td>
<td>23</td>
<td>21</td>
<td>N/A</td>
<td>17</td>
<td>32</td>
<td>39</td>
</tr>
<tr>
<td>11–12 Jul</td>
<td>21:26</td>
<td>26</td>
<td>20</td>
<td>14</td>
<td>13</td>
<td>30</td>
<td>32</td>
</tr>
</tbody>
</table>
Figure 2. Mean (+SE) number of specimens (A) and species (B) collected from the meadow and forest habitats of Fairbanks Creek at the various time intervals. Asterisks denote significantly highest means for the meadow site and Xs denote highest means for the forest site (1-way Analysis of Variance with post-hoc Tukey test, $P < 0.01$ for all). Other groups of time intervals not marked due to the substantial overlap between them. Sample size was 5 through the 2:00 sample, 4 through the 4:00 sample, and 3 through the 6:00 sample.
but not the fundamental flight periodicity. Wright et al.’s (2013) study on the flight periodicity of 18 caddisflies on the Manistee River found that each species maintained a consistent flight pattern on each evening, except that warmer nights yielded a greater specimen abundance.

We sampled only during nights with dusk temperature ≥18°C, considerably warmer than the established 8–10°C low dusk temperature threshold. Even our low temperatures during morning sampling periods were ≥13°C (Table 1). Even within our warm range, however, caddisfly flight periodicity appeared related to temperature. Our positive correlation of both specimen abundance and species richness with dew point reflected nights when temperatures remained fairly constant, allowing for large collections throughout the sampling periods. In contrast, low dew point evenings began warm but dropped in temperature more quickly, leading to lower abundances. Thus, species richness did not correlate to daytime high, low, or dusk temperature.

The meadow and forest habitats of our study both exhibited the same basic patterns in their nocturnal species richness and specimen abundance, despite composing fundamentally different species assemblages. Although the two sites are only separated by ~100m, the abrupt changes in canopy cover (Fig. 1) promotes an assemblage dominated by shredder species in the forest site, and one dominated by filtering collector species in the meadow site (Houghton and Wasson 2013). A similar result was found in our study, as the 5 most abundant species in the meadow site were filtering collectors and the 5 most abundant species of the forest site were shredders (Fig. 4). The top 10 most abundant
species in Wright et al.'s (2013) study of the 40m wide Manistee River had no overlap with either assemblages of our study, yet exhibited the same peaks in species richness and specimen abundance. Resh et al. (1975) also found that peak caddisfly flight activity occurred within the first 3 hours after sunset in a Kentucky stream. Thus, the general flight periodicity pattern probably applies to different species assemblages in different habitat types.

Despite a similar basic pattern, there were some subtle differences between the flight periodicities of our two assemblages. The higher abundance of specimens at the forest site during the early sampling periods was due to the presence of Protoptila tenebrosa (Walker) (Glossosomatidae), which was more abundant at the forest site than the meadow site, and flew almost entirely during the early periods. The higher specimen abundance at the meadow site during the other sampling periods was a little enigmatic. These 2 assemblages have been studied extensively for several years using ultraviolet light traps set out for 1 h after dusk (Houghton and Wasson 2013 and additional unpublished data). The total number of caddisfly species known from the forest site is actually higher than that of the meadow site. It is possible that the open canopy of the meadow site may have allowed our ultraviolet lights to attract specimens from a greater distance throughout the night than at the forest site. This hypothesis is supported
by the accumulated species curves of the two populations. That the number of total species caught from the meadow site habitat continued to increase several hours after the forest site had reached maximum species richness suggests that additional species were being drawn to the light throughout the night, perhaps from a greater distance.

Our secondary peaks in species richness and specimen abundance have not been previously documented in caddisflies. It is possible that these peaks were spurious due to our small sample size after 02:00 when the peaks occurred. Thus, our result should be treated as tentative. There was, however, no significant difference in the overall standard error values for species ($P = 0.29$) or specimens ($P = 0.20$) between samples caught before 02:00 and those after 02:00 (Two-sample T-test). This result suggests that, despite the smaller sample size, the later samples were not unduly influenced by outlier samples relative to the earlier samples (Zar 2010).

Bimodal flight peaks have been frequently observed in the Lepidoptera. For example, Helicoverpa armigera (Hübnner) peaked in flight activity 15 minutes after sunset, declined, and then increased slightly during the second half of the night. The second peak was attributed to males in search of mates (Riley et
al. 1992). Lingren et al. (1977) observed four moth species, two of which had mating periods that occurred between 22:00 and 04:00, thus increasing in flight activity during that time. Several other studies (summarized in Fullard and Napoleone 2001) have noted a general increase in adult moth abundance within 1–4 hours before sunrise.

Due to their demonstration in the Lepidoptera and their occurrence in the two habitats of our study, we suspect that bimodal flight peaks may be common in caddisfly populations. Previous studies may have missed the second peak by not sampling throughout the night. It is not clear why Wright et al.’s (2013) study did not document a second peak, although their large river caddisfly assemblage—which had very few species in common with our 2 small stream assemblages and was dominated (77% of total specimens) by 3 species—may exhibit a different flight behavior due to the different individual species involved. Differences in flight periods likely relate to mating and other adult behaviors, and need substantial further study.

Our data suggest that ultraviolet light sampling may need to be employed for a longer period of time throughout the night than logic would indicate. For example, sampling until the point of decreasing specimen abundance (23:00) would have missed ~25% of the total species richness from both of our study sites. Sampling for 2 hours after sunset, which is a common time period in the literature (Nakano and Tanida 1999, Houghton 2004), would have missed 12% of the species richness of the forest site and nearly 20% of the species richness of the meadow site.

Thus, the ideal time period to sample adult caddisflies will depend on whether or not exhaustive sampling is needed. For biological monitoring studies, exhaustive sampling may not be necessary as long as samples accurately reflect the overall population (e.g., Cao and Hawkins 2011), although our data suggest that non-exhaustive samples should be of similar time interval. For faunistic studies, where an exhaustive sampling of species is the goal, it would be prudent to sample later into the night. In the case of stream sites with an open canopy, additional species may well be collected almost until sunrise.

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Literature Cited


