

Hudsonian Emerald (*Somatochlora hudsonica*, Hagen) in Boulder County

December 8, 2017

Kristofor Voss, Department of Biology, Regis University, [kvoss@regis.edu](mailto:kvoss@regis.edu)  
Katrina Loewy, Department of Research and Conservation, Butterfly Pavilion,  
[kloewy@butterflies.org](mailto:kloewy@butterflies.org)

## **Abstract**

Dragonfly conservation in parks serves the dual purpose of protecting iconic species of aesthetic value to park visitors as well as preserving aquatic ecosystem function. The Hudsonian emerald dragonfly (*Somatochlora hudsonica*, Hagen). *S. hudsonica* is the only Colorado dragonfly listed as sensitive by the US Forest Service. Little is known about *S. hudsonica*'s habitat associations, distribution, and life history, all essential for future management of the species. We began answering those basic questions with literature-based habitat suitability models followed by a ground-truthing survey of adults across Boulder County Parks and Open Space (BCPOS) properties that span the suitability gradient to determine the local habitat variables that influence probability of occurrence. To determine breeding habitat, we also conducted an exuvial survey, and set the groundwork for captive rearing. The information collected as part of this project will provide critical baseline data necessary for BCPOS to draft habitat management and monitoring plans for the Hudsonian emerald.

## **Introduction**

In the Anthropocene, human activities that destroy and degrade habitat are extirpating species at alarming rates, resulting in unprecedented levels of global biodiversity loss<sup>1</sup>. While iconic charismatic megafauna typically serve as the poster children for species preservation<sup>2</sup>, the large balance of global animal biodiversity resides in terrestrial and aquatic insects<sup>3</sup>. Compared to terrestrial species, those of aquatic origin are particularly vulnerable to human threats due to their highly endemic distributions and typically restricted environmental requirements<sup>4</sup>. One such order of aquatic insects, the odonates (damselflies and dragonflies), are well-recognized by even casual observers as iconic freshwater inhabitants. Not only do dragonflies serve to add aesthetic value to freshwater habitats, but they function as apex predators of invertebrates and prey for fish, amphibians, and birds, thereby linking aquatic and terrestrial habitats<sup>5</sup>. Thus, dragonfly conservation serves the dual purpose of preserving ecosystem function and enhancing the aesthetic value of aquatic resources.

Of 453 total species of North American odonata (dragonflies and damselflies), fewer than 20 have fully recorded life cycles<sup>6</sup>. The Colorado Natural Heritage Program and Colorado Parks and Wildlife published a list of sensitive dragonfly species in an addendum to their Wildlife Action Plan<sup>7</sup>. For most dragonfly species in the plan, the State listed lack of information as a threat to their survival. Lack of knowledge certainly threatens the Hudsonian emerald (*Somatochlora hudsonica*), a dragonfly found in Boulder County and listed as a Tier 2 Species

of Greatest Concern by Colorado Parks and Wildlife and as a sensitive species in Region 2 by the USDA Forest Service<sup>7,8</sup>.

The Hudsonian emerald is an uncommon species found throughout Canada and mountainous regions of Alaska, Montana, Wyoming and Colorado<sup>8,9</sup>. Within Colorado *S. hudsonica* has only been observed within Park, Larimer, and Boulder Counties, the southernmost end of its distribution. Because these counties lie on the periphery of the Hudsonian emerald's distribution, individuals tend to be locally restricted and not commonly found. Consequently, while *S. hudsonica* is stable globally, the species is vulnerable to habitat degradation in areas where it occurs within the state<sup>10</sup>. Indeed, as of 2005 very few specimens had been collected and vouchered within Colorado, most of which were collected decades earlier<sup>8</sup>. Within Boulder County, confirmed sightings or collections occurred at Rainbow Lakes, Brainard Lake, and Red Rock Lake<sup>11</sup>. However, within BCPOS properties, *S. hudsonica* has not been officially documented in recent odonate surveys<sup>12-14</sup>, but based on habitat requirements is potentially present in or near the following BCPOS areas: Steamboat Mountain, Heil Valley Ranch (Geer Canyon & Marrietta Canyon), El Dorado Springs (South Draw), Caribou Ranch, and Reynolds Ranch (Giggey Lake)<sup>15</sup>.

The 2005 assessment cited seven instances of *S. hudsonica* in Colorado at altitudes of over 1,524 m. The closest BCPOS parcels with significant water sources are Barron, Duck Lake, and Caribou Ranch. Habitat use in the United States is extrapolated from those few adult sightings as well as observations in Canada where the species occurs more widely<sup>16</sup>. At northern latitudes, *S. hudsonica* inhabit bogs, lakes, ponds, and (especially for larvae) the edges of woodland streams<sup>17</sup>. An early guide to the genus suggested that *Somatochlora* larvae only develop in water with summer temperatures of 16–20 °C (61-68 °F)<sup>18</sup>. Within its range, the Hudsonian emerald typically inhabits elevations above 1500 m in lentic (i.e. still water) habitats, but has been incidentally found in some small mountain streams within pool microhabitats<sup>8</sup>. The lentic habitats have been described as sedge-bordered, boggy lakes, ponds and streams with nearby or adjacent forest for foraging and mating<sup>8 19</sup>.

Like many dragonflies, *S. hudsonica*'s habitat use changes over its life cycle. Larvae are aquatic, pre-reproductive adults leave the water source and hunt among the tree tops, and reproductive adults return to water to breed<sup>9,20</sup>. The rate of natal philopatry and dispersal distance remain unknown. Females may exploit different habitats than males<sup>21</sup>. We need knowledge of habitat associations for all ages and genders, and the dispersal ability of adults for preservation or restoration of *S. hudsonica*.

Until a detailed study occurs, threats to *S. hudsonica* remain speculative. Hypothesized threats to the Hudsonian emerald habitat include those that impact water quality (i.e. from sedimentation, mining, or pesticide application) or vegetation loss (i.e. from livestock grazing, trampling or tree loss)<sup>8</sup>. If adults require trees close to the banks where they emerge, as other *Somatochlora* species do, clearing land near water sources could threaten their survival<sup>8</sup>. Predation by fish or other dragonflies could prevent larvae from persisting in ponds or streams<sup>22,23</sup>. Lack of sufficient cover by aquatic vegetation could increase predation rates.

The life history of *S. hudsonica* also remains unknown, including the number of years for larvae to reach adulthood and if eggs overwinter. However, based on traits of congeners, Walker estimated that the larval phase of Hudsonian emeralds lasts two full seasons and eggs overwinter. He also estimated that adults live 1.5-2 months<sup>18</sup>. All adult specimens in the region were found in July; the dragonflies could start emerging in mid-June<sup>8</sup>.

This lack of basic ecological information is compounded by the lack of recent survey/occurrence data from areas within the county, especially from those areas managed by BCPOS. Thus, at this point we have limited information about **where and when** the Hudsonian emerald is found and **the ecological requirements** of the species. To monitor and manage habitat for Hudsonian emerald, these three critical pieces of information should be formally assessed for BCPOS areas. The goal of this study is to fill this critical research gap.

## **Objectives**

- 1.) To determine the presence or absence of *S. hudsonica* on Boulder County Parks and Open Space land.
- 2.) To conduct a habitat assessment for the Hudsonian emerald in Boulder County Parks and Open Space (BCPOS) areas with the purpose of providing a map of estimated habitat suitability throughout Boulder County. Using this map, to conduct a pilot ground-truthing study that surveys Hudsonian emeralds in BCPOS areas that span the habitat suitability gradient. The goal of this survey will be to estimate site occupancy and local habitat factors that correlate strongly with occurrence of Hudsonian emeralds.
- 3.) To conduct an exuvial survey to determine the breeding habitat of *S. hudsonica*, including a) correlation with adjacent forest b) correlation with fish stocking, and c) co-occurrence with other dragonfly species. To successfully rear *Somatochlora* species and other common dragonflies in captivity to assess potential for “head-starting” *S. hudsonica* and other sensitive odonates.

- 4.) To successfully rear *Somatochlora* species and other common dragonflies in captivity to assess potential for “head-starting” *S. hudsonica* and other sensitive odonates.

### **Questions and Hypotheses**

This research aims to answer four questions:

**Q1. In which areas of Boulder County Open Space is the Hudsonian emerald predicted to occur?**

*H1a. A comprehensive habitat suitability model will provide a data-driven approach to assess potential habitat for the species. We expect to find higher suitability in areas that possess boggy ponds and lakes above 1500 m in elevation.*

*H1b. We expect to find *S. hudsonica* in Caribou Ranch and Barron parcels, near historical sightings.*

**Q2. How well does the habitat suitability model (Q1) reflect current occupancy by the Hudsonian emerald?**

*H2. Given the limited occurrence data for the Hudsonian emerald, we expect that the habitat suitability model may overestimate presence of the dragonfly in certain areas. Ground-truthing of the model with on-the-ground surveys enable us to assess the success of the model.*

**Q3. What local-scale habitat features (e.g. water quality, vegetation management, etc.) tend to correlate strongly with presence of Hudsonian emeralds?**

*H3: Extremely limited data has been collected to assess the local factors that make suitable habitat for the Hudsonian emerald. Collection of such data during ground-truthing surveys will likely show that Hudsonian emeralds respond positively to better water quality and protection of riparian areas from livestock watering and grazing.*

**Q4: How does proximity of forested area, presence of fish, and co-existence with other anisopterans impact breeding habitat?**

*H4: Breeding habitat will occur in areas a) within 200 m of a forested area, b) without stocked fish, and c) without other dragonfly species, except the mountain emerald (*S. semicircularis*).*

## **Methods**

### *Habitat Suitability Modeling*

We used a two-pronged approach to construct habitat suitability models to forecast areas where the Hudsonian emerald likely occurs. First, we used an approach where we chose several habitat variables that have been shown (or are assumed) to correlate positively or negatively with Hudsonian emerald occurrence. While we attempted to find a comprehensive set of articles about *S. hudsonica* habitat requirements, the primary source for our scoring system was information reported by Packauskas in 2005<sup>8</sup>. The habitat variables we used and scored were: (1) proportion of forest within 500-m (from National Land Cover Database, 0% = 0, 100% = 1), (2) proximity to lentic or lotic water source (from National Hydrography Dataset, 0 m = 1, 500 m = 0), (3) proximity to forested wetland (from National Wetland Inventory, 0 m = 1, 500 m = 0), (4) elevation (from National Elevation Dataset, scaled from 0 to 1 between 1500 and 3000 m, decreasing after 3000 m), (5) proportion of developed land within 500 m (from National Land Cover Database, 0% = 1, 100% = 0), (6) proportion of rangeland/pasture (from National Land Cover Database, 0% = 1, 100% = 0), and (7) distance to nearest road (0 m = 0, 500 m = 1). Using ArcGIS, we scored each of the habitat variables as indicated above and combined them into a habitat suitability index using two methods, the geometric mean and the arithmetic mean<sup>23</sup>. The geometric mean is more restrictive than the arithmetic mean because any attribute scored as a 0 is indicated as unsuitable. The arithmetic mean is more permissive allowing compensation by attributes. Essentially this technique uses information from a literature review to create a scoring system for each habitat attribute where higher numbers indicate more suitable habitat.

While this approach was useful in the absence of a many occurrence records, it is based on expert judgement. Consequently, we supplemented the literature-based method with a traditional habitat suitability model that relates habitat variables to the probability of occurrence of Hudsonian emeralds within North America<sup>24,25</sup>. To do so, we curated a collection of occurrence records from known summaries of occurrences<sup>8</sup>, digital collections (iDigBio, iNaturalist), and other odonate sighting data at Odonata Central known from local naturalists. These digital records collate records in the database from some museums. All records were confirmed by third-party taxonomic experts and by the authors using provided photographs.

After georeferencing these occurrences, we built a species distribution model from lower dimensional variables defined by principal components analysis (PCA) of bioclimatic data and land use data (e.g., summaries of temperature, precipitation, land use, and nearby lentic

habitat). We used nine well-known models for species distribution modeling using a randomly assigned subset of 80% of the data for model-building (Bioclim, Domain, Mahalanobis, generalized linear models, generalize additive models, maxent, boosted regression trees, random forest, and support vector machine). We used synthetic PCA variables rather than the raw variables because of the high degree of correlation among the variables. In this way, the model uses orthogonal, uncorrelated summaries of climate and land use within the study area as the major sources of variation across the landscape. We combined the presence-absence maps from each of the models, weighting each model by its area under the curve (AUC) calculated from a plot of the true positive rate versus the false positive rate in a cross-validation that predicted presence-absence from the remaining 20% of the data. The AUC is a measure of model accuracy describing how well the model predicts presence/absence in the 20% holdout dataset not used to train the model. Each model uses species occurrence data as presence data and randomly generated “pseudo-absences” to build a model that predicts probability of occurrence from the habitat parameters. This model can then be used to project the probability of occurrence across the landscape into a map. We then used these maps in conjunction with recent occurrence records in Boulder County to identify candidate sites for a ground-truthing study.

#### *Ground-Truthing Adult Pilot Survey*

At each site identified from habitat suitability mapping (see Results), we conducted Hudsonian emerald surveys along transects that circled the perimeter of each pond, lake, or pond complex. We used established protocols that control for time of day, weather, and walking speed<sup>26,27</sup>. Briefly, the perimeter of the water body was divided into 20-m or 50-m transects which were walked in opposite directions by two observers. Each observer recorded a count of the number of Hudsonian emeralds, other dragonflies (not identified), and damselflies. Additionally, each observer visually estimated the percent sun to the nearest 10%, the time of day, and the depth one meter toward the lake center. Sites were visited from June 26, 2017 to August 19, 2017, a period identified as the known flight time of adult Hudsonian emeralds (mid-July to mid-August)<sup>19</sup>. We revisited each site twice to repeat transect surveys over the course of the summer. While 90% of transects were visited between 9:30am and 3:30 pm, we did attempt to revisit sites at different times of day on subsequent visits. The first time we found a Hudsonian emerald at a site, we photographically confirmed presence by catching, photographing, and releasing the specimen.

### *Habitat and Water Quality Analysis*

At each of the study sites, a brief local habitat survey was conducted on August 14, 2017 or August 15, 2017 to assess the extent of emergent vegetation cover, proximity to forest habitat, other noticeable disturbances, and water quality (dissolved oxygen, TDS, pH, temperature, nitrate, phosphate, alkalinity, metals). Water samples were taken just under the water surface by syringe near the edge of the pond or lake in clean, acid-washed bottles and brought back to the lab or sent out for analysis according to standard EPA methods. To determine which habitat variables corresponded to presence/absence of *S. hudsonica*, we used two methods. First, using a bootstrap resampling procedure, we compared the mean difference in habitat variables between sites where *S. hudsonica* was observed and sites where *S. hudsonica* was not observed. Secondly, we conducted a non-metric multidimensional scaling ordination of habitat variables on the Gower's distance matrix of habitat variables among sites. Gower's distance allows a distance between sites to be calculated when different types of variables are in the data table (i.e. categorical, ordinal scale, numeric, asymmetric binary). This allowed us to show whether sites where *S. hudsonica* was observed and sites where it was not observed differed in multivariate habitat space.

### *Exuvial Surveys and Analysis*

We conducted an exuvial study in randomized 2 m X 2 m plots along water features with emergent vegetation in Caribou Ranch, Barron and Duck Lake parcels. We walked the perimeter of potential habitats in early June (July for Caribou Ranch locations due to access restrictions) and used GPS units (Garmin, Canton of Schaffhausen, Switzerland) to map areas of potential dragonfly emergence. After uploading the resulting lines to ArcMaps, we used ArcGIS tools to assign ten randomized sample plots per site. We chose small plots to avoid unnecessarily trampling of sensitive aquatic vegetation. We drew this technique from an exuvial study on Hine's emerald dragonflies<sup>29</sup>.

Sampling occurred from June 17<sup>th</sup> to August 18<sup>th</sup>, 2017. We attempted to visit each site once a week to collect exuviae. A previous study noted that exuvial persistence decreased exponentially after three weeks<sup>30</sup>. We collected all anisopteran exuviae within the plots in small plastic vials, which we brought to Butterfly Pavilion for identification. We identified Corduliid exuviae to species, and all other dragonfly exuviae to genus using two different dichotomous keys<sup>17,31</sup>.



### *Marking Method Test*

As we collected exuviae, we also attempted to capture *Somatochlora* species adults. We held several adult males briefly to affix a queen bee marker (Bee Works, Oro-Medonte, ON, Canada) to their thorax behind the head and to the side. Researchers marking *S. hineana* moved from using colored paint on wings to small, numbered tags (Fig 1), and we replicated their marking procedure.



Figure 1: *Somatochlora hineana* with numbered tag. Photographer: Daniel A. Soluk.

### *Rearing Methods*

Butterfly Pavilion staff assembled a rearing setup to support dragonfly eggs and larvae through emergence. The odonata rearing setup was built on a metal shelving unit. The three central shelves hold hydroponics trays (0.6m by 1.2m by 11.4 cm), Chlorophyll, Denver, CO, USA). The bottom shelf holds a sump tank that contains a Eflux DC Flow pump (Current, Vista, CA, USA) in addition to the intake pump/hose and outtake hose for a ¼ HP chiller (JBJ Arctica; TransWorld Aquatic Enterprises Inc., Inglewood, CA, USA). The trays are connected to each other and the pump with PVC pipes. The three central shelves are lit by three 91.4 cm Trulumen Pro LED strips 12000K (Current, Vista, CA, USA) on photoperiod timers. The timers are updated periodically to reflect actual sunrise and sunset times in Colorado.

We collected eggs from females of two common dragonflies: mountain emeralds (*Somatochlora semicircularis*), and eastern or western pondhawks (*Erythemis* spp.). Females released eggs into plastic vials (20 mL Clear Polystyrene Plastic Vials with White Caps; Freund Container and Supply, Lisle, IL, USA) of pond water upon contact of water with their ovipositors. The eggs were kept shaded and cool until arrival at the Butterfly Pavilion lab. We counted all *S. semicircularis* eggs using a microscope at X40 magnification (OMAX). We then transferred the eggs to plastic vials ¾ full of reverse osmosis, deionized water treated with Replenish (Seachem, Madison, GA, USA) in groups of no more than 34 eggs per vial. Labeled vials with

eggs stayed submerged in the temperature and photoperiod controlled larva shelves and were only removed for short bi-weekly checks.

Upon discovering hatchling(s), we separated *S. semicircularis* larvae into individual 0.15 L plastic cups. The cups nest securely into trimmed cup bases affixed with silicon into 10 in (25.4 cm) plastic underwater planter baskets (Pond Boss, West Palm Beach, FL, USA). The planter baskets sit, partially submerged, in the trays. This allows temperature controlled water to circulate around the cups without water exchange, without the risk of losing a larva into the larger system, or of exposing hatchlings to the scent of larger larvae.

Hatchlings are fed small *Daphnia* sp. three times a week, and get 10% water changes tri-weekly. Due to their small size and lack of fat reserves, we plan to keep them at 10°C over the winter and continue to feed them. Alternatively, the remaining *S. semicircularis* and *Erythemis* eggs will be slowly lowered to 4 °C by December and kept at that temperature until April to simulate overwintering and stimulate continued development. We expect eggs to hatch once we begin to raise the temperature in Spring of 2018.

### *Data Analyses*

We used Excel 2013 (Microsoft, Redmond, WA) and R (R Development Core Team, 2017) for all statistical analyses and calculations.

Exuviae relative abundance was calculated as mean exuviae per plot (2m X 2m, or 4m<sup>2</sup>) for the selected taxon divided by total mean exuviae per plot. We used exuvial discovery date as a proxy for dragonfly emergence date. Since we visited each site weekly, we expected the actual emergence to be no more than one week off. The major exception was exuviae collected during the first visit to a site, which may have been there for significantly longer.

There were so few entries for just *S. hudsonica* that we combined those points with *S. semicircularis* into a single entry for *Somatochlora* spp. to facilitate emergence time comparisons. To find peak emergence time by taxon, we log transformed exuvial density, then calculated the peak time from 2<sup>nd</sup> degree parabolic lines of best fit. We chose to use quadratic polynomials because they have a single line of symmetry and, therefore, display a single “best time” for emergence monitoring. The standard quadratic equation is  $y = ax^2 + bx + c$ . In this equation, a and b are coefficients, and c is the y-axis line intercept. On a graph in which x represents time, and y represents exuvial density, the peak emergence time is calculated as  $b \div (-2a)$ .

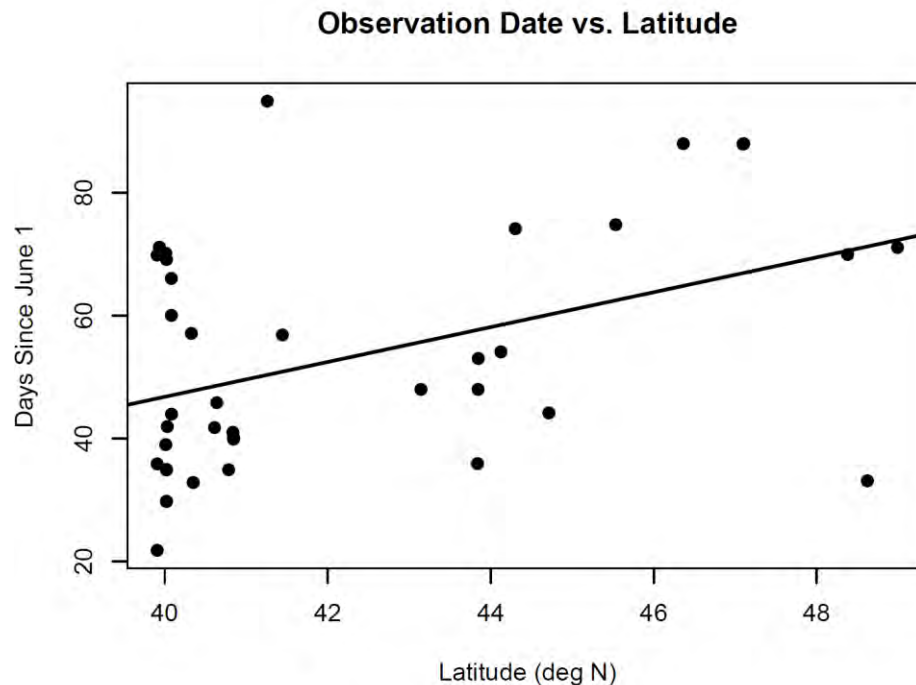
We expect some species and even more genera to exhibit polymodal emergence times in nature, thus the calculation only answers the question, “What is the *single best time* to find

evidence of the taxon emerging, based on exuvial survey data?" The  $R^2$  value included with each equation addresses how well the quadratic equation fits the data.

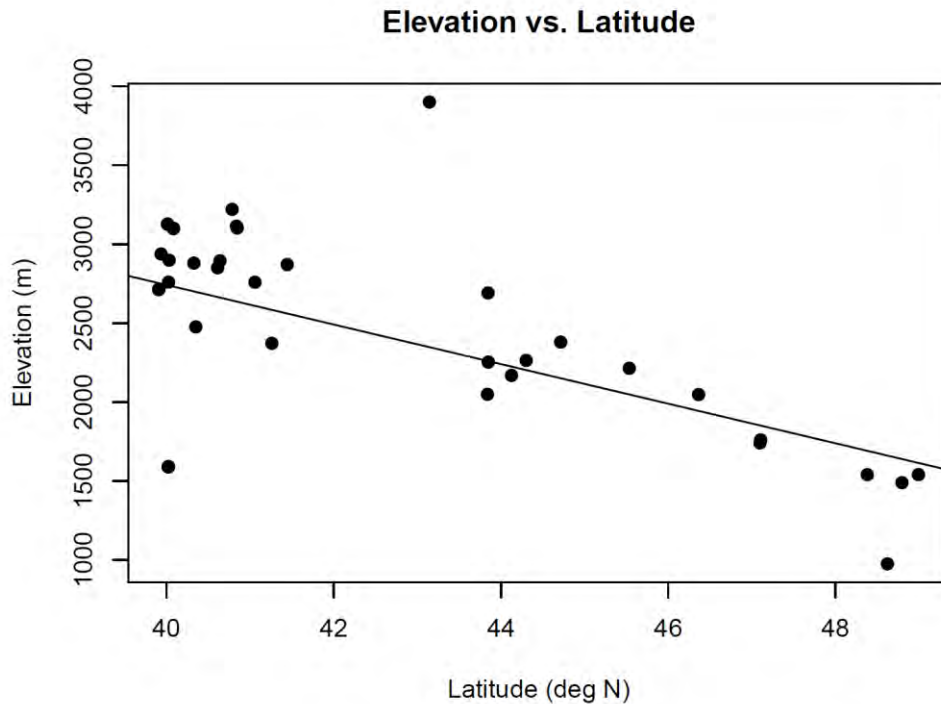
## Results

Using records from multiple databases, we collated 35 unique locations where *Somatochlora hudsonica* specimens have been collected or identified in the continental United States over the last century (1914 – 2014). These specimens were collected from four states (37% Colorado, 23% Montana, 11% Utah, and 29% Wyoming) at a median elevation of 2702 m. Specimens were collected from June 23 to September 4.

Specimens at higher latitudes were found significantly later in the season ( $p = 0.006$ , Fig 2). Linear regression of specimen latitude on observation date (Fig 2) indicates that at 40° latitude (the southern edge of Boulder County), individual specimens could be found from June 12 to August 23. For each 0.5° increase in latitude, specimen observation date increases by 2.8 days (95% CI: 0.8 – 4.8 days). Additionally, we found a strong negative relationship between the elevation and latitude where specimens were found ( $p = 0.00008$ ). Linear regression of latitude on elevation (Fig 3) indicates that at 40° latitude (the southern edge of Boulder County), specimens are likely to be found from 2524 to 2983 m. For each 0.5° increase in latitude, average elevation decreases by 125m (95% CI: 68 – 183 m).



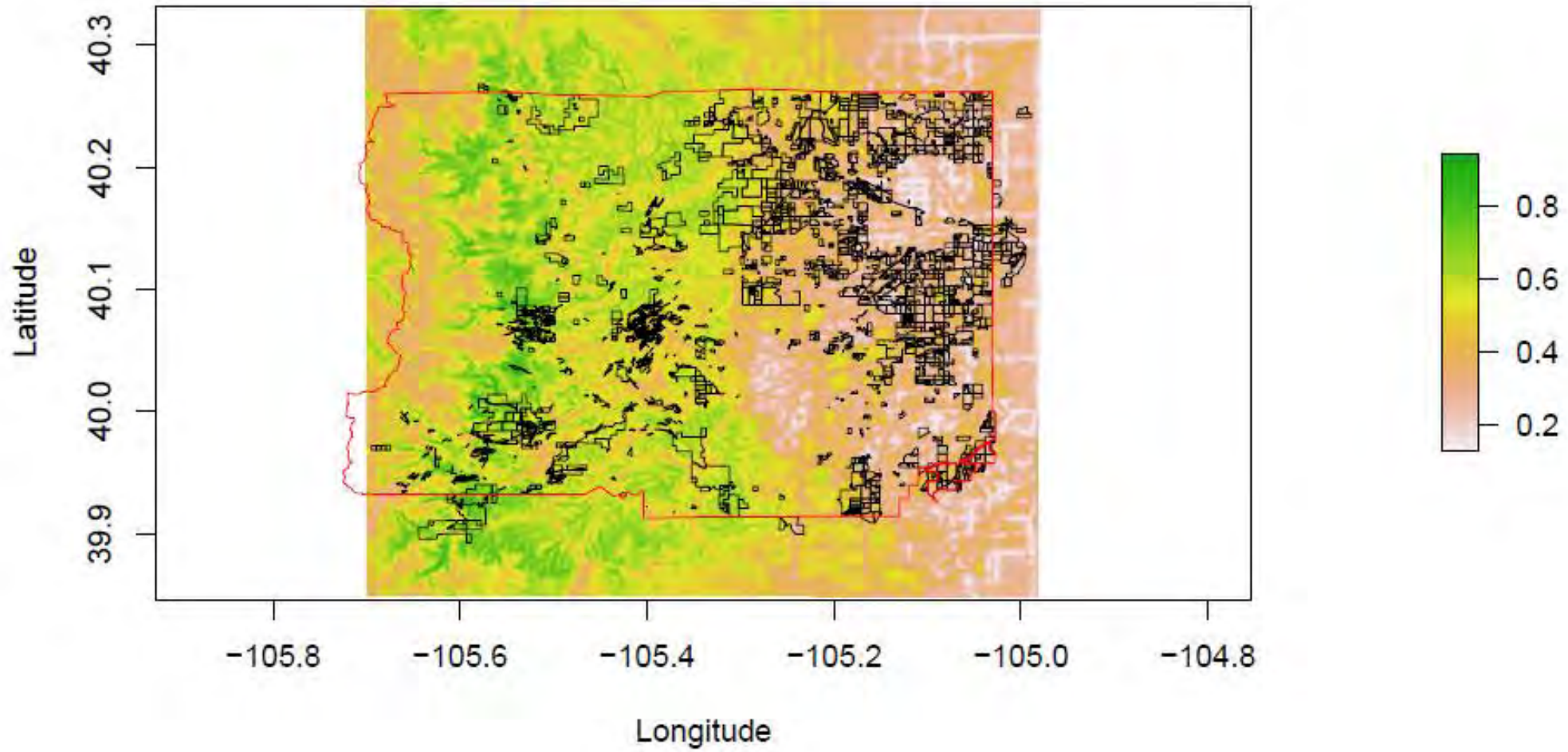
**Figure 2.** *S. hudsonica* observation date increases at higher latitudes.



**Figure 3.** Specimens are found at lower elevations at higher latitudes.

We constructed three habitat suitability maps using the arithmetic mean habitat suitability index (Fig 4), the geometric mean habitat suitability index (Fig 5), and the proportion of bioclimatic models that predicted *S. hudsonica* presence (Fig 6). The average habitat suitability score across all parcels was  $0.424 \pm 0.120$ ,  $0.115 \pm 0.149$ , and  $0.303 \pm 0.309$  for each of the three indices respectively. Based on these models, prior occurrences of *S. hudsonica* within Boulder County and initial site reconnaissance, we chose eight sites at which surveys for exuvia and/or adults would be conducted: Barron NE (exuviae and adults, 40.0975 °N, 105.5144 °W), Barron SW (exuviae and adults, 40.0926 °N, 105.5212 °W), Caribou North (exuviae and adults, 40.0087 °N, 105.5422 °W), Delonde Ponds (exuviae and adults, 39.9899 °N, 105.5302 °W), Duck Lake (exuviae and adults, 40.0834 °N, 105.5129 °W), Giggey West (adults, 39.9499 °N, 105.4737 °W), Minnick-Thompson (adults, 40.0008 °N, 105.5022 °W), and Mud Lake (adults, 39.9777 °N, 105.5098 °W). Habitat suitability scores for all BCPOS parcels can be found in Appendix A.

### Arithmetic HSI for *S. hudsonica*



**Figure 4.** Arithmetic habitat suitability index

# Geometric HSI for *S. hudsonica*

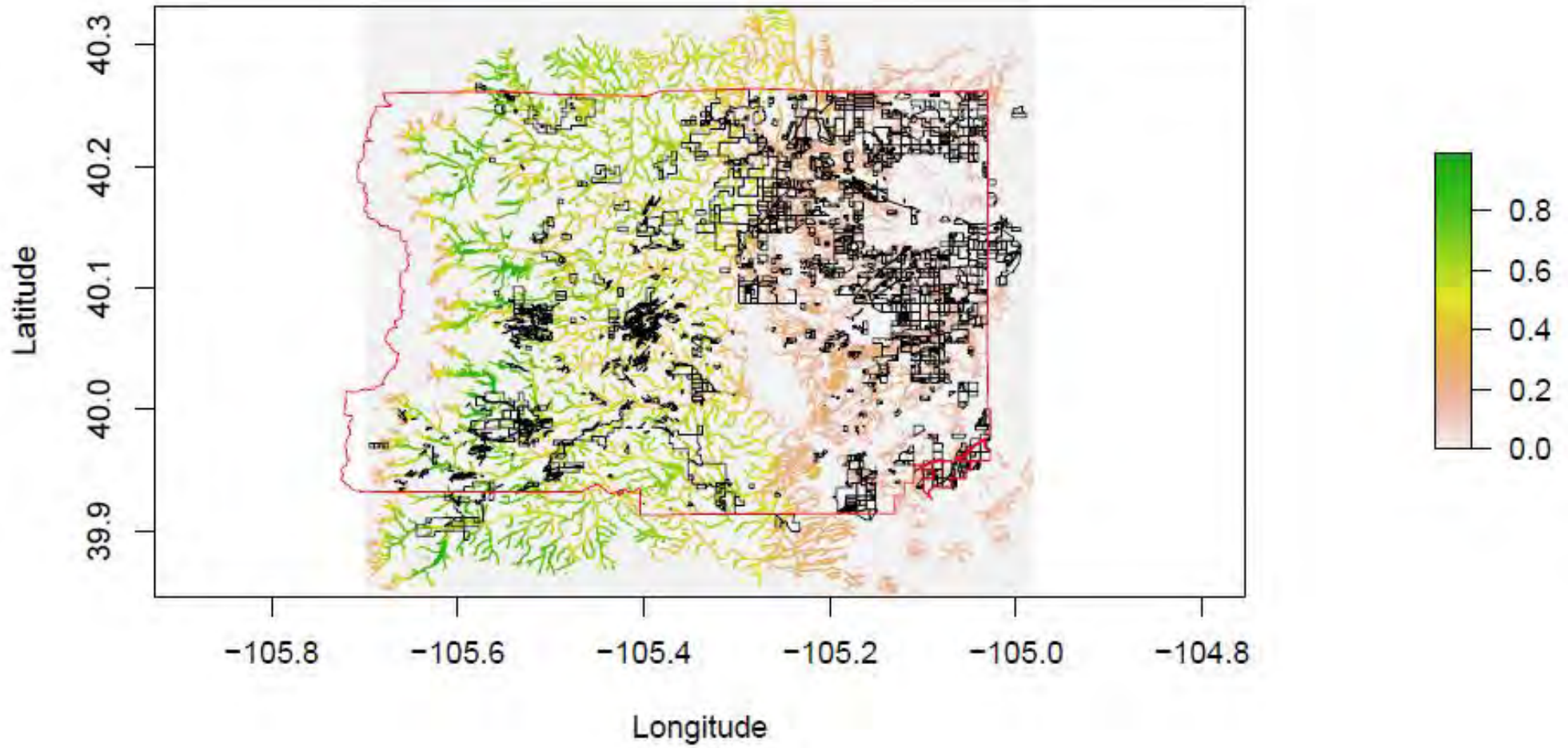


Figure 5. Geometric habitat suitability index

# Model HSI for *S. hudsonica*

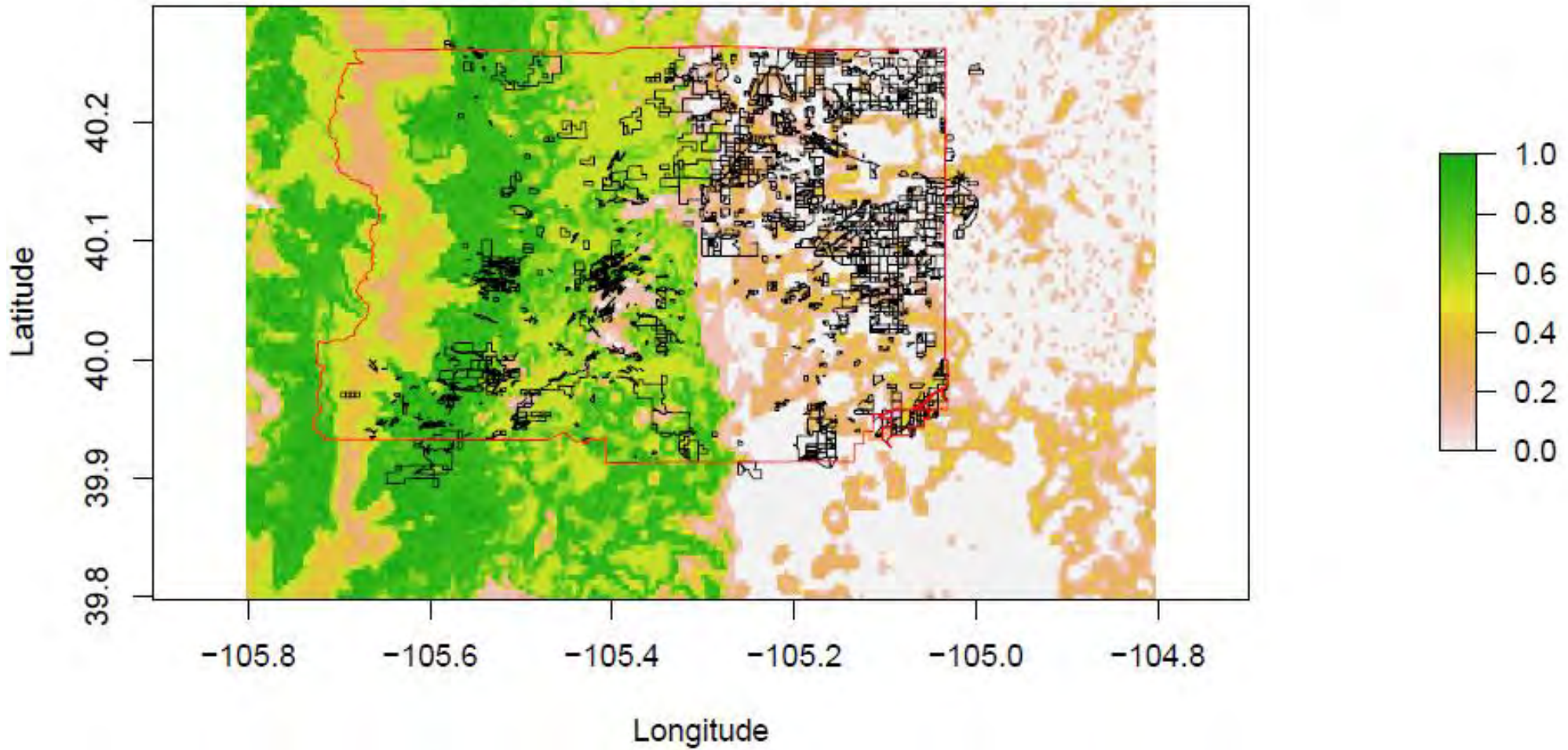


Figure 6. Model average habitat suitability

## Exuvial Survey Results

### *Rarity of Somatochlora hudsonica*

Out of 236 dragonfly (Suborder: Anisoptera) exuviae from five locations, two belonged to *S. hudsonica* (see Table 1). One exuvia was retrieved from Barron SW on June 30th, 2017. It was one of 71 dragonfly exuviae recovered from Barron SW during 2017. The second *S. hudsonica* exuvia came from Delonde Ponds on July 12th, and was one of only 7 total dragonfly exuviae recovered from that location. See all raw exuvial survey data in Appendix B.

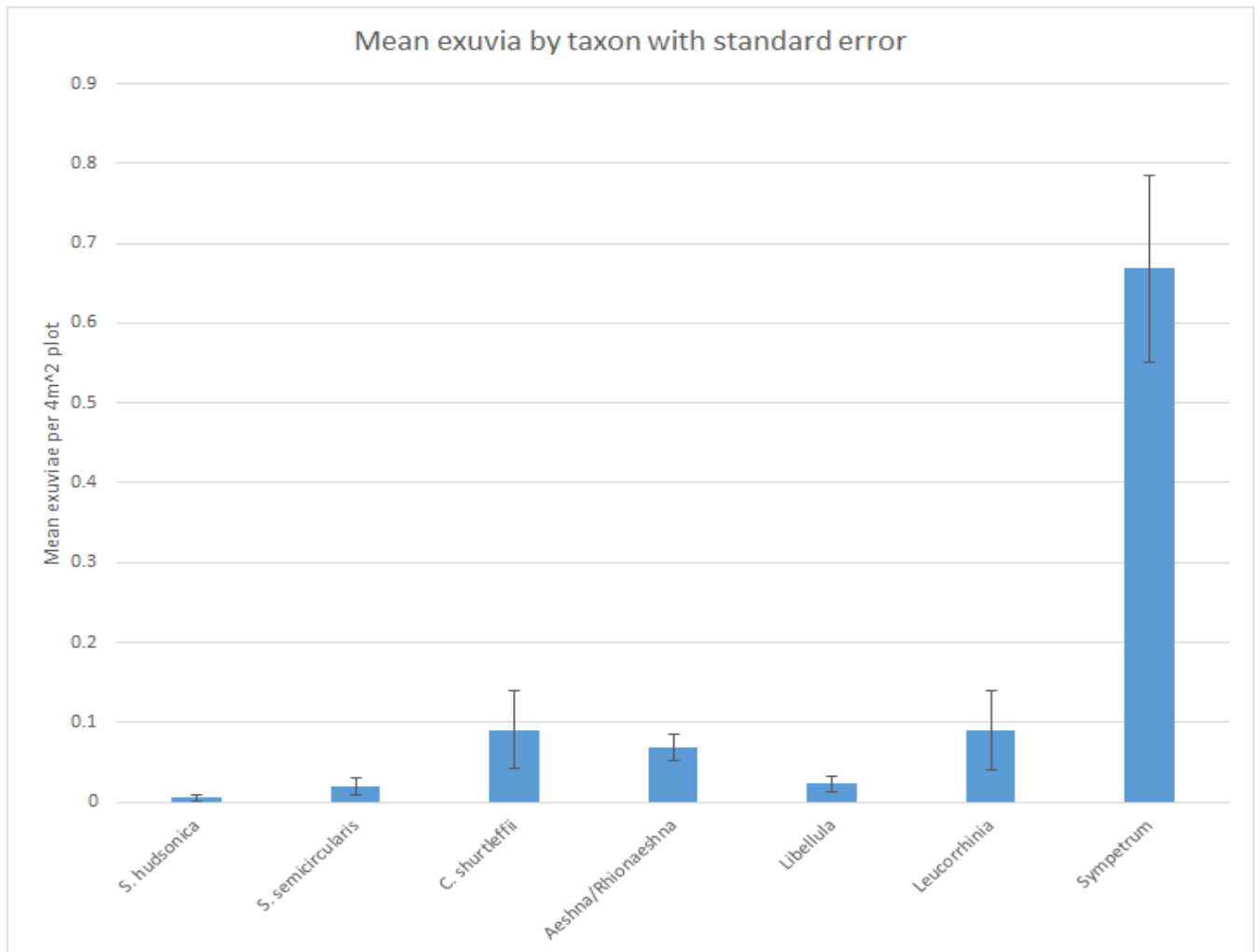
Across five sites, relative abundance of *S. hudsonica* exuviae was 0.59% (Table 1). Genus *Sympetrum* was 26 times more dominant than genus *Somatochlora* (Fig 7).

**Table 1.** Raw summary of dragonfly exuviae collected by location. The counts are *not* controlled by number of site visits and number of plots sampled. Relative Abundance reported in this table is based on density, which considers the number of site visits and plots sampled.

Site	Somatochlora hudsonica (Hudsonian Emerald)	Somatochlora semicircularis (Mountain Emerald)	Cordulia shurtleffii (American Emerald)	Genus: Aeshna/Rhionaeshna	Genus: Libellula	Genus: Leucorrhinia	Genus: Sympetrum
Barron NE	0	0	0	19	2	4	49
Barron SW	1	3	28	0	1	23	15
Caribou Kettle	0	4	0	0	3	4	170
Delonde Ponds	1	0	1	3	0	0	2
Duck Lake	0	0	3	2	2	1	0
<b>Total Counts</b>	<b>2</b>	<b>7</b>	<b>32</b>	<b>24</b>	<b>8</b>	<b>32</b>	<b>236</b>
<b>Relative Abundance (%)</b>	<b>0.59</b>	<b>2.05</b>	<b>9.38</b>	<b>7.04</b>	<b>2.35</b>	<b>9.38</b>	<b>69.21</b>

The relative abundances of *S. semicircularis* and *Cordulia shurtleffii* (American Emerald) of Family Corduliidae were analogous with other dragonfly taxa. The relative abundance of *C. shurtleffii* exuviae was the same as that of *Leucorrhinia* (white face) species, and *S. semicircularis* was only 0.3% less abundant than *Libellula* spp. However, *S. hudsonica* stands out as the least abundant taxon (Table 1 and Fig 7).

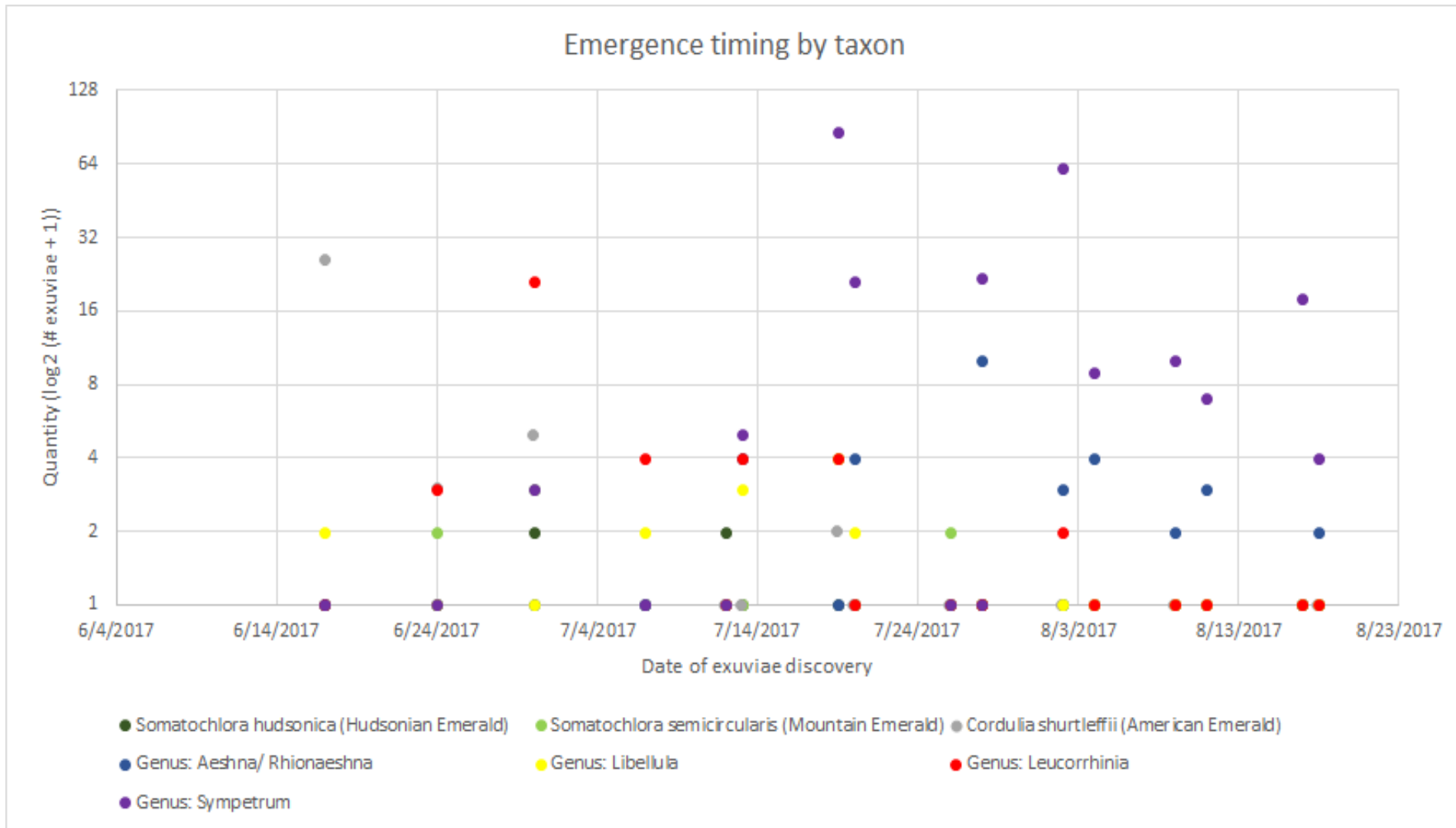




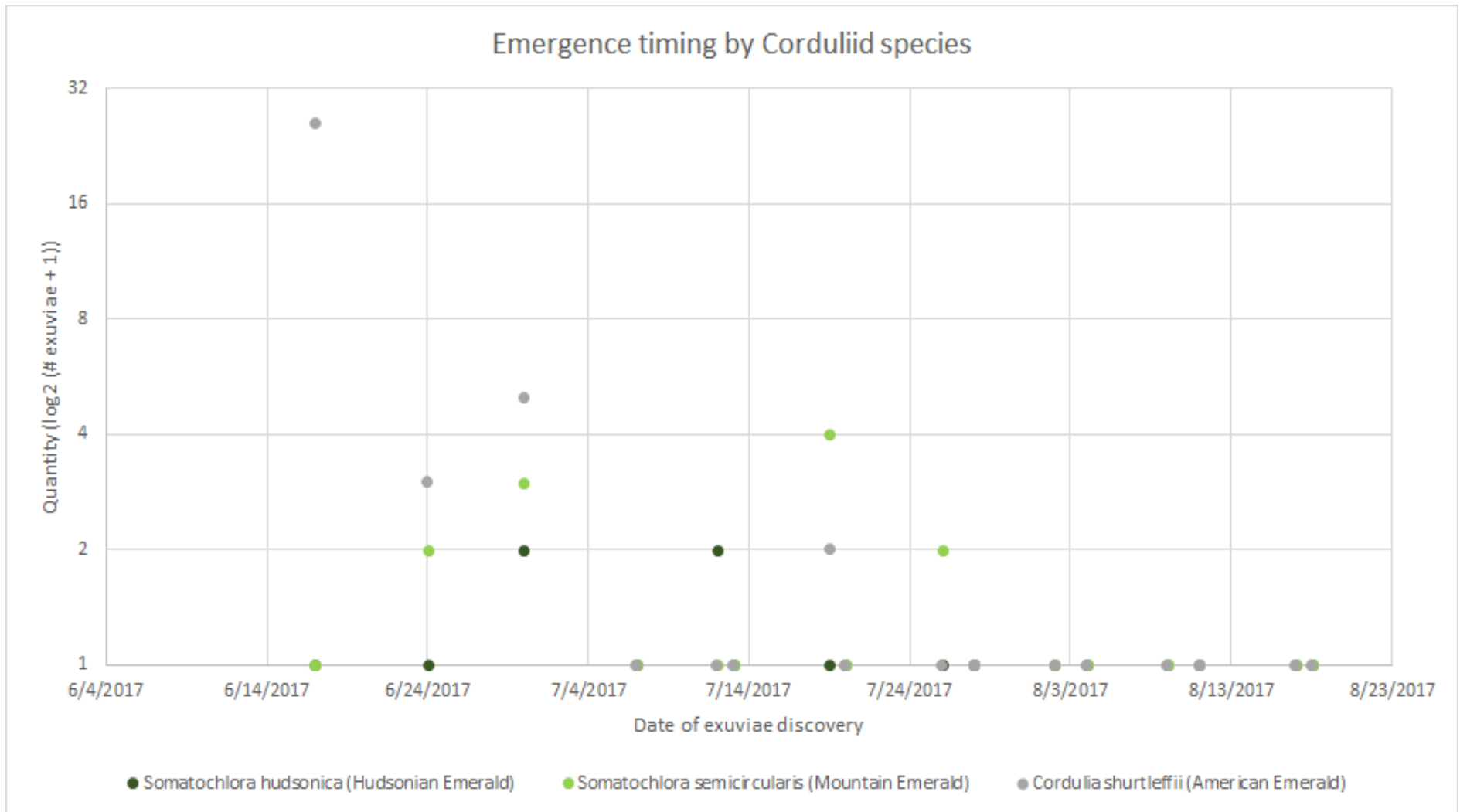
**Figure 7.** Mean exuviae per plot separated by species (Corduliidae) and genus (all other dragonflies). Error bars shown are standard error.

### *Emergence Timing*

Here, we use exuvial discovery date as a proxy for dragonfly emergence date. Since we visited each site weekly, we expect the actual emergence to be no more than one week off. The major exception is exuviae collected during the first visit to a site, which may have been there for significantly longer. For a possible example, see *Cordulia shurtleffii* in Figure 9.

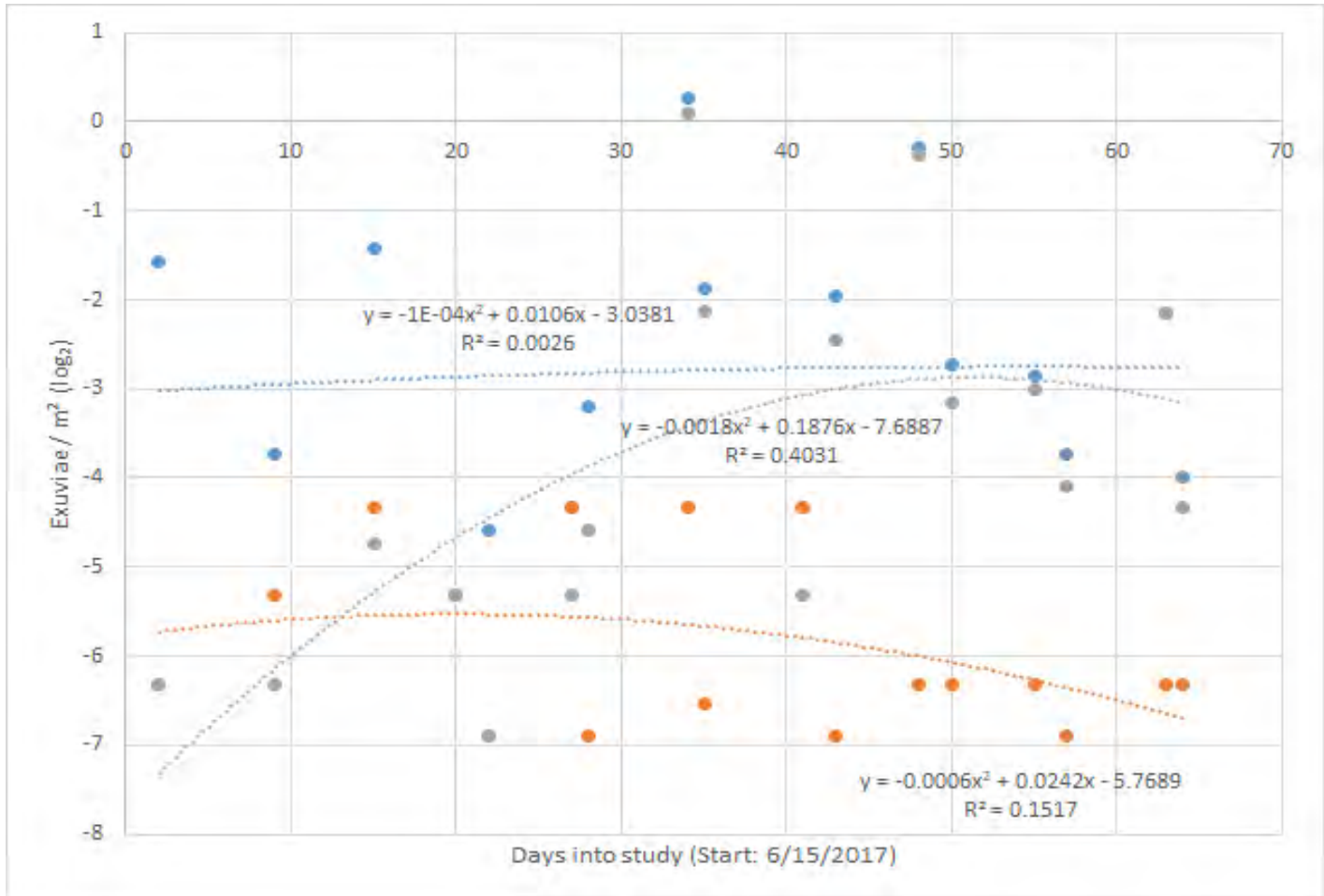


**Figure 8.** Exuviae of all anisopteran taxa discovered by calendar date. All quantities were increased by 1 because zeros are not represented on the log transformed y axis.



**Figure 9.** Exuviae of Corduliid species discovered by calendar date. All quantities were increased by 1 because zeros are not represented on the log transformed y axis.

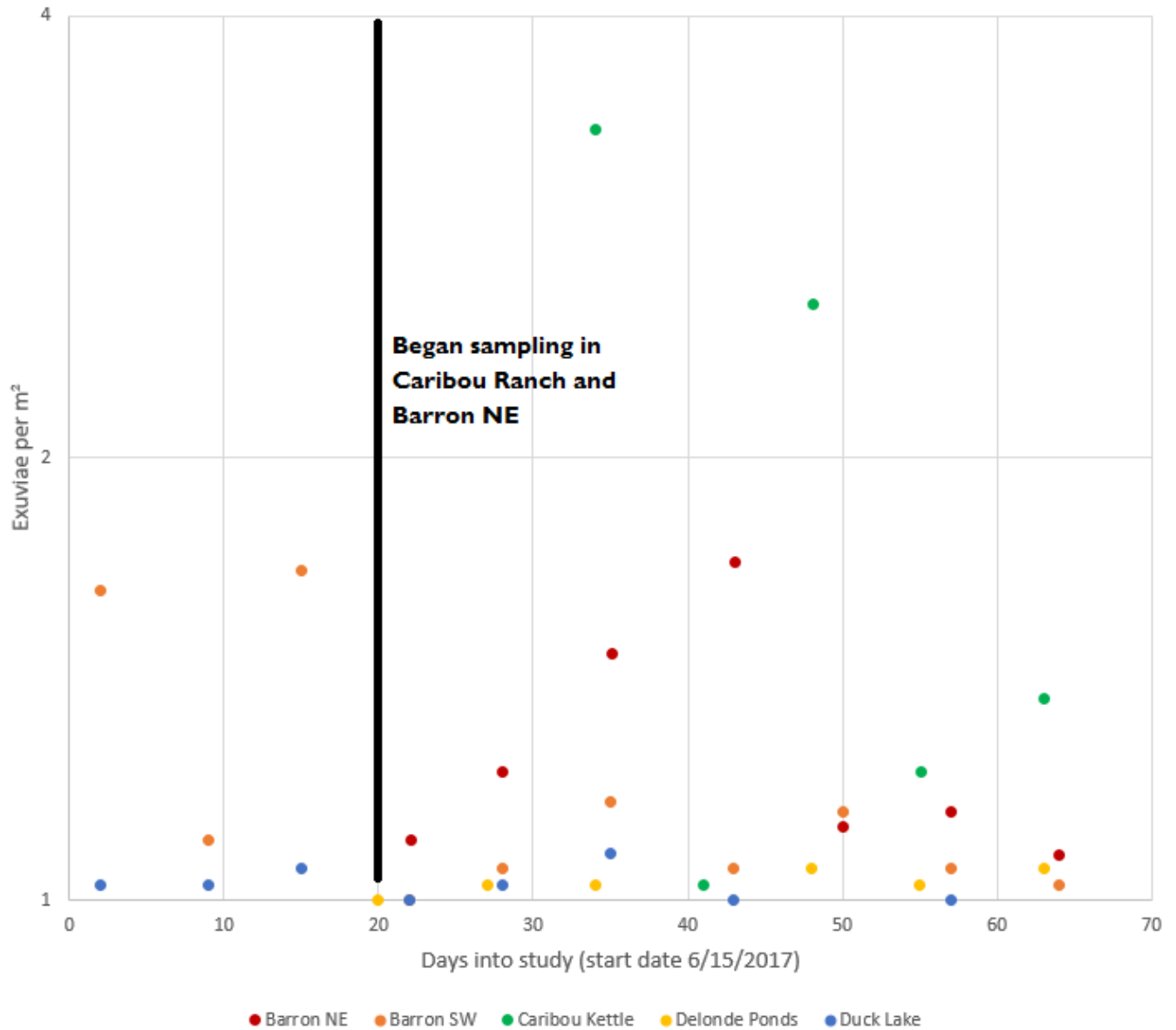
*Somatochlora* emergence peaks at 20 days (7/5/2017). 53 days (8/7/2017) is the peak of all dragonfly emergence. 52 days (8/6/2017) is the peak time for *Sympetrum* emergence. (Fig. 10). Peak emergence time for all dragonflies is driven by *Sympetrum* spp. The low R<sup>2</sup> for the gently sloping parabola of best fit for all dragonflies suggests that different species were emerging regularly throughout the 2017 sampling season.



**Figure 10.** Emergence times for *Somatochlora* sp. (orange), *Sympetrum* sp. (gray), and all dragonflies (blue) with parabolic lines of best fit, equations of those lines, and R<sup>2</sup> values. To accommodate calculations, dates are represented on the x axis as the number of days after 6/15/2017.

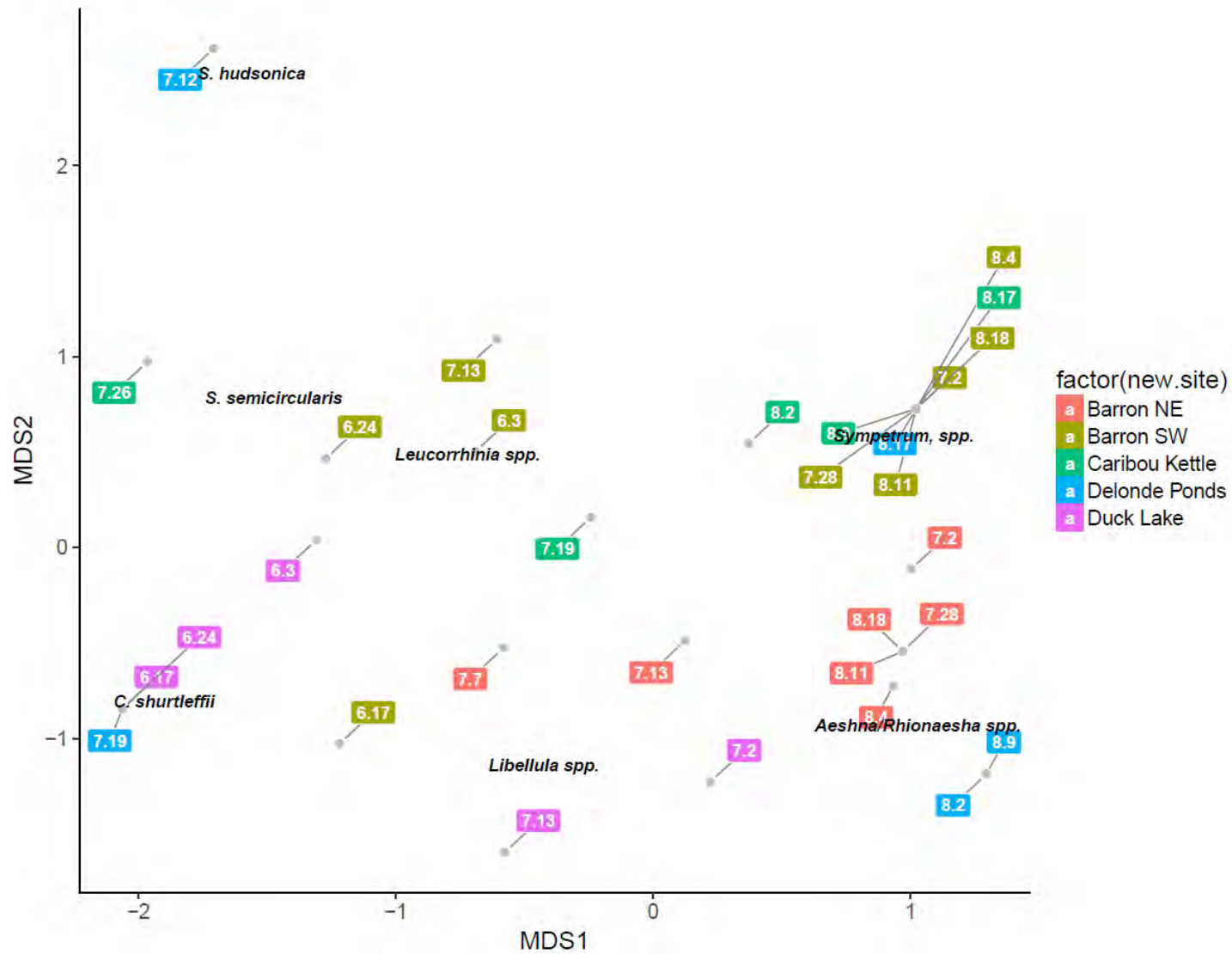
### Site Variation in Exuvial Density

Some sites were far more productive than others. We discovered the majority of exuviae at Caribou Kettle Pond, Barron North East, and Barron South West (Fig. 11). Bias was introduced by the late discovery of Barron NE for exuvia sampling, and late entry onto seasonally closed Caribou Ranch (Fig. 11).



**Figure 11.** Density of exuviae - all dragonfly taxa - over time. Broken down by collection site. Log<sub>2</sub> y scale transformation to increase visibility of low density sites. Exuvial density was increased by one to appear on logarithmic y axis.

The temporal and spatial dynamics of exuvial surveys is summarized by a two-dimensional non-metric dimensional scaling ordination (Figure 12).



**Figure 12.** Spatiotemporal variation in exuvial community structure.

#### *Habitat Associations from Exuvial Survey*

The two *S. hudsonica* exuviae came from two different sites: Barron SW, an isolated, rocky-bottomed, high-altitude kettle wetland (precipitation-fed) in the Barron parcel, and Delonde Ponds, a lower-altitude string of mucky ponds along Delonde Creek near the well-traveled Delonde homestead. The two sites are significantly different from one another (see Figure 18). Because of the very small sample size (n=2), and the diversity of the sites, it is

difficult to draw any conclusions about habitat associations. Exuvial survey data combined with adult surveys informs habitat association analysis in Figure 18 and Table 4.

**Table 2.** Summary of the two sites where *S. hudsonica exuviae* were recovered, regarding the habitat association hypotheses of this paper.

	<b>Barron SW</b>	<b>Delonde Ponds</b>
Forested area within 200 m of water?	Yes, all around	Yes in some parts, not in others
Presence of fish?	No	Yes
<i>S. semicircularis</i> exuviae?	Yes	No, but adults were captured
Presence of other dragonfly taxa?	Yes	Yes

#### *Captive Breeding of Somatochlora sp. at Butterfly Pavilion*

We collected eggs from three female *S. semicircularis* at Barron NE on 7/7/17, 7/13/17, and 7/20/17 respectively. They are labeled chronologically as broods 1, 2, and 3. Hatchlings were observed swimming among the eggs of broods 1 and 3 starting on 8/29/2017. As of November 15th, 2017, all 24 *S. semicircularis* larvae that were discovered as living hatchlings remain living. That represents a 64% survival rate for hatchlings from Brood 1, 37% survival rate for hatchlings from Brood 3, and an overall survival rate of 49% (Table 3). Brood 2 was very small (3 eggs) and none of them hatched in the fall. Most eggs in each brood contain developing embryos visible through a microscope (x40), and will diapause over winter (Table 3).

Most wild dragonfly larvae die before they emerge as adults. Among the most generous estimates is that “fewer than 10%” or 3-10% survive to emergence (measured for *Plathemis lydia*, *Libellula luctuosa*, *Ladona deplanata*, *Epitheca cynosure*, *Epitheca semiquea*, and *Celithemis fasciata*)<sup>32,33</sup>. Long-lived *Cordulia aenea amurensis* experienced 99.8% mortality over five years spent as an aquatic juvenile<sup>34</sup>. Soluk and DeMots estimated that Hine’s Emeralds survival rate from egg to mature larvae is less than 1-5.5%<sup>35</sup>. Most mortality in the wild is due to predation, including from conspecifics<sup>36</sup>. Much of early mortality in this case can be explained by cannibalism. The 100% survival of *S. semicircularis* after separation of hatchlings is a positive indicator of the Butterfly Pavilion’s ability to raise *Somatochlora* larvae in captivity.

**Table 3.** Summary of findings from captive rearing of *Somatochlora semicircularis* from eggs in 2017.

	Brood #		
	1	2	3
Oviposition date	7/7/2017	7/13/2017	7/20/2017
Total eggs	62	3	143
Live hatchlings (days since oviposition)	14 (53)	0*	6 (40); 7 (43); 10 (63)**
Hatched/broken eggs by November 15, 2017	22	0	27
Unfertilized eggs	0	0	9
Remaining viable eggs by November 15	40	3	107
Proportion eggs hatched pre-winter	35%	0%	19%
Larval survival past 2nd instar	64%	n/a	37%
Range larval lengths on November 15 in mm	2.5 - 3.5	n/a	1.3 - 3.0
Mean larval length on November 15 in mm (n)	3.0 (5)	n/a	2.3 (8)

\* Brood 2 includes only three eggs, none of which have hatched as of November 15th, but all appear fertilized (darkened).

\*\* Numbers of hatchlings are additive. In this case, larvae hatched on three occasions, producing 6, 1, and 3 live hatchlings for a total of 10.

#### Marking Trial

We chose one site, Barron NE, to mark individuals over a two week (two visit) period. On July 13<sup>th</sup> and July 20<sup>th</sup>, 2017, we captured three total adult male *S. hudsonica*, which we marked and released taking care to minimize handling time (Fig 14). The numbered markers appeared well affixed, and once released, the dragonflies flew quickly and strongly high into the trees of the adjacent forest. During following weeks, we searched for the marked individuals at each exuvial study site, but did not see or recapture them.

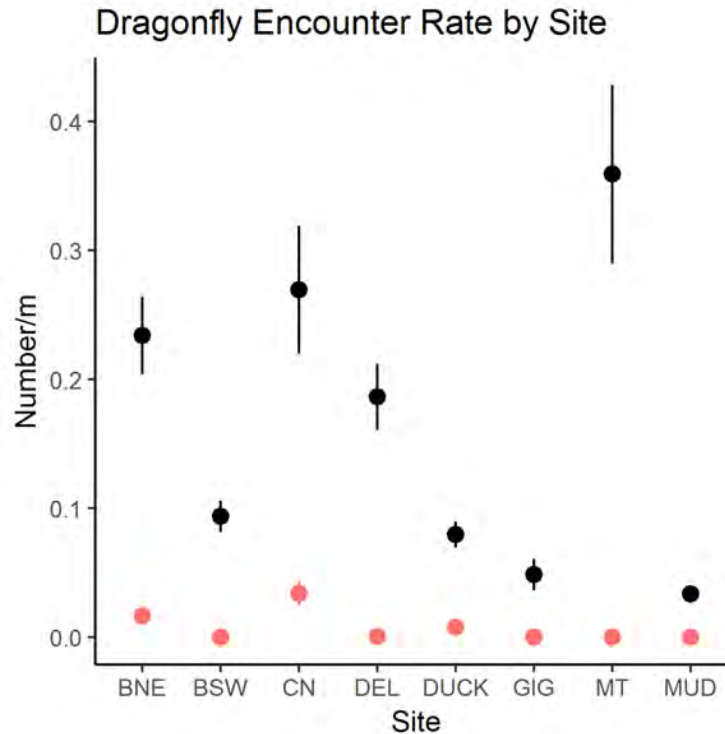




Figure 14: Marked *S. hudsonica*. Photograph by Katrina Loewy and Nick Coon

### Adult Survey Results

After conducting three transect surveys at each of the eight survey locations, we caught and released *S. hudsonica* adults at four sites: Barron NE, Caribou North, Delonde Ponds, and Duck Lake. Across all eight sites, the relative abundance of *S. hudsonica* compared to total dragonflies (damselflies excluded) is 4.8%. Including damselflies, the relative abundance of *S. hudsonica* is only 1.2% on average across all eight sites. If we focus only on sites where *S. hudsonica* was found, these average numbers rise to 6.6% and 1.8% respectively. Encounter rates for dragonflies (i.e. number of dragonflies/m) and *S. hudsonica* varied significantly by site (Fig. 15). Our highest encounter rate for dragonflies occurred at Barron NE, Caribou North, Delonde Ponds, and Minnick-Thompson. *S. hudsonica* encounter rate was most prominent at Caribou North and Barron NE.

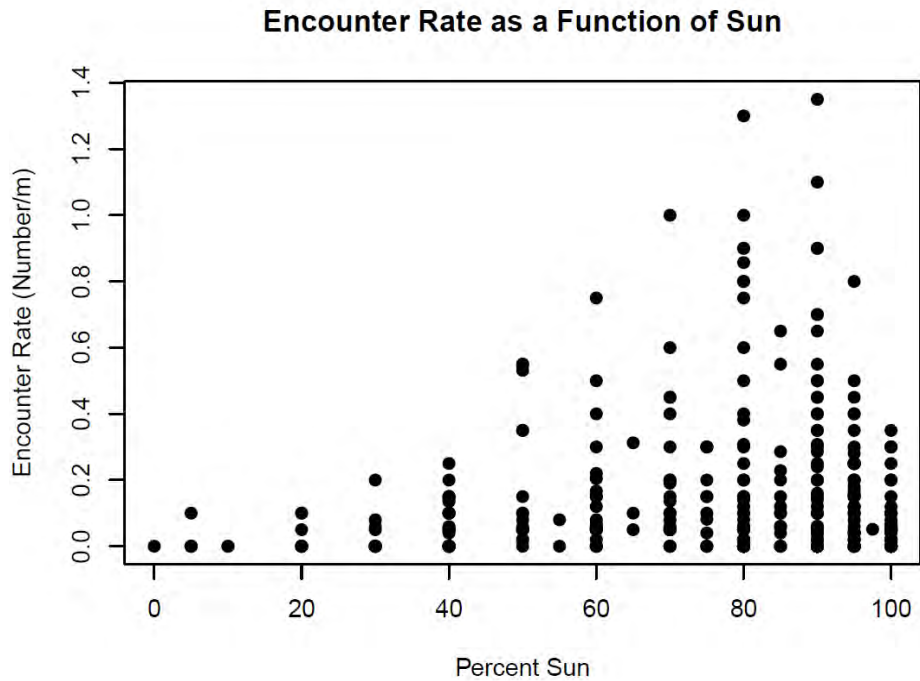


**Figure 15.** Average encounter rates by site (black = all dragonflies, red = *Somatochlora hudsonica*)

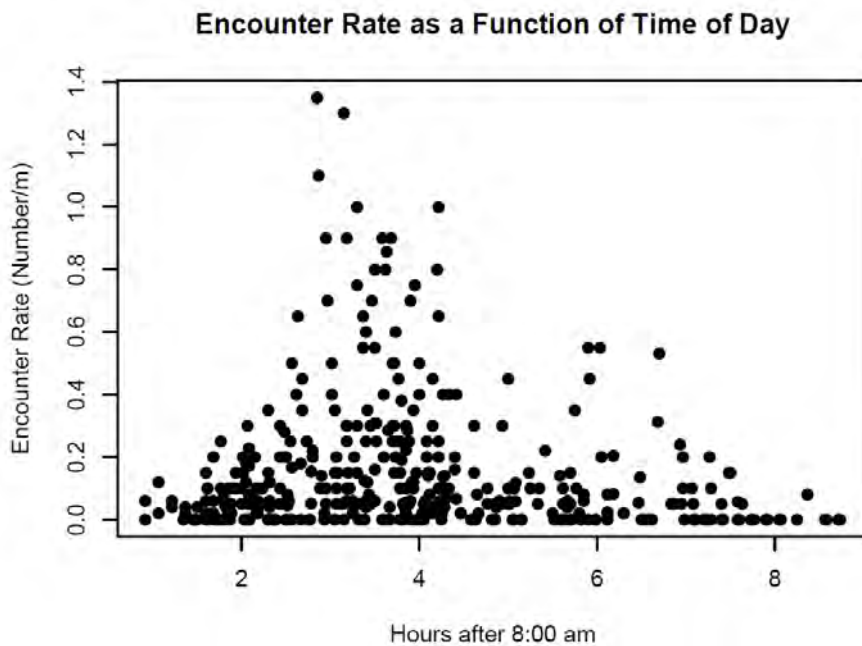
For all dragonflies and *S. hudsonica*, we modeled the  $\log(x+1)$  encounter rate using a linear mixed model. The fixed effects in the model included percent sun, days since June 15, and quadratic time of day, average habitat score, and an interaction between percent sun and time of day. The random effects included observer, site, and transect within site. For all dragonflies we find a positive relationship between % sun and encounter rate ( $p = 0.0034$ ) such that a 10% increase in sun exposure corresponds to a 20% increase in the median encounter rate of dragonflies (Fig. 16). Furthermore, we found a significant quadratic relationship with time of day ( $p = 0.0004$ ), indicating a peak encounter rate at roughly 12:30 pm (Fig 17). We did not find a significant effect of habitat score ( $p = 0.95$ ), days since June 15 ( $p = 0.21$ ), or the interaction between percent sun and time of day ( $p = 0.31$ ) in our model. Residual random variation in  $\log(\text{encounter rate})$  is driven by all four random effects: 34% due to variation by sites, 10% due to variation in transects nested within sites, 20% due to interobserver variation, and 26% to residual variation.

The same fixed effects were not significant in a similar model of encounter rate of *S. hudsonica* in sites where it was found. Only days since June 15 showed a marginally significant negative effect on encounter rate ( $p = 0.098$ ) such that median encounter rate decreases by 8%

for every month that elapses during the summer. Residual random variation in log(encounter rate) for Hudsonian emeralds is driven by three random effects: 49% due to variation by sites, 14% due to variation in transects nested within sites, and 37% due to residual variation. Limited interobserver variability occurred for Hudsonian emerald encounter rate.



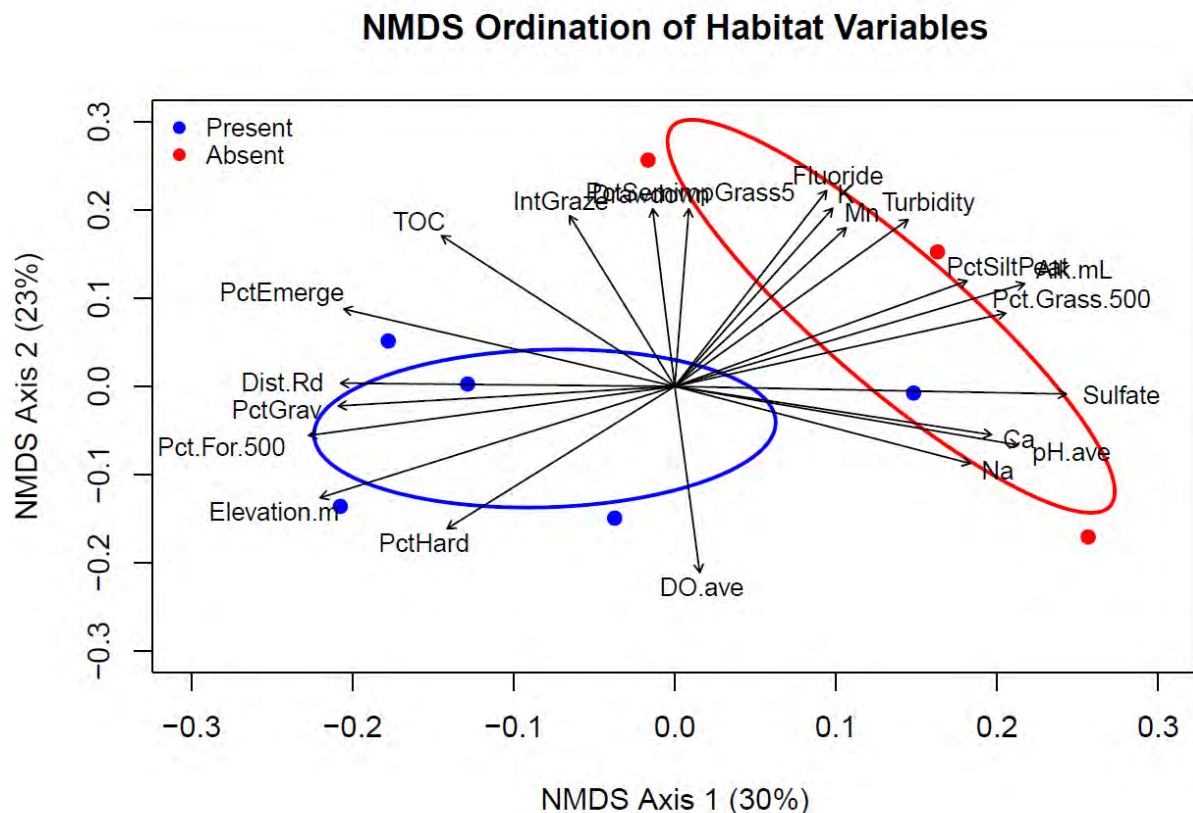
**Figure 16.** Total dragonfly encounter rate increases as % sun increases.



**Figure 17.** Total dragonfly encounter rate as a function of time of day.

## Habitat Associations

We also examined those habitat factors (both physical habitat and water quality) that differ between those sites where we observed and did not observe *S. hudsonica*. A two-dimensional NMDS ordination of the habitat distance (Gower's) among sites explains 53% of the variation in habitat among sites. Notably, sites where we observed *S. hudsonica* were distinct in ordination space from those where we did not observe the species ( $R^2 = 0.32$ , Fig. 18). Sites where we observed the species tended to be higher in elevation, forest land cover, emergent vegetation, substrate size (% gravel, % bedrock). In terms of water quality, sites where we observed *S. hudsonica* have lower pH and lower dissolved ions than those sites where we did not observe the species. Significant differences among habitat variables at  $\alpha = 0.05$  between areas where the Hudsonian emerald was found compared to where it was not found are indicated in Table 4.



**Figure 17.** Sites where *Somatochlora hudsonica* was found differ in physical habitat and water quality from those where *Somatochlora hudsonica* was absent.

**Table 4.** Significant differences in habitat variables between ponds where *Somatochlora hudsonica* is present and where it is absent.

Variable	90% Lower	90% Upper	Mean Absent	Mean Present
Elevation (m)	141.73	328.07	2591.67	2834.20
% of Margin with Overhanging Veg.	-19.17	-2.83	15.00	4.00
Turbidity - Visual	-1.27	-0.17	2.17	1.43
Percent Silt/Peat Substrate	-54.67	-10.67	90.00	57.67
Percent Hard/Bedrock Substrate	10.67	38.00	0.00	23.67
Percent Semi-Improved Grassland within 5 m	-36.67	-3.33	20.00	0.00
Water Quality for Amphibians - Visual	0.40	1.40	2.83	3.77
Potassium (mg/L)	-5.95	-1.70	5.33	1.50
Sodium (mg/L)	-28.39	-4.14	18.70	2.66
Magnesium (mg/L)	-11.59	-3.02	8.67	1.40
Calcium (mg/L)	-29.99	-6.09	23.40	5.56
Chloride (mg/L)	-123.59	-8.94	66.43	0.17
Fluoride (mg/L)	-0.20	-0.03	0.13	0.02
Total Dissolved Solids (mg/L)	-141.07	-33.45	102.72	15.71
Distance to nearest Road (m)	87.00	431.53	128.00	389.00
Percent Forest within 500m	6.00	28.67	71.67	90.00
Percent Grassland within 500 m	-27.00	-8.00	25.00	7.00
Percent Barren within 500 m	-5.00	-1.67	3.33	0.00
Alkalinity (mL titrant)	-8.81	-5.14	12.40	5.38

Finally, as an independent assessment of our *a priori* habitat suitability scores, we examined the average differences in habitat suitability between ponds where we observed *Somatochlora hudsonica* and ponds where we did not. Sites where the Hudsonian emerald was found had significantly higher ( $p < 0.1$ ) values of all three habitat suitability scores including a composite score consisting of the the sum of arithmetic, geometric, and model-based. All but the geometric mean score also significantly correlated with the NMDS ordination of habitat factors in our study ponds in the same direction as ponds where *S. hudsonica* was observed.

## Discussion

Prior to this study, we knew little of the whereabouts and ecological requirements of *S. hudsonica* in Boulder County. Not only have we confirmed the presence of this rare dragonfly species on Boulder County Parks and Open Space lands, but we have also learned more about the basic biology of this organism through a combined modelling and field approach. This newfound knowledge of the habitat associations, emergence timing and finer scale distribution of *S. hudsonica* can be used along with our burgeoning program of captive rearing to establish management and monitoring plans for its protection.

For the first time, we have documented the occurrence of *S. hudsonica* on Boulder County Parks and Open Space properties notably in Caribou Open Space, Duck Lake, and Barron land parcels. Both exuvial and adult field surveys indicate that *S. hudsonica* is quite rare. Because Boulder County lies at the southern-most edge of the known distribution of the species, it is unsurprising that the species comprises no more than 1-5% of the dragonfly assemblage in our exuvial and adult field surveys. The relative rarity of *S. hudsonica* highlights both the importance of identifying prime habitat for the species and the need for this study describing its habitat requirements and biology.

Based on past studies and observations of *S. hudsonica* and other *Somatochlora* species, we made several predictions regarding the habitat *S. hudsonica* would prefer in our region. Our observations and analysis corroborates Walker's prediction that *S. hudsonica* aquatic habitat would be found very near highly forested areas<sup>18</sup>. This finding indicates not only that forest is likely important for the species to forage away from the water, but also as a buffer against changes in water quality. Specifically, four out of the five sites where we observed *S. hudsonica* are sheltered ponds and lakes nearly surrounded by forest. Three of these are quite small kettle ponds that have lower alkalinity, dissolved ions, and pH in comparison to ponds where we did not observe *S. hudsonica*. These low concentrations not only highlight the need for pristine water conditions, but also the vulnerability of these waters to any changes to the surrounding land, such as by forest thinning or burning. Consequently, protecting forested buffer areas around small ponds will be of prime importance. In addition to these variables, larger substrate size and a higher proportion of emergent vegetation also appear to be important local-scale variables for *S. hudsonica* to thrive either because of its own habitat requirements or that of its prey. These are likely important for larval development and emergence because they might protect early instar larvae or serve as vegetation for emergence.

Other predictions we made based on literature on other congeners, did not prove true for *S. hudsonica*. For example, the congener *Somatochlora hineana* often dominates the dragonfly assemblage in habitats where it is found because it exploits habitats other dragonflies do not<sup>30</sup>. Conversely, we found both exuviae and adults of *S. hudsonica* at sites with many other dragonfly species. We also presumed that fish presence might exert top-down control on *S. hudsonica* breeding habitat because dragonfly larvae often make up a significant portion of fish diets<sup>33</sup>. However, we found *S. hudsonica* in two locations where fish are also present, Duck Lake (adults) and Delonde Creek (exuviae and adults).

Future monitoring efforts can be guided by the results we report in this study. The habitat scoring system we constructed in this study can be used as a way to prioritize new areas for *S.*

*hudsonica* reconnaissance. We showed that significantly higher suitability scores were indeed found in areas where *S. hudsonica* is present and where local habitat is suitable for the species. Thus, if we target small heavily forested ponds from 2500-3000 meters in elevation, we are likely to also find local conditions which favor presence of *S. hudsonica*.

Finding appropriate monitoring locations (i.e. where?) is no more important than monitoring at the right time of year (i.e. when?). Our findings support an earlier emergence period than previously reported for *S. hudsonica*. While Ann Cooper reported a flight period of mid-July through early August in the Colorado Front Range<sup>19</sup>, Dennis Paulson reported flight seasons for Yukon (June - August), British Columbia (May - August) and Montana (July - August) in Canada and the United States<sup>9</sup>. Our analysis of occurrence records shows earlier emergence at lower latitudes, and our field surveys support earlier flight times for the species. We first observed a mature adult male on June 28, 2017, which means it would have had to emerge at some point prior to that. The first *S. hudsonica* exuvia (of two) was found on June 30, 2017, and the peak emergence for *Somatochlora* sp. was estimated to be about July 5, 2017. Further corroborating this finding, we observed a decline in the encounter rate of *S. hudsonica* over the course of our monitoring throughout the summer. This implies that our study began after the peak in emergence. In future monitoring, we recommend moving the start date to early June or late May. Furthermore, our findings also recommend that adult surveys take place within the 10 am -2 pm timeframe under high sun conditions.

Curiously, the adult and exuvial surveys differed in their report of *S. hudsonica* occurrence, a finding which indicates the importance of studying a species throughout its life cycle. For example, peak exuvial discovery time was about 10 days earlier than peak adult observations, which could reflect the time it takes *Somatochlora* spp. to mature. Additionally, we collected an exuvia at one location (Barron SW) where no adults were observed. That could be explained by the rarity of *S. hudsonica* – adults were not observed at the site because they are uncommon in general - or it could be due to adult dispersal to more suitable habitats. It is also possible that the quality of the site for mating and oviposition may have changed over the (estimated) three years it takes for a larva to mature and emerge.

The more common trend was to find adults at locations with no *S. hudsonica* exuviae. While exuvial sampling provides the best evidence of breeding habitat, there are limitations with it as well. Exuvia sampling significantly underestimates species abundance. Our method of sampling once a week meant that we likely missed many exuviae, especially after storms and in unsheltered areas. Again, we may have missed emergences that happened before we accessed the sites. Variation among sites in exuvial density was extreme. We only collected

seven total dragonfly exuviae from Delonde Ponds, although many adults were observed, including teneral that, at other sites, were observed within inches of their molts. This discrepancy may be related to higher moose and elk grazing pressure that disturbs recent exuvial molts.

In sum, our analysis strongly indicates that *S. hudsonica* is imperiled by living on the edge of its distributional range. We showed that at the southern edge of its range, *S. hudsonica* can only be found at higher elevations. Thus, in the face of a warming climate, we can only expect that *S. hudsonica* would shift its distributions to higher elevations in order to maintain its thermophysiology. If so, an absolute barrier of tree line would preclude establishment of *S. hudsonica* at higher elevation. Such thermal restriction highlights the necessity of protecting small, snow-fed mountain ponds from other anthropogenic disturbances that could prevent them from providing adequate habitat. Such disturbances include deforestation by thinning and burning, livestock grazing, pollution from nearby roads and other point sources as well as more severe effects like dredging and filling. Given this finding, presence of *S. hudsonica* within its elevational range might be used to indicate high quality aquatic habitat along forest-aquatic ecotones within montane forests throughout the county. Conversely, absence of the species could hint at recreational or forestry related impacts to aquatic resources.

Despite the significant amount of knowledge gained from our joint collaboration on evaluating *S. hudsonica* habitat, many questions still remain unanswered with regard to the basic ecology of this imperiled species. To unravel these mysteries, we recommend a focused in-depth study earlier in the year at the Barron NE pond where we found numerous *S. hudsonica* specimens. Not only would this limit disturbance to potentially high suitability areas, but it would allow a different set of questions to be answered. Future studies might involve:

- (1) A concerted effort to find females to support captive rearing of *S. hudsonica* in the same manner as current, thriving *S. semicircularis* have been reared at the Butterfly Pavilion.
- (2) A more dedicated mark-recapture study to estimate population size at ponds. In 2017, we marked three male *S. hudsonica*, which we never saw or captured again, which highlighted the need for greater focus on this aspect of the study.
- (3) Determine fine scale habitat associations (vegetation diversity, emergence, substrate sizes at emergence site) for larvae in ponds.



## Acknowledgements

Thank you to Boulder County Parks and Open Space, which contributed both financially and logistically. We thank Butterfly Pavilion Intern, Nick Coon, and volunteers Rebecca Otey and Wendy Elliott, who contributed significantly to sample collection, record keeping, and captive dragonfly care. We also appreciate Mary Ann Colley and Rich Reading of the Butterfly Pavilion for their support. We thank Regis students Andrew Pitluck, Alyssa Herrin, Colin Martin, Jesse Rosso, and Catherine Devitt for field assistance and GIS expertise. We also thank Colorado Mountain College and Colorado School of Mines for conducting water quality analyses.

## References

1. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* (80-. ). **345**, 401–406 (2014).
2. Martin-Lopez, B., Montes, C. & Benayas, J. The non-economic motives behind the willingness to pay for biodiversity conservation. *Biol. Conserv.* **139**, 67–82 (2007).
3. Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B. & Worm, B. How many species are there on Earth and in the ocean? *PLoS Biol.* **9**, 1–8 (2011).
4. Strayer, D. L. & Dudgeon, D. Freshwater biodiversity conservation: recent progress and future challenges. *J. North Am. Benthol. Soc.* **29**, 344–358 (2010).
5. Simaika, J. P. & Samways, M. J. in *Dragonflies & damselflies: Model organisms for ecological and evolutionary research* (ed. Cordoba-Aguilar, A.) (Oxford University Press, 2008).
6. Tennessen, K. What to feed newly-hatched dragonfly nymphs? *Argia* **28**, 19–22 (2016).
7. Colorado Natural Heritage Program. *Colorado Wildlife Action Plan : Rare Plant Addendum By the Colorado Natural Heritage Program.* (2015).
8. Packauskas, R. J. Hudsonian Emerald Dragonfly (*Somatochlora hudsonica*): A Technical Conservation Assessment. *USDA For. Serv. Rocky Mt. Reg.* (2005).
9. Paulson, D. *Dragonflies and Damselflies of the West.* (Princeton Field Guides, 2009).
10. Colorado Natural Heritage Program. *Conservation status handbook: Colorado's animals, plants, and plant communities of special concern.* (1999).
11. Abbot, J. C. OdonataCentral: An online resource for the distribution and identification of Odonata. (2017).
12. Cooper, A. *Dragonfly and damselfly surveys on Boulder County Open Space.* (2014).
13. Cooper, A. *Dragonfly and damselfly surveys on Boulder County Open Space.* (2015).
14. Cooper, A. *Dragonfly and damselfly surveys on Boulder County Open Space.* (2016).
15. Boulder County Parks and Open Space. *Description of critical wildlife habitat areas.* (2013).
16. Dunkle, S. W. *Dragonflies through binoculars.* (Oxford University Press, 2000).
17. Needham, J. G., Westfall, M. J. J. & May, M. L. *Dragonflies of North America.* (Scientific Publishers, 2000).
18. Walker, E. M. *The North American Dragonflies of the Genus Somatochlora.* (University of Toronto Press, 1925).
19. Cooper, A. *Dragonflies of the Colorado Front Range.* (Boulder County Nature Association, 2014).

20. Corbet, P. S. *Dragonflies: Behavior and Ecology of Odonata*. (Cornell University Press, 1999).
21. Foster, S. E. & Soluk, D. A. Protecting more than the wetland: The importance of biased sex ratios and habitat segregation for conservation of the Hine's emerald dragonfly, *Somatochlora hineana* Williamson. *Biol. Conserv.* **127**, 158–166 (2006).
22. Šigutová, H., Šigut, M. & Dolný, A. Intensive fish ponds as ecological traps for dragonflies: an imminent threat to the endangered species *Sympetrum depressiusculum* (Odonata: Libellulidae). *J. Insect Conserv.* **19**, 961–974 (2015).
23. DeMots, R. Personal interview.
24. US Fish & Wildlife Service. *Habitat evaluation procedures handbook*. (1981).
25. Peterson, T. A. *et al.* *Ecological niches and geographic distributions*. (Princeton University Press, 2011).
26. Franklin, J. *Mapping species distributions: Spatial inference and prediction*. (Cambridge University Press, 2009).
27. Moore, N. W. & Corbet, P. S. Guidelines for monitoring dragonfly populations. *J. Br. Dragonfly Soc.* **6**, 21–23 (1990).
28. Ausden, M. & Drake, M. in *Ecological census techniques* (ed. Sutherland, W. J.) (Cambridge University Press, 2006).
29. Foster, S. E. & Soluk, D. A. Evaluating exuvia collection as a management tool for the federally endangered Hine's emerald dragonfly, *Somatochlora hineana* Williamson (Odonata: Cordulidae). *Biol. Conserv.* **118**, 15–20 (2004).
30. Aliberti Lubertazzi, M. A. & Ginsberg, H. S. Persistence of Dragonfly Exuviae on Vegetation and Rock Substrates. *Northeast. Nat.* **16**, 141–147 (2009).
31. Cashatt, E. D. & Vogt, T. E. Description of the larva of *Somatochlora hineana* with a key to the larvae of the North American species of *Somatochlora* (Odonata: Corduliidae). *Int. J. Odonatol.* **4**, 93–105 (2001).
32. Wissinger, S. A. Comparative population ecology of the dragonflies *Libellula lydia* and *Libellula luctuosa* (Odonata: Libellulidae). *Can. J. Zool.* **67**, 931–936 (1989).
33. Benke, A. C. Dragonfly Production and Prey Turnover. *Ecology* **57**, 915–927 (1976).
34. Ubukata, H. Survivorship curve and annual fluctuation in the size of emerging population of *Cordulia anenea amuriensis* Selys (Odonata: Corduliidae). *Japanese J. Ecol.* **31**, 335–346 (1981).
35. U.S. Fish and Wildlife Service. *Hine's Emerald Dragonfly, Somatochlora hineana (Odonata: Corduliidae) 5-Year Review: Summary and Evaluation*. (2013).
36. Benke, A. C. Interactions Among Coexisting Predators--A Field Experiment with Dragonfly Larvae. *J. Anim. Ecol.* **47**, 335–350 (1978).