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Thermally moderated firefly activity is delayed by precipitation extremes

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20 **Abstract**

21 The timing of events in the life history of temperate insects is most typically primarily cued by one of
22 two drivers: photoperiod or temperature accumulation over the growing season. However, an insect's
23 phenology can also be moderated by other drivers like rainfall or the phenology of its host plants. When
24 multiple drivers of phenology interact, there is greater potential for phenological asynchronies to arise
25 between an organism and those it interacts with. We examined the phenological patterns of a highly
26 seasonal group of insects, the Eastern Firefly (*Photinus pyralis*) over a 12-year period (2004–2015) across
27 10 plant communities to determine if interacting drivers could explain the variability observed in the
28 adult flight activity density (*i.e.* mating season) of this species. We found that temperature accumulation
29 was the primary driver of phenology with activity peaks usually occurring at a temperature accumulation
30 of ~800 degree days (base 10°C), however, our model found this peak varied by nearly 180 degree day
31 units between years. This variation could be explained by a quadratic relationship with the accumulation
32 of precipitation in the growing season; in years with either high and low precipitation extremes at our
33 study site, flight activity was delayed. More fireflies were captured in general in herbaceous plant
34 communities with minimal soil disturbance (alfalfa and no-till field crop rotations), but only weak
35 interactions occurred between within-season responses to climatic variables and plant community. The
36 interaction we observed between temperature and precipitation accumulation suggests that, although
37 climate warming has potential to disrupt phenology of many organisms, changes to regional
38 precipitation patterns can magnify these disruptions.

39 **Keywords: Lightning bug, lampyridae, phenology, ecoinformatics, LTER**

40

41 Introduction

42 Much can be learned about biological systems by observation alone (Rosenheim et al., 2011),
43 and observational data are often captured incidentally as a result of human activity (Bahlai and Landis,
44 2016). Incidental data can range from the very informal and uncontrolled (e.g. comments on a topic in a
45 web forum) to highly controlled and meticulously collected (e.g. unused data from scientific
46 experiments). Indeed, research activities can produce systemic observational data of very high quality;
47 for instance, insect trapping systems seldom only capture target taxa. This 'by-catch' can provide data
48 which supports investigations into entirely uninvestigated phenomena. In this study we examine one
49 such 'by-catch' data set: a 12-year time series of firefly observations in southwestern Michigan for their
50 responses to environmental and habitat conditions.

51 Over 2,000 species of firefly (Coleoptera: Lampyridae) have been identified across various
52 temperate and tropical environments around the world (Wang et al., 2007). As larvae, species within the
53 family Lampyridae spend much of their time living underground feeding on earthworms, mollusks, and
54 other subterranean invertebrates (Wing, 1989). As adults, most species abstain from feeding (Hess,
55 1920), with the exception of the species *Photuris pennsylvanica*, of which the female is a voracious
56 predator of both con-specifics as well as other insects (Eisner et al., 1997; Hess, 1920; Williams, 1917).
57 Few studies been conducted on firefly conservation and broader-scale ecology in relation to changing
58 environments and land uses, and little is known about how environmental parameters drive firefly life
59 history. However, it has been demonstrated that the life history of at least one species of firefly is
60 temperature-dependent; researchers found that *P. pennsylvanica* adult emergence could be artificially
61 accelerated by exposing larvae to increased soil temperature (Keiper and Solomon, 1972). Much of the
62 primary research on fireflies has focused on the bio-luminescent properties of the firefly abdomen.
63 These studies include, but are not limited to, the molecular/genetic properties of bio-luminescence
64 (Branchini et al., 2002; Schaap and Gagnon, 1982), spectral emission and quantum yield of bio-

65 luminescence (Seliger et al., 1964) and the use of bio-luminescence in firefly mating ecology (Branham
66 and Wenzel, 2003; Lall et al., 1980; Lloyd, 1997) .

67 In addition to the scientific importance of the Lampyridae for their bio-luminescent properties
68 and as model organisms for evolutionary investigations, fireflies are also among the most widely
69 recognized and culturally valued insect families among non-scientists. Two US states have designated a
70 firefly as their “State Insect” (National Museum of Natural History, 2013). Notably, fireflies also feature
71 prominently in Japanese culture, where they have been designated as national natural treasures in
72 many districts and have been used to generate support of biodiversity conservation efforts in Japanese
73 agricultural regions (Kobori and Primack, 2003; Takada, 2011; Takeda et al., 2006). They have also been
74 touted as useful classroom tools for sparking student interest in biology (Faust, 2004). Because of their
75 popular appeal, it is unsurprising that public concern has grown about apparent declines of firefly
76 populations from regions around the world where they occur (Gardiner, 2009).

77 Considering the paucity of ecological information about fireflies, widespread popularity, ease at
78 which they are observed, and concerns about their population viability, fireflies represent an ideal
79 species for citizen science investigations. Citizen science efforts are currently underway seeking to gain
80 information about the status, geographic distribution, and phenology of fireflies (Chow et al., 2014;
81 “Firefly Watch,” 2016; Scagill, 2016) and peer-reviewed publications on fireflies have already been
82 produced based on these volunteer-generated data (Faust and Weston, 2009; Picchi et al., 2013). The
83 popularity of fireflies gives them great potential as a flagship and umbrella conservation species and
84 potentially an indicator species of ecological degradation in agricultural regions (Guiney and
85 Oberhauser, 2008). However, to our knowledge, no long term systematic study of firefly phenology and
86 responses to environmental drivers has been published.

87 Phenology plays a significant role in regulating species abundance, distribution, and biodiversity
88 (Diez et al., 2012; Miller-Rushing et al., 2010). The timing of phenological events in insect life histories is
89 strongly linked to climatic conditions (Parmesan, 2006; Root et al., 2005; Rosenzweig et al., 2008) such
90 as temperature and precipitation (Crimmins et al., 2010, 2008; Diez et al., 2012). Changes in
91 phenological timing can have community-wide consequences, and differential responses among various
92 species within a community can lead to trophic mismatches (Miller-Rushing et al., 2010; Parmesan,
93 2006). For example, the timing of larval winter moth (*Operophtera brumata*) emergence was formerly
94 largely synchronized with oak (*Quercus robur*) bud burst. Caterpillars that emerge too early lack a
95 sufficient food source and will starve, while caterpillars that emerge too late will be exposed to older,
96 poor quality leaves, leading to negative physiological implications (Visser and Holleman, 2001).
97 Increased spring temperature has resulted in changes in the timing of oak bud burst. However, the
98 winter moth has yet to adapt to changing temperatures, which has led to disrupted synchrony between
99 these two species (Visser and Holleman, 2001). Thus, phenological shifts can have both top-down and
100 bottom-up consequences extending throughout multiple trophic levels. Long term observations are
101 important for understanding ecological trends and the merit of phenology as a predictor of ecological
102 consequences. A long term study on the Genji firefly (*Luciola cruciate*) in Japan found that populations
103 fluctuated in response to rainfall, potentially leading to early larval emergence and reduced foraging
104 (Yuma, 2007). However, the ways in which climate change and other environmental events have
105 impacted firefly species is less understood.

106 Developing a model for the emergence of adult fireflies is key to developing our understanding
107 of firefly phenology, which can then be used to expand firefly conservation efforts, educational
108 outreach, environmental research, and to predict peak firefly display. In this study, we examine a ‘by-
109 catch’ dataset documenting captures of fireflies at the Kellogg Biological Station over a 12-year period

110 and place it in the context of other available data to gain insights into the long-term dynamics and
111 phenology of this charismatic, but understudied taxon.

112

113 **Methods**

114 ***Data sources***

115 Data were obtained through two publicly available data sets—a weather data set which
116 included daily maximum and minimum temperature and precipitation, as well as a data set that focuses
117 on ladybeetle observations, but also documents captures of the other insect species. Both data sets
118 arise from Michigan State University's Kellogg Biological Stations (KBS), located in southwestern
119 Michigan. The firefly abundance data were collected as a part of the KBS Long Term Ecological Research
120 (LTER) site within the Main Cropping System Experiment (MCSE) and forest sites starting in 2004.
121 Fireflies were recorded to family alone, however, from spot-checks of the collected data, it appears the
122 majority of fireflies collected belonged to the species *Photinus pyralis*, the common eastern firefly.

123 Within the MCSE, seven plant community treatments were established in 1989 ranging from a
124 three-year rotation of annual field crops (maize, soybean, wheat) under four levels of management
125 intensity (conventional, no-till, reduced input, or biologically based) to perennial crops including alfalfa,
126 poplar and early successional vegetation (*i.e.* abandoned agricultural fields maintained in an early
127 successional state by yearly burnings; Table 1). Each of these treatments is replicated six times across
128 the MCSE site with each replicate consisting of a 1 ha sized plot. We also included three forest sites in
129 our analysis, these sites were established in 1993 within 3 km of the MCSE site on KBS and represent
130 one of three plant community treatments: conifer forest plantations; late successional deciduous forest;
131 and successional forest arising on abandoned agricultural land (Table 1). Forested treatment plots are
132 also 1 ha in size but are replicated three times for each treatment.

133 Observations were taken on a weekly basis throughout the sampling season at five sampling
134 stations within each replicate (both MCSE and forest sites). These insect abundance data are available
135 publicly, online at <http://lter.kbs.msu.edu/datatables/67>. Insect abundance monitoring was done using
136 un-baited two-sided yellow cardboard sticky cards (Pherocon, Zoecon, Palo Alto, CA) suspended from a
137 metal post within each sampling station 1.2m above the ground. Cards were deployed each week for a
138 one-week exposure for the duration of the growing season (14 ± 1 weeks, on average, per year).

139 In addition to plant community treatment management information, we also included weather
140 as environmental factor to explain firefly abundance. These data were also obtained through a publicly
141 available data set, online at <http://lter.kbs.msu.edu/datatables/7>.

142 ***Data pre-processing***

143 All analyses performed are available as an R script at <https://github.com/cbahlai/lampyrid/>.
144 Analyses presented in this manuscript were run in R 3.3.1 “Bug in Your Hair” (R Development Core Team
145 2016). Firefly data were extracted from the database held at the KBS data archive and combined with
146 relevant agronomic data (which are encoded in plot and treatment numbers in the main database) and
147 are hosted at figshare at <https://ndownloader.figshare.com/files/3686040>.

148 Data were subject to quality control manipulations to remove misspellings in variable names
149 which had occurred with data entry. Observations with missing values for firefly counts were excluded
150 from analysis. Because subsample data was zero-biased, we used reshape2 (Wickham, 2014) to sum
151 within date, within plot numbers of captures, and created an additional variable to account for sampling
152 effort (which was usually consistent at five traps per plot per sampling period, but on occasion traps
153 were lost or damaged).

154 Weather data (daily maximum and minimum temperatures were reported in °C and daily
155 precipitation in mm) were downloaded directly from the Kellogg Biological Station Data archive

156 (<http://lter.kbs.msu.edu/datatables/7.csv>). To overcome errors in calculations requiring accumulated
157 annual weather data caused by rare missing data points (most often occurring during winter, in periods
158 of extreme cold leading to equipment malfunction), we created a function to replace missing values in
159 the temperature data with the value that was observed for that variable from the day before the
160 missing observation.

161 We created a dummy variable for ‘start day’ to enable the user to easily test the sensitivity of
162 our conclusions to varying our within-year start of accumulation of environmental conditions. We
163 empirically determined that March 1 (start = 60) provided the best compromise between capturing early
164 growing season weather variation and negating brief variation in winter conditions, however, the
165 selection of the precise day did not dramatically influence the overall trends in the results.

166 We then created a function to calculate daily degree day accumulation and season-long degree
167 day accumulation based on Allen’s (Allen, 1975) double sine function, using our daily maximum and
168 minimum temperature data. We created a dummy variable for our minimum development threshold to
169 facilitate sensitivity analysis, but set it to a default value of 10°C. We did not use a maximum
170 development threshold in our calculation, assuming temperatures exceeding its hypothetical value
171 (often >35°C for temperate insects) were rare. Accumulations were calculated from the start day
172 variable, as described above. We also created functions that calculated the accumulation of
173 precipitation over the sampling week, the accumulation of precipitation over the growing season, from
174 the start date, and the number of rainy days in a sampling period. Weather data were merged with
175 firefly data to facilitate subsequent analyses.

176 ***Data analysis***

177 We used ggplot2 (Wickham, 2009) to visualize trends in captures of fireflies by plant community
178 treatment over years. We then conducted a multivariate analysis to determine if firefly plant community

179 use patterns changed within or between years, and what environmental factors were associated with
180 plant community use patterns. To accomplish this, data were cast as a date-by-treatment matrix at two
181 resolutions (weekly observations and yearly observations), transformed using the Wisconsin
182 standardization, and Bray-Curtis differences were subjected to non-metric multi-dimensional scaling
183 (NMDS) in vegan (Oksanen et al., 2013). Environmental parameters were fit to the NMDS plots using
184 envfit to determine if patterns were influenced by weather.

185 To examine patterns in firefly captures over time, and the interactions of these captures with
186 environmental variables, we visualized trends in capture data by sampling week and degree day
187 accumulation. Noting that degree day accumulation was associated with the clearest patterns in firefly
188 captures (see results), with some variation due to plant community, we built a generalized linear model
189 with a negative binomial structure to explain these patterns. The model included the degree day
190 accumulation in linear and quadratic forms as continuous variables, year and plant community
191 treatment as factors, and trapping effort as an offset variable (to account for lost or compromised
192 traps). After fitting the model, we used the resultant regression parameters to generate predicted
193 values, so we could visually compare the performance of the model to the raw data.

194 Because the model found year-to-year variation in the activity peak that was not explained by
195 degree day accumulation, we extracted the activity peaks from each year as predicted by the model to a
196 new data frame, and matched these data to other relevant environmental variables in the weather
197 matrix (week the peak occurred in, precipitation variables corresponding to that week). We visualized
198 the relationship between activity peak and other variables, and then constructed a generalized linear
199 model for a quadratic relationship between the activity peak, by degree days, and the precipitation
200 accumulation at the activity peak.

201 For all frequentist analyses, a significance level of $\alpha = 0.05$ was used.

202

203 **Results**

204 Visualizations of firefly capture data by treatment and time period revealed several patterns.
205 Numbers of fireflies captured in each trap varied by plant community type and across samples (Figure
206 1), but in general, more fireflies were captured in alfalfa and no-till row crop treatments. Average
207 numbers of fireflies captured per trap also demonstrated variation by year independent of plant
208 community treatment. Overlaid plots of average captures for all treatments against year (Figure 2)
209 suggest a 6–7 year firefly population cycle that appears uncorrelated with environmental variables.

210 Non-metric multi-dimensional scaling revealed only weak trends in patterns of capture between
211 plant community treatments at both the yearly and weekly resolutions. At the yearly resolution (Figure
212 3A), plant community treatment use varied slightly with the number of rainy days in the growing season
213 ($R^2 = 0.16$, $p = 0.006$, 2-D NMDS stress = 0.14) with herbaceous habitat use generally associated with
214 greater amounts of rainfall. At the weekly resolution (Figure 3B), 2D-NMDS stress was higher (0.19), but
215 a general trend away from forest plots was observed with increasing degree day accumulation ($R^2 =$
216 0.15 , $p = 0.001$) and week ($R^2 = 0.15$, $p = 0.001$).

217 When plotting firefly abundance by week of capture, the timing of the peaks in firefly
218 emergence show asynchrony among years (Figure 4A), indicating that week of year (and, by proxy, day
219 length) is not a strong driver of firefly emergence. However, plotting firefly numbers instead against
220 degree day accumulation dramatically reduced the asynchrony of emergence peaks (Figure 4B). Thus,
221 degree day accumulation appears to be a better predictor of firefly populations than week of year or
222 associated variables.

223 Our model for firefly activity incorporating degree day accumulation, crop, and year, performed
224 well at predicting the timing of the activity peaks (Figure 5), accounting for more than 40 percent of the

225 variation in the raw data. However, model selection favored the inclusion of a year term as a factor,
226 suggesting that another factor in addition to degree day accumulation was varying from year to year,
227 and impacting firefly activity. Activity peaks varied from year to year by nearly 180 degree-day units,
228 varying from 720 ± 38 DD in 2004 to 898 ± 55 DD in 2012 (Figure 6). However, we found the year-to-year
229 variation was well-explained by precipitation accumulation: a quadratic relationship occurs between
230 degree day at peak emergence and precipitation accumulation (pseudo- $R^2 = 0.456$, $p = 0.026$; Figure 7).

231

232 Discussion

233 The greatest proportion of fireflies were captured in alfalfa and no-till plant communities (Figure
234 1), indicating that areas with moderate soil disturbance and primarily herbaceous plant communities
235 favored firefly emergence. This result was unexpected; because fireflies spend much of their life cycle in
236 the soil, it may be expected that plots with little soil disturbance (coniferous, deciduous and successional
237 forests) would foster the greatest populations of fireflies. However, these plots produced capture rates
238 similar to those observed in the intensively managed and tilled conventional row crop plots. Our result
239 contrasted with observations of another genus of fireflies in Malaysia (*Pteroptyx*), where researchers
240 found that plant canopy structure was the most important determinant of abundance (Jusoh et al.,
241 2010). Also surprising was the relatively low capture rate in early successional plots, which are primarily
242 herbaceous, with no tillage regime. Thus, the yearly burnings may play a role in suppressing firefly
243 populations in these plots. An alternative explanation for these variations in captures could be
244 differences in trapping efficiencies between plant communities. However, if this were the case, we
245 would expect trapping efficiencies in the three other row crop treatments (conventional, organic and
246 reduced input management) not to differ appreciably from that of the no-till row crop plant community.

247 When plotted over sample years (Figure 2), captures of fireflies by treatment seem to suggest an
248 intriguing cyclical dynamic, with alternating peaks and troughs in captures on an approximately 6-year
249 cycle. Our time series only spans 12 years, meaning more data will be required to elucidate this pattern
250 and its drivers. Similarly, analysis of plant community use patterns was inconclusive (Figure 3). At the
251 weekly resolution there was a trend away from woody treatments over the growing season (Figure 3B;
252 *i.e.* with both increasing week and increasing degree day accumulation). Although this pattern was not
253 strong, it could result from fireflies overwintering in forest habitats and then moving to lower-canopy
254 herbaceous habitats for mating displays. We observed very similar performance of both degree day and
255 week, likely due to autocorrelation between the two variables that cannot be resolved at the sampling
256 resolution used over the course of the study.

257 Although both photoperiod and degree day accumulation can both play a role in the phenology
258 of insects, our results suggest that degree day accumulation is the dominant driver of firefly flight
259 activity. The model was unable to account for between trap variation within a single sampling day
260 (Figure 5), though it was able to capture the overall trends in activity quite well, using only degree day
261 accumulation, plant community treatment, and year as predictors. Nevertheless, degree day
262 accumulation was not the sole driver in within season variability. Our model found year-to-year
263 variability in activity peaks that could not be explained by degree day accumulation alone. We found
264 that this variation in activity peak by degree day accumulation had a quadratic relationship with
265 precipitation, indicating that both drought and heavy rainfall in the time period leading up to their
266 activity peak can delay the peak (Figure 7). Assuming a $\sim 20^{\circ}\text{C}$ daily average temperature at this site in
267 late June and early July, this could translate to a ten-or-more day change in activity peak due to
268 precipitation extremes in any given year.

269 In this study, we have clearly demonstrated a species whose phenology varies in response to
270 multiple drivers. Species with phenologic responses to multiple drivers are not rare (Wolkovich et al.,

271 2012). Yet ecological interactions among species with multiple drivers of phenology may be prone to
272 asynchrony (Hua et al., 2016), potentially leading to dire consequences in a changing environment
273 (McLaughlin et al., 2002). Our study examined the phenological responses to environmental conditions
274 of adult fireflies; however, data on larvae or sex of the adults was unavailable. Adult *Photinus* fireflies
275 are non-feeding (Lloyd, 1997), so shifts in their activity are unlikely to have direct consequences on
276 herbivores through phenological asynchronies. Shifts in adult activity likely correspond to shifts in
277 development or activity among larvae, potentially leading to asynchronies between larvae-prey
278 populations at this critical development time period. Resources acquired during the predaceous larval
279 stage are important in determining mating success among adult fireflies: males provide an energetically
280 costly nuptial gift to the female in the form of a spermatophore (Lewis et al., 2004). If sex differences in
281 phenological responses to environmental conditions exist, asynchronies between males and females
282 may additionally reduce mating success and fecundity, thus this should be an area of emphasis in future
283 study. Additionally, phenological shifts in fireflies may lead to consequences at other trophic levels. For
284 example, generalist ground dwelling predators like firefly larvae and other predaceous beetles are
285 known to have dramatic effects on the establishment of agricultural pests early in the growing season
286 (Safarzoda et al., 2014). Similarly, although distasteful and avoided by many predators, some birds,
287 lizards and frogs are known to feed on adult fireflies (Lloyd, 1973), thus shifts in firefly activity may have
288 dietary consequences for animals at higher trophic levels.

289

290 **Conclusions**

291 Fireflies are a charismatic and important taxon with ties to trophic function, economic
292 importance, and culture. Although empirical evidence of specific declines of *Photinus* fireflies has not
293 been clearly demonstrated in longitudinal studies, naturalists and citizen scientists perceive a decline in

294 their number (Chow et al., 2014), leading to interest in their conservation. Our study has offered new
295 insight to support conservation efforts and to direct future research. *Photinus pyralis* appears to thrive
296 in habitats with moderate soil disturbance. Thus, efforts to foster no-till and perennial agricultural
297 systems (Werling et al., 2014, 2011) will likely benefit the species. Climate warming may advance the
298 activity of fireflies to earlier and earlier in the growing season, but other extremes of climate in the form
299 of precipitation may introduce unpredictable elements to this, and add the possibility of inducing
300 asynchrony with other systems.

301 The availability of long term observational data, made freely accessible to the public, was an
302 essential factor in the discoveries made in this study. Although the study that provided these data were
303 not initiated with this purpose in mind, we were able to empirically demonstrate and disentangle the
304 effect of multiple drivers on firefly phenology simply because we had the statistical power to do so.
305 Although species that respond to multiple, interacting environmental drivers are relatively common,
306 data supporting investigations of this kind are rare (Strayer et al., 2006). We therefore encourage all
307 practicing ecologists to curate their species observation data and make them publicly available, to foster
308 long term, broad scale investigations in the future (Hampton et al., 2015, 2013; Michener and Jones,
309 2012).

310

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- 452
- 453

454 Table 1

Crop Type	Plant Community Treatments	Description
Annual	Conventional	Rotated crop field (corn-soybean-wheat), with conventional chemical input which is chisel plowed
	No-Till	Rotated crop field (corn-soybean-wheat), with conventional chemical input, with no tilling.
	Reduced Input	Biologically based rotated crop field (corn-soybean-wheat), with low input chemical control and a winter cover crop (leguminous). Plots are treated with banded herbicide and starter N at planting
	Organic	Biologically based rotated crop field (corn-soybean-wheat), low input chemical control with winter cover crop (leguminous). Certified Organic
Perennial	Poplar Trees	10-year rotation cycle of a fast growing <i>Populus</i> clone
	Alfalfa	Continuously grown alfalfa
	Early Successional	Abandoned field from 1989, left to grow into native successional plants which are annually burned
Forest	Successional	40-60 year old successional forest, left from former agricultural fields
	Coniferous	40-60 year old conifer plantations
	Deciduous	Late successional deciduous forest

455

456

457 **Figure captions**

458 **Figure 1: Box plot of average firefly captures, 2014-2015, by plant community treatment.**

459 Yearly average number of adult fireflies captured on weekly sampled yellow sticky cards across ten plant
460 community treatments at Kellogg Biological Station. Median firefly density in each treatment is
461 represented by the bold line, and upper and lower margins of each box represent the upper and lower
462 quartiles in that treatment, respectively.

463

464 **Figure 2: Average firefly captures, 2004-2015, by plant community treatment, by year.**

465 Yearly average number of adult fireflies captured on weekly sampled yellow sticky cards across ten plant
466 community treatments at Kellogg Biological Station. Loess smoother lines represent smoothed captures
467 within a given treatment and are used to illustrate general trends in population across treatments.

468

469 **Figure 3: Two-dimensional non-metric multidimensional scaling and environmental fitting of plant
470 community treatment plot use by fireflies over time.** A) At the yearly resolution, a 2D NMDS stress of
471 0.14 was observed. B) At the weekly resolution, a 2D-NMDS stress of 0.19 was observed.

472

473 **Figure 4: Average number of adult fireflies per trap across all sampled treatments at Kellogg Biological
474 Station plotted by year.**

475 Samples were taken weekly over the growing season from 2004–2015, and plotted by A) week of
476 capture; and B) degree day accumulation at capture. Loess lines represent smoothed capture trends for
477 a given year and were used to assess consistency of response to a given variable between years.

478

479 **Figure 5: Number of firefly adults captured, as predicted by GLM and as observed, by observation**
480 **number.**

481 Predicted values were generated using GLM accounting for variability due to plant community
482 treatment degree day accumulation, and year as a factor variable. Details of GLM can be found in data
483 analysis section in Materials and Methods.

484

485 **Figure 6: Degree day accumulation at peak firefly activity by year.**

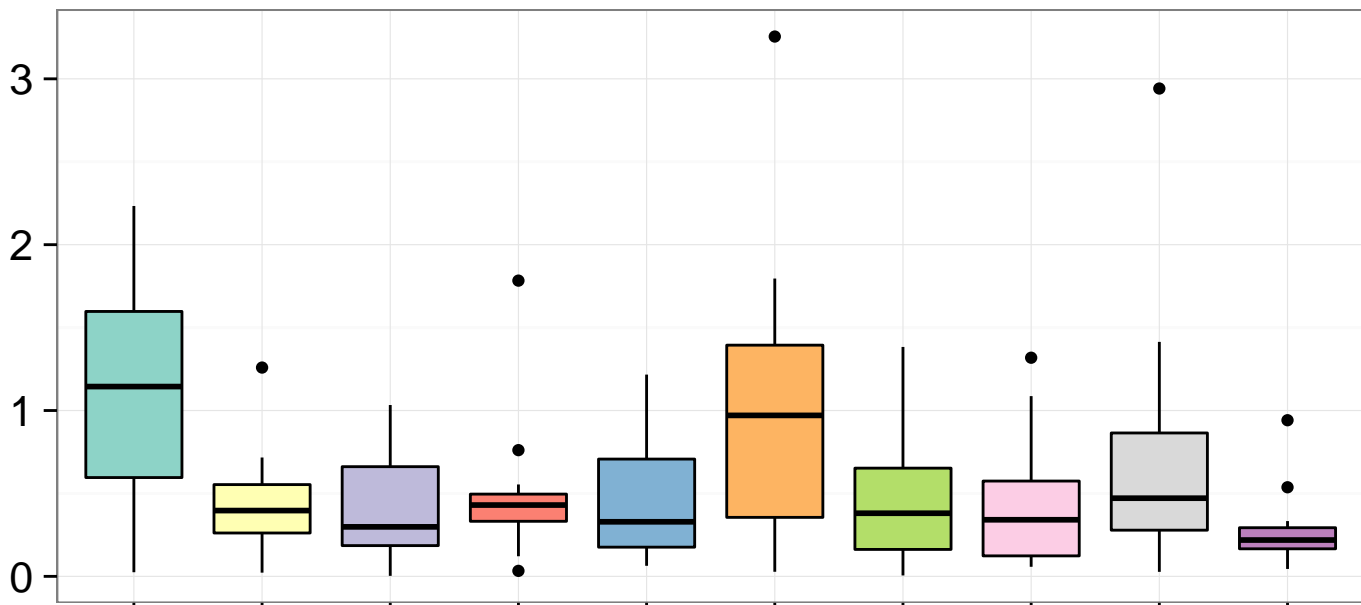
486 Degree day accumulation (\pm SEM) at peak emergence of firefly adults varied by sample year. Activity
487 peaks were extracted from regression coefficients from GLM.

488

489 **Figure 7: Firefly activity peaks by precipitation accumulation.**

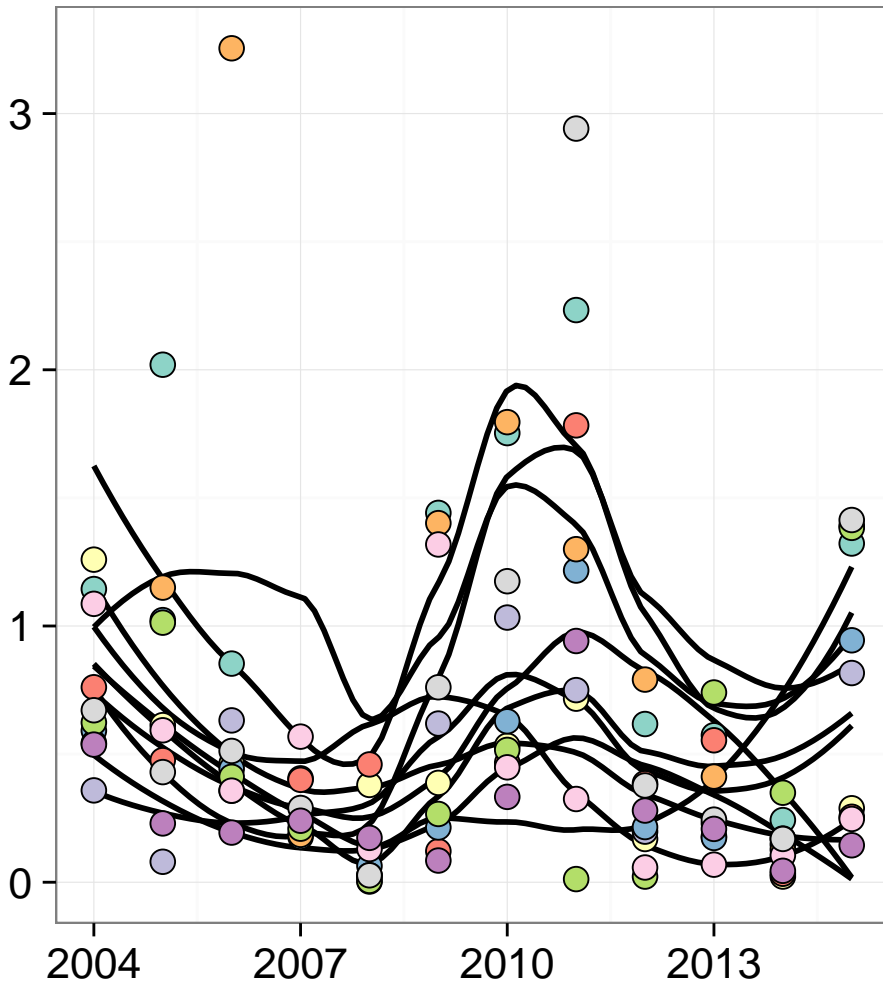
490 Firefly activity peak degree day accumulation had a quadratic relationship with precipitation
491 accumulation (pseudo- $R^2 = 0.456$, $p = 0.026$).

Adults per trap



Treatment

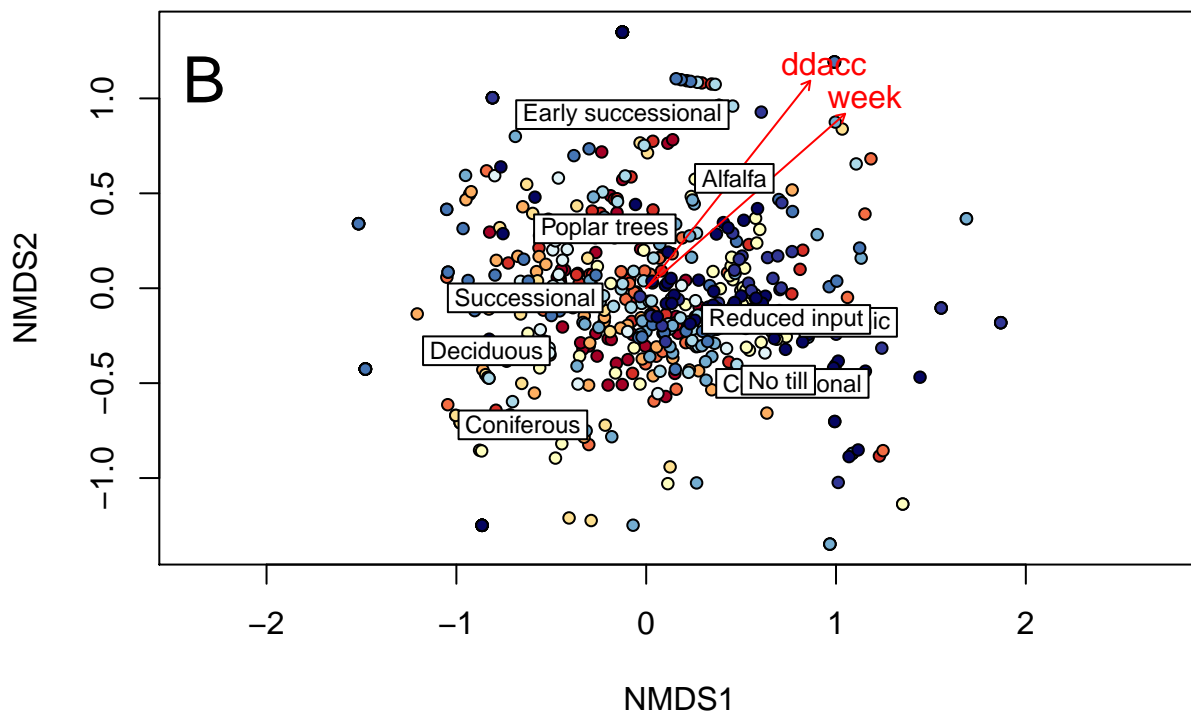
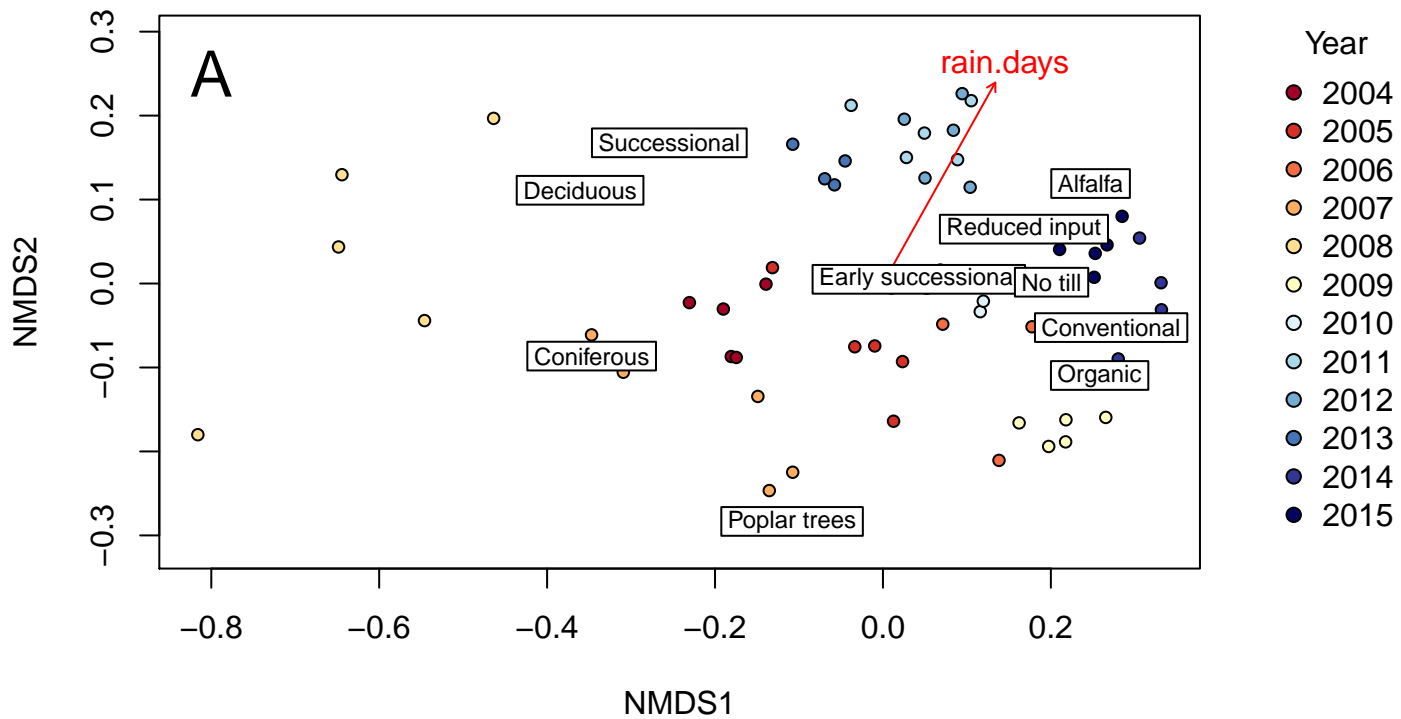
Adults per trap

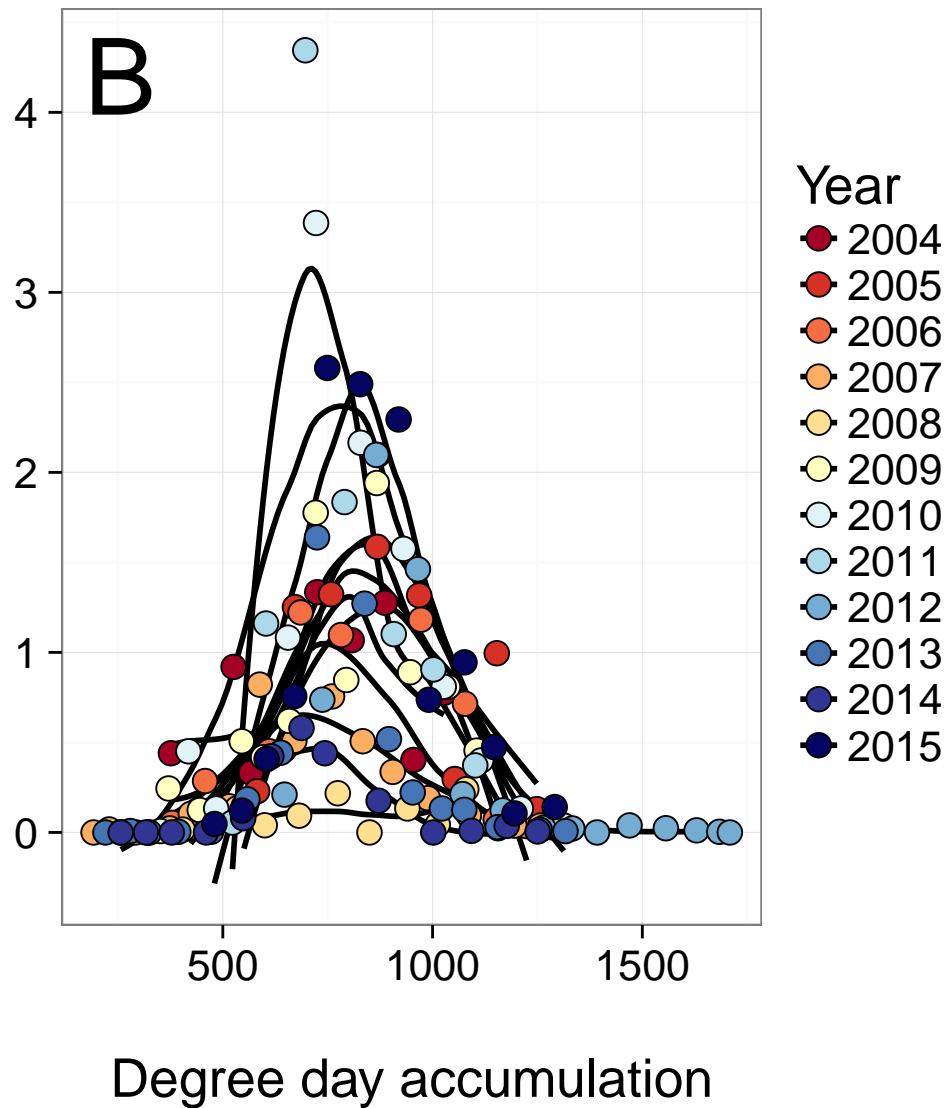
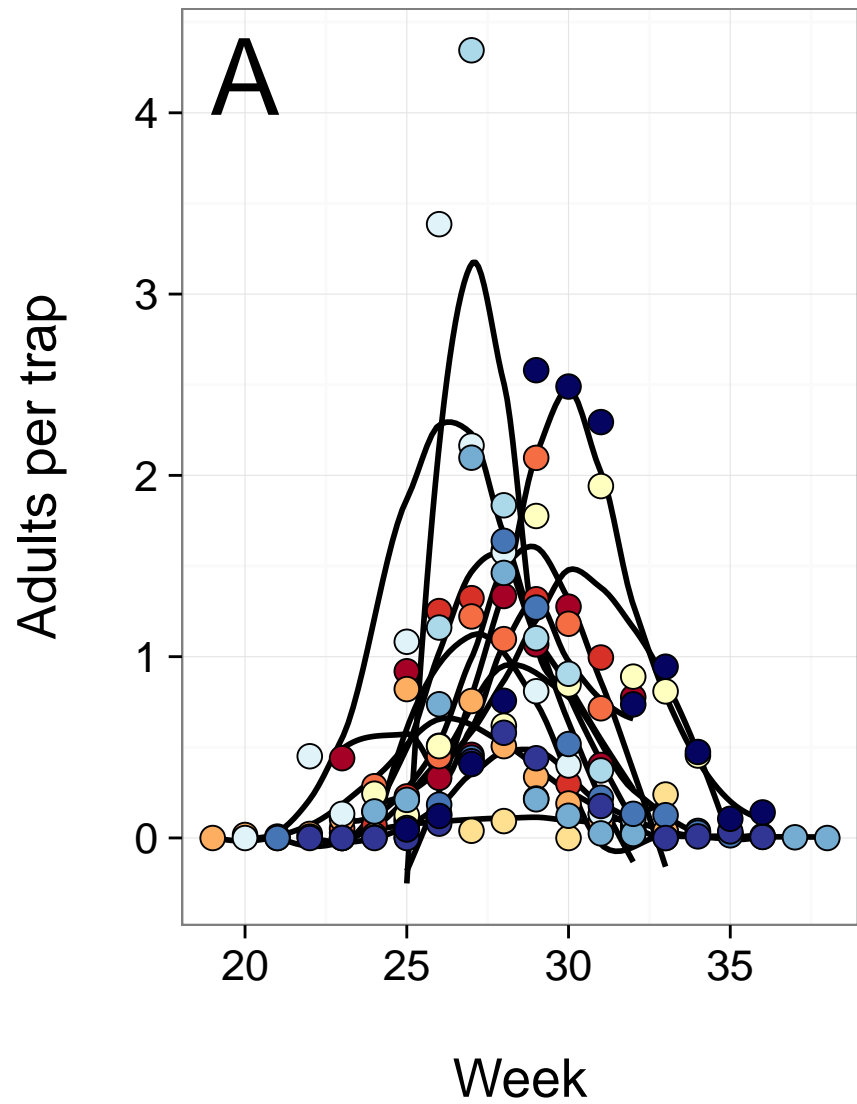


Treatment

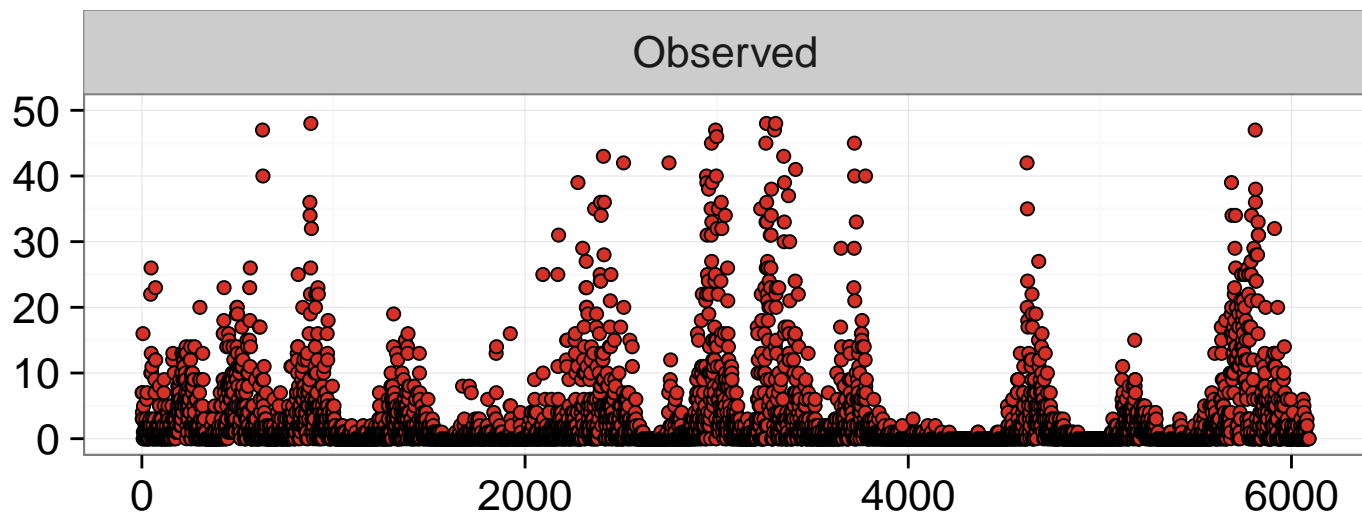
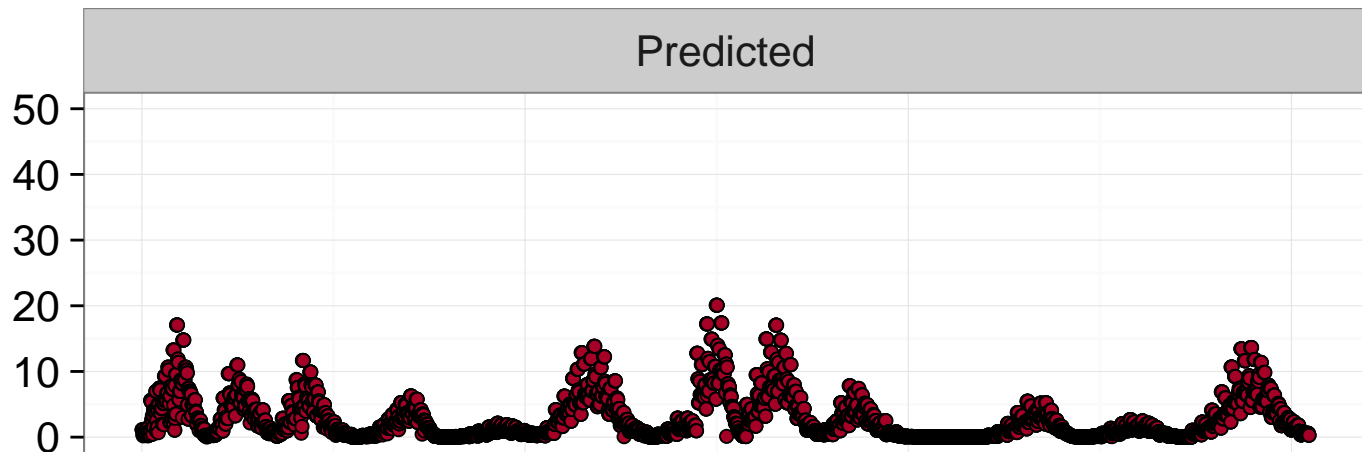
- Alfalfa
- Coniferous
- Conventional
- Deciduous
- Early successional
- No till
- Organic
- Poplar trees
- Reduced input
- Successional

Year



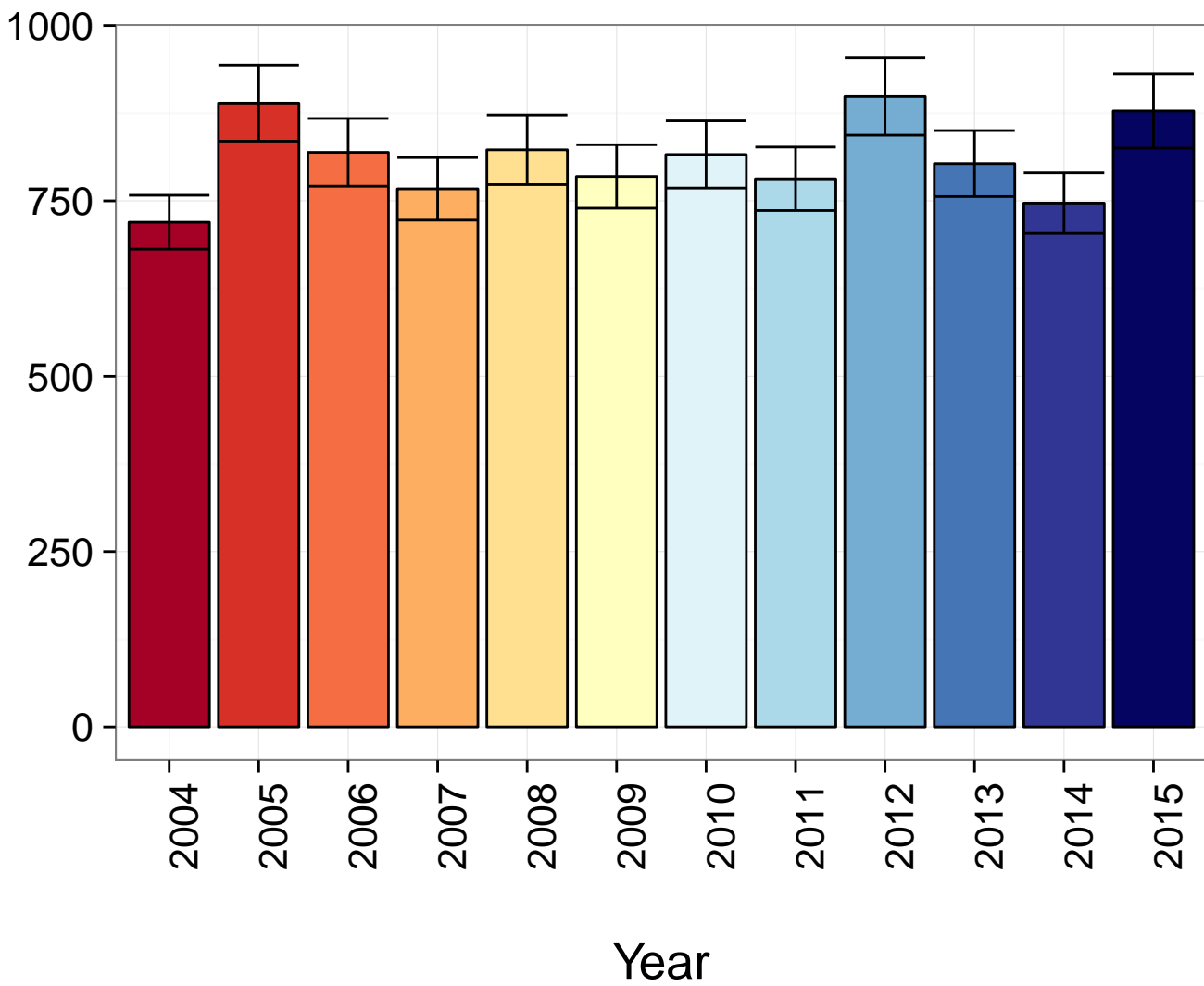


Adults captured

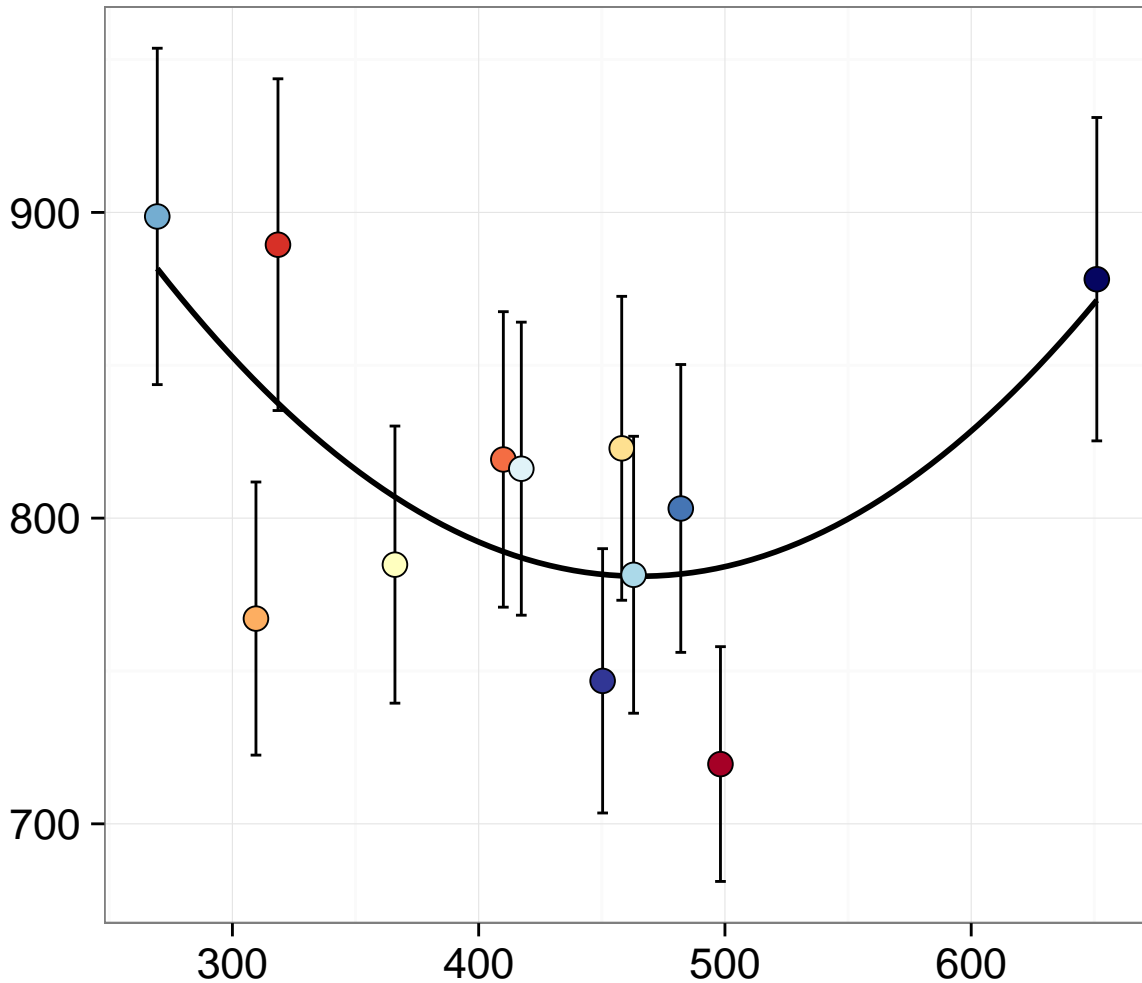


Observation number

DD at peak emergence



DD at peak emergence



Year

- 2004
- 2005
- 2006
- 2007
- 2008
- 2009
- 2010
- 2011
- 2012
- 2013
- 2014
- 2015

Precipitation accumulation (mm)