Abstract

Migratory bird species must coordinate their migration and breeding to coincide with a period of peak resource availability in the location where they raise their young. Recent evidence suggests that migratory birds have been responding to climate change at different rates than their arthropod food sources. This can lead to a phenological mismatch, where the timing of resource availability produced by a lower trophic level does not align with the timing of resource need of a higher trophic level. Migratory bird species are unable to feed their hatchlings, inhibiting reproductive success. We characterized the seasonal variation of foliage arthropods over the summers of 2015 and 2016 at the North Carolina Botanical Garden in Chapel Hill, NC and the Prairie Ridge Ecostation in Raleigh, NC. Timing and magnitude of peaks in occurrence varied with arthropod order, year, and survey method. Caterpillars and orthopterans had peaks of greater intensity than combined orders of arthropods that represent "bird food." Timing of peaks were then compared to spring greenup and temperature. Later greenup corresponded with later arthropod peak occurrence with one survey method at both sites, but this was not true for the other survey method or for arthropod peak occurrence comparisons to temperature. The arrival of some bird species aligned with temperature, greenup, and arthropod peak occurrence. These findings help to improve the characterization of arthropod phenology in future studies, and they also demonstrate the importance of testing a network of phenological variables when considering how communities are affected by climate change.

Introduction

The consequences of climate change for bird species is a topic of rising importance, as many anthropogenic processes are negatively impacting populations in ways that are not fully understood (Walther et al. 2002). Migratory bird species are especially sensitive to climate change as they must time their migration, breeding, and raising of young to coincide with a period of peak resource availability in a distant location, and the climatic and environmental cues they have historically relied on may no longer be reliable. Therefore, two key questions are (1) how have birds been responding to the environmental cues of spring temperature and foliage greenup (the greening of plant matter), and (2) to what extent have they been responding in a manner similar to the arthropods on which they depend?

Temperature plays a key role in the timing of foliage greenup (Zhang et al. 2003), and is affecting arthropod and bird phenology as well (Hinks et al. 2015, Lany et al. 2015, Visser & Holleman 2001, Visser & Holleman 2006). For every $1°C$ rise in spring temperature, migratory bird species in North America are shifting their breeding ground arrival date on average 0.8 days earlier, with some species arriving as much as 3 to 6 days earlier per $1°C$ rise (Hurlbert & Liang 2012). Though birds are shifting their migration timing, they may be adjusting too little or too much. A number of studies show climate change-induced mismatches in phenological shifts across trophic levels. For example, in the Netherlands, the peak date in caterpillar abundance has been advancing faster than the breeding dates of the bird species that rely on them (Both et al. 2009). Visser and Both (2005) summarized multiple studies on the response of species to a phenological yardstick, such as oak budburst for the winter moth or the caterpillar biomass peak for great tits. They found that species often respond too much or too little to changes in timing of their specific yardstick (Visser & Both 2005). The inability to adjust appropriately can be

detrimental; many bird species that are unable to adjust their migration patterns show decreasing population trends (Møller et al. 2008).

While large-scale, high-resolution data exist on temperature (Hart & Bell 2015), greenup (Tuck & Phillips 2016), and bird phenology (Sullivan et al. 2009), there are no standardized datasets available on the phenology of foliage arthropods. The citizen science project Caterpillars Count! was created to address this data gap. I present here the results from this two-summer study of arthropod seasonal abundance, providing a first glimpse into characterization of arthropod abundance phenology. The goals of this study are to (1) characterize arthropod phenology, while also comparing phenologies between arthropod order, site, year, and method, (2) characterize greenup and spring temperature at sites since 2000, (3) compare greenup and spring temperature to estimates of arthropod peak occurrence date, (4) compare greenup and spring temperature to estimates of bird arrival date, and (5) compare estimates of arthropod peak occurrence date to bird arrival date. Exploring these characterizations and relationships will begin to provide answers to the key questions mentioned previously. I predict higher peaks for the individual orders (caterpillars and orthopterans) than combined "bird food" (caterpillars, orthopterans, spiders, beetles, and true bugs), because arthropods peak at various stages of the summer and adding more orders could add noise to any individual peaks in abundance. I also predict differences due to methodology to be order-specific, because arthropod orders respond to the surveying methods differently. Peak intensity and timing differences due to year may be due to spring greenup or temperature, and this will be explored as well. I predict later arthropod peak dates to correspond with later greenup more strongly than temperature, as most arthropods are directly relying on fresh leaves as food. Using bird arrival date as an estimation for the timing of reproductive events, I predict bird arrival dates to align with greenup more so than temperature, as this is a more direct yardstick. Even though spring temperature has been shown to affect bird

arrival date (Hurlbert & Liang 2012), greenup should have a more direct effect on the availability of arthropod food. Species that are not following trends in arthropod abundance might be expected to have decreasing population trends in NC. Relevance to migrating birds and their peak resource need is discussed, along with future goals of large-scale arthropod data collection.

Methods

Arthropods

In both 2015 and 2016, foliage arthropods were surveyed from mid-May to late July twice a week by trained scientists (including PI Hurlbert and students of the Hurlbert Lab) at the Prairie Ridge Ecostation in Raleigh, NC and the North Carolina Botanical Garden in Chapel Hill, NC. Survey trees were distributed in groups ("circles") of five around each of the two sites in a semi-standardized fashion (Figure 1). The center tree in each circle was chosen based on the existence of sufficient nearby vegetation for sampling. To obtain an unbiased representation of the woody vegetation at the site, the four remaining survey trees in each circle were chosen by identifying the first suitable tree (≥50 leaves, each ≥5 cm long) at least 5 meters away in each of the four cardinal directions from the circle center. A total of 60 survey trees were selected at Prairie Ridge, and 40 survey trees at the Botanical Garden.

Two types of survey methods were used: 50-leaf visual surveys and beat sheet surveys. For the visual surveys, observers checked the top and bottom of 50 leaves and associated twigs of the survey branch from standing height, and recorded the identity (to order) and length of all arthropods greater than 2 mm. Observers conducted beat sheet surveys by beating a branch over a 2' x 2' white sheet, and then recording the identity and length of all arthropods observed, as well as the number of leaves sampled by the beat sheet on that particular branch.

Cleaning and analysis of the arthropod data was conducted in R (R Core Team 2015). Phenology was characterized using two different variables: mean density per survey by day, and fraction of surveys on which the taxon occurred by day. Mean density is useful in that it takes into account the abundance of the arthropod taxon at each survey, a factor that birds may be relying on. Occurrence, or the fraction of surveys, was used in this study because large outliers that were surveyed do not affect the possible trends in the data. Note that the occurrence here represents the average over a week of surveying, so that each point is the mean arthropod occurrence of the whole week at the middle Julian day (numbered days of the year with January 1 = Julian day 1) of that week. This was done to compare this data to weekly volunteer data, which will be analyzed in another study. Peak occurrence was estimated by fitting a spline to the phenology curves and noting the date of the peak in the spline fit (Figure 2C).

Temperature

Average daily temperature data at a 4 km resolution was downloaded for each site from PRISM using the prism package in R (Hart & Bell 2015). Growing degree day (GDD) units are used in phenology studies to predict the timing of stages of development, often for plants (Bonhomme 2000). GDDs were calculated with the temperature data by taking a cumulative sum over a full year of consecutive daily average temperatures that are above 7 degrees Celsius and below 30 degrees Celsius (McMaster & Wilhelm 1997), with the date at which 1000 GDDs (GDD1000) was reached serving as a comparison point (Figure 2A). This threshold, although arbitrary, was chosen because 1000 GDDs typically accumulates between June 5th and June 15th, and is a good proxy for whether spring temperatures accumulated early or late in a given year.

Spring greenup

Enhanced Vegetation Index (EVI) data at a 250 m resolution was downloaded for each site with the MODISTools package in R (Tuck & Phillips 2016). EVI is a remotely sensed index of greenness, and usually follows a logistic trajectory into the summer and then a browndown period in the fall, where the greenness falls quickly. The date of spring greenup was calculated by fitting a logistic curve to the first 200 days of the year (with EVI data occurring every 16 days) and finding the date of the inflection point (Figure 2B).

Bird arrival

Bird arrival dates were estimated using data from the citizen science website and online database, eBird (Sullivan et al. 2009). Users of eBird submit checklists of bird species and abundance they see at a location with unique longitude-latitude coordinates, and indicate how far they travelled and how long they were birding. Data from eBird for the years 2007 - 2016 was used to estimate bird arrival dates to the two sites using the general methods described in Hurlbert and Liang (2012). Focal bird species used include indigo bunting, red-eyed vireo, common yellowthroat, and blue-gray gnatcatcher, as these species are all migrants that rely on foliage arthropods and are seen frequently at the two sites. Estimates for bird arrival dates were found by fitting logistic curves to plots of the proportion of eBird checklists including the focal bird species, and finding the Julian day of the inflection point (Figure 2D). The proportion of checklists were used because this adjusted the presence of the focal bird species based on the amount of birding activity. There is a general tradeoff between estimating bird arrival dates at a fine spatial scale so as to better pair with the on-the-ground collected field data versus using a larger spatial scale that would include more observations, and therefore a better estimate of arrival for more years of data. Using a 4 x 4 km box around the coordinates of each site, there

was sufficient data in the last three to eight years for these focal bird species to estimate bird arrival date.

Results

Arthropod phenology

Between years, seasonal patterns were present at Prairie Ridge. Caterpillar occurrence was highest around Julian day 170 both years (Figure 3A, 3B), and orthopterans consistently peaked later in both years (Figure 3C, 3D). The intensities of the peaks were also similar between years. The bird food category showed no obvious peak in either year (Figure 3E, 3F). Occurrence was also usually higher for the beat sheet surveys compared to the visual surveys at Prairie Ridge (note the green line's placement compared to the brown line, Figure 3).

At the Botanical Garden, seasonal patterns between years were less consistent. Intensity of the peak in caterpillar occurrence varied between years, especially for visual surveys (peak occurrence of 0.19 in 2015 versus 0.09 in 2016 according to spline fits, Figure 4A, 4B). Timing of peaks also appears less consistent between years than it does at Prairie Ridge. With visual surveys, the bird food category at the Botanical Garden has clear peaks, unlike the patterns seen at Prairie Ridge (Figure 4E, 4F).

The relationship between peak date estimated by visual surveys versus peak date estimated by beat sheet surveys gives indication of how survey method might impact estimation of peak occurrence dates (Figure 5). The two survey methods are generally correlated ($r = 0.45$, $p = 0.14$). Most combinations of arthropod and site fall below the 1:1 relationship in 2015, while most combinations of arthropod and site fall above the 1:1 relationship in 2016 (Figure 5).

GDD and greenup comparisons between sites

To test whether years with earlier temperature accumulation correspond to years with earlier greenup, I compared estimates of spring greenup date and GDD1000 date between each other and at both sites. Deviations from the mean at each site for each predictor variable were calculated for easier comparison. The deviations for GDD1000 date and spring greenup date are strongly correlated with each other (r = 0.53, p < 0.01) with estimates generally falling close to the 1:1 line (Figure 6A). This indicates that years with later accumulation of temperature also tend to have later greenup. Exceptions include the Botanical Garden in 2004 and 2013, when greenup was later or earlier, respectively, than what would be expected by the GDD1000 date.

Spring temperature was similar between the two sites across years (r = 0.98, p < 0.01), with the Botanical Garden usually reaching GDD1000 3 days before Prairie Ridge (Figure 6B). Greenup date was not strongly correlated between sites (r = 0.22, p = 0.41), although most points were above the 1:1 line, indicating that greenup at the Botanical Garden usually preceded greenup at Prairie Ridge (Figure 6C).

Arthropod peak comparisons to greenup, GDD

To test whether arthropod phenology is corresponding with temperature accumulation and spring greenup, I compared estimates of these two predictor variables to the timing of arthropod peak occurrence. The predicted pattern of later predictor variables corresponding with later arthropod peak occurrence was seen with greenup for all orders at both sites when surveyed by beat sheet (Figure 7D), and the opposite relationship was seen with GDD for all orders at both sites when surveyed by beat sheet (Figure 7B). The trends based on visual survey data were more variable between site and order (Figure 7A, 7C).

Bird arrival and greenup, GDD

Over Julian day, the proportion of checklists with the focal bird species started at 0, and then started rising to higher proportions at a date dependent on the species (Figure 2D). The scale parameters of the logistic fits usually spanned a time period less than two days, indicating that the rise in the logistic fits were sharp. Points with narrower 95% confidence intervals on arrival date were weighted more heavily for the linear models comparing GDD1000 date or greenup date to bird arrival date. Birds usually arrived later in years with later GDD1000 dates or greenup dates (Figure 8), even if the relationships had low R^2 and high p-values (Table 1). Relationships of the bird arrival date to the predictor variable were tighter with GDD (mean $R^2 = 0.57$) than greenup (mean $R^2 = 0.41$) (Figure 8, Table 1). The common yellowthroat and blue-gray gnatcatcher showed the predicted positive relationship across all four combinations of site and predictor variable, the red-eyed vireo exhibited a positive relationship at three of the four combinations, and the indigo bunting only one of four (Figure 8). Arrival date is variable for the four focal species, but especially the common yellowthroat.

Bird arrival and arthropod peak occurrence

The red-eyed vireo arrives later at both sites with later arthropod peak occurrence according to beat sheet surveys (Figure 9D). The opposite occurs for the common yellowthroat and blue-gray gnatcatcher according to beat sheet surveys (Figure 9F, 9H). The visual surveys are similar to these three bird species' relationships to arthropod peak occurrence date at the Botanical Garden, but are variable at Prairie Ridge (Figure 9C, 9E, 9G). The indigo bunting had identical estimates of arrival date in both years despite variation in both GDD1000 date and greenup date (Figure 9A, 9B).

Discussion

The arthropod phenology dataset that was collected and used in this study is novel in its ability to address important questions in climate change ecology, as arthropod abundance is the missing link in a chain of phenological events that impact birds and other organisms. Furthermore, this is one of the first studies in North America to simultaneously consider bird migration phenology with respect to arthropod phenology, spring greenup, and temperature.

Seasonal peaking of arthropod availability is present, differing in timing and intensity with order, site, and year. Most groups of arthropods (caterpillars, orthopterans, and bird food) exhibit a peak during the summer season. The bird food category exhibited a broader peak at Prairie Ridge, likely due to different orders peaking at various stages throughout the summer. Within an order, variability between species in phenological timing might also contribute to how broad a peak in abundance or occurrence may be. This matters because a narrow phenological peak in resource availability for a migrating bird species might make it more susceptible to phenological mismatch. The broader the peak in arthropod abundance, the higher chance that nesting timing will overlap with a time of greater resource availability (Miller-Rushing et al. 2010). Caterpillars and orthopterans are often listed as key arthropod orders in an insectivorous bird species' diet (Poole 2005), but more work must be done in characterizing the diets of hatchlings specifically. If more is known about what is required for feeding a hatchling during the critical period of resource need, there will be a better understanding of how reproductive success is affected by changes in arthropod phenology, as we will be able to predict which bird species are phenologically mismatching with their specific arthropod prey. Still, it is significant that caterpillars and orthopterans, composing a large fraction of the prey that is needed for feeding hatchlings in general, experience relatively high peaks over the summer. The same

amount of food resources is thus not always available to birds depending on the timing of their migrations and reproductive events.

The nature of the survey method likely caused differences in the results for beat sheet surveys and visual surveys. With a visual survey, there is more room for human error while checking each leaf. Arthropods that are able to camouflage themselves are likely to be missed in the count. With the beat sheet surveys, arthropods that are particularly mobile when the branch is disturbed might fly or hop away and not be observed on the beat sheet. This includes orthopterans that can jump in any direction when a branch is hit. Arthropods that are able to cling to a leaf strongly might also be missed in the beat sheet counts, such as caterpillars.

Peak occurrence dates for arthropods did not consistently track GDDs or spring greenup, although there was a trend of later arthropod peak dates correlating with later greenup date according to beat sheet surveys at both sites (Figure 7D). With only two years of data, I was unable to fully evaluate the effects of spring greenup and GDD on arthropod phenology. Peaks in arthropod phenology are predicted to correlate more with spring greenup rather than GDD, because arthropods, especially caterpillars, are directly affected by greenup as a food source. Yet, the relationship between GDD and spring greenup ($r = 0.53$, $p < 0.01$) indicates that temperature might also indirectly affect arthropod phenology. If arthropods shift in peak timing in response to the timing of greenup and GDD, I would expect positive slopes for all plots. It is relevant to note that the occurrence was used to calculate timing of peaks, when it might be more accurate to use biomass phenology data, since birds are interested in the amount of energy they gain when consuming prey. Dates of peak occurrence also occasionally do not occur within the relevant time window for migrating birds. For example, beat sheet surveys of caterpillars in 2016 showed a loosely increasing occurrence over the summer, causing the "peak date" to just be the

edge of the time window. Patterns relating to the tendency of an arthropod order to peak over the summer would be more evident with more sites and years of collecting data.

Bird arrival dates tracked GDDs and spring greenup, but most relationships were not significant, likely due to low sample size. It was thought that bird arrival would have a stronger relationship with greenup because this is a more directly related yardstick, yet there was a tighter relationship with GDD. In terms of the variability of arrival date, the species that show more variability, such as the common yellowthroat, may be able to track environmental cues better. For some species, migration timing may be more internal or instinctive so they arrive the same time every year, making them more prone to mismatch. Most species were variable in their arrival dates, at least at this scale. The sample size for most species was small due to the size of the sites and the frequency of activity of birders, making any patterns difficult to discover.

Some bird species showed patterns in their arrival date related to arthropod peak date, and this relationship has the potential, with the continuation of this project, to explain population trends of these species in NC. The indigo bunting, red-eyed vireo, and common yellowthroat all show decreasing population trends in North Carolina from 2005 to 2015 (-1.77, -0.87, and -2.12, respectively) (BBS). The common yellowthroat, with the most decreasing population trend, was one of the species that had patterns of later arrival with earlier arthropod peak date. However, the blue-gray gnatcatcher also had these patterns and has a population trend of +0.93. The red-eyed vireo was the only bird in this study with frequent patterns of later arrival in response to later arthropod peak occurrence, and it had the least decreasing population trend. The red-eyed vireo might be better at picking up on cues that will directly affect their reproductive success, while other species could be following trends that are not going to aid the success of their breeding season. This species has also been noted as one of the best at shifting its migration timing in

relation to temperature (Hurlbert & Liang 2012). It also has a slow migration speed, so it may be picking up on environmental cues more thoroughly than other species (Hurlbert & Liang 2012).

There are complications involved in measuring and interpreting avian phenology. The effect of arthropod abundance phenology on reproductive success is likely to vary based on the broadness of the diet of the hatchlings of that species. Species that are generalists would be able to adapt better to changes in phenology than species that are specialists. Likewise, migratory species are more prone to being affected by changes in arthropod phenology, compared to resident species, because they do not have the same amount of time to pick up on cues in the spring before starting their breeding period. It is also relevant to note the scale that these interactions are occurring at. Occurrence was calculated across the field site, when birds may be constrained to much smaller ranges while feeding their hatchlings (Hinks et al. 2015). Also, due to limitations in data, I only looked at bird arrival date, though this date is assumed to be parallel to reproductive timing.

There is more work to be done to gauge how much arthropod peak occurrence timing is affected by temperature and spring greenup, and how much bird arrival date is affected by temperature, spring greenup, and arthropod peak occurrence. The arthropod phenology results from these two summers can be used to determine how to efficiently set up new field sites and survey routines. It is possible that beat sheets are picking up on any existing trends more easily than visual surveys because arthropods are more visible to the surveyor. More frequent surveying throughout the summer also may have the potential to pick up on nuanced phenologies. More years of arthropod phenology data will be helpful in identifying how spring greenup and GDD relate to seasonal peaks in arthropod abundance. Quantifying the intensity of arthropod peaks and comparing this between order would provide a better understanding of the patterns regarding the shape of phenological curves that may be relevant to breeding birds.

The earth continues to warm, and plants are following this trend with earlier greening (Schwartz et al. 2006) Climate change has been shown to be predictor of arthropod phenology (Cayton et al. 2015), and has also played a significant role in decreasing population trends of North American birds (Reif 2013), with migratory birds especially at risk (Møller et al. 2008). The results here, along with other phenology studies (Hinks et al. 2015, Lany et al. 2015, Visser & Holleman 2001, Visser & Holleman 2006), indicate that birds and arthropods are responding to changes in their resources, illustrating a need to address climate change and its impact on ecosystems.

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Appendix

R scripts used for this project can be found in the Caterpillars Count GitHub repository,
https://github.com/hurlbertlab/caterpillars-count-analysis. Relevant scripts include:
summary_functions.r, data_cleaning.R, prism_10year.R, modis_10year.R, spline_thesis.R,
eBird.R, eBird_logistics.R, phenology_thesisplots.R, and compilation_thesis.R.
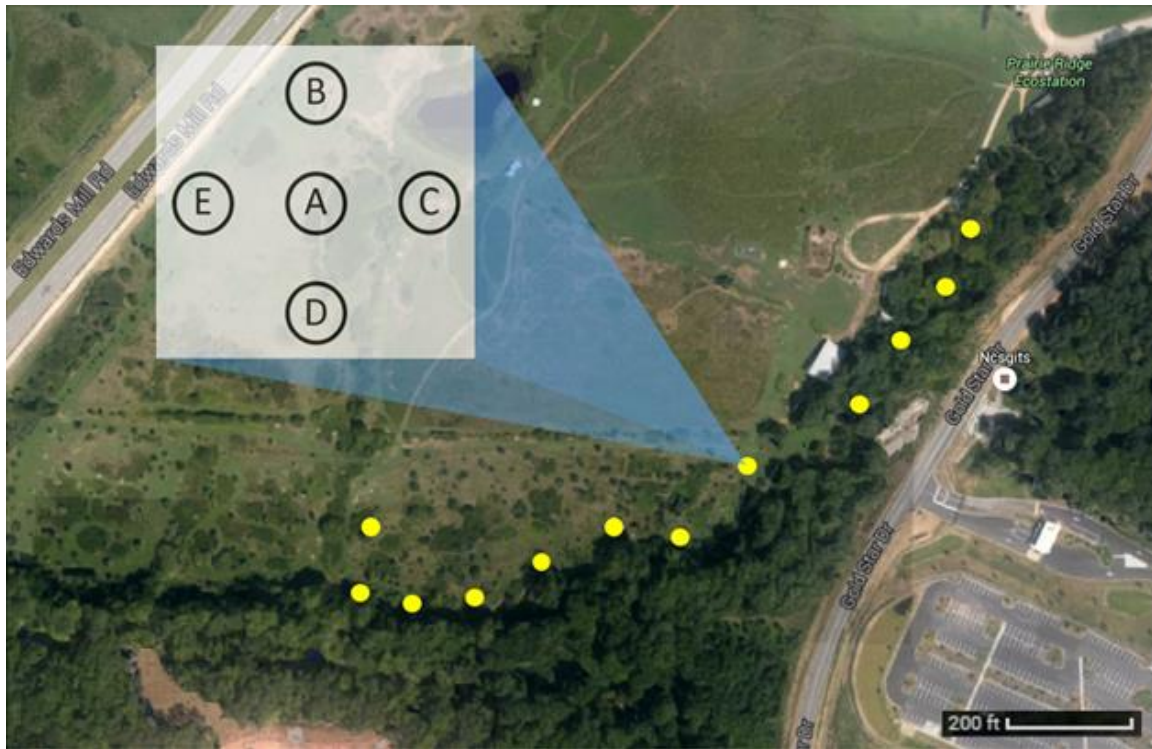
Figure 1. Map of Prairie Ridge Ecostation (top) and North Carolina Botanical Garden (bottom) including survey circle locations. Each yellow dot represents a set of five surveys (see inset).
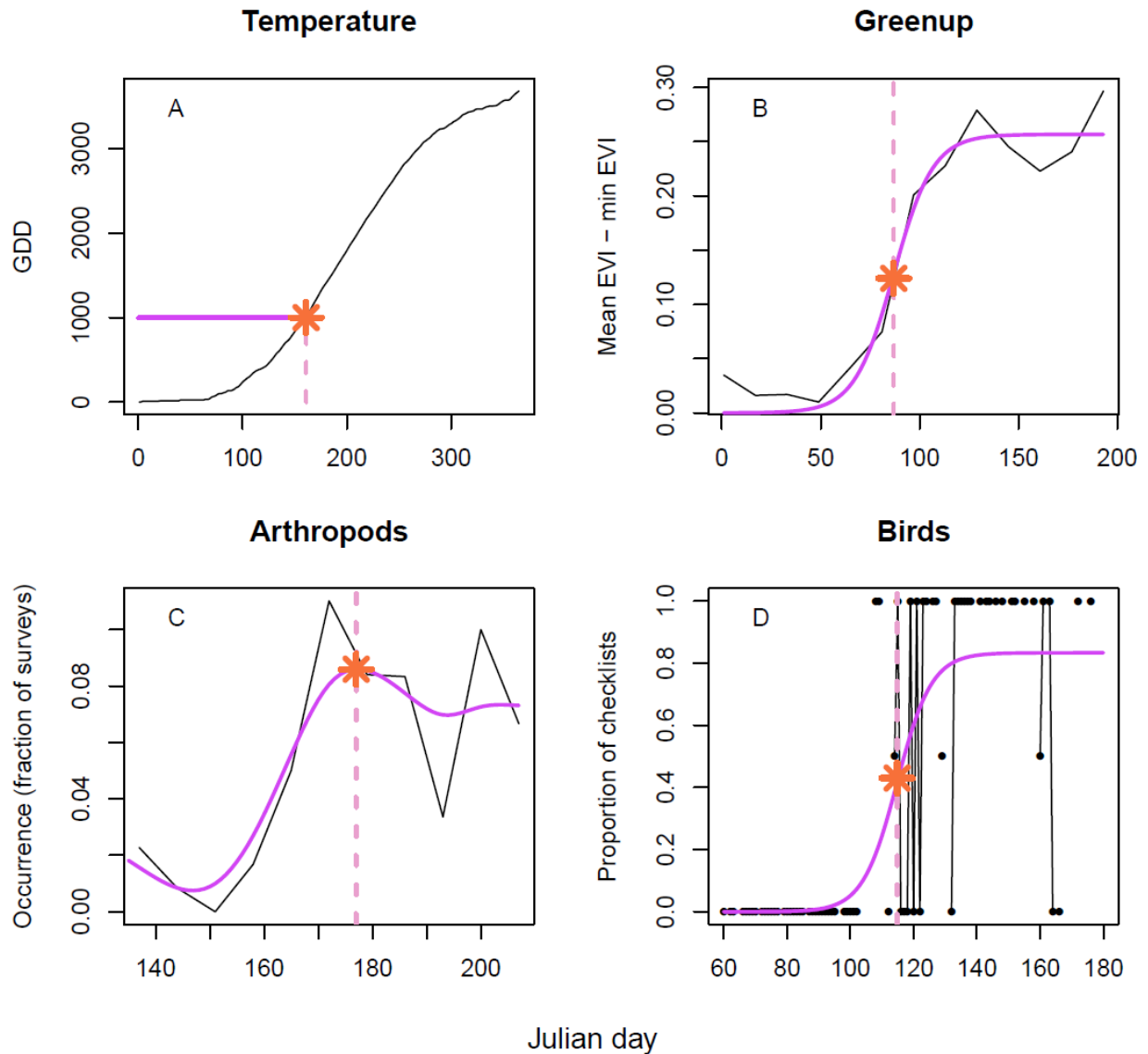
Figure 2. An illustration of methods for estimating phenological dates in this study. A. The date at which 1000 growing degree days above a minimum threshold of 7 degrees Celsius and below 30 degrees Celsius have been accumulated. B. A logistic curve is fitted to the trajectory of the Enhanced Vegetation Index (EVI) over time, and the location of the inflection point is used as the estimate of greenup date. C. A spline is fit to the arthropod occurrence data, and the maximum of that curve (over the summer interval) is used as the estimate of arthropod peak occurrence date. D. A logistic curve is fit to the proportion of checklists that recorded the focal bird species on a given day, and the location of the inflection point is used as the estimate of bird arrival date.
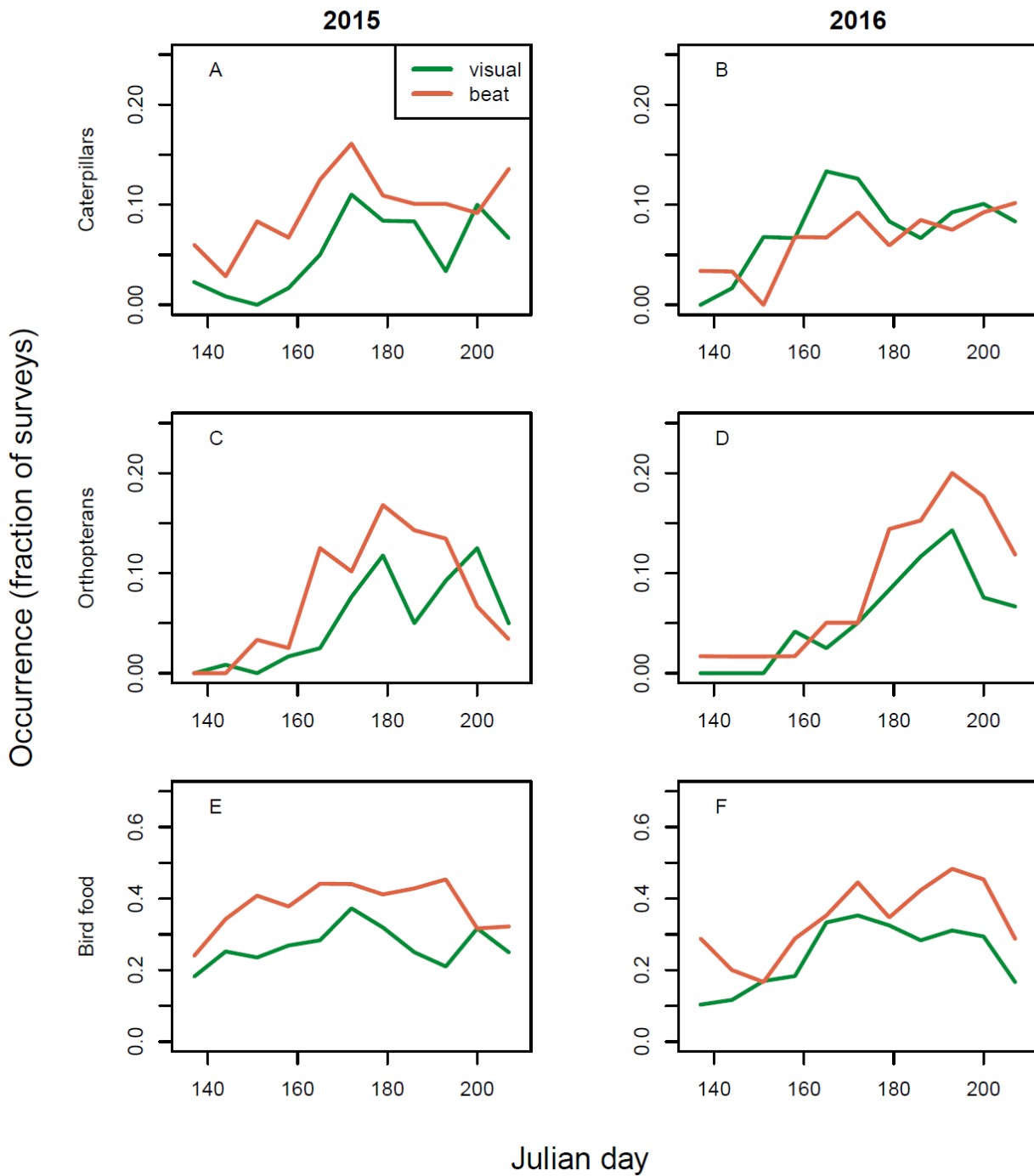
Figure 3. Fraction of surveys in which the selected arthropod order was observed over the late spring and summer at the Prairie Ridge Ecostation in 2015 (left column) and 2016 (right column). Estimates based on visual surveys are shown in green and estimates based on beat sheet surveys in brown. Correlation coefficients (r) between the two survey types are in the top right corner of each plot.
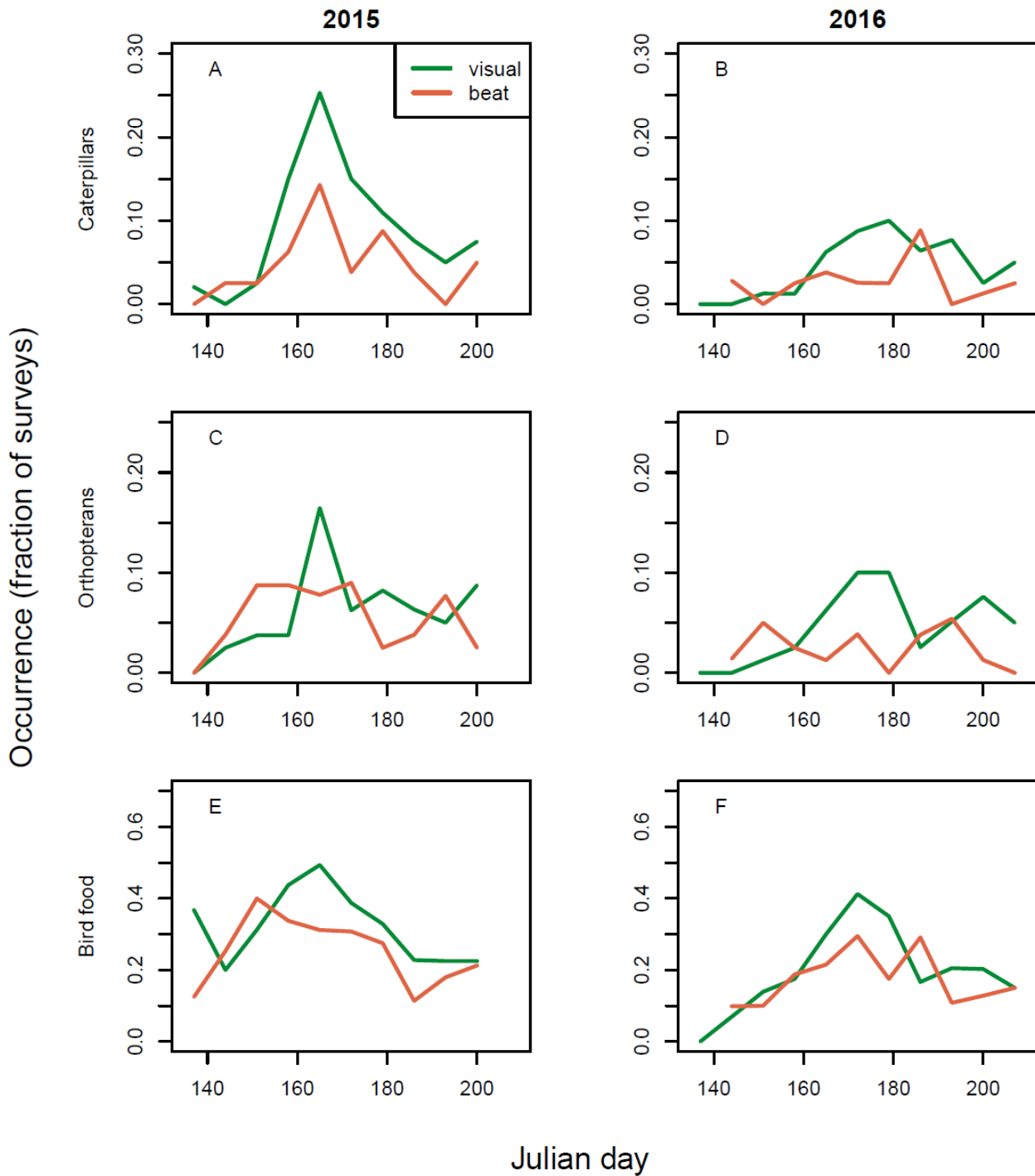
Botanical Garden

Figure 4. Fraction of surveys in which the selected arthropod order was observed over the late spring and summer at the NC Botanical Garden in 2015 (left column) and 2016 (right column). Estimates based on visual surveys are shown in green and estimates based on beat sheet surveys in brown. Correlation coefficients (r) between the two survey types are in the top right corner of each plot.
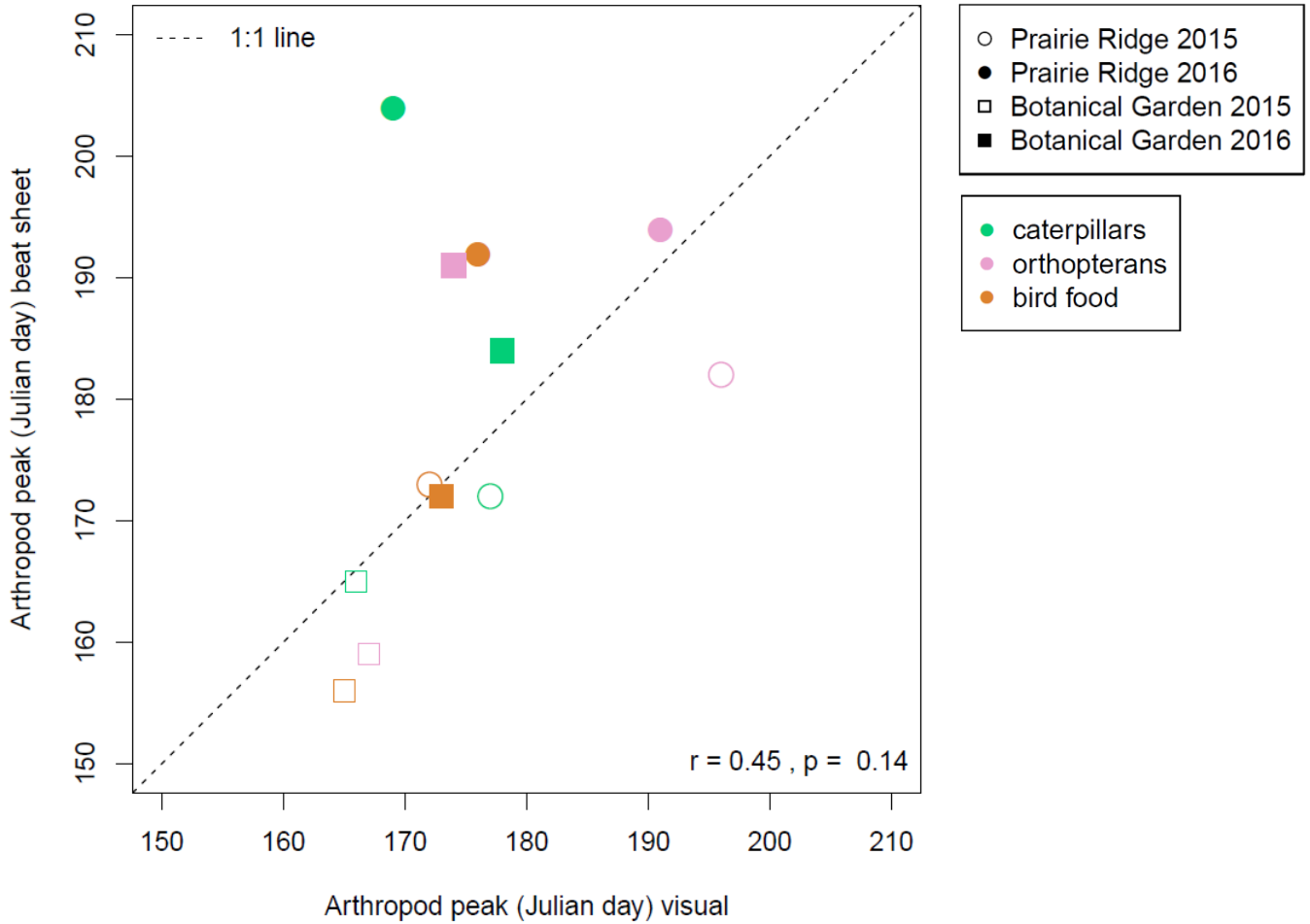
Figure 5. Comparison of arthropod peak occurrence date based on beat sheet data to arthropod peak occurrence date based on visual survey data. Each point indicates a year (open shapes, 2015; closed shapes, 2016) for a given site (circles, Prairie Ridge; squares, Botanical Garden) and arthropod group (colors).
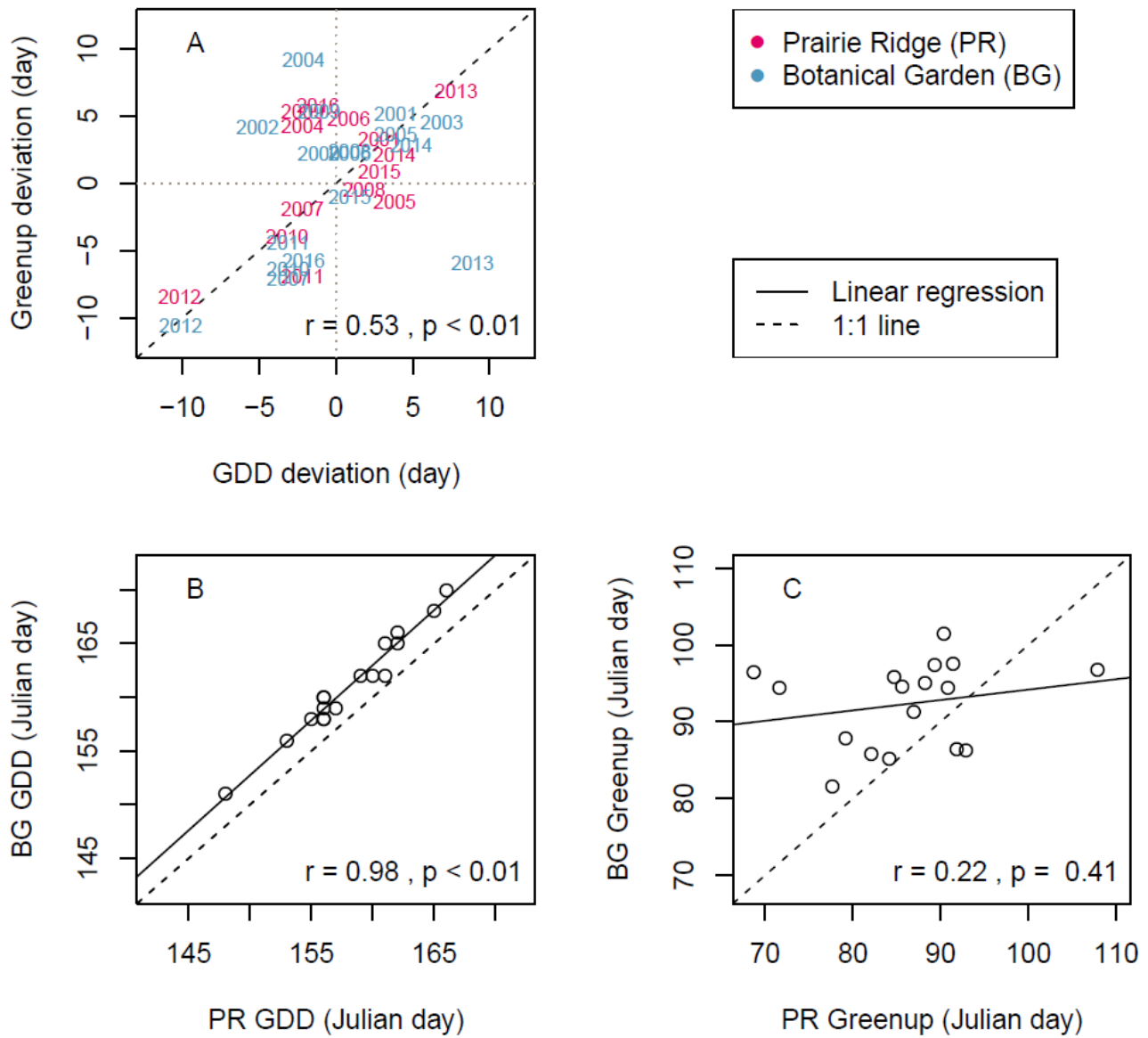
Figure 6. A. Greenup date plotted against GDD1000 date for Prairie Ridge (red) and the Botanical Garden (blue). Deviation from the mean for these datasets was plotted for 2000-2016. B. Comparison of GDD1000 date between Prairie Ridge (PR) and the Botanical Garden (BG). C. Comparison of greenup date between PR and BG. Dashed line is 1:1 and solid line is regression line.
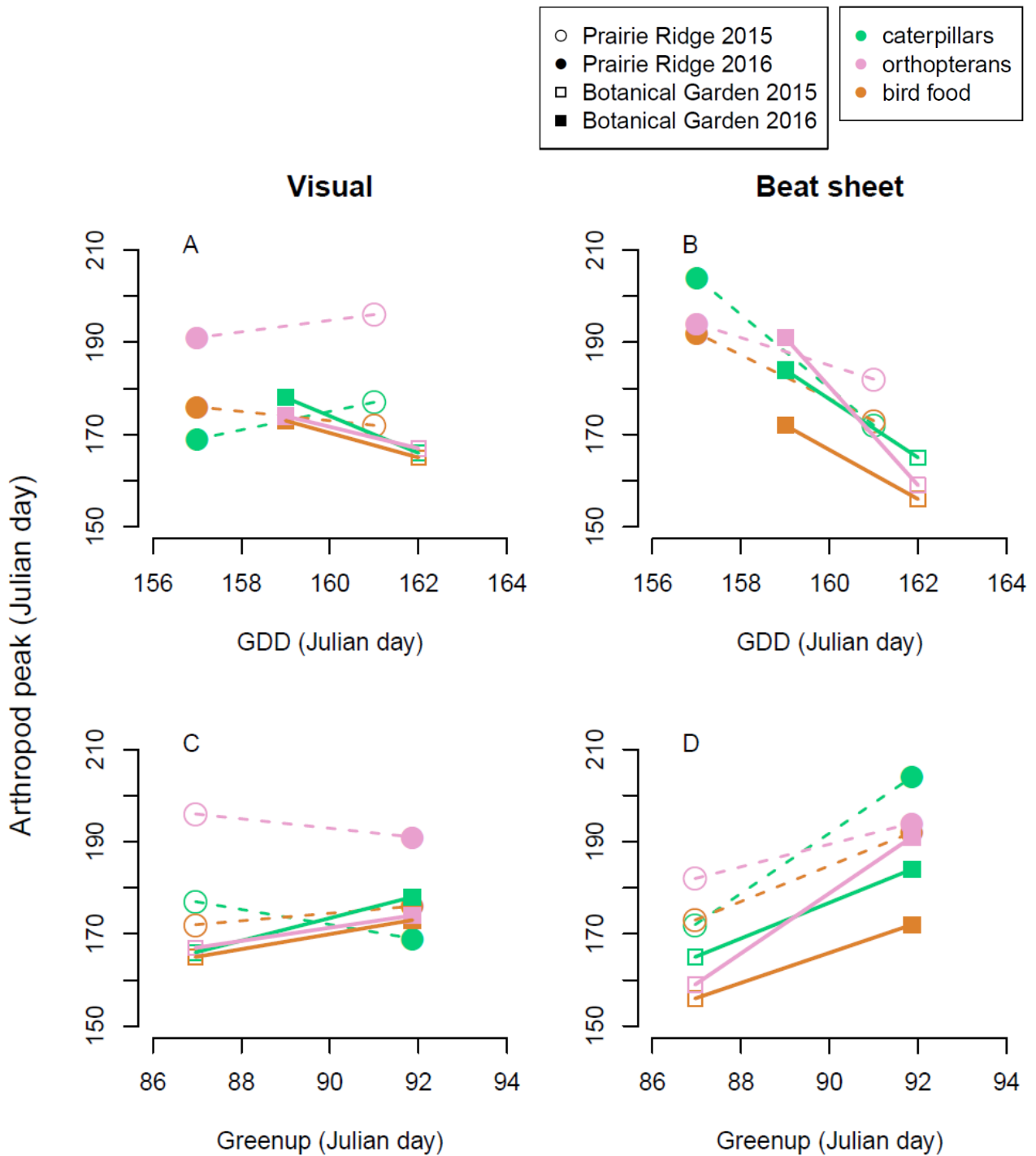
Figure 7. A, B. Julian day of the peak date of caterpillar (green), orthopteran (pink), or bird food (orange) occurrence as a function of GDD1000 date. C, D. Julian day of the peak date of caterpillar, orthopteran, or bird food occurrence as a function of spring greenup date. Peak arthropod occurrence dates are based on visual surveys (left column) and beat sheets surveys (right column). Segments connected between years (open shapes, 2015; closed shapes, 2016) for a given site (circles, Prairie Ridge; squares, Botanical Garden) and arthropod group (colors).
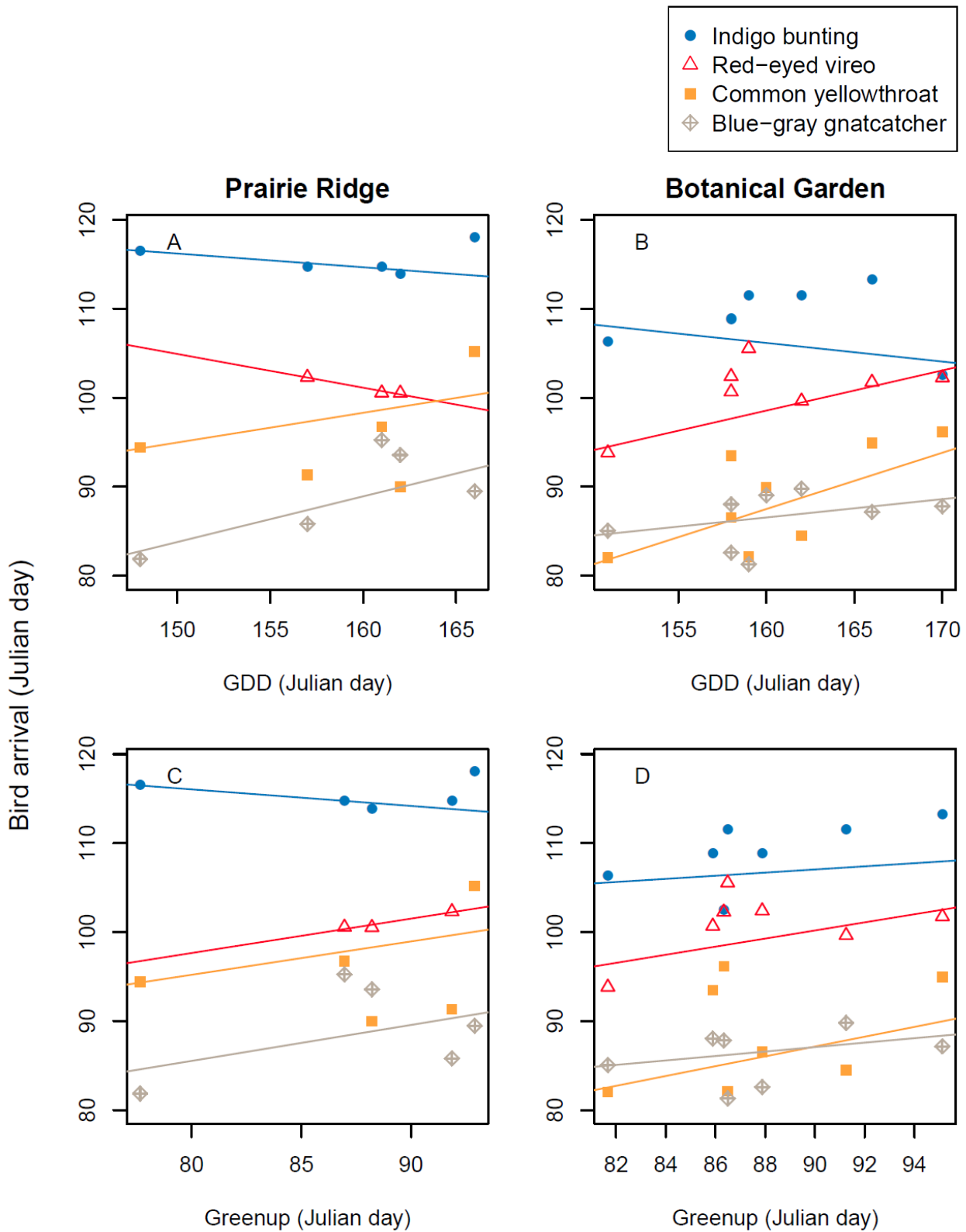
Figure 8. Bird arrival date of four focal species as a function of GDD1000 date (A, B) or greenup date (C, D) at Prairie Ridge (A, C) and the NC Botanical Garden (B, D). For the linear regression, points were weighted inversely to the confidence interval of the logistic fit.

Species	Site	Metric	R2	p
Indigo bunting	PR	GDD	0.68	0.09
Red-eyed vireo	PR	GDD	0.97	0.11
Common yellowthroat	PR	GDD	0.47	0.31
Blue-gray gnatcatcher	PR	GDD	0.58	0.13
Indigo bunting	BG	GDD	0.3	0.21
Red-eyed vireo	BG	GDD	0.86	0
Common yellowthroat	BG	GDD	0.55	0.04
Blue-gray gnatcatcher	BG	GDD	0.19	0.29
Indigo bunting	PR	Greenup	0.62	0.11
Red-eyed vireo	PR	Greenup	0.93	0.17
Common yellowthroat	PR	Greenup	0.53	0.28
Blue-gray gnatcatcher	PR	Greenup	0.26	0.38
Indigo bunting	BG	Greenup	0.02	0.74
Red-eyed vireo	BG	Greenup	0.45	0.1
Common yellowthroat	BG	Greenup	0.46	0.06
Blue-gray gnatcatcher	BG	Greenup	0.18	0.3

Table 1. R^2 and p-values for weighted linear models for each bird species as a function of GDD or greenup at both sites.
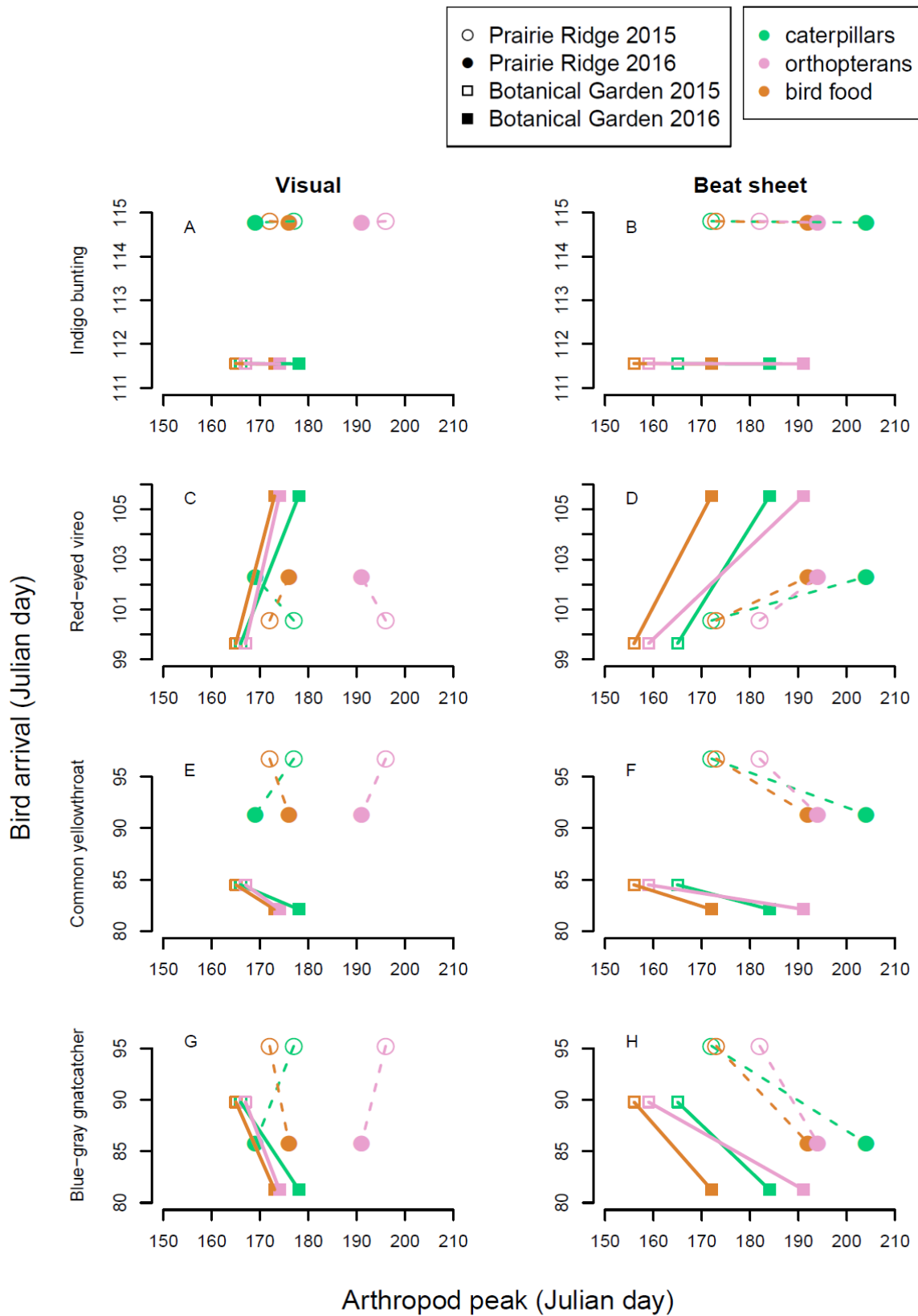
Figure 9. Julian day of indigo bunting (A, B), red-eyed vireo (C, D), common yellowthroat (E, F) and blue-gray gnatcatcher (G, H) arrival date as a function of peak occurrence date for arthropods: caterpillars (green), orthopterans (pink), or bird food (orange). Peak arthropod occurrence estimated from visual surveys plotted in left column, and from beat sheets in right column. Segments connected between years (open shapes, 2015; closed shapes, 2016) for a given site (circles, Prairie Ridge; squares, Botanical Garden) and arthropod group (colors).