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Insights from citizen science into the spatiotemporal dynamics of Batesian mimicry in the context of climate change

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Thesis

**INSIGHTS FROM CITIZEN SCIENCE INTO THE
SPATIOTEMPORAL DYNAMICS OF BATESIAN MIMICRY
IN THE CONTEXT OF CLIMATE CHANGE**

by

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DEDICATION

For being the first in three generations of women in science, and for her love for butterflies, I dedicate this to my grandmother, Diana Lee.

Love, 婷玲

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Sean Mullen, for his support and expertise throughout this project. Sean kindly welcomed me into his lab last year and quickly provided me with many opportunities to get involved in a number of amazing research projects. It has been a pleasure to be involved in work with the Mullen Lab, and I am deeply grateful for my time here.

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Thank you as well to my amazing committee members, Dr. Fred Wasserman and Dr. Pete Buston, for all of their helpful feedback and support in this project. And a big thank you to Dennis Milechin from Boston University Research Computing Services for providing invaluable software support and assistance with GIS-related questions. I would also like to express my gratitude to Dr. Leslie Ries and PhD candidate Vaughn Shirey of Georgetown University for their invaluable insights during the formative stages of this project.

Finally, I would also like to thank Butterflies and Moths of North America and iNaturalist for their free provision of citizen science data used in this project.

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ABSTRACT

Climate has a demonstrable impact on species distributions, with changes in climatic oscillations often producing complex downstream effects due to species-specific tolerances to changes in temperature and precipitation. In general, barring physiological or environmental barriers, species are predicted to migrate polewards, and possibly also upwards in elevation, in response to general equatorial warming (Walther *et al.* 2002). A major challenge to substantiating this predicted relationship between temperature and distribution, especially for highly mobile or nomadic species, has been the lack of suitable techniques for tracking species distributions with sufficiently high resolution to assess for evidence of range shifts over decadal timescales. However, the recent rise in the volume and availability of citizen science data has demonstrated its strong potential as a tool for elucidating responses to environmental change on large temporal and spatial scales (Champion *et al.* 2018; Hurlbert & Liang 2012; Soroye *et al.* 2018). Here we assessed the strengths and weaknesses of three different citizen science datasets in addressing questions relating to historical range shifts in two butterfly species endemic to the eastern United States: the pipevine swallowtail (*Battus philenor*) and its Batesian mimic, the red-spotted purple (*Limenitis arthemis astyanax*). Motivated by the prediction that there would be a quantifiable northward latitudinal range shift in both *B. philenor*

and *L. a. astyanax* in response to historical regional warming, we ultimately analyzed twenty-four years of observational survey data from the North American Butterfly Association and found evidence to suggest that, surprisingly, from 1998 to 2021, there is no indication of a directional range shift in either the model or its mimic. However, consistent with expectations from classic mimicry theory we found evidence of a tight historical correlation between the ranges of *B. philenor* and *L. a. astyanax* over the years surveyed. Furthermore, we found that the annual variance in the ratio of models to mimics is significantly lower at the model's northern range limit than in other parts of its range. This suggests that phenological coupling between these two species is subject to more intense selection at the range edges and that climate-induced changes in phenology likely have stronger fitness consequences in areas where the model species, *Battus philenor*, is relatively rare. Taken together, our results support the potential of citizen science data as a powerful resource for tracking historical spatiotemporal changes in highly vagile insect populations, particularly in tracking patterns linked to the long-term effects of climate change.

TABLE OF CONTENTS

DEDICATION.....	<i>iv</i>
ACKNOWLEDGEMENTS.....	<i>v</i>
ABSTRACT.....	<i>vi</i>
LIST OF FIGURES	<i>x</i>
INTRODUCTION	<i>1</i>
Climate Change and Monitoring Dispersive Species	1
Study Species and Predictions of Mimicry Theory	2
Applications of Citizen Science Data	4
Purpose of This Study	5
MATERIALS AND METHODS.....	8
Assessment of Citizen Science Datasets.....	8
Data Quality Control and Filtering	13
Species Home Range Percent Overlap Estimates	16
Annual Variance in Ratio of Relative Abundance.....	17
RESULTS	20
DISCUSSION.....	22
Strengths and Weaknesses of Citizen Science Data	23
Model-Mimic Home Range Overlap	23
Variability of Model-Mimic Relative Abundance is Influenced by Degree of Sympatry with Respect to the Model’s Distribution	25
CONCLUSION.....	28

Future Directions	29
SUPPLEMENTARY MATERIALS	<i>31</i>
BIBLIOGRAPHY.....	<i>33</i>
CURRICULUM VITAE.....	38

LIST OF FIGURES

Figure 1. Study Species and Data Source Summary Statistics	12
Figure 2. MCP Range Overlap Estimates	15
Figure 3. Variance in Model-Mimic Ratio of Relative Abundance.....	17
Figure S1. Comparison of Sightings to Sampling Effort.....	31
Figure S2. Distribution of Sightings	32

INTRODUCTION

Climate Change and Monitoring Dispersive Species

Anthropogenic climate change can have complex ecological consequences. Shifting seasonal and annual temperatures and increasing severity of meteorological events have been shown to contribute to phenological shifts in many species (Walther *et al.* 2002). Examples include earlier first occurrence and breeding time for avian and insect species (Stemkovski *et al.* 2022), earlier spawning time in amphibians (Carey & Alexander 2003), and earlier shooting of flowering plants (Piao *et al.* 2019). However, predicting the timing and severity of impact due to regionally shifting climate regimes remains challenging due to the complexities of short- and long-term environmental stochasticity as well as population- and community-level processes at play (Walther *et al.* 2002). Previous work has furthermore demonstrated that the downstream effects of climate change vary by species, often presenting as phylogenetically biased patterns of species loss (Willis & Primack 2008). Therefore, addressing the downstream implications of climate change often must be done on a per-species basis.

The urgency of the global climate crisis necessitates methodological advancements for both characterizing historical trends and predicting future population-level changes in endangered, threatened, and indicator species. However, due to differences in anatomy and life history, certain species have proven more challenging to monitor than others. Accurately characterizing the spatial distributions of migrant and nomad species remains especially difficult due to their high mobility and sometimes unpredictable, opportunistic migratory behaviors (Runge *et al.* 2014; Runge *et al.* 2015). The issue is further

complicated by the fact that environmental stressors have the potential to quickly reshape the year-to-year spatial distributions of these very same populations, an adaptive behavior that is seen in numerous nomadic species (Dostine *et al.* 2014; Runge *et al.* 2014). Even when possible, traditional tracking methods such as banding and radio telemetry – common techniques for monitoring birds – have low return rates and are frequently inadequate in capturing movements across large areas (Donovan *et al.* 2006). Advances in satellite telemetry may be promising for tracking migratory patterns in larger species but are ill-suited for smaller species such as insects (Webster *et al.* 2002). Other more contemporary methods such as genetic analysis and stable isotope chemistry have potential to be used in tandem with satellite data but are often insufficient on their own due to the high level of variability in genetic differences across populations and biogeochemical variations across localities (Webster *et al.* 2002).

Study Species and Predictions of Mimicry Theory

This study uses citizen science data to interrogate historical trends in species distributions by mapping changes in sighting locations over time. We specifically chose to focus on the mimetic relationship of two species of butterfly, the pipevine swallowtail (*Battus philenor*) and its Batesian mimic, the red-spotted purple (*Limenitis arthemis astyanax*), as a lens for examining the interplay between ecological and evolutionary dynamics in the context of climate change.

Batesian mimicry occurs when a palatable species (the mimic) co-opts a warning signal, via convergent evolution, from a defended species (the model) in order to deceive potential predators (Bates 1862, p. 511; Ceccarelli 2018; Pfennig & Mullen 2010). The

core prediction of Batesian mimicry theory is that the mimic's protection from predation will erode in the absence of the model, or when the mimic becomes more abundant relative to the model, in relation to the model's level of unpalatability (Pfennig & Mullen 2010; Pfennig *et al.* 2007). As a consequence, the distribution of a mimetic species is predicted to be geographically confined by the distribution of its model (Pfennig *et al.* 2001). In reality, mimetic relationships are highly nuanced, and many examples of allopatric mimics exist, posing a paradox to the original theory (Conant & Collins 1998; Pfennig & Mullen 2010; Prudic *et al.* 2002). Hypotheses for why allopatric mimicry occurs are numerous. For example, in some instances, it is possible that selection incidentally favors the mimetic phenotype beyond the range of the model. This scenario is most likely to occur if both the model and mimic species have independently converged on the same phenotype for reasons other than protection from predation or because predator behavior, such as innate, unlearned avoidance of a general aposematic phenotype, is the driver for allopatric mimicry. Alternatively, changes to the ecological niches of the model or the mimic populations could also play a role in the persistence of allopatric mimicry. For instance, if a model population experiences a sudden range contraction, the mimic population may be unable to maintain sympatry with the model. Finally, it has been hypothesized that gene flow from a sympatric population of mimics to a neighboring allopatric population could maintain the mimetic phenotype beyond the extent of the model's range (Pfennig & Mullen 2010).

The relationship between the *B. philenor* and its mimic, *L. a. astyanax*, is one such example of allopatric Batesian mimicry. This relationship has been clearly demonstrated

both in early ecological and behavioral studies (Brower 1958; Brower & Brower 1962; Platt & Brower 1968) and in more recent work involving observational field data (Ries & Mullen 2008). *Limenitis arthemis* is a polytypic species complex including the mimetic subspecies *L. arthemis astyanax* and its conspecific, the non-mimetic white admiral (*L. arthemis arthemis*). The former phenotypically resembles the highly toxic pipevine swallowtail, as both species are characterized by predominantly black melanization on the forewings and hindwings, with blue-green iridescent scales on the distal regions of the hindwings (Fig. 1a – b). Both *L. a. astyanax* and *B. philenor* exist largely sympatrically in the eastern United States (Ries & Mullen 2008).

Applications of Citizen Science Data

As previously mentioned, a fundamental constraint to answering questions dealing with historical changes in distribution and abundance lies in the dearth of available techniques for tracking entire populations of highly abundant, vagile species (El Sheikha 2019; Kokko & Sepulcre 2006). Given these limitations, there is a strong interest in using citizen science data to leverage the statistical power offered by large historical data sets (Tulloch *et al.* 2012).

Citizen science is most concisely defined as the engagement of the public in a scientific project (Kobori *et al.* 2016). Such projects are typically either organized field-based censuses or less structured, opportunistic data collection events conducted by casual volunteers (Tulloch *et al.* 2012). Records from citizen science projects have potential to offer novel insights into the nuanced life-histories of a wide range of populations and communities. For example, some historical records, such as the annual

cherry blossom blooms in Kyoto, Japan, date as far back as 1200 years (Aono & Kazui 2007). In the United States, the National Audubon Society's Christmas Bird Count and the Xerces Society's Fourth of July Butterfly Counts have occurred annually, respectively, since 1900 and 1975. Both are nationwide, volunteer-based community censuses (Swengel *et al.* 1990; Tulloch *et al.* 2012). Volunteer-based citizen science projects have also been shown to exceed most federal-funded studies in the sheer breadth of their temporal and taxonomic extent, and these projects can furthermore amount to billions in their equivalent economic value in labor and resources (Theobald *et al.* 2015). Citizen science projects have also become increasingly well-funded in recent years, as prominent research funding agencies have begun to place more emphasis on the necessity of public engagement in their research funding goals (Golombic *et al.* 2017). For these reasons, citizen science data has great potential to both provide historical context for long-term studies and act as a powerful statistical framework for answering questions on both ecological and evolutionary timescales.

Purpose of This Study

In order to persist, theory predicts that mimicry complexes require spatial and temporal overlap between the model and mimic species. Consequentially, climate change may have an especially strong effect on this type of interspecific dynamic, particularly on the phenological synchrony of the actors involved (Hassall *et al.* 2019). Climate data obtained from NOAA indicates a generalized increase in both precipitation and annual temperatures in the eastern United States over the past 30 years, from 1991 to 2020 (NOAA 2023). These findings prompted our interest in identifying regional changes to

species spatiotemporal relationships over the same time period.

Butterflies are particularly suitable model organisms for studying climate change because they are ectothermic animals that thermoregulate through a combination of behavioral, physiological, and phenotypic traits. Past studies have demonstrated that different species of Lepidopterans respond uniquely to climate change; some expand their ranges, while others experience range contractions (Hill *et al.* 2021). Greater wing melanism – as seen in both of our study species – has also been shown to increase the risk of thermal stress under increasing temperatures (Kingsolver & Buckley 2015). Because ectotherms display temperature-limited growth (Belitz *et al.* 2020), and because species tend to migrate polewards in response to general warming (Walther *et al.* 2002), we initially predicted that there would be significant northward range expansions in both *B. philenor* and *L. a. astyanax* due to the rise of regional annual temperatures over the aforementioned time period. We furthermore sought to identify potential hotspots within the mimicry complex at potentially greater predisposition to stress under the effects of rising annual temperatures. We did so by quantifying annual variability in the relative frequency of models versus mimics, predicting that lower variability in relative abundance of the two species would be seen at the northern edge of the model's range.

This exploratory study presents a novel approach to testing classic mimicry theory using citizen science data. Because most of the existing literature on the sympatry of model and mimic species is based on field experiments, anecdotal observations, and museum records (Harper & Pfennig 2007; Pfennig *et al.* 2001), citizen science data may prove a strong additional resource for modeling large-scale trends in population

dynamics, with additional potential to be used in tandem with more targeted monitoring strategies (Whipple *et al.* 2022). By examining the strengths and limitations of three different citizen science datasets that employ contrasting methods of data collection, we were able to address the efficacy of each of these data sources in representing current trends and predicting future changes to the spatial distributions and relative abundance of two species of mimetic butterfly. In working with the historical citizen science datasets used in this study, our objectives were threefold: (1) to test for geographical overlap and (2) evidence of historical range shifts in our study species, and (3) to compare variance in the ratio of models to mimics within different regions of the mimicry complex.

MATERIALS AND METHODS

We began our analysis by collecting summary statistics on each of the three datasets to determine their usefulness in answering these two fundamental questions. From there, we selected the data source with sufficient historical records for historical analysis. With this data, we analyzed minimum convex polygon (MCP) range approximations using the *adehabitatHR* package in R (ver. 4.2.1) to determine if there was evidence of geographical range overlap and historical range shifts in either species (Calenge 2006). Following methods outlined by Ries & Mullen (2008), we furthermore calculated the variance in relative abundance of models to mimics at selected focal sites within the mimicry complex in order to identify patterns of change over time in model-mimic frequency across the model's geographic range. To further support our findings, we also generated a linear regression model relating variance in the ratio of relative abundance to distance from the heart of the model's range.

Assessment of Citizen Science Datasets

We initially analyzed three separate data sets from Butterflies and Moths of North America (BAMONA), iNaturalist, and the North American Butterfly Association (NABA) for suitability in our study of model-mimic temporal dynamics. BAMONA is a North American citizen science project primarily based on photographic submissions from the volunteers and supplemented by historical records from museum specimens, personal collections, and published literature. This dataset is easily available upon request, and quality control for data is provided by lepidopterists who act as regional coordinators. The data is further verifiable due to the fact that recorded sightings are

typically accompanied by either a photograph or an indication that the specimen belongs to a collection. Species that cannot be distinguished by phenotype alone require a specimen for identification (BAMONA 2023). Of the three datasets evaluated in this study, the BAMONA dataset also contains the most historical data, with the oldest record dating back to 1824. However, due to the comparatively small size of this dataset (437,717 dated observations) and the lack of data collection protocols for participants, there were statistical drawbacks to using this dataset as a stand-alone resource. A cursory overview of historical data also revealed that locational data may be approximate at best for older specimens. Coordinate data for sighting locations occasionally reflect the current location of the specimen — such as the location of the museum in which the specimen is currently housed — rather than the true original site of collection. These biases were some of the factors we took into consideration when assessing the viability of this data source for the purposes of our study.

Unlike BAMONA, iNaturalist is not exclusive to Lepidoptera and is also a much more recent citizen science dataset. Established in 2002, iNaturalist is a globally available, app-based citizen science platform that allows users to directly upload GPS-tagged observations of flora and fauna. According to the organization's website, observations are deemed “verifiable” if they are: dated, georeferenced, have photos or sounds, and are not a captive or cultivated organism (iNaturalist 2023). When at least two of three identifiers agree on taxon, an observation is deemed “research-grade”. Only research-grade observations were used in this study. iNaturalist is a robust resource due to the sheer size of its dataset, with over 14 million recorded observations of butterflies

and moths to date (iNaturalist 2023). The data is also free to the public and can be pulled directly from iNaturalist's website. Prior to download, data can easily be culled to include only research-grade observations. Most observations are additionally corroborated with either a photograph or an audio recording for further independent verification of taxonomic identification. However, similar to BAMONA, this dataset presents its own challenges due to the high variability of data collection methods. Because absences of a particular species at a given time and location are not recorded, this type of data is considered "presence-only". For the purposes of population-level data analysis, absences of data points cannot be interpreted as true zeros, as they would be with pure survey data. Furthermore, due to the app-based nature of this platform, submissions may potentially be limited by availability of cell service, internet connection, or general access to technology.

The third dataset used in our initial analysis came from the North American Butterfly Association (NABA). NABA is a purportedly non-profit organization that has run annual butterfly counts since 1993. The data provided by NABA is exclusively privately accessible. Approximately 450 yearly NABA counts occur at established count sites in the United States, Canada, and Mexico. During a count event, volunteers record all sightings of butterflies and moths within a 15-mile diameter circle of the count site center, and all data is collected within a one-day period. The center of the count site is used as an approximate location for all sightings recorded during the count event. Some count sites may be surveyed by multiple parties within a given day, and the total number of survey hours are tracked and recorded for each count event (NABA 2017; NABA

2021). In comparison with BAMONA and iNaturalist, the NABA dataset is collected under the most standardized protocols and therefore qualifies as true survey data. As the NABA data is not “presence-only”, species absences can be interpreted as true zeros. However, due to the fact that NABA survey data cannot be corroborated with specimens, photographic evidence, or sound files, observations are not independently verifiable. Despite this shortcoming, the NABA dataset is a larger historical dataset than the dataset provided by BAMONA, and of the three datasets in this study, it is based on the most consistent collection techniques. Because NABA provides data from as early as 1977, their dataset also offers a more consistent historical perspective than either the BAMONA or iNaturalist datasets.

To understand the distribution of data and compare sample sizes across all three datasets, we first plotted total observations per year for each entire dataset using the *ggplot* package in R. This initial analysis revealed that, although BAMONA provided the farthest-reaching historical records (with the oldest recorded specimen collected in 1824), the sample size for historical data was too small to be useful in this study. BAMONA’s entire dataset only became consistently robust enough for historical analysis in the early 2000s. Similarly, the iNaturalist dataset did not provide adequate sample sizes until around 2019 (*Fig. 1c – d*). Of the three, the NABA dataset provided the best record for analysis of historical trends, with consistent sample sizes from about 1998 through 2021. Since NABA also provides estimates of sampling effort, recorded as total party hours per survey event, we created a linear regression model to compare party hours per year with the number of annual observations for the NABA data used in this study. We found

trends in the number of observations to be unrelated to the total party hours per annum ($R^2 = 0.007$). Therefore, we were confident that annual variations in sighting frequency were unrelated to yearly sampling effort with this dataset (Fig. S1). Because the NABA dataset was the only dataset of the three with a sufficient number of annual observations for examining historical trends, we chose to conduct the remainder of this study exclusively using this dataset.

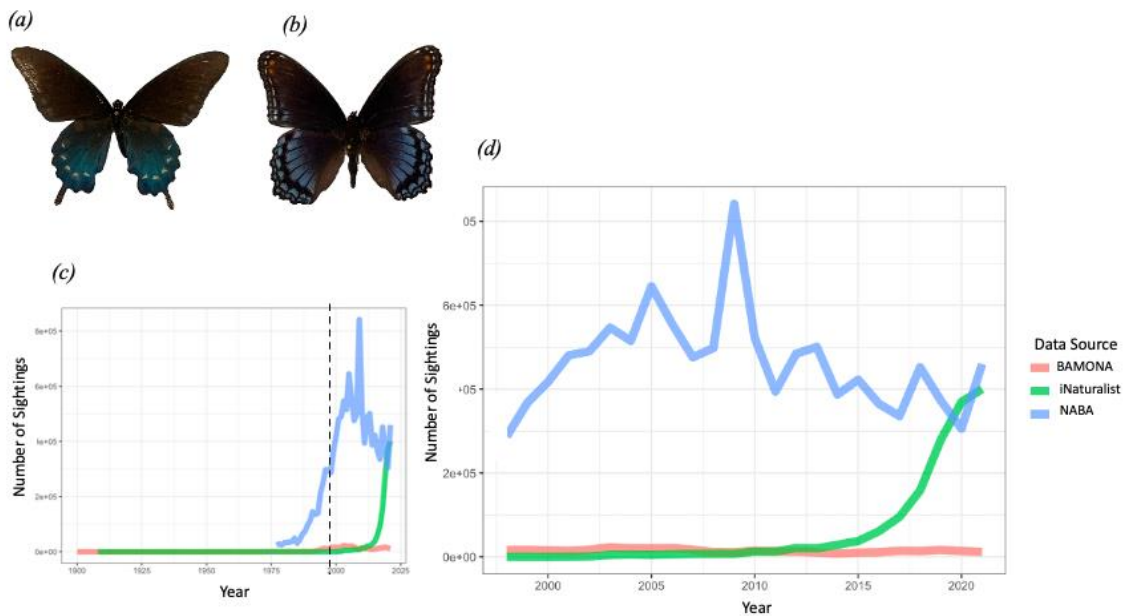


Figure 1. Study species and data source summary statistics. (a) A model, *Battus philenor*, and its Batesian mimic, (b) *Limenitis arthemis astyanax*. Photographs © 2022 by Abby Robinson and Jessica Herrmann, taken at the McGuire Center for Lepidoptera & Biodiversity, Gainesville, FL. (c) Comparison of annual sightings across all three data sources. Vertical dashed line marks the year 1998, beyond which point there was a consistently high enough number of annual observations in the NABA dataset for our historical analysis. (d) Annual sightings per data source for the years 1998 – 2021.

Data Quality Control and Filtering

To correct data entry errors, we created a filtered dataset that corrected for errors (e.g. GPS location input errors). We also filtered the dataset to reduce the likelihood of artificial inflation of total yearly observations of *B. philenor* and *L. a. astyanax* in the southern regions of their home ranges. Due to climatic differences in the northern versus southern regions of both species' ranges, the populations in the eastern United States typically have one to two summer flight periods in the northern parts of their ranges (from approximately June through August) and are multivoltine throughout the year in the southern parts of their ranges (LeGrand & Howard 2023; North American Moth Photographers Group 2022). Since NABA typically only surveys each site once per year, their data was unsuitable for studying phenological trends. We instead used data from iNaturalist for further verification by comparing the number of monthly sightings of *B. philenor* and *L. a. astyanax* in the northern and southern regions of their overlapping home ranges (Fig. S2). In order to control for these temporal differences across both species' ranges, we used the *lubridate* package to subset the entire dataset to exclusively include observations from the months of June through August, peak season for both *B. philenor* and *L. a. astyanax*.

To accurately assess temporal changes in geographic ranges across our 24-year period, we only included site locations that were sampled every year between 1998 and 2021. We began by excluding data from NABA sites that were not repeatedly surveyed each year throughout our 1998 – 2021 study period so that inconsistent site sampling, or potential additions of new survey locations throughout the duration of the time course,

would not bias the observed trends in sighting locations. This step was especially crucial to our calculations of species range limits. And since the range of the mimicry complex is limited to the eastern US and southern Canada, we chose to filter by US states and Canadian provinces encompassing the extent of the mimicry complex. These were: Ohio, Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, Pennsylvania, New York, New Jersey, Delaware, Maryland, West Virginia, Virginia, Kentucky, Tennessee, North Carolina, South Carolina, Georgia, Florida, Mississippi, Alabama, and Ontario, Canada. We found that there were 34,937 observations of butterflies and moths at sites within this region sampled annually from 1998 through 2021, within the summer months. In total, there were thirty-seven NABA sites matching our criteria, and of the initial thirty-seven, one or both of our species of interest had at least one recorded observation at a total of thirty sites within the chosen twenty-four-year timeframe (*Fig. 2a*).

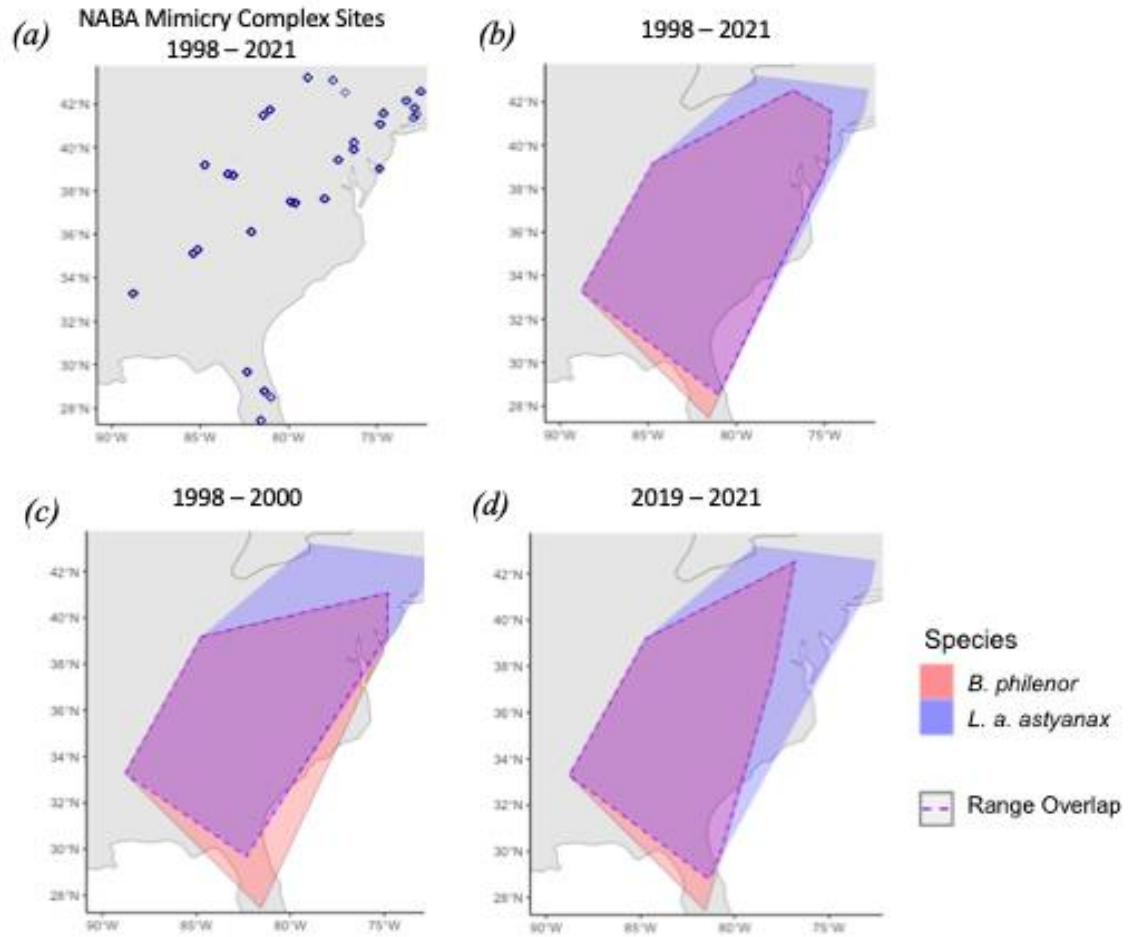


Figure 2. MCP range overlap estimates. (a) A map of all thirty NABA sites encompassing the *B. philenor* mimicry complex, 1998 – 2021. (b) An MCP plot of cumulative estimated species home ranges for the years 1998 – 2021. Red and blue polygons represent the distributions of *B. philenor* and *L. a. astyanax*, respectively. The purple polygon enclosed by dashed lines indicates estimated home range overlap between the two species. (c) – (d) MCP plots estimating species distributions for 1998 – 2000 and 2019 – 2021, respectively.

Species Home Range Percent Overlap Estimates

To examine small-scale temporal trends in species distribution, we grouped the data into eight three-year increments as follows: 1998 – 2000, 2001 – 2003, 2004 – 2006, 2007 – 2009, 2010 – 2012, 2013 – 2015, 2016 – 2018, and 2019 – 2021. Due to the size of the dataset, smaller grouping of one to two years would have provided an insufficient number of sightings. We then used the *adehabitathr* package to plot minimum convex polygons (MCPs) of each species' distribution for every three-year increment. MCPs are typically used to estimate species home ranges and are generated by connecting the outermost coordinate points in a dataset, thereby providing putative range boundaries based on the available coordinate data for a given species. Because NABA's data are collected at fixed sampling sites, we could not soundly interpolate population density at locations between sites or beyond the range of the outermost sites. Therefore, we opted not to use kernel density estimations (KDEs) and instead calculated the total MCP areas and percentage overlap between the *B. philenor* and the *L. a. astyanax* MCPs for each of the three-year time periods. Percentage overlap was calculated as the percentage of the *B. philenor* MCP occupied by the *L. a. astyanax* MCP, a proxy for the degree of sympatry between the model and the mimic. We also calculated the minimum and maximum observed latitude for each species at each three-year interval.

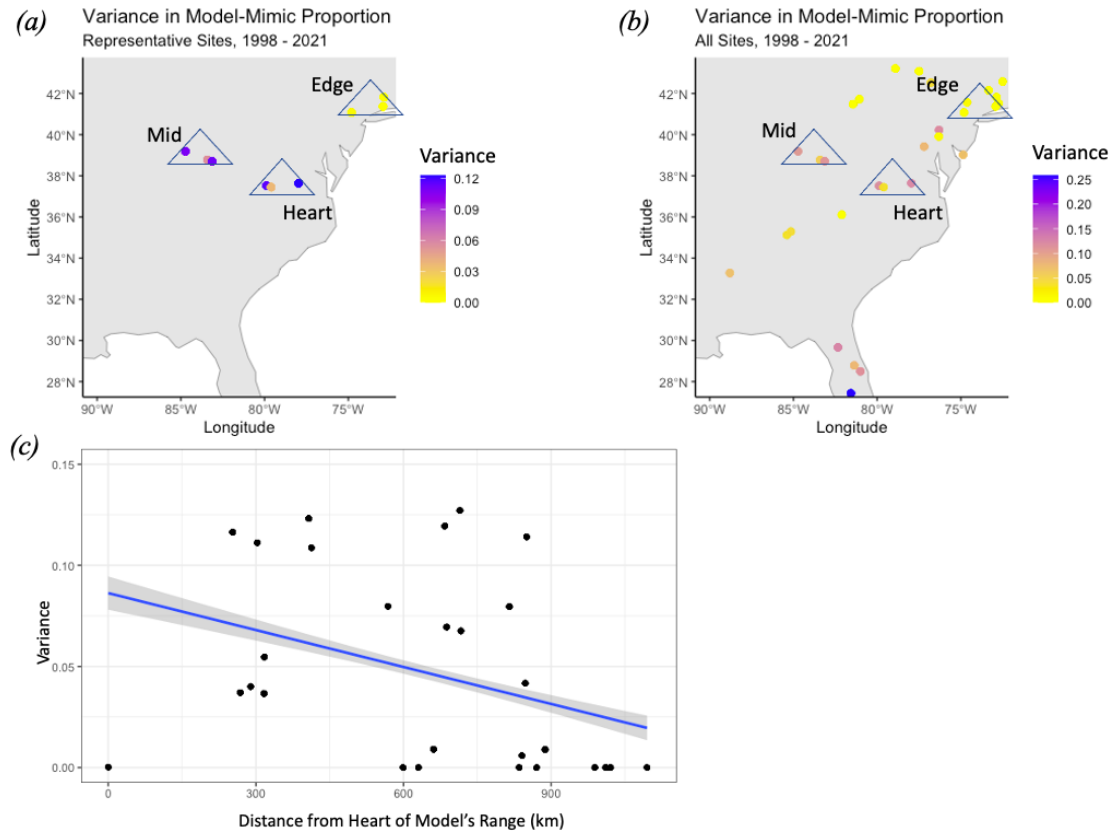


Figure 3. Variance in mimic-model ratio of relative abundance. (a) Variance in model-mimic proportion across all 24 years. Triangles outline each three-site cluster used to compare the different regions of the model's range. (b) Variance in ratio of model-mimic relative abundance across all 30 NABA sites encompassing the mimicry complex. (c) Linear regression model demonstrating a negative correlation between distance from the heart of the model's range and variance in the ratio of model-to-mimic relative abundance.

Annual Variance in Ratio of Relative Abundance

We next tested our prediction that the variance in the relative ratio of models to mimics should decrease with greater distance from the heart of the model's range. To investigate changes in relative abundance over time, we calculated the yearly ratio of models to mimics (hereafter referred to as ratio of relative abundance) for each of the thirty sites of interest. Because absences are not recorded in survey data, we were missing

years for which neither the model nor the mimic were observed at a given site. For this reason, the dataset for all thirty sites was modified to include years in which there were no sightings of either *B. philenor* or *L. a. astyanax*.

Next, we selected three sites that fell within the heart of the model's range and three sites at the northern edge of the model's range. An additional three-site cluster that fell between these two locations was chosen to represent an intermediate latitude between the heart and edge of *B. philenor*'s range. Relative locations of each representative cluster were based on preliminary range maps for both species created using the BAMONA, iNaturalist, and NABA datasets, as well as on species distribution data from LeGrand & Howard 2023 and the North American Moth Photographers Group. The sites comprising each three-site cluster were chosen based on relative proximity, and each cluster was intended to be an approximate spatial replica of the others. However, given the limited number of suitable survey locations, the exact distance between sites within each cluster varied. The total area covered by each cluster ranged from 194,425.3 km² to 3,919,519.6 km². Our selected sites in the heart of the model's range were located in Fincastle, Peaks of Otter, and Maidens, Virginia. The sites we chose to represent the edge of the range were located in Farmington Valley and Southern New Haven County, Connecticut, and Springdale, New Jersey. The intermediate sites, all located in Ohio, were Adams County, Shawnee State Park and Forest, and Western Hamilton County Parks. We first calculated the average ratio of model-to-mimic relative abundance per three-site cluster. Next, we calculated the average variance in this ratio over the twenty-four-year timespan for all nine representative sites and compared the variance of this ratio across each of the three-

site clusters. We then used a two-sided F-test to test for significance in the differences between variance values calculated for all three locations.

To further substantiate our findings, we additionally modelled the relationship between distance from the heart of the model's range and variance in the ratio of relative abundance. We first identified the NABA site in Roan Mountain, Tennessee, as the site with the highest average and maximum recorded sightings of *B. philenor* over the years of interest. This site was selected to represent the heart of the model's range. Note that this site was not included in the three-site cluster representing the heart of the range because there was an insufficient number of neighboring sites to pair with it in the previous test. We then used the coordinates for the Roan Mountain site as an estimated centroid for the model's range and used the *dism* function in the *geosphere* package in R to calculate the distance in kilometers of each of the remaining twenty-nine NABA sites from this central site. Next, we plotted a linear regression model to test the relationship between distance from the central site and variance in the model-mimic ratio over the twenty-four-year timespan.

RESULTS

Based on the evidence in this preliminary study, our data revealed no clear evidence in support of a historical range shift in either *B. philenor* or *L. a. astyanax* from the years 1998 through 2021. MCP estimates of total range area for both the model and the mimic remained consistent throughout the study period, with only a slight decrease in the range area for *B. philenor* between the years 2001 and 2009 (*Fig. 2b – d*). The percentage overlap of *L. a. astyanax*'s range with *B. philenor*'s range remained consistently in the low 90% range, with the exception of the years 1998 through 2000, in which the percentage overlap was an estimated 81.1%. The average percent overlap for all twenty-four years, 1998 – 2021, was 93.1%. The upper and lower range limits for both species also remained consistent throughout the time course of this study. The lowest observed latitudes for *B. philenor* remained between 27.43°N and 28.78°N, and the upper range limit for the species remained consistently between 40.23°N and 41.07°N. As expected, the range for *L. a. astyanax* trended more northward than the range of *B. philenor*, with a lower range limit between 28.5°N and 29.67°N and an upper limit between 42.15°N and 43.21°N. Despite a lack of evidence for large-scale directional trends in the ranges of *B. philenor* and *L. a. astyanax* over our selected time course, there was evidence of small-scale annual fluctuation in the ranges of both species.

As expected, our analysis of model-to-mimic relative abundance further suggested that the proportion of *B. philenor* to *L. a. astyanax* was significantly more variable for sites located in deep sympatry than for the sites in edge sympatry, with respect to the model's range (*Fig. 3a – b*). The average ratios of models to mimics in the sites

representing the heart and middle of the model's range were 0.51 and 0.68, respectively. Conversely, the average ratio at the edge of the range was 0.01. The average variance in the ratio of relative abundance seen at the intermediate sites was also greater than the variance at the edge of the model's range. The mean variance in ratios for the sites in both the heart and middle of the model's range ($\sigma^2 = 0.092$) was significantly greater ($P = 2.2 \times 10^{-16}$) than the mean variance ($\sigma^2 = 0.002$) calculated for the sites at the northern edge of *B. philenor*'s home range. Though less indicative of a strong trend ($R^2 = 0.023$), our linear regression model also revealed a negative correlation between distance from the centroid of the model's range and variance in the ratio of relative abundance (*Fig. 3c*).

DISCUSSION

Here, we analyzed two publicly available data sets and one privately accessible data set to investigate the hypothesis that there has been an appreciable historical shift in the range of *B. philenor* and its mimic, *L. a. astyanax*, over the years 1998 through 2021. Our results indicate that, consistent with classical expectations of Batesian mimicry theory, there is a strong historical correlation between the geographic ranges of *B. philenor* and *L. a. astyanax*. We also found that the yearly variation in model-to-mimic relative abundance was lower in sites located closer to the edge of the model's home range. This suggests potentially tighter phenological coupling at the range edge, presumably due to stronger natural selection on the mimic in areas where the model is generally rare, than in the heart of the model's range where inter-annual variation in the model's relative abundance has less effect on the mimic's overall fitness. Surprisingly, we found no clear evidence of a directional range shift in either species over the time period of interest. While this result is contradictory to our expectation that climatic warming should facilitate range expansions of *Battus philenor*, and subsequently a northward expansion of the selective advantage for the mimetic form of *Limenitis arthemis*, it may indicate a lag between rapid warming of annual temperatures, happening on an ecological timescale, and the evolutionary response of these two butterfly populations. However, further assessment of this hypothesis will require statistically modeling of species occupancy to address some of the limitations of the citizen science data sets, detailed below.

Strengths and Weaknesses of Citizen Science Data

We found significant heterogeneity in the quality and consistency of our citizen science data, resulting in inconsistent correlations across our three data sets. These inconsistencies were largely due to variability in data collection methodologies. Due to the lack of formalized collection methods, BAMONA and iNaturalist data are potentially affected by significant ascertainment bias. Data sets from these sources, which provide information about species presence but no confirmation of absence, are therefore challenging to analyze for changing patterns in species distribution and abundance over time because they may contain a large number of false negatives (e.g. examples where species were present but not reported). Secondly, the low data density, or complete lack of historical data, from the two datasets precluded us from drawing meaningful conclusions about spatial trends over timescales extending more than a few years before present. This contrasts with standardized climate records (such as NOAA climate normals), that are typically summarized over thirty-year periods (NCEI 2023). Given these limitations, we based the majority of our statistical analyses on the historical survey data provided by NABA, as this organization provided the most robust and uniformly collected historical Lepidoptera data.

Model-Mimic Home Range Overlap

Because the spatial relationship between model *B. philenor* and mimic *L. a. astyanax* represents a known case of allopatric mimicry (Pfennig & Mullen 2010), we did not expect perfect overlap in the ranges of these two species. Despite this, our results indicate that there has been a highly consistent historical overlap between the home ranges of the

model and its mimic from at least the late 1990s through the present. As predicted, the majority of the mimic's range coincides with the range of the model. However, consistent with Ries & Mullen (2008), we found that *L. a. astyanax*'s range extends beyond the northern range limit of *B. philenor*. This finding is important because it confirms the utility of citizen science data for addressing fundamental question about species ranges and supports a core prediction classic mimicry theory. Furthermore, this pattern demonstrates that protection for the mimic quickly erodes beyond the outer reaches of the model's range, as predators that do not regularly encounter the model also do not recognize the warning coloration of the mimic (Pfennig & Mullen 2010).

Despite expectations, our data did not provide evidence of a clear directional shift in the home ranges of either *B. philenor* or *L. a. astyanax* over the twenty-four-year time frame of interest. We did, however, see evidence of small-scale range shifts in both species, though it was difficult to decisively correlate these minute range shifts. It is likely that the small-scale changes we observed result from numerous ecological factors at play, namely environmental stochasticity, host plant availability, and year-to-year variation in climate and precipitation. Since inter-seasonal environmental variability can limit a population's evolutionary responses to climate change (MacLean *et al.* 2016), it may have been the case that the time frame referenced in this analysis was simply not broad enough to reveal the full long-term effects of climate change on our two species of interest. This result was not entirely unexpected, given that previous studies of North American and European butterflies have shown no evidence of universal northward range

expansions in response to climate change. Rather, only a subset of butterfly species has exhibited a quantifiable pattern of northward colonization (Parmesan & Yohe 2003).

Variability of Model-Mimic Relative Abundance is Influenced by Degree of Sympatry with Respect to the Model's Distribution

Though the data did not reveal evidence of a historical range shift, there was evidence to point towards future hotspots for climate-driven phenological change within the mimicry complex. Our comparison of variance in the ratio of models to mimics throughout *B. philenor*'s home range produced results that agreed with our prediction. Because the population density of a model is highest in the heart of its range, mimicry theory predicts strong protection for mimics because predators are expected to frequently encounter and quickly learn to avoid the convergent warning signals of the model and mimic. Therefore, selection pressure against mimics is expected to be lower in the heart of the model's range than at the range edges (Harper & Pfennig 2007). If so, annual fluctuations in the relative abundance of the model, as long as the model is relatively common, should not erode protection for the mimic because of predator learning and avoidance. This is what we found. Our analysis indeed gives evidence to suggest that the highest variance in model-to-mimic relative abundance occurs in the heart of the model's range, the region in which the model and mimic are in deep sympatry with one another. In regions of edge sympatry, where *L. a. astyanax* was present but *B. philenor* was relatively scarce, there was a notably lower degree of annual variation in the relative proportion of models to mimics.

However, due to the limited number of suitable count sites included in this study,

there is still some possibility that our chosen site clusters were not fully representative of the relative abundance of *B. philenor* to *L. a. astyanax* across the entirety of *B. philenor*'s range. There were several variables we were unable to thoroughly control for in this part of our study: location of sites, area covered by each three-site cluster, topography within and across sites, and relative sample sizes in the north compared to the south. In general, there were fewer NABA sites that coincided with the heart of the model's range, as compared to the number of sites representative of the edge of the range. Therefore, our representations of the heart, middle, and northern edge of the model's range are approximate at best. The statistical power of our linear regression model was likely also weakened by the low number of suitable study sites used to model the relationship between distance from the center of the model's range and variance in the relative proportion of models to mimics. Variation in area covered by each cluster of sites was another variable we were unable to completely account for in this study. As such, there is a significant range in area covered by each representative cluster of sites. Differences in elevation across sites and within individual sites may also have affected the trends we observed, given that butterflies with higher wing melanism – such as our study species – tend to be found in greater abundance at higher elevations, where darker coloration is a physiological advantage conferring more efficient thermoregulation and higher UV protection (Clusella-Trullas *et al.* 2020). Finally, it is important to acknowledge that differences in annual sample size for both species in different regions of the model's home range may also have affected the apparent trends in the ratio of relative abundance. Because both species (particularly *B. philenor*) are less abundant in the north, low

variance in the apparent ratios of relative abundance may have been an artifact of lower sample sizes in this region. Future work should address this issue, potentially by directly comparing the raw number of observations of both species, rather than calculating variance in a ratio of their relative abundance.

Nonetheless, these findings highlight areas of the mimicry complex that are at a potentially heightened risk for future perturbation due to the downstream effects of climate change. In particular, the model's northern range limit is a likely candidate for future phenological instability because: (1) there is a lower threshold for annual fluctuation in the relative abundance of models to mimics in this region, and (2) there is also preliminary evidence of tighter phenological synchrony in this part of the model's range (*Fig. S2*). These two factors suggest that future shifts in regional climate regimes may have stronger impact on the model and mimic subpopulations at the edge of the model's range, as the relationship between these two species in this particular region is characterized by a relatively more rigid ecological and phenological relationship than seen elsewhere in the model's range.

CONCLUSION

Here, we have demonstrated the potential advantages of citizen science data as a tool in the analysis of spatial and temporal trends in large, vagile insect populations.

Despite the wealth of valuable information citizen science data has to offer, working with this type of data also presents unique statistical challenges. Because of the lack of protocols and participant training, there is no standardization in sampling effort, area surveyed, and best practices for data collection. For many members of the scientific community, this lack of standardization disincentivizes the use of citizen science data in publication-grade research (Burgess *et al.* 2016; Sullivan *et al.* 2013). It is likely that the average citizen scientist is more likely to report conspicuous, charismatic species more often than less eye-catching or highly ubiquitous species, leading to significant ascertainment bias. Data contributed by hobbyists and collectors has an even greater likelihood of bias towards certain specific taxa of interest. Some collectors may engage in “community sampling” or sampling all species at a given site regardless of taxon, whereas others may only be interested in only a particular taxon or species, known as “targeted sampling” (Shirey 2021). Ascertainment bias is also compounded by the fact that a greater density of data points will correspond to areas of greater human population density (Cornell Lab of Ornithology 2023), as well as to areas with greater access to technology and awareness of citizen science programs. Another major pitfall accompanying the lack of standardized data collection procedures is the “presence-only” nature of the data. When species go unreported, there is no certainty that they were not present, only that they were not accounted for. As such, zeroes in citizen science datasets

cannot be treated as true non-detections. Understanding true absences is critical to painting an accurate picture of species' distribution and abundance. Therefore, it is necessary to either restructure citizen science data collection protocols — or more feasibly — build models that retroactively estimate absence data and account for inconsistencies in sampling effort. In this study, we circumvented the above issues by opting to use volunteer-collected survey data from the NABA dataset. However, in the interest of supporting citizen science projects and the wealth of free, open-source data they provide, future work should include the use of models bespoke to citizen science data in order to substantiate and build upon the findings of this preliminary study.

Future Directions

Occupancy-detection models, or occupancy models, offer a new strategy for dealing with citizen science datasets by incorporating statistical methods to account for inconsistencies in collection effort through space and time. Occupancy modeling involves incorporation of the probabilities of community sampling events and sampling history frequencies to construct a model built upon “occupancy intervals”. Occupancy intervals are records grouped by space and time that allow for the retroactive estimation of discrete sampling events, therefore allowing one to model true non-detections from a presence-only dataset (Shirey 2021). The use of occupancy modeling would open doors to the future use of open-source datasets such as BAMONA and iNaturalist for research purposes. Especially in an era of increasingly rapid environmental change, there is a greater need to understand large-scale spatiotemporal trends affecting population and community structures. Expanding the accessibility of citizen science projects to the

public also provides a powerful way to ensure community involvement and interest in conservation and the natural sciences. Furthermore, encouraging the use of citizen science data within the scientific community yields access to a vast array of specialized datasets that, as of yet, go widely underutilized.

SUPPLEMENTARY MATERIALS

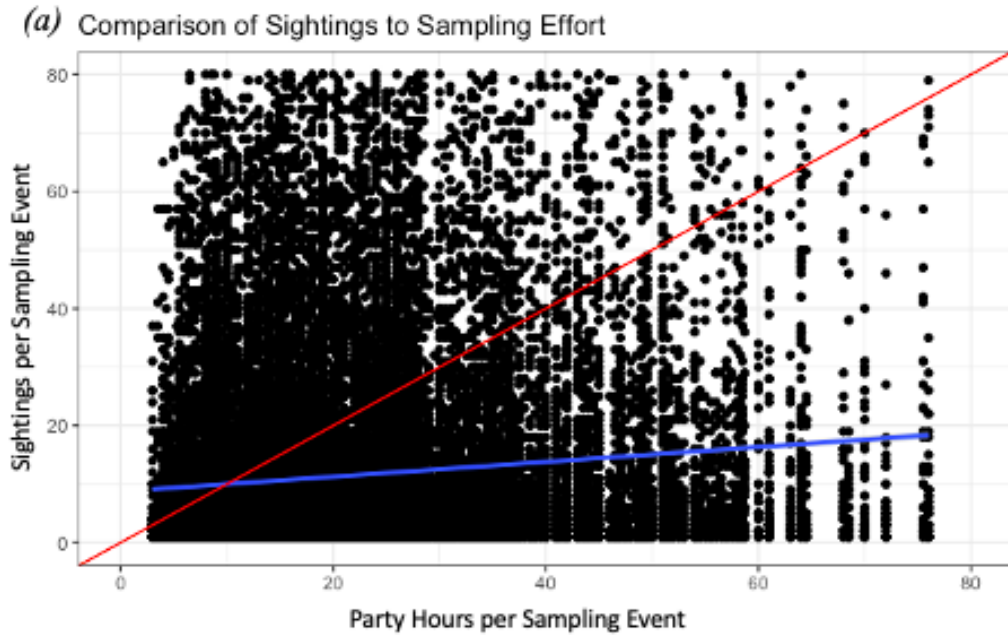


Figure S1. Comparison of sightings to sampling effort. (a) A linear regression model (blue line) showing negligible correlation between the number of sightings and party hours (sampling effort) per sampling event. The red line represents the null hypothesis, a significant positive correlation between sightings and sampling effort. Plot generated from NABA data used in this study, from the years 1998 – 2021.

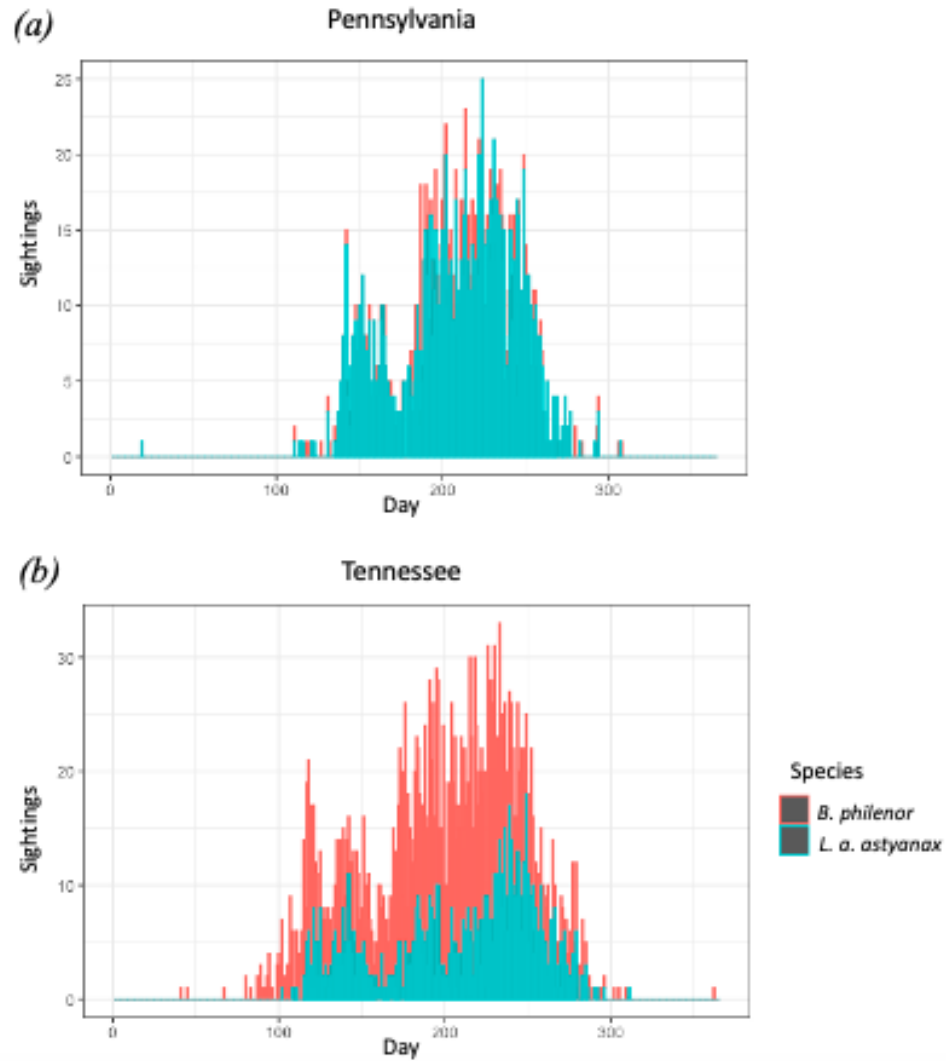


Figure S2. Distribution of sightings. (a) Distribution of annual sightings of *B. philenor* and *L. a. astyanax* in Pennsylvania, representative of the northern region of both species' ranges. (b) Annual sightings of both species in Tennessee, representative of the southern region of both species' ranges. Both plots were generated using all research-grade iNaturalist data for each species. Note that the northern subpopulations of each species exhibit historical bivoltinism, whereas the southern subpopulations are multivoltine and appear to be less phenologically synchronous.

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CURRICULUM VITAE

