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The Effect of Climate on Population Dynamics of Butterfly Species across Southeastern Virginia

A thesis submitted in partial fulfillment of the requirement for the degree of Bachelors of Science in Biology from The College of William & Mary

By

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ABSTRACT

Local climate affects the occurrence and turnover of butterfly populations in a variety of ways, demonstrating a need to explore these interactions in the face of climate change. This study aimed to investigate the influence of climate variation on the population dynamics of five butterfly species with differing life history traits (number of broods and overwintering strategy) and diet preference (sap vs. nectar). Detection/non-detection data were gathered for four consecutive years (2012-2015) across six annual surveys on 67 different sites. I used multi-season occupancy models to analyze the detection/non-detection data. Occupancy models estimate the probability that a species occupies a given area, but also the probability of expansion (previously unoccupied locations become occupied in current year) and contraction (previously occupied locations become unoccupied in current year). To construct multi-season occupancy models for each species, detection probabilities (the probability that a species is detected given that it is present at a given location) were first modeled to account for heterogeneity in the detection conditions across surveys. I then related 30 different climate variables to probability of expansion and contraction while keeping the top detection model constant. Variables that produced the best univariate models were added to a candidate set. From the candidate set of climate variables for each species, multivariate models were generated and model averaged. Model averages informed which climate variables most strongly influenced inter-annual population dynamics. I found that the population dynamics of sap feeders were not driven by climate variability, while nectar feeders were driven by climate variability. The population dynamics for two of the three nectar-feeding butterflies correlated strongly with spring total rainfall. I found no difference in the effect of climate variability on overwintering strategy (pupae vs. larvae) and number of broods. The results from my research can be used to forecast
distributions of these species under various future climate scenarios and provides hypotheses for future research to investigate the specific mechanisms driving population dynamics of these species.
INTRODUCTION

Variation in local climate affects population dynamics of organisms across all taxa (Parmesan et al 2000, Sandvik et al 2012, Ficetola 2016). Ectothermic organisms are reliant on external factors and often more drastically influenced by variation in climate (Boggs 2012). Climate can drive insect populations to fluctuate rapidly on relatively short time scales, leading to near extinction events and then total reestablishment between generations (Martinat et al 1987). These fluctuations designate insects as ideal study organisms to understand the abiotic factors that drive population dynamics. Identifying the strength of external factors, such as weather, on insect populations allows for predictions of population viability in the face of climate change (Cannon 1998).

Ecological field studies often use butterflies to evaluate effects of variation in climate on population dynamics (Cappuccino and Kareiva 1985, Breed et al 2012). Adult butterflies are diurnal and, for many species, are easily identifiable in the field (Kaufman and Brock 2006). Within a temperate ecosystem, adult butterflies emerge and mate during a finite period of time, typically the warmest season of the year (Robinson et al 2012). Monitoring schemes in temperate ecosystems allow scientists to study adult butterfly presence only during summer seasons (Robinson et al 2012, Puntenney and Schorr 2016). Butterfly species in these ecosystems spend all other seasons in diapause, defined as a period of arrested development driven by environmental factors (Andrewartha and Birch 1954). Butterflies can diapause as an egg, larva, pupae, or adult (Opler and Krizek 1984). Each life stage requires and tolerates different environmental thresholds, making phenology an imperative component when studying insect population dynamics (Weiss et al 1993). Long-term monitoring programs on adult butterfly
presence allow for inferences on factors driving population dynamics throughout the life cycle of a butterfly (Gonzalez-Megias et al 2008).

Different life history strategies of butterflies provide characteristics to compare and contrast to population dynamics (Breed et al 2012). Analyzing life history traits across multiple species determines the strength of certain traits in relation to others. Brood number represents a variable life history trait often studied in butterflies (Slansky 1974, Altermatt 2009). Brood numbers typically range from one to upwards of five generations per breeding season (Opler and Krizek 1984). Univoltine species reproduce only once during the breeding season (Settele et al 2009). Univoltine species emerge from diapause in the spring to metamorphose into adults (Settele et al 2009). These adults breed, lay eggs, and emergent larvae enter diapause under the appropriate environmental conditions. Sufficient environmental conditions for diapause are determined primarily by photoperiod and secondarily by other cues, such as temperature (Andrewartha and Birch 1954). In contrast, bivoltine species reproduce twice during the breeding season (Settele et al 2009). Bivoltine species emerge from diapause in the spring to metamorphose into adults. These adults breed, lay eggs, and emergent larvae undergo a full life cycle during that same breeding season. Once adults, these butterflies produce a second generation before the conclusion of the breeding season. The second generation then enters diapause at the end of the breeding season (Andrewartha and Birch 1954). Consequently, multivoltine species reproduce three or more times in a breeding season (Settele et al 2009). Environmental conditions define the number of broods each year, but multivoltine species complete at least three full life cycles within a breeding season (Altermatt 2009).

Different butterfly species also enter diapause at varying life stages (Opler and Krizek 1984). Butterflies overwinter at particular life stages, arrested in development, and do not begin
to develop again until appropriate environmental conditions cease diapause in the spring (Andrewartha and Birch 1954). Entering and exiting diapause are critical moments in the life cycle of a butterfly, as well as enduring the duration of diapause (Posledovich et al 2014). Successfully reaching the adult stage can hinge on the conditions before, during, and after diapause (Kim et al 2014). Different life stages may also respond in diverse ways to these conditions. Overwintering as a pupa, for example, may be advantageous during spring emergence (Stalhandske et al 2015). Butterflies emerge from their chrysalides as adults, wasting no time or energy on metamorphosis to another life stage. Adverse conditions during this emergence, such as phenological mismatch of adult emergence and nectar producing plants, however, can also hinder the success of a generation (Stalhandske et al 2015). Overwintering as a larva, in contrast, may be energetically costly when larvae emerge in the spring and then must search for host plant resources (Clark and Platt 1969). Then larvae must pupate to eventually emerge as adults during the breeding season. Building up extra energy reserves, however, may also benefit the eventual adult butterfly (Boggs 1997). For instance, male butterflies often fly further and more frequently than females, requiring greater energy resources (Kingslover 1983). If larvae are given more time to feed and store energy resources, this may allow for greater mating success in adult male butterflies (Boggs 1997). Overwintering strategies can significantly influence overall butterfly population dynamics (Breed et al 2012).

Adult food resources also greatly differ between butterfly species (Settele et al 2009). Adult butterflies rely on the availability of food resources to harness energy in order to locate mates and reproduce (Kingslover and Daniel 1979). Many adult butterflies consume nectar, defined as the sugary fluid produced in the flower of plants to encourage pollination (Watt et al 1974). Other adult butterfly species consume sap, known as the watery fluid that contains
dissolved sugars and flows in the vascular system of plants (Omura 2001). Butterflies are unable
to access sap on their own and rely on consistent external sap flows in large woody plants
(Omura 2001). Sap moves through plants most readily during days of greatly fluctuating
temperatures (Cermak et al 2004). External sap flows in plants occur typically in response to an
injury (Cermak et al 2004). Sap flows attract adult butterflies to directly consume sap from the
bark of a woody plant (Corke 1999). Differential availability of these adult food resources can
drive population dynamics and therefore makes it a critical characteristic for all butterfly species
(Wiklund 2005).

Life history traits and food preferences across multiple butterfly species influence
variation in population dynamics. However, life history traits are also differently affected by
external factors, such as climate (Diamond et al 2014). Climatic conditions can directly and
indirectly influence butterfly life history traits (Boggs and Inouye 2012). Responses of life
history traits to climate can therefore affect population dynamics. One life history trait across
many species may respond in uniform or dissimilar ways to climate, providing critical insight
into important ecological processes (Vegvari et al 2014, Breed et al 2012).

Temperature and rainfall are the two variables most frequently studied in butterfly
population dynamics (Pollard 1988). Temperature is closely linked to diapause and plant
Butterflies respond to longer day lengths and warmer temperatures in the spring to end diapause
(Clark and Platt 1969). Relying solely on these two environmental cues, butterflies have no
perception of host plant or adult food resource availability. Although the phenology of plants
often aligns with the phenology of butterflies, imperfect timing with plant phenology can affect
insect populations (Peterson 1997, Roy et al 2001). Plants may respond differently to spring
temperature fluctuations than butterflies, resulting in early or late bud emergence in relation to butterfly emergence (Singer et al 2010). Rainfall can also influence the timing of plant phenology and growth, thus affecting butterfly population dynamics (Ehrlich et al 1980, Hellman 2002, Robinson et al 2012). Too little rainfall, for example, may stunt plant growth in the spring, which prevents both adults and larvae from locating food resources (Nagy et al 2013).

During the adult breeding season, rainfall also plays a key role in providing wet, sandy or rocky surfaces for male butterflies (Otis et al 2006). On these surfaces, males can soak in critical salts, proteins, and minerals; this behavior is referred to as puddling (Otis 2006). Puddling allows for males to supplement their diet and strengthen the nutrient composition of their sperm (Pivnick and McNeil 1987). After mating with a female, the extra salts and minerals from the male improve the viability of the newly fertilized egg (Pivnick and McNeil 1987). The ability of males to find nutrients and transmit them to the next generation is critical for population persistence (Lederhouse et al 1990, WallisDeVries et al 2011). If rainfall throughout the breeding season decreases so much so that males are unable to find nutrients and mate, the populations of univoltine, bivoltine, and multivoltine species may be affected in different ways. A univoltine species, for example, could be completely unharmed by a decrease in rainfall if its larvae are already in diapause (Hidaka et al 1971). Bivoltine or multivoltine species, however, could be influenced in different ways, depending on the timing of diapause (Friberg et al 2012). Conversely, prolonged rainfall during the breeding season can also influence realized fecundity (Kingslover 1989). Adult butterflies live on average for about a week (Opler and Krizek 1984). During this time period, butterflies do not fly to forage or mate when it rains (Pellet 2007). Instead, they take refuge under a leaf and wait until the storm passes to resume normal activity (Opler and Krizek 1984). Therefore, after an adult butterfly emerges from its pupa, there is a
critical window of opportunity for the butterfly to reproduce. If there are numerous consecutive
days of rainfall during the breeding season, butterflies are unable to mate (Kingsolver 1989).
Moreover, fertilized females may be prevented from finding host plants and laying eggs during a
prolonged rainy period (Kingsolver 1989). Significant increases or decreases in the amount of
rainfall during the breeding season can affect butterfly population dynamics across different life
history traits.

The conclusion of a breeding season also influences butterfly population dynamics. The
viability of the population is dependent on success at the end of the breeding season to increase
the likelihood of population success in the following breeding season. Larvae and pupae
generally enter diapause at the end of the summer and are dependent on certain climatic
conditions to successfully begin their arrested development (Andrewartha and Birch 1954).
Temperature is one condition, which is closely linked to plant phenology. Larvae are completely
dependent on host plants and must consume enough host plant material to grow large enough to
successfully enter diapause (Hunter and McNeil 1997). Sudden decreases in temperature,
however, can signal to plants to begin to senescence, or lose their leaves (Fleishman et al 2000).
Timing of host plant senescence at the end of the breeding season can affect foraging larvae
(Singer 1972). If temperatures decrease too rapidly and plant leaves respond with earlier
senescence, larvae may not have enough time to feed and then diapause (Dobkin et al 1987).
Host plant senescence at the end of the breeding season can thus negatively affect butterfly
survival (Goehring 2002).

Another direct effect of sudden cold temperatures at the end of the breeding season is on
the physiology of larvae or pupae (Frankos et al 1976). Gradual cooling signifies to larvae or
pupae to decrease their water content and increase glycerol accumulation, which allows for them
to withstand colder temperatures in the winter without freezing over (Frankos et al 1976). Sudden cold, however, may leave larvae or pupae unprepared physiologically and cause them to freeze over before entering diapause.

Climatic conditions during the winter, when butterflies are in diapause, can also affect population dynamics (Scriber et al 2012). Extreme temperature decreases can be fatal for larvae or pupae, but most species possess specific mechanisms to combat average annual low temperatures (Bale 1996). The cold hardiness of larvae or pupae is imperative for population viability, so most species are well-adapted to low winter temperatures. Low winter temperatures during diapause may actually be beneficial to butterflies in diapause. When butterflies overwinter in high densities on a host plant, they may be subjected to the spread of disease (Myers et al 2016). Low winter temperatures can kill potential diseases and prevent them from spreading in the butterfly population. Low winter temperatures also provide strong metabolic cues for butterflies in diapause (Diamond 2014). If late winter and early spring temperatures warm too early in the season, larvae or pupae may experience contradictory cues (Diamond 2014). On one hand, photoperiod signals indicate to larvae or pupae to continue diapause; on the other, temperature signals inform them to end diapause. The overall effect is a waste of metabolic energy and later emergence dates (Diamond 2014; Williams 2012). Late emergence from diapause may lead to a phenological mismatch with host plants or food resources (Singer and Parmesan 2010). Therefore, larvae or pupae demand consistent low winter temperatures until the appropriate time: when photoperiod and temperature cues can align.

The objective of this study was to explore how variation in climate affects population dynamics of five butterfly species that differ in life history traits and food preference (Table 1). Species differ in number of broods (univoltine, bivoltine, and multivoltine), overwintering
strategy (pupae vs. larvae), and in adult food resources (nectar vs. sap). Each characteristic is subject to the influence of climate, potentially at different times throughout the phenology of the species. Within these time periods, different climate variables may also act more strongly than other variables to regulate population dynamics. This exploratory study will relate a set of climate variables to the population dynamics of each of the five species and compare the strength of the variables against each other.

Patterns in explanatory climate variables are predicted to emerge based on life history traits and food preferences. I predict bivoltine and multivoltine species are more susceptible to climate than univoltine species, specifically at the end of the breeding season. Bivoltine and multivoltine species rely on favorable environmental cues as larvae to pupate and continue on for another brood during the breeding season. Univoltine species, however, will enter diapause as fourth or fifth instar larvae, regardless of the environmental signals. Radical changes in environmental conditions can therefore affect bivoltine or multivoltine larvae that are unprepared for diapause, whereas univoltine species are more likely to already be in diapause by the fall season.

I also predict that species which overwinter as pupae are more likely to be affected by climate than species which overwinter as larvae. Climate can metabolically and pathogenically affect both butterfly larvae and pupae throughout the winter, as discussed above. I predict, however, that climate will play a greater role in the spring emergence of butterfly species that overwinter as pupae when compared to those that overwinter as larvae. Butterflies overwintering as pupae emerge from diapause as adults and their short lifespan as adult butterflies demands availability of both host plant and adult food resources at the time of emergence. A mistiming with the plant phenology of either host plants or adult food resources inhibits reproduction and
the persistence of the population. Species that overwinter as larvae rely only on host plant availability when emerging from diapause, halving their reliance on aligning their emergence times with plant phenology when compared with species that emerge as adults.

Finally, I predict that nectar-feeding species are more susceptible to variation in climate than sap-feeding species. Throughout the breeding season, numerous herbaceous plants flower at different times and under optimal climate conditions, such as sufficient amounts of rainfall. Without an optimal climate, herbaceous plants will flower at lower abundance and nectar-feeding species cannot access food resources. Woody plants containing an abundance of sap also rely on climate conditions, but much less so to produce sap because it is vital for plant productivity. Sap resources are hypothesized to be affected less by climate variables than nectar resources.

Because this study is exploratory, its major contribution is to provide hypotheses for further investigation on mechanisms that drive population dynamics under different climatic regimes. Demonstrating contrasting influences of climate across butterfly species highlights the need to study these organisms on a species level. Understanding how the populations of each species respond to climate given an individual set of life history traits furthers knowledge on butterfly population dynamics and allows forecasting of population dynamics under climate change.

**METHODS**

*Study Area*

Four years (2012 to 2015) of detection/non-detection data were collected on adult butterfly species in southeastern Virginia. Sixty-seven 500-m transects were randomly placed
along an urban to rural gradient and forest type (riparian vs upland forest) in nine publically accessible areas: Beaverdam Park (5 transects), Chickahominy Park (8), Colonial Williamsburg (4), Dragon Run State Forest (7), Fort Eustis Military Base (7), Newport News Park (16), New Quarter Park (4), Sandy Point State Forest (6), and the College of William and Mary (10). Starting point of each transect was randomly placed on overgrown service roads and trails. Direction of transect was also randomly selected to follow either up or down a road or trail (Fig. 1). Transect were uploaded to a handheld Global Positioning System (GPS) for tracking in the field. All spatial analyses were performed in ArcGIS 10.2 (ESRI 2014).

I sampled butterflies on four types of transects: edge, forest gap, forest interior, and riparian (Appendix 1) that predominantly bisected upland coniferous and deciduous forests as well as riparian forests. The canopy of upland coniferous forests was dominated by loblolly pine (Pinus taeda) and, in early successional stands, sweetgum (Liquidambar styraciflua) (Monette and Ware 1983, Weakly 2012). Dominant canopy species in upland deciduous forests were American beech (Fagus grandifolia) and oaks (Quercus spp.). Loblolly pine, tulip popular (Liriodendron tulipifera), and sweetgum also were present (Monette and Ware 1983, Weakly 2012). The composition of the canopy in riparian forests depends on hydrology and soil drainage. Common species were red maple (Acer rubrum), birch (Betula spp.), black walnut (Juglans nigra), sweetgum, tulip popular, water tupelo (Nyssa aquatica), black tupelo (N. sylvatica), sycamore (Platanus occidentalis), and oaks (Weakly 2012).

Butterfly survey

Pollard walks were employed to monitor butterfly species (Rhopalocera: Papilionoidea and Hesperioidea) on transects (Pollard 1977; Pollard and Yates 1993). Species were marked as detected if seen within a 5-m area surrounding transects. Individuals were either identified by
sight or captured with a net for closer examination. I visited each transect about every two weeks, during the flying period between mid-May through mid-August. Transects were sampled between the hours of 0900 and 1700 on days without precipitation or strong winds, as butterflies do not fly during these conditions (Pollard and Yates 1993). Transects were walked at a moderate pace for 10 - 15 min in one direction and another 10 - 15 min in the opposite direction along the same path. Each transect was surveyed six times each year (i.e. sampling period) between 2012 and 2015, totaling 24 surveys for each transect.

Species Selection

Five out of the seventy butterfly species documented in the study area were chosen for this analysis based on their life history traits and feeding behavior (Table 1). This allowed me to evaluate how climate affected population dynamics of species that differ in life history traits. Species were selected on the basis of number of broods (1 univoltine, 2 bivoltine, and 2 multivoltine species), overwintering strategy (2 species overwinter as pupae and 3 species as larvae), and adult food resources (3 species forage on nectar and 2 species forage on sap; Table 1). The first species selected for analysis was Epargyreus clarus (Family Hesperiidae, Subfamily Pyrginae), the only skipper chosen for this study (Table 1). Skippers (Suborder Rhopalocera, Superfamily Hesperiidea) morphologically differ from true butterflies (Suborder Rhopalocera, Superfamily Papilionoidea), although all are considered butterflies and defined to differ from moths by the suborder Rhopalocera (Opler and Krizek 1984). Skippers have stouter bodies and are typically smaller than true butterflies. The clubbed portion of the antennae is also bent inwards on skippers, which differs from true butterflies. E. clarus is one of the most widespread skipper species in North America, ranging from southern Quebec west to southern British Columbia and then south to Florida, the Gulf Coast, Texas and Northern Mexico (Opler and
Krizek 1984). *E. clarus* occurs in a variety of habitats, including forest edges, fields, and gardens (Opler and Krizek 1984). Host plants include suckers of various locust trees (*Robinia* spp), including black locust (*Robinia pseudacacia*); also other legumes, including beggar’s ticks (*Desmodium* spp), wisteria (*Wisteria* spp), hog peanut (*Anphicarpa braceata*), and kudzu (*Pueraria thunbergii*) (Kaufman and Brock 2006). Larvae of *E. clarus* are also known to build leaf shelters as protection from predators and pupate in leaf shelters as well (Opler and Krizek 1984).

The second species chosen for analysis was *Papilio glaucus* (Family Papilionidae, Subfamily Papilioninae) (Table 1). *P. glaucus* is a sexually dimorphic species; both males and females display distinctive bands of yellow and black coloring, but only the females show a large band of blue along the bottom of the hindwing (Kaufman and Brock 2006). The range of *P. glaucus* extends throughout the eastern half of the United States, from Vermont south to Florida and as far west as Colorado (Opler and Krizek 1984). Preferred habitats consist of deciduous forests, streams, rivers, fields, and gardens. Host plants include wild cherry (*Prunus serotina*), sweet bay (*Magnolia virginiana*), tulip poplar (*Liriodendron tulipifera*), ash (*Fraxinus nigra*), spicebush (*Lindera benzoin*), and birch (*Betula* spp) (Kaufman and Brock 2006).

The third species chosen for this study was *Phyciodes tharos* (Family Nymphalidae, Subfamily Nymphalinae) (Table 1). *P. tharos* belongs to a group of butterflies referred to as ‘crescents,’ which are smaller butterflies with rounded forewings, orange and black patterning, and a crescent-shaped spot near the margin of the hind wing (Kaufman and Brock 2006). The range of *P. tharos* extends from southeastern Alberta to southern Maine and then south to Florida and west to Texas (Opler and Krizek 1984). *P. tharos* typically inhabits open spaces, such as roadsides, pastures, fields, and open pine woods (Opler and Krizek 1984). Host plants include
smooth-leaved true asters of a wide variety, including Aster pilosus, A. ericoides, A. laevis, A. solidagineus, A. texanus, and A. prealtas (Kaufman and Brock 2006).

The fourth species analyzed was the Carolina satyr, Hermeuptychia sosybius (Family Nymphalidae, Subfamily Satyrinae) (Table 1). The subfamily of H. sosybius consists of the satyrs, small to medium-sized brown butterflies (Kaufman and Brock 2006). Adult satyrs generally have short proboscises, limiting their ability to find nectar of flowering plants (Opler and Krizek 1984). Instead, adult satyrs prefer to feed on sap flows, as well as fermenting fruit or dung (Opler and Krizek 1984). H. sosybius displays brown unmarked wings dorsally and a series of small, black, yellow-rimmed eyespots ventrally (Kaufman and Brock 2006). The range of H. sosybius extends from southern New Jersey down to Florida and west to Southern Texas and into tropical and temperate portions of the Americas (Opler and Krizek 1984). H. sosybius lives primarily in forested areas, ranging from pinewoods and oak forest to wooded river bottoms (Opler and Krizek 1984). Host plants include a variety of grasses, including centipede grass (Eremochloa ophiuroides), St. Augustine grass, (Stenotaphrum secendatum), and Kentucky bluegrass (Poa pratensis) (Kaufman and Brock 2006).

The final species selected for analysis is the Appalachian eyed brown, Satyrodes appalachia (Family Nymphalidae, Subfamily Satyrinae) (Table 1). S. appalachia is a medium-sized satyr with a distinct line of eyespots on the rim of the ventral wings and duller eyespots on the dorsal wings (Kaufman and Brock 2006). Adults of S. appalachia feed on sap flows (Opler and Krizek 1984). The range of S. appalachia extends from Central New England and southern Quebec west to eastern Minnesota and south through the Appalachians and coastal plain to Florida, Alabama, and Mississippi (Opler and Krizek 1984). The habitat of S. appalachia consists of a variety of wet, wooded areas, such as swamp forest, shrub swamp, clearings along
slow-moving streams, and bottomlands near streams (Opler and Krizek 1984). Host plants include a variety of sedges (Family: Cyperaceae), including *C. lacutris*, *C. lupulina*, *C. gracillima*, and *C. tuckermanii* (Kaufman and Brock 2006).

**Climate Data**

Daily climate data were downloaded from weather underground (https://www.wunderground.com/), which were collected at four different airport regions within the study area (Fig. 1). Transects were grouped into regions based on proximity to airports (Fig. 1).

The variables of interest for this study included: total rainfall, maximum and minimum temperature, and maximum and minimum humidity. Each of these variables was shown to affect butterfly population dynamics in other studies. Pollard (1988) analyzed the abundance of butterfly species in relation to temperature and rainfall, finding that high temperatures in the summer and increased rainfall in the spring of the previous year correlate positively to numbers of butterflies. Another study analyzing butterfly communities in the Mediterranean found minimum humidity and extreme temperature values to influence observed butterfly species (Schwartz-Tzachor et al 2008).

To evaluate how climate variables affect population dynamics of the selected butterfly species, I first defined six different seasons (Figure 2). The first season defined was winter (November 1-March 31). The beginning and ending of winter were set by the days in which temperatures reached freezing conditions. Only between November 1 and March 31 did temperatures fall below 0 °C within this study area. Next, the three summer windows were defined around the six sampling surveys. Hence, spring and fall composed the months between summer and winter.
Climate data were then averaged across each year and temporal window. Each temporal window was hypothesized to have a different effect on population dynamics (Table 2). Spring, summer III, fall, and winter, for example, were predicted to influence population expansion. These temporal windows can drive inter-annual dynamics in a variety of ways. Each temporal window was also hypothesized to relate to different climate variables. Total rainfall and minimum temperature, for instance, were selected variables for fall. All climate variables within each temporal window were then predicted to affect estimates directly or indirectly through a prior year offset. I tested the hypothesis that climatic variation in fall of 2012 influences the expansion or contraction observed in 2013, or that climatic variation in fall of 2011 influences the expansion or contraction observed in 2013.

Introduction to Occupancy Models

Detection/non-detection data provide useful insight on the distribution of species in a given area and estimates occupancy adjusted for imperfect detection (MacKenzie et al. 2006). Occupancy is defined as the proportion of area occupied by a species or fraction of landscape units where the species is present, whereas detection is defined as the probability of detecting a species given that it is present (MacKenzie et al. 2006). Occupancy models offer numerous advantages to study butterfly populations dynamics. Occupancy models mathematically quantify and test hypotheses on the behavior of a system based on defined parameters. Following this, mechanistic studies on the system of interest can further confirm the conclusions of an occupancy model. Defining the behavior of a system also allows for predictions about how the system responds to perturbations, such as habitat degradation or climate change.

Occupancy modeling aims to correct for imperfect detections, that is, to account for species not detected but present (MacKenzie et al. 2006). While detecting a species in a given
areas is unambiguous, surveys resulting in non-detection lead to ambiguity in the data. Essentially, if a species is not detected on a particular survey this can lead to two different conclusions: the species does not occupy the study area, or the species does occupy the study area but the observer was not able to detect the species. Non-detection, therefore, can indicate a ‘true-absence’ or ‘false-absence’ of the species (MacKenzie et al. 2006). If a dataset does not correct for false-absences in non-detection data, this can bias estimates of occupancy. A model may therefore incorrectly predict the occupancy of species in a given study area if it does not take into account the probability of false-absences (MacKenzie et al. 2006).

Occupancy models typically assume a closed population (MacKenzie et al. 2006). A closed population supposes that a species does not exit or enter the study area throughout the sampling period. Therefore, if a species is detected on one site during one survey and not detected on subsequent surveys at that same site, the model assumes closure, meaning the species was present on the site but not detected. Conversely, only if the species is never detected at a particular site, the closed population model estimates the probability that the species does not occupy the area as well as the probability that the species occupies the area and was never detected. Below are examples of detection/non-detection data and the structure of corresponding models estimating occupancy and detection:

<table>
<thead>
<tr>
<th>Sampling Period</th>
<th>(\Psi (p_1)(p_2)(p_3))</th>
<th>(\Psi (1-p_1)(1-p_2)(p_3))</th>
<th>(\Psi (1-p_1)(1-p_2)(1-p_3) + (1-\Psi))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 1 1</td>
<td>(\Psi (p_1)(p_2)(p_3))</td>
<td>(\Psi (1-p_1)(1-p_2)(p_3))</td>
<td>(\Psi (1-p_1)(1-p_2)(1-p_3) + (1-\Psi))</td>
</tr>
</tbody>
</table>
The first example (111) shows an occupancy estimate (denoted by $\Psi$) and three separate detection probability estimates for each survey occasion ($p_1$, $p_2$, and $p_3$). This example shows the probability the species occupies the site and the probabilities the species was detected on every survey at that site during the sampling period. The next example (001) shows the probability the species occupies the site and the probabilities that the species was not detected on the first two surveys, but was detected on the final survey. And the last example (000) shows the probability the species occupies the site, but was never detected, plus the probability that the species does not occupy the site.

To derive estimates for occupancy and detection probabilities, occupancy models use frequencies of encounter histories (MacKenzie et al. 2006). Encounter histories describe the detection/non-detection data for a particular site. Each of the three examples above describes three distinct encounter histories. The number of unique encounter histories in a sampling period is defined by $2^n$. The ‘2’ represents possible outcomes during a survey (detecting or not detecting a species) and ‘n’ represents the number of surveys repeated during a sampling period (in the example above, there are 3 surveys). Therefore, in the example above, there are 8 unique encounter histories that a site may experience during the sampling period. The frequencies of these encounter histories across all sites in a study area are used to estimate a log likelihood, or the most likely estimate given the data, to then derive estimates for each parameter ($\Psi$, $p_1$, $p_2$, and $p_3$) (MacKenzie et al 2006). Transects for my study were visited on 6 separate surveys, totaling to 64 unique encounter histories for one sampling period.

Multi-season occupancy models make inferences about population dynamics across multiple sampling periods in addition to estimating occupancy adjusted for imperfect detection (MacKenzie et al 2006). Occupancy probability estimates in these models, however, are only
derived for the first sampling period (see Appendix 3 for conceptual model). Encounter histories from every subsequent sampling period are used to estimate two additional parameters: expansion ($\gamma_i$) and contraction ($\varepsilon_i$), where $i$ indexes sampling period. These parameters estimate the probability the range of a species has expanded or contracted. Expansion, for example, estimates the probability that sites unoccupied in the first sampling period are occupied in the second sampling period. Contraction estimates the exact opposite scenario, defining the probability that sites occupied during the first sampling period become unoccupied during the second sampling period. Below are examples of encounter histories and what parameters they estimate across two sampling periods:

<table>
<thead>
<tr>
<th>Sampling Period 1</th>
<th>Sampling Period 2</th>
<th>Encounter History Terms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 1</td>
<td>1 1</td>
<td>$\Psi_1 \ (p_{1,1}) \ (p_{1,2}) \ (1-\varepsilon_1) \ (p_{2,1}) \ (p_{2,2})$</td>
</tr>
<tr>
<td>0 0</td>
<td>1 0</td>
<td>$\Psi_1 \ (1-p_{1,1}) \ (1-p_{1,2}) \ (1-\varepsilon_1) \ (p_{2,1}) \ (p_{2,2}) + (1-\Psi_1) \ (\gamma_1) \ (p_{2,1}) \ (1-p_{2,2})$</td>
</tr>
<tr>
<td>0 0</td>
<td>0 0</td>
<td>$\Psi_1 \ (1-p_{1,1}) \ (1-p_{1,2}) \ (1-\varepsilon_1) \ (1-p_{2,1}) \ (1-p_{2,2}) + \Psi_1 \ (1-p_{1,1}) \ (1-p_{1,2}) \ (\varepsilon_1) + (1-\Psi_1) \ (1-\gamma_1) + (1-\Psi_1) \ (\gamma_1) \ (p_{2,1}) \ (1-p_{2,2})$</td>
</tr>
</tbody>
</table>

The first example (11 11) estimates the probability the site was occupied by the species in the first sampling period ($\Psi_1$), the probabilities the species was detected on the first and second surveys during the first sampling period ($p_{1,1}$ and $p_{1,2}$), the probability the site range did not contract between the first and second sampling period ($1-\varepsilon_1$), and the probabilities the species was detected on the first and second surveys during the second sampling period ($p_{2,1}$ and $p_{2,2}$). Because the species was detected during the first sampling period and the site is known to be occupied, this encounter history cannot estimate the probability of expansion. The range of the species cannot expand into this site, so an estimate can only be derived for the probability the site did not contract the range of this species (see Appendix 3 for conceptual model).
The next example (00 10) estimates the probability the site was occupied in the first sampling period \( (\Psi_1) \), the probabilities the species was not detected on the first and second surveys \( (1-p_{1,1} \text{ and } 1-p_{1,2}) \), the probability the range did not contract between the first and second sampling periods \( (1-\epsilon_1) \), and the probabilities the species was detected during the second sampling period on the first survey and not detected on the second survey \( (p_{2,1} \text{ and } 1-p_{2,2}) \). These probabilities are then added to the probability the site was unoccupied in the first sampling period \( (1-\Psi_1) \), the probability the range expanded between the first and second sampling periods \( (\gamma_1) \), and the probabilities the species was detected during the second sampling period on the first survey and not detected on the second survey \( (p_{2,1} \text{ and } 1-p_{2,2}) \). Expansion and contraction probabilities are both estimated for this site because no detections in the first sampling period leave ambiguity in the data. If treated as ‘true absences,’ these zeros describe that the site was not occupied during the first sampling period and an expansion event allowed for the site to become occupied in the second sampling period. In contrast, if treated as ‘false absences,’ these zeros describe that the site was occupied during the first sampling period but the species was never detected. Both are plausible situations and therefore both must be estimated (see Appendix 3 for conceptual model).

The final example (00 00) details an encounter history when the species was never detected across any surveys or sampling periods. The first part of the equation estimates the probability of occupancy \( (\Psi_1) \), the probabilities the species was never detected during the first sampling period \( (1-p_{1,1} \text{ and } 1-p_{1,2}) \), the probability the range of the species did not contract \( (1-\epsilon_1) \), and the probabilities the species was never detected during the second sampling period \( (1-p_{2,1} \text{ and } 1-p_{2,2}) \). These probabilities are added to the probability the site was \( (\Psi_1) \), the species was never detected during the first sampling period \( (1-p_{1,1} \text{ and } 1-p_{1,2}) \), and the probability the range of
the species contracted \((e_i)\). Next, these probabilities are added to the probability the site was not occupied in the first sampling period \((1 - \Psi_i)\) and the range of the species never expanded to this site \((1 - \gamma_i)\). Lastly, these probabilities are added to the probability the site was unoccupied during the first sampling period \((1 - \Psi_i)\), the probability the range of the species expanded to this site \((\gamma_i)\), and the probabilities that the species was never detected during the second sampling period \((1 - p_{2,1} \text{ and } 1 - p_{2,2})\). These estimates detail all possible scenarios when the species is never detected across multiple sampling periods in a closed system (see Appendix 3 for conceptual model).

Assuming closure conveniently structures estimates within a sampling period, but it is known that birds (Klemp 2003, Dale et al. 2005, Betts et al. 2008) and many other highly mobile species, including butterflies (Bried and Pellet 2012, Fernandez-Chacon et al. 2014), violate the closure assumption. Adult butterflies are highly driven by the availability of nectar or sap resources. When plant species flower or produce sap at variable times and locations, adult butterflies will move to different transects throughout the summer. It is false to assume no immigration or emigration in butterfly populations throughout the breeding season, and therefore, adult butterflies within this study area violate the closure assumption.

To correct for violations of the closure assumption, this study utilized an open-population multi-season occupancy model structure. The open-population model continues to estimate occupancy, detection, expansion, and contraction probabilities but, in addition, also estimates entry and departure probabilities (Chambert et al. 2015). Entry \((e)\) and departure \((d)\) estimate intra-annual population fluctuations, which parallel the inter-annual estimates of expansion \((\gamma)\) and contraction \((e)\). Entry \((e)\) is defined as the probability a species enters a site between surveys within a given sampling period. Departure \((d)\) is defined as the probability a species departs from a site between surveys within a given sampling period. Entry and departure estimates allow the
model to estimate detection more precisely as fewer false absences are included in the detection histories.

Detection probability estimates are significantly lowered in the closed-population model when a species is detected once on a site and then not detected on subsequent surveys (MacKenzie et al. 2006). The assumption of false absences in this situation results in low detection probability estimates. Low detection probability estimates alter the estimates of all other parameters in the model. Entry and departure estimates alleviate this problem and account for both true and false absences (Chambert et al. 2015). For instance, if an encounter history begins with a single detection and is then followed by multiple non-detections in subsequent surveys, the open-population model allows for these non-detections to no longer only represent that the species was present on the site but not detected. Instead, this model represents presence but non-detection as well as the probability the species departed the site before the end of the sampling period. In this way, true and false absences within a sampling period are estimated in a staggered entry model. An example encounter history is shown below:

<table>
<thead>
<tr>
<th>Sampling Period 1</th>
<th>Sampling Period 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 1 1</td>
<td>1 0 1</td>
</tr>
</tbody>
</table>

\[ \Psi_1 \left[ \{e_{1,0}(1-p_{1,1})(1-d_{1,1}) + e_{1,1}(1-e_{1,0})\} \times p_{1,2}(1-d_{1,2})P_{1,3} \right] \times (1-\varepsilon_1) \times \left[ e_{2,0}(p_{2,1})(1-d_{2,1})(1-p_{2,2})(1-d_{2,2})p_{2,3} \right] \]

The encounter history is used to first estimate the probability the site is occupied (\(\Psi_1\)), the probability the species entered the site before the first survey during the first sampling period (\(e_{1,0}\)), the probability the species was not detected (1-p_{1,1}), the probability the species did not depart from the site (1-d_{1,1}), plus the probability the species entered the site by the end of the first survey (\(e_{1,1}\)) and the probability the species did not enter before the first survey (1-e_{1,0}). These
probabilities estimate the non-detection during the first sampling period and account for both a true and false absence. The encounter history then is used to estimate the probability the species was detected during the second survey of the first sampling period \((p_{1,2})\), the probability the species did not depart the site \((1-d_{1,2})\), and the probability the species was detected on the third survey of the first sampling period \((p_{1,3})\). Next, the probability the range of the species did not contract \((1-\epsilon_1)\) is estimated to account for inter-annual variation. The model then estimates the probability the species entered the site before the first survey of the second sampling period \((e_{2,0})\), the probability the species was detected during the first survey of the second sampling period \((p_{2,1})\), the probability the species did not depart the site \((1-d_{2,1})\), the probability the species was not detected during the second survey of the second sampling period \((1-p_{2,2})\), the probability the species did not depart \((1-d_{2,2})\), and the probability the species was detected during the third survey of the second sampling period \((p_{2,3})\).

**Modeling Approach**

I first derived \(P^*\), or the probability of detecting a species at least once during a sampling period (MacKenzie et al. 2006). An occupancy estimate for a given sampling period is estimated by dividing a naïve occupancy estimate by the probability of detecting a species at least once across all surveys \((p^*)\) (MacKenzie et al. 2006). \(P^*\) differs subtly from regular detection probability estimates. Detection probabilities estimate the probability of detecting a species on a given survey during a particular sampling period. In contrast, \(p^*\) estimates the probability across all surveys in a given sampling period that the species will be detected at least once. The formula to derive \(p^*\) is:

\[
1-(1-p)^n
\]

where \(n\) equals the number of surveys.
A low estimate of $p^*$ means that detection probability estimates across a particular sampling period were low as well. Low estimates for detection probabilities essentially show that the model has difficulty interpreting the zeros of the detection/non-detection data. The model cannot discern if these zeros are true or false absences. Low detection probability estimates in turn lead to low estimates of $p^*$, which result in drastic differences between naïve occupancy estimates and model-derived occupancy estimates. As the formula above shows, the closer a $p^*$ estimate is to one, the closer model-derived and naïve occupancy estimates will be to each other (MacKenzie et al 2006). In general, when $p^* < 0.85$, more surveys within a sampling period are needed to improve precision of the detection probability. When $p^* > 0.85$, too many surveys are conducted and the number of surveys can be reduced to decrease sampling cost.

Multi-season occupancy models were separately constructed for each of the five butterfly species ($E. clarus$, $P. glaucus$, $P. tharos$, $H. sosybius$, and $S. appalachia$) using the free online software PRESENCE (Hines 2006). To determine the best model structure, I first evaluated model fit for the closed-population multi-season model (MacKenzie et al. 2006) and the open-population multi-season model (Chambert et al. 2015) structure. The models were compared on the basis of null models for the closed-population multi-season model ($\Psi[.]$, $\gamma[.]$, $\varepsilon[.]$, $p[.]$) and the open-population multi-season model ($\Psi[.]$, $\gamma[.]$, $\varepsilon[.]$, $\epsilon[.]$, $d[.]$, $p[.]$). I selected the best model on the basis of Akaike’s Information Criteria (AIC) adjusted for small sample size ($AIC_c$, specifically $\Delta AIC_c$), to determine which models best supported the data (Burnham and Anderson 2006).

I then determined the best model structure to estimate detection probabilities. For each species, in addition to the null model (i.e. detection probability does not vary within and among sampling periods), I also evaluated model fit for sampling season effect, survey effect, an
additive model of sampling period and survey effect, and a model with a sampling period and
survey interaction (Appendices 4, 5, 6, and 7). The model with the lowest AICc value (Burnham
and Anderson 2006) was carried forward to the next step of the modeling process and is referred
to as the ‘null model’ for each species. I did not include any covariates to model variation in
detection probability as this was not the focus of the study.

The next phase of the modeling process involved evaluating which climate covariates
(Appendix 8) best fit expansion and contraction data. Climate covariates were centered and
standardized (observation – mean/standard deviation) for each region. I used univariate models
in which only one other parameter was varied among models with the best detection model held
constant across all candidate models. I also kept entry and departure estimates as a null model, as
explaining intra-annual variation in these parameters was not the focus of this study.

To evaluate model fit of 30 climate variables (Appendix 2), I used three types of design
matrices (Appendices 9, 10, and 11). I tested model fit by always starting with the most complex
design (i.e., separate estimates of intercept and slopes for each sampling period, Appendix 9), but
resorted to less complex design matrices (Appendix 10 and 11) if regression coefficient slopes
and variation estimates exceeded 4. I included all covariates in the candidate set if AICc values
were < null model and within 4 ΔAICc.

The final step in the modeling process was to evaluate best model fit on the basis of
multivariate models. Multivariate models included all combinations of covariates from the
expansion and contraction variable candidate set. Multivariate models maintained occupancy,
entry, and departure parameters as null models and retained the best detection design matrix
among final candidate models. All possible combinations of expansion and contraction
covariates were run and models were compared against one another and the null model on the
basis of their ΔAIC value. I did not include additive models of climate variables to avoid overfitting models (Hosmer and Lemeshow 2000). Because the climate data came from four regions (n = 4), I only included one variable for each estimated parameter.

All multivariate models with a ΔAICc < 4 were model averaged (Burnham and Anderson 2002, Arnold 2010) to produce12 estimates of expansion and contraction estimates for each species. The 12 estimates for expansion and contraction represent three inter-annual estimates across four regions. I also used conditional model averaging for slope estimates of climate covariates and unconditional model averaging for the standard errors of those slopes (Burnham and Anderson 2002). AIC weights were then summed across all models that represented a particular climate covariate in expansion or contraction parameters. The summed AIC weight of a climate covariate across multivariate models demonstrated the strength of the variable in explaining expansion or contraction estimates: weakly supported variables summed to an AIC weight < 0.25, moderately supported variables ranged from a summed AIC weight of 0.25-0.75, and strongly supported variables showed a summed AIC weight > 0.75 (Burnham and Anderson 2002). I then estimated annual occupancy on the basis of model-averaged annual probabilities of expansion and contraction:

\[ \Psi_{(t+1)} = \Psi_t (1 - \varepsilon) + (1 - \Psi_t) \gamma. \]

I estimated variance of \( \Psi_{(t+1)} \) using the delta method, which estimates variance on the basis of the derivative of the algorithm estimating \( \Psi_{(t+1)} \) (Cooch and White 2016).

**RESULTS**

*Weather*

Weather patterns differed among years and regions (Fig. 1 and Appendix 8). During my study, compared to average rainfall in 2012, 2013, and 2015, spring total rainfall in 2014 was
twice as high and in 2011 twice as low. Fall total rainfall continuously decreased across all five years. Climate variability was synchronous for spring total rainfall but climate variation was asynchronous for other variables. For example, Region 1 is the most northern and generally slightly colder than all other regions, particularly during fall and winter seasons. Summer III maximum humidity in Region 1 was either higher in 2012 and 2013 or lower in 2014 and 2015. Similarly, spring minimum temperatures were cooler between 2012 and 2015 in Region 1 and Region 2 had higher minimum temperature during the Fall of 2011 and 2013.

**Multi-Season Occupancy Model Structure**

The open-population model fit the data best for *E. clarus* (Appendix 12), *P. tharos* (Appendix 14), *H. sosybius* (Appendix 15), and *S. Appalachia* (Appendix 16). For *P. glaucus*, the closed-population model had a lower AIC value than the open-population model (Appendix 13). In the end, I selected the open-population model because it consistently had fewer issues when estimating detection, expansion, and contraction probabilities.

**Naïve Occupancy and Detection**


Detection probabilities from top detection models (Appendix 12 – 16) were used to estimate P*. I examined whether P* was > or < than 0.85, the critical threshold defining
sampling design adequacy (MacKenzie et al. 2006). For *E. clarus*, *H. sosybius*, and *S. appalachia*, \( P^* \) was > 0.85 in all sampling periods (Fig. 3), indicating adequate sampling. \( P^* \) was < 0.85 for *P. tharos* and *P. glaucus* in 2014 (Fig. 3), indicating too few surveys in my sampling design (MacKenzie et al. 2006).

**Univariate Models**

Univariate expansion model results are reported for each species in Appendices 17 - 21 and results for univariate contraction models are shown in Appendices 22 - 26. Initially I started with 30 climate variables for both expansion and contraction (Table 2). For *E. clarus*, 21 climate variables performed poorly in expansion models and two models had AIC\(_c\) values > null model, resulting in an expansion candidate set of nine variables: spring minimum temperature \( t \), summer III maximum humidity \( t-1 \), and fall minimum temperature \( t-1 \) (Appendix 17). Six variables performed poorly in contraction models and 16 models had \( \Delta\text{AIC}_c \) values > 4, resulting in a contraction candidate set of eight variables: spring minimum temperature \( t \), winter minimum temperature \( t-1 \), fall minimum temperature \( t-1 \), spring maximum humidity \( t-1 \), days below freezing \( t-1 \), summer III minimum humidity \( t-2 \), fall rainfall \( t-2 \), and spring maximum temperature \( t-1 \) (Appendix 22).

For *P. glaucus*, one variable performed poorly in an expansion model, 12 variables had AIC\(_c\) values > null model, and 15 variables had \( \Delta\text{AIC}_c \) values > 4, resulting in two variables included in the contraction candidate set: spring rainfall \( t-1 \) and winter rainfall \( t-2 \) (Appendix 18). Four variables performed poorly in contraction models and an additional 11 variables had AIC\(_c\) values > null model. After removing variables with \( \Delta\text{AIC}_c \) values > 4, three variables were retained in the contraction candidate set: spring rainfall \( t-1 \), summer III minimum humidity \( t-2 \), and spring rainfall \( t \) (Appendix 23).
For *P. tharos*, four variables performed poorly in the expansion models and 22 variables had AIC\(_c\) value > null model. The remaining four variables were included in the expansion candidate set: summer III rainfall \((t - 1)\), spring minimum humidity \((t - 1)\), summer III maximum humidity \((t - 1)\), and fall minimum temperature \((t - 2)\) (Appendix 19). All contraction models were within 4 ΔAIC\(_c\), but only two variables were included in the candidate set because their AIC\(_c\) value < null model: spring maximum temperature \((t)\) and spring rain \((t)\) (Appendix 24).

For *H. sosybius*, 27 expansion models had ΔAIC\(_c\) < 4, but their AIC\(_c\) values were > null model and were therefore excluded from the expansion candidate set. The only variable carried forward to the expansion candidate set was summer III maximum humidity \((t - 2)\) (Appendix 20). Five variables in the contraction models were excluded because their AIC\(_c\) values > null model and four model had ΔAIC\(_c\) values > 4. The 21 remaining variables were included in the contraction candidate set: fall minimum temperature \((t - 1)\), summer III maximum humidity \((t - 2)\), summer III minimum humidity \((t - 2)\), days below freezing \((t - 1)\), winter minimum temperature \((t - 1)\), spring minimum temperature \((t)\), summer III rainfall \((t - 2)\), winter rainfall \((t - 2)\), spring minimum humidity \((t)\), days below freezing \((t - 2)\), fall rainfall \((t - 2)\), spring minimum temperature \((t - 1)\), summer III maximum temperature \((t - 2)\), summer III rainfall \((t - 1)\), winter minimum temperature \((t - 2)\), summer III maximum temperature \((t - 1)\), fall minimum temperature \((t - 2)\), summer III minimum humidity \((t - 1)\), spring minimum humidity \((t - 1)\), spring rainfall \((t - 1)\), and winter rainfall \((t - 1)\) (Appendix 25).

For *S. appalachia*, 20 expansion models had ΔAIC\(_c\) values > 4 and were removed from the expansion candidate set. Of the remaining variables, nine variables had ΔAIC\(_c\) values < 4 but AIC\(_c\) values > null model, leaving one variable, spring maximum temperature \((t - 1)\), to be included in the expansion candidate set (Appendix 21). For contraction, 21 model had ΔAIC\(_c\) values > 4
and of the remaining nine models, none had an AIC<sub>c</sub> value < null model (Appendix 26). Therefore, no variables were included in the contraction candidate set.

**Multivariate Models**

*E. clarus* - The final models included three variables for expansion and eight variables for contraction, totaling 24 multivariate models (Appendix 27). I excluded five models because they had estimation problems and three that had ΔAIC<sub>c</sub> values > 4. Estimates of expansion and contraction parameters were then model averaged on the basis of 16 models.

Overall, variables explaining heterogeneity in expansion were more important than variables for contraction (Fig. 4). Of the three variables included for expansion multivariate model, summer III maximum humidity<sub>(t-1)</sub> and spring minimum temperature<sub>(t)</sub> were moderately supported whereas fall minimum temperature<sub>(t-1)</sub> was weakly supported. For contraction, all variables showed weak support (Fig. 4). Two of three variables showed negative association with expansion whereas two of seven variables related negatively with contraction (Fig. 4).

The two top expansion variables, summer III maximum humidity<sub>(t-1)</sub> and spring minimum temperature<sub>(t)</sub>, varied asynchronously among regions (Fig.8). Summer III maximum humidity<sub>(t-1)</sub> was positively associated with expansion (Fig. 4) and correlated with higher humidity levels in Region 1 across all three intervals (Appendix 8). Summer III maximum humidity<sub>(t-1)</sub> dropped from 100% in 2013 to 85% in 2014, resulting in an approximately 50% reduction in the probability of expansion for Region 1 (Fig. 8). Spring minimum temperature<sub>(t)</sub> was negatively associated with expansion (Fig. 4). Between 2012 and 2015, spring minimum temperatures were consistently lower in Region 1 (Appendix 8), resulting in higher estimates of expansion in this region (Fig. 8).
P. glaucus - Final models included two variables for expansion and three variables for contraction, totaling six multivariate models (Appendix 28). All six models were included for model averaging.

Overall, variables explaining expansion were more important than variables explaining contraction (Fig. 5). Spring rainfall \(_{(t-1)}\) was the top variable for both expansion and contraction estimates. For expansion, spring rainfall \(_{(t-1)}\) was strongly supported whereas winter rainfall was weakly supported. Of the three variables included in the contraction multivariate model, two were moderately supported whereas one was weakly supported (Fig. 5). All expansion variables related negatively to estimates of expansion and all contraction variables related positively to contraction.

The top expansion and contraction variable, spring rainfall \(_{(t-1)}\), followed synchronous annual trends across regions (Fig. 8). Spring rainfall remained relatively constant in 2012 and 2013, but showed a drastic increase in 2014 (Appendix 8). Correlating to the 2014 increase in rainfall, the 2014/15 interval showed a significant decrease in expansion across all regions (Fig. 8) because expansion estimates related negatively to spring rainfall \(_{(t-1)}\) (Fig. 5). Conversely, spring rainfall \(_{(t-1)}\) related positively to contraction estimates (Fig. 5). Contraction estimates in the 2014/15 interval increased across all regions (Fig. 8).

P. tharos - The final models included four expansion variables and two contraction variables, totaling eight multivariate models (Appendix 29). Model averages were comprised of all eight models.

Overall, variables explaining expansion and contraction were equally important (Fig. 6). Three expansion variables were weakly supported (Fig. 6) and one expansion variable was moderately supported (summer III rainfall \(_{(t-1)}\)). For contraction, both variables (spring maximum
temperature \( t_0 \), spring rainfall \( t_0 \) showed moderate support (Fig. 6). Three out of four variables related negatively to expansion while one out of two variables related negatively to contraction (Fig. 6).

Summer III rainfall \( t_{-1} \) explained the most variation in expansion estimates and varied asynchronously across regions (Fig. 8). Summer III rainfall \( t_{-1} \) was positively associated with expansion (Fig. 6) and each interval correlated with the region experiencing the highest levels of rainfall in 2012, 2013, and 2014 (Appendix 8). For example, Region 4 received more rainfall than any other region in 2013 and also showed the highest probability of expansion in 2013/14 (Fig. 8). The top contraction variables, spring rainfall \( t_0 \) and spring maximum temperature \( t_0 \), showed synchronous and asynchronous variation across regions, respectively (Fig. 8) Spring rainfall \( t_0 \) was negatively associated with contraction (Fig. 6) and correlated with low amounts of rainfall across all regions in 2013 and 2015 (Appendix 8). Synchronous increases in rainfall in 2014 (Appendix 8) also correlated with synchronous decreases in contraction probabilities (Fig. 8). In contrast, spring maximum temperature \( t_0 \) related positively to estimates of contraction and varied asynchronously across regions (Appendix 8). Regions 3 and 1 were consistently cooler, while Regions 2 and 4 were consistently warmer (Appendix 8). Across all three intervals, contraction probabilities for \( P. \) tharos showed Regions 2 and 4 to be higher than Regions 3 and 1 (Fig. 8).

\textit{H. sosybius}- The final models included one expansion variable and 21 contraction variables, totaling 21 multivariate models (Appendix 30). I excluded seven models because they had estimation problems and one model that had \( \Delta \text{AIC}_c \) value > 4. The final model candidate set included 14 models that were used to derive model averaged expansion and contraction parameter estimates (Fig. 8).
Overall, climate variables explained little heterogeneity in expansion and contraction estimates, as evidenced by a lack of variable candidates for expansion and weakly supported AIC weights for contraction variables (Fig. 7). No correlations were drawn from climate data because all variables lacked strength of support.

*S. appalachia*- Only one expansion variable was carried forward to the multivariate candidate set (spring maximum temperature \(t_{-1}\); Appendix 21). For contraction, the null model produced the lowest AIC value (Appendix 26). Because the candidate set included so few variables, no multivariate models were constructed. The null model estimated expansion and contraction (Fig. 8).

*Occupancy Estimates*

Occupancy estimates across all four years were also derived for each species (Fig. 9). Estimates of occupancy for *P. glaucus* varied more than any other species; occupancy estimates increased by 50% between 2012 and 2013. Occupancy estimates for *S. appalachia* varied the least over time and were substantially lower than estimates for all other species across time.

**DISCUSSION**

The five butterfly species analyzed in this study all responded to climate variability idiosyncratically. Life history traits, such as overwintering strategy (pupae vs. larvae) or number of broods (univoltine, bivoltine, and multivoltine), did not consistently explain differences in responses of species to climate variation. In contrast, I found that the effects of climate variation on population dynamics varied among sap-feeding and nectar-feeding species. This effect is supported by synchronous and asynchronous climate patterns across the four regions, which greatly affect butterflies (Ehrlich et al 1980, Nice et al 2014).
Climate variables were found to correlate to population range expansion and contraction estimates for *E. clarus*, *P. glaucus*, and *P. tharos*. Typically, populations at the fringe of their range are responding strongly to climate variability (Breed et al. 2012). Because the range of the three species is centered on my study area, it less likely that responses by these species to variation in climate could be explained by dynamics of populations at either their northern or southern limit of their range. The three species demonstrating a response to climate include butterflies that consume nectar resources as adults. In contrast, the two species that did not demonstrate a clear response to climate were species that consume sap resources as adults (*H. sosybius* and *S. appalachia*). This result confirms my prediction that sap-feeding butterfly populations are less driven by climate than nectar-feeding butterflies. To my knowledge nobody has demonstrated differential population dynamics on the basis of adult dietary preference.

The lack of response in sap-feeders indicates that climate directly or indirectly fails to affect population dynamics. Direct mortality or survival in sap-feeding butterfly populations may not be influenced by climate fluctuations. In contrast, an indirect effect would indicate that sap resources in woody plants do not react to climate and respond differently than herbaceous plants to climate variation. An alternate mechanism driving population dynamics and turnover is habitat configuration and composition (Krauss et al 2003, Thomas et al 2001). Behavioral studies on the flight patterns of *S. appalachia* suggest that it remains almost exclusively in riparian forest habitat, occasionally crossing to upland forest areas when necessary (Kuefler et al 2010). A similar study on the movement patterns of multiple woodland butterfly species found similar habitat-driven responses in both *H. sosybius* and *S. appalachia* (Kuefler and Haddad 2006). Yet another study on habitat restoration and conservation of *S. appalachia* populations found a strong correlation between increased abundance of *S. appalachia* and damming of streams in addition to
tree removal (Aschehoug et al 2015). The host plants of *S. appalachia* are grasses (Opler and Krizek 1984), so tree removal increased host plant abundance. However, this action alone did not increase *S. appalachia* populations. Only when tree removal was coupled with damming did researchers find substantial increases in *S. appalachia* populations. They hypothesize that damming decreased insect predator access via moving water to eggs and juveniles. Interactions between insect predators and prey highlight another potential explanation for my results. Butterfly larvae and pupae are often preayed upon by vertebrates and insect predators, such as parasitoid wasps (Settele et al 2009). Climate variables may drive populations of these organisms and an indirect effect may be shown in the population dynamics of the butterflies. Overall, these studies corroborate the findings of my research and suggest that the range of *S. appalachia* may remain relatively constant over time because the species is less likely to leave a particular area if favorable habitat resources are abundant.

For nectar-feeding butterflies, *E. clarus, P. glaucus,* and *P. tharos,* climate variables correlated strongly with population dynamics across the four sampling periods. A likely mechanism explaining observed population dynamics is that climate factors regulate nectar availability. Herbaceous plants rely more strongly on climatic factors for growth than woody plants (Engemann et al 2016). Ideal climate conditions, therefore, may cause more herbaceous plants to flower in certain regions, promoting range expansion by these butterfly species to forage on the newly abundant resources. In contrast, poor climate conditions can reduce the numbers of flowering herbaceous plants in a given region (Nagy et al 2013) and potentially cause contraction in the range of these species.

The nectar-feeding butterfly species, *E. clarus, P. glaucus,* and *P. tharos,* analyzed in this study showed distinct responses to variability in climate. Variation in climate did not consistently
explain differences in life history traits but species responded mainly to two seasons: spring and summer III. Although variables from both fall and winter appeared in multivariate models for all three species, these variables were weakly supported. The lack of explanatory power in fall and winter climate variation suggests that overwintering as pupae or larvae may not be affected by climate but that variation in spring climate may affect emergence from pupae differently than emergence from diapause as a larva.

The importance of variation of spring climate may indicate that overwintering emergence is differentially affected. For instance, spring rainfall \((t-1)\) explained variation in expansion and contraction probabilities for *P. glaucus*, which overwinters as a pupa. Spring rainfall \((t)\) also explained the most variance in contraction estimates for *P. tharos*, which overwinters as a larva. The year offset shows that the previous spring rainfall affects *P. glaucus* emergence in the following year. Pollard (1988) also found that spring rainfall from the previous year affected observed butterfly populations. Another study also found that rainfall in the previous year drove contraction in a butterfly population, but offered no specific mechanism to account for the year offset (McLaughlin et al 2002). Increasing rainfall in the spring may reduce number adults emerging from diapause thereby reducing number of adults in second brood of the same flying period. This could result in lower occupancy in the following year.

In contrast, the positive effect of spring rainfall \((t)\) on *P. tharos* populations indicates that larval survival benefits from increased spring rainfall. Rainfall may drive greater host plant growth, allowing more larvae to forage in the spring and successfully pupate into adult butterflies. In contrast to these results, Dobkin et al (1987) related increased rainfall to a decrease in the ability of post-diapause larvae to forage on host plants before leaves senescence. A possible explanation for the contrasting results is simply that larvae of different butterfly species
or their host plants thrive under variable climate conditions. My study suggests this in the populations of *P. glaucus* and *P. tharos*, which are likely driven by spring rainfall under contrasting mechanisms. I postulate that these mechanisms relate to differing overwintering stages.

The summer III season also correlated with expansion estimates for both *E. clarus* and *P. tharos*. Falling at the end of the breeding season, summer III may provide insights on the effect of brood number on population dynamics. Summer III maximum humidity related positively to expansion estimates in *E. clarus*. As a bivoltine species, *E. clarus* will lay eggs in the late summer season that eventually overwinter as pupae. High relative humidity has been shown to increase the survival of butterfly eggs (Karlsson 1985). Therefore, as a bivoltine species, it is likely critical that *E. clarus* eggs do not desiccate during late summer to maintain occurrence of the population in the following year. Conversely, summer III rainfall related positively to expansion estimates in *P. tharos* populations. This species may experience a similar but distinct climatic effect during late summer because as a multivoltine species, the adults may still be flying in search of mates and food resources. Late summer rainfall may therefore affect puddling and nectar resources available to *P. tharos* adult butterflies. An abundance of these resources could cause range expansion in *P. tharos* populations allowing this species to lay eggs in regions unoccupied in the previous flying periods. Another study also demonstrated a decrease in butterfly abundances in years with less rainfall and greater temperatures (Robinson et al 2012). This study attributes decreases in butterfly abundance to lack of viable host plant resources for adults to lay eggs.

Overall, my study demonstrates a direct correlation between butterfly population dynamics and local climate. Differences in the response of species to climate exhibit the
complexity of these interactions between biotic and abiotic factors. Future directions of research may look to determine the specific mechanisms suggested by my research. Advancing knowledge on butterfly population dynamics in response to local climate allows for predictions of population viability in the face of climate change.

ACKNOWLEDGMENTS

I would first like to thank my advisor, Matthias Leu, for all of his guidance and support throughout the process of writing this thesis. Many thanks as well to my committee members: Joshua Puzey, Brad Lamphere, and Leah Shaw. I would also like to acknowledge the Applied Conservation and Ecology Research (ACER) Lab, particularly Angela Zappalla, Elena Bischak, and Meghan Mulroy. All of you made the fieldwork so enjoyable and Angela, thank you for being such a phenomenal mentor. Financial support for this project was provided by the Strategic Environmental Research and Development Program (RC-2202).

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Table 1: Life history traits and adult food source for *Epargyreus clarus*, *Papilio glaucus*, *Phyciodes tharos*, *Hermeuptychia sosybius*, and *Satyrodes appalachia*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Brood Number</th>
<th>Overwinter</th>
<th>Adult Food Sources</th>
</tr>
</thead>
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<tr>
<td><em>Epargyreus clarus</em></td>
<td>Bivoltine</td>
<td>Pupae</td>
<td>Nectar</td>
</tr>
<tr>
<td><em>Papilio glaucus</em></td>
<td>Bivoltine</td>
<td>Pupae</td>
<td>Nectar</td>
</tr>
<tr>
<td><em>Phyciodes tharos</em></td>
<td>Multivoltine</td>
<td>Larvae</td>
<td>Nectar</td>
</tr>
<tr>
<td><em>Hermeuptychia sosybius</em></td>
<td>Multivoltine</td>
<td>Larvae</td>
<td>Sap</td>
</tr>
<tr>
<td><em>Satyrodes appalachia</em></td>
<td>Univoltine</td>
<td>Larvae</td>
<td>Sap</td>
</tr>
</tbody>
</table>
Table 2: Predictions of which season and climate variables affect population dynamics of *Epargyreus clarus, Papilio glaucus, Phyciodes tharos, Hermeuptychia sosybius*, and *Satyrodes appalachia*. Rain = rainfall (total precipitation [mm]), Temp = temperature (°C), Hum = humidity (relative humidity), and DBF = days below freezing. For starting and ending dates for each season, see Fig. 2.

<table>
<thead>
<tr>
<th>Variables included</th>
<th>Spring</th>
<th>Summer I</th>
<th>Summer II</th>
<th>Summer III</th>
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<th>Winter</th>
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<td>Contraction</td>
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<td>t₂</td>
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<td>t₂</td>
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</tr>
<tr>
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<tr>
<td>Hum_{max}</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
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</table>
Figure 1: Geographical proximity of weather stations (Region 1: Middle Peninsula Regional Airport, Region 2: Williamsburg/Jamestown Airport, Region 3: Felker Army Air Field, and Region 4: Newport News/Williamsburg International Airport.) to 500-m transects. In total, there are four regions for which climate data were derived independently. Butterfly transects were associated with nearest weather station.
Figure 2: Temporal climate windows defined by the general phenology of butterflies in this study, as well as the sampling design. Spring Season extends from April 1 to April 30. Summer I Season: May 1 - May 31. Summer II Season: June 1 – June 30. Summer III Season: July 1 – July 31. Fall: August 1 – October 31. Winter: November 1 – March 31.
Figure 3: Probability of detecting a species at least once during the sampling period ($P^*$) for five species of butterflies: *Epargyreus clarus* (EPCL), *Hermeuptychia sosybius* (HESO), *Papilio glaucus* (PAGL), *Phyciodes tharos* (PTH), and *Satyrodes appalachia* (SAAP) from 2012–2015. $P^*$ was similar among years for *E. clarus* and *S. Appalachia* but varied greatly for *P. glaucus*. $P^*$ was < 0.85, indicating too few surveys (MacKenzie et al. 2006), for *H. sosybius* in 2015, for *P. tharos* in 2014, and for *P. glaucus* in 2014 and 2015. $P^*$ was calculated on the basis of the ($\psi . \gamma . \varepsilon . \delta . \rho$ [interaction of sampling period and survey]) model for *E. clarus*, the ($\psi . \gamma . \varepsilon . \delta . \rho$ [interaction of sampling period and survey]) model for *P. glaucus*, the ($\psi . \gamma . \varepsilon . \delta . \rho$ [interaction of sampling period and survey]) model for *H. sosybius*, and the ($\psi . \gamma . \varepsilon . \delta . \rho$ [survey]) model for *S. appalachia*. Standard errors are not shown to improve clarity of illustration but are provided here for 2012, 2013, 2014, and 2015, respectively: *Epargyreus clarus* (0.26, 0.04, 0.12, 0.16), *Hermeuptychia sosybius* (0.05, 0.06, 0.06, 0.12), *Papilio glaucus* (0.10, 0.01, 0.10, 0.09), *Phyciodes tharos* (0.02, 0.08, 0.18, 0.07), and *Satyrodes appalachia* (0.04, 0.04, 0.04, 0.04).
Figure 4: Summed AIC model weights, conditional model-averaged regression coefficients ($\hat{\beta}$) and unconditional standard errors (SE) for variables included in the most strongly supported multivariate models of colonization and extinction for *Epargyreus clarus*. Intercepts for expansion = $-2.62 \pm 1.46$ and for contraction = $-1.91 \pm 1.11$. 

**Epargyreus clarus Expansion (γ)**

- Fall Min Temp, t-1: $-1.59 (1.55)$
- Summer III Max Hum, t-1: $1.81 (1.70)$
- Spring Min Temp, t: $-0.14 (0.15)$

**Epargyreus clarus Contraction (ε)**

- Days Below Freezing, t-1: $-0.03 (0.06)$
- Winter Min Temp, t-1: $0.06 (0.10)$
- Spring Min Temp, t: $0.14 (0.20)$
- Spring Max Temp, t-1: $0.19 (0.29)$
- Spring Max Hum, t-1: $0.14 (0.15)$
- Fall Rain, t-2: $0.14 (0.15)$
- Fall Min Temp, t-1: $0.36 (0.43)$
Figure 5: Summed AIC model weights, conditional model-averaged regression coefficients ($\beta$) and unconditional standard errors (SE) for variables included in the most strongly supported multivariate models of colonization and extinction for *Papilio glaucus*. Intercepts for expansion = $-0.46 \pm 0.96$ and for contraction = $-2.63 \pm 0.78$. 
Figure 6: Summed AIC model weights, conditional model-averaged regression coefficients ($\hat{\beta}$) and unconditional standard errors (SE) for variables included in the most strongly supported multivariate models of colonization and extinction for *Phyciodes tharos*. Intercepts for expansion = -4.02 ± 1.45 and for contraction = -1.17 ± 0.40.
Figure 7: Summed AIC model weights, conditional model-averaged regression coefficients ($\beta$) and unconditional standard errors (SE) for variables included in the most strongly supported multivariate models of colonization and extinction for *Hermeuptychia sosybius*. Note that AIC weight for expansion is skewed because it was the only variable included in this model. Intercepts for expansion 2012/13 = $-1.92 \pm 0.87$; 2013/14 = $-3.54 \pm 1.46$; 2014/15 = $-3.57 \pm 1.38$; and for contraction 2012/13 = $-3.03 \pm 1.43$; 2013/14 = $-4.03 \pm 1.99$; 2014/15 = $-1.87 \pm 1.48$. 
Figure 8: Interval-specific model-averaged estimates of probability of expansion (E) and contraction (C) for *Epargyreus clarus*, *Papilio glaucus*, *Phyciodes tharos*, *Hermeuptychia sosybius*, and *Satyrodes appalachia* sampled in four regions (Region 1 = blue, Region 2 = red, Region 3 = black, and Region 4 = green). Geographical locations are provided in the upper-right panel.
Figure 9: Probability (± SE) of occupancy of *Epargyreus clarus, Papilio glaucus, Phyciodes tharo, Hermeuptychia sosybius*, and *Satyrodes appalachia* across four seasons (2012-2015). Occupancy for four of five species was relatively stable whereas it increased nearly twofold in 2013 for *P. glaucus*. Estimates for *E. clarus* were based on the ($\psi \cdot \gamma \cdot \varepsilon \cdot \delta \cdot p$ [season + survey]) model, for *P. glaucus* were based on the ($\psi \cdot \gamma \cdot \varepsilon \cdot \delta \cdot p$ [season + survey]) model, for *P. tharo* were based on the ($\psi \cdot \gamma \cdot \varepsilon \cdot \delta \cdot p$ [interaction of sampling period and survey]) model, for *H. sosybius* were based on the ($\psi \cdot \gamma \cdot \varepsilon \cdot \delta \cdot p$ [interaction of sampling period and survey]) model, and for *S. appalachia* were based on the ($\psi \cdot \gamma \cdot \varepsilon \cdot \delta \cdot p$ [survey]) model.
APPENDICES

Appendix 1: Number of transects within each land cover type and description of land cover type for 67 random transect stratified along a rural urban gradient.

<table>
<thead>
<tr>
<th>Land cover type</th>
<th>Number of transects</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge</td>
<td>8</td>
<td>Transect along the edge of a transition from forest to some other ecological condition</td>
</tr>
<tr>
<td>Forest gap</td>
<td>32</td>
<td>Forest transect in which the opening of the pathway through the forest has caused the conditions on the transect to be different from the surrounding forest</td>
</tr>
<tr>
<td>Forest interior</td>
<td>21</td>
<td>Forest transect in which the conditions on the transect itself are little different from the surrounding forest</td>
</tr>
<tr>
<td>Riparian</td>
<td>6</td>
<td>Transect that follows a riparian corridor</td>
</tr>
</tbody>
</table>
### Appendix 2: Nomenclature of climate variables used to estimate population turnover.

<table>
<thead>
<tr>
<th>Season</th>
<th>Climate Variable</th>
<th>Year</th>
<th>Presence Input</th>
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</thead>
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<tr>
<td>Spring</td>
<td>Total Rainfall</td>
<td>Current Sampling Year</td>
<td>sprain_t</td>
</tr>
<tr>
<td></td>
<td>Minimum Temperature</td>
<td></td>
<td>spmint_t</td>
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<tr>
<td></td>
<td>Maximum Temperature</td>
<td></td>
<td>spmaxt_t</td>
</tr>
<tr>
<td></td>
<td>Minimum Humidity</td>
<td></td>
<td>spminh_t</td>
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<tr>
<td></td>
<td>Maximum Humidity</td>
<td></td>
<td>spmaxh_t</td>
</tr>
<tr>
<td>Spring</td>
<td>Total Rainfall</td>
<td>First Year Prior to Sampling</td>
<td>sprain_t-1</td>
</tr>
<tr>
<td></td>
<td>Minimum Temperature</td>
<td></td>
<td>spmint_t-1</td>
</tr>
<tr>
<td></td>
<td>Maximum Temperature</td>
<td></td>
<td>spmaxt_t-1</td>
</tr>
<tr>
<td></td>
<td>Minimum Humidity</td>
<td></td>
<td>spminh_t-1</td>
</tr>
<tr>
<td></td>
<td>Maximum Humidity</td>
<td></td>
<td>spmaxh_t-1</td>
</tr>
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<td>Summer III</td>
<td>Total Rainfall</td>
<td>First Year Prior to Sampling</td>
<td>3_surain_t-1</td>
</tr>
<tr>
<td></td>
<td>Maximum Temperature</td>
<td></td>
<td>3_sumaxt_t-1</td>
</tr>
<tr>
<td></td>
<td>Minimum Humidity</td>
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<td>3_suminh_t-1</td>
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<td></td>
<td>Maximum Humidity</td>
<td></td>
<td>3_sumaxh_t-1</td>
</tr>
<tr>
<td>Summer III</td>
<td>Total Rainfall</td>
<td>Second Year Prior to Sampling</td>
<td>3_surain_t-2</td>
</tr>
<tr>
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<td>Maximum Temperature</td>
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<td>Fall</td>
<td>Total Rainfall</td>
<td>First Year Prior to Sampling</td>
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<tr>
<td></td>
<td>Minimum Temperature</td>
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<td>fmint_t-1</td>
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<tr>
<td>Fall</td>
<td>Total Rainfall</td>
<td>Second Year Prior to Sampling</td>
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<td>Minimum Temperature</td>
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<td>Winter</td>
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<tr>
<td></td>
<td>Days Below Freezing</td>
<td></td>
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<td>Minimum Temperature</td>
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<tr>
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<td>Maximum Temperature</td>
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<td>wmaxt_t-2</td>
</tr>
</tbody>
</table>
Appendix 3: Conceptual outline for multi-season model across four sampling periods. $\Psi_1$ denotes the probability a site is occupied during the first sampling period. $1 - \Psi_1$ denotes the probability a site is unoccupied during the first sampling period. Four separate inter-annual events can then be estimated between sampling period one and sampling period two: the probability that contraction did not occur ($1 - \varepsilon_1$), the probability contraction did occur ($\varepsilon_1$), the probability expansion did occur ($\gamma_1$), and the probability that expansion did not occur ($1 - \gamma_1$). The same four parameters are estimated between each subsequent sampling period. Specific encounter histories determine which parameters are estimated for a given site. Adapted from MacKenzie et al. (2006).
Appendix 4: Example of a design matrix to evaluate sampling period effect on detection probability (where C refers to column).

<table>
<thead>
<tr>
<th>Survey</th>
<th>C1</th>
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Appendix 5: Example of a design matrix to evaluate survey effect on detection probability (where C refers to column).

<table>
<thead>
<tr>
<th>Survey</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>C4</th>
<th>C5</th>
<th>C6</th>
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</thead>
<tbody>
<tr>
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<tr>
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Appendix 6: Example of a design matrix to evaluate additive effects of sampling period and survey on detection probability (where C refers to column).

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<th>C3</th>
<th>C4</th>
<th>C5</th>
<th>C6</th>
<th>C7</th>
<th>C8</th>
<th>C9</th>
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<tr>
<td>p_{12}</td>
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<td>0</td>
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<td>1</td>
<td>0</td>
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<tr>
<td>p_{13}</td>
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Appendix 7: Example of a design matrix to evaluate interaction between sampling period and survey on detection probability (where C refers to column).

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</tbody>
</table>

67
Appendix 8: Annual variation of total rainfall, maximum temperature, minimum temperature, maximum humidity, and minimum humidity measured at four weather stations spread throughout the study area (Fig. 1). Averages for each variable were calculated based on seasons defined in Fig 2.
Appendix 9: Design matrix to estimate regression coefficients for contraction and expansion on the basis of separate intercepts and slopes for each sampling period

<table>
<thead>
<tr>
<th>Inter-Annual Estimate</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>C4</th>
<th>C5</th>
<th>C6</th>
</tr>
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<tbody>
<tr>
<td>$\gamma_1 / \varepsilon_1$</td>
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<td>0</td>
<td>covar_1</td>
<td>0</td>
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<tr>
<td>$\gamma_2 / \varepsilon_2$</td>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>covar_2</td>
<td>0</td>
</tr>
<tr>
<td>$\gamma_3 / \varepsilon_3$</td>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>covar_3</td>
</tr>
</tbody>
</table>
Appendix 10: Design matrix to estimate regression coefficients for contraction and expansion on the basis of a constant intercept and slopes for each sampling period.

<table>
<thead>
<tr>
<th>Inter-Annual Estimate</th>
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<th>C2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_1 / \varepsilon_1$</td>
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<td>covar_1</td>
</tr>
<tr>
<td>$\gamma_2 / \varepsilon_2$</td>
<td>1</td>
<td>covar_2</td>
</tr>
<tr>
<td>$\gamma_3 / \varepsilon_3$</td>
<td>1</td>
<td>covar_3</td>
</tr>
</tbody>
</table>
Appendix 11: Design matrix to estimate regression coefficients for contraction and expansion on the basis of separate intercepts for each sampling period but a constant slope for each sampling period

<table>
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<tr>
<th>Inter-Annual Estimate</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>C4</th>
</tr>
</thead>
<tbody>
<tr>
<td>𝛾₁ / 𝜖₁</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>covar_1</td>
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<td>𝛾₂ / 𝜖₂</td>
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<td>1</td>
<td>0</td>
<td>covar_2</td>
</tr>
<tr>
<td>𝛾₃ / 𝜖₃</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>covar_3</td>
</tr>
</tbody>
</table>
Appendix 12: Strengths of support for open and closed multi-season occupancy models and detection probability models for *Epargyreus clarus*. Psi = occupancy, p = detection, gam = colonization, eps = extinction, e = entry, d = departure, AICc = Akaike’s Information Criterion adjusted for small sample size, ΔAIC = difference from the model with the lowest AIC, and AICω = model weight, season = sampling period effect (Appendix 4), within = survey effect (Appendix 5), within_6 = additive model of sampling period and survey (Appendix 6), full_id = interaction between sampling period and survey (Appendix 7).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AICω</th>
<th>Parameters</th>
<th>Log Likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ψ(·), γ(·), ε(·), e(·), d(·), p(within_6)</td>
<td>711.10</td>
<td>0</td>
<td>0.50</td>
<td>14</td>
<td>683.10</td>
</tr>
<tr>
<td>Ψ(·), γ(·), ε(·), e(·), d(·), p(within)</td>
<td>711.50</td>
<td>0.40</td>
<td>0.41</td>
<td>11</td>
<td>689.50</td>
</tr>
<tr>
<td>Ψ(·), γ(·), ε(·), e(·), d(·), p(full_id)</td>
<td>714.61</td>
<td>3.51</td>
<td>0.09</td>
<td>29</td>
<td>656.61</td>
</tr>
<tr>
<td>Ψ(·), γ(·), ε(·), p(full_id)</td>
<td>722.48</td>
<td>11.38</td>
<td>&lt;0.001</td>
<td>27</td>
<td>668.48</td>
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<tr>
<td>Ψ(·), γ(·), ε(·), p(within_6)</td>
<td>726.00</td>
<td>14.90</td>
<td>&lt;0.001</td>
<td>12</td>
<td>702.00</td>
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<td>Ψ(·), γ(·), ε(·), p(within)</td>
<td>728.07</td>
<td>16.97</td>
<td>&lt;0.001</td>
<td>9</td>
<td>710.07</td>
</tr>
<tr>
<td>Ψ(·), γ(·), ε(·), p(season)</td>
<td>756.06</td>
<td>44.96</td>
<td>&lt;0.001</td>
<td>7</td>
<td>742.06</td>
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<tr>
<td>Ψ(·), γ(·), ε(·), p(·)</td>
<td>758.51</td>
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<td>&lt;0.001</td>
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<td>Ψ(·), γ(·), ε(·), e(·), d(·), p(season)</td>
<td>758.90</td>
<td>47.80</td>
<td>&lt;0.001</td>
<td>9</td>
<td>740.90</td>
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<td>760.39</td>
<td>49.29</td>
<td>&lt;0.001</td>
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<td>748.39</td>
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</table>
Appendix 13: Strengths of support for open and closed multi-season occupancy models and detection probability models for *Papilio glaucus*. Psi = occupancy, p = detection, gam = colonization, eps = extinction, e = entry, d = departure, AICc = Akaike’s Information Criterion adjusted for small sample size, ΔAIC = difference from the model with the lowest AIC, and AICω = model weight, season = sampling period effect (Appendix 4), within = survey effect (Appendix 5), within_6 = additive model of sampling period and survey (Appendix 6), full_id = interaction between sampling period and survey (Appendix 7).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AIC ω</th>
<th>Parameters</th>
<th>Log Likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{within}_6) )</td>
<td>1226.22</td>
<td>0</td>
<td>0.63</td>
<td>12</td>
<td>1202.22</td>
</tr>
<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), e(\cdot), d(\cdot), p(\text{within}_6) )</td>
<td>1227.78</td>
<td>1.56</td>
<td>0.29</td>
<td>14</td>
<td>1199.78</td>
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<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), d(\cdot), p(\text{full_id}) )</td>
<td>1231.33</td>
<td>5.11</td>
<td>0.05</td>
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<td>1173.33</td>
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<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{full_id}) )</td>
<td>1231.98</td>
<td>5.76</td>
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<td>1177.98</td>
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<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), d(\cdot), p(\text{season}) )</td>
<td>1272.84</td>
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<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{season}) )</td>
<td>1285.63</td>
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<td>&lt; 0.001</td>
<td>7</td>
<td>1271.63</td>
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<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), e(\cdot), d(\cdot), p(\text{within}) )</td>
<td>1319.59</td>
<td>93.37</td>
<td>&lt; 0.001</td>
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<td>1297.59</td>
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<tr>
<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{within}) )</td>
<td>1324.90</td>
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<td>155.65</td>
<td>&lt; 0.001</td>
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<td>1373.87</td>
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</table>
Appendix 14: Strengths of support for open and closed multi-season occupancy models and detection probability models for *Phyciodes tharos*. Psi = occupancy, p = detection, gam = colonization, eps = extinction, e = entry, d = departure, AICc = Akaike’s Information Criterion adjusted for small sample size, ΔAIC = difference from the model with the lowest AIC, and AICw = model weight, season = sampling period effect (Appendix 4), within = survey effect (Appendix 5), within_6 = additive model of sampling period and survey (Appendix 6), full_id = interaction between sampling period and survey (Appendix 7). I fixed survey two in sampling period three at zero because the lack of detections during that particular survey prevented an estimation of this parameter.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AICw</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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</thead>
<tbody>
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<td>0.98</td>
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<td>950.10</td>
</tr>
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<td>0.02</td>
<td>14</td>
<td>988.44</td>
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<td>11</td>
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<td>1005.44</td>
</tr>
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<td>37.57</td>
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<td>9</td>
<td>1027.67</td>
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<tr>
<td>Ψ(.), γ(.), ε(.), e(.), d(.), p(.)</td>
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<td>6</td>
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<tr>
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<td>82.49</td>
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<td>1082.59</td>
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</table>
Appendix 15: Strengths of support for open and closed multi-season occupancy models and detection probability models for *Hermeuptychia sosybius*. \( \Psi \) = occupancy, \( p \) = detection, \( \gamma \) = colonization, \( \epsilon \) = extinction, \( e \) = entry, \( d \) = departure, \( \text{AICc} \) = Akaike’s Information Criterion adjusted for small sample size, \( \Delta \text{AIC} \) = difference from the model with the lowest AIC, and \( \text{AIC}\omega \) = model weight, \( \text{season} \) = sampling period effect (Appendix 4), \( \text{within} \) = survey effect (Appendix 5), \( \text{within}_6 \) = additive model of sampling period and survey (Appendix 6), \( \text{full}_id \) = interaction between sampling period and survey (Appendix 7).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>( \Delta \text{AIC} )</th>
<th>( \text{AIC}\omega )</th>
<th>Parameters</th>
<th>Log Likelihood</th>
</tr>
</thead>
<tbody>
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<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), e(\cdot), d(\cdot), p(\text{full}_id) )</td>
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<td>1332.07</td>
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<td>91.34</td>
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<td>( \Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{season}) )</td>
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<td>1447.18</td>
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Appendix 16: Strengths of support for open and closed multi-season occupancy models and detection probability models for *Satyrodes appalachia*. \( \Psi = \) occupancy, \( p = \) detection, \( \gamma = \) colonization, \( \varepsilon = \) extinction, \( e = \) entry, \( d = \) departure, \( \text{AICc} = \) Akaike’s Information Criterion adjusted for small sample size, \( \Delta \text{AIC} = \) difference from the model with the lowest AIC, and \( \text{AIC}_\omega = \) model weight, \( \text{season} = \) sampling period effect (Appendix 4), \( \text{within} = \) survey effect (Appendix 5), \( \text{within}_6 = \) additive model of sampling period and survey (Appendix 6), \( \text{full}_id = \) interaction between sampling period and survey (Appendix 7).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>( \Delta \text{AIC} )</th>
<th>( \text{AIC}_\omega )</th>
<th>Parameters</th>
<th>Log Likelihood</th>
</tr>
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<tbody>
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<td>( \Psi(.), \gamma(.), \varepsilon(.), e(.), d(.), p(\text{within}) )</td>
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<td>544.91</td>
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<td>566.44</td>
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Appendix 17: Strengths of support for univariate expansion ($\gamma$) models for *Epargyreus clarus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

<table>
<thead>
<tr>
<th>Model</th>
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<th>ΔAIC</th>
<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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<tbody>
<tr>
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<tr>
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<td>5.00</td>
<td>0.04</td>
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<td>670.98</td>
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<tr>
<td>$\gamma$ (wrain_t-2_b)</td>
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<td>679.55</td>
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<tr>
<td>Null Model</td>
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<td>15.12</td>
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<td>683.10</td>
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<tr>
<td>$\gamma$ (frain_t-1_b)</td>
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<td>16.83</td>
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<td>682.81</td>
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Appendix 18: Strengths of support for univariate expansion (γ) models for *Papilio glaucus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

<table>
<thead>
<tr>
<th>Model</th>
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<th>ΔAIC</th>
<th>AIC ω</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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<td>γ (spmaxint_t_b)</td>
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<td>1196.51</td>
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<tr>
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<td>19.66</td>
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<td>1199.78</td>
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</table>
Appendix 19: Strengths of support for univariate expansion ($\gamma$) models for *Phyciodes tharos* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
</tr>
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<tbody>
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<td>0.05</td>
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<td>947.95</td>
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Appendix 20: Strengths of support for univariate expansion ($\gamma$) models for *Hermeuptychia sosybius* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “a” see Appendix 9 and for matrix “c” see Appendix 11. Any models that lacked robustness in parameter estimates were removed.

<table>
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<th>Log Likelihood</th>
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Appendix 21: Strengths of support for univariate expansion (γ) models for *Satyrodes appalachia* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “a” see Appendix 9 and for matrix “c” see Appendix 11. Any models that lacked robustness in parameter estimates were removed.

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Appendix 22: Strengths of support for univariate contraction ($\varepsilon$) models for *Epargyreus clarus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

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Appendix 23: Strengths of support for univariate contraction ($\varepsilon$) models for *Papilio glaucus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

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Appendix 24: Strengths of support for univariate contraction ($\varepsilon$) models for *Phyciodes tharos* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

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Appendix 25: Strengths of support for univariate contraction (ε) models for *Hermeuptychia sosybius* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “a” see Appendix 9 and “c” Appendix 11. Any models that lacked robustness in parameter estimates were removed.

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Appendix 26: Strengths of support for univariate contraction ($\varepsilon$) models for *Satyrodes appalachia* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “a” see Appendix 9 and “c” Appendix 11. Any models that lacked robustness in parameter estimates were removed.

<table>
<thead>
<tr>
<th>Model</th>
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<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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Appendix 27: Strengths of support for multivariate expansion ($\gamma$) and contraction ($\varepsilon$) models for *Epargyreus clarus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

<table>
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<tr>
<th>Model</th>
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<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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Appendix 28: Strengths of support for multivariate expansion ($\gamma$) and contraction ($\varepsilon$) models for *Papilio glaucus* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

<table>
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<tr>
<th>Model</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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Appendix 29: Strengths of support for multivariate expansion ($\gamma$) and contraction ($\varepsilon$) models for *Phyciodes tharos* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “b” see Appendix 10. Any models that lacked robustness in parameter estimates were removed.

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<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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*Null Model*  
1008.10  
4.31  
0.03  
29  
950.10
Appendix 30: Strengths of support for multivariate expansion ($\gamma$) and contraction ($\epsilon$) models for *Hermesyphtchia sosybius* while keeping the best detection model constant and keeping the occupancy, entry and exit model as null models. For full name of covariates see Appendix 2. For full design of matrix “a” see Appendix 9 and “c” see Appendix 11. Any models that lacked robustness in parameter estimates were removed.

<table>
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<tr>
<th>Model</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>AIC $\omega$</th>
<th>Parameters</th>
<th>Log Likelihood</th>
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<td>$\gamma$ (3_sumaxh_t-2_c), $\epsilon$ (fmint_t-1_c)</td>
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<td>0</td>
<td>0.15</td>
<td>35</td>
<td>1184.01</td>
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<td>0.13</td>
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<td>0.12</td>
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<td>1.20</td>
<td>0.08</td>
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<td>3.12</td>
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