One size does not fit all: Family specific differences in seasonal patterns of abundance and

behavior in butterfly communities

Authors: Grace E. Hirzel, Ashlyn E. Anderson, and Erica L. Westerman

Affiliation: Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701

Short title: Seasonality in butterfly communities

Keywords: Lepidoptera, long term research, insect, pollinator, intra-annual change

Abstract

Animal communities can undergo seasonal shifts in assemblage, responding to changes in their

environment. Animal behavior can also shift due to seasonal environmental variation, with the

potential to shape ecosystems. However, it is unclear if similar environmental factors and time

scales affect both abundance and behavior. We examined how butterfly abundance and

behavior change seasonally in temperate prairies and a butterfly garden, and if the factors

driving variation differ between taxonomic families. We conducted monthly abundance surveys

year-round and biweekly abundance and behavior surveys during the summer and fall, in 2017-

2021 and 2018-2020 respectively. We also determined how ambient light, temperature,

precipitation, and time of year interact to affect butterfly abundance and behavior. We found

increased temperature and light levels correlate with increases in general butterfly abundance.

Unlike the greater community, Lycaenidae abundance decreased as weekly precipitation

increased, and Papilionidae abundance did not respond to changes in environmental factors.

Only Nymphalidae changed behavior in response to environmental factors, increasing

thermoregulatory behaviors as temperature and light levels decreased. These results indicate

that lineages may differ in their sensitivity to environmental factors, which could result in

disproportionate changes in their abundances in response to future climate change and

anthropogenic-driven disturbance.

Introduction

Habitats can change drastically with the seasons, either to the benefit or detriment of

their animal inhabitants (Campuzano et al. 2020; Wettlaufer et al. 2023). As a result,

community structure can shift throughout the year, as animal populations respond to seasonal

environmental changes (see Cerda et al. 1997; Desmond et al. 2002). Shifts in the community

can be measured via animal abundance and diversity, revealing both intra- and inter-annual

differences (Highland et al. 2016; Turley et al. 2022). Surveying animal behavior in conjunction

to abundance can also provide useful information about animal communities (Toft et al. 2007;

Sawyer et al. 2017). Many animals' first responses to environmental change are alterations in

behavior, which may lead to shifts in abundance, species interactions, or ecosystem services

(reviewed in (Wong and Candolin 2015)). Thus, understanding changes in behavior and when

they occur can help predict community health.

Seasonal shifts in community structure have been documented across many

ecosystems, from terrestrial to aquatic and tropical to temperate environments. Tropical bird

communities at higher elevations decrease in species richness from the breeding to

nonbreeding season (Liang et al. 2021). Near shore fish communities in the north Atlantic are

composed of different species in the winter and spring vs the summer and fall (Lazzari et al.

1999). Likewise in Panama, orchid bee communities also show seasonal changes in assemblages

throughout the year (Roubik and Ackerman 1987). However, multiple environmental factors

covary with season and may have interactive effects that are hard to detect in a laboratory

setting. This can make it difficult to determine which seasonal factors are impacting community

composition and abundance.

For example, abiotic factors such as temperature, light, and precipitation can co-vary

and interact, affecting animal communities directly, or indirectly through biotic factors (Dai et

al. 1999; Kleypas et al. 1999; Bae and Park 2019; La Sorte and Graham 2021). In marine

ecosystems, temperature and pH change seasonally and can cause shifts in the dominant

animal species (Dijkstra et al. 2011). Within terrestrial systems, seasonal precipitation and

vegetation can affect abundance of tropical insects (Wolda 1978), and seasonal soil humidity

can affect species richness in litter dwelling arthropod communities (Wiwatwitaya and Takeda

2005). Adding further complexity, response to seasonal factors may not be immediate, such as

the increase in herbivorous tropical insect abundance two months after major precipitation

events (Grøtan et al. 2012). Some of the environmental factors that affect abundance, such as

day length or degree days, cannot be isolated from time of year in natural settings (Rohde and

Pilliod 2021). However, identifying the seasonal factors that drive shifts in community

assemblages is important, as many of these environmental factors may change in timing and

intensity due to phenomena such as climate change and other human disturbances ((Zhang et

al. 2004), reviewed in (Trenberth 2011)).

While studies of seasonal shifts in abundance are more common, animal communities

also exhibit seasonal shifts in behavior. For example, large African carnivores show seasonal

patterns in movement to avoid competing or dominant species (Vanak et al. 2013). In tropical

environments, fruit feeding bats change their diets to take advantage of abundant food

resources, becoming pollinators instead of strict frugivores (Heithaus et al. 1975). Diets

amongst tropical ground dwelling frog species are also seasonal, overlapping less during the dry

season compared to the wet season (Toft 1980). Animals may also change their diurnal patterns

of activity throughout the year; for example, temperate water snakes are nocturnal in summer

but are diurnal in cooler months (Mushinsky et al. 1980). By affecting predator-prey

interactions, pollination events, and the abundances of plant and animal heterospecifics,

seasonal shifts in behavior of these animal communities have the potential to shape

ecosystems.

A community's structure depends on the varied responses (including behaviors) of

individual species, affecting interactions between predators, prey, and competitors

(Nagelkerken and Munday 2016). Animals often change their behavior before changes in

abundances occur, as is observed when animals face anthropogenic disturbance (Tuomainen

and Candolin 2011). Research on behaviors of individual species highlights how understanding

behavioral patterns can help predict changes to species assemblages and ecosystems. For

example, bivalves are valuable ecosystem engineers and their behavior (burrowing depth) is a

better predictor of larval recruitment than adult densities are ((van Gils et al. 2009; Compton et

al. 2016). Predator behavior can also shape communities, as in the case of rat snakes, which are

predicted to increase nest predations as nocturnal temperatures increase due to climate

change (DeGregorio et al. 2015). Scaling up to examine behavioral patterns at the community

level is critical to optimizing predictive models and management strategies for entire

ecosystems. As environmental conditions change throughout the year, observing community

behavior in a seasonal context will give us a more complete understanding of ecosystem health.

Butterflies offer a unique system in which to study both abundance and behavior at the

community level. They are relatively easy to survey with minimal disturbance and will perform

feeding, flying, and thermoregulating behaviors in view of human observers. The abundance

and behavior of butterflies are also of special interest because of their ability and tendency to

disperse long distances, carrying pollen between plant populations (Courtney et al. 1982;

Ghazanfar et al. 2016). The phenology of butterfly abundance also has important implication

for bird communities, as butterfly and other lepidoptera larvae make up the majority of

passerine nestling diets (Kennedy 2019). Because of their ecological importance, abundance,

and ease of survey, butterflies have been used as indicators of decline in biodiversity in several

western European countries (Brereton et al. 2011).

Butterflies from a wide variety of habitats are sensitive to shifts in abiotic conditions and

plant communities. Both yearly temperature and precipitation can explain interannual

differences, with high temperatures and low precipitation causing annual declines in North

American butterfly populations (Woods et al. 2008; Robinson et al. 2012). Environmental

conditions can also cause butterfly abundance to fluctuate within a given year. In butterfly

communities found in neotropical dry-forests and Brazilian mountain forests, seasonal changes

in temperature and precipitation affect abundance (Checa et al. 2014; Beirão et al. 2021).

Similarly plant diversity and number of degree days above freezing shape alpine butterfly

communities (Pellissier et al. 2013). As environments shift due to changes in land use and

climate, butterfly communities may also change, particularly in terms of timing of adult

emergence and when peak abundance occurs.

115   In addition to changes in abundance, butterflies also respond behaviorally to

environmental factors. For example, decreases in covarying factors light and temperature can

cause corresponding decreases in courting, patrolling, and ovipositing in individual butterfly

species from multiple taxonomic families (McDonald and Nijhout 2000; Ide 2002; Vives-Ingla et

al. 2023). Likewise, at the community level, flying and nectaring behaviors increase in grassland

butterflies at warmer temperatures (Kral-O'Brien et al. 2021). A meta-analysis of mark-

recapture studies showed that time of year also affects behavior, as the time butterflies spend

on reproductive behaviors changes throughout the season for a wide range of species (Vlašánek

et al. 2018). These findings highlight the sensitivity of butterfly species and butterfly

communities to changes in their environment. However, butterfly communities are often

species rich and comprised of species from multiple taxonomic families (Simonson et al. 2001;

Wittman et al. 2017; Subedi et al. 2021). For example, in temperate North America butterfly

communities often consist of 25 to 50 species (Myers et al. 2012; Smith and Cherry 2014). It

remains unclear how such diversity impacts both community-wide behavioral changes and

family-specific responses to abiotic environmental factors and seasonal change.

130   A butterfly's response to its' environment may be associated with its taxonomic family

status and broad evolutionary history. Biological differences between taxonomic families

include size and wing morphology, which affect flight speed (Hawkins and Lawton 1995; Le Roy

et al. 2019). Families also differ in ability to thermoregulate, with Pieridae and Papilionidae

buffering against greater changes in temperature and Hesperiidae tolerating higher

temperatures compared to other butterfly families (Bladon et al. 2020; Ashe-Jepson et al.

2023). Butterfly families also vary in their sensitivity to color (Stavenga and Arikawa 2006),

which mediates a range of behaviors including mate choice, host plant selection, background

matching, and finding nectar sources (Obara and Hidaka 1968; Snell-Rood and Papaj 2009; Pohl

et al. 2011; van Bergen and Beldade 2019). Some behaviors, such as mate locating strategies,

also appear to be influenced by taxonomic family (Tiple et al. 2010). Due to these family specific

variations in physiology and anatomy, we predicted that we would observe seasonal patterns of

abundance and behavior that differ between butterfly families.

In this long-term study we examined how both butterfly abundance and butterfly

behavior change with season in Northwest Arkansas, a region that historically consisted of both

Ozark woodlands and tallgrass prairies but is now being rapidly developed for urban use. In

conjunction with animal surveys, we assessed how abiotic factors, including temperature,

precipitation, and light environment, changed throughout the year at our prairie and botanical

garden field sites. Since these factors can affect both butterflies' ability to thermoregulate and

vision mediated behaviors, we predicted that seasonal or daily changes in temperature,

precipitation, or light environment would influence patterns of thermoregulation behaviors or

cause lower levels of activity. Lastly, to account for other potentially important seasonal factors

that we did not measure, such as day length and vegetation height and types, we asked if

temperature, precipitation, or light environment interacted with time of year to correlate with

changes in abundance and behavior.

Methods

Field Sites:

Survey sites included three prairie sites and one botanical garden in Northwest Arkansas, USA.

Woolsey Wet Prairie Restoration Area (Woolsey) is a 50 acre restored wet prairie owned by the

city of Fayetteville, AR, located at 36°3'52''N and 94°13'57''W. Chesney Prairie Natural Area

(Chesney) is an 80 acre tallgrass prairie under the control of the Arkansas Natural Heritage

Commission located at 36°13'10''N and 94°28'58''W. Stump Prairie is a privately owned 20 acre

remnant tallgrass prairie, located at 36°12'18''N and 94°29'43'' W. Woolsey is near the edge of

Fayetteville surrounded by fallow fields slowly being developed into housing. Stump and

Chesney are surrounded by wheat fields and pasture. The Botanical Garden of the Ozarks (BGO)

is a 44 acre botanical garden with a native butterfly house in Fayetteville, AR, located at

36°08'12"N and 94°07'06"W.

Study animals:

We identified the observed adult butterflies to the lowest taxon possible, which varied

depending on the species, genus, and family. Survey members varied in levels of identification

expertise, but all survey members could confidently identify all animals to families Hesperiidae,

Nymphalidae, Lycaenidae, Papilionidae, and Pieridae. For monthly surveys we could identify up

to 38 species with confidence. (See fig. 1 for examples of butterflies from our study sites).

Transect Walks:

We counted butterflies on transect surveys based on Pollard Yates Walks (Pollard & Yates 1993)

to examine how the composition of butterfly communities changed throughout the season and

across years. We conducted monthly surveys in small groups from July 2017 to December 2021

at the BGO and Woolsey. Survey groups usually ranged from 3 to 6 people, though in 2020 and

2021 some surveys groups were only 1 or 2 people in size because of the Covid-19 pandemic.

Group surveys took place the first Thursday or Friday of the month. On days with heavy rain, we

delayed surveying until the next day with suitable conditions. Surveys began at approximately

09:00 at the BGO. Surveys at Woolsey began after finishing surveys at the BGO and driving to

the site, typically starting between 10:00 and 10:30. Transect walks were conducted at a slow

walking pace. During these surveys we identified butterflies to the lowest taxon possible.

We also conducted surveys every other week in 2018, 2019, and 2020 from late May to early

November. For these surveys, a single individual walked transects at Woolsey, Chesney, and

Stump prairies. Each site had three transects. In 2018, transects were 183 meters long. In 2019

and 2020 most transects were in the same location, but lengthened by 27 meters to 210

meters. We moved Woolsey Transect 1 in 2019 after a new utility road intersected the transect.

We moved Chesney Transect 3 in 2019 after analysis of 2018 data indicated that Transect 3 had

significantly lower numbers of butterflies than the two other Chesney transects. We walked

transects in the span of approximately 10 minutes, but times varied between 8 and 10 minutes,

depending on number of butterflies. For biweekly surveys we conducted surveys in the time

period between solar noon and 150 minutes after solar noon. During a survey week we visited

every site once. We counted butterflies observed within 5 meters to the front and sides of the

observer during biweekly transects.

Behavior:

We collected behavioral data to investigate how seasonal and other environmental conditions

affected the behavior of different butterfly taxa. We recorded behavior during our biweekly

visits to Woolsey, Chesney, and Stump prairies in 2019 and 2020. During the first transect we

walked for each visit, we recorded the first behavior observed for every butterfly we counted.

We categorized behavior as *flying, resting, basking, nectaring, courting, chasing, rejecting,*

mating, hovering, ovipositing, and *startled*. Butterflies were categorized as *chasing* whether

they were following other butterflies or being followed. While *chasing* behavior can be part of

courting in some species, for this study we defined *courting* as butterflies hovering and

fluttering over another butterfly (Scott 1975). *Rejecting* was defined as butterflies that were

fluttering their wings while being courted (Scott 1975). We recorded *resting* behavior when we

observed inactive butterflies that had closed wings and *basking* behavior when we observed

inactive butterflies that had open wings. We recorded butterflies as *startled* when we observed

butterflies flying from a stationary position or flying within 0.5 meters from the observer in

thick vegetation and could have been startled from a stationary position.

Abiotic factors:

To examine how seasonal light environment affected abundance and behavior of butterflies

from different families, we measured absolute solar irradiance during visits to sites with a Jaz

spectrophotometer (Ocean Optics). During monthly visits we measured irradiance at four

predetermined spots along our transects at both the BGO and Woolsey that stayed consistent

across all years. For biweekly surveys, we included an additional spot for measurements at

Woolsey and also took irradiance measurements at five predetermined locations along our

transects at Chesney and Stump prairies. Locations for irradiance measurements mainly stayed

consistent throughout the study; however, we moved one measurement location at Chesney

between 2018 and 2019. Instead of measuring irradiance at the beginning of the Transect 3 we

walked in 2018, we took measurements at the end of the new Transect 3 walked in 2019 and

2020. At each designated irradiance location, we recorded three irradiance measurements. (We

took up to six measurements if we suspected technical problems with saving measurements.)

We also examined how temperature and precipitation affected butterfly abundance and

behavior. We used temperature and precipitation data captured by a regional weather station

at Northwest Arkansas National Airport that is available online through NOAA

(https://www.ncei.noaa.gov/cdo-web/datatools/lcd). For monthly surveys we used the

temperature measured immediately before conducting the surveys (around 08:50 for BGO and

09:50 for Woolsey). For biweekly surveys we used the temperature measurements around

13:50, because this time always fell within the start and end points of a survey visit. For

precipitation we used total levels of precipitation that fell for the Julian Week of the survey.

Data Processing and Statistical Analysis:

Irradiance data was extracted and processed using R 3.6.3 (R Core Team 2018). Using the

photobiology and *photobiologyInOut* packages (Aphalo 2015), we extracted properties of

ambient light (UV and total solar irradiance levels). These packages extracted the calibrated

("Processed") data in the rightmost column of the *.JazIrrad files. After extracting data we used

the e_irrad() function to find irradiance values for all wavelengths from 290 to 800 nm and 290

to 400 for total irradiance and ultraviolet wavelengths (UV), respectively. We determined

relative levels of UV by dividing the UV irradiance by total irradiance. We averaged the

measurements taken at a single measurement location during each survey visit. When

comparing irradiance values to abundance and behavior, all site measurements were then

averaged together.

We completed subsequent analysis of abundance and environmental data with R 4.2.2 (R Core

Team 2018). Before we tested whether environmental factors, including time of year, total

solar irradiance, relative UV levels, temperature, weekly precipitation, survey year, and site,

affected abundance or behavior, we ran a correlation matrix to determine the correlations

between these environmental factors. Correlated factors ($R^2 > 0.20$) were then used in a

principal component analysis. Sampling dates with missing data (eg. weather or abundance)

were dropped from the analysis. Principal Components (PCs) were included in generalized

linear models with the glm() function from the *lme4* package (Bates et al. 2015) to determine

the effects of our PCs on abundance (monthly and biweekly data) and behavior (biweekly) of

the entire butterfly community, as well as the abundance and behavior of butterfly members of

each of the five families we observed (Hesperiidae, Nymphalidae, Lycaenidae, Papilionidae, and

Pieridae). Models were run with a quassipoisson distribution and chi square test. To account

for multiple testing we used a Bonferroni correction (α = .05, p = 0.0016). To further examine

behavioral responses to specific factors and to visualize behavioral data we ran posthoc

nominal regressions in JMP Pro 17.0.0 (JMP 2021). Non behavioral data were visualized with

ggplot2 in R (Wickham 2016).

Ethical Statement

No butterflies were handled during this research. Permission to survey at Stump was granted by

Ozark Ecological Restoration Inc and permission to survey at Woolsey was provided by

Environmental Consulting Operations, Inc. We surveyed at Chesney with permission from the

Arkansas Natural Heritage Commission under research permits S-NHCC-18-023, S-NHCC-19-015,

and S-NHCC-20-010. The BGO permitted us to survey on their property.

Results:

We walked 109 monthly survey transects from 2017-2021 and saw species from 5

butterfly families (see fig. 1). We counted 2,919 Nymphalidae, 1,141 Hesperiidae, 837

Lycaenidae, 606 Pieridae, and 262 Papilionidae (fig. S1A) We walked 342 biweekly survey

transects from 2018-2020. We counted a total of 3,559 Nymphalidae, 1,195 Hesperiidae, 561

Lycaenidae, 373 Pieridae, and 95 Papilionidae (fig. S1B).

Abiotic factors covary and change throughout the year

Many, but not all, of the abiotic factors we measured changed throughout the year.

Ambient temperature was highest from June to September in monthly surveys (fig. 2A) and

highest in July for biweekly surveys (fig. 2B). Precipitation during the week of the survey did not

change significantly from month to month or week to week for either monthly or biweekly

surveys (fig. 2C, D). Total irradiance was highest in June and August in monthly surveys and

highest for the entire period from May through July in biweekly surveys (fig. 2E, F). Relative UV

did not change significantly throughout the year for monthly surveys, but changed seasonally

for biweekly surveys, with relative UV levels peaking at the end of May (fig 2G, H).

Time of year and weather conditions can be highly correlated. To investigate how these

factors interacted and affected butterfly abundance and behavior, we ran principal component

analyses. Survey time of year (month/week), survey year, temperature, precipitation, total

irradiance, and relative UV were correlated with each other for both monthly (table S1) and

biweekly (table S2) surveys and were included in principal component analyses. Site was

correlated to total irradiance in monthly surveys, but we did not include it in the principal

component analysis. Our two sites, Woolsey and the BGO, differ in factors other than light

environment, such as plant species and human disturbance. To better understand differences in

abundance between sites, we instead included site as an independent variable in our models. In

biweekly surveys, site did not correlate to any of the other variables we measured and was

included as an independent variable in our models.

Butterfly abundance increases with absolute irradiance and temperature in year round

surveys

Principal Component 1 (PC1), PC2, and PC3 accounted for 75.3% of the total variance in

abiotic data for monthly surveys (table 1). PC1 accounted for 32.2% of variance and primarily

comprised of equal loadings of temperature, total irradiance, and negative relative UV. Lower

weightings were given to year and survey months, with little impact of precipitation. We

interpreted this to mean that high PC1 values represent "sunny conditions." PC2 accounted for

23.7% of variance and predominately comprised of equal loadings of survey month and survey

year, which were negatively correlated. Lower weightings were given to temperature, total

irradiance, and precipitation, with little impact of relative UV. PC3 accounted for 19.5% of

variance and comprised largely of increasing weekly precipitation. Other factors were equally

loaded and contributed to a lesser extent.

Table 1: Loadings for principal components analysis of monthly survey abiotic data

	PC1	PC2	PC3	PC4	PC5	PC6
Year	0.314	-1.616	-0.284	0.405	1.400	0.284
Survey Month	0.289	1.456	-0.341	0.656	-2.459	0.154
Temperature	0.598	0.824	0.361	0.250	4.310	-0.038
Weekly Precipitation	-0.134	-0.504	0.805	0.633	-2.085	0.032
Total Irradiance	0.631	0.085	0.301	-0.783	-2.031	0.218
Relative UV	-0.699	0.755	0.158	-0.161	1.868	0.350
Proportion of Variance	0.322	0.237	0.195	0.125	0.069	0.054
Cumulative Proportion	0.322	0.558	0.753	0.877	0.946	1.000

For models of monthly survey abundance, we included three principal components (PC1, PC2,

and PC3) and site. PC1 had a positive effect on total butterfly abundance (fig. 3A, table 2).

When data were analyzed by Lepidoptera family, we recovered a strong positive correlation

between PC1 and Hesperiidae, Nymphalidae, and Pieridae abundances, with other families

showing significant but weak (<0.1) correlations (fig. 3D, 3G, 3J, 3M, 3P, table 2). PC2

significantly affected butterfly abundance for most families, but changes in PC2 did not strongly

correlate to changes in abundance (R^2 less than 0.1 for all families) (fig. 3B, 3E, 3H, 3K, 3N, 3Q,

table 2). PC3 (precipitation) had a negative effect on Lycaenidae abundance and had significant

weak (<0.1) effects on Nymphalidae and Pieridae (fig. 3C, 3F, 3I, 3L, 3O, 3R, table 2). Butterfly

abundance was significantly higher at Woolsey than at the BGO for families Hesperiidae and

Papilionidae (fig 4A, table 2).

Table 2: Generalized linear model analyses of monthly survey abundance data

	PC1	PC2	PC3	Site
All Families	$p < 0.001$*	$p < 0.001$*	$p < 0.001$*	$p = 0.671$
	$R^2 = 0.27$	$R^2 = 0.09$	$R^2 = 0.05$	
Hesperiidae	$p < 0.001$*	$p < 0.001$*	$p = 0.226$	$p = 0.003$*
	$R^2 = 0.14$	$R^2 = 0.06$	$R^2 < 0.01$	
Lycaenidae	$p < 0.001$*	$p = 0.002$*	$p < 0.001$*	$p = 0.020$
	$R^2 = 0.07$	$R^2 = 0.04$	$R^2 = 0.19$	
Nymphalidae	$p < 0.001$*	$p < 0.001$*	$p = 0.015$	$p = 0.154$
	$R^2 = 0.24$	$R^2 = 0.07$	$R^2 = 0.03$	
Papilionidae	$p = 0.004$*	$p < 0.001$*	$p = 0.329$	$p = 0.006$*
	$R^2 = 0.06$	$R^2 = 0.09$	$R^2 = 0.01$	
Pieridae	$p < 0.001$*	$p < 0.001$*	$p < 0.001$*	$p = 0.138$
	$R^2 = 0.20$	$R^2 = 0.05$	$R^2 = 0.08$	

'* denotes significance after Bonferroni corrections

Time of year, temperature, and light cause changes in butterfly abundance in surveys

conducted during the flight period

In our biweekly surveys, four principal components explained 89.9% of variance of abiotic data

(table 3). Principal Component 1 (PC1) accounted for 32.7% of variance and was comprised of

equal loadings of temperature, total irradiance, relative UV, and negative survey week. We

interpreted PC1 to represent "seasonality." PC2 accounted for 28.0% of variance and comprised

primarily of weekly precipitation, relative UV, and negative total irradiance and survey year. We

interpreted PC2 to represent "cloud and rain levels." PC3 accounted for 15.0% of variance and

was comprised primarily of survey year. PC4 accounted for 14.2% of variance and comprised of

primarily weekly precipitation.

We included five factors in our models of biweekly abundance (PC1, PC2, PC3, PC4, and

site). Only PC1 significantly affected and had a strong correlation with butterfly abundance. As

PC1 increased, total butterfly abundance decreased (fig. 5A, table 4). This was also observed for

families Lycaenidae and Nymphalidae when families were analyzed individually (fig. 5B-F, table

4).

Basking behavior changes with light and temperature, but only in Nymphalidae

We included these same five variables (PC1, PC2, PC3, PC4, and Site) in our models when

analyzing our biweekly behavioral data. When analyzing the butterfly community as a whole,

only PC2 affected behavior (table 5). At lower levels of PC2, butterflies were more likely to be

seen basking; at higher levels they were more likely to be seen nectaring (fig. 6G). When

families were analyzed individually, PC2 also affected Nymphalidae behavior, but not the

behavior of the other families (table 5). Nymphalidae behavior mirrored the overall community

trend and were more likely to be seen basking at lower PC2 levels and more likely to be seen

nectaring at higher PC2 levels (fig. 6H). None of the principal components significantly affected

Hesperiidae or Lycaenidae behavior (table 5). There were not enough data to analyze the

behavior of Pieridae or Papilionidae individually.

Table 3: Loadings for principal components analysis of biweekly survey abiotic data

	PC1	PC2	PC3	PC4	PC5	PC6
Year	-0.468	1.513	1.124	0.004	-0.125	0.139
Survey Week	-1.570	0.446	-0.355	0.030	0.496	0.319
Temperature	1.343	1.219	0.135	0.007	0.831	-0.036
Weekly Precipitation	-0.196	-1.752	0.287	0.737	0.192	-0.054
Total Irradiance	0.906	1.889	-0.391	0.423	-0.386	0.252
Relative UV	0.986	-2.316	0.201	-0.201	-0.008	0.380
Proportion of Variance	0.327	0.280	0.150	0.142	0.075	0.026
Cumulative Proportion	0.327	0.607	0.758	0.899	0.974	1.000

364   **Table 4:** Generalized linear model analyses of butterfly abundance during biweekly surveys

	PC1	PC2	PC3	PC4	Site
All Families	$p < 0.001$*	$p = 0.013$	$p = 0.311$	$p = 0.755$	$p < 0.001$*
	$R^2 = 0.13$	$R^2 = 0.03$	$R^2 < 0.01$	$R^2 < 0.01$	
Hesperiidae	$p = 0.066$	$p = 0.013$	$p = 0.561$	$p = 0.265$	$p = 0.107$
	$R^2 = 0.02$	$R^2 = 0.03$	$R^2 < 0.01$	$R^2 < 0.01$	
Lycaenidae	$p < 0.001$*	$p = 0.348$	$p = 0.754$	$p = 0.009$	$p < 0.001$*
	$R^2 = 0.17$	$R^2 < 0.01$	$R^2 < 0.01$	$R^2 = 0.02$	
Nymphalidae	$p < 0.001$*	$p = 0.094$	$p = 0.295$	$p = 0.821$	$p < 0.001$*
	$R^2 = 0.14$	$R^2 = 0.01$	$R^2 < 0.01$	$R^2 < 0.01$	
Papilionidae	$p = 0.003$*	$p = 0.078$	$p = 0.490$	$p = 0.918$	$p = 0.483$
	$R^2 = 0.06$	$R^2 = 0.02$	$R^2 < 0.01$	$R^2 < 0.01$	
Pieridae	$p = 0.439$	$p = 0.011$	$p = 0.527$	$p = 0.571$	$p = 0.200$
	$R^2 < 0.01$	$R^2 = 0.06$	$R^2 < 0.01$	$R^2 < 0.01$	

365   * denotes significance after Bonferroni corrections.

371   **Table 5:** Generalized linear model analyses of behavior during biweekly surveys

	PC1	PC2	PC3	PC4	Site
All Families	$p = 0.822$	$P < 0.001*$	$p = 0.122$	$p = 0.037$	$p = 0.344$
Hesperiidae	$p = 0.020$	$p = 0.683$	$p = 0.560$	$p = 0.561$	$p = 0.368$
Lycaenidae	$p = 0.468$	$p = 0.358$	$p = 0.374$	$p = 0.568$	$p = 0.150$
Nymphalidae	$p = 0.139$	$p < 0.001*$	$p = 0.177$	$p = 0.851$	$p = 0.245$

* denotes significance after Bonferroni corrections.

Discussion:

We found that seasonal environmental factors affect butterfly abundance and behavior

in wet and dry prairie communities as well as in botanical gardens. In the course scale (monthly)

year-long surveys, we found that as temperature and sunny conditions increase, total butterfly

abundance increases. Both these abiotic factors affected abundance more than time of year in

the monthly surveys. We observed a similiar pattern in fine-scale (biweekly) sampling efforts

during the flight period (late spring through fall); biweekly abundance decreased in response to

the covarying decrease in temperature and total irradiance as the flight period progressed.

Community-wide patterns were reflected in Nymphalidae. Hesperiidae, Lycaenidae, and

Pieridae abundances also followed community wide patterns but only in one of the survey data

sets. Lycaenidae abundance was also negatively affected by increased precipitation.

Conversely, Papilionidae did not respond to any of the environmental conditions we measured.

We also found seasonal effects on community-wide butterfly behavior, with butterflies as a

whole decreasing basking behavior as temperature and light increase and relative UV levels

decrease. However, when we examined families individually, we found that only nymphalids

show changes in behavior in response to any of the abiotic factors we measured. When

combined, our results suggest that while temperature and light affect both overall butterfly

abundance and behavior, butterfly family (and associated evolutionary history) may play an

important role in how butterflies respond to their environments.

Our finding that butterfly communities in mid-latitude prairies and botanical gardens

change in abundance with changes in temperature may reflect global patterns and complexities

encountered when assessing communities in other habitats and seasonal temperature regimes.

In both tropical and temperate ecosystems butterfly abundance generally increases as

temperatures increase (Checa et al. 2009; Rohde and Pilliod 2021). We saw this reflected in our

analyses of monthly data as abundance increases with temperature. In our biweekly surveys,

time of year also is important, since butterfly abundance decreased as the season progressed

and temperature decreased. Time of year and temperature interact to affect abundance in

other butterfly communities. In tropical systems, butterflies respond to interactions between

temperature and seasonal precipitation, with abundance increasing or decreasing with

precipitation levels depending on the habitat type (Checa et al. 2009; Beirão et al. 2021).

Interactions between time of year and temperature appear in other North American grasslands,

where day length and growing degree days interact with temperature to not only affect

abundance of butterflies and moths, but also abundance of bees and flies (Rohde and Pilliod

2021). Interactions between temperature and other seasonal factors are not limited to

butterfly and terrestrial communities: in marine ecosystems temperature interacts with pH to

cause seasonal changes in invertebrate communities (Dijkstra et al. 2011). In our study survey

month and survey week served as proxies for important seasonal factors that we might not

have considered. Although we measured seasonal light and weekly precipitation, animal

communities can also be affected by such seasonal factors as vegetation and soil moisture

(Wolda 1978, Wiwatwitaya and Takeda 2005). Future studies could examine whether seasonal

temperature interacts with other aspects of seasonality and time of year to differentially affect

certain groups of ectotherms and other temperature sensitive animals within their

communities.

We also found that butterfly abundance increases with total light and decreases with

relative UV. Changes in solar irradiation and canopy cover can explain changes in butterfly

abundance across different habitats and within forest habitats; whether the effect of light is

negative or positive depends on the scale and habitat type (Waltz and Covington 2004;

Houlihan et al. 2013; Grundel et al. 2020). Here we show that light environment also covaries

with time of year and other aspects of seasonality to affect butterfly abundance, and that these

effects differ for relative UV light and total irradiance. In the monthly surveys increased relative

UV could have been from either increased shade or cloud cover, since some surveys took place

at a botanical garden with shaded areas. In our biweekly surveys increased relative UV was only

from increased cloud cover, as these prairie sites lacked shade. However, increased relative UV

across all sites caused a decrease in butterfly abundance, indicating that regardless of cause,

butterflies respond to this aspect of light environment. Previous studies show butterfly

abundance changes with qualitative or estimated shifts in canopy and cloud cover (Fischer and

Fiedler 2001; Grundel et al. 2020). By measuring quantitatively, we were able to show that

canopied and cloudy environments may affect animals similarly, possibly due to changes in

their visual environment. Changes in canopy cover also influence changes in abundance in

other animals capable of seeing UV, including birds and other insect pollinators like bees and

flies (McCabe et al. 2019) (Patten and Smith-Patten 2012). Often changes in canopy cover are

framed in the context of changing temperature, it would be interesting to examine how

communities of other animals respond to relative UV, which we show is an important aspect of

increased shade and cloud cover. This is especially important now, since canopy cover is

decreasing in the tropics and increasing in other parts of the globe, causing wide-ranging shifts

in light environments (Song et al. 2018).

While temperature and light environment affected the butterfly community at large, we

found it particularly interesting that they did not affect the abundances of all families equally

and had no effect on the abundance of Papilionidae in either the monthly or biweekly surveys.

In general, Papilionidae are better at thermal buffering (maintaining specific body temperature)

than other butterfly species (Ashe-Jepson et al. 2023). Thermal buffering may be useful when

temperatures fluctuate, but is also associated with a narrower thermal niche, meaning that

higher temperatures may affect Papilionidae more negatively than other families (Ashe-Jepson

et al. 2023). This may indicate that climate change will affect populations of species in

Papilionidae in different ways than populations of species in other butterfly families. In

general, butterflies have a relatively narrow thermal niche compared to other, smaller insect

pollinators which may thrive at cooler temperatures that butterflies cannot tolerate (Kühsel

and Blüthgen 2015). However, the differences in family responses to temperature may be more

indirect; for example, bird species that eat animals decline in abundance with colder winter

temperatures while other bird species do not (Reif et al. 2010). Butterflies also have a wide

variety of diets, both as larvae and adults (Dyer et al. 2007, Krenn 2008, Opler and Krizek 1984).

If host plant abundance changes due to environmental change, butterfly populations may

respond in kind (Yamamoto et al. 2007). Future studies could explore the mechanisms behind

family specific responses to temperature and light, whether it be physiological or indirectly

caused, for example by diet.

Lycaenidae also expresses a family specific response to abiotic factors, as it is the only

family in the monthly surveys that decreases in abundance as weekly precipitation increases. In

studies taking place in the tropics, butterfly abundance increases due to precipitation events,

but this increase can lag behind precipitation events by two months (Grøtan et al. 2012). Yearly

precipitation can also increase overall butterfly abundance in temperate habitats (Robinson et

al. 2012). In contrast to these studies, our analysis examined the more immediate response of

butterflies to precipitation. Lycaenidae contains some of the smallest butterflies in our area, so

this family may be more sensitive to certain conditions than other families containing larger

butterflies (Spencer 2006, Bladon et al. 2020, Ashe-Jepson et al. 2023). It will be important to

determine if Lycaenidae are more greatly impacted by precipitation events, especially since

precipitation is predicted to increase at higher latitudes and decrease at lower latitudes in

current climate models (Trenberth 2011). Further research can explore the possible

physiological mechanisms that are disproportionally affecting Lycaenidae compared to larger

butterflies or those from other families.

Butterfly behavior also responded to environmental conditions. Unlike what we

observed for biweekly abundance, biweekly behavior was more strongly affected by

temperature and light, rather than time of year. Still, biweekly behavior and monthly

abundance both were affected by similar conditions. Behavioral surveys could be used in future

surveys as indicators of community health, if abundance and behavior respond to similar

factors. Other animals, including other pollinators, change their behaviors seasonally (Vanak et

al. 2013, Heithaus et al. 1975, Toft 1980). We found a seasonal change in *basking*, a

thermoregulatory behavior. Like in our butterflies, seasonal behaviors in other ectotherms may

be related the thermoregulation (Mushinsky et al. 1980). In general, while behavioral changes

may result in changes to abundance of the study taxon (van Gil et al. 2009, Tuomainen &

Candolin 2011), there may be greater implications for other species in the ecosystem, especially

if the study taxon are important predators, prey, or competitors (DeGregorio et al. 2015,

Reviewed in Nagelkerken & Munday 2015). Surveying seasonal behavior may help describe

mechanisms behind behavioral change and in the future, predict changes in abundance.

The butterfly community at large responded behaviorally to changes in environmental

conditions, though this was only reflected in Nymphalidae at the family level. Nymphalid

behavior changed significantly in response to environmental factors: mainly temperature,

weekly precipitation, total irradiance and relative UV. In contrast to nymphalid abundance,

nymphalid behavior was not strongly affected by time of year. In our area Nymphalidae is the

most speciose family (Spencer and Simons 2006), so it could be that patterns of nymphalid

behavior are due to covarying shifts in nymphalid assemblages. An alternate hypothesis is that

the community changes its behavior in response to different environmental conditions, while

remaining relatively stable in composition. Many Nymphalidae species are sensitive to changes

in environmental conditions and exhibit seasonal wing colors and behaviors (Brakefield and

Reitsma 1991; Smith 1991; Davis 2009; McElderry 2016; Järvi et al. 2019). We suspect the

observed Nymphalidae-wide changes in behavior are probably due to both proposed

mechanisms: intraspecific plasticity and changes in community assemblage. However, since

different principal components are responsible for changes in behavior and abundance and

only abundance was affected by survey site, it is unlikely that changes in assemblage alone

cause changes in behavior. Future studies could target specific species to compare between

families and determine mechanisms. If butterfly families differ in response to light and

temperature conditions, this has important implications for butterfly conservation and

management strategies, especially if family specific differences are due to differing sensitivity

to environmental factors.

Conclusions:

We found that seasonal conditions affect both butterfly abundance and behavior. This

indicates that the degree to which communities are affected by seasonal change is not just a

matter of how many animals are present, but also what they are doing. Scale of sampling

affected our results: while temperature and light were better predictors of abundance for the

entire year during monthly sampling, this was not true when we surveyed animals biweekly

during the time of year that they were most abundant. Instead, survey week (a proxy for

unmeasured seasonal conditions) and temperature were better predictors of biweekly butterfly

abundance. Our data suggest that some butterfly families are more sensitive to ambient

environmental conditions than other others, a hypothesis that could be tested in future

comparative studies. Examining how seasonal conditions influence family specific responses in

behavior and abundance may help predict which groups of animals are most vulnerable as

climate change and habitat degradation cause abiotic factors to shift.

Acknowledgements

We thank all who participated in monthly surveys over the years of this project: Dylan Meyer,

Deonna Robertson, Timothy Sullivan, Peyton Rather, Abbigail Herzog, Brandon Allen, Gabriella

Agcoaili, Ciara Parenzin, David Ernst, Mallory Kim, Jarrod Varnell, Taryn Tibbs, Matthew

Murphy, Sushant Potdar, Yi Ting Ter, and Kiana Kasmaii. We thank Jessica Proctor for assistance

with data curation. Neelandra Joshi, Sarah DuRant, and Jeffrey Lewis provided thoughtful

feedback on early versions of these analyses. We thank the Botanical Gardens of the Ozarks for

allowing us to gather data on the premises, especially during lockdown. Thank you to the City of

Fayetteville for the use of Woolsey Prairie. Special thanks to Pooja Panwar for help locating

prairie field sites and for Joe Woolbright at Ozark Ecological Restorations and Arkansas Natural

Heritage Commission for permission to survey at Stump and Chesney respectively. This work

was funded by an Arkansas Game and Fish Commission Conservation Scholarship to GEH, a

Distinguished Doctoral Fellowship through the University of Arkansas to GEH, a University of

Arkansas Honors College Research Grant to AEA and ELW, and the University of Arkansas.

Data Accessibility Statement

538   Code used to run analyses reported in this article is available on github at XXXXXXX. Data are

539   available on Dryad XXXXXX

Supplemental Material

541   All other data presented within this manuscript are available above and as Supplemental

542   Materials.

Competing Interests

544   The authors declare no competing interests.

Literature Cited

Ashe-Jepson, E., S. A. Cobo, Y. Basset, A. J. Bladon, B. C. Laird-Hopkins, I. Kleckova, A. Mcfarlane,

et al. 2023. *Tropical butterflies use thermal buffering and thermal tolerance as alternative*

strategies to cope with temperature increase (preprint). Preprints.

Aphalo, P. J. 2015. The r4photobiology suite. UV4Plants Bulletin 2015(1): 21-29.

DOI:10.19232/uv4pb.2015.1.14

Bae, M.-J., and Y.-S. Park. 2019. Evaluation of precipitation impacts on benthic

macroinvertebrate communities at three different stream types. Ecological Indicators 102:446–

456.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using

lme4. Journal of Statistical Software 67(1): 1–48. doi:10.18637/jss.v067.i01.

Beirão, M. V., F. S. Neves, and G. W. Fernandes. 2021. Climate and plant structure determine

the spatiotemporal butterfly distribution on a tropical mountain. Biotropica 53:191–200.

Bladon, A. J., M. Lewis, E. K. Bladon, S. J. Buckton, S. Corbett, S. R. Ewing, M. P. Hayes, et al.

2020. How butterflies keep their cool: Physical and ecological traits influence thermoregulatory

ability and population trends. Journal of Animal Ecology 89:2440–2450.

Brakefield, P. M., and N. Reitsma. 1991. Phenotypic plasticity, seasonal climate and the

population biology of Bicyclus butterflies (Satyridae) in Malawi. Ecological Entomology 16:291–

303.

Brereton, T., D. B. Roy, I. Middlebrook, M. Botham, and M. Warren. 2011. The development of

butterfly indicators in the United Kingdom and assessments in 2010. Journal of Insect

Conservation 15:139–151.

Campuzano, E. F., G. Ibarra-Núñez, S. Machkour-M´Rabet, A. Morón-Ríos, and M. L. Jiménez.

2020. Diversity and seasonal variation of ground and understory spiders from a tropical

mountain cloud forest. Insect Science 27:826–844.

Cerda, X., J. Retana, and S. Cros. 1997. Thermal Disruption of Transitive Hierarchies in

Mediterranean Ant Communities. The Journal of Animal Ecology 66:363–374.

Checa, M. F., A. Barragán, J. Rodríguez, and M. Christman. 2009. Temporal abundance patterns

of butterfly communities (Lepidoptera: Nymphalidae) in the Ecuadorian Amazonia and their

relationship with climate. Annales de la Société entomologique de France (N.S.) 45:470–486.

Checa, M. F., J. Rodriguez, K. R. Willmott, and B. Liger. 2014. Microclimate Variability

Significantly Affects the Composition, Abundance and Phenology of Butterfly Communities in a

Highly Threatened Neotropical Dry Forest. Florida Entomologist 97:1–13.

Compton, T. J., W. Bodnar, A. Koolhaas, A. Dekinga, S. Holthuijsen, J. ten Horn, N. McSweeney,

et al. 2016. Burrowing Behavior of a Deposit Feeding Bivalve Predicts Change in Intertidal

Ecosystem State. Frontiers in Ecology and Evolution 4.

Courtney, S. P., C. J. Hill, and A. Westerman. 1982. Pollen Carried for Long Periods by

Butterflies. Oikos 38:260.

Dai, A., K. E. Trenberth, and T. R. Karl. 1999. Effects of Clouds, Soil Moisture, Precipitation, and

Water Vapor on Diurnal Temperature Range. Journal of Climate 12:2451–2473.

Davis, A. K. 2009. Wing Color of Monarch Butterflies (Danaus plexippus) in Eastern North

America across Life Stages: Migrants Are "Redder" than Breeding and Overwintering Stages.

Psyche: A Journal of Entomology 2009:1–5.

DeGregorio, B. A., J. D. Westervelt, P. J. Weatherhead, and J. H. Sperry. 2015. Indirect effect of

climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation.

Ecological Modelling 312:239–246.

Desmond, J. S., D. H. Deutschman, and J. B. Zedler. 2002. Spatial and temporal variation in

estuarine fish and invertebrate assemblages: Analysis of an 11-year data set. Estuaries 25:552–

569.

Dijkstra, J. A., E. L. Westerman, and L. G. Harris. 2011. The effects of climate change on species

composition, succession and phenology: a case study: CLIMATE CHANGE DESTABILIZES

COMMUNITIES. Global Change Biology 17:2360–2369.

Dyer, L. A., M. S. Singer, J. T. Lill, J. O. Stireman, G. L. Gentry, R. J. Marquis, R. E. Ricklefs, et al.

2007. Host specificity of Lepidoptera in tropical and temperate forests. Nature 448:696–699.

Fischer, K., and K. Fiedler. 2001. Spatio-temporal dynamics in a population of the copper

butterfly Lycaena hippothoe (Lycaenidae). Nota lepidopterologica 24:77–86.

Ghazanfar, M., M. F. Malik, M. Hussain, R. Iqbal, and M. Younas. 2016. Butterflies and their

contribution in ecosystem: A review. Journal of Entomology and Zoology Studies 4:115–118.

Grøtan, V., R. Lande, S. Engen, B.-E. Saether, and P. J. DeVries. 2012. Seasonal cycles of species

diversity and similarity in a tropical butterfly community. Journal of Animal Ecology 81:714–723.

Grundel, R., G. S. Dulin, and N. B. Pavlovic. 2020. Changes in conservation value from grasslands

to savannas to forests: How a temperate canopy cover gradient affects butterfly community

composition. PLOS ONE 15:e0234139.

Hawkins, B. A., and J. H. Lawton. 1995. Latitudinal gradients in butterfly body sizes: is there a

general pattern? Oecologia 102:31–36.

Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging Patterns and Resource Utilization

in Seven Species of Bats in a Seasonal Tropical Forest. Ecology 56:841–854.

Highland, S. A., J. C. Miller, and J. A. Jones. 2016. Determinants of moth diversity and

community in a temperate mountain landscape: vegetation, topography, and seasonality.

Houlihan, P. R., M. E. Harrison, and S. M. Cheyne. 2013. Impacts of forest gaps on butterfly

diversity in a Bornean peat-swamp forest. Journal of Asia-Pacific Entomology 16:67–73.

Ide, J.-Y. 2002. Mating behaviour and light conditions cause seasonal changes in the dispersal

pattern of the satyrine butterfly *Lethe diana*: Seasonal change in dispersal of a butterfly.

Ecological Entomology 27:33–40.

JMP®, Version 17.0.0. 2021. SAS Institute Inc., Cary.

Järvi, V. V., K. R. L. van der Burg, and R. D. Reed. 2019. Seasonal Plasticity in Junonia coenia

(Nymphalidae): Linking Wing Color, Temperature Dynamics, and Behavior. The Journal of the

Lepidopterists' Society 73:34.

Kennedy, Ashley C. 2019. *Examining Breeding Bird Diets To Improve Avian Conservation Efforts*.

University of Delaware.

Kleypas, J. A., J. W. Mcmanus, and L. A. B. Meñez. 1999. Environmental Limits to Coral Reef

Development: Where Do We Draw the Line? American Zoologist 39:146–159.

Kral-O'Brien, K. C., J. P. Harmon, and A. K. Antonsen. 2021. Snapshot observations demonstrate

within- and across-year weather related changes in butterfly behavior. Climate Change Ecology

1:100004.

Kühsel, S., and N. Blüthgen. 2015. High diversity stabilizes the thermal resilience of pollinator

communities in intensively managed grasslands. Nature Communications 6:7989.

La Sorte, F. A., and C. H. Graham. 2021. Phenological synchronization of seasonal bird migration

with vegetation greenness across dietary guilds. (J. Chapman, ed.)Journal of Animal Ecology

90:343–355.

Lazzari, M. A., S. Sherman, C. S. Brown, J. King, B. J. Joule, S. B. Chenoweth, and R. W. Langton.

1999. Seasonal and Annual Variations in Abundance and Species Composition of Two Nearshore

Fish Communities in Maine. Estuaries 22:636.

Le Roy, C., V. Debat, and V. Llaurens. 2019. Adaptive evolution of butterfly wing shape: from

morphology to behaviour. Biological Reviews brv.12500.

Liang, D., X. Pan, X. Luo, C. Wenda, Y. Zhao, Y. Hu, S. K. Robinson, et al. 2021. Seasonal variation

in community composition and distributional ranges of birds along a subtropical elevation

gradient in China. (J. Fischer, ed.)Diversity and Distributions 27:2527–2541.

McCabe, L. M., E. Colella, P. Chesshire, D. Smith, and N. S. Cobb. 2019. The transition from bee-

to-fly dominated communities with increasing elevation and greater forest canopy cover. (M. E.

Saunders, ed.)PLOS ONE 14:e0217198.

McDonald, A. K., and H. F. Nijhout. 2000. The effect of environmental conditions on mating

activity of the buckeye butterfly, Precis coenia. The Journal of Research on the Lepidoptera

35:22–28.

McElderry, R. M. 2016. Seasonal life history trade-offs in two leafwing butterflies: Delaying

reproductive development increases life expectancy. Journal of Insect Physiology 87:30–34.

Mushinsky, H. R., J. J. Hebrard, and M. G. Walley. 1980. The Role of Temperature on the

Behavioral and Ecological Associations of Sympatric Water Snakes. Copeia 1980:744.

Myers, M. C., B. J. Hoksch, and J. T. Mason. 2012. Butterfly response to floral resources during

early establishment at a heterogeneous prairie biomass production site in Iowa, USA. Journal of

Insect Conservation 16:457–472.

Nagelkerken, I., and P. L. Munday. 2016. Animal behaviour shapes the ecological effects of

ocean acidification and warming: moving from individual to community-level responses. Global

Change Biology 22:974–989.

Patten, M. A., and B. D. Smith-Patten. 2012. Testing the microclimate hypothesis: Light

environment and population trends of Neotropical birds. Biological Conservation 155:85–93.

Pellissier, L., N. Alvarez, A. Espíndola, J. Pottier, A. Dubuis, J.-N. Pradervand, and A. Guisan.

2013. Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in

the western Swiss Alps. Ecography 36:541–550.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for

Statistical Computing, Vienna. URL https://www.R-project.org/.

Robinson, N., S. Armstead, and M. Deane Bowers. 2012. Butterfly community ecology: the

influences of habitat type, weather patterns, and dominant species in a temperate ecosystem.

Entomologia Experimentalis et Applicata 145:50–61.

Rohde, A. T., and D. S. Pilliod. 2021. Spatiotemporal dynamics of insect pollinator communities

in sagebrush steppe associated with weather and vegetation. Global Ecology and Conservation

29:e01691.

Roubik, D. W., and J. D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae:

Euglossini) in Panama. Oecologia 73:321–333.

Sawyer, H., N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer

and energy development-Long-term trends of habituation and abundance. Global Change

Biology 23:4521–4529.

Scott, J. A. 1975. Variability of courtship of the Buckeye Butterfly, Precis coenia (Nymphalidae).

The Journal of Research on the Lepidoptera 14:142–147.

Simonson, S. E., P. A. Opler, T. J. Stohlgren, and Chong, Geneva W. 2001. Rapid assessment of

butterfly diversity in a montane landscape. Biodiversity and Conservation 10:1369–1386.

Smith, K. C. 1991. The effects of temperature and daylength on the rosa polyphenism in the

buckeye butterfly, Precis coenia (Lepidoptera Nymphalideae). Journal of Research on the

Lepidoptera 30:225–236.

Smith, L. M., and R. Cherry. 2014. Effects of Management Techniques on Grassland Butterfly

Species Composition and Community Structure. The American Midland Naturalist 172:227–235.

Song, X.-P., M. C. Hansen, S. V. Stehman, P. V. Potapov, A. Tyukavina, E. F. Vermote, and J. R.

Townshend. 2018. Global land change from 1982 to 2016. Nature 560:639–643.

Spencer, L.A. and D. R. Simons. 2006. *Arkansas butterflies and moths*. 2nd Ed. University of

Arkansas Press, Fayetteville.

Stavenga, D. G., and K. Arikawa. 2006. Evolution of color and vision of butterflies. Arthropod

Structure & Development 35:307–318.

Subedi, B., A. B. Stewart, B. Neupane, S. Ghimire, and H. Adhikari. 2021. Butterfly species

diversity and their floral preferences in the Rupa Wetland of Nepal. Ecology and Evolution

11:2086–2099.

Tiple, A. D., S. V. Padwad, L. Dapporto, and R. L. H. Dennis. 2010. Male mate location behaviour

and encounter sites in a community of tropical butterflies: taxonomic and site associations and

distinctions. Journal of Biosciences 35:629–646.

Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical

environment. Oecologia 45:131–141.

Toft, J. D., J. R. Cordell, C. A. Simenstad, and L. A. Stamatiou. 2007. Fish Distribution,

Abundance, and Behavior along City Shoreline Types in Puget Sound. North American Journal of

Fisheries Management 27:465–480.

Trenberth, K. 2011. Changes in precipitation with climate change. Climate Research 47:123–

138.

Tuomainen, U., and U. Candolin. 2011. Behavioural responses to human-induced environmental

change. Biological Reviews 86:640–657.

Turley, N. E., D. J. Biddinger, N. K. Joshi, and M. M. López-Uribe. 2022. Six years of wild bee

monitoring shows changes in biodiversity within and across years and declines in abundance.

Ecology and Evolution 12:e9190.

van Gils, J. A., C. Kraan, A. Dekinga, A. Koolhaas, J. Drent, P. de Goeij, and T. Piersma. 2009.

Reversed optimality and predictive ecology: burrowing depth forecasts population change in a

bivalve. Biology Letters 5:5–8.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013.

Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores.

Ecology 94:2619–2631.

Vives-Ingla, M., J. Sala-Garcia, C. Stefanescu, A. Casadó-Tortosa, M. Garcia, J. Peñuelas, and J.

Carnicer. 2023. Interspecific differences in microhabitat use expose insects to contrasting

thermal mortality. Ecological Monographs.

Vlašánek, P., Z. F. Fric, K. Zimmermann, D. Novotný, O. Čížek, I. Klečková, P. Vrba, et al. 2018. Do

Butterfly Activity Data from Mark-Recapture Surveys Reflect Temporal Patterns? Journal of

Insect Behavior 31:385–401.

Waltz, A. E. M., and W. W. Covington. 2004. Ecological Restoration Treatments Increase

Butterfly Richness and Abundance: Mechanisms of Response. Restoration Ecology 12:85–96.

Wettlaufer, J. D., A. Ye, H. A. MacMillan, and P. R. Martin. 2023. A test of the competitive

ability–cold tolerance trade-off hypothesis in seasonally breeding beetles. Ecological

Entomology 48:55–68.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, New

York.

Wittman, J., E. Stivers, and K. Larsen. 2017. Butterfly Surveys are Impacted by Time of Day.

Journal of the Lepidopterists' Society 71:125–129.

Wiwatwitaya, D., and H. Takeda. 2005. Seasonal changes in soil arthropod abundance in the dry

evergreen forest of north-east Thailand, with special reference to collembolan communities.

Ecological Research 20:59–70.

Wolda, H. 1978. Seasonal Fluctuations in Rainfall, Food and Abundance of Tropical Insects. The

Journal of Animal Ecology 47:369.

Wong, B. B. M., and U. Candolin. 2015. Behavioral responses to changing environments.

Behavioral Ecology 26:665–673.

Woods, J. N., J. Wilson, and J. R. Runkle. 2008. Influence of Climate on Butterfly Community and

Population Dynamics in Western Ohio. ENVIRONMENTAL ENTOMOLOGY 37.

Yamamoto, N., J. Yokoyama, and M. Kawata. 2007. Relative resource abundance explains

butterfly biodiversity in island communities. Proceedings of the National Academy of Sciences

104:10524–10529.

Zhang, X., M. A. Friedl, C. B. Schaaf, Alan H. Strahler, and A. Schneider. 2004. The footprint of

urban climates on vegetation phenology. Geophysical Research Letters 31:L12209.

Figure 1: Representatives of butterfly families surveyed including Hesperiidae (A), Lycaenidae (B),
Nymphalidae (C), Pieridae (D), and E) Papilionidae (E). F) Map of field sites in Arkansas.

Figure 2: Abiotic factors for monthly and biweekly surveys. Temperatures from a local regional airport from the hour closest to survey time for both monthly (A) and biweekly (B) surveys. Precipitation levels from a local regional airport from the week proceeding survey weeks for both monthly (C) and biweekly (D) surveys. Absolute irradiance measurements for monthly (E) and biweekly (F) surveys and relative UV measurements for monthly (G) and biweekly (H) surveys that were collected at field sites.

Figure 3: Effect of abiotic factors on butterfly abundance. A) Overall butterfly abundance increases as
PC1 (temperature and absolute irradiance vs relative UV levels) increases, but does not strongly

correlate with changes in PC2 (B) or PC 3 (C). Hesperiidae, Nymphalidae, and Pieridae abundance
increase with PC1 (D, J, P), but do not strongly correlate with PC2 (E, K, Q) or PC3 (F, L, E). Lycaenidae
abundance does not correlate strongly with PC1 (G) or PC2 (H), but decreases as PC3 (weekly
precipitation) increases (I). Papilionidae abundance did not correlate strongly with any PC (M-O).

Figure 4: Butterfly abundance by site. Woolsey had more butterflies in both monthly (A) and biweekly
(B) surveys.

Figure 5: Effect of PC1 (temperature vs survey week) on biweekly butterfly abundance but not
behavior. As PC1 decreases in biweekly surveys butterfly abundance decreases overall (A) and for
families Lycanidae (C) and Nymphalidae (D), but not for families Hesperiidae (B), Papilionidae (E), and
Pieridae (F). G) PC1 did not affect behavior.

788   **Figure 6: Effect of PC2 (year/temperature and absolute irradiance vs weekly precipitation and relative**
789   **UV levels) on biweekly butterfly behavior but not abundance.** Changes in biweekly butterfly

790   abundance do not correlate with changes in PC2 (A-F). However, as PC2 increases basking behavior

791   decreases overall (G) and in Nymphalidae (H).

PC1

# of Butterflies

A — All Families

B — Hesperiidae

C — Lycaenidae

D — Nymphalidae

E — Papilionidae

F — Pieridae

PC Values

G

Proportion of Butterflies

PC Values

Legend:
- Flying
- Nectaring
- Flushed
- Chasing
- Basking
- Mating
- Resting
- Courting
- Ovipositing
- Slow Fluttering

PC2

# of Butterflies

Flying
Nectaring
Flushed
Chasing
Basking
Mating
Resting
Courting
Ovipositing
Slow Fluttering