



Long-term population dynamics of an endangered butterfly are influenced by hurricane-mediated disturbance

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ABSTRACT

Effective species conservation requires understanding an organism's population dynamics and natural history, but long-term data are challenging to collect and maintain. As a result, conservation management decisions are frequently made using short-term data which are insufficient to accurately assess population trends in most species. For less-studied taxa, including most invertebrates, inadequate understanding of life and natural history impedes conservation efforts. Long-term studies are highly valuable for improving conservation decisions for target species as they serve as a model for other understudied species. We use mark-recapture data collected over 36 years to examine weather drivers of population patterns for a population of an endangered butterfly, Schaus' swallowtail (*Heracleides ponceanus*), and to enhance our understanding of its natural history. We show that the population size of Schaus' swallowtail was highly variable, ranging from under 100 to over 10,000 individuals. Population size was influenced by wind events and population size in the previous year. Population size was lower immediately following high wind events but was positively influenced by high wind events four years prior, with notable population increases following tropical cyclone events. This study reveals the potentially beneficial role of hurricane-mediated disturbance on Schaus' swallowtail populations potentially due to increased treefall gaps and the resulting shifts in plant communities. This remarkable data set represents one of the longest-term studies on a tropical insect and highlights the need for further study of tropical cyclone disturbance on insect populations.

1. Introduction

Understanding the long-term population dynamics and natural history of organisms is fundamental in ecology (Magurran et al., 2010; Siddig et al., 2016). In the face of global climate change and the current biodiversity crisis (Manes et al., 2021; McLaughlin et al., 2022), this information is critical to biodiversity conservation, especially for species which are already vulnerable to extinction (Nielsen et al., 2009). One conservation challenge, particularly for invertebrates, is a lack of understanding of the natural history of organisms that are under threat of extinction (Cardoso et al., 2011; Hochkirch et al., 2021). Conservation of

organisms with complex life histories, such as insects, requires comprehensive understanding of their natural history because different life stages often have disparate ecological niches (Wilbur, 1980; Nakazawa, 2015). Partial information about species life and natural history, for example knowledge of only one life stage (e.g. adult butterflies but not their caterpillars), leads to misinformed conservation decisions. For example, in the case of the large blue butterfly (*Phengaris arion* Linnaeus, 1758) in Europe, conservationists inadvertently excluded herbivores which are important to maintaining suitable habitat for the butterfly's obligate ant host when they erected fences to keep out human collectors of the rare butterfly (Thomas, 1980). The importance of herbivores was

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only revealed decades later through intensive ecological studies; this discovery was central to the success of reintroduced populations of this butterfly in Great Britain (Thomas et al., 2009). Similarly, conservation of St. Francis satyr butterfly (*Neonympha mitchellii francisci* Parshall and Kral, 1989) in North Carolina, USA, was impeded by a lack of understanding of the important role that habitat disturbance by fire played in the persistence of populations, which was revealed through long-term studies (Haddad, 2018). Both cases illustrate the importance of a deep understanding of natural history and ecological disturbance in species conservation.

The role of disturbance on the population dynamics of many organisms is notable, especially those which are adapted to and benefit from ecological disturbances such as fire, wind, or flooding (Hobbs and Huenneke, 1992). Insects are often especially sensitive to impacts from disturbance (Brown, 1997; Schowalter, 2012), including those deriving from climate change such as rising temperatures, changes in precipitation patterns, and the increasing frequency and severity of extreme weather events (Nielsen and Papaj, 2015; Forrest, 2016; Renner and Zohner, 2018). Due to their life history and dependence on plants throughout their life cycle, butterflies represent a group of insects particularly sensitive to and reliant upon ecological disturbances such as fire (Mason et al., 2021) and grazing (Vogel et al., 2007). Insect disturbance ecology is best understood for temperate taxa, but largely unknown for most tropical taxa despite the high diversity of tropical insects (Lamarre et al., 2020; Slade and Ong, 2023).

Tropical cyclones are an ecologically important form of disturbance that are projected to increase in severity in the Atlantic Basin due to anthropogenic climate change (Bender et al., 2010; Knutson et al., 2010; Walsh et al., 2016). The impact of tropical cyclones on insect communities is highly variable. This is particularly evident in coastal ecosystems which are vulnerable to habitat destruction and sea level rise

(Henry et al., 2020; Rippel et al., 2021). The influence of tropical cyclones on insect communities is well-studied at Luquillo Experimental Forest in eastern Puerto Rico, USA, where experiments on the role of disturbance from hurricanes as well as experimental forest gap creation have been ongoing since the 1980s (Shiels et al., 2015). Studies in this system demonstrate that long-term population dynamics of insects are determined largely by hurricane-mediated disturbance and subsequent forest succession (Shiels et al., 2015; Schowalter et al., 2021; Pandey and Schowalter, 2022). Other studies of insect communities following tropical cyclones corroborate findings from Luquillo; increases in insect abundance and diversity following tropical cyclones likely occur due to increased heterogeneity in forest structure and resulting increases in resources (e.g., new plant growth, increased floral abundance) (Mullany et al., 2018; Novais et al., 2018; Badon et al., 2022).

Southern Florida, USA, contains a mixture of Caribbean and continental North American flora and fauna and is one of few subtropical ecological communities in the continental United States (Myers and Ewel, 1990), with many plant and insect species colonizing South Florida from Cuba and the Bahamas (Peck, 1989; Gillespie, 2006). The Florida Keys, an archipelago located off the coast of southern Florida (Fig. 1A), comprises part of the Caribbean biodiversity hotspot, which has a high rate of endemism in a relatively small geographic area, along with high rates of habitat destruction and land use change (Myers et al., 2000). South Florida experienced dramatic land use change in the 20th century, with deforestation of upland habitats concentrated along the coast due to massive human population increases (Walker et al., 1997). The area also experiences regular impacts from tropical cyclones with a major hurricane occurring approximately every 30 years in this region and less severe storm events occurring in most years (Doyle and Girod, 1997).

Given the biogeographical context and high human development

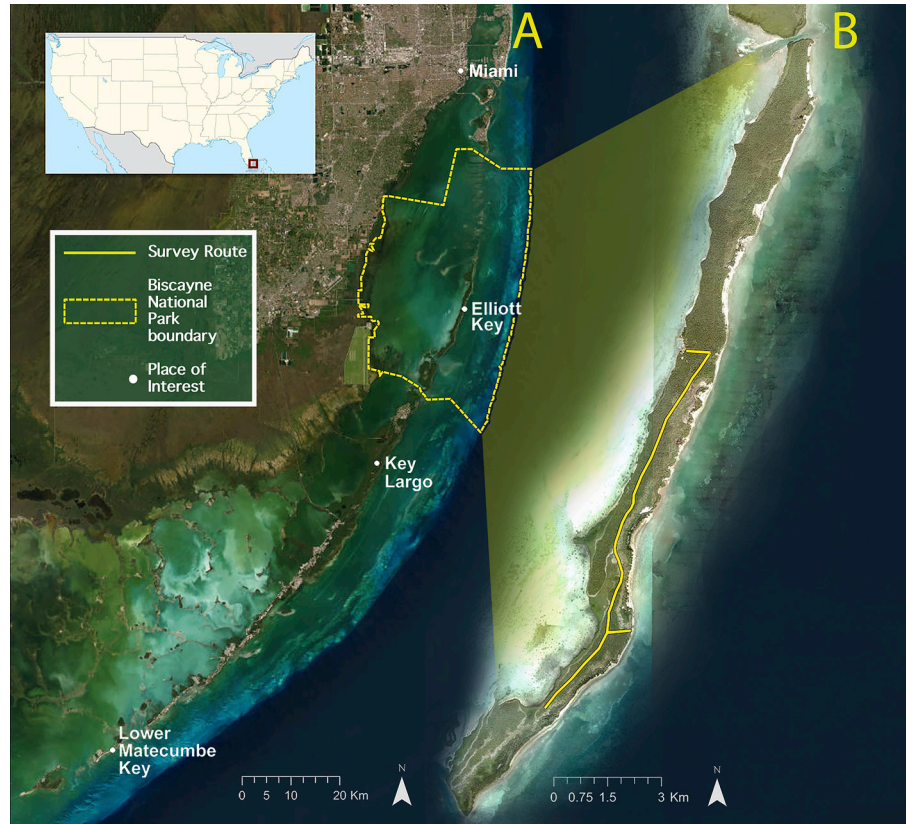


Fig. 1. (A) Map showing the historic range of Schaus' swallowtail butterfly. Schaus' swallowtail historically occupied hardwood hammocks from Miami to Lower Matecumbe Key but is only extant in northern Key Largo and several islands within Biscayne National Park. (B) Map showing the study site, Elliott Key and the linear survey route which covers much of the butterfly's habitat on the island. Imagery courtesy Esri and Wikimedia Commons.

pressure in South Florida, it is unsurprising that many of the endemic taxa in the region's forests are imperiled. These include charismatic mammals such as the Florida panther (*Puma concolor coryi*) and the Key deer (*Odocoileus virginianus clavium*), but also dozens of other species including plants, reptiles, small mammals, and invertebrates (Florida Natural Areas Inventory, 2010). Most endemic taxa in this region are dependent upon scarce freshwater resources and upland forests, including several insects listed as federally endangered: Bartram's scrub-hairstreak butterfly (*Strymon acis bartrami* Comstock and Huntington, 1943) (Emmel and Minno, 1993), Florida leafwing butterfly (*Anaea troglodyta florldalis* Johnson and Comstock, 1941) (Minno and Emmel, 1993), Miami tiger beetle (*Cicindelia floridana* Cartwright, 1939) (Brzoska et al., 2011), and Schaus' swallowtail butterfly (*Heraclides ponceana*) (Minno and Emmel, 1993).

In this study, we examine the population dynamics of a narrow-range endemic butterfly in the Florida Keys, USA, Schaus' swallowtail (*Heraclides ponceana* (Schaus, 1911) Zhang et al., 2020; Fig. 2A). We use *Heraclides ponceana* throughout this manuscript, though some prefer *Heraclides aristodemus ponceanus* (Schaus, 1911); these two names refer to the same entity. Using intensive monitoring data collected over a 36 year-long period on Elliott Key in Biscayne National Park (Fig. 1), we explore possible weather drivers of these patterns and aim to better understand the natural history of this butterfly. This study is likely the longest-term intensive monitoring effort for an imperiled tropical butterfly and is an apt study system for research on tropical cyclone disturbance on insect populations. These data are also central to informing ongoing conservation and recovery efforts for this endangered butterfly (U.S. Fish and Wildlife Service (USFWS), 2019).

2. Material and methods

2.1. Study species

Schaus' swallowtail is a federally endangered papilionid endemic to extreme southeastern Florida (USFWS, 1984, 2021). This species was once found from Miami, Florida to Lower Matecumbe Key, Florida (Fig. 1A). Since the extirpation of many populations in the early-mid 20th century due to habitat destruction and impacts from insecticides used for mosquito control (USFWS, 1984; Eliazar and Emmel, 1991), current extant populations are only found within the conservation lands of Biscayne National Park and Key Largo (USFWS, 2021). The butterfly is found in hardwood hammock forests (Fig. 2B), a type of seasonally dry subtropical forest which contain this species' larval host plants, *Amyris elemifera* L. and *Zanthoxylum fagara* (L.) Sarg., both of which are understory trees in the family Rutaceae (Wunderlin and Hansen, 2011).



Fig. 2. (A) A male Schaus' swallowtail butterfly (*Heraclides ponceana*) in habitat, perched on its primary larval host plant, sea torchwood (*Amyris elemifera*). Inset: A 5th instar larva everting its osmeteria, a defense mechanism. Photograph courtesy of Kristen Grace/Florida Museum (B) Typical Schaus' swallowtail habitat in our study area, consisting of subtropical hardwood hammock forest on Elliott Key along the Spite Highway trail.

Hardwood hammock forests occur at the highest elevations in the Florida Keys, areas that are most desirable for human development. This has resulted in the loss of most upland habitat across the butterfly's range (Karim and Main, 2009).

Schaus' swallowtail has one, or possibly two broods per year, with the greatest number of adults present in May and June, corresponding with the beginning of the wet season in South Florida (Loftus and Kushlan, 1984; Glassberg et al., 2000). While adults have been observed in August and September, it is unknown whether this represents a true second brood or sporadic asynchronous termination of diapause (Covell Jr, 1977; Loftus and Kushlan, 1984). The species has been documented to remain in pupal diapause for up to two years in field conditions (Loftus and Kushlan, 1984) and even longer in captivity under laboratory conditions (Daniels, unpublished data). Pupae also appear to be tolerant of sea water flooding and other seemingly detrimental impacts of disturbance (National Park Service (NPS), 2019).

2.2. Study site

Elliott Key (25.433, -80.202; Fig. 1B) is the largest island within Biscayne National Park; it is approximately 12 km long and 0.75 km wide and is composed of fossilized coral. Average elevation above sea level on Elliott Key is about 3 m, and maximum elevation is approximately 5 m (Klein, 1970). Several groups of indigenous people were known to inhabit this area by 8000 BCE; the island was later settled in the 19th century for pineapple cultivation (Brown Leynes and Cullison, 1998). A six-lane highway was planned for Elliott Key in the 1960s for which a seven-mile-long swath of forest was cleared. Further construction was halted in 1968 with the establishment of Biscayne National Monument, now Biscayne National Park (NPS, 2017). The remaining linear clearing is known as "Spite Highway" which is maintained by the NPS and serves as the transect for surveying Schaus' swallowtails.

2.3. Mark-release-recapture study

Surveys were conducted by trained observers along a 6 km section of trail (Fig. 1B) between 9:00 and 17:00, when butterflies were observed to be most active. Survey parties consisted of between one and four people traveling either on foot or in an all-terrain vehicle along the transect searching for, capturing, and marking butterflies. For each survey, the most experienced surveyor was designated the primary observer. Surveys were conducted between April and June, the main flight period for Schaus' swallowtail. In some years, additional surveys were conducted in August and September following new observations of butterflies during those months, though the number of observations was too small to include in this analysis. Surveys were not conducted during inclement weather. Between 1985 and 2021, researchers conducted 411 individual surveys, producing 23 years of mark-release-recapture data with a median of 10 survey days per year (range of 3–29 survey days per year). Some years have missing or low-quality data due to factors including equipment failure, personnel availability, and the COVID-19 pandemic.

Observers attempted to capture every Schaus' swallowtail sighted along the trail with an aerial insect net, though many butterflies evaded capture even by experienced surveyors. When captured, butterflies were carefully removed from the net and marked with a unique 3-digit ID number on the ventral surface of both hindwings using a fine-tip permanent marker. Data including sex, time of capture, and location were recorded for each capture and recapture event. For a subset of years (1986–2009), forewing length was also measured using digital calipers (Mitutoyo Corp., Illinois, USA). Butterflies were promptly released at the same location where they were captured or recaptured. Recaptured individuals were identified using the unique ID, and time and location of capture was recorded for each capture and recapture event. Butterflies seen but not captured were recorded, but not assigned a unique ID nor used in the analyses presented, since these observations could not be

linked to an individual butterfly.

Mark-release-recapture (MRR) models were fit for each year with recaptures in R version 4.2.3 (R Core Team, 2020) using the RMark interface (Laake, 2013) and Program MARK (White and Burnham, 1999). We fit POPAN models, a type of Jolly-Seber model, which themselves are an open population capture-recapture model capable of estimating population size (Schwarz and Arnason, 1996). The POPAN Jolly-Seber model estimates four parameters, (1) detection probability (p_t ; the probability of detecting an individual at time t if it is alive), (2) apparent survival (Φ_t ; the probability of an individual surviving to the next time step), (3) super population size (N_{super} ; the total number of individuals available to enter the study), (4) probability of entry through births and immigration (pent_t ; probability of new individuals from the super-population entering at time t). We included several potential covariates into estimating the probability of detecting an individual (p_t) to account for detection differences across male and female butterflies, differing expertise of surveyors, and survey effort. These covariates include the sex of the individual butterfly, the primary observer of a survey date, and the total number of butterfly species observed by the surveyors on a survey date (i.e., list length (Breed et al., 2013)). We included the sex of the individual butterfly as a covariate that could impact the estimation of the survival (Φ_t). We did not include any covariates in the probability of entry submodel (pent_t). Year-specific MRR models were selected based on AICc values (Burnham and Anderson, 2004). Two year-specific population estimates had confidence intervals far too large to be informative due to a lack of recapture data and these estimates were removed from further analyses. In total, we had 23 years with population estimates spanning 1985 to 2021 (Table S1).

2.4. Weather data

We obtained daily values of minimum and maximum temperature and precipitation values for Elliott Key from 01 January 1985–31 December 2021 from Daymet (Thornton et al., 2016). Daily wind speed values came from the second Modern-Era Retrospective analysis for Research and Applications (MERRA-2), a NASA atmospheric reanalysis with data available from 1980 (Global Modeling and Assimilation Office, 2015). MERRA-2 estimates surface wind speed (m s^{-1}) at two-hour intervals, which we aggregated to the maximum daily wind speed. We included temperature, precipitation, and wind covariates in our modeling framework used to estimate population dynamics. These covariates were selected based on our understanding of the species' biology and the literature indicating that weather impacts butterfly abundance and population dynamics (Roy et al., 2001; WallisDeVries et al., 2011; Mills et al., 2017).

Given the uncertainty of how weather affects Schaus' swallowtail (or other tropical butterfly) population dynamics, we used daily weather data to generate a variety of predictor variables that were included in exploratory models estimating potential drivers of population dynamics. Year-specific mean minimum temperature and mean maximum temperature values were calculated across three different time periods within a calendar year reflecting the times of year Schaus' swallowtail were expected to be in different life stages since weather variables partitioned by butterfly life stage have been demonstrated to impact survivorship and the subsequent abundance of adult butterflies (Santos et al., 2020; Konvicka et al., 2021). For each year, we averaged the daily minimum and maximum temperature over key time periods for adult butterflies (day of year [DOY] 121 to 212; i.e., May through July), larvae (DOY 91–181; i.e., April through June), and pupae (DOY 213–273; i.e., August through September). Year-specific precipitation values summed the daily precipitation accumulated over two time periods representing the wet and dry seasons. The wet season corresponds to May 15 through October 15 (DOY 135–288) on a non-leap year. The dry season corresponds to October 16 through May 14 (DOY 289_{y-1} and 134). For example, the dry season precipitation calculation for the year 2019

would sum the total precipitation accumulated from October 16, 2018 to May 14, 2019.

The two wind variables, maximum wind speed and extreme wind events, were quantified over the entire year. Maximum wind was calculated as the maximum daily wind speed observed in a year, and extreme wind events were calculated as the number of days in which the maximum daily wind speed exceeded 15 m s^{-1} , corresponding to frequent gusts that classify as a 'moderate' high wind threat level on the National Oceanic and Atmospheric Administration's wind threat categories (National Weather Service, 2023). Temporal lags in species' response to disturbance and conservation actions are common (Watts et al., 2020), so we also included time lags of weather variables as potential predictor variables in downstream modeling. For the temperature and precipitation variables, we included variables with a one-year lag ($t-1$), and for the wind variables, we included variables with up to a 4-year lag ($t-4$) since plant communities may take multiple years to recover following large hurricanes (Rastetter et al., 2021). All predictor variables were scaled to a mean of zero and standard deviation of one to facilitate the interpretation of their relative influence.

2.5. Statistical analysis

2.5.1. Modeling population dynamics

We fit exploratory (sensu Tredennick et al., 2021) generalized linear models using the negative binomial distribution to estimate potential drivers of Schaus' swallowtail population dynamics. In these models, we use the number of survey days as a weight in fitting our regression to give higher weights to years with more sampling effort. Our response variable in these models was the population estimate generated from the MRR model. Predictor variables were the temperature, precipitation, and wind variables described above. We fit all combinations of two-variable models using these variables to quantify the effect of these covariates on the estimated population size. We included a maximum of two predictor variables in our competing models to adhere to the 10 data points per predictor rule, because we were limited to 23 years with a population estimate. Residual diagnostic tests of the model with the lowest AICc were conducted to ensure that model assumptions were met (Fig. S1) and variance inflation factors (VIF) were calculated to ensure top models did not have problematic collinearity.

We also fit models to test the importance of density dependence on Schaus' swallowtail population dynamics. To do so, we first identified years with consecutive population estimates, which allowed us to include a population estimate of the prior year as a predictor variable. Given this data structure, we calculated a population growth rate parameter, instantaneous rate of population increase $r = \log(N_1/N_0)$; when N_0 = population size at time zero and N_1 = population size at time 1, which we used as the response variable for this set of models. In total we had 14 years with a population estimate that was also estimated for the year prior. Here, we built 3 competing two-variable models predicting population growth rate using the Gaussian distribution based on the two variables retained in the top population estimate model described above and also included the new density dependence predictor variable (population estimate at $t-1$). Residual diagnostic tests of the model with the lowest AICc were conducted to ensure that model assumptions were met (Fig. S2).

2.5.2. Modeling forewing size

To test if forewing size was influenced by weather conditions, we built a linear model with forewing size as a response variable using the following two continuous predictors: mean maximum temperature during the larval time period and precipitation during the wet season in the year prior. We also included butterfly sex as a categorical predictor.

3. Results

3.1. Population dynamics

The population estimates of Schaus’ swallowtail varied considerably over time, with the smallest population size estimated for the year 2007 (56 [95 % CI 41–77]), and the largest population size estimated for the year 1987 (11,360 [95 % CI 4505–28,673]). The population estimates did not show a consistent positive or negative trend through time (Fig. 3A). Males were nearly twice as likely to be captured as females (median p_t value across all years: 0.126 for males, 0.072 for females). Males also had a higher daily survivorship probability than females (median Φ value of 0.738 for males and 0.653 for females).

The top model estimating Schaus’ swallowtail population size consisted of two wind variables: maximum wind the previous year and maximum wind four years prior. This model strongly outperformed all other models with a model weight > 0.999 and an AICc value 22 below the second ranked model. These two wind variables affected population size differently depending on the temporal lag since the wind event occurred. Maximum wind in the previous year negatively impacted Schaus’ swallowtail population size, while population size was higher four years after a year with high winds (Fig. 4A).

The top model estimating variation in growth rate of Schaus’ swallowtail on Elliott Key consisted of the following two variables: population size the year prior (i.e., density-dependence) and maximum wind the previous year. Population growth rate from one year to the next was lower in years when population size was higher the previous year, indicating negative density-dependence (Fig. 4B). Growth rate was also

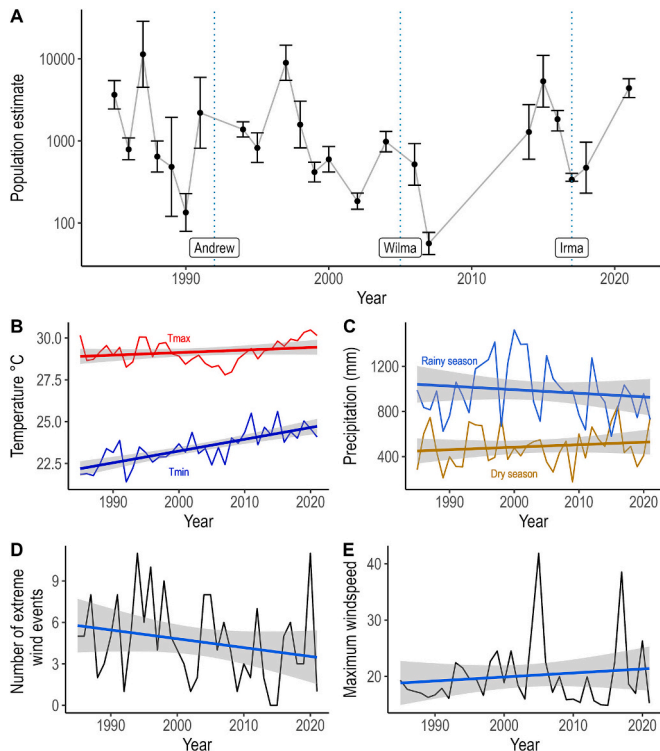
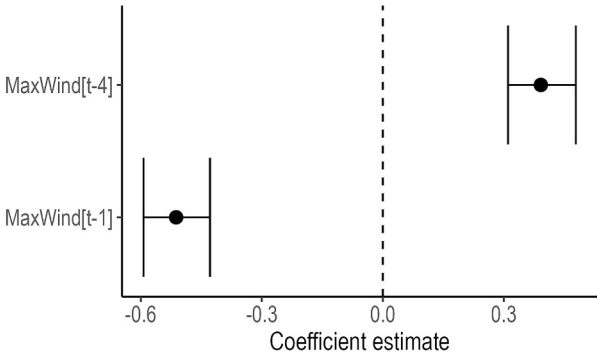


Fig. 3. Variation of Schaus’ swallowtail population estimates and weather variables from 1985 to 2021. Schaus’ swallowtail population estimates show large variation across years, but no significant trend (A). Maximum temperature during the larval stage has remained relatively consistent across our study period (red), but minimum temperature has been increasing (blue) (B). Wet season (blue) and dry season (bronze) annual precipitation (C), number of extreme wind events (D), and maximum wind speed (E) had large interannual variation but no long-term trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A) Population size



B) Growth rate

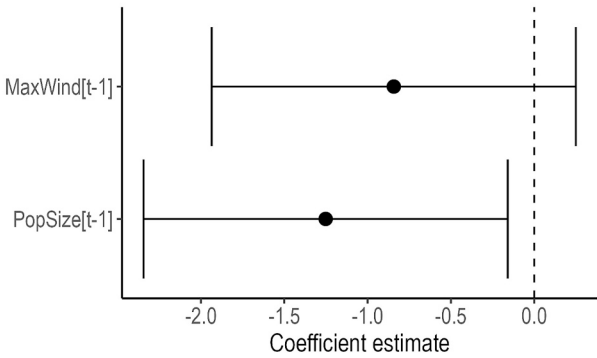


Fig. 4. Coefficient estimates and associated 95 % confidence intervals of top models predicting Schaus’ swallowtail population size (A) and population growth rate (B). DensityDependence refers to the population size the previous year. MaxWind[t-1] refers to the maximum windspeed the previous year and MaxWind[t-4] refers to the maximum windspeed four years prior. Predictor variables were mean centered and rescaled to have a standard deviation of one.

lower in years following a year with high winds, although this coefficient estimate encompassed zero (Fig. 4B, Table 1). Among the competing models, this top model had a weight of 0.77 and an $\Delta AICc$ value 2.77 below the second ranked model (Table 1). Our models provide evidence that density-dependence influences the growth rate of Schaus’ swallowtail, as the model without the density-dependent variable had a model weight of only 0.03 (Table 1).

3.2. Variation in forewing size

Sex, temperature, and precipitation were all important in estimating variation in Schaus’ swallowtail forewing length (Table S2). Schaus’ swallowtails are sexually dimorphic; female butterflies are larger than

Table 1

Model	$\Delta AICc$	Weight
DensityDependence (–1.25 95% CI –2.34, –0.16) + MaxWind [t–1] (–0.84 95% CI –1.93, 0.25)	0.00	0.77
DensityDependence (–1.14 95% CI –2.33, 0.05) + MaxWind [t–4] (0.34 95% CI –0.85, 1.53)	2.77	0.19
MaxWind [t–1] (–0.60 95% CI –1.98, 0.78) + MaxWind[t–4] (0.06 95% CI –1.13, 1.45)	6.37	0.03

males (male coefficient estimate -4.17 [95 % CI $-4.38 - -3.95$]; Fig. 5A). Our model estimating forewing length of individual butterflies found that forewings were smaller in years for which the larvae experienced warm temperatures (coefficient estimate -0.29 [95 % CI $-0.38 - -0.20$]; Fig. 5B). Our model results also estimate forewing length to be larger in years following more precipitation in the wet season the year prior (coefficient estimate 0.63 [95 % CI $0.54-0.73$]; Fig. 5C). Overall, sex was the most important variable in explaining variation in forewing length, while weather variables explained far less variation in forewing length ($R^2 = 0.03$ in a two variable model that does not include sex). Together, the three variable model had an $R^2 = 0.37$.

4. Discussion

The endangered Schaus' swallowtail is a flagship of insect conservation, as it was among the first butterfly species to be listed as under the Endangered Species Act in the United States and is a key umbrella species for tropical hardwood hammocks in South Florida. Our study leverages a remarkable dataset, likely the longest running mark-recapture dataset of any tropical butterfly, to provide ecological insights into species biology and population dynamics. We provide quantitative evidence of long-held speculations, including that females are larger than males, and uncover a complex response of Schaus'

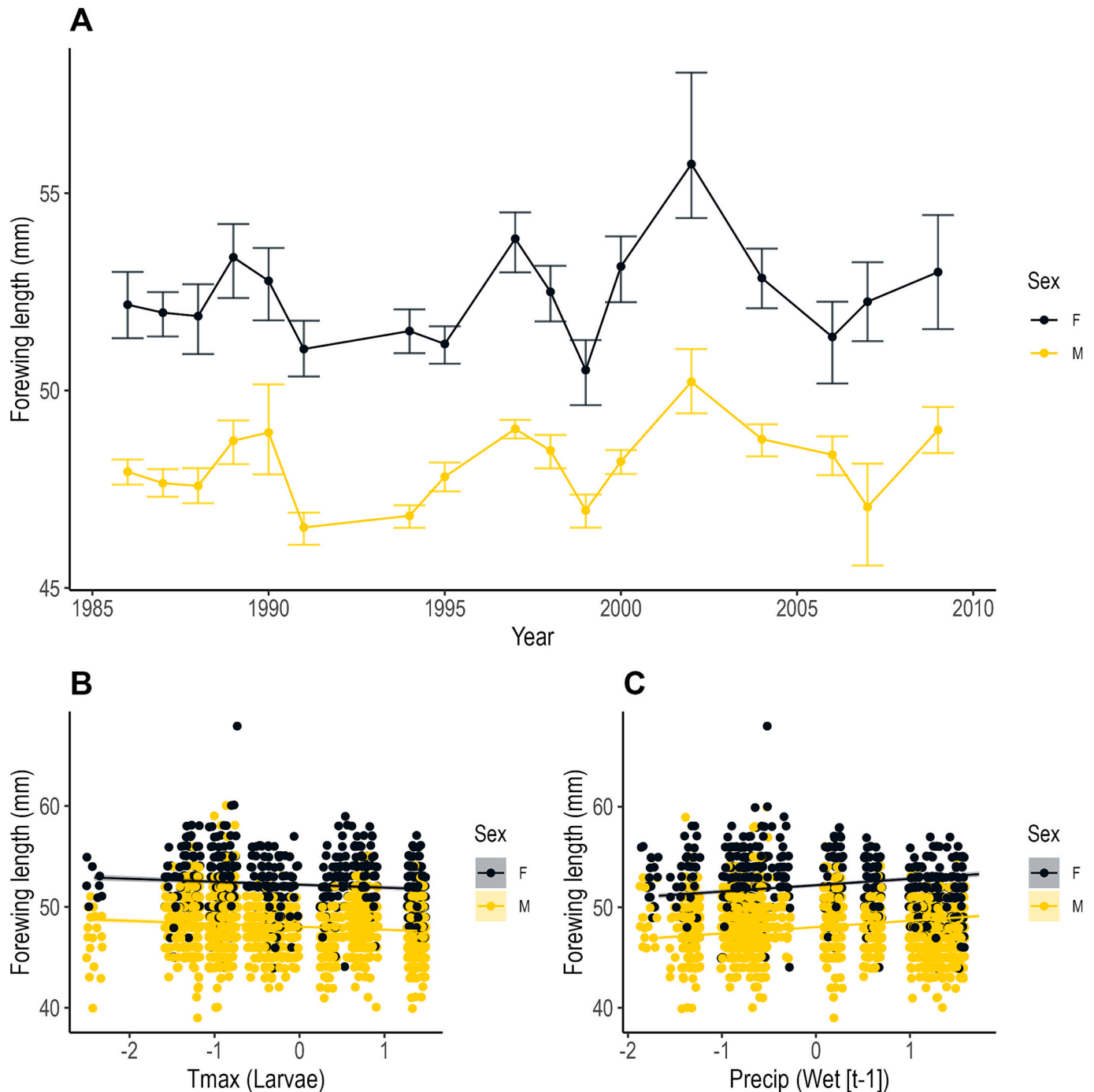


Fig. 5. Measurement of Schaus' swallowtail forewing length (and 95 % bootstrapped CIs) for a subset of study years (A). Model predictions show forewing length was smaller following warmer years during the adult larval stage (B), but forewing length was larger in years with more rain in the wet season the year prior (C). Females were on average larger than males. Points are jittered to show density of data.

swallowtail to hurricane-mediated disturbance. Specifically, we report evidence that high winds associated with tropical cyclones immediately decrease Schaus' swallowtail population size, but the longer-term effects of the disturbance leads to increases in population size several years following a tropical cyclone event.

The 36-year dataset reveals that this population of Schaus' swallowtail has been stable over the long term, which was only revealed due to the long-term nature of this study. Conclusions regarding population status and trend may have differed significantly had the study only been conducted for a subset of the whole dataset. In the short term, population size was highly variable, with population estimates ranging from under 100 individuals to over 10,000 individuals. Basing conclusions on only a few years would demonstrate 'the snapshot effect' in which population trend estimates can be greatly influenced by the choice of contemporary time-points (Didham et al., 2020). We echo the calls of others (Dolný et al., 2021; Hellmann et al., 2003) to interpret the results of population trends using short time-series data, especially for insects, with caution given the limited statistical power of such data.

This study demonstrates that the Elliott Key population of Schaus' swallowtail is highly resilient to both environmental and demographic stochasticity. Population dynamics are most influenced by population size in the previous year and high wind events in both the previous year and four years prior to butterfly data collection. The association of Schaus' swallowtail population dynamics with recent high wind events is perhaps to be expected since this butterfly is endemic to South Florida, a region that experiences frequent hurricanes (Doyle and Girod, 1997). During the study period analyzed, dozens of hurricanes tracked through southeastern Florida, with the most notable being Hurricane Andrew, a compact Category 5 storm that made landfall on Elliott Key in August 1992 with a sustained wind speed of 269 km/h. (National Oceanic and Atmospheric Administration, 2024). Hurricane Andrew was a devastating storm for Biscayne National Park, with virtually all large trees located in hardwood hammock forests defoliated and about 25 % windthrown or badly broken (NPS, 2019). Despite the enormous magnitude of this disturbance and likely mortality of butterflies due directly to high winds and storm surge as well as decreased resources in the months following Hurricane Andrew, population numbers rebounded only a few years later. Schaus' swallowtail abundance also responded to disturbance resulting from Major Hurricanes Wilma in 2005 and Irma in 2017 (Fig. 3A), which tracked further from Biscayne National Park (National Oceanic and Atmospheric Administration, 2024) but had large wind fields and impacted our study site with tropical storm force winds between 63 and 118 km/h (Pasch et al., 2006; Cangialosi et al., 2021).

One mechanism which could explain an increase in the population of Schaus' swallowtail several years following a hurricane is an increase in floral resources that result in increased nectar availability for adult butterflies. It is well-established that the high wind and heavy precipitation associated with tropical cyclones create treefall gaps which can result in higher local plant diversity (Lugo, 2008; Mitchell, 2013; Murphy et al., 2014; Shiels et al., 2015). In the 2–3 years after Hurricane Andrew at nearby study sites in Everglades National Park and elsewhere in the Upper Florida Keys, early successional woody and herbaceous species dominated previously closed-canopy hardwood hammock forests and understory trees flowered much more extensively than prior to the hurricane (Armentano et al., 1995; Ross et al., 2001). Although the impact of hurricanes on plant flowering and fruiting phenology is highly variable (Rathcke, 2000; Gandhi et al., 2007), one study showed an increase in flowering of a common understory shrub in southeastern Florida 2–3 years after Hurricane Andrew in hurricane-damaged populations, while nearby undamaged populations did not flower at all (Pascarella, 1998). Increased nectar resources result in higher butterfly survivorship and fecundity (Hill and Pierce, 1989; Boggs and Ross, 1993; Romeis et al., 2005); nectar can be a limited resource in nature (Schultz and Dlugosch, 1999; Erhardt and Mevi-Schütz, 2009). We believe this could be the case in the closed canopy forest habitat of

Schaus' swallowtail, where butterflies are frequently observed nectaring on the flowers of herbaceous plants along trails, treefall gaps, and other clearings with high light availability. Population decreases the year following high winds is likely due to increased mortality across all life stages from storm surge inundation and vegetation defoliation from high winds which decrease oviposition habitat and larval resources. Negative density dependence is common but not ubiquitous among Lepidoptera and other insects (Dempster, 1983; Stiling, 1988). In this case, negative density dependence could be explained by intraspecific competition (Nowicki et al., 2005; Flockhart et al., 2012) or parasitism (Daniels et al., 1993).

As we demonstrate here with Schaus' swallowtail, taxa in the Caribbean Basin are well-adapted to persist with frequent hurricane events (Schowalter et al., 2021). Global climate change is projected to increase the intensity of hurricane events in the Atlantic Basin (Bender et al., 2010) and sea level rise will exacerbate storm surge risk (Walsh et al., 2016). Although Schaus' swallowtail and other organisms that inhabit this region are clearly well-adapted to be resilient to tropical cyclone events (Donihue et al., 2018), ecological disturbance events can increase the risk of extinction for taxa with small and fragmented populations (Casagrandi and Gatto, 2002; Ovaskainen and Meerson, 2010), particularly for narrow-range endemics and taxa that are already endangered due to human factors (Goulding et al., 2016; Crain et al., 2019). This seems to be the case for endemic Caribbean birds such as the Puerto Rican parrot (*Amazona vittata*), which became endangered due to human factors (Snyder et al., 1987) while also suffering massive mortality after severe hurricanes (Beissinger et al., 2008; Martínez and Logue, 2020). The complexity of tropical cyclone disturbances and the interaction of disturbance from tropical cyclones and anthropogenic threats should be considered in the creation of conservation plans. Within the field of species and ecosystem management, tropical cyclones are often considered to be deleterious events (Maxwell et al., 2019). We recommend that conservation practitioners and managers consider the role of tropical cyclone events in their ecological context as disturbance events that have positive, negative, and neutral impacts on ecological communities, species, and populations. Continued efforts to understand the mechanisms of how tropical cyclones impact insect population dynamics could inform management actions.

This study provides valuable insights into the natural and life history of Schaus' swallowtail and substantiates many anecdotal observations made by researchers. We confirm sexual dimorphism in this butterfly, with females having a consistently larger forewing length than males. This female-biased sexual size dimorphism is common in arthropods and is generally attributed to the greater fecundity of larger females (Shine, 1989; Head, 1995; Teder and Tammaru, 2005). We also confirm the presence of adult butterflies in August and September. Although data were insufficient to understand population size of this second flight period, these observations raise the question of whether this butterfly could have two generations per year rather than one generation per year, as previously thought. Further exploration of the prevalence of a secondary flight period is warranted for this taxon.

Across the study period, males were nearly twice as likely to be captured as females, and the probability of recapturing males was also higher than the probability of recapturing females. This finding, combined with anecdotal observations of apparent patrolling behavior along the trail by males with individual males often sighted repeatedly at the same location, indicates that male Schaus' swallowtails are likely territorial; male territoriality has been observed in many other butterflies (Pinheiro, 1990; Merckx and Van Dyck, 2005; Lehnert et al., 2013). We conjecture that males may be patrolling the increased nectar flower resources available along canopy openings such as trails, which are attractive to foraging females, making males more likely to be encountered by researchers than females. When encountered, females often appeared to be searching for or evaluating host plants for oviposition. The primary host plant for Schaus' swallowtail is found throughout the forest in areas that are far from the trail and difficult to access due to the

thick vegetative growth which may account for the sex bias in captures.

As is common with data collected over multiple decades, survey effort was variable and dependent upon fluctuating funding. This resulted in some years with large confidence intervals surrounding population estimates and years for which population size could not be estimated. Across the entire study period, there were dozens of observers with varying levels of experience which led to differing capture rates between observers. Additionally, this butterfly is the subject of past and ongoing efforts to restore populations through releases of individuals head started under laboratory conditions. During 1995–97, over 1000 butterflies were released within Biscayne National Park, North Key Largo, Miami, and other locations within the historical range for Schaus' swallowtail. In 2014–21, over 1300 individuals were released in Biscayne National Park and nearby areas. To support these releases, several dozen individuals, usually larvae, were removed from the wild in the year prior to releases. We use an open population model to account for migration, but these releases may represent an additional source of uncertainty in population estimates. Many of the head started butterflies were released during the larval stage which are subject to a high rate of predation (Clayborn and Koptur, 2017), so the number of head started individuals that contributed to population estimates is likely much smaller than the total number released.

The persistence of the Schaus' swallowtail population on Elliott Key highlights the success of past and ongoing efforts to conserve and manage remaining butterfly populations and hardwood hammock forests within their range – critical conservation efforts particularly given the destruction of much of this habitat in the 20th century (Walker et al., 1997). Persistent efforts to control invasive plants found throughout forests within Biscayne National Park were likely beneficial to the conservation of Schaus' swallowtail butterfly due to the creation of canopy openings. Our study site, Elliott Key, supports what is likely the most robust population of Schaus' swallowtail across its range. Although population estimates on other islands within Biscayne National Park and on Key Largo have not been conducted, community science surveys of Key Largo indicate that Schaus' swallowtail's main host plant is less abundant than on Elliott Key and numbers of butterflies observed during Pollard transects are indicative of smaller populations in Key Largo than Elliott Key (unpublished data). This unprecedented continuous dataset spanning 36 years between 1985 and 2021 not only sheds light on the natural history and ecology of a charismatic and endangered insect; it also permits us to examine truly long-term population trends. Our dataset allows us to see the volatility of population dynamics while contextualizing them as that – volatility around a long-term stable population size and not true trends. This study underscores the role that tropical cyclone disturbance plays in species population dynamics. Although tropical cyclones occur across large areas of the planet, their role in shaping and maintaining tropical biodiversity is poorly understood, particularly for insects and other invertebrates. Since butterflies are comparatively data rich when compared to other insect groups, datasets on butterflies in areas impacted by frequent tropical cyclones represent an opportunity to further explore the effects of these natural disturbances on species of conservation concern as well as ecological communities.

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CRedit authorship contribution statement

Sarah R. Steele Cabrera: Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation. **Michael Belitz:** Writing – review & editing, Writing – original draft, Visualization, Software, Formal analysis. **Thomas C. Emmel:** Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Emily S. Khazan:** Writing – review & editing, Writing – original draft, Investigation. **Matthew J. Standridge:** Project administration, Investigation. **Kristin Rossetti:** Project administration,

Investigation. **Jaret C. Daniels:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data and code necessary to recreate results and figures (Belitz, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.13714961>. We have not included raw butterfly mark-recapture data because they include personal information of individual surveyors. Instead, we provide population estimates for each year that can then be used to recreate subsequent analyses.

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