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Life history variations and seasonal polyphenism in *Eumaeus atala* (Lepidoptera: Lycaenidae)

Sandy Koi^{1,*} and Jaret Daniels^{2,3}

Abstract

Insects are excellent indicator species for documenting changes in ecosystems and biodiversity, and south Florida is a recognized “hotspot” for hundreds of rare and endemic taxa. The capacity of native invertebrate species to adapt to changing ecological factors may be the dynamic that either strengthens their fitness or drives their extirpation or extinction. Variable life strategies may evolve that enable those taxa to persist, in spite of, or in response to, unstable or stochastic features in their changing ecosystems. Florida insects are subject to many extremes: drought, flooding, hurricanes, and high-wind tropical storms, as well as urban threats such as pesticide use and fragmented remnant habitats. The Atala, *Eumaeus atala* (Poey) (Lepidoptera: Lycaenidae), which was once believed to be extinct, is still considered to be an insect of conservation concern in southeast Florida for those reasons. In this study, environmental chambers were programmed to simulate the widely varying climatic conditions found in southeast Miami, Florida, to understand the ranges in the life history and development of the Atala. Results indicated that pupal and adult male polyphenism and variations in development time are determined by seasonal changes in temperature, humidity, and photoperiod; these factors may indicate stress-adaptive responses increasing pupal survival and male mating success.

Key Words: climate change; butterfly; Florida; pine rockland

Resumen

Las especies de insectos son excelentes indicadores para documentar los cambios en los ecosistemas y la biodiversidad, y el sur de la Florida es un “punto clave” reconocido por cientos de taxones raros y endémicos. La capacidad de las especies de invertebrados nativos para adaptarse a los factores ecológicos cambiantes puede ser la dinámica que fortalece su desempeño o dirige su extirpación o extinción. Pueden desarrollarse estrategias de vida variables que permitan a esos taxones persistir a pesar de, o en respuesta a, características inestables o estocásticas en sus ecosistemas cambiantes. Los insectos de la Florida están sujetos a muchos extremos: sequía, inundaciones, huracanes y tormentas tropicales de alto viento, así como amenazas urbanas como el uso de pesticidas y los hábitats remanentes fragmentados. El Atala, *Eumaeus atala* (Poey) (Lepidoptera: Lycaenidae), antes considerado extinto, todavía se considera un insecto de la preocupación de la conservación en el sureste de la Florida por esas razones. Las cámaras ambientales fueron programadas para simular las condiciones climáticas muy variadas que se encuentran en el sureste de Miami, Florida, para comprender las amplias variaciones en la historia de vida y desarrollo de la Atala. Los resultados indicaron que el polifenismo de la pupa y del macho adulto y las variaciones en el tiempo de desarrollo están determinados por cambios estacionales en temperatura, humedad y fotoperiodo; estos factores pueden indicar respuestas adaptativas al estrés aumentando la sobrevivencia de la pupa y el éxito del apareamiento del macho.

Palabras Clave: cambio climático; mariposa; Florida; tierra rocosa de pino

Climate change, land-use alteration, human population growth and the anthropomorphic modifications that accompany these factors are sources of significant stress to indigenous biota (Hanski 1999; Hardy & Dennis 1999; Walther et al. 2002; Hanski et al. 2006; Algar et al. 2009; Gaston 2009; Thomas 2011; Lemes & Loyola 2013). Insects are excellent indicator species for documenting changes in ecosystems and biodiversity, environmental degradation, as well as the benefits of habitat restoration (Kremen 1992, 1994; McGeoch 1998; Thomas 2011; Gerlach et al. 2013); as their small size, short generation time, wide distribution, and immediate relationship to their surroundings make them respond quickly to changes in the environment (Noss 1990; Kremen 1994; McGeoch 1998; Peck et al. 1998; Gerlach et al. 2013).

Variable life strategies may enable taxa to persist in spite of, or in response to, unstable or stochastic features in their changing ecosystems, as well as determine their range and distribution (Walker 1986; Kingsolver 1995; Abrams et al. 1996; Brakefield 1996; Davis et al. 1996;

Fischer & Fielder 2002; Hanski et al. 2006; Gaston 2009; Thomas 2011; Xu et al. 2012). The capacity of native invertebrate species to adapt to changing ecological factors may be the driver that either strengthens their fitness, or leads to their extirpation or extinction (Hardy & Dennis 1999; Schultz et al. 2008; Thomas 2011). There are documented changes in dispersal and range records for many species (Blau 1981; Gaston 2009; Walther et al. 2002) because of environmental changes, which lead to variations in survival, size, and fecundity, as well as altered interactions within the interspecies community, such as avian migration and bud break, or senescence (Walther et al. 2002). Seasonal polyphenism, a change in larval, pupal or adult butterfly color, pattern or form, in response to changes in temperature, photoperiod, humidity, and other environmental factors, has been documented globally in many butterfly species (Shapiro 1976; Brakefield 1996), including *Polygonia c-album* Linnaeus (Wiklund & Tullberg 2004), *Eurema daira* (Godart) (Daniels 1999), and *Pontia occidentalis* (Reakirt) (Kingsolver

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1995). Beneficial aspects of seasonal polyphenism may include increased survival via thermoregulation, or cryptic coloration, as well as better mating success because of enhanced wing patterns in adults.

Many Florida butterflies are in serious decline due to a variety of factors (Schwartz et al. 1995; Minno 2010; IBWG 2011; Schweitzer et al. 2011; Minno 2012). Those that inhabit remnant natural areas such as pine rocklands, tropical hardwood hammocks, coastal salt marshes or other specialized niches, are particularly vulnerable (New 1993; Dennis et al. 2004; Minno 2010; Schweitzer et al. 2011; Minno 2012). Lycaenids are especially sensitive to micro-habitats in their specialized biomes because of their extreme vulnerability to changes in temperature, humidity, host plant density, and other elements in their environment; furthermore, they exhibit complex relationships with their adult and larval food sources (New 1993). Stress-tolerant butterflies are able to persist or even thrive in spite of environmental degradation. The Atala butterfly, *Eumaeus atala* (Poey) (Lepidoptera: Lycaenidae), once thought to be extinct (Klots 1951) and still considered to be a species of special concern in Florida, has persisted in spite of climate change, extreme anthropomorphic landscape modifications in southeast Florida, and the consequent fragmented remnant natural habitats.

The Atala is a tropical species associated with pine rockland and tropical hardwood hammocks in southeast Florida, an area considered to be a “hotspot” for biodiversity (Myers et al. 2000). Both of these ecosystems are currently found in isolated remnant fragments. Pine rocklands are considered globally endangered (Snyder et al. 1990; USFWS 1999, 2015a,b; Miami-Dade 2014, undated). However, the Atala has increased its populations in Florida in recent years with assisted relocation programs into remaining natural areas as well as domestic gardens (Koi 2013; Koi & Daniels 2015; Koi & Hall 2016; Ramírez-Restrepo et al. 2016). While most of the federally endangered butterflies in southern Florida such as the Miami blue, *Cyclargus thomasi bethunebakeri* (Comstock & Huntington), the Schaus swallowtail, *Papilio aristodemus ponceanus* (Schaus), the Bartram’s scrub-hairstreak, *Strymon acis bartrami* (Comstock & Huntington), and the Florida leafwing, *Anaea troglodyta floridalis* (Johnson & Comstock), have remained confined to their historical ecosystems, the Atala has expanded its traditional habitats to include high-traffic urban parks and natural areas, as well as domestic and botanical gardens (Koi 2013; Koi & Daniels 2015; Koi & Hall 2016; Ramírez-Restrepo et al. 2016). The Atala is currently listed as imperiled by the Florida Wildlife Conservation Commission through the Imperiled Butterfly Work Group and is tracked by the Florida Natural Area Inventory. The Atala butterfly may exhibit extreme biannual crash-eruption cycles, establish ephemeral colonies, and periodically disappear from a site for years before suddenly re-appearing in what may indicate a classic chaotic pattern. It is still unknown whether every extant population now found in southeast Florida originated with the wild colony that was rediscovered off Key Biscayne in 1979, or if the meta-populations are occasionally re-stocked by deliberate or accidental immigrants from the Bahamas or Cuba, or if there were more remnant populations simply overlooked for many years in unknown refugia.

The Atala’s ability to utilize new territories in urbanized landscapes is aided in part by the increased use of its larval host plant, *Zamia integrifolia* L. (Zamiaceae), commonly known as coontie, in both private homes and developments as ornamental foliage. This is both a boon for the species and a potential problem for management of herbivory on the host plant. To its benefit, more colony locations help sustain a minimum population needed for dispersal between isolated and fragmented natural areas and for supporting genetic variability. Larger range areas could prove to be critical for species survival in the event of severe hurricanes or tropical storms, which have impacted

colonies in the past (Rawson 1961; Covell & Rawson 1973; Emmel & Minno 1993; New 1993; Davis et al. 1996; Platt et al. 2000; Minno 2011; NOAA 2015; Koi unpublished data).

However, increased host plant use may be problematic as the herbivory is often severe, leading to an increased need to manage herbivory for the health or aesthetics of the plant. While integrated pest management practices for protected species can be designed to control the insect without damaging the environment, the insect population or the plant (Culbert 1994; Pimentel & Hart 2001; Koi 2013), it is often challenging to successfully navigate management without negatively impacting one or another aspect of the biotic community (Pimentel & Hart 2001).

Re-introduction ventures in the past were limited (Rawson 1961; Covell & Rawson 1973; Emmel & Minno 1993; New 1993; Hammer 1995) and additional colony sites were unknown. Past re-establishment projects also were thwarted by hurricanes, such as Hurricane Donna in 1960 and Hurricane Andrew in 1992, both of which caused significant environmental and economic damage that was difficult to assess regarding the impact on imperiled butterfly populations in natural areas and pine rocklands (Davis et al. 1996; Platt et al. 2000; Minno 2011; NOAA 2015).

A re-location of Atala butterflies from erupting sites into Everglades National Park occurred between 2004 and 2008, and several other re-introductions have been attempted, but the butterfly has not persisted in that location (Koi unpublished data). New colonies also were distributed into privately owned sites, primarily using local conservation groups and butterfly clubs up to 2008. Currently, another re-location project is underway with help from Citizen Science volunteers, monitored by members of local butterfly clubs and native plant societies in Miami-Dade, Broward and Palm Beach counties (Koi unpublished data). Because there are sites, such as cycad gardens or commercial properties with cycads, where the Atala is not welcome because of the severe herbivory, these sites often request removal; other private home owners who wish to host the butterfly are contacted, and a transfer is made to the new location. This program has been in effect since 2004, and new locations are vetted to assure that there are adequate food resources for both larvae and adults (Koi 2008, 2013).

Climate change, environmental degradation and stochastic weather events affect the ecological stability and the range and distribution of the Atala butterfly. To address potentially beneficial or deleterious effects of changing temperatures on the butterfly, as well as to explore the possibility of an increased range and distribution, the effect of seasonal climate needed to be studied regarding life stage development time and mortality rate. Understanding the potential impact of seasonal stress to the butterfly’s overall fitness will help natural areas managers and home owners utilize the best strategies to optimize survival of introduced colonies.

Recently published research established that not only does the lifespan of the butterfly exceed previously known reports by weeks, there is a wide variation in the development duration of the life stages (Koi 2013; Koi & Daniels 2015; Koi & Hall 2015). To document better understanding of this butterfly’s life stages, these variable life history traits were monitored under controlled temperature, light and humidity levels programmed to simulate southeast Florida seasons. Results of this experiment will aid in determining optimal periods of the year for re-introduction objectives aimed at restoring the butterfly into previously inhabited sites. In addition, this research may act as a template for other imperiled southeast Florida taxa indigenous to pine rocklands, including the federally listed endangered Bartram’s Scrub-hairstreak and Florida leafwing (USFWS 2015a).

Materials and Methods

ORGANISM LIVESTOCK

Adults of *E. atala* reared from wild larval stock collected in south-east Florida from several sites on private property in Palm Beach, Broward and Miami-Dade counties were housed in a 182 cm² floor area flight cage (Greenhouse Castle Cage, LiveMonarch Foundation, Boca Raton, Florida) and allowed to oviposit freely on whole leaf fronds of their native host plant, coontie (*Z. integrifolia*). Coontie were maintained in a screenhouse located on the grounds of the Entomology and Nematology Department at the University of Florida (Gainesville, Florida) in ambient outdoor temperatures. Leaf fronds for ovipositing were collected and replaced in the cages daily. The flight cage for the adults was housed indoors in temperatures ranging from 24 to 26 °C, a relative humidity of 25 to 42% depending on season, and an approximately 8:16h L:D cycle that varied occasionally to 10:14 h L:D. Daylight lamps also were provided to encourage mating and ovipositing, programmed for cycles of 1 h on and 2 h off during the day. A fan, similarly programmed, helped project plant volatiles and mating signals between adults. See Koi and Daniels (2015) for further details on the rearing protocol.

Environmental chambers (Percival, Advanced Intellus, Environmental Controller, Perry, Iowa), housed at the United States Department of Agriculture (USDA) Agricultural Research Service (ARS) Invasive Plant Research laboratory in Gainesville, Florida (29.6513889°N, 82.3247222°W) were programmed to simulate south Florida seasonal variations in temperature, humidity, and daylight, based on mean values for 4 seasons obtained from archived weather data for southeast Miami for the years 2009 to 2011 (NOAA 2015). Chambers were set to characterize the seasons based on the first day of fall, winter, spring, and summer (Table 1). The winter chamber was re-programmed and used again for fall conditions the day after the winter experiments were completed.

Twenty five to twenty eight eggs were haphazardly chosen from host leaves in the flight cage from free-flying females and were deposited inside each environmental chamber daily. Although ovipositing females were not identified individually, because of the egg-laying pattern, clusters of eggs used in the experiment were likely laid from the same female; however, it is unlikely that every batch of approximately 25 eggs collected daily was from the same female(s), as the flight cage contained between 50 to 100 adult females. Eggs were collected sequentially for 5 d for each chamber so that each chamber housed at least 25 newly laid eggs as biological replicates in 1 d increments. Leaflets from the host plant fronds containing 25 to 28 eggs were placed into a 9 cm plastic Petri dish lined with grade 1 filter paper (Whatman[®] International, Ltd., Filter Papers No. 1, GE Health Care Companies, Maidstone, United Kingdom) cut to size and moistened with deionized water. Petri dishes were sealed with cotton string until the larvae emerged in order to maintain humidity and prevent larvae from escap-

ing. The Petri dishes were placed in the appropriate chamber within 30 min of collection. Each cohort of eggs was placed in a separate fabric cage measuring 30.5 cm² (Castle Cage Size JUMBO, LiveMonarch Foundation, Boca Raton, Florida), so that each chamber contained 5 cages as technical replicates, totaling at least 125 individuals per chamber (Fig. 1).

Broods were monitored every day from egg collection until adult emergence. Development stages were recorded and individuals were counted. Unhatched eggs were considered non-viable at 13 d post-installation, based on prior hatch rates in the laboratory, and removed from the cohort.

Enclosed larvae were housed in generic restaurant style clear plastic “deli boxes” (approx. 20 cm L × 20 cm W × 7.6 cm H) with hinged lids and lined with paper toweling, which was replaced daily, to preserve moisture and provide a clean substrate (Fig. 1). Larvae were given fresh host plant leaves from the screen house plant colony ad libitum. Deli boxes were confined within the fabric cages to prevent accidental escape and placed inside the appropriate environmental chamber. Deli box lids were kept closed until the larvae reached third instar to prevent loss of larvae and moisture, at which point the boxes were opened and larvae were allowed to wander within the confines of the fabric cages. Deli boxes were cleaned daily of frass (larval excrement). Larvae were counted and the development stage recorded before being returned to the chamber immediately after monitoring.

Emerged adults were sexed and the left forewing length was measured. Wing length was measured in a straight line from the basal sclerite on the left forewing from where it attaches to the thorax to the apex of the forewing.

Following quarantine protocols, all adults were immediately placed into glassine envelopes, euthanized in a -80 °C freezer and later fumigated with pesticide (methyl bromide) before being removed from the laboratory; voucher specimens were deposited in the collections of the McGuire Center for Lepidoptera and Biodiversity, University of Florida, Gainesville, Florida.

STATISTICAL ANALYSES

Statistical analyses included life table statistics, egg, larval and pupal development time (*t*-tests were used to compare cohorts), as well as adult wing length measurements, to determine differences under varying humidity, photoperiod, and temperature conditions in environmental chambers programmed to simulate southeast Florida seasonal climatic changes. Mean values were presented with the standard deviation (SD).

Results

The results presented are life table statistics and adult measurements. Development time varied significantly for all treatments except between the summer and fall chambers (Table 2). Summer and fall broods developed at nearly the same rates (*t*-test, *df* = 1, *P* < 0.390) and showed the highest brood survival (Table 2). There was no significant difference in sex ratio between the seasons, although slightly more adults successfully emerged in warmer seasons than in cooler seasons. All development stages took significantly longer in the spring chamber than any other chamber (Table 2) (*t*-test, *df* = 1, *P* < 0.001) and females in particular grew larger than in the other chambers (Table 3). Life tables (Southwood & Henderson 2009) showed a strong growth rate for all seasons (Tables 4–7). In all seasons, it took 4 generations for

Table 1. Temperature, photoperiod, and relative humidity (RH) were programmed in Percival Environmental Chambers to simulate South Florida seasonal variations for rearing *Eumaeus atala*.

Parameter	Summer	Fall	Winter	Spring
Temperature (°C)	26.9	28.9	23.6	23.0
Range	23.2–30.0	27.2–31.1	23.3–25.0	19.4–23.8
Photoperiod (L:D)	16:8	12:18	9:15	10:14
RH	76.3%	69.5%	71.9%	73.0%
Range	65–82%	59–79%	59–83%	58–97%

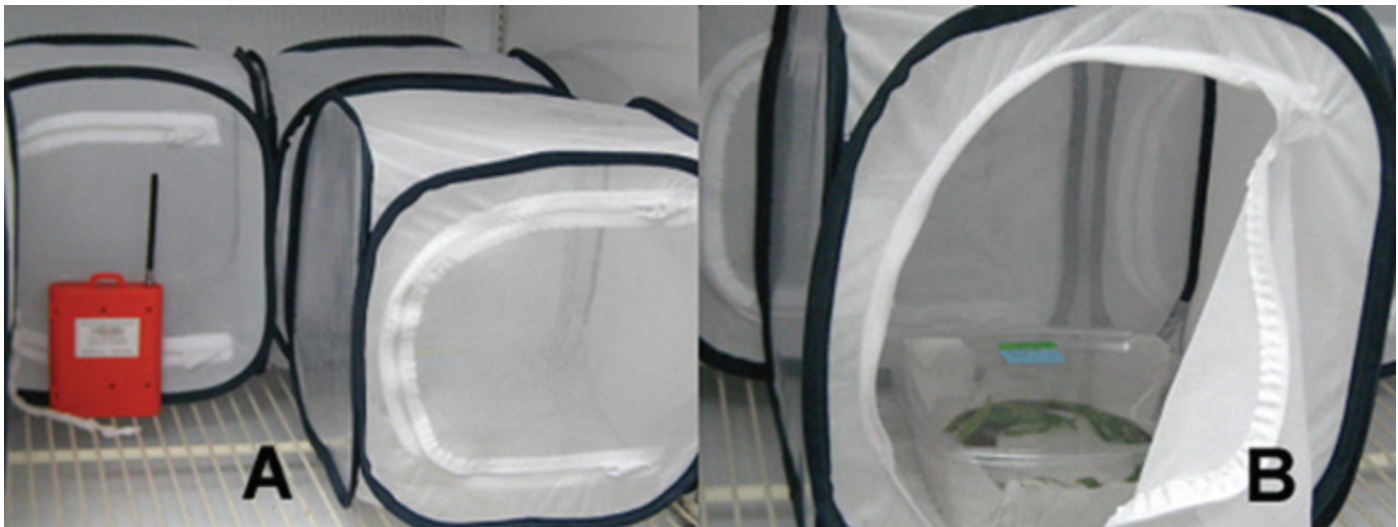


Fig. 1. Percival environmental chambers housing *Eumaeus atala*. A) Interior view of fabric housing cages in the Percival chambers and B) plastic 'deli-box' larval cages inside with host plant material and young *Eumaeus atala* larvae.

the population to experience an exponential growth rate of 94 to 98%. Temperatures in the chambers were monitored daily to match simulated southeast Florida temperatures as closely as possible (Fig. 2).

EGG AND LARVAL DEVELOPMENT

Survival plots of the egg stage (Fig. 3) display the beginning of a noticeable seasonal difference between summer to fall and winter to spring development. Each step in the graph represents the occurrence of hatching events in days. The y-axis steps indicate the proportion of unhatched individuals at that time. When the value on the y-axis is equal to zero this indicates that all the eggs have hatched, and shows that the summer eggs hatched first, the fall eggs hatched second, the winter eggs hatched third, and the spring eggs hatched last. A 99% confidence interval for life stage development in the different seasons is found in Table 8.

LARVAL DEVELOPMENT

Larval development (Fig. 4) displays an even greater discrepancy between the warm summer to fall seasons and cool winter to spring seasons. Each step in the graph represents the day after hatching at which time the larva became a pre-pupa (i.e., no longer a larva), not true mortality. In this graph, the last summer and fall larva pre-pupated between days 13 and 17 after hatching, while the last spring larva did not become a pre-pupa until day 19 after hatching. When the value on the y-axis is equal to zero this indicates that all the larvae became pre-pupa.

PRE-PUPAL AND PUPAL DEVELOPMENT

Pupal development (Fig. 5) displays an obvious visual difference between the development time of the summer to fall broods and that

Table 2. Development times of *Eumaeus atala* immature life stages under environmental conditions simulating southeast Florida seasons.

Season	Egg development (d)	Larval development (d)	Pre-pupae formation (d)	Pupal development (d)	Total development (d)	Number of Females	Number of Males
Summer	<i>n</i> = 125	<i>n</i> = 114	<i>n</i> = 84	<i>n</i> = 84	<i>n</i> = 84	43	41
Mean	6.55	11.15	2.17	12.23	31.87		
SD	1.21	0.86	0.86	0.86	0.84		
Range (d)	5–10	8–13	1–4	10–14	31–33		
Fall	<i>n</i> = 129	<i>n</i> = 110	<i>n</i> = 106	<i>n</i> = 106	<i>n</i> = 103	50	53
Mean	6.79	10.81	2.54	12.04	31.65		
SD	1.46	1.04	0.99	0.713	2.21		
Range (d)	6–12	7–12	1–3	11–15	30–35		
Winter	<i>n</i> = 125	<i>n</i> = 117	<i>n</i> = 87	<i>n</i> = 87	<i>n</i> = 87	49	38
Mean	8.67	14.85	3.80	15.67	42.81		
SD	1.07	0.73	0.68	1.00	2.14		
Range (d)	7–11	13–17	3–5	14–18	40–48		
Spring	<i>n</i> = 125	<i>n</i> = 115	<i>n</i> = 88	<i>n</i> = 88	<i>n</i> = 86	46	40
Mean	9.50	15.59	5.32	17.62	47.59		
SD	1.32	1.63	1.63	1.45	1.65		
Range (d)	8–13	13–19	2–8	14–20	44–53		

Total development (d) was equal to the adult emergence (d).

Significantly different development times were between fall and spring ($P < 0.0001$), fall and winter ($P < 0.0001$), winter and spring ($P < 0.0001$), and summer and spring ($P < 0.001$). Summer and fall showed no significant difference in development time ($P < 0.3895$).

Table 3. Wing length of *Eumaeus atala* females and males reared under environmental conditions simulating southeast Florida seasons. Sex ratio did not change seasonally, but male dorsal wing color varied.

Season	Wing cord length (cm) in females	Wing cord length (cm) in males	Wing cord length (cm) in blue males	Wing cord length (cm) in green males
Summer	<i>n</i> = 43	<i>n</i> = 41	<i>n</i> = 38	<i>n</i> = 3
Mean	2.37	2.37	2.24	2.23
SD	0.12	0.09	0.09	0.10
Range (cm)	2.1–2.6	2.0–2.4	2.0–2.4	2.1–2.3
Fall	<i>n</i> = 50	<i>n</i> = 103	<i>n</i> = 50	<i>n</i> = 3
Mean	2.40	2.23	2.23	2.30
SD	0.08	0.34	0.34	0.14
Range (cm)	2.2–2.5	2.0–2.4	2.2–2.5	2.2–2.4
Winter	<i>n</i> = 49	<i>n</i> = 38	<i>n</i> = 24	<i>n</i> = 14
Mean	2.51	2.28	2.28	2.36
SD	0.13	0.43	0.43	0.05
Range (cm)	2.0–2.7	2.2–2.5	2.2–2.5	2.3–2.5
Spring	<i>n</i> = 46	<i>n</i> = 40	<i>n</i> = 21	<i>n</i> = 19
Mean	2.60	2.39	2.39	2.39
SD	0.14	0.05	0.05	0.13
Range (cm)	2.2–2.7	1.9–2.5	2.1–2.5	1.9–2.5

Significantly different wing cord lengths in *Atala* were observed between fall females and males ($P < 0.000$), winter females and males ($P < 0.001$), and spring females and males ($P < 0.000$). There was no significant difference in the wing cord length between blue males and green males regardless of season. There was no significant difference between summer females and males.

Table 4. Life table of *Eumaeus atala* brood reared in an environmental chamber programmed to simulate Miami-Dade summer conditions. The generation time ($\Sigma lxbx/\Sigma lxbx$) was 4 and the growth rate ($r = \ln(Ro)/G$) was 0.9403.

Stage (x) ^a	<i>n</i> x ^b	<i>l</i> x ^c	<i>d</i> x ^d	<i>q</i> x ^e	<i>b</i> x ^f	$\Sigma lxbx$ (Ro) ^g	$\Sigma lxbx^h$
Egg (0)	125	1	11	0.088	0	0	0
Larva (1)	114	0.912	30	0.263	0	0	0
Pre-pupa (2)	84	0.737	0	0	0	0	0
Pupa (3)	84	1	0	0	0	0	0
Adult (4)	84	1	0	0	43	43	172

^aThe pooled number of individuals in each life stage wherein the analysis begins. For example stage (0) being the number of unhatched, newly laid eggs placed in each chamber.

^bThe number of individuals in that life stage.

^c*l*x is calculated by dividing the surviving number of individuals by survivors from the previous day and indicates the proportion of individuals surviving at the start of interval x.

^d*d*x is the number of individuals dying from x to x+1.

^e*q*x shows the mortality (*d*x/*n*x).

^f*b*x is the number of females per brood; males are not counted as females will determine the future brood size via fecundity/fertility and therefore the consequent growth of the colony.

^gThe sum of *l*x*b*x ($\Sigma lxbx$) determines the net reproductive rate (Ro) or number of daughters in the brood.

^hThe sum of *l*x*b*x*x* ($\Sigma lxbx^h$) is the projected generation time.

The generation time (G), the length of time between the birth of the parents and the birth of offspring, is calculated by dividing the projected generation time ($\Sigma lxbx^h$) by the net reproductive rate ($\Sigma lxbx$). In all seasons, the calculated generation time was only 4, which quickly leads to exponential growth in the equation ($r = \ln(Ro)/G$) to determine “r”, which is the rate of increase.

Table 5. Life table of *Eumaeus atala* brood reared in environmental chamber programmed to simulate Miami-Dade fall conditions. The generation time ($\Sigma lxbx/\Sigma lxbx$) was 4 and the growth rate ($r = \ln(Ro)/G$) was 0.9830.

Stage (x) ^a	<i>n</i> x ^b	<i>l</i> x ^c	<i>d</i> x ^d	<i>q</i> x ^e	<i>b</i> x ^f	$\Sigma lxbx$ (Ro) ^g	$\Sigma lxbx^h$
Egg (0)	129	1	19	0.147	0	0	0
Larva (1)	110	0.853	4	0.036	0	0	0
Pre-pupa (2)	108	0.982	0	0	0	0	0
Pupa (3)	106	1	0	0	0	0	0
Adult (4)	106	1	0	0	51	51	204

^aThe pooled number of individuals in each life stage wherein the analysis begins. For example stage (0) being the number of unhatched, newly laid eggs placed in each chamber.

^bThe number of individuals in that life stage.

^c*l*x is calculated by dividing the surviving number of individuals by survivors from the previous day and indicates the proportion of individuals surviving at the start of interval x.

^d*d*x is the number of individuals dying from x to x+1.

^e*q*x shows the mortality (*d*x/*n*x).

^f*b*x is the number of females per brood; males are not counted as females will determine the future brood size via fecundity/fertility and therefore the consequent growth of the colony.

^gThe sum of *l*x*b*x ($\Sigma lxbx$) determines the net reproductive rate (Ro) or number of daughters in the brood.

^hThe sum of *l*x*b*x*x* ($\Sigma lxbx^h$) is the projected generation time.

The generation time (G), the length of time between the birth of the parents and the birth of offspring, is calculated by dividing the projected generation time ($\Sigma lxbx^h$) by the net reproductive rate ($\Sigma lxbx$). In all seasons, the calculated generation time was only 4, which quickly leads to exponential growth in the equation ($r = \ln(Ro)/G$) to determine “r”, which is the rate of increase.

Table 6. Life table of *Eumaeus atala* brood reared in environmental chamber programmed to simulate Miami-Dade winter conditions. The generation time ($\Sigma lxbxx/\Sigma lxbx$) was 4 and the growth rate ($r=\ln(Ro)/G$) was 0.9780.

Stage (x) ^a	nx ^b	lx ^c	dx ^d	qx ^e	bx ^f	$\Sigma lxbx$ (Ro) ^g	$\Sigma lxbxx$ ^h
Egg (0)	125	1	8	0.064	0	0	0
Larva (1)	117	0.936	30	0.256	0	0	0
Pre-pupa (2)	87	0.744	0	0	0	0	0
Pupa (3)	87	1	0	0	0	0	0
Adult (4)	87	1	0	0	50	50	200

^aThe pooled number of individuals in each life stage wherein the analysis begins. For example stage (0) being the number of unhatched, newly laid eggs placed in each chamber.

^bThe number of individuals in that life stage.

^clx is calculated by dividing the surviving number of individuals by survivors from the previous day and indicates the proportion of individuals surviving at the start of interval x.

^ddx is the number of individuals dying from x to x+1.

^eqx shows the mortality (dx/nx).

^fbx is the number of females per brood; males are not counted as females will determine the future brood size via fecundity/fertility and therefore the consequent growth of the colony.

^gThe sum of lxbx ($\Sigma lxbx$) determines the net reproductive rate (Ro) or number of daughters in the brood.

^hThe sum of lxbxx ($\Sigma lxbxx$) is the projected generation time.

The generation time (G), the length of time between the birth of the parents and the birth of offspring, is calculated by dividing the projected generation time ($\Sigma lxbxx$) by the net reproductive rate ($\Sigma lxbx$). In all seasons, the calculated generation time was only 4, which quickly leads to exponential growth in the equation ($r=\ln(Ro)/G$) to determine "r", which is the rate of increase.

of the winter to spring broods. Each step in the graph represents the number of days after becoming a pre-pupa that the pupa eclosed as an adult. When the value on the y-axis is equal to zero this indicates that all pupae have become adults.

ADULT ECLOSURE

The last of the summer brood emerged first, between 13 to 16 d after the onset of pupation, and the last of the fall brood followed closely behind, eclosing 16 to 17 d after pupation. However, the last emergent in the winter brood did not eclose until approximately day 22 after pupation and the final spring emergent occurred on day 26 after pupation.

Pupae exhibit a seasonal polyphenism with summer and fall pupa developing a "warm honey brown" case with soft black speckles (Fig. 6). Winter and spring pupal cases displayed a heavily melanized integument and a darker brown casing (Fig. 6).

ADULT MEASUREMENTS

Male Atala adults exhibited seasonal polyphenism (Table 3 and Fig. 7), with cooler environmental conditions associated with a green color and warmer conditions associated with a blue color. The polyphenism may be partially explained by genetics and partly as a seasonal response, as green and blue males eclosed consistently at a 50:50 ratio

in the laboratory; however, broods often exhibited one color or the other. Green males eclosed more often in cooler seasons in the chambers than did blue males (Table 3).

Females were the largest in spring. The wing length did not vary significantly between females and males in the summer season but did vary significantly in the other 3 seasons ($P < 0.001$) (Table 3). There was no significant difference in wing length between the green males and blue males ($P < 0.855$).

Discussion

Plasticity in life history traits in all life stages is an important adaptive response to changing ecological situations, especially in species that inhabit harsh environments and stochastic weather patterns (Abrams et al. 1996; Fischer & Fiedler 2002). In this study, the Atala has displayed a wide variety of adaptive traits that are advantageous for its reproductive fitness and colony survival.

Within 1 generation, a summer Atala colony may experience a growth rate of 94% and has the potential to erupt into 3,612 individuals. We have seen eruptions of this type, with several thousand adult individuals in self-established wild colonies in southeast Florida (Koi unpublished).

Summer season butterflies had a 94% growth rate, fall butterflies showed a 98% growth rate, winter butterflies exhibited a 97% growth

Table 7. Life table of *Eumaeus atala* brood reared in environmental chamber programmed to simulate Miami-Dade Spring conditions. The generation time ($\Sigma lxbxx/\Sigma lxbx$) was 4 and the growth rate ($r=\ln(Ro)/G$) was 0.9521.

Stage (x) ^a	nx ^b	lx ^c	dx ^d	qx ^e	bx ^f	$\Sigma lxbx$ (Ro) ^g	$\Sigma lxbxx$ ^h
Egg (0)	125	1	10	0.08	0	0	0
Larva (1)	115	0.92	27	0.23	0	0	0
Pre-pupa (2)	88	0.77	0	0	0	0	0
Pupa (3)	88	1	0	0	0	0	0
Adult (4)	86	0.98	2	0.02	46	45.08	180.3

^aThe pooled number of individuals in each life stage wherein the analysis begins. For example stage (0) being the number of unhatched, newly laid eggs placed in each chamber.

^bThe number of individuals in that life stage.

^clx is calculated by dividing the surviving number of individuals by survivors from the previous day and indicates the proportion of individuals surviving at the start of interval x.

^ddx is the number of individuals dying from x to x+1.

^eqx shows the mortality (dx/nx).

^fbx is the number of females per brood; males are not counted as females will determine the future brood size via fecundity/fertility and therefore the consequent growth of the colony.

^gThe sum of lxbx ($\Sigma lxbx$) determines the net reproductive rate (Ro) or number of daughters in the brood.

^hThe sum of lxbxx ($\Sigma lxbxx$) is the projected generation time.

The generation time (G), the length of time between the birth of the parents and the birth of offspring, is calculated by dividing the projected generation time ($\Sigma lxbxx$) by the net reproductive rate ($\Sigma lxbx$). In all seasons, the calculated generation time was only 4, which quickly leads to exponential growth in the equation ($r=\ln(Ro)/G$) to determine "r", which is the rate of increase.

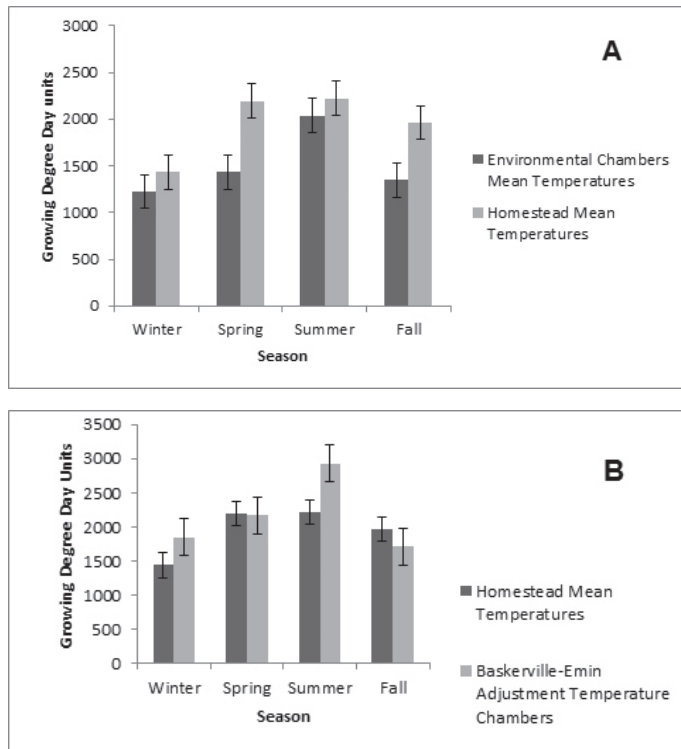


Fig. 2. Seasonal temperatures as programmed in environmental chambers. A) Temperatures in the chambers were programmed to match Homestead, Miami temperatures as closely as possible (see discussion) and B) degree-day units were analyzed using a Baskerville–Emin adjustment (see discussion). Bars indicate standard error.

rate, and spring butterflies displayed a 95% growth rate. Generations in all seasons had the potential to quickly exhibit exponential growth without such mitigating factors as host plant depletion, drought, predation, etc. There was a high mortality in the immature stages, with increased survival in late larval and pupal stages, with little variation between seasons.

The expansion in *Atala* ranges from what once were historic locations in Miami-Dade County to new self-established sites as far north as Martin County is probably related to climate change (Walther et al. 2002). At least one of these new sites is in a power line “right-of-way” area containing abundant host plants and weedy nectar resources. The populations at this site periodically erupt into thousands

Table 8. Development times (d) for *Eumaeus atala* life stages in environmental chambers programmed for southeast Florida seasons.

Stage	Season	Development (d)	99% CI
Egg	Summer	6.55	6.27–6.83
	Fall	6.79	6.45–7.13
	Winter	8.67	8.42–8.92
	Spring	9.50	9.19–9.81
Larvae	Summer	11.20	10.69–11.61
	Fall	10.80	10.55–11.07
	Winter	14.90	14.67–15.02
	Spring	15.60	15.19–15.99
Pre-pupae	Summer	2.17	1.92–2.42
	Fall	2.54	2.29–3.99
	Winter	3.80	3.61–3.99
	Spring	5.32	4.86–5.78
Pupa	Summer	31.63	31.63–32.11
	Fall	11.86	11.86–12.22
	Winter	15.39	15.39–15.95
	Spring	17.62	17.31–18.03

of adults. Ironically, the original *Atala* colonies were located in south Miami-Dade County, which is now a heavily populated city containing 2.7 million people (USCB 2016), with fragmented, and often degraded natural areas, which lack suitable corridors for natural dispersal. The butterfly has instead dispersed into domestic gardens containing its host plant. Between 2004 and 2008, thousands of *Atala* in all life stages were released into Everglades National Park, where there is abundant host plant and nectar, but there is little evidence that a viable colony ever persisted in the park (Koi 2013). However, there are colonies persisting in areas just a few miles north of the park in Homestead (Koi unpublished data), which is from where the climatic data used for the environmental chambers was taken.

The chambers followed the Homestead temperatures fairly well (Fig. 2A), but for analysis, the values were adjusted using the Baskerville–Emin formula, which compensates for possible discrepancies caused by lower on-going temperatures (Fig. 2B). The important factor in development is the “growing degree day”, which is the amount of growth that takes place under different temperature regimes. The standard formula is maximum temperature minus the minimum temperature squared, divided by the baseline temperature, which in normal circumstances has been determined as 10 °C. This is the temperature

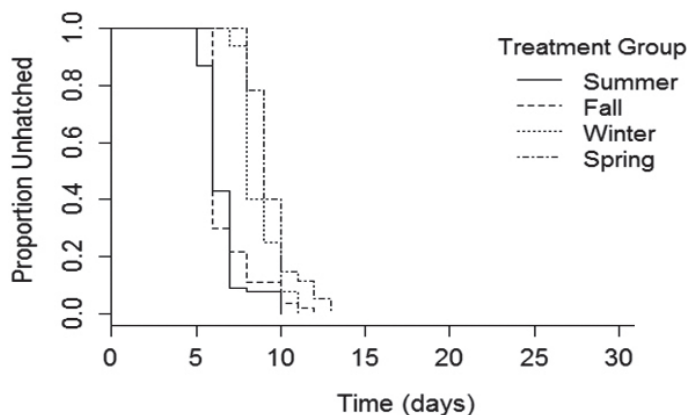


Fig. 3. *Eumaeus atala* egg development time (d) for different seasons is indicated by different line styles. A separation in development is starting to show between warm season (summer to fall) and cool season (winter to spring).

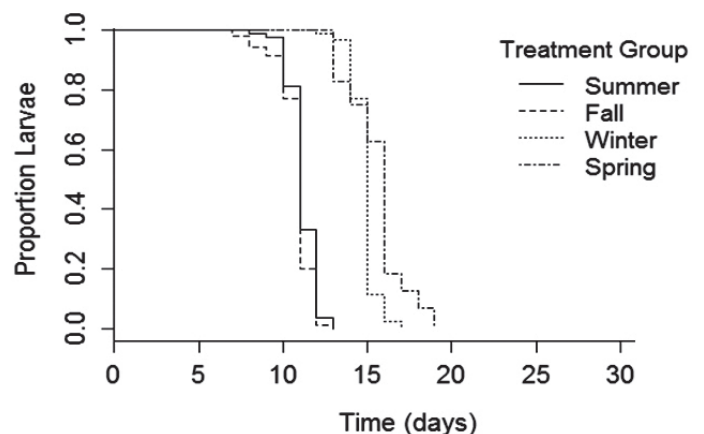


Fig. 4. *Eumaeus atala* larval development time (d) for different seasons is indicated by the different line styles. The separation between the warm season (summer to fall) and cool season (winter to spring) development is showing clearly.

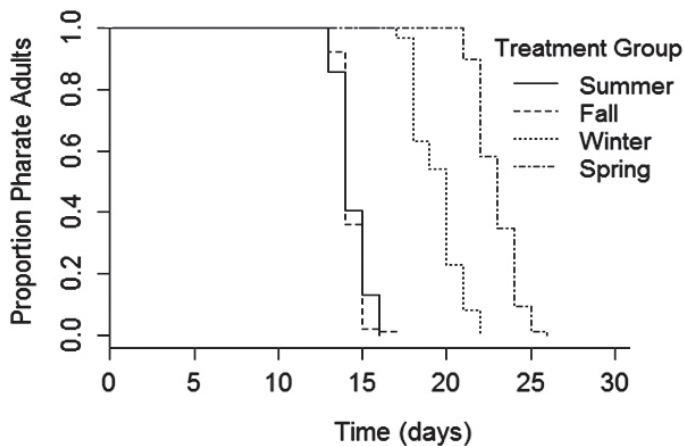


Fig. 5. *Eumaeus atala* pupal development time (d) for different seasons is indicated by the different line styles. Two distinct groups of development are present, the warm season (summer to fall) and cool season (winter to spring).

at which most insect development stops. However, in south Florida, the minimum temperature for which the winter chambers could be

programmed was 23 °C. However, the lowest temperatures in Homestead were much lower than 23 °C at 1.7 °C. Because the chambers could not be programmed that low, we adjusted the numbers for the comparison by using the actual lowest temperature for Homestead instead of the hypothetical minimum temperature for the generic baseline usually used.

Although chamber data show, for instance, that an egg will hatch between 6.27 and 6.83 d, there were eggs in the laboratory that hatched in 4.00 or 5.00 d, and conversely there were eggs in adverse colder outdoor temperatures that did not hatch for as long as 13.00 d. This variation was most likely an artifact of environmental factors as well as how well the eggs were provisioned by the female (Blau 1981; Abrams et al. 1996; Fischer & Fiedler 2002).

Seasonal polyphenism is a combination of the effects of temperature, photoperiod, and humidity. This experiment was not designed to tease out the effects of the separate factors. Polyphenism is seen in many species of butterflies (Shapiro 1976; Kingsolver 1995; Brakefield 1996; Daniels 1999; Wiklund & Tullberg 2004; Daniels et al. 2012) and performs in different ways. It may be a mating signal, with the color indicating the species' mating season, and may be particularly important for univoltine species recognition where the season is short and mating must be accomplished without hesitation. Darker colors, such

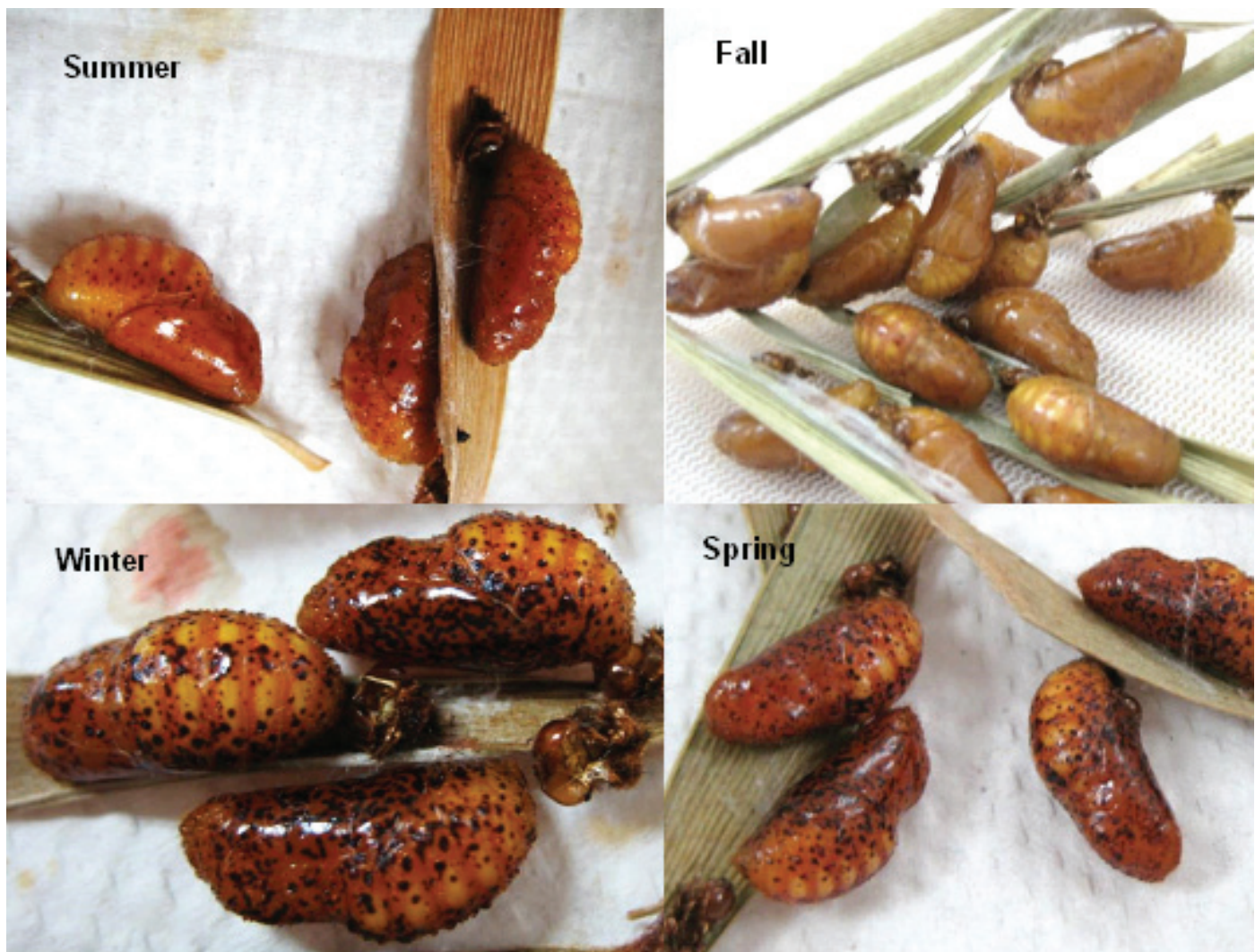


Fig. 6. Polyphenism in *Atala*, *Eumaeus atala*, pupae. Increased melanization is associated with cooler temperatures. All pupae were 10 d old when the photographs were taken.



Fig. 7. Seasonal polyphenism in the dorsal wing color of male Atala, *Eumaeus atala*. Green (left photo) is predominantly found in cooler winter and spring south-east Florida temperatures.

as the melanization evident in the cooler season pupae, are strongly associated with increased absorption of sunlight in the shorter days of winter and spring, which affects thermoregulation and development.

In addition, the larger size of females in cooler seasons is related to the longer development time spent as a larva and pupa. A larger size is a distinct advantage for female Atala, as they are multivoltine, displaying consecutive and overlapping generations. A larger size female would be able to lay larger and more robust eggs, resulting in larger, more robust larvae, than a smaller female (Abrams et al. 1996; Daniels 1999; Daniels et al. 2012). Additionally, a larger size would allow for increased feeding, development of larger fat bodies and improved general health of the female, contributing to her overall fitness.

Because these butterflies were reared at a laboratory in a quarantine facility, they were euthanized soon after emergence, immediately after the necessary biological parameters were measured. It would have been interesting to follow the individuals to observe whether there were differences in the lifespan, and what the difference in mating success may have been between green or blue males, regarding male aggression and female preference.

Both the winter and fall programs were installed in the same environmental chamber (winter first, and then fall after the last winter adult emerged). This could have potentially affected the second program or the results may have been an artifact of the actual chamber programming itself. The chambers were not programmed to vary at all during the season, so the early settings remained in effect for the entire time frame. In the natural environment, the photoperiod, humidity, and temperatures would not only fluctuate by season but also daily. This was not accounted for in the chambers. If repeating this experiment we would re-program the settings to follow daily fluctuations to reflect previous temperature means for the week in another year. Ideally, a mean for the day for the entire 3 mo period could be programmed into the chambers and would give a much stronger data set. Nonetheless, the values recorded in the chambers are valuable in documenting the tremendous range in variability in Atala development rates. However, examining additional archived weather patterns from southeast Florida may show as much variability in weather patterns as the Atala has in life history strategies.

Seasonal changes do not take into account the other environmental factors that indirectly influence development, plasticity, survival, and fitness such as the urban heat sink (Dennis et al. 2004) that permeates most of southeast Florida, completely enclosing the biogeographical

“islands” of remnant pinelands, hammocks and wetlands. Southeast Florida has historically hosted farming communities around the remnant pinelands, but the landscape is changing drastically and natural areas are being squeezed out of existence by planned communities and developments. Although urbanization may help reduce potential run-off or drift from the agricultural use of chemicals (e.g., fertilizers, pesticides and herbicides), it may ultimately be as detrimental to the environment because of increased use of the same or similar chemicals by homeowners or commercial developments (Bortleson and Davis 1997; Salvato 2001; Hoang et al. 2011; Bargar 2012).

Urbanized areas, however, regardless of possible increases in artificial fertilizers, may be beneficial because there may be an increase in host plants and nectar resources. In the early 1980’s it was thought that the pine rocklands in Everglades National Park did not support coontie growth very well and that could explain why the introduced Atala have not persisted (Covell personal communication). Now that there are so many developments hosting a wide variety of non-native cycad host plants as ornamentals, and different nectar plants, this may have a direct influence on Atala fitness regardless of seasonal fluctuations in native flower abundance or the normal poor state of coontie in winter. Ornamental and exotic cycad installations in botanical and private gardens also have allowed the butterfly to persist in areas where native sources would be less than desirable for sustenance in the winter. Mechanistic factors such as these may act as drivers for Atala dispersal and persistence in urbanized areas rather than in historically occupied sites.

Dennis et al. (2004) states that having access to multiple host plants, including secondary host plants, increases species’ exposure to a wider variety of survival strategies, many of which may offer novel evolutionary paths and channels that could lead away from a specialist life style. “Loss of variability in host use with habitat loss implicates the reverse: vulnerability of species leads to extinction,” he concludes (Dennis et al. 2004). Season may play a less important role in the butterfly’s evolutionary tract than these other factors.

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