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9 Seasonal life history trade-offs in two leafwing
10 butterflies: delaying reproductive development increases
11 life expectancy
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23
24 **Abstract**
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26 Surviving inhospitable periods or seasons may greatly affect fitness. Evi-
27 dence of this exists in the prevalence of dormant stages in the life cycles of
28 most insects. Here I focused on butterflies with distinct seasonal morpholog-
29 ical types (not a genetic polymorphism) in which one morphological type, or
30 form, delays reproduction until favorable conditions return, while the other
31 form develops in an environment that favors direct reproduction. For two
32 butterflies, *Anaea aidea* and *A. andria*, I tested the hypothesis that the de-
33 velopment of each seasonal form involves a differential allocation of resources
34 to survival at eclosion. I assayed differences in adult longevity among sum-
35 mer and winter forms in either a warm, active environment or a cool, calm
36 environment. Winter form adults lived 40 times longer than summer form
37 but only in calm, cool conditions. The magnitude of this difference provided
38 compelling evidence that the winter form body plan and metabolic strategy
39 (i.e. resource conservatism) favor long term survival. This research suggests
40 that winter form adults maintain lowered metabolic rate, a common feature
41 of diapause, to conserve resources and delay senescence while overwintering.
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47 *Keywords:* Life history trade-off; seasonal life history; longevity;
48 reproductive diapause; resource allocation; *Anaea spp.*
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1. Introduction

In variable environments, survival of harsh conditions has the greatest impact on fitness, especially for short-lived organisms (Morris et al., 2008). The ability of organisms to store nutrients and energy can provide an important buffer against the difficulties presented by environments that change state on a temporal scale that is shorter than the lifetime of organisms. One important example is seasonality, a pattern in which the environment changes state on a regular basis each year. In response to seasonality, many insects are capable of entering into diapause or a similar dormant state in which they can endure periods of otherwise unsuitable conditions (Hahn and Denlinger, 2011). Diapause serves not only to allow insects to endure unsuitable conditions, but also synchronizes the life cycle with seasonal resource dynamics (Hahn and Denlinger, 2011). In addition to storing resources, diapausing insects can reduce their metabolism to conserve energy reserves (Hahn and Denlinger, 2011). Although diapause has typically received attention in temperate regions, where unsuitable conditions occur during the winter, diapause has also gained attention for its prevalence during summer (Masaki, 1980) and also among tropical species where dry seasons may restrict suitable conditions (Denlinger, 1986).

In this paper, I explored adult longevity in leafwing butterflies, genus *Anaea* (Nymphalidae). I focused on two leafwing species with broad geographic distributions, one from tropical latitudes, and the other from temperate latitudes. Co-occurrence of these *Anaea* in Texas provides the opportunity to compare seasonality between a tropical and temperate butterfly in a subtropical climate. There are two distinct seasonal forms of adult *Anaea* (Riley, 1980) that diverge in life history. Winter form adults develop in the fall and survive the winter to reproduce in the spring, while summer form adults develop in the spring and reproduce in the summer and fall (Riley, 1980). The development of each seasonal form is day length dependent (Riley, 1988a), so they do not represent genetic-based polymorphisms. These seasonal forms are morphologically (Riley, 1980) and physiologically distinct (Riley, 1988b), suggesting the differential allocation of resources to survival and reproduction. Summer form *Anaea* are reproductively viable as early as two days following adult emergence, while winter form individuals are reproductively non-viable for at least one month after emerging (pers. obser., Riley, 1988b).

Many butterflies depend on the resources acquired as caterpillars (Boggs,

1997), meaning the energy budget is set before eclosing as adults. Thus resource allocation to survival and reproduction has typically been evaluated simply by the pattern of resource distribution throughout the bodies of adults at eclosion. In general larger female butterflies allocate an increased proportion of both biomass and nitrogen to the abdomen for reproduction (Wickman and Karlsson, 1989), suggesting that when butterflies obtain sufficient resources to survive, any remaining resources are allocated to reproduction. However, in butterfly seasonal forms the allocation patterns differ in the proportion of resources invested in either survival or reproduction. An experiment comparing winter and summer forms in *Polygonia c-album*, a butterfly with similar life history to *Anaea*, found that winter form adults invested a higher proportion of resources to the thorax compared with the abdomen (soma versus reproduction) (Karlsson and Wickman, 1989). In other words, winter form adults allocate resources preferentially to survival. Summer form females invested a higher proportion of body mass and total nitrogen to the abdomen relative to the thorax (Karlsson and Wickman, 1989), representing preferential investment in reproduction. Within these seasonal forms there is a clear switch in investment strategies, but to evaluate whether or not this switch constitutes a trade-off, we need to evaluate the fitness cost.

A trade-off, by definition, is an observed negative association between life history traits that implies differential allocation of limited resources to one function vs another at particular times in the life cycle (Zera and Harshman, 2001). The observed allocation is expected to be the one that has the highest fitness, such that alternative allocations would have lower fitness (Stearns, 1989). For example if a species allocates all its energy to growth and survival during the early years, but allocates a substantial portion of energy to reproduction later in life, it is expected that altering this allocation pattern, for example reproducing early, would result in lower fitness. The link between the preferential investment in the abdomen and fecundity has been well established across insects, with increased abdomen size resulting in increased fecundity (Garca-Barros, 2000; Karlsson and Wickman, 1990; Wickman and Karlsson, 1989). However, increased life expectancy resulting from preferential investment in the somatic tissues has not been experimentally verified, although winter form butterflies do seem to live longer in nature. I asked if summer form adults are capable of achieving the same life expectancy if provided the same living conditions as winter form adults. Important to this question is the finding that preferential allocation of larval-obtained resources to the abdomen decreases in species that forage for nitrogen-rich food

as adults (Boggs, 1981). Several butterflies, including *Anaea* and *Polygonia* feed on potentially nitrogen rich foods, e.g., rotting fruit, fermenting sap, or dung (Scott, 1992). If resources are not limiting, then how important is the preferential investment in reproduction over survival at eclosion if adult feeding can balance resource needs?

I tested the hypothesis that the development of each seasonal form involves differential allocation of resources to survival at eclosion, which will result in differences in life expectancy. Using the fact that the development of each seasonal form is photoperiod dependent (Riley, 1988a), I created each seasonal form in the laboratory. I recorded adult size at eclosion and measured the time to death for each adult under two experimental living conditions. I subjected adults of each seasonal form to either a warm, sunny environment that encouraged an active lifestyle similar to foraging adults in the summer, or to a cool, calm environment that encouraged inactivity of individuals similar to quiescence in winter. To remove resource limitation, I continuously supplied adults with fermenting bananas and water. I presumed that adult size at eclosion corresponds to the size of resource reserves and included size as a covariate in the analysis to control for differences in adult life expectancy due to adult size alone. I predicted summer form adults will survive better in the active conditions, and winter form adults will survive better when inactive. Further, I expected larger adults to live longer based on resource allocation patterns documented for *Polygonia* (Karlsson and Wickman, 1989). Although adult feeding and lack of reproductive activity in summer form adults might offset resource needs in favor of surviving, I expected that winter form adults would have longer life expectancy due to delayed reproductive development (Riley, 1988b).

2. Methods

I studied adult longevity for two leafwing butterflies *Anaea andria* and *A. aidea* (Nymphalidae), each from a different climate, temperate and tropical, respectively. *Anaea andria* (temperate leafwing) is distributed throughout the southeastern United States and *Anaea aidea* (tropical leafwing) is distributed throughout Central America (Scott, 1992). *Anaea* endure the winter as adults, as opposed to a majority of temperate butterflies that overwinter in a juvenile stage (Scott, 1992). *Anaea aidea* and *A. andria* exhibit two seasonal morphological types of adults called either winter and summer forms or dry and wet forms (Comstock, 1961). Day length regulates whether pupae

will develop into summer versus winter form adults with photoperiods of at least 14 hours and winter form adults with photoperiods no longer than 12 hours (Riley, 1988a).

115 2.1. Rearing of Butterflies

I collected *Anaea* caterpillars from natural populations in Gainesville, Florida and Austin, Texas, and transported caterpillars along with local host plants *Croton spp.* to Miami, FL where I established a captive *Anaea* population. In Austin, I collected caterpillars from the Brackenridge Field Laboratory (30°17'00"N, 97°46'44"W), and in Gainesville, I collected caterpillars from San Felasco Hammock Preserve (29°42'38"N, 82°27'04"W). I collected temperate leafwing from Gainesville and Austin, and tropical leafwing from Austin only on three separate occasions, April 2011, October 2012, and April 2013. The temperate leafwing was collected only from Gainesville in 2011 and in subsequent years only from Austin.

Once in Miami, I cultivated all host plants in a shade house at Fairchild Tropical Botanic Garden in Miami, FL. I placed wild-collected and captive-bred eggs and caterpillars along with the leaf or a sprig of the host where they were attached in petri dishes with moistened filter paper. Each caterpillar was segregated into a separate petri dish and provided leaf material from the host plant on which it was found. I checked all individuals each day and cleaned the petri dish and replenished leaf material as needed. I moved all new fifth instar larvae from 9 cm diameter petri dishes to 15 cm dishes. After each caterpillar pupated, I inserted a cylindrical mesh screen between the bottom and lid of the petri dish to create a small cage (15 cm height × 15 cm diameter). Adult butterflies emerged in these small cages still inside of the growth chamber and I provided each individual with a small puddle of water and fermenting banana mash for food (about 2 mL of each).

Caterpillars grew in a growth chamber (Percival Scientific I-35), under temperature conditions programmed to mimic natural conditions during the month of April. The temperature schedule in the growth chamber started each day with a slow increase from 20°C to 30°C over 7 hours after the lights turned on. After remaining at this warm temperature for three hours, the temperature then gradually dropped back down to 20°C in a series of steps over the next 10 hours. The temperature then remained at the minimum of 20°C, and then the diurnal cycle repeated. Average daily temperature was 24.85°C. The lighting schedule was constant for each cohort of caterpillars, but differed among cohorts to produce each seasonal form. I set

the photoperiod to 14L:10D to produce summer form adults and 12L:12D to produce winter form adults (Riley, 1988a). Cohorts were maintained in identical conditions to reduce the chance of spurious differences between cohorts. Sample sizes for summer and winter form adults, respectively, were as follows: temperate (24 and 11 females, 16 and 2 males) and tropical (41 and 41 females, 40 and 51 males) leafwings.

To test for differences in life expectancy, I subjected adults of each seasonal form to one of two experimental living conditions. Experimental conditions were meant to mimic either (1) the conditions endured by summer form adults that do not enter a quiescent state or (2) the conditions endured by winter form adults that are quiescent through the winter and become active in the spring. To encourage an active life style, I kept butterflies outside in a shade house to represent a warm, sunny (20% sunlight) environment where metabolism would be increased with warmth and activity, and individuals were free to fly in 1 m³ cages. Average summer temperatures in South Florida remain around 33°C, and about 200 mm of rain falls on average each month from May to October (Chen and Gerber, 1990). To encourage an inactive life style, I kept butterflies inside the cool, dim laboratory where metabolism would be decreased, and individuals were essentially unable to fly in the small cylindrical cages. Conditions in the laboratory remained fairly consistent with an average temperature of 22°C, and I provided a diurnal lighting schedule with a small full spectrum fluorescent light set to a 12L:12D photoperiod. Butterflies of both seasonal forms were isolated at all times, preventing mating which could alter the allocation of resources. I checked each individual every day, and supplied fresh water and fermenting banana mash as needed until all butterflies died.

2.2. Statistical analyses

I used accelerated failure-time regression to evaluate adult life expectancy, i.e., the number of days from eclosion to death, in response to age, leafwing species, seasonal form, sex, forewing length, and experimental living conditions. Accelerated failure-time models are generalized linear models for which a number probability distributions can be tested, each with a direct link to how the probability of mortality and the instantaneous risk of mortality changes with age (Fox, 2001). I evaluated the appropriateness of four probability distributions, and in doing so I tested three alternative hypotheses; mortality was constant over all ages (exponential), mortality increased or decreased monotonically (Weibull), or mortality increased to maximum at

some age then decreased (log-logistic and lognormal). To select among these probability distributions, I evaluated statistical significance of the scale parameter, which estimates the age effect on mortality (Fox, 2001), and also compared the values of each model's Akaike's information criteria (AIC), which estimates the fit of the model relative to the number of parameters used (Burnham and Anderson, 2002).

I used a backward stepwise regression approach to reduce the full model. The full factorial model had 33 parameters, which with 226 adults in this study means less than 7 data points contributed to each parameter estimate. In this process, I sequentially removed statistically non-significant parameters in steps, starting with higher level interaction terms, and repeated the process until no non-significant parameters could be removed. Lower level interaction parameters and main effects were not removed if higher level parameters that included these lower level parameters were significant. To cross-validate the results of step-wise model reduction, I evaluated the AIC values corrected for small sample size (AICc) of the model at each step.

Leafwing, seasonal form, sex, and experimental living condition were each categorical factors, and forewing length was a covariate. Forewing length was highly correlated with pupal mass ($\rho = 0.803$, $t = 17.03$, $df = 160$, $p < 0.001$). I preferred forewing length as a measure of adult size, because it better represented the quality of the adult at eclosion. To control for differences in starting quality, I standardized forewing length and used analysis of deviance of the best failure-time model to evaluate the effect of each factor at the mean forewing length. The fact that there were no significant interactions with forewing length made this approach possible, and enabled me to evaluate the effect of each factor and their interactions while holding constant the influence of adult size on life expectancy.

3. Results

The log-logistic probability distribution provided the best fit to the data (ΔAIC : exponential = 88, Weibull = 35, log-logistic = 0, lognormal = 41), indicating that mortality increased to a maximum at some age, then decreased. Using backward stepwise regression for model reduction, I excluded 22 non-significant interaction terms, and arrived at a model that included all factors and only four interactions. AIC model selection metrics supported this model with 65% likelihood relative to the other models in my stepwise approach (Table 1). Although forewing length explained only a fraction of

the deviance that seasonal form and living conditions explained, it did explain a statistically significant amount of deviance (Table 2). Larger adults lived longer on average, and this result was not dependent on any other factor, i.e., all interactions were non-significant; so I evaluated the effect of all other factors at the mean forewing length to control for size effects. The significant interactions terms: treatment $\times$ season, treatment $\times$ sex, and treatment $\times$ season $\times$ sex, indicated that differences in life expectancy between winter and summer seasonal forms and also between the sexes depended on the experimental living conditions (treatment in Table 2). The interaction between season and sex indicates that seasonal differences in life expectancy are sex dependent, and the lack of significant interactions including leafwing species indicates that the effects of these factors and their interactions do not differ between the temperate and tropical leafwings (Table 2).

Winter form adults had the longest life expectancy, outliving summer form adults by a factor of almost 40 (Figure 1). However, this only occurred in the cool, dim environment, where individuals were encouraged to be inactive. In the warm, sunny environment, where individuals were encouraged to be active, winter form adults had much lower life expectancy than summer form adults (Figure 1). There was a much smaller difference in life expectancy for summer adults between active and inactive living conditions than there was for winter form adults, but similar to winter adults, summer adults did live longer when encouraged to be inactive (Figure 1). This pattern was more pronounced for males than it was for females (Figure 1). Females lived longer on average, but had lower life expectancy than males when inactive and in the winter form. Tropical leafwing lived longer than temperate leafwing regardless of sex, seasonal form, or activity level (Figure 1), but this result was marginally significant.

4. Discussion

For butterflies with seasonal forms, winter (dry) season forms delay reproductive maturity to survive until breeding season conditions return in spring (Brakefield and Reitsma, 1991; Karlsson and Wickman, 1989; Torres et al., 2009). I experimentally verified for both *Anaea aidea* (tropical) and *A. andria* (temperate) that by delaying reproductive development, winter form adults do achieve much greater live expectancy than summer form adults that do not delay reproductive development. The maximum life span achieved was 466 days (oviposition to death). Fruit feeding butterflies have been shown

to have relatively long lives in nature with one individual observed living at least 293 days (Molleman et al., 2007). The great disparity in life expectancy between seasonal forms provides compelling evidence that the winter form body plan and metabolic strategy favors long term survival. Resources used for reproduction are not available for maintenance (Stearns, 1989; Zera and Harshman, 2001), and the fact that winter form leafwing delay reproductive maturity (Riley, 1988b) and increase life expectancy in doing so suggested that these resources were used for maintenance to survive.

My research also showed that adult feeding had little impact on the differences between seasonal forms, which seems contradictory to research showing increased life expectancy with high quality diets (e.g., Molleman et al., 2008a,b). Karlsson (1994) linked food quality with the change in thorax to abdomen as butterflies age, showing that aging *Heliconius hecale* increased in thorax and abdomen mass due to a nitrogen-rich diet of pollen, while two nectar feeders, *Parage aegeria* and *Speyeria mormonia*, decreased primarily in abdomen mass. However, restricted diet and mass were not predictors of life expectancy in *S. mormonia* in a study by Boggs and Ross (1993), which the authors suggest was due to decreased reproductive output to reallocate resources to survival. Similarly, (Molleman et al., 2008a) showed decreased life expectancy with increased reproductive rate for *Bicyclus anynana*, but Molleman et al. (2008b) did not find this cost for *Charaxes fulvescens*. My results demonstrated that adult feeding did not offset the cost of reproductive development paid by summer form adults. Winter form adults delayed this cost, and achieved greater life expectancy. The finding that adult size in my study was positively correlated with life expectancy suggests some reliance on stored resources obtained as larvae. However, life expectancy only changed a small amount relative to changes in adult size. A millimeter difference in forewing length predicted little more than an extra day of life on average, and the maximum difference in forewing length among adults was only 12 mm.

The energy budget of diapausing, aestivating, or quiescent adults responds to resource reserves, income, and conservation. The results reported here discount large effects of either reserves or income, but strongly support a difference in resource conservation. Differing morphology between seasonal forms already suggested different physiology, e.g. delayed reproductive development (Riley, 1988b), and the extreme difference in life expectancy between seasonal forms was striking. Summer form adults were simply unprepared to survive as long as winter form adults. The fact that this result was only

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9 true in a cool calm environment supports resource conservation, given that
10 warmer temperatures increase metabolism. Lower temperatures have been
11 linked to decreased resting metabolic rates for adults (Pijpe et al., 2007) and
12 greatly increases life expectancy (Bauerfeind et al., 2009; Hahn and Den-
13 linger, 2011; Wikström et al., 2009). Lowered metabolic rate decreases re-
14 source demands reducing the need to be active, which also conserves energy.
15 Insects have multiple physiological pathways for sensing resource reserves
16 (Hahn and Denlinger, 2011), and starvation as adults actually increases life
17 expectancy of fruit-feeding butterflies (Pijpe et al., 2007, 2008). The level of
18 feeding activity varied among individuals in our study, but most butterflies
19 appeared at rest most of the time, and fed infrequently. The inability to
20 survive in the warm, active environment shows that the longevity of winter
21 form adults required quiescence to achieve high life expectancy, which is im-
22 portant when considering the effects of warming climates on overwintering
23 butterflies (see WallisDeVries et al., 2011).
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26 Summer form adults lived short lives whether active or inactive, which
27 indicates that these butterflies would only have limited aestivation abilities
28 to survive during inhospitable periods. The fact that I did not allow mating
29 for either seasonal form controlled for seasonal differences that would result
30 from the cost of reproduction. The age of the oldest summer form adult was
31 126 days which is very similar to the time between spring and fall breeding
32 seasons, about 120 days from May to September. Austin has a subtropical
33 climate with two inhospitable seasons (NWS, 2015), which differs from either
34 temperate climates to the north where *A. andria* occurs or tropical climates
35 to the south where *A. aidea* occurs. The wet-dry seasons in Mexico are
36 comparable in timing and duration to the summer-winter seasons in United
37 States, meaning the tropical *A. aidea* is able to endure either winter or the
38 dry season depending on its latitude. However, summers may be especially
39 hot and dry in Texas, making recruitment difficult for butterflies when fresh
40 foliage is hard to find and creating a situation where survival strategies are
41 optimal. Similar to other Texas butterflies in this environment (Gilbert,
42 1985), leafwing likely retreat to wetter, shaded habitats along rivers and
43 streams, where conditions are more favorable. This behavior has also been
44 documented for tropical butterflies (Brakefield and Reitsma, 1991; Denlinger,
45 1986).
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4.1. Conclusions

I found a striking difference in life expectancy between seasonal morphological types of adults for a tropical and temperate leafwing, *A. aidea* and *A. andria*, in a subtropical environment. Although the tropical leafwing outlived the temperate leafwing, the pattern of differences in response to sex, season, and living conditions was unchanged between species. Winter adults outlived summer adults, but only in a calm, cool environment. My results suggest that winter adults achieved high life expectancy not just through resource storage, but also resource conservatism.

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Tables

Table 1: Model selection criteria among competing models predicting time to death of adult butterflies with leafwing species, seasonal form, sex, and living conditions as factors and the covariate forewing length. The column Step indicates the step in the backward stepwise regression model reduction process. The best model had the following structure: $\log(\text{time to death}) = \text{treatment} + \text{season} + \text{leafwing} + \text{sex} + \text{forewing length} + \text{treatment} \times \text{season} + \text{treatment} \times \text{sex} + \text{season} \times \text{sex} + \text{treatment} \times \text{season} \times \text{sex}$, where treatment refers to the experimental living conditions and season refers to the seasonal form

Model	Step	# Par.	AICc	AICc	Weight
1	6	11	1684	0.00	0.65
2	5	12	1685	1.67	0.28
4	3	20	1689	5.71	0.04
5	4	17	1691	7.29	0.02
6	2	21	1692	8.10	0.01
7	1	26	1703	19.53	0.00
8	0	29	1708	24.84	0.00

Table 2: Analysis of deviance table for the accelerated failure-time model predicting time to death of adult butterflies with the factors, leafwing species, seasonal form, sex, and living conditions and the covariate forewing length (Model 1, Table 1). I used a χ^2 test for the significance of the amount of deviance explained by each factor. The fit of the model to the data, i.e., the total deviance explained, was significant ($df = 9$, $\chi^2 = 363.78$, $p < 0.001$).

Factor	df	Deviance	Residual df	Residual Deviance	p-value
Treatment	1	145.3	223	1879	<0.001
Season	1	32.8	222	1846	<0.001
Leafwing	1	3.9	221	1842	0.048
Sex	1	13.8	220	1828	<0.001
Forewing Length	1	14.8	219	1813	<0.001
Treatment Season	1	137.6	218	1676	<0.001
Treatment Sex	1	6.9	217	1669	0.009
Season Sex	1	2.4	216	1667	0.120
Treatment Season Sex	1	6.2	215	1660	0.013
Intercept only			224	2024	

Figure captions

Figure 1. Interaction plots comparing the mean ($\pm$ SE) life expectancy between males (dashed) and females (solid) of each seasonal form of the temperate, *A. andria* (A), and tropical, *A. aidea* (B), leafwings. Living conditions refers to one of two experimental conditions for adults. Active conditions were maintained outside in a shade house and represent a warm, sunny environment where butterflies were able to fly. Inactive conditions were maintained inside a laboratory and represent a cool, low light environment where butterflies were unable to fly.