Predictive Adaptive Responses: Condition-Dependent Impact of Adult Nutrition and Flight in the Tropical Butterfly *Bicyclus anynana*

Marjo Saastamoinen,[1,2,*] Dominique van der Sterren,[1] Nienke Vastenhout,[1] Bas J. Zwaan,[1] and Paul M. Brakefield[1]

1. Institute of Biology, Leiden University, P.O. Box 9505, 2300 RA, Leiden, The Netherlands; 2. Metapopulation Research Group, Department of Biological Sciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland

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abstract: The experience of environmental stress during development can substantially affect an organism's life history. These effects are often mainly negative, but a growing number of studies suggest that under certain environmental conditions early experience of such stress may yield individuals that are less sensitive to environmental stress later on in life. We used the butterfly *Bicyclus anynana* to study the effects of limited larval and adult food and forced flight on individual performance measured as reproduction and adult life span. Larvae exposed to food stress showed longer development and produced smaller adults. Thus, they were not able to fully compensate for the food deprivation during development. Females that experienced food stress during development did not increase tolerance for adult food limitation. However, females exposed to food stress during development coped better with forced flight compared with the control group. The apparent absence of costs of flight in poor-quality females may be a by-product of an altered body allocation, as females experiencing both food stress treatments had increased thorax ratios, compared with controls, and increased flight performances. The results reveal an important plasticity component to variation in flight performance and suggest that the cost of flight depends on an individual's internal condition.

Keywords: environment, flight, life history, nutrition limitation, stress, trade-off.

Introduction

Organisms in the wild are constantly faced with a wide range of environmental variation. For example, changes in resource availability or ambient temperature vary from short-term fluctuations during an individual's lifetime to longer-term changes across generations (Lopez-Maury et al. 2008). Any environmental change that acts to reduce the fitness of an organism is defined as environmental stress (Koehn and Bayne 1989; Bijlsma and Loeschke 1997). Although the ability to sense, cope with, or even adapt to environmental variation or stress is essential for the survival of individuals and populations, we still know very little about the possible strategies and mechanisms underpinning such processes (Boggs 2009).

Environmental change, such as variation in ambient temperature and precipitation, will have an effect on resource availability for herbivores via its influence on phenology and plant growth (Parmesan 2006). This may consequently increase food limitation and starvation risks for herbivores. Effects of food limitation can be long lasting, as the environment experienced during the key periods of development may strongly influence adult physiology and life-history trajectories (reviewed in Monaghan 2008; Boggs 2009). This is especially so in holometabolous insects, as resources acquired during larval development are allocated during metamorphosis to different adult body parts, including the reproductive organs, fat bodies, and flight muscles (Boggs 2009). Poor nutritional conditions during development have often been shown to have a negative impact: individuals developing under such stressful conditions perform more poorly than those developing under favorable conditions (e.g., Hamel et al. 2009). Individuals may attempt to counteract short-term resource limitation, for example, via accelerated or compensatory growth once resource availability improves (reviewed in Wilson and Osbourn 1960; Metcalfe and Monaghan 2001). Such compensatory growth during development has been suggested to be adaptive as it minimizes variation in adult body size and the costs of being small (Roff 2002). Smaller individuals are often of lower quality and, therefore, reproduce later and have fewer offspring and a shorter life span than larger individuals of higher quality (Roff 2002). However, compensatory growth itself can also have costs, such as an increased metabolic rate (Criscuolo et al. 2008)

* Corresponding author; e-mail: marjo.saastamoinen@helsinki.fi.

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and reduced immune function (De Block and Stoks 2008), both of which consequently decrease individual life span (reviewed in Metcalfe and Monaghan 2001).

Life-history strategies and reproductive decisions of an individual should match environmental conditions (e.g., density, food availability, predation risk, and weather condition) and the adult phenotype (e.g., body size and foraging efficiency; Roff 2002). Therefore, one can predict that organisms will evolve an ability to perceive differences in the environmental conditions (e.g., habitat quality) and rely on such cues in making life-history decisions involving both developmental and adult plasticity responses (Stearns 1992; Kisdi et al. 1998; Clobert et al. 2009). A growing number of studies suggest that under some circumstances the environmental conditions experienced during development may shape an individual's phenotype so that it is better prepared for conditions it will encounter later in life (the so-called predictive-adaptive response; reviewed in Monaghan 2008). Whether such phenotypic alterations can be expected to be beneficial depends on how closely the conditions experienced during development predict those later in life. Poor nutritional conditions experienced during growth could provide an honest signal of poor habitat quality to come in later life and can be used to yield increased stress tolerance response. Changes in hormone levels (e.g., in birds; McGlothlin and Ketterson 2008), fat storage (e.g., in cockroaches; Barrett et al. 2009), and metabolic rate (e.g., in butterflies; Pijpe et al. 2008) could all provide potential underlying mechanisms.

Alternatively, poor environmental conditions during development and growth could be used as a cue to increase dispersal ability (e.g., Meylan et al. 2009). Rather than modifying the phenotype to better deal with the local conditions, this strategy would involve alterations in body composition, morphology, or behavior in a way that enhances an individual's ability to escape from a poor environment (Meylan et al. 2009). Dispersal itself and the maintenance of dispersal-related traits, such as high flight metabolic rate and large wing muscles, are in general costly (Zera and Harshman 2001; Roff and Fairbairn 2007). Therefore, selection might be expected to promote an individual's ability to increase allocation to dispersal-related traits under those environmental conditions in which dispersal is likely to occur. Chin et al. (2009) found that in the European starling (*Sturnus vulgaris*), juveniles exposed to embryonic corticosterone, a maternal stress hormone, had increased flight performance. Comparable environmentally induced changes have been associated in wing-dimorphic insects, with the development of the dispersive, winged individuals under harsh environmental conditions (see Roff and Fairbairn 1991). Quantifying dispersal ability or propensity in wing-monomorphic insects (e.g., fruit flies, butterflies, and moths) is very difficult. Therefore proxies, such as relative thorax mass (e.g., Berwaerts and Van Dyck 2004), flight endurance (e.g., Parker and Gatehouse 1985*b*), or flight metabolic rate (e.g., Niitepõld et al. 2009), that often correlate with dispersal or flight ability have been used. Nevertheless, few studies on wing-monomorphic species have also demonstrated some adaptive plasticity in flight capacity or related morphological traits (Parker and Gatehouse 1985*a*; Woodrow et al. 1987; Senger et al. 2008; Pellegroms et al. 2009).

Here we use the tropical butterfly *Bicyclus anynana* to examine whether environmental conditions experienced during development alter individuals' physiology or life history (phenotypic plasticity) so that they are better able to cope with stress later on in life. Previous experiments in *B. anynana* have shown how adverse environmental conditions experienced during juvenile and adult stages are major factors affecting heterogeneity in important life-history traits, behavior, and reproductive capacity (e.g., Bauerfeind and Fischer 2005*b*, 2009). We specifically address the following questions: (1) Can larvae compensate for short interruption in food supply through a subsequent increase in growth when food is available, or do they remain smaller as adults? (2) Does experiencing short-term nutritional stress during the juvenile stage enhance the ability to tolerate food limitation experienced later in life, or will high-quality individuals (i.e., those from optimal larval conditions) always perform better? (3) Does an increased forced flight inflict condition-dependent costs, or does adaptive plasticity in flight-related traits or capacity occur?

Material and Methods

Study Species and Larval Rearing

Bicyclus anynana is a butterfly from tropical and subtropical east Africa, which as an adult feeds on decaying fruit (Brakefield et al. 2009). The butterfly exhibits two seasonal morphs, which function as an adaptation to alternate wet-dry seasonal environments (seasonal polyphenism; Brakefield and Larsen 1984; Brakefield and Frankino 2009). The two forms differ in morphology and in many life-history traits, as wet-season morphs are smaller, reproduce faster, and have a shorter life span compared with the dry-season morph (e.g., Brakefield and Reitsma 1991; Brakefield and Kesbeke 1997; Pijpe et al. 2006). The butterflies used in our experiment originated from the stock population at Leiden University, which was established in 1988 from over 80 gravid females collected in Malawi (Brakefield et al. 2009). Several hundred butterflies are reared in each generation to sustain high levels of heterozygosity (Van't Hof et al. 2005).

We used larvae from the stock population, and hence

they represent multiple different families. Larvae were reared in an environmental chamber at a constant temperature of 27°C (relative humidity [RH] 70%; 12L : 12D), resembling the natural environmental conditions during the wet season. Larvae were kept in gauze sleeves and fed on maize in groups of approximately 20 individuals per plant. This density is relatively low compared to what has been used in other studies (e.g., Stelgenga and Fischer 2007; Bauerfeind and Fischer 2009), as the aim was to rear the larvae at this stage under optimal nonstressful conditions. The small sleeve cages also ensured that larval food was never limited, and the sleeves were checked daily and fresh plants were provided to ensure ad lib. feeding conditions.

Treatments

Larval Food Stress. Larvae were randomly assigned to two larval food treatments, food stress ($N = 387$) and control ($N = 398$), on the day they moulted to the final (fifth) instar. Individual larvae were transferred to a petri dish with either fresh maize leaves (control) or a piece of agar (1.5 cm^3 to ensure high humidity; food stress) and kept under these conditions for 2 consecutive days. A 2-day stress treatment was used, as previous studies have shown that such stress is enough to have a negative impact on the fitness of *B. anynana* females (Bauerfeind and Fischer 2009) and that a 3-day food stress treatment decreases larval survival dramatically (Brakefield 1997). After the 2 days of larval food treatment, individuals were transferred back to maize plants with food available ad lib. Larvae from the two different treatment groups and from the different days were kept separate to record development time for each individual. Individuals were sexed and weighed 1 day after pupation, after which female pupae were placed individually in small containers until eclosion. For logistical reasons, only females were used in our experiment.

Adult Food Stress. On the day of eclosion, females were randomly assigned to two adult food-treatment groups: adult food stress or control ($N = 367$ and $N = 363$, respectively). Females were individually marked on the ventral hind wing and placed in the environmental chamber (constant temperature of 27°C; RH 70%; 12L : 12D) in cylindrical hanging cages (diameter = 30 cm, height = 40 cm; 20 females/cage), keeping the groups separate. The control group had moist banana available ad lib., whereas females in the food-limitation group had water available at all times but received banana only on every fourth day. Adult food stress was chosen, as previous results on *B. anynana* have indicated that such food limitation reduces female fitness (Bauerfeind and Fischer 2009). The adult food treatment continued until the death of the butterflies.

Flight Treatment. On the second day after eclosion, females were randomly assigned to two flight treatments: subjected to or not subjected to 5 min of forced flight. In the forced-flight treatment, each butterfly was placed individually in a hanging cage (diameter = 30 cm, height = 40 cm; in the environmental chamber with constant temperature of 27°C; RH 70%; 12L : 12D) and forced to fly for 5 min. The abdomen of the butterfly was gently touched with a paintbrush to stimulate flight, and then every time the butterfly settled it was forced to continue flying (five females refused to fly for the required 5 min, and they were omitted; see below). The number of times the butterfly was forced to take off over 5 min was recorded as an index for the average length of the flight bouts. This 5-min forced-flight treatment was chosen as it allowed the measurement of flight ability or endurance of a large number of females per day. In addition, we needed a flight treatment significant enough to inflict a cost (in case tradeoffs between flight and other life-history traits exist in this species) but not so significant that some females would not be able to endure it. Results from a pilot experiment showed that many females cannot fly for more than 7 min without total exhaustion. In this context, it is important to realize that during these 5 min of forced flight, females need to take off multiple times, as in a cage this size the average flight bouts are relatively short. Takeoff is energetically very costly, and hence this flight exercise uses many more resources than continuous flight in the same amount of time (Dudley 2002).

Life-History and Morphological Traits Measured

In addition to development time and pupal mass, we also recorded early-life fecundity and egg size, life span, and relative allocation to thorax or abdomen. Three days after eclosion (i.e., 1 day after the flight treatment), one-third of the females were randomly sampled and stored at −80°C for body composition analyses (see below). The remaining females were mated randomly with males from the optimal larval food-treatment group. All matings were observed, and couples were then placed in a transparent pot with a gauze lid. Males were removed after mating, and females were provided with food, according to the adult food treatment, and with a fresh standard-sized cutting of *Oplismenus* spp. grass in water for oviposition. Female fecundity was measured as the number of eggs the female laid during the first 5 days after mating (early-life fecundity; this is known to be highly correlated with lifetime fecundity in *B. anynana* in laboratory culture; Brakefield et al. 2001). Approximately 15 of these eggs were

collected at random from each female and used to measure egg size (cross-sectional area [mm^2], using a Leica DC200 digital camera connected to a binocular microscope). *Bicyclus anynana* eggs are almost perfectly spherical, and this measure correlates very well with egg mass (Fischer et al. 2002). The remainder of the eggs were kept in an environmental chamber to check their fertility. After 5 days of oviposition, females were transferred back to cages, each with fewer than 20 females to avoid density effects, to record their life span. Finally, thorax mass, abdomen mass, and thorax ratio (thorax dry mass/total dry mass) were assessed for those females that were sampled 3 days after eclosion after drying to constant weight (60°C for 24 h).

Data Analysis

Statistical analyses were performed with SAS (ver. 9.1.3.; SAS Institute 1999). As all explanatory variables were normally distributed, linear models were used to examine whether larval food treatment affected development time and pupal mass (GLM procedure in SAS). We used χ^2 tests to analyze whether larval or pupal survival differed between the larval food treatments. Linear models (GLM procedure in SAS) were also used to test the effect of larval and adult food and flight treatment on early-life fecundity, egg size, life span, and thorax ratio, with pupal mass included as a covariate. Starting with the full model including all interactions, model selection was done by backward elimination of nonsignificant factors. Only females that laid fertile eggs were used in the final analysis (60 females were omitted). An additional five females were omitted from the final model, as they refused to fly for the required 5 min. out including the omitted females, but the results were not qualitatively different, nor were the females from any particular treatment group. Additional comparisons between the larval treatment groups of abdomen and thorax size corrected for pupal mass were conducted to confirm whether the observed differences were primarily due to differences in body size.

Many of the traits that we have included in our study can potentially show correlations that may hinder a direct interpretation of effects. Although, where possible, we have used covariates in our analyses, we additionally performed a principal component analysis (PCA). The multivariate data set is described in a few principal components (PCs), and the loadings of the traits in these components greatly facilitate the interpretation of the effects of larval and adult food stress and the flight treatment on the life-history phenotype. PCA was run on JMP (ver. 5.0.1), using the mean values of development time, pupal mass, early-life fecundity, egg size, thorax mass (corrected for body size), and life span for the pooled data of each treatment group. Mean values were used, as thorax mass values were not available for the same individuals for which fitness measures were obtained. All PCs with eigenvalues higher than 1.0 were included. For each treatment group, the scores for the PC components were stored and used to describe the distribution along the axes defined by the estimated PCs.

Results

Table 1 summarizes the mean statistics for life-history and the morphological traits for the different treatment groups.

Larval and Pupal Survival, Larval Development Time, and Pupal Mass

A 2-day period of food limitation in the early final instar larva produced a small but significant decrease in both larval and pupal survival (from 94% to 91%, $\chi^2 = 6.69$, $P < .01$, and from 89% to 85%, $\chi^2 = 4.44$, $P < .04$, respectively). It also prolonged the mean developmental time from 30 to 33 days, with the final instar being extended from 6 to 9 days on average. The difference was caused entirely by the effect on the final instar, with the pupal period not differing between the two treatments ($t = 0.03$, $P = .974$). Although food-stressed larvae took longer to develop, the resulting pupal mass was significantly lower ($F_{1,781} = 42.42$, $P < .0001$).

Body Allocation

Both larval and adult food stress reduced the total dry weight of the females sampled on day 3 after eclosion (i.e., 1 day after the potential flight treatment; $F_{1,229} = 38.7$, $P < .0001$, and $F_{1,229} = 179.0$, $P < .0001$, for the larval and the adult treatments, respectively). Flight treatment had no effect on total dry mass ($F_{1,228} = 0.0$, $P = .951$), nor were any of the interactions significant.

The decrease in body mass due to nutritional stress was not evenly distributed between the body parts as proportionally more weight was lost from the abdomen than from the thorax. In general, smaller females had a higher thorax ratio than larger females (table 2). However, irrespective of body mass, females that had experienced food limitation during their development had a higher thorax ratio compared with those of the control group (table 2; fig. 1*A*). Comparisons of the thorax and abdomen masses (corrected for pupal mass) among the food-treatment groups demonstrate that more variation arises from the abdomen than from the thorax mass (larval treatment; $F_{1,230} = 3.63$, $P = .058$, and $F_{1,229} = 31.9$, $P < .0001$, for relative thorax and abdomen, respectively). Hence, although resources to be allocated during growth are limited, individuals seem to maintain thorax mass at the expense of

Table 1: Mean ± SD values of the physiological and life-history traits in *Bicyclus anynana* females in the different treatment groups

	Adult optimal		Adult stress	
	No flight	Flight stress	No flight	Flight stress
Larval optimal:				
Development time	29.7 ± 1.2 ($N = 93$)	29.6 ± 1.2 ($N = 77$)	29.8 ± 1.2 ($N = 88$)	29.8 ± 1.2 ($N = 93$)
Pupal mass (mg)	220.5 ± 20.8 ($N = 92$)	222.0 ± 18.7 ($N = 76$)	217.8 ± 20.5 ($N = 88$)	219.5 ± 20.0 ($N = 93$)
Thorax ratio (%)	24.1 ± .7 ($N = 31$)	24.8 ± .6 ($N = 28$)	29.9 ± .5 ($N = 29$)	30.0 ± .4 ($N = 27$)
No. eggs	169.9 ± 44.4 ($N = 60$)	155.8 ± 54.6 ($N = 43$)	127.1 ± 46.4 ($N = 56$)	107.7 ± 51.5 ($N = 65$)
Egg size (mm^2)	.641 ± .05 ($N = 33$)	.638 ± .04 ($N = 28$)	.631 ± .05 ($N = 31$)	.630 ± .04 ($N = 43$)
Life span (days)	30.1 ± 10.1 ($N = 59$)	26.8 ± 9.6 ($N = 42$)	20.7 ± 5.7 ($N = 57$)	19.6 ± 6.0 ($N = 64$)
Average flight time (s)	…	1.8 ± .06 ($N = 75$)	…	2.0 ± .04 ($N = 93$)
Larval stress:				
Development time	33.3 ± 1.3 ($N = 94$)	33.2 ± 1.2 ($N = 93$)	33.3 ± 1.2 ($N = 93$)	33.1 ± 1.2 ($N = 84$)
Pupal mass (mg)	208.1 ± 23.3 ($N = 94$)	209.6 ± 21.3 ($N = 92$)	206.7 ± 23.1 ($N = 92$)	208.7 ± 20.2 ($N = 83$)
Thorax ratio (%)	25.7 ± .6 ($N = 30$)	26.5 ± .6 ($N = 30$)	31.7 ± .5 ($N = 29$)	31.2 ± .4 ($N = 30$)
No. eggs	138.1 ± 40.0 ($N = 60$)	148.0 ± 43.5 ($N = 60$)	105.2 ± 43.3 ($N = 59$)	109.2 ± 38.8 ($N = 52$)
Egg size (mm^2)	.631 ± .05 ($N = 56$)	.639 ± .04 ($N = 57$)	.616 ± .04 ($N = 58$)	.619 ± .03 ($N = 51$)
Life span (days)	28.0 ± 8.0 ($N = 60$)	30.6 ± 8.6 ($N = 59$)	20.9 ± 6.7 ($N = 59$)	20.1 ± 5.4 ($N = 52$)
Average flight time (s)	…	1.9 ± .04 ($N = 93$)	…	2.1 ± .08 ($N = 84$)

Note: Sample sizes are in parentheses.

abdomen mass, for any given pupal mass (fig. 2; similar slopes, different intercepts). Similarly, experiencing adult food limitation increased thorax ratio (table 2; fig. 1*A*). Adult food stress had no effect on the thorax mass, so the difference was solely due to the decrease in abdomen mass ($F_{1,229} = 194.1$, $P < .0001$, and $F_{1,229} = 0.97$, $P = .327$, for abdomen and thorax dry mass, respectively). Flight treatment had no effect on thorax ratio ($F_{1,228} = 0.25$, $P = .619$), nor were the interactions between the treatments significant.

Fecundity

The mean value for early-life fecundity was 133 eggs (SD ± 50 eggs; $N = 448$). Egg number declined with body mass (table 2). Irrespective of body mass, experiencing food stress during development further depressed early-life fecundity. Additionally, adult food stress reduced female fecundity (table 2; fig. 1*B*). There was no significant interaction between adult and larval food treatment on early-life fecundity ($F_{1,445} = 0.3$, $P = .617$). Flight treatment alone had no significant effect ($F_{1,445} = 1.69$, $P = .194$), but its effect on fecundity differed between the two larval treatment groups. Fecundity was decreased by the increased flight treatment in females from the larval control group only (table 2; fig. 3*A*), whereas those that had experienced larval nutritional stress were not affected by the increased flight in terms of early-life fecundity. Other interactions were not significant.

Egg size decreased with decreasing body mass (table 2), and there was no independent effect of larval food stress on egg size ($F_{1,349} = 0.92$, $P = .339$). Additionally, females that experienced adult food stress laid smaller eggs than those of the control group (table 2; fig. 1*C*). Egg size was not affected by the flight treatment ($F_{1,349} = 0.19$, $P = .667$) or by any of the potential interactions.

Table 2: ANCOVAs for the effects of larval food limitation, adult food limitation, and flight stress on thorax ratio, early-life fecundity, egg mass, and life span of *Bicyclus anynana* females

	df	*F*	*P*	Effect direction
Thorax ratio:				
Larval food stress	1, 229	14.81	.0002	+
Pupal mass	1, 229	9.21	.003	+
Adult food stress	1, 229	204.05	<.0001	+
Early-life fecundity:				
Larval food stress	1, 445	5.97	.015	−
Pupal mass	1, 445	13.66	.0002	+
Adult food stress	1, 445	96.90	<.0001	−
Flight treatment	1, 445	1.69	.194	
Larval food stress × flight treatment	1, 445	6.49	.011	−[a]
Egg size:				
Pupal mass	1, 349	11.95	.0006	+
Adult food stress	1, 349	14.27	.0002	−
Life span:				
Larval food stress	1, 447	.60	.434	
Adult food stress	1, 447	139.30	<.0001	−
Flight treatment	1, 447	.50	.468	
Larval food stress × flight treatment	1, 447	4.64	.035	−[a]

Note: Pupal mass was included as a covariate if significant.

[a] Direction for control group.

Life Span

Life span was not affected by the larval food stress (table 2; fig. 1*D*) or by body mass ($F_{1,442} = 2.18$, $P = .140$), whereas experiencing food stress as an adult significantly decreased female life span (table 2; fig. 1*D*). Life span was not affected by the flight treatment alone, but there was a significant interaction between larval stress and flight treatment (table 2; fig. 3*B*). Experiencing increased flight decreased the life span of females from the control group but did not affect the life span of females that had experienced larval food stress. Indeed, comparing only flight-treatment females, those that had experienced food stress during their larval stage lived longer than those from the control group (fig. 3*B*; $t = -2.78$, $P < .01$). None of the other interactions were significant.

Flight Performance

Smaller females had increased flight performance as measured by the average length of flight bouts during the 5 min of forced flight ($F_{1,338} = 9.76$, $P < .002$). Larval stress treatment, independently of body mass, had no effect on flight performance ($F_{1,338} = 2.67$, $P = .103$). However, if the covariate of body mass was removed from the analysis, females that had been stressed as larvae flew better ($F_{1,339} = 6.43$, $P = .012$), indicating that the effect of larval food stress on flight performance is mediated partially through its effect on body mass. Adult food stress treatment also had a significant effect on flight performance, as females that experienced adult food limitation flew better than the controls ($F_{1,229} = 10.1$, $P < .002$). Flight performance had no effect on early-life fecundity, egg size, or life span, and none of the interactions were significant.

Principal Component Analysis

The PCA describing the patterns of variation in larval and adult life-history traits from the different treatment groups enabled us to reduce the variation to two main PCs, together accounting for 97% of the total variation (table 3). Principal component 1 (PC1) can be interpreted as the "reproductive" component: egg size and early-life fecundity correlate positively with pupal mass and life span and negatively with developmental time and thorax size. Principal component 2 (PC2) is the "growth" component, in which developmental time contrasts with pupal mass and thorax size and with very low loadings for early-life fecundity and egg size. The average scores along the two PCs were used to compare each of the treatment groups (fig. 4; see "Discussion").

Discussion

The aim of our study was to assess whether the tropical butterfly *Bicyclus anynana* responds to environmental stress during the final stages of its development in a predictive manner that could be adaptive in natural environments. We will first summarize the main results (see also table 2) and then focus on the predictive adaptive response to the developmental food stress.

Even though stressed individuals developed more slowly, they were not able to fully compensate for the poor conditions and attained a smaller adult size than unstressed controls. Even a short-term nutritional limitation during development may result in decreased body mass, especially when nutritional limitation is experienced during the final stages of larval development, when growth rate is highest (e.g., Boggs and Freeman 2005; Bauerfeind and Fischer 2009; Pellegroms et al. 2009), as was the case in our study. Larvae that experienced food limitation also changed their body allocation: thorax mass was unaffected, but allocation was reduced to the abdomen, resulting in an increased thorax ratio (thorax dry mass/total dry mass). This may indicate that the females stressed during development preserve thoracic muscles, and thus flight ability, at the expense of decreased reproduction, as abdomen size, in general, correlates very strongly with fecundity in insects (e.g., Wickman and Karlsson 1989). Consequently, females stressed during development had lower early-life fecundity

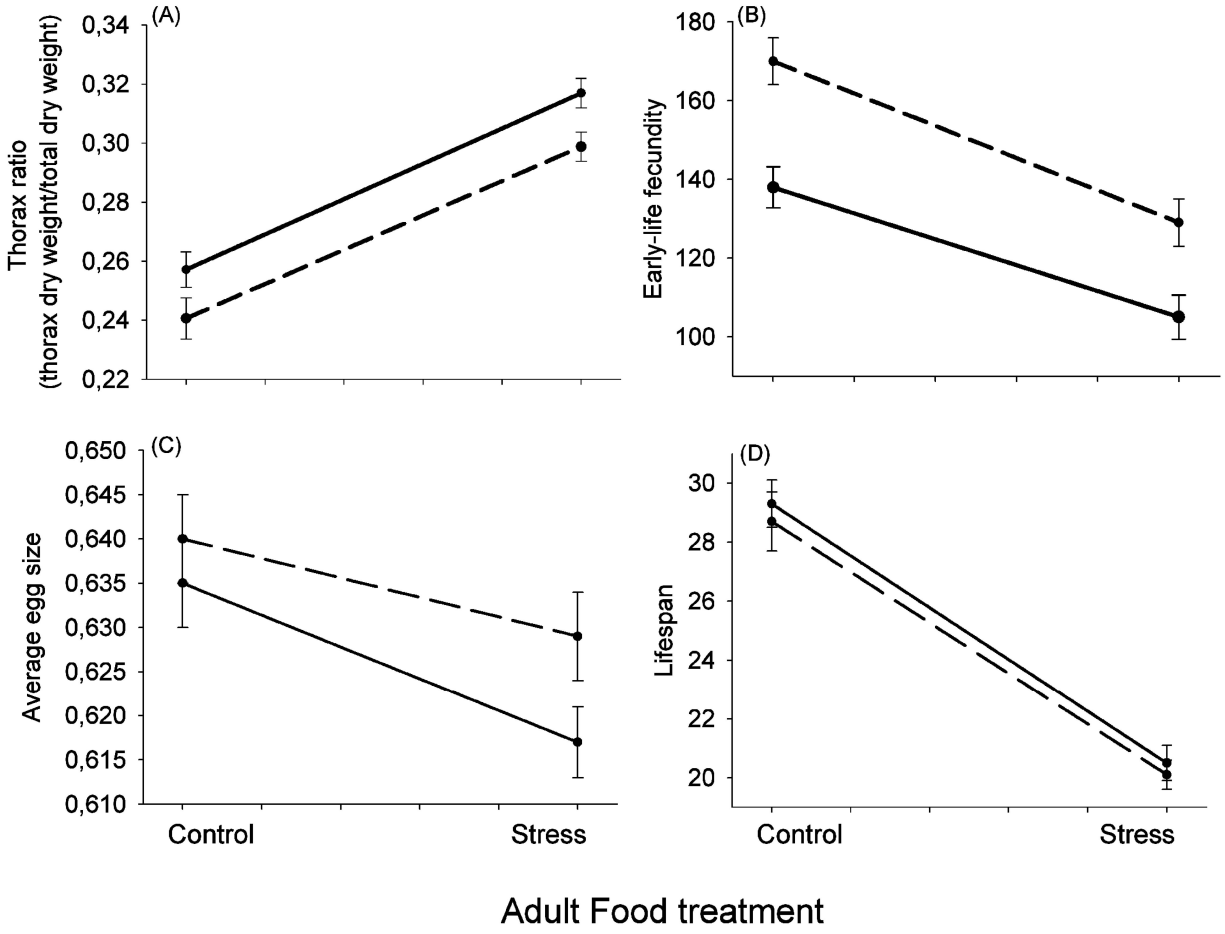

Figure 1: Effects of larval and adult food stress on thorax ratio (*A*), early-life fecundity (*B*), egg size (*C*), and life span (*D*) of female *Bicyclus anynana*. Dashed and solid lines represent larval control and stress treatment, respectively.

(fewer eggs that also tended to be smaller) than females that had experienced optimal conditions. It is unlikely that decreased fecundity is confounded by changes in the dynamics of reproductive output since females with low early-life fecundity also had shorter life span. The negative effect of larval food limitation on body allocation and fecundity was not mediated solely through a reduction in body size, as, for a given pupal mass, the stress treatments yielded females with a lowered allocation to the abdomen and thus to reproduction (fig. 2*A*). Adult life span was unaffected by the juvenile environment, suggesting that poor-condition individuals can compensate for a bad start if they experience optimal conditions as adults.

As predicted from previous studies using *B. anynana* (Fischer et al. 2004; Bauerfeind and Fischer 2005*a*), food-limited females laid fewer and smaller eggs and had a shorter life span than those that had experienced optimal conditions. Consistently, adult food-stressed females lost mass mainly from their abdomen compared with the controls. The effect of forced-flight treatment varied between the treatment groups, as females exposed to food stress during larval development coped better with the forced flight than did those from the control group.

Predictive Adaptive Response to Food Stress

The concept of predictive adaptation has been developed to explain the relationship between early-life events and the risk of later-life stress (e.g., in the context of disease, see Gluckman et al. 2005). According to this idea, adult performance is influenced not only by an individual's genetic background and adult condition but also by environmental factors experienced earlier in development. These factors can act through the processes of developmental plasticity. Thus, variation in food quality or quantity during development could trigger changes in physiology (e.g., via

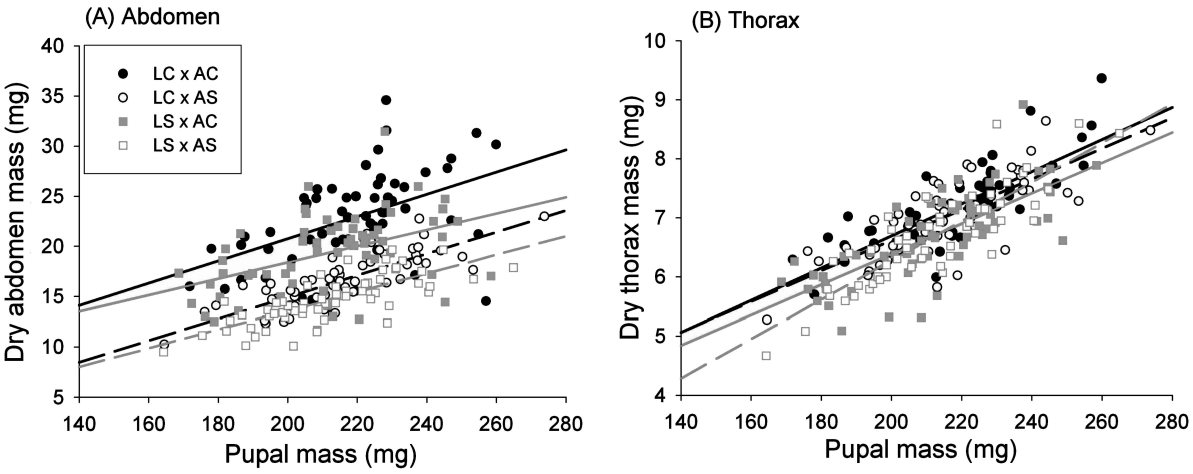

Figure 2: Relationships between pupal mass and dry abdomen (*A*) and thorax (*B*) mass for different treatment groups (LC = larval control, LS = larval stress, AC = adult control, and AS = adult stress). Gray and black lines represent larval stress and control lines, respectively, and dashed and solid lines represent adult stress and control treatment, respectively.

hormones, allocation patterns) or life-history traits so that individuals can cope more effectively with expected stress later in life (Monaghan 2008). The predictive adaptive response concept and its generality for explaining developmental plasticity is still very much under debate (e.g., Wells 2007). Individuals of *B. anynana* experience one of two alternative environments occurring in a seasonal cycle that is highly predicable on the basis of temperatures experienced in late larval development, and therefore this organism is suitable for testing the predictive adaptive response concept.

The results from our experiment showed that in terms of early-life fecundity, egg size, and life span, high-quality females (i.e., those that experienced no larval food stress) always performed better than females that had experienced poor conditions (i.e., a silver-spoon effect; Metcalfe and Monaghan 2001). Hence, experiencing food shortage during development did not enable females to buffer against food shortage experienced later on in life. Interestingly, a previous study on *B. anynana* showed that females that had been starved for 2 days during the final instar (but not 2 consecutive days, as in our experiment) suffered less from subsequent adult food limitation in terms of fecundity (Bauerfeind and Fischer 2005*b*). An experience of 2 consecutive days of food limitation may be more stressful and difficult to compensate for than 2 days separated in time. Additionally, larvae in our experiment experienced nutritional limitation in the first 2 days of the final instar, compared with a less controlled period of food stress by Bauerfeind and Fischer (2005*b*). If the first 2 days of the final instar are an exceptionally sensitive period of larval development, we may have induced a stronger stress response compared with Bauerfeind and Fischer (2005*b*). Another notable difference between our study and that of Bauerfeind and Fischer (2005*b*) is the intensity of the adult food stress since food-stressed adults in our study received banana on every fourth day compared with every other day. This indicates that buffering against mild adult food limitation resulting from food shortage experienced earlier in development may be possible in *B. anynana*. The mechanisms by which such buffering occurs require further research.

The alternative predictive response to food shortage during development as examined in our study is a potential increase in allocation of resources to morphological and physiological traits that could favor dispersal ability. An increased flight ability would be expected to enhance the ability of individuals to move away from a poor-quality habitat patch and thus to locate a more favorable environment (Clobert et al. 2009). Our results showed that females that had experienced food shortage during development had an increased thorax ratio, which has been shown to indicate an increased allocation to flight and dispersal ability in some Lepidoptera (e.g., Thomas et al. 1998; Berwaerts et al. 2002). Indeed, females with a higher thorax ratio in our experiment consistently had longer flight bouts during the forced-flight treatment, suggesting an enhanced flight performance. Finally, females that had experienced food shortage during their development did not suffer in terms of either early-life fecundity or life span due to the forced-flight treatment, whereas forced-flight treatment decreased both of these traits in control females. Statistical analysis supports this interpretation (fig. 4). PC1, representing the reproductive component, clearly

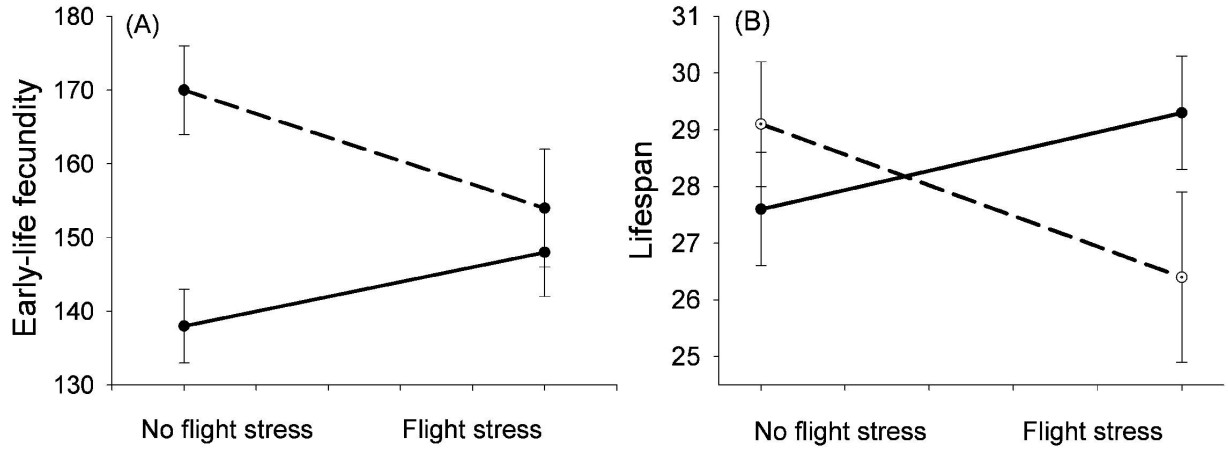

Figure 3: Effects of larval and flight stress on early-life fecundity (*A*) and life span (*B*) of female *Bicyclus anynana*. Dashed and solid lines represent larval control and stress treatment, respectively.

separates the adult stress and control groups, with the pattern of change in direction along this axis for the effect of forced flight being reversed relative to that for the larval stress and control groups. As expected, only the PC1 values are affected by the flight treatment, as the mean values for PC2 represent the larval growth components that cannot be influenced by the adult flight treatment.

Importantly, in our experiment we measured thorax ratio and flight ability only in a small cage. Further studies are required to confirm the link between these traits in *B. anynana* in a more natural flying arena under various flight conditions. Similarly, the effect of nutritional limitation on other flight traits including more long-distance dispersal should be performed since dispersal entails costs far beyond its physiological demands (Hanski et al. 2006). In addition to flight performance, we used the flight treatment to assess the energetic costs it imposes to the females (see also Gibbs and Van Dyck 2010). Here, it is important to note that the effect of 5 min of continuous flight was increased by forcing the females to take off every time they tried to land (Dudley 2002). The takeoff in insects is energetically the most expensive part of the flight and, hence, explains why even 5 min of forced flight can have such a strong effect (Dudley 2002). A similar 5-min flight treatment was recently used in the speckled wood butterfly and was shown to have strong negative fitness effects, partly dependent on the landscape of origin (Gibbs and Van Dyck 2010). Other studies have also found changes in dispersal-related morphological traits in Lepidoptera (e.g., an allometric relationship between body mass and wing length, wing loading, wing shape) in response to food quality, food quantity, or rearing density during development (Woodrow et al. 1987; Boggs and Freeman 2005; Pellegroms et al. 2009). In general, studies demonstrating that flight capability in wing-monomorphic species may also be a phenotypically plastic trait remain few in number, especially in comparison to the studies on wing-dimorphic species (reviewed in Zera and Denno 1997). Whether the increased flight ability or the ability to buffer against the energetic costs of the forced flight of the females that had experienced stress during development in our experiments is an adaptive predictive response to food shortage remains to be tested. This will require more functional and mechanistic understanding of the physiological processes underlying the phenotypic responses (Lessells 2008). It is, for example, possible that increased thorax ratio due to poor developmental conditions resulted from some direct, nonadaptive physiological (energetic) constraint on development (Marshall and Uller 2007). Both thorax mass and abdomen mass were decreased due to larval food deprivation, but the decline in thorax mass was not as large as that in abdomen mass. Altered allocation patterns to female body parts in response to food deprivation have also been shown in other insects. In a caddisfly (*Agrypnia de-*

Table 3: Results of principal component (PC) analysis

	PC1	PC2
Eigenvalue	3.64	2.17
Cumulative percentage	60.67	96.90
Development time	−.22	−.62
Pupal mass	.28	.58
Early-life fecundity	.52	−.04
Egg size	.51	.06
Relative thorax mass[a]	−.38	.44
Life span	.46	−.31

[a] Dry thorax mass corrected for total dry mass.

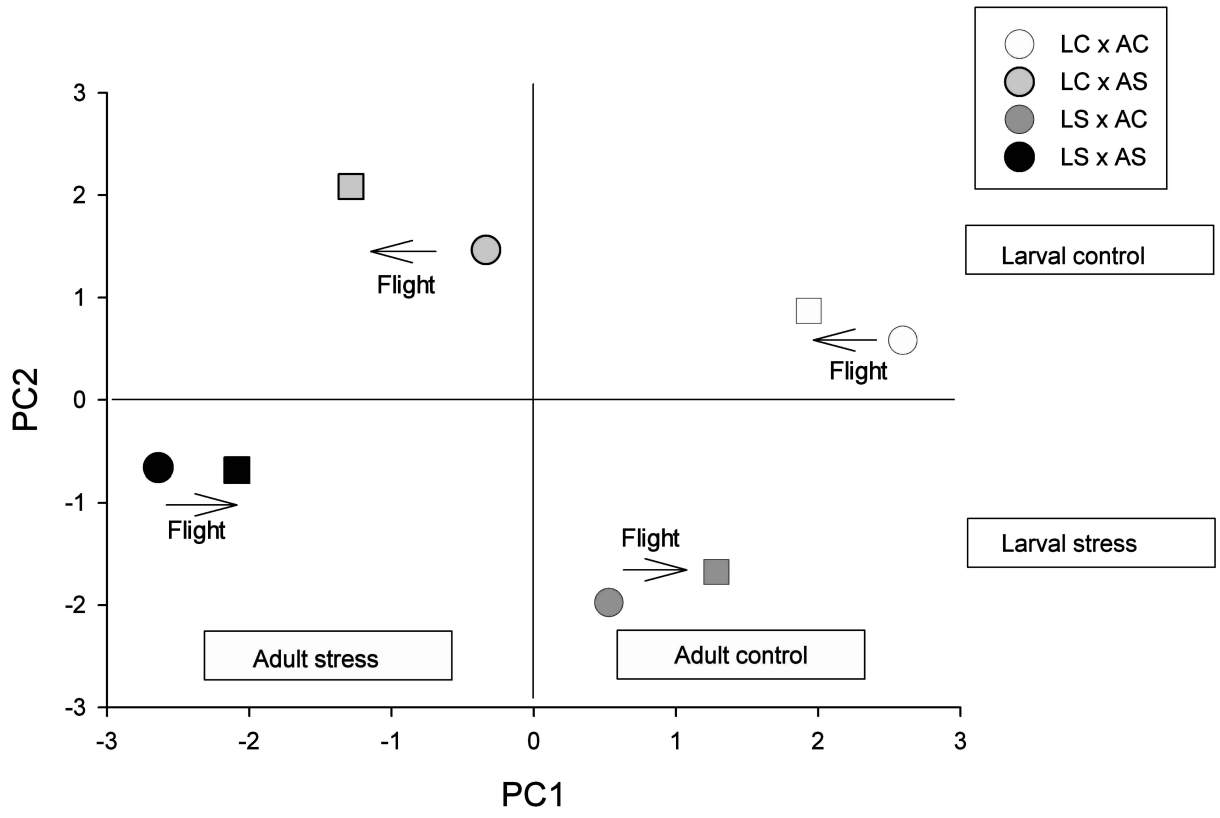

Figure 4: Distribution of the different treatment groups (LC = larval control, LS = larval stress, AC = adult control, and AS = adult stress) according to their scores for the first two principal components (PCs) defined by the principal component analysis. Squares and circles indicate females that did and did not experience flight-stress treatment, respectively. PC1 is the reproductive component, with early-life egg size and fecundity correlating positively with pupal mass and life span and negatively with developmental time and thorax size. PC2 is the growth component in which developmental time contrasts with pupal mass and thorax size.

flata), resource reduction during development resulted in resources being allocated away from the thorax into the abdomen (Jannot et al. 2007), which is in the opposite direction from our results. This difference may be due to life-history differences between the organisms, as in general caddisflies are short-lived capital breeders (mainly feed only during larval stage; Wiggins 1998) and hence seem to preserve reproduction at the expense of flight capability (see also Boggs 2009).

Environmental conditions experienced during the final instar may, however, provide a reliable prediction of the environmental conditions, for example, in terms of habitat quality that an individual will experience as an adult. Therefore, an increased ability to move away from a poor habitat could reflect an adaptive response. This might be especially important for *B. anynana* during the wet season in Africa, when resources in general are more plentiful and hence the likelihood of finding resources elsewhere is high (Brakefield and Reitsma 1991). Comparative studies under dry season conditions will be valuable, as the predictive adaptive responses to developmental food limitation may be very different under circumstances when resources, both larval and adult, are scarce in general. The involvement of hormones (e.g., juvenile hormone and adipokinetic hormone) in the regulation of migratory physiology in general is evident (Rankin 1991), and hence more research into the interaction between developmental stress and hormone regulation is required.

Perspective

Our results emphasize the potential role of phenotypic plasticity in shaping flight or dispersal abilities (Dufty et al. 2002; Clobert et al. 2009). In insects with adult flight and dispersal as a continuous trait (wing-monomorphic species), an individual's flight ability has typically been perceived to be a fixed trait (e.g., Berwaerts et al. 2002; Hughes et al. 2003; Hanski et al. 2006). Growing numbers

of studies are, however, demonstrating that dispersal ability is condition dependent and may vary in response to such factors as body condition, age, and mating status (Meylan et al. 2002; Bonte et al. 2008; Stevens et al. 2010). Although in our study females from initially poor conditions appear to have been preadapted or more prepared for flight, the opposite pattern (i.e., the silver-spoon effect; Metcalfe and Monaghan 2001) in which better-conditioned individuals from a developmental environment with lower stress are more able to disperse successfully is also possible. Thus, it is important to note that while "silver-spooned" individuals may outperform lower-quality ones, the responses of the latter animals may increase their adaptedness in the face of lower traits values; the low-quality individuals appear to be making the most of their available resources (Monaghan 2008).

It is clearly extremely important to consider dispersal, or flight ability as measured here, as a plastic condition-dependent trait in studies of life-history theory (McNamara and Houston 1996) and the evolution of dispersal (Clobert et al. 2009), because one of the core assumptions of both bodies of theory is trade-offs between energetically expensive life-history traits such as flight and reproduction (review in Roff and Fairbairn 2007). It is generally assumed that if resources, such as nutrients and energy, become limited, an increase in resource allocation to one trait inevitably leads to a decrease in allocation to the other (van Noordwijk and de Jong 1986). Intuitively, one would therefore assume that high-quality individuals can better cope with the energetic costs of flight, as they have more resources available. If, however, individuals are able to alter their physiology or life-history depending on the quality of their environment in a way that increases their flight ability, as was demonstrated in our experiment (see the crossing reaction norms in fig. 3), dispersal costs may actually be decreased in lower-quality individuals. Such phenomena will need to be accounted for in future studies of the evolution of life histories in general and of dispersal in particular.

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Female *Bicyclus anynana.* Photograph by Oskar Brattström.