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The Predictive Adaptive Response: Modeling the Life-History Evolution of the Butterfly *Bicyclus anynana* in Seasonal Environments

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ABSTRACT: A predictive adaptive response (PAR) is a type of developmental plasticity where the response to an environmental cue is not immediately advantageous but instead is later in life. The PAR is a way for organisms to maximize fitness in varying environments. Insects living in seasonal environments are valuable model systems for testing the existence and form of PAR. Previous manipulations of the larval and the adult environments of the butterfly *Bicyclus anynana* have shown that individuals that were food restricted during the larval stage coped better with forced flight during the adult stage compared to those with optimal conditions in the larval stage. Here, we describe a state-dependent energy allocation model, which we use to test whether such a response to food restriction could be adaptive in nature where this butterfly exhibits seasonal cycles. The results from the model confirm the responses obtained in our previous experimental work and show how such an outcome was facilitated by resource allocation patterns to the thorax during the pupal stage. We conclude that for *B. anynana*, early-stage cues can direct development toward a better adapted phenotype later in life and, therefore, that a PAR has evolved in this species.

Keywords: predictive adaptive response, developmental plasticity, energy allocation model, life history, stochastic dynamic programming.

Introduction

Developmental plasticity is the ability of a genotype to direct development in response to changes in its environment (Stearns 1982; Piersma and Drent 2003; West-Eberhard 2003). Plasticity is adaptive when the resultant change

in the phenotype causes a fitness benefit in the new environment (Ghalambor et al. 2007). The predictive adaptive response (PAR) is a specific type of developmental plasticity where the response to a cue is advantageous at a later life stage rather than immediately (Gluckman and Hanson 2004a, 2004b; Gluckman et al. 2005). The concept of PAR was first introduced in the context of human development. It is suggested that the human fetus evolved an ability to interpret cues from the early-life environment that results in development of a phenotype better matched to the environment predicted to occur later in life (Gluckman and Hanson 2004a, 2004b; Gluckman et al. 2005). Some empirical data support the idea of PAR in humans (e.g., Jasienska et al. 2006), but its general validity remains uncertain. Concerns involve factors such as honesty of cue, mother offspring conflict, and environmental variance (Wells 2006, 2007; Rickard and Lummaa 2007; but see Gluckman et al. 2005, 2008). Theoretical work suggests that plasticity is less likely to evolve when the relationship between cue and late-life environment weakens (Reed et al. 2010; but see Moran 1992; Sultan and Spencer 2002).

One of the best candidates for PAR is the development of meadow vole (*Microtus pennsylvanicus*) fur, which is thicker in autumn-born voles than in those born in the spring (Lee and Zucker 1988). There is no immediate advantage of the differential fur thickness, as the nest temperatures are similar in autumn and spring. However, when the voles mature and leave the nest, the external temperatures are very different. Other possible examples of PAR include the dispersal response in the desert locust *Locusta migratoria* (Pener and Yerushalmi 1998; Simpson et al. 1999, 2001) and in the great tit *Parus major* (Tschirren

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et al. 2007), alteration of morphology of water flea *Daphnia cucullata* (Agrawal et al. 1999), and growth rate and developmental time in the guppy *Poecilia reticulata* (Gosline and Rodd 2008). Even though such examples demonstrate that organisms respond to environmental cues by changes in physiology and/or life-history traits, what is often lacking is a definitive test of the adaptive value of the responses. This may be partially explained by the fact that measuring fitness in the field can be logistically difficult and that interpretations of such data may be confounded by environmental and genetic factors (Monaghan 2008).

Ideal opportunities to test the presence of evolved PARs exist in organisms experiencing seasonal environments, particularly when generation times are relatively short compared to the seasonal variation. Moreover, in testing PAR it is important that the environment can be easily manipulated and that extensive knowledge exists about the ecology to which the adaptive suitability of the observed response can be related (Rickard and Lummaa 2007). One example of such an organism is the tropical butterfly *Bicyclus anynana* (Brakefield and Zwaan 2011). This species exhibits seasonal polyphenism, appearing in two distinct phenotypes (wet and dry season morphs), which differ in a number of morphological and life-history traits (Brakefield and Larsen 1984; Brakefield and Frankino 2009). The dry season form is, on average, larger and longer-lived, with delayed reproduction and higher metabolic rate and fat content, and it is better camouflaged on its resting background (Brakefield et al. 2007). Seasonal variation is highly predictable, with warm, wet seasons of abundant food alternating with cool, dry seasons when there is no food for larvae.

Recently, Saastamoinen et al. (2010) conducted an experiment on *B. anynana* to assess whether poor nutritional conditions during development shaped the adult phenotype so that it could better deal with stressful conditions later in life. Results from this experiment showed that females experiencing food restriction during larval development did not increase their tolerance for adult food limitation but did alter their body allocation via an increased thorax ratio (i.e., thorax mass/body mass) that led to an enhanced flight performance (Saastamoinen et al. 2010). These results reveal a substantial effect of plasticity in response to larval nutrition on variation in adult flight performance. They also suggest that such plasticity may be adaptive, as food-stressed individuals could disperse more effectively to higher-quality habitats when this is favored.

Here we describe a state-dependent energy allocation model of the life history of *B. anynana*, in which organisms can evolve strategic decisions based on their physiological state and the state of the environment (McNamara and Houston 1996). Individuals respond dynamically to con-

dition from the past and present, providing a basis to predict and adapt to future environments. We address whether the life-history traits, as observed for *B. anynana* in nature, are predicted to evolve and whether the responses observed in the experiment of Saastamoinen et al. (2010) are likely to be adaptive.

Methods

Overview of the Model

In the model, we characterize an individual in one of a set of states that describes variables such as weight, developmental time, and biological age, which are known to affect the biological outcomes of interest. Transitions between states and options such as feeding and egg production are described by mathematical relationships, using energy as a common currency. Environmental factors, such as temperature, predator pressure, and resource abundance, are also included in the model. We use a daily time step, and each day the individual makes decisions concerning, for example, larval development time, pupal allocation pattern, and adult behavior, which will affect its future state. The optimal decisions in a given environment are determined using stochastic dynamic programming (SDP; Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). We assume that natural selection acts to optimize the life history of an individual by maximizing the number of progeny that the individual produces. Once the optimal decisions have been found, the traits of the individuals that define its state in the different environments can be modeled by forward simulation. As nutritional status at the larval stage influences allocation strategies in the pupal and adult stages, all these stages of the life cycle are modeled. Figure 1 presents an overview of the model. We first explain how environmental variation is addressed and then briefly describe each stage of the life cycle. Further mathematical details are provided in the appendix.

Environmental Variation

Generations of *B. anynana* live in two alternating seasons, the dry and the wet seasons. A year in the model consists of 366 time steps, each representing 1 day. During most of the dry season, which lasts 6 months, there are no host plants for larvae to feed on. At the start of the wet season, ambient temperature increases, followed by an increase in rainfall (Windig et al. 1994) and an increase in host plant density. Hence, during the wet season at every time step a proportion of the patches changes in quality. As the wet season progresses, temperature, rainfall, and the number of host plants decrease. For each time step in the model,

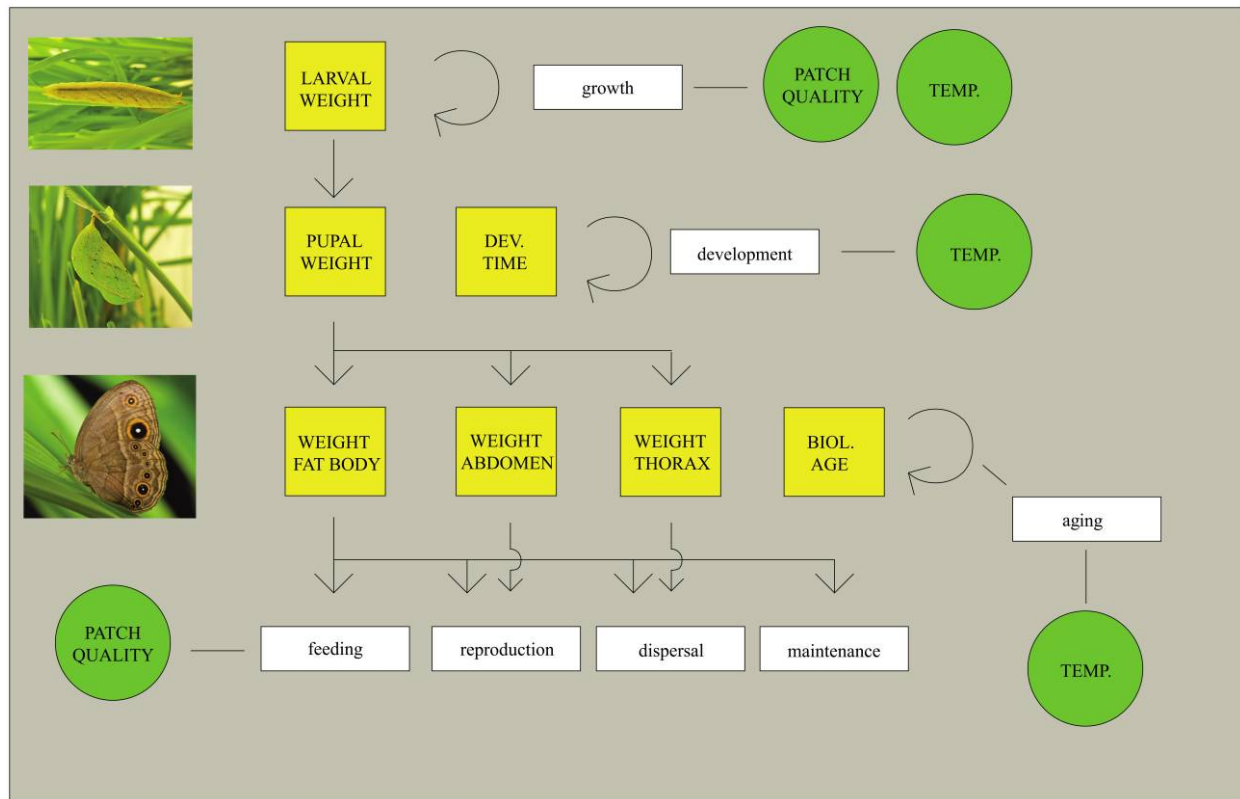


Figure 1: Overview of the model. The different stages of the butterfly's life history (larva, pupa, adult) are shown from top to bottom. Individuals at each stage are characterized by the traits shown as yellow squares (biol. age = biological age). The processes in the model are shown as white rectangles. The environmental factors are shown in green circles. Photos by Oskar Brattström.

we assigned a temperature (table S1, fig. S1, available online) and a proportion of good patches based on climate information available for Malawi, from where the laboratory population of *B. anynana* was derived (Windig et al. 1994). A good patch contains host plants where larvae can feed: see table S1 and figure S1. Every patch becomes good and bad once a year, with the percentage of good patches fixed for a given day. A good patch remains a good patch unless the proportion of good patches decreases. We let

$$\lambda_{gb}(t) = \Pr(\text{good patch at time } t \text{ is followed by bad patch at time } t + 1). \quad (1)$$

This probability is

$$\lambda_{gb}(t) = \frac{\varphi_g(t) - \varphi_g(t+1)}{\varphi_g(t)}, \quad (2)$$

where $\varphi_g(t)$ is the proportion of good patches at time t (table S1). The chance that a good patch remains a good patch is $1 - \lambda_{gb}(t)$. Equivalent relationships hold for the probability of a patch being bad.

The probability that a butterfly reaches a good patch by dispersal is equal to the relative frequency of good patches present in the next time step and is therefore equal to $\varphi_g(t+1)$, if the butterfly disperses at time t . This is independent of the patch quality from the point of dispersal, and therefore there is no spatial correlation. The chance of reaching a bad patch is $1 - \varphi_g(t+1)$. The seasonal variation is predictable in the sense that when a good patch turns into a bad patch, this patch does not become a good patch again until the next wet season. Hence, the only chance of reaching a good patch is by dispersal. At the very end of the wet season there are so many bad patches that the chance of reaching a good patch is negligible. From year to year, the time at which a specific patch becomes good or bad is variable.

In our model, we separate data by generation, which is possible since we can trace each individual from birth. Individuals born from parents surviving the dry season are called, "first generation, wet season morphs." The offspring they produce are called "second generation, wet season morphs." These produce the individuals that survive the dry season, and these individuals are therefore

called the “third generation, dry season morphs.” Butterflies sometimes survive longer than one generation, but lose the ability to reproduce, so in reality no overlap in generations exists.

Larval Stage

During the larval stage, the state of an individual is described by its body weight. Larvae are located in either a good or a bad patch, with food being available only in a good patch. The growth of a larva depends on its current weight, the availability of food, and temperature. At every time step (day) a larva consumes an amount of food that is partitioned between daily costs and growth. This is modeled as

$$w_L(t + 1) = w_L(t) + E_L(p) \times [i_1 w_L(t)^{i_2 + i_3 T(t)} - c_1 w_L(t)^{c_2 + c_3 T(t)}], \quad (3)$$

where $w_L(t)$ is the weight of the larva with an initial value 1 mg and $E_L(p)$ is the effect of patch quality in the larval stage, taking the value of 0 in a bad patch and 1 in a good patch. The constants i_1 , i_2 , and i_3 relate larval weight and temperature (T) to daily intake and c_1 , c_2 , and c_3 to daily costs. We select the values of these constants so that the model behavior corresponds to larval growth in Lepidoptera. Larval growth follows an S-shaped curve (Parker and Johnston 2006) with an exponential initial phase (Mackey 1978). At lower temperatures growth rate decreases, but final size at pupation increases due to longer development time (Atkinson 1994; Davidowitz and Nijhout 2004; see also fig. A1), and this is also true for *B. anynana* (Oostra et al. 2010). Therefore, we model growth as being faster at higher temperatures but with a lower asymptote of final weight. Pupation can be initiated when a larva reaches a weight larger than the critical weight for pupation, which is assumed to be independent of temperature, but see Davidowitz et al. (2004) and Nijhout et al. (2006). Alternatively, the larva can keep growing and pupate later. These two possibilities generate two different relationships for fitness that are compared in the SDP.

We let $F_L(t, p, w_L)$ denote the maximum accumulated reproductive success of an adult that ultimately emerges from a larva with weight w_L , in patch p at time t . For a larva opting to grow at time t , future fitness is

$$V_{\text{grow}}(t, p, w_L) = \sum_{p'=g}^b \lambda_{pp'}(t + 1) F_L(t + 1, p', w_L) \times S[\mu_L, p(t), p(t - 1)]. \quad (4)$$

We calculate the fitness of this individual for the cases that the patch will be a good patch or a bad patch at time $t + 1$ and sum over these two options using the proba-

bilities ($\lambda_{pp'}$) from equation (2), where p' indicates the patch quality at time $t + 1$. Survival (S) depends on daily mortality (μ_L), which is constant and thus independent of weight, and patch quality at this time step and the former time step ($t - 1$). Starvation is known to increase mortality rates for *Bicyclus* larvae (Bauerfeind and Fischer 2009), which is modeled by a severe reduction in survival if a bad patch is experienced for more than 1 day; they also tend to increase for insect larvae at higher temperatures (Oloumi-Sadeghi and Levine 1989; Padmanabha et al. 2011). See the appendix, available online, for further details.

We let $F_p(t, p, w_p, d)$ denote the maximum accumulated reproductive success of the adult that ultimately emerges, given that the pupa is in a patch of kind p , with pupal mass w_p and developmental state d at time t . Thus, for a larva that pupates, future fitness is

$$V_{\text{pupate}}(t, p, w_L) = \sum_{p'=g}^b \lambda_{pp'}(t + 1) F_p(t + 1, p', w_p, d) \times S[\mu_L, p(t), p(t - 1)]. \quad (5)$$

The developmental state of the pupa is initially zero ($d = 0$), and the pupa will start development in the next time step. Survival is equal to that in equation (4). Again the fitness is summed over both kinds of patches with probabilities (λ) that the individuals will be in a good or bad patch as in equation (4).

The optimal decision (to grow or pupate) is then determined by the larger of the fitness values in equations (4) and (5):

$$F_L(t, p, w_L) = \max(V_{\text{grow}}(t, p, w_L), V_{\text{pupate}}(t, p, w_L)). \quad (6)$$

Pupal Stage

During the pupal stage, an individual’s state is described by weight and pupal developmental state. The development state is temperature- and time-dependent as a fixed number of degree-days are required before the adult can eclose and at higher temperatures it takes fewer days to complete pupal development (Koch et al. 1996; Oostra et al. 2010). For simplicity, pupal mortality (μ_p) is assumed to be constant as there are no data available for *Bicyclus* and data concerning the relationship between pupal size and survival in other Lepidoptera are inconsistent (Tamaru et al. 2002). Using the definition for $F_p(t, p, w_p, d)$ provided in equation (5), future fitness for a pupa that does not eclose and continues to develop is

$$V_{\text{develop}}(t, p, w_p, d) = \sum_{p'=g}^b \lambda_{pp'} F_p(t+1, p', w_p, d') \exp(-\mu_p), \tag{7}$$

where the developmental state increases from d to d' in both a good and a bad patch, given by probability (λ), and survival is given by $\exp(-\mu_p)$.

At the end of the pupal stage, the pupal weight is partitioned into thorax, abdomen, and fat, which represents the second strategic choice in the model. During the pupal stage, the costs for development, growth, and maintenance differ among tissues (Kooijman 2009), which is implemented in the model as follows: for each 10 mg of pupal weight, 10 eggs of 0.1 mg each can develop. This yields a weight ratio from the pupal to the adult stage of 10 : 1 for abdominal tissue; for muscle tissue the corresponding ratio is 2 : 1 and for fat 1 : 1. Although no direct comparison can be made to data, a 90% decrease in muscle tissue in de-alated crickets only led to a doubling of the number of eggs produced (Tanaka 1991). Thus, egg production is most costly, as eggs not only consist of proteins but also need to be maintained in a damage-free condition (Kooijman 2010). The actual tissue-specific costs are unknown, but since exploration of a range of costs shows no qualitative change in the results, we continue with the ones described above, which we consider to be reasonable estimates.

Fitness at the end of the pupal stage depends on the amount of resource allocated to fat, abdomen, and thorax and biological age X (see eq. [11] below) of the adult. Thus, if $F_A(t+1, p', w_f, w_a, w_t, x)$ represents the maximum accumulated reproductive success of an adult that is in patch of kind p with fat, abdominal, and thorax masses w_p, w_a, w_t and biological age x at time t the fitness value of eclosing is

$$V_{\text{eclose}}(t, p, w_p, d) = \sum_{p'=g}^b \lambda_{pp'} F_A(t+1, p', w_f, w_a, w_t, 0) \exp(-\mu_p). \tag{8}$$

The conversion of pupal mass (w_p) to fat, abdominal, and thorax masses depends on the allocation pattern as described above.

If the pupae are in a developmental state lower than the boundary (d_{max}) at which they will eclose, the fitness during this development (eq. [9a]) is equal to that described in equation (7). When the developmental state is equal to or larger than this boundary, the fitness value (eq. [9b]), at eclosion, is determined by the optimization of the allocation to the different adult tissues as described in equation (8). Therefore,

$$F_p(t, p, w_p, d | d < d_{\text{max}}) = V_{\text{develop}}(t, p, w_p, d), \tag{9a}$$

$$F_p(t, p, w_p, d | d \geq d_{\text{max}}) = \max_{\text{allocation}} (V_{\text{eclose}}(t, p, w_p, d)), \tag{9b}$$

where “allocation” refers to all possible ways the energy acquired during the larval stage can be allocated to the adult tissue fat (w_f), abdomen (w_a) and thorax (w_t) as described in equation (8).

Adult Stage

During the adult stage, the state of a butterfly is described by the weight of its tissues (fat, abdomen, and thorax) and its biological age. At every time step, an adult can undertake one of three behaviors, B : to feed, disperse, or reproduce. When feeding, the weight of fat increases. This increase in fat decreases with biological age so as to reflect lower feeding rates (Wong et al. 2009). If the butterfly disperses, fat decreases by an amount dependent on total weight, weight of the thorax, and temperature. Reproduction decreases the number of eggs present in the abdomen, and additionally, the development of these eggs costs 1 mg of fat per egg. The effect of the different strategic choices on the daily changes in fat is summarized as feeding:

$$w_f(t+1) = (1 - q)w_f(t) + I_A - C_A, \tag{10a}$$

dispersing:

$$w_f(t+1) = (1 - q)w_f(t) - C_A - T(t) \times f\{w_f(t), w_t(t), w_a(t)\}, \tag{10b}$$

and reproducing:

$$w_f(t+1) = (1 - q)w_f(t) - C_A - N_{\text{eggs}}, \tag{10c}$$

where $w_f(t)$ is the weight of fat at time t , I_A is daily intake for feeding individuals, C_A are the daily costs, T is temperature, and N_{eggs} represents the cost for laying eggs. The function that relates the weight of fat, abdomen, and thorax to cost of dispersal ($f\{w_f(t), w_t(t), w_a(t)\}$) increases with weight of fat and abdomen, but decreases with thorax. Thus a relatively larger thorax ensures that dispersal is less costly. The variable q represents the proportion of fat used for maintenance and repair, which affects the rate of increase in biological age, $X(t)$. The actual value of q is a strategic choice for adults and can change every time step. Biological age is irreversible and increases at every time step by an amount determined by the energetic investment

in maintenance and repair processes, total weight, and temperature:

$$X(t + 1) = X(t) + \frac{a_1 w_{\text{total}}(t) + a_2 (T(t) - a_3)}{r q w_f(t)}. \quad (11)$$

The parameter r is a conversion constant relating an amount of fat ($w_f(t)$) to an amount of damage repair. Damage increases faster for individuals with more tissue and at higher temperatures. Further constants a_1 , a_2 , and a_3 are also introduced.

Mortality during the adult stage is dependent on predator pressure, biological age, and weight of the adult. Predator pressure is lower in the bad patches compared to good patches corresponding to field observations (Lyytinen et al. 2004; Brakefield and Frankino 2009; Joiris et al. 2010). We model total mortality rate as

$$\mu_{\text{total}} = \mu_x(X(t)) + \mu_{\text{pred}}(p) + \mu_w(w_{\text{total}}), \quad (12)$$

where intrinsic mortality (μ_x) depends on biological age ($X(t)$), predation-related mortality ($\mu_{\text{pred}}(p)$) depends on patch quality, and weight-related mortality ($\mu_w(w_{\text{total}})$) depends on total weight. The latter sets a lower boundary for the weight at which butterflies can still survive. Mortality due to biological age is

$$\mu_x(X(t)) = a_4 + a_5 \exp(a_6 X(t)), \quad (13)$$

where a_4 , a_5 , and a_6 are constants.

The future fitness for an adult following behavior B (see eq. [10]) is

$$V_{B,q}(t, p, w_f, w_a, w_t, X) = \sum_{p'=g}^b \lambda(B) F_A\{t + 1, p', w'_f, w'_a, w'_t, X'\} + N_{\text{eggs}}(B) F_L(t, p, 1) \Delta(B) \exp(-\mu_{\text{total}}), \quad (14)$$

where B represents the decision for behavior (see eq. [10]). The chance of reaching a certain type of patch in the next time step (λ) is dependent on behavior since in the adult stage the adult can either feed or reproduce, and λ will then be calculated using equation (1), or disperse, when λ will be calculated using equation (2). When individuals lay eggs, $N_{\text{eggs}}(B)$ is 10; otherwise it is 0. Each egg, equivalent to a larva of weight 1 mg, provides a fitness benefit of $F_L(t, p, 1)$, which is dependent on patch quality (p) and (t) and equivalent to the fitness of a larva with a weight of 1 mg from equation (3). The reason for modeling $F_L(t, p, 1)$ as dependent on patch quality and time is that larvae cannot survive in the dry season. Therefore, eggs laid by a butterfly in the dry season would be expected to result in a lower fitness benefit than those laid in the wet season.

Survival ($\exp(-\mu_{\text{total}})$) is multiplied by a term ($\Delta(B)$), which is required because survival is affected by dispersal and takes a value of 0.75 for individuals that disperse, otherwise it is 1. The change in biological age from X to X' depends on q , the amount of energy allocated to maintenance and repair.

The optimal decisions for B and q give the maximum accumulated reproductive success of an adult, $F_A(t, p, w_f, w_a, w_t, x)$:

$$F_A(t, p, w_f, w_a, w_t, x) = \quad (15)$$

$$\max_{B,q} V_{B,q}(t, p, w_f, w_a, w_t, x).$$

Backward Iteration

We determine the optimal strategies by finding the maximum value for fitness from equations (6) for the larval stage: 9 for pupae and 15 for adults. The SDP algorithm, which works backward in time, is initiated at a nominal time horizon by assigning the fitness for all larvae with a weight of 1 mg (newly born) a value of 1, that is, $F_L(t, p, 1) = 1$ in equation (4). The fitness of all other states are 0. As the environmental parameters between years for a given time step are the same, the fitness values on a specific day for each combination of states converge to a single value. Following convergence, the fitness values and optimal strategies for each state are stored to be used for forward simulations.

Forward Simulation

In the forward simulation we model two scenarios. Firstly, individuals are simulated by the introduction of 100 larvae of a size of 1 mg at the start of the wet season (time step 175). The temperature and proportion of good patches used for these simulations are the same as those used in the backward iterations; see table S1, available online. The output is the numbers of individuals, their life-history strategies, and their traits. Second, we simulate the experimental setup of Saastamoinen et al. (2010). In our model, there are good and bad patches, and during the backward optimization, the patches vary seasonally. In the laboratory experiment, one group was fed optimal food as larvae throughout development, while another was starved in the last stage of larval development. For the model, all patches are assumed to be good at the start of a forward simulation but all turn into bad patches when food manipulation during the larval stage is needed. In the optimization, the adults can choose to feed, fly, or reproduce. During the forward simulation, adults are forced to perform a series of flight bouts by fixing their strategy to flight rather than following their optimal strat-

Table 1: Life-history traits and strategies separated by generation and patch quality

	Wet season form 1		Wet season form 2		Dry season form	
	Good	Bad	Good	Bad	Good	Bad
Larval and pupal strategies	<i>N</i> = 19,759	<i>N</i> = 407	<i>N</i> = 83,486	<i>N</i> = 11,484	<i>N</i> = 863	<i>N</i> = 200,274
Size at pupation	138.7 (17.9)	151.2 (21.9)	145.8 (22.9)	141.8 (18.8)	239.5 (1.2)	179.9 (32.5)
Allocation fat	.48 (.02)	.45 (.01)	.46 (.022)	.46 (.04)	.45 (.00)	.47 (.02)
Allocation abdomen	.47 (.02)	.41 (.02)	.49 (.023)	.44 (.02)	.45 (.00)	.47 (.02)
Allocation thorax	.05 (.00)	.14 (.03)	.05 (.01)	.10 (.05)	.10 (.00)	.06 (.02)
Adult optimal behavior	<i>N</i> = 60,782	<i>N</i> = 42,396	<i>N</i> = 55,912	<i>N</i> = 67,411	<i>N</i> = 127,158	<i>N</i> = 526,666
Proportion feeding	.78 (.002)	1.00 (.000)	.67 (.001)	.99 (.000)	1.00 (.00)	1 (0)
Proportion reproducing	.21 (.002)	0 (0)	.29 (.002)	0 (0)	.00 (.00)	0 (0)
Proportion dispersing	.01 (.000)	.00 (.000)	.00 (.001)	.01 (.000)	.00 (.00)	0 (0)
Body composition adults	<i>N</i> = 60,782	<i>N</i> = 42,396	<i>N</i> = 55,912	<i>N</i> = 67,411	<i>N</i> = 127,158	<i>N</i> = 526,666
Proportion fat	.37 (.002)	.40 (.002)	.39 (.002)	.31 (.002)	.03 (.000)	.28 (.001)
Proportion abdomen	.48 (.002)	.43 (.002)	.50 (.002)	.61 (.002)	.84 (.001)	.63 (.001)
Proportion thorax	.15 (.001)	.17 (.002)	.11 (.001)	.08 (.001)	.13 (.001)	.09 (.001)
Adult traits	<i>N</i> = 60,782	<i>N</i> = 42,396	<i>N</i> = 55,912	<i>N</i> = 67,411	<i>N</i> = 127,158	<i>N</i> = 526,666
Fecundity	44.6 (16.9)	40.6 (3.2)	23.3 (27.1)	3.9 (12.8)	1.1 (3.1)	.0 (.2)
Age	16.9 (14.8)	57.5 (26.5)	16.9 (38.6)	79.6 (63.4)	230.3 (32.6)	88.7 (61.0)
Biological age	16.6 (15.9)	51.0 (20.2)	9.7 (19.3)	30.1 (30.1)	105.4 (38.6)	23.0 (25.2)
Fat used per day for repair	.24 (.13)	.26 (.06)	.66 (.55)	.63 (.33)	.20 (.09)	.87 (.49)

Note: Average values (SD) of indicated strategies and traits for the different stages (larval, pupal, and adult) of the three generations in good and bad patches. Larval and pupal traits are measured once, while those of the adults were measured every day in the life of the individual. The *N* indicates the number of individuals in a single simulation.

egy in the first few time steps but can then behave optimally according to when in the seasonal cycle they live (first, second, or third generation).

States and Strategic Decision Possibilities

We discretize state variables as detailed in the supplemental material (table S2). For the strategies, in every time step, larvae can choose to start pupation. Pupae can allocate from 5% to 90% to every tissue, in steps of 5% with the total constrained to 100%. Adults can choose one behavior from feeding, dispersal, reproduction in each time step. Also they can reallocate energy to maintenance and repair for 0%–8% of the fat tissue every day in 10 steps between 0% and 8%. In initial runs of the model, no individual ever spent more than 8% on maintenance and repair; therefore, we reduce the choice to this number.

Typically in a state dependent model a robustness test is performed. This is carried out by altering the parameters systematically and checking whether the optimal strategic decisions and overall results show dramatic changes. If such sensitivity is displayed, then the generality of the

results is limited; however, if the results are stable, the generality is increased. In the appendix, available online, a detailed description is given of the robustness tests we perform. Most of the results are qualitatively stable, except for the number of generations, which can be altered by varying larval growth rates (i.e., by changing parameter $E_L(p)$ in a good patch, eq. [3]).

Results

Population and the Seasonal Life-History Strategies Based on the Model

The numbers of larvae, pupae, and adults in good and bad patches in the model are shown in table 1 and figure 2. As in the wild, the dry season morph survives throughout the dry season without reproducing, and reproduction is initiated at the start of the next wet season. The first wet season generation of butterflies will produce the second wet season generation, which in turn produces offspring that survive over the next dry season.

Most larvae (98.0%) in the first wet season generation

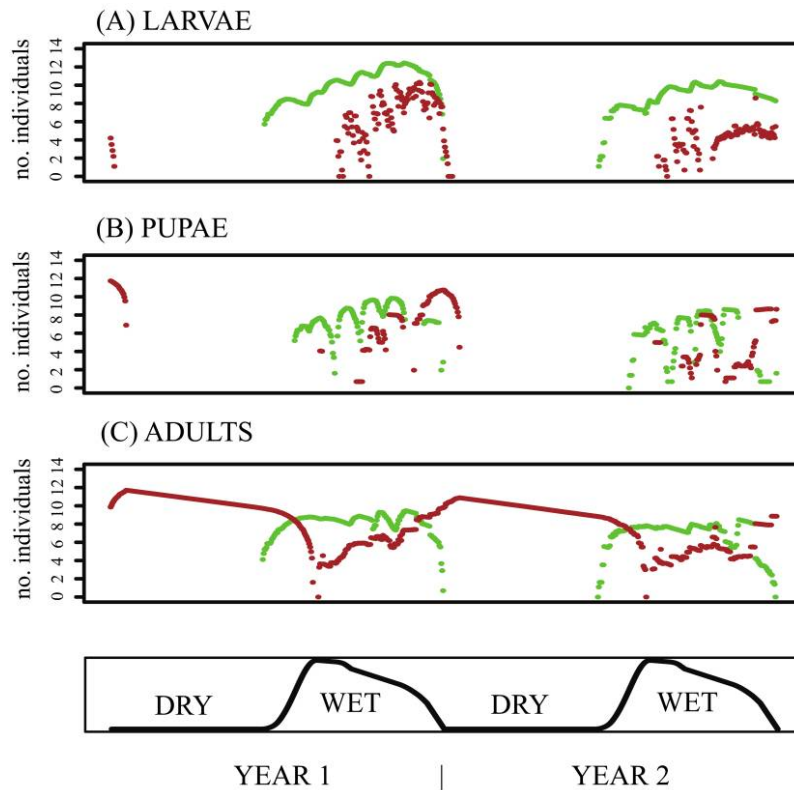


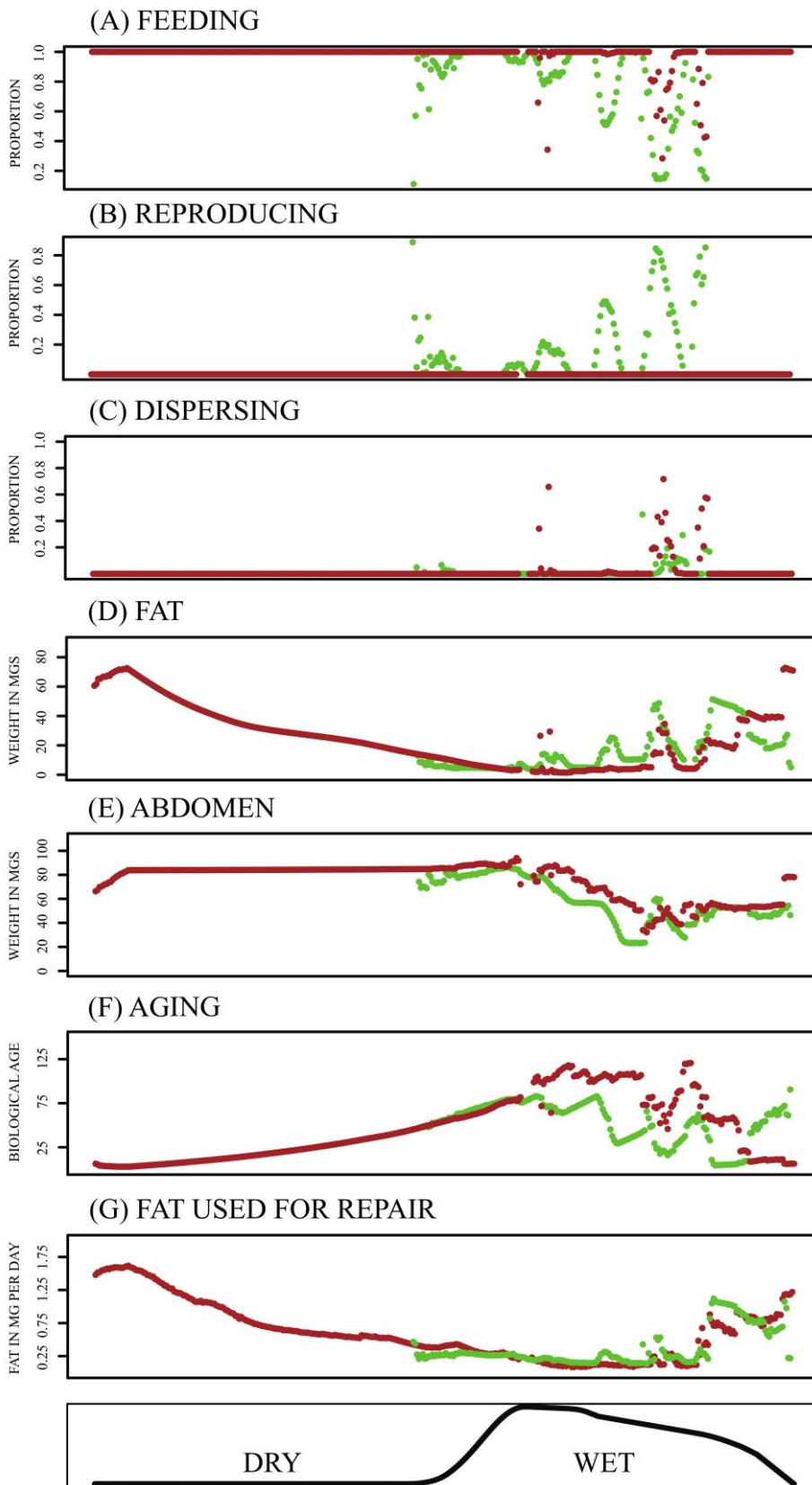
Figure 2: Number (log transformed) of individuals (A, larvae; B, pupae; C, adults) across the seasons in good (green) and bad (brown) patches. Each point indicates the number of individuals on a specific time step (day) during the simulation. Two years are simulated, consisting of two dry and two wet seasons, as indicated below the graphs. In the lowest panel, the line represents the proportion of good patches in each time step.

pupate in good patches, while this number is reduced (87.9%) in the second generation. If during larval growth a patch changes from good to bad, larvae initiate pupation. In the dry season generation, most larvae are in a patch that changes from good to bad, and therefore, they start to pupate in a bad patch (99.5%). Based on our model, the average pupation size is larger in the first than in the second wet season generation (table 1; fig. S2, available online). Individuals in the third generation (dry season) are on average the largest (table 1; fig. S2). Those larvae of the second wet season generation that pupate later, do so at a smaller size even in good patches, which explains the variation in size. Within the dry season, higher variance is explained by habitat heterogeneity and consequently by the fact that some individuals are able to prolong their growth and increase their size, whereas others run out of food and remain small.

Life-history strategies (summarized in table 1) are determined by the resource allocation patterns of individuals, as those with larger abdomens can lay more eggs, while those that allocate resources into thorax require less energy

for a single dispersal event between patches. Fat is used as storage to support activities such as egg production, dispersal, and damage repair. During the pupal stage, individuals of the first wet season generations allocate more to fat than abdomen when they are in good patches, while this is reversed in the second wet season generation (table 1; fig. S3). Individuals of the two wet season generations in bad patches allocate more resources to fat than to abdomen, while dry season individuals allocate equal to fat and abdomen in good and bad patches (table 1; fig. S3). Individuals of the wet season generations allocate much more to thorax in bad, compared to good patches, indicating investment in dispersal (table 1; fig. S3).

As adults, individuals have a choice of feeding (acquiring more resources), reproducing, or dispersing, and these behaviors are highly dependent on season and patch quality. Since only bad patches are available during the dry season, all individuals feed in order to survive the dry season (fig. 3A). Reproduction is not beneficial in terms of fitness, as the larvae would not survive. Reproduction only takes place in good patches (table 1; fig. 3B). Individuals in the wet



season that are still able to reproduce but are in a patch that changes from good to bad, disperse (table 1; fig. 3C). In every generation some individuals also disperse from good to bad patches (table 1; fig. 3C), but these individuals have lost the capacity to reproduce as they have insufficient fat storage (not shown), and hence their behavior does not influence their fitness or the number of larvae in the population. Young individuals without fat reserves can take up energy and regain the capacity to reproduce, whereas old individuals that survived the dry season cannot.

In the wet season, adults use fat mostly for reproduction (fig. 3D), whereas in the dry season, individuals do not reproduce or disperse and rather use fat to reallocate resource to maintenance and repair (fig. 3G). Therefore, butterflies age more rapidly in the wet season compared to the dry season (fig. 3F).

Finally, the average life span differs among the three generations and is highest in the dry season morph, when butterflies can only reproduce at an advanced age as the next wet season begins (table 1; fig. 2). Due to lower survival and reproduction at an older age, the average fecundity in the dry season generation is much lower than in the two wet season generations (table 1; fig. 2). Within the wet season, individuals of the first generation have a lower life span but higher fecundity compared to the second generation (table 1). In good patches, fat used for maintenance and repair per day is highest in the second wet season generation, while in bad patches, it is highest in dry season individuals (table 1).

Predictive Adaptive Response

We test whether food shortage during the larval stage or an increase in dispersal events during the adult stage influenced life span and fecundity. Figure 4 shows the effect of larval food manipulation on thorax ratio and early fecundity compared to the previous laboratory experiment. Both in the experiment and in the model, the thorax ratio is higher for individuals that were restricted during late larval development (fig. 4A, 4B). In the experiment, early fecundity was lower for individuals that were food restricted (fig. 4C). In the model, the abdomen weight (proxy for fecundity) is also lower for restricted individuals (fig. 4D). The percentage of thorax in the experimental butterflies was 24.1% and 25.7% of the total body weight for ad lib. and restricted individuals, respectively (Saastamoinen et al. 2010), while in the model these values are lower, 5.0% and 10.0%. The standard de-

viation of the thorax ratio is larger in the bad patch individuals in the model prediction. This is because the timing of encountering a bad patch varies widely among individuals, leading to higher variation in their weight compared to those in good patches.

Figure 5 shows the effect of larval and adult manipulation on life span and fecundity. These two traits are less affected by the adult treatment (forced flight events) when larvae had experienced food limitation, compared to individuals with an optimal larval period in the wet season (fig. 5). This is because in both wet season generations, allocation to the thorax is higher for individuals deprived of food in the late larval stage (data not shown). In the wet season, life span is positively related to flight events, while fecundity is negatively related to flight events for individuals with an optimal larval period (fig. 5). For individuals that experience food shortage during the larval stage, life span and fecundity are both largely unaffected by the adult treatment. Larval treatment groups do not respond differently to adult treatment for dry season individuals (fig. 5). When comparing the results between model and experiment, the effects of flight on fecundity are more similar than those on life span (fig. 5), as the optimally reared individuals have decreased fecundity when forced to fly, both in the model and in the experiment. Fecundity and life span within a larval treatment group are negatively related in the model, while in the experiment they were positively related.

Discussion

In this study we describe a state-dependent energy allocation model of the life history of *Bicyclus anynana*, which we use to test whether a specific plastic response observed under laboratory conditions could potentially be adaptive in nature. Food-restricted larvae in both the experiment and the model allocated more energy to dispersal ability, which in the model made them more likely to reach a good-quality patch and hence reproduce successfully. We thus conclude that a predictive adaptive response evolved in *B. anynana*. However, this specific predictive adaptive response is likely to be only adaptive in one of the seasons, the wet season, as in the dry season no extra allocation to dispersal ability occurred in response to larval food restriction. This is expected as the benefit of increased dispersal is lacking in this season due to lack of good-quality habitat patches.

Figure 3: A–C, Proportion of individuals feeding, reproducing, and dispersing (in respective order). D, E, Average weight of fat tissue and abdomen; F, G, variation in aging and the amount of fat used for repair. The data represent individuals in good (green) and bad (brown) patches dependent on the seasonal variation, which is indicated by the bar below the graph (where the line represents the proportion of good patches in each time step).

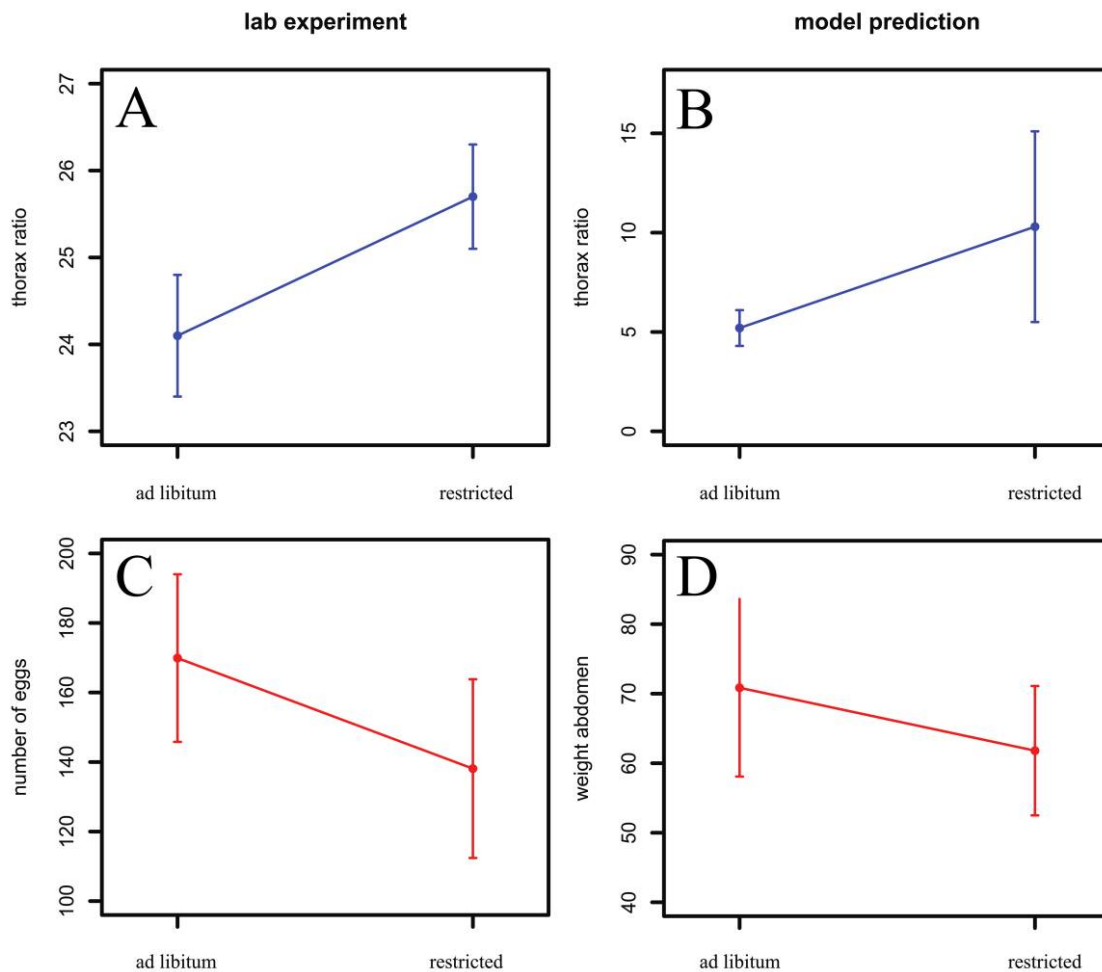


Figure 4: Comparison between the experimental data and the model predictions. *A, B*, Average thorax ratio (\pm SD) in the experiment and in the model, respectively, from one simulation. The lower panels show the mean number of eggs (\pm SD) during the first 2 weeks in the experiment (*C*) and the weight of the abdomen in the model (*D*).

Life History and Seasonal Variation

Seasonal change in our model consists of variation in temperature and the percentage of good patches, both of which are lowest in the dry season and peak in the wet season. This pattern is comparable to measurements taken from the site where *B. anynana* has been studied in Malawi (Brakefield and Reitsma 1991; Windig et al. 1994). Similarly, predicted seasonal population dynamics emerge from the model as the dry season form adults delay their first reproduction and initiate it only early in the wet season to yield the first generation of the wet season form. This generation then produces a second wet season generation, which is followed by a new dry season generation.

An important question for any state-dependent energy-allocation model is to consider the relationship between the assumed physiological rules and the inferred optimal

behavior. In our model, larval growth is influenced by temperature, so that at higher temperatures growth rate is higher but maximum possible size is lower, as is common for insects (Atkinson 1994; Davidowitz and Nijhout 2004). In the dry season, individuals are, on average, larger, and temperature is lower. Therefore, we expect the optimal life-history decision to be to prolong larval growth. This is partly facilitated by the assumed physiology in the model, since larvae can reach a higher plateau of size at lower temperatures. In a version of the model in which temperature do not influence larval growth, the size differences between the different generations of butterflies remain, suggesting that another factor additional to the assumed physiology contributed to the size variation. A possible explanation is that optimal size varies between seasons, and that larger body size is favored in the dry season.

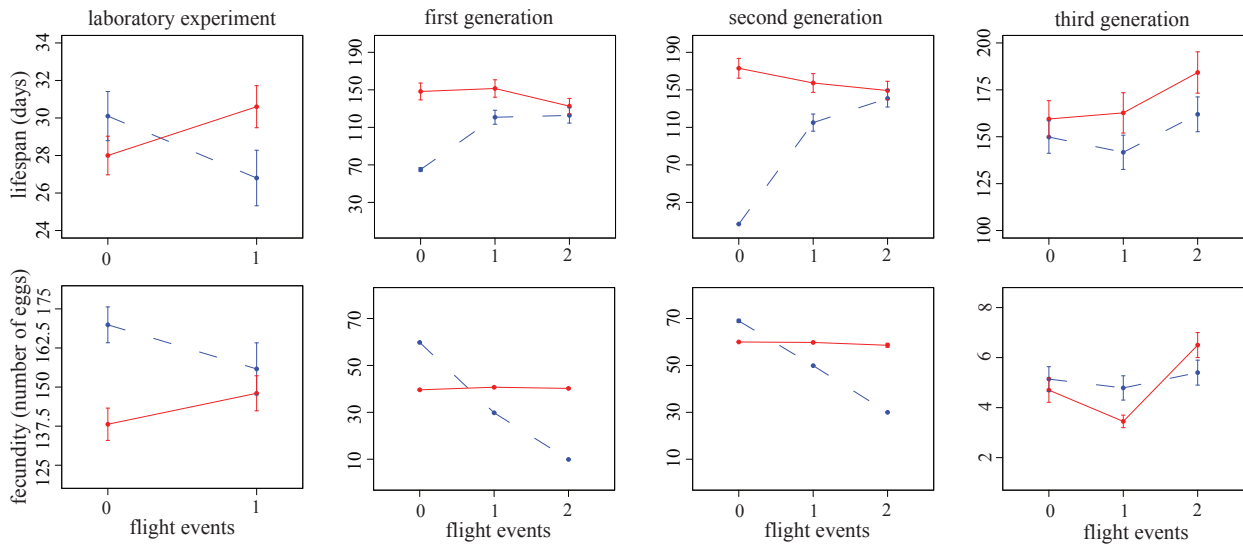


Figure 5: Comparison of the data acquired in the laboratory experiment and the first, second, and third generation of butterflies in the model. Top and bottom rows present life span and fecundity, respectively. Note that the Y-axis might differ per subgraph. Individuals that were food restricted as larvae are shown in red (solid lines), and individuals from the optimal larval treatment are shown in blue (dashed lines). Error bars indicate standard errors for mean values.

In addition to variation in size, we also find variation in allocation patterns, which vary with the generation and the quality of the patches in which the larvae are present. We find a large number of larvae in the second wet season generation in patches that change from good to bad in quality. Our model shows that when this occurs, individuals allocate more resources to their thorax during the pupal stage, which is comparable to the findings of earlier laboratory studies (Saastamoinen et al. 2010). An increased thorax ratio allows individuals to disperse more easily to a new, good-quality patch, where they can successfully reproduce. In our model, we presume that individuals that allocate more to thorax during the pupal stage use less energy per flight event based on the observation that individuals with a higher thorax ratio are better fliers (Marden 2000). Thus the cue of food deprivation during the larval stage directs the allocation pattern in the pupal stage towards a more optimal phenotype (i.e., higher thorax ratio). The pupae of the dry season generation do not show this allocation pattern, since the allocation to thorax is equal in bad- and good-patch individuals. The model's prediction is thus that in the field, pupae from dry patches with low-quality plants will allocate more to the thorax during the middle of the wet season when some good patches remain. Later in the wet season, this allocation to the thorax becomes less favorable because the likelihood of reaching a good patch decreases as the number of bad-quality patches increases.

Predictive Adaptive Response

The second aim of the model is to test whether the environment of *B. anynana* is expected to favor evolution of a predictive adaptive response. Experiments had previously shown that individuals reared as the wet season form had an increased resistance to adult manipulation (flight stress) when food restricted during the final larval stage (Saastamoinen et al. 2010). Interestingly, in our model, individuals are also less affected by this adult treatment if they are food restricted during the final larval stage. The increased ability to cope with forced flight events is facilitated by an increase allocation to thorax in the model, consistent with what was observed in the experiment (Saastamoinen et al. 2010). The relationship between food limitation, increased thorax ratio, and resistance to increased flight events does not appear in the model for the dry season generation.

The patterns of relative response to food manipulation in the experiment and in the model with respect to allocation to thorax are thus very similar. However, the thorax ratio in the model is, on average, lower than in the experiment (fig. 4A, 4B). This difference can be explained by a lack of detailed realism concerning the function of the thorax in the daily routine movement of a butterfly. In the model, the thorax is not necessary in the search for food or mating partners but only for dispersal. However, the argument that increasing thorax ratio in restricted conditions is adaptive is supported by the model, which suggests that these adaptations can be studied in this type of model.

In addition, Oostra et al. (2010) showed that the relative thorax weight is higher for individuals reared on good-quality plants as dry season morphs compared to wet season morphs, which is true in our model for the individuals in good patches (but not in bad patches; fig. S3).

There are also differences between the model and experiment in the results concerning the relationship between fecundity and life span, a positive correlation between these traits being found only in the experiment. This difference may be partially due to any allocation to fecundity leading to a larger increase in intrinsic mortality rate in the model. In reality, a number of other traits are also likely to covary with fecundity and life span (e.g., immunological responses, metabolic rate, activity, stress resistance; Boggs 2009), but such relationships are not included here. Since the larvae in both the model and experiment are treated equally, the inconsistency is unlikely to be caused by a difference in acquisition during the larval stage, which may potentially also lead to positive relationships between life-history traits (De Jong and Van Noordwijk 1992).

We have modeled an organism that lives for a short time compared to the length of the seasonal period (i.e., shorter than a year). Besides sampling the environment directly (Krebs et al. 1978; Mangel and Roitberg 1989), information can additionally be passed on via maternal effects. Whether it is adaptive to pass on information from one generation to the next is very much dependent on the life span compared to the length of a seasonal period (Lachmann and Jablonka 1996). The type of maternal effect that evolves is likely to be highly dependent on parameters such as life expectancy, environmental fluctuations and predictability, presence of parent-offspring conflict, and constraint and costs of producing offspring with specific phenotypes (Marshall and Uller 2007). These will be quite different between long-lived organisms and short-lived insects, and therefore, it is unlikely that any maternal effects in the modeled organism could be translated to the cases of long-lived organisms. A model as described here can be made for long-lived organisms though, when agreement is reached about the relevant ecological parameters. Such an approach is likely to benefit the discussion around PAR.

In conclusion, the evolution of developmental plasticity resulting in the two distinct adult morphs emerged as a robust prediction of the model. In addition, we show that a short-lived organism, such as *B. anynana*, living in a seasonal environment can evolve a PAR. The model is based on the considerable biological and ecological knowledge we have on this species, accumulated through extensive field and laboratory studies. However, even without this extensive knowledge state-dependent modeling is a valuable tool as it allows for freedom of parameters. The combination of modeling and experiments promises to be a constructive

way to test the adaptive value of plasticity in this species and potentially in others, as it facilitates the evolutionary and ecological interpretation of laboratory experiments.

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Bicyclus anynana. Photo by Oskar Brattström.