Appendix from J. van den Heuvel et al., "The Predictive Adaptive Response: Modeling the Life-History Evolution of the Butterfly *Bicyclus anynana* in Seasonal Environments"

Mathematical Equations

In this appendix, mathematical descriptions of metabolism and the effect of strategic decisions on the traits are given. Energy uptake and use for specific processes depend on the environment and state of the organism. Strategic choices can influence how energy is invested. The different strategic choices represent either genetic variation or plastic responses. The model calculates which strategy is the best in which environment. The equations of which the model consists will be described for each stage (larva, pupa, adult) of the life history. We then describe how the environment is modeled with respect to patch quality and its changing nature. All constants and variables that take two levels (patch quality, predation pressure) are listed in table A1.

Larval Stage

The most important feature of larvae is that they feed. There are also daily costs that are directly paid from intake. Growth is modeled as income minus the daily costs. In a bad patch, no food for larvae is available.

In this model every time step (day) a larva consumes an amount of food that is partitioned between daily costs and growth. This is modeled as,

$$w_L(t + 1) = w_L(t) + E_L(p)[i_1 w_L(t)^{i_2+i_3 T(t)} - c_1 w_L(t)^{c_2+c_3 T(t)}], \tag{A1}$$

where w_L is the weight of the larvae and $E_L(p)$ is the effect of patch quality that varies between 0 and 1 bad and good patches. The constants i_1, i_2, and i_3 relate weight and temperature with intake and constants c_1, c_2, and c_3 relate weight and temperature to maintenance costs. These constants are chosen in such a way that larvae grow faster at higher temperatures but can reach a larger size at lower temperatures (Parker and Johnston 2006).

Figure A1 shows the effect of temperature on larval growth. Because the value of i_3 is lower than c_3, the plateau reached in the late stage of growth is higher at lower temperatures. The manipulation of the constants i_1 and c_1 together lead to a change in relative growth rates between temperatures but not in the plateaus the larvae can reach. In the power functions, the effect of temperature is multiplied by i_3 and c_3 and then added to i_2 and c_2 because otherwise the effect of an increase in temperature would lead to a very large decrease in the final growth plateau, which is not biologically realistic.

Intake is dependent on surface area of the organism and daily costs depend on volume (Kooijman 2010). In the model this is realized by a larger value of $c_2 + c_3 T(t)$ than $i_2 + i_3 T(t)$. The growth curves at different temperatures have an S shape (fig. A1). Larvae grow slower at lower temperatures but can potentially reach a higher weight because of a higher growth plateau at lower temperatures, as has also been shown for larvae of the phantom midge (*Chaoborus flavicans*; Hanazato and Yasuno 1989; Atkinson 1994).

To test robustness, the parameters $E_L(p)$, i_2, i_3, c_2 and c_3 are varied. When $E_L(p)$ increases, overall growth rate also increases. This changes the number of generations from three to four, but does not increase the size of each generation. The size difference between the first and second wet-season generations remains similar. Also, the average size of the dry season form is larger than any other generation of butterflies. Another test is whether the size differences between generations are influenced by temperature dependent growth. Constants i_3 and c_3 are reduced to zero, and i_2 and c_2 increased to maintain the same average growth rate. Absolute size differences between generations of butterflies are altered, but relative differences remain the same.

Larval mortality is dependent on predation risk, food availability, and temperature, when larvae are deprived of food. Predation risk is independent of size. Although tests have been done that relate predation risk to weight in butterfly

larvae, this risk may vary between species and is dependent on the type of predator and background (Mand et al. 2007; Remmel and Tammaru 2009). Here we model predation risk as

$$\mu_L = P_L, \tag{A2}$$

where P_L is predation risk of larvae. Survival of larvae in a good patch is equal to survival in a bad patch if it is the first day for the larvae in a bad patch:

$$S = \exp(-\mu_L). \tag{A3}$$

When the larvae continue to be in the bad patch for more than 1 day, survival is further reduced. This is modeled as

$$S = \{s_1 + s_2 T(t)\} \exp(-\mu_L). \tag{A4}$$

The constants s_1 and s_2 relate the survival decrease in a bad patch to $T(t)$, which is temperature. This extra reduction in survival is necessary since larvae cannot live very long without food. The constants we use are based on an experiment where larvae of *Bicyclus anynana* were starved for different numbers of days (Bauerfeind and Fischer 2009). Increase in temperature negatively affects survival under starvation (Oloumi-Sadeghi and Levine 1989; Padmanabha et al. 2011); therefore, in our model constant s_2 is negative.

At a point called the "critical weight," the larvae have reached a size at which they can start pupation. The critical weight is associated with a decline in growth rate and in this model is assumed to be independent of environmental factors, but see Davidowitz et al. (2004) and Nijhout et al. (2006). In the model, the extra weight increase after the critical weight is not fixed. As a strategic choice, the model admits the possibility of further growth. Individuals that choose to grow larger are less likely to reach the pupal stage, because it takes more days to grow, and thus, the cumulative mortality is higher. During the larval stage individuals thus have a choice along the axis of trade-off between the size at pupation (and thus adult size) and the chance to survive until pupation and adulthood.

Pupal Stage

During the pupal stage the individuals develop the organs specifically needed for adult life. The amount of time needed is dependent on temperature. A fixed number of degrees of temperature multiplied by number of days, is necessary to complete this developmental stage. This is modeled as

$$D(t + 1) = D(t) + d_1 T(t), \tag{A5}$$

where D represents the developmental state during pupal stage in units degrees $\times$ days. At higher temperatures, pupal development is shorter (Koch et al. 1996; Oostra et al. 2010). Weight is positively related to survival in the laboratory and negatively related to survival in a test with predators for *Orygia* species (Tammaru et al. 2002), but the field situation is not known for *Bicyclus*. Pupal survival is modeled as a fixed predatory pressure with

$$\mu_P = P_P, \tag{A6}$$

and survival is modeled as for the larval stage, that is,

$$S = \exp(-\mu_P). \tag{A7}$$

Because at lower temperatures development takes longer, the cumulative survival of pupae at lower temperatures is reduced.

As pupae become fully developed, they must divide their energy between tissue (which becomes fat as storage; abdomen, which contains eggs; and thorax for dispersal ability). These tissues are not uniformly costly. To produce one egg, 1 mg of pupal energy must be paid. During the adult stage, to produce an egg, this egg has to be matured, which also costs 1 mg. The weight of an egg when it is not matured is 0.1 mg, which makes egg production 10 times more costly than mere weight. One milligram of pupal weight can be developed into 0.5 mg of thorax tissue. Fat can be transferred from the pupal to adult stage as a 1 : 1 ratio. These ratios of tissue conversion mean that pupae will generally lose weight and adults become lighter in weight than pupae.

Because measurements of the costs of specific tissues are not yet available, a robustness test is done with equal costs

for fat, abdomen, and thorax. This leads to an increase in fat in all generations of butterflies but does not alter the allocation differences and behavior between good- and bad-patch individuals.

Adult Stage

Adults can feed, disperse, or reproduce. Each activity has different effects on the amount of fat storage. Energy can also be put into reducing ageing and thus the intrinsic mortality rate.

Adult weight is divided in three parts:

$$w_{\text{total}} = w_{\text{f}} + w_{\text{a}} + w_{\text{t}}, \tag{A8}$$

where w_{f} is the weight of the fat, w_{a} is the weight of the abdomen, which contains the eggs, and w_{t} is the weight of the thorax, which enables dispersal.

During each time step, adults must pay daily costs. This is modeled as

$$C_{\text{A}} = f(T)c_4 w_{\text{total}}^{c_5}, \tag{A9}$$

where C_{A} are the daily costs, constants c_4 and c_5 relate weight to the costs, and $f(T)$ is a function of temperature:

$$f(T) = 1 + t_1\{T(t) - T_{\text{min}}\}, \tag{A10}$$

where t_1 and T_{min} are constants. Although the actual costs for specific processes within and between organisms might differ, costs decrease overall with a decrease in temperature (Kooijman 2010). In the model, temperature is also positively related to intake (eq. [A17]) and daily costs (eq. [A9]) at each time step through $f(T)$ (eq. [A10]).

Intrinsic mortality rate is modeled as an indicator of biological age. Biological age, X, increases with each time step, which depends on repair, temperature, and weight. This is modeled as

$$X(t + 1) = X(t) + \frac{a_1 w_{\text{total}}(t) + a_2(T(t) - a_3)}{rq w_f(t)}, \tag{A11}$$

where a_1, a_2, and a_3 are constants. The constant r relates the amount of repair to an amount of energy allocation from fat. A part of the fat, q, is used to repair damage and thus to decrease the rate of aging. As in other models, the increase in biological age increases partly as a function of volume, which is here represented by weight (Mangel 2008). Intrinsic mortality rates in *Drosophila melanogaster* were previously shown to be positively related to temperature at a population level (Miquel et al. 1976) as well as the molecular level (Jacobson et al. 2010).

Adult mortality has three different causes. The first is intrinsic mortality that increases exponentially with biological age as

$$\mu_X(X(t)) = a_4 + a_5 \exp(a_6 X(t)), \tag{A12}$$

where a_4, a_5, and a_6 are constants.

The second mortality cause is predation, which is a constant that depends on the patch quality, since the butterflies have a conspicuous coloring in a good (green) background but a cryptic one in a bad (brown) background (Brakefield and Frankino 2009):

$$\mu_{\text{pred}}(p) = P_{\text{A}}(p), \tag{A13}$$

where $P_{\text{A}}(p)$ is a function of patch quality. Predation pressure takes values 0.02 and 0.01 in a good and bad patch, respectively.

The third cause of mortality is associated with weight. There is a lower boundary for weight, below which butterflies cannot survive. Weight-dependent mortality is modeled as

$$\mu_{\text{W}}(w_{\text{total}}) = \frac{w_1 \exp(w_2 w_{\text{total}})}{w_3 + \exp(w_2 w_{\text{total}})}, \tag{A14}$$

where w_1, w_2, and w_3 are constants.

Total adult mortality per time step is thus

$$\mu_{\text{total}} = \mu_X(X(t)) + \mu_{\text{pred}}(p) + \mu_{\text{w}}(w_{\text{total}}), \tag{A15}$$

and survival is modeled as

$$S = \exp(-\mu_{\text{total}}). \tag{A16}$$

Adults can exhibit a range of behaviors, each associated with some additional considerations, as follows.

Feeding

Feeding adults gain an intake-based income dependent on weight, biological age, and temperature. Income increases with temperature and decreases with biological age and is modeled as

$$I_A = E_A(p)i_4 W^{i_5} f(T)f(X), \tag{A17}$$

where $E_A(p)$ is the effect of patch quality in the adult stage, i_4 and i_5 are constants that relate weight to intake (Molleman et al. 2005), $f(T)$ is a function of temperature according to equation (A10) and $f(X)$ is a function of biological age according to

$$f(X) = 1 - a_7 X. \tag{A18}$$

The rates of several processes linked with intake and food digestion are positively associated with temperature in a variable number of taxa (Angilletta 2009). Biological age is negatively related to intake because it is expected to relate to all functions including feeding. In fruit flies, feeding has been shown to decrease with age (Wong et al. 2009).

Daily costs are subtracted from the amount of fat, while income is added to the fat, which is modeled as

$$w_f(t+1) = (1-q)w_f(t) + I_A - C_A, \tag{A19}$$

where I_A is income and C_A represents daily costs. The weight of the thorax and abdomen does not change while feeding. The fraction of the fat that remains after allocation to repair is $(1-q)$.

Flying

For flying individuals, fat is reduced further, according to

$$w_f(t+1) = (1-q)w_f(t) - C_A - T(t)f_1 \frac{f_2 + w_f(t) + w_a(t)}{w_t(t)^{f_3}}, \tag{A20}$$

where f_1, f_2, and f_3 are constants; w_a is the weight of the abdomen; and w_t is the weight of the thorax. When the weights of the fat and abdomen are high, flying is more costly. With a larger thorax, flying is less costly. Total weight has been shown to influence the costs of moving (Bejan and Marden 2006), and butterflies with higher thorax ratios have a better flight performance (Berwaerts et al. 2008). Flight is considered to be a cost for storage since it can influence how fast energy can be allocated to other functions such as reproduction, which has also been shown to need energy from the fat body in the butterfly *Pararge aegeria* (Gibbs et al. 2010).

Reproducing

When an individual reproduces, the number of eggs present in the abdomen decreases, and fat decreases by an amount of 1 mg per egg. Fat is further depleted by reallocation of energy to repair and maintenance and daily living costs:

$$w_f(t+1) = (1-q)w_f(t) - C_A - N_{\text{eggs}}, \tag{A21}$$

where N_{eggs} is the number of eggs produced by a female.

The abdomen contains the eggs. When an individual reproduces the abdomen is decreased in a similar fashion,

$$w_a(t+1) = w_a(t) - 0.1 N_{eggs}. \tag{A22}$$

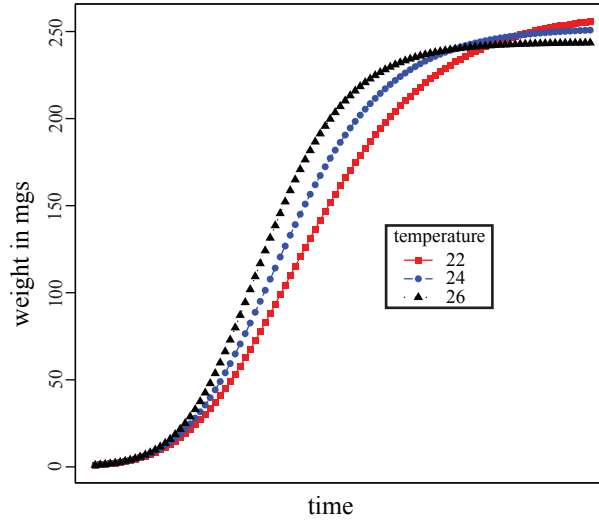Because one egg weighs 0.1 mg, abdomen is reduced 0.1 mg per egg.

Figure A1: The effect of temperature on growth of the larvae. Different colors, shapes, and lines indicate growth at different constant temperatures given in degrees Celsius.

Table A1. Model Constants and Their Values

Constant	Value
a_1	2.5
a_2	.1
a_3	15
a_4	.0025
a_5	.0005
a_6	.025
a_7	.001
c_1	.045
c_2	.8
c_3	.021
c_4	.025
c_5	1
d_1	1.5
d_{max}	540
$E_L(p = good)$	1
$E_L(p = bad)$	0
$E_L(p = good)$	3
$E_L(p = bad)$	2.5
f_1	.4
f_2	20
f_3	2.5
i_1	.27
i_2	.5
i_3	.02
i_4	.022
i_5	.9
P_L	.015
P_P	.0075
$P_A(p = good)$	.02

Table A1 (*Continued*)

Constant	Value
$P_A(\text{p} = \text{bad})$	.01
s_1	1.125
s_2	.03125
t_1	.05
$T_{\min}$	15
R	12.5
W_1	.01
w_2	$-.12$
w_3	.7
Δ (feeding)	1
Δ (reproducing)	1
Δ (dispersing)	.75

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