Modeling caterpillar growth and behavior under inducible plant defense

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Abstract

- Many herbivores have the ability to defoliate an entire plant within days. In response to herbivory, some plants generate toxic chemicals in their leaves. These inducible defenses are unique for each species of plant. For example, tobacco, *Nicotiana attenuate,* increases nicotine production when the caterpillar, *Manduca sexta,* starts to feed on it. We explored caterpillar growth and feeding behavior in the context of inducible plant defenses by creating a dynamic state variable model. At each time step the caterpillar had a "choice" to either stay on the current plant or move to a new plant. We compared the optimal life histories of caterpillars growing on plants with a low induction rates to those growing on plants with high induction rates. Caterpillars that were adapted to a lower induction rate tended to stay on a plant longer and achieve higher average fitness than caterpillars adapted to a higher induction rate. However, when caterpillars that were adapted to a low induction rate were exposed to an environment with a high induction rate, they achieved lower average fitness than caterpillars adapted to that environment, even though they displayed similar behavior. Similarly, caterpillars adapted to a high induction rate tended to remain on low induction rate plants for a longer time, but could not match the average fitness level of caterpillars adapted to the less stressful environment. Thus, variation in the inducible defenses has the potential to act as a selective force on caterpillar behavior. The generality of the model will also allow future studies to examine whether caterpillar behavior can change in response to inducible communication between plants.

Introduction

- In the field of behavioral ecology, dynamic state variable models are frequently used to model behavioral trade-offs in variable environments. Dynamic state variable models are based on the optimal foraging theory. The theory assumes that if energy supplies are limited, organisms cannot simultaneously maximize all of life's functions; for example, allocation of energy for growth reduces the amount of energy available for defense (Molles 2006). We focused on the tobacco hawkmoth, *Manduca sexta,* and its interactions with the tobacco plant, *Nicotiana attenuate.* The flow diagram below illustrates the complexity of the system; our model focuses only on the effects of inducible defenses. In this case the tobacco plants increase nicotine production in response herbivory to a level that is toxic to caterpillars. The model predicts the decisions that the larvae will make, given their physiological state based on models of caterpillar growth and foraging trade-offs. These trade-offs are represented by foraging equations that incorporate the state variables and other parameters that can affect a larvae's decision.

- We used Matlab to model a 20 day developmental period of a *Manduca* larva. During these 20 days the caterpillars were faced with two choices: stay on the currently induced plant or forage in hopes of finding a less harmful plant. The choices were based on estimated and calculated parameters from the literature. To evaluate the optimal fitness outcome for each choice given a current state, we used a backwards iteration procedure which assumed that subsequent behavior maximized fitness. The result was a multi-dimensional matrix of optimal decisions for any given combination of state variables.

- These decision matrices were used to predict how the behavior of caterpillars adapted to plants with low inducible defenses would differ from that of caterpillars adapted to plants with high inducible defenses. We evaluated the impact of these behavioral differences on fitness by performing a "reciprocal transplant" simulation experiment.

Results

- The figures represent the effects of inducible defense on the average mass, storage and foraging percent of a *Manduca sexta*. Two environments were looked at: a low induction environment and a high induction environment; every possible combination of the environments was tested to see which environmental pair produced the highest fitness.

- Overall size and storage (our fitness measure) depended on the rearing environment, not on the behavioral strategy of the caterpillar (Figure 1 & 2).

- However, the behavioral differences between the two environments were modest (Figure 3).

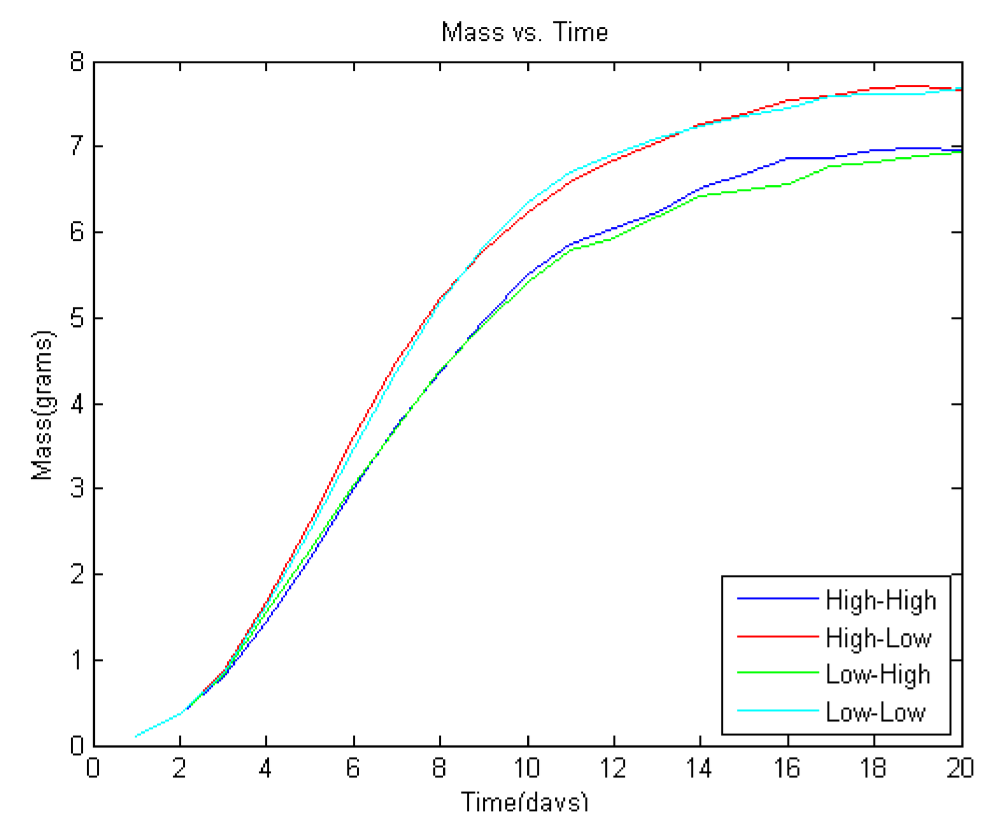

Figure 1. The effects of inducible defense on the average mass of *Manduca sexta*, for a period 20 days. Each line represents a sample size of 1,000 caterpillars. High induction rate (r) = 1.0, low induction rate (r) = 0.15

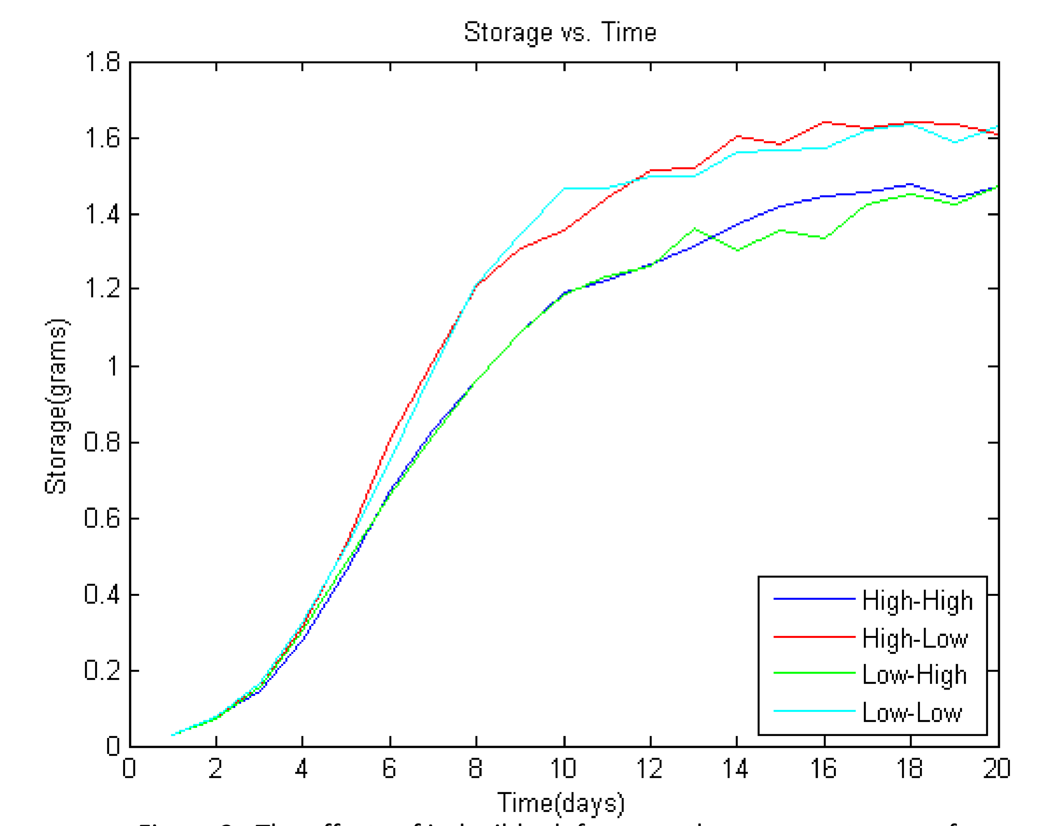

Figure 2. The effects of inducible defense on the average storage of *Manduca sexta* for a period of 20 days. Each line represents a sample size of 1,000 caterpillars. High induction rate (r) = 1.0, low induction rate (r) = 0.15

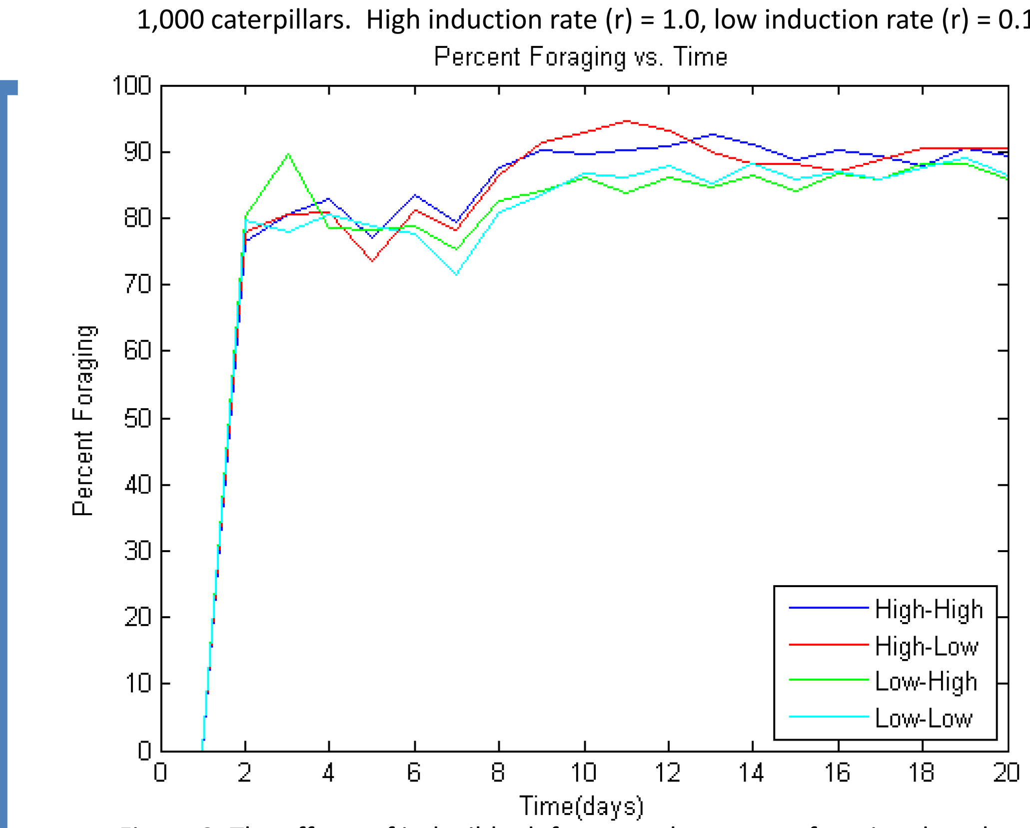

Figure 3. The effects of inducible defense on the percent foraging done by a *Manduca sexta* for a period of 20 days. Each line represents a sample size of 1,00 caterpillars. High induction rate (r) = 1.0, low induction rate (r) = 0.15.

The Model

- The growth equation (G) factors in a detoxification cost that the caterpillar must pay due to exposure from nicotine on an uninduced plant, the allometric scaling of growth metabolism and a maintenance cost.

$$G = \left[1 - \left(\frac{s}{s_{\max}}\right)^{y}\right] * \left(ax^{\frac{3}{4}}\right) - bx$$

- The fitness for staying on the current plant is equal to the amount of storage the caterpillar has plus its expected net resource uptake minus the energy needed for growth.

$$F_{stay} = z + U_{Net} - G$$

- The fitness for foraging also factors in a foraging cost.

$$F_{forage} = z + U_{Net} - \left(Ax^{\frac{3}{4}}\right) - G$$

- Given a combination of state variables, the caterpillars choose to stay or forage by selecting the behavior that maximizes expected fitness over the entire developmental period.

$$F(x, z, s, d, t) = \max(F_{stay}, F_{forage})$$

- The expected resource uptake is based on summing over the distribution of nicotine concentration in the induced plants. The shape of the distribution depends on how long the larva has been on the plant.

$$U_{net} = \sum P(s) * \left(ax^{\frac{3}{4}}\right) * \left[1 - \left(\frac{s}{s_{\max}}\right)^{y}\right] - bx$$

Table 1. Summary of parameters and functions used in the model

Parameters	Definition	Value
	State variables	
x	Biomass of herbivore	0.1-10 (0.1)
z	Total stored energy of herbivore	0-3 (0.03)
s	Nicotine concentration of plant	0-20
d	Herbivore's time on plant	0-20
t	Time (days)	0-20
	Caterpillar and Plant parameters	
A	Foraging Cost coefficient	0.07
s_0	Initial Nicotine concentration of plant	1.0
v	Adds variance in Nicotine concentration	3.55
y	Adds variance in detoxication concentration	1.5
pd	Mortality risk	0.01
s_{max}	Threshold of Nicotine concentration that herbivore cannot exceed	21
r	Induction rate	0.35
a	Growth coefficient	3.5

Conclusion & The Future

- In our current experiments, differences in induction rate were not sufficient to produce large differences in caterpillar strategy or fitness outcomes. However, the model did confirm the existence of fitness differences between environments differing in their induction rate.

- Looking to the future, we will be adjusting the model to incorporate the effects of plant communication into the model. It has been theorized that when a plants undergoes induction nearby plants can sense that these inducible defenses are occurring, therefore they will start to induce themselves. This would create a harsher environment for the caterpillar because the longer it spends on a given plant the higher the probability it has of running into plants with higher toxin concentrations.

Acknowledgments

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References Cited:

(1) Clark, C.W. and Mangel, M. 2000. *Dynamic State Variable Models in Ecology.* Oxford: Oxford University Press.
(2) Kerkhoff, A.J. 2004. Expectation, explanation and masting. *Evolutionary ecology research*, **6:** 1003-1020.
(3) Molles Jr., Manuel C. Ecology: Concepts and Applications. Fourth ed. New York, NY: McGraw-Hill,2006.
(4) Shelton, A.L. 2000. Variable Chemical defenses in plants and their effects on herbivore behavior. *Evolutionary ecology research*, **2:** 231-249.
(5) Shelton, A.L. 2004. Variable Chemical defenses of plants may improve the effectiveness of defenses. *Evolutionary ecology research*, **6**: 709-726.