

THE INFLUENCE OF HERBIVORY ON THE NET RATE OF INCREASE OF GYPSY MOTH ABUNDANCE: A MODELING ANALYSIS

Harry T. Valentine

Research Forester, Northeastern Forest Experiment Station, Center for Biological Control of Northeastern Forest Insects and Diseases, 51 Mill Pond Road, Hamden, CT 06514

A differential equation model of gypsy moth abundance, average larval dry weight, and food abundance was used to analyze the effects of changes in foliar chemistry on the net per capita rate of increase in a gypsy moth population. If relative consumption rate per larva is unaffected by herbivory, a reduction in the nutritional value of foliage reduces the net rate of increase at relatively low larval densities, and increases the larval density needed to bring about starvation. This result is achieved by reducing larval assimilation efficiency, or by increasing larval death rate, or both, in response to declining nutritional value of foliage associated with herbivory. An increase in relative consumption rate in response to herbivory reduces the larval density needed to bring about starvation, and reduces the net rate of increase of the larval population at all higher larval densities.

Introduction

Oak (*Quercus* spp.) foliage is the principal food of the gypsy moth (*Lymantria dispar* (L.)) in Eastern North America. Herbivory causes changes in the concentrations of suspected primary and secondary metabolites of gypsy moth in the foliage of oaks (Schultz and Baldwin, 1982; Valentine et al., 1983). Late-instar gypsy moths that feed on severely defoliated oaks are smaller at pupation, and less fecund, than gypsy moths that feed on essentially undefoliated trees (Wallner and Walton, 1979). Together, these results suggest that changes in foliar chemistry induced by herbivory influence the population dynamics of gypsy moth during outbreaks and the subsidences of outbreaks. The exact nature of the influence is neither known nor obvious because it is intermingled with the influences of parasites, predators, disease, and food shortage. However, it should be possible to discern some of the effects of induced changes in foliar chemistry on gypsy moth population dynamics through modeling.

The Model

The basic model that I use consists of a system of differential equations. The equations describe changes in larval dry weight, larval

abundance, and available foliage with respect to time measured in days (t), where 1 day is assumed to equal 15 Celsius degree days (threshold = 4.4°). The equations are initialized at the start of each larval generation and solved over the interval $0 \leq t \leq 44$. It is assumed that all larvae hatch and start feeding coincident with budbreak at $t=0$, and that all surviving larvae pupate at $t=44$. The values of the components at $t=44$ are used to predict the initial values of the components for the next generation. For example, the initial number of larvae next year is predicted from the number of pupae this year.

The variables of the model are:

$W(t)$ = average dry weight of a larva (mg)
 $F(t)$ = expected dry weight of a leaf (mg)
 $F^*(t)$ = total amount of foliage available (mg)
 $X(t)$ = number of gypsy moth larvae feeding on $F^*(t)$

$C_{\max}(t)$ and $C_{\text{act}}(t)$ are maximum and actual consumption rates (mg/day) of the larval population, which are defined in terms of the variables of the model.

The variables are related as follows:

$$C_{\max} = a_1 W X \quad (1)$$

$$C_{\text{act}} = \min(C_{\max}, a_2 F^*) \quad (2)$$

$$dX/dt = -X(a_3 + a_4(1 - C_{\text{act}}/C_{\max})) \quad (3)$$

$$dW/dt = E(C_{\text{act}}/X) - a_5 W \quad (4)$$

$$dF/dt = a_6 F(\ln F)(1 - (\ln F)/a_7) \quad (5)$$

$$dF^*/dt = (F^*/F)dF/dt - C_{\text{act}} \quad (6)$$

In the absence of a shortage of food, the consumption rate of a larva is $a_1 W$ (Valentine and Talerico, 1980), and the consumption rate of the larval population (C_{\max}) is $a_1 W X$ (eq. 1). If the consumptive demand of the larval population approaches or exceeds available foliage (i.e., $C_{\max} > a_2 F^*$), herbivory is constrained at rate $a_2 F^*$ (eq. 2), and the consumption rate of a larva is $a_2 F^*/X$.

Since gypsy moth is univoltine, and dispersal is assumed nil, all changes in the abundance of feeding larvae are negative. By equation (3), larvae die at rate a_3X from the effects of density-dependent agents, and, during a food shortage, larvae cease to feed (and starve) at rate $a_4(1-C_{act}/C_{max})X$.

Average larval growth (eq. 4) is equal to the average larval anabolic rate minus the average larval catabolic rate (a_5W). The anabolic rate is the product of the larval consumption rate (C_{act}/X) and assimilation efficiency (E). Foliage quality should influence larval growth through its effect on E ; various predictors of E are described in the next section.

Equation (5) describes the growth of an average-size leaf (Valentine, 1983), and equation (6) describes the collective growth of (say) N leaves available to the larval population. In the absence of larval feeding, the relative rates of increase in dry weight in the average leaf and the N leaves are equal (i.e., $dF^*/F^*/dt = dF/F/dt$), and the solutions of (5) and (6) are related as $F^*(t) = NF(t)$. When the gypsy moth feeds, the growth of available foliage is reduced by the rate of consumption (C_{act}), and $F^*(t) < NF(t)$ for $t > 0$. Rationale for the formulation of (6) was reported by Goldstein and Van Hook (1972), Nagy (1978), and Valentine (1978). Apparent herbivory (H) can be calculated from the solutions of (5) and (6) as:

$$H = (1 - (F^*(t)/N)/F(t)) \quad (7)$$

The solution of equation (5) can be written as

$$\ln F(t) = a_7/(1 + \exp(a_8 - a_6t)) \quad 0 \leq t \quad (8)$$

Therefore, (5) can be eliminated from the model by substituting for $(dF/dt)/F$ on the right hand side of (6) with:

$$(dF/dt)/F = a_6a_7(\exp(a_8 - a_6t)/(1 + \exp(a_8 - a_6t))^2) \quad (9)$$

At budbreak ($t=0$), average leaf dry weight is

$$F(0) = \exp(a_7/(1 + \exp(a_8))) \quad (10)$$

To initialize $F^*(t)$, it is convenient to put the variables of the model on a per-ha basis. If we denote the asymptotic dry weight of mature foliage per ha as F^*_{max} , then total available foliage at budbreak is:

$$F^*(0) = F(0)F^*_{max}/\exp(a_7) \quad (11)$$

To solve the model over a period of years, a function is needed that predicts initial larval abundance ($X(0)$) in year $n+1$ from pupal abundance ($X(44)$) in year n , viz.:

$$X(0)_{n+1} = a_9W(44)_nX(44)_n \quad (12)$$

The parameter a_9 subsumes survival rates of pupae, adults, and eggs, and the proportion of females in the adult population; egg production is a linear function of pupal weight (Hough and Pimentel, 1978).

Solutions of the Model

One way to discern the effects of food quality on gypsy moth population dynamics is to compare solutions of the model with and without the effects of food quality included, while holding other effects constant. Unless noted otherwise, the following solutions were computed with the parameter values listed in table 1, and with $W(0) = 0.2$ mg, and $F^*_{max} = 10^5$ mg/ha.

Assuming that food quality is invariant between years and unaffected by herbivory, a purely empirical expression describing assimilation efficiency of larvae for eq. (4) is the cubic polynomial (adapted from Valentine and Talerico, 1980):

$$E = a_{10} + a_{11}t + a_{12}t^2 + a_{13}t^3 \quad (13)$$

The model of gypsy moth abundance without food quality effects is now completely defined.

Inspection of the model shows that where food is unlimited, the net per capita rate of increase (1/yr) in the abundance of feeding larvae (X) from $t=0$ in year n to $t=0$ in year $n+1$ is constant:

$$\ln(X(0)_{n+1}/X(0)_n) = -a_344 + \ln(a_9) + \ln(W(44)_n) \quad (14)$$

When the initial larval density in year n is sufficient to cause a food shortage, the right hand side of (14) no longer applies, as the net per capita rate of increase declines precipitously (Fig. 1). Over a period of years, $X(0)$ assumes a pattern such as depicted in Figure 2; i.e., $X(0)$ increases exponentially from year to year until food becomes limiting to late-instar growth and survival, causing a catastrophic decline in $X(0)$ the following year, and a resumption of exponential population increase. However, it is evident in Figure 1 that the net per capita rate of increase can be zero, so a steady state population is theoretically possible.

As was noted, herbivory causes changes in foliar chemistry which reduce larval growth and pupal weight. We can produce such an effect by forcing larval assimilation efficiency to decrease as herbivory increases. The only change we need to make is to substitute E' for E in (4) where

$$E' = E(1 - a_{14}H) \quad 0 < a_{14} < 1 \quad (15)$$

Under the assumptions and constraints of the model, it is obvious that this function will cause per capita fecundity to decline with increased herbivory, because fecundity is a

Table 1.--Values of parameters used to generate solutions of the model.

Parameter	Value	Source of value or data
a_1	1.003	Valentine and Talerico (1980)
a_2	0.5^a	Sensitivity Analysis
a_3	0.08	Campbell (1981)
a_4	4.0^a	Sensitivity Analysis
a_5	0.0192	Valentine and Talerico (1980)
a_6	0.265	Valentine (1983)
a_7	6.109	Valentine (1983)
a_8	0.893	Valentine (1983)
a_9	2.5	Campbell (1981)
a_{10}	0.2885	Valentine and Talerico (1980)
a_{11}	-1.0635×10^{-2}	Valentine and Talerico (1980)
a_{12}	2.4861×10^{-4}	Valentine and Talerico (1980)
a_{13}	-2.3609×10^{-6}	Valentine and Talerico (1980)

^aValues of a_2 and a_4 were guessed and then adjusted to give larvae that survived starvation a reasonable dry weight.

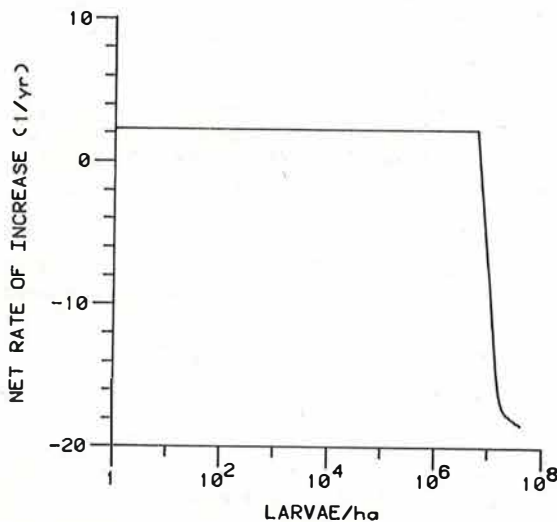


Figure 1.--Net rate of increase in larval density versus larval density as predicted by the model without foliage quality effects included.

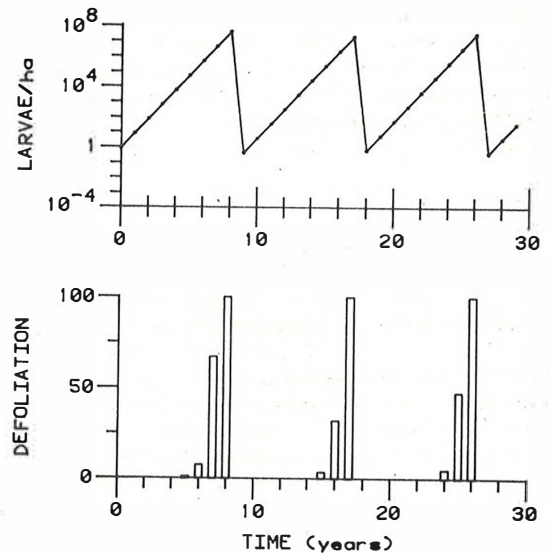


Figure 2.--Time-series of larval densities and defoliation as predicted by the model without foliage quality effects included.

linear function of pupal weight. The effect of this function on the net per capita rate of increase of the population is less obvious, but is shown in Figure 3 for a_{14} equal to 0 (no effect), 0.09, and 0.18. On the basis of experimental results reported by Wallner and Walton (1979) and by Valentine et al. (1983), I estimate the true value of a_{14} to be 0.09.

At relatively low initial larval densities, the net per capita rate of increase (for $a_{14} > 0$) is less than the corresponding rate that would be expected in the absence of a larval response ($a_{14}=0$) to changes in foliar chemistry induced by herbivory (Fig. 3). However, at relatively high larval densities, the net rate of increase is greater with a

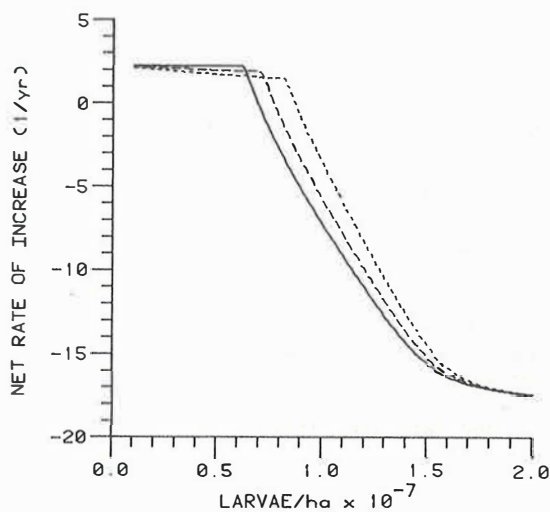


Figure 3.--Net rate of increase in larval density versus larval density when a reduction in larval assimilation efficiency associated with herbivory is included in the model (see eq. (15)). The 3 curves represent no response to herbivory (solid, $a_{15}=0.0$), the estimated true response to herbivory (long dash, $a_{15}=0.09$), and an exaggerated response to herbivory (short dash, $a_{15}=0.18$), respectively.

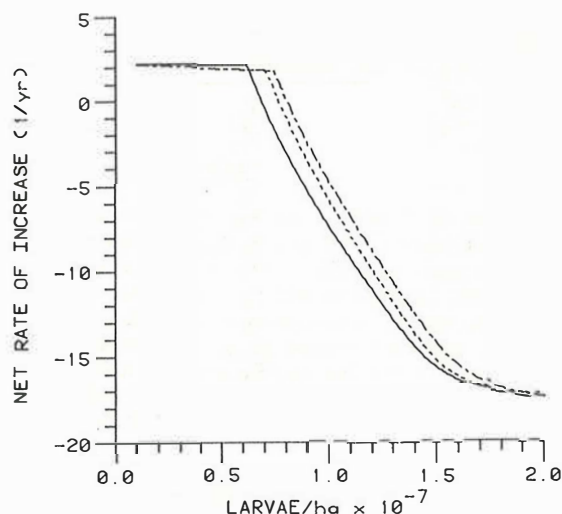


Figure 4.--Effects on herbivory on the net rate of increase in larval density. No effect (solid line); reduced assimilation efficiency with no change in relative consumption rate (short dash), and no change in assimilation efficiency, but a reduction in relative consumption rate (short dash, long dash).

response to herbivory because fewer individuals die from starvation. Average larval consumption rate is proportional to larval weight, so starvation becomes less likely at a given population density if larvae respond to herbivory with a reduction in assimilation efficiency, but no change in relative consumption rate. The relatively inefficient assimilators weigh less than they would in the absence of the response and, therefore, are less likely to eat all the available foliage. Consequently, a reduction in larval abundance due to starvation may be postponed by a year, affording the gypsy moth additional opportunity to spread its infestation through the dispersal of first instars. The reduction in the net rate of increase in response to herbivory also tends to reduce the chance of starvation during the early instars of the next generation, and increase the chance that a larva will live to pupation. Therefore, reductions in the population through starvation may be smaller with a response to herbivory than without one. At very high initial larval densities, the model indicates that changes in foliar chemistry have virtually no effect on the net rate of increase.

The most plausible explanation for the decline in larval growth associated with herbivory is a reduction in larval assimilation efficiency. However, it is possible that assimilation efficiency is unaffected and larvae simply reduce their feeding rate in response to herbivory. The models for the two cases are similar, but not identical. Assuming no food shortage, where assimilation efficiency is affected by herbivory, we have

$$C_{\max} = a_1 W X \quad (17)$$

and

$$dW/dt = E(1-a_{14}H)a_1W-a_5W \quad (18)$$

If feeding rate is reduced, but assimilation efficiency is unaffected, we have

$$C_{\max} = a_1(1-a_{14}H)WX \quad (19)$$

and

$$dW/dt = Ea_1(1-a_{14}H)W-a_5W \quad (20)$$

Thus, in both cases, larval growth (dW/dt) is the same. However, the feeding rate (C_{\max}) of the larval population declines with herbivory in the latter case and, therefore, larval death due to starvation is less likely at a given larval density (Fig. 4).

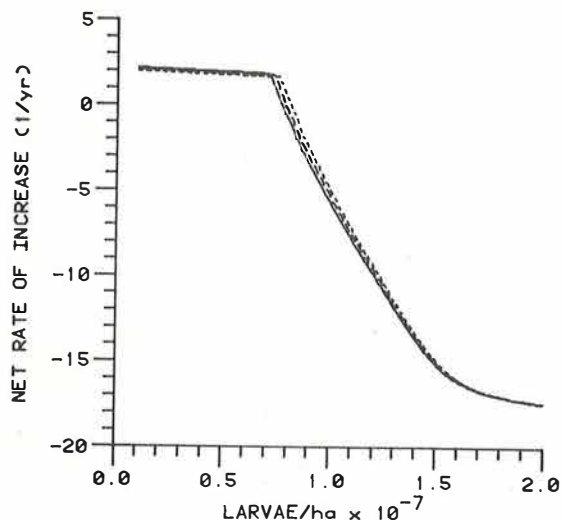


Figure 5.--Net rate of increase in larval density versus larval density when the effect of defoliation in the prior year (long dash) or 2 prior years (short dash) is added to the model (see eq. (21)). Both curves are estimated true responses. No effect due prior defoliations is represented by the solid line.

Additional reductions in pupal weight and fecundity due to consecutive defoliations (as reported by Wallner and Walton, 1979) tend to exacerbate the response of the larval population to herbivory in terms of its net per capita rate of increase (Fig. 5). The effects shown in Figure 5 were achieved by replacing a_{10} in eq. (13) with a_{10}' where

$$a_{10}' = a_{10} - a_{15}H(44)_{n-1}(1+H(44)_{n-2}) \quad (21)$$

A parameter value of $a_{15} = .002$ gives percentage reductions to $W(44)_n$ due to defoliations in year $n-1$ and year $n-2$ consistent with the results of Wallner and Walton (1979). The implicit assumption here is that changes in foliar chemistry due to defoliation in the prior year or 2 prior years affects the assimilation efficiency of larvae in the current year. If we solve the model over a period of years, the time series of $X(0)$ is so similar to that shown in Figure 1 that it does not warrant a figure of its own. However, the more or less constant 9-year cycle shown in Figure 1 becomes an alternating 8- or 9-year cycle when food quality effects are added.

It has been hypothesized that changes in foliar chemistry induced by herbivory increase the rate of death of larvae from malnutrition, parasitism, and disease (e.g., Podgwaite, 1981; Schultz and Baldwin, 1982). If we assume that the per capita death rate increases with herbivory, we can assess the consequences of this larval response by replacing a_3 on the right hand side of eq. (3) by a_3' where

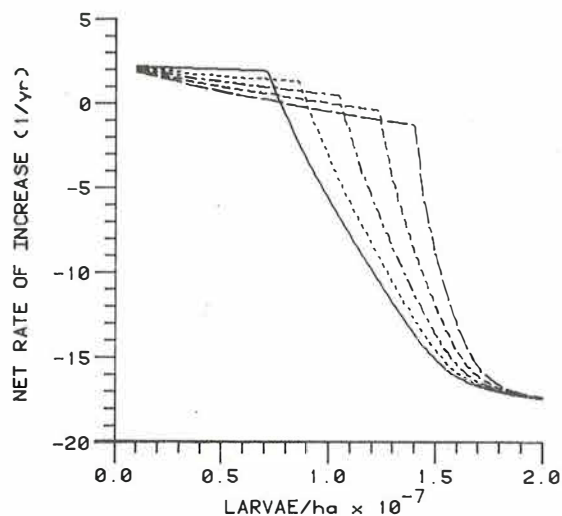


Figure 6.--The effect of an increase in larval death rate associated with herbivory (see eq. (22)) on the relation between net rate of increase in larval density and larval density for $a_{16}=0.0$ (solid), 0.02 (short dash), 0.04 (dot dash), 0.06 (mid-sized dash), and 0.08 (longest dash).

$$a_3' = a_3 + a_{16}H \quad (22)$$

The effect of an increase in larval death rate associated with herbivory on the net rate of increase of the population is shown in Figure 6 for a_{16} equal to 0 (no effect), 0.02, 0.04, 0.06, and 0.08. The result is a familiar one; the net rate of increase of the population is reduced by the increase in death rate until the larval density is reached where starvation would be manifested in the absence of the increase. At higher larval densities, the net per capita rate of increase is greater because reductions in the population due to starvation are either postponed or buffered by death of larvae from other causes. Indeed, when a_{16} was assigned a value of 0.06 or 0.08, the increased death rate associated with herbivory effectively prevented the population from growing large enough to collapse from starvation (Fig. 7); instead, the population settled into a steady state. As a_{16} is increased further, the steady-state population is smaller and severe defoliation is prevented, but this is contrary to our experience with gypsy moth.

It is not known whether gypsy moth larvae respond to a reduction in the nutritional value of foliage with an increase in relative consumption rate, but Scriber and Slansky (1981) indicated that tree feeders are limited in their ability to do this. The only structural change we need to make to the model to assess the effects of increased larval consumption rate is to replace a_1 in eq.

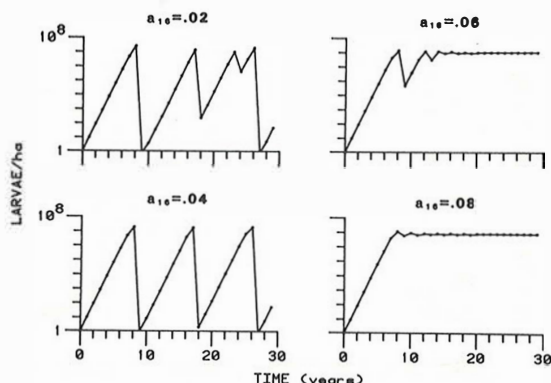


Figure 7.--Time-series of larval densities with increases in larval death rate associated with herbivory included in the model.

(1) by a_1' where

$$a_1' = a_1 + a_{17}H \quad (23)$$

Any increase in consumption rate associated with herbivory requires a compensatory reduction in assimilation efficiency so that $W(44)$ will equal its expected value. Thus, the parameter a_{14} of eq. (15) will vary directly with a_{17} , though not linearly. The effect of this hypothesized larval response on the net per capita rate of increase of the larval population (given $a_{16}=0$) is shown in

Figure 8 for $a_{14}=0.09$, $a_{17}=0$; $a_{14}=0.18$,

$a_{17}=0.1$; $a_{14}=0.26$, $a_{17}=0.2$; and $a_{14}=0.40$,

$a_{17}=0.4$. At low larval densities, where herbivory is negligible, the effect of the larval response on the net rate of increase also is negligible. However, increases in larval consumption rate reduce the larval density needed to bring about starvation, and reduce the net rate of increase of the larval population at all higher larval densities.

Summary and Conclusions

If the parametrization of the model is adequate, the following conclusions can be drawn from this analysis. Where larval density is insufficient to cause starvation, larval response to herbivory results in a reduction in per capita fecundity, which singly, or in combination with increased larval death rate, reduces the net rate of increase in gypsy moth abundance. Unless larval relative consumption rate increases in response to herbivory, the net rate of increase in gypsy moth abundance is

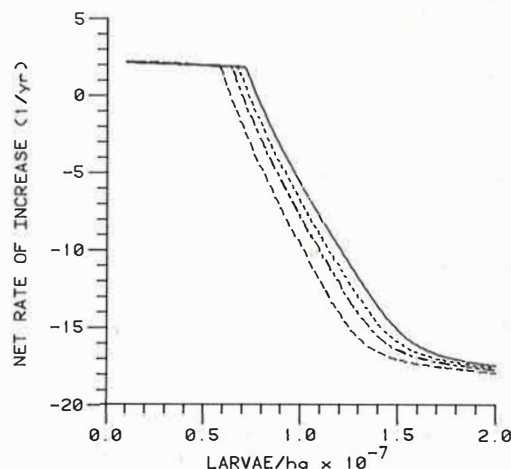


Figure 8.--Net rate of increase in larval density versus larval density where larval relative consumption rate increases with herbivory (see eq. (23)). Solutions are plotted for $a_{17}=0$ (solid), 0.1 (dot), 0.2 (dot-dash), and 0.4 (dash).

greater at all larval densities where larval starvation would ensue in the absence of any larval response, because a reduction in assimilation efficiency or feeding rate--or an increase in larval death rate--in response to herbivory effectively reduces the cumulative consumption of the larval population. If larval relative consumption rate does increase in response to herbivory, then, compared to no increase, the larval density needed to bring about starvation is reduced and the net rate of increase is reduced at all higher densities.

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