ORIGINAL PAPER

Size-dependent fitness trade-offs of foraging in the presence of predators for prey with different growth patterns

Kathryn J. Montovan[1] · Natasha Tigreros[2] · Jennifer S. Thaler[3]

Abstract

Prey species make choices about whether to employ costly predator avoidance behaviors throughout their growth and lifecycle. Here, we explore the effects of prey size at a given age (ontogenetic size) and prey growth on optimal behavior using a dynamic optimization model. Under the assumption that prey experience greatest predation risk at intermediate or large sizes, and that growth is fastest at intermediate or large sizes, we find that prey should generally forage when they are small in size and hide when they are larger due to a critical *strategy switching size threshold*. But this is dependent both on the mortality risks and on the rate of growth. Higher background mortality rates or lower predator-induced detection costs of foraging reduce the size at which prey switches from foraging to hiding. Rapid initial growth leads to decreased overall survival and a wider range of conditions under which the prey hides from the predator. As a test case, the model is parametrized with data and applied to understand differing risk-reducing behaviors between cannibal and non-cannibal *Leptinotarsa decemlineata*, Colorado potato beetle, larvae. The model predicts that a wide range of parameter values lead to differing behaviors of cannibals and non-cannibals of the same age due to differences in ontogenetic size. We also see that individuals with swifter early growth switch to hiding at larger sizes but will often have earlier strategy switching times. This increases survival of cannibals to the critical pupation size with the largest increases occurring when the baseline death rate is high. Our findings suggest that ecological factors that affect the rate of growth during development, even if final size is not affected, may have an important role in prey responses to predators.

Keywords State-dependent foraging · Growth models · *Leptinotarsa decemlineata*

Introduction

Most animals face the challenge of acquiring the necessary nutritional resources to grow and reproduce while also avoiding being eaten. When foraging, prey are more likely to be detected and killed by predators, leading to a fundamental trade-off between foraging and risk of predation (reviewed in Lima and Dill 1990; Brown and Kotler 2004; Verdolin 2006). While feeding reductions constitute an important form of predator avoidance across diverse animal species (Elvidge et al. 2014; Nelson et al. 2004), reducing energy

intake comes with substantial fitness costs, especially when slowing down the growth of juvenile prey (Stoks et al. 2012). Research in the last decades indicates that prey organisms are able to adaptively balance the costs and benefits of such trade-offs, by adjusting their responses to predation risk. Indeed, a vast body of literature has linked shifts in prey responses to variation in predator pressure (Ferrari and Chivers 2009; Hermann and Thaler 2014; Lima 1998; Rudolf 2008; Winnie and Creel 2017) and prey's nutritional state or body condition (Pettersson and Brönmark 1993; Lima 1998; Barnett et al. 2007; Houston 2010; Heithaus et al. 2007). Few studies, however, have considered how prey optimal responses may shift as the growth rate changes over ontogeny (but see Moschilla 2018), even though the costs and benefits in the foraging-predation risk trade-off are likely to change with prey size and developmental stage or age.

With growth, the risk of being consumed by a predator often decreases due to gape limitations of potential predators

✉ Kathryn J. Montovan
kmontovan@bennington.edu

[1] Bennington College, 1 College Drive, Bennington 05257, VT, USA

[2] University of Arizona, Tucson 85721, AZ, USA

[3] Cornell University, Ithaca 14850, NY, USA

or reduced ability to handle larger prey successfully (Nowlin et al. 2006; Urban 2007). At the same time, the risk of being found by a predator may increase with ontogenic growth, e.g., if larger prey are more easily detected by visual predators (Mänd et al. 2007; Karpestam et al. 2014). Thus, prey responses to predators (to forage or hide) may change as prey grow and passes through windows of increased vulnerability to predators. Importantly, costs associated with feeding reductions, in terms of decreasing prey growth, may also vary with ontogeny. This is especially important given the fact that most organisms follow s-shaped rather than exponential growth trajectories (West et al. 2001; Kerkhoff 2012). Here, a juvenile's growth-reducing predator avoidance through reduced foraging would carry greater costs when foraging is associated with greater mass gains and greater benefits when their ontogenetic size puts them at high risk of predation from the focal predator. Empirical and theoretical studies in invertebrates have traditionally assumed that juvenile prey grow exponentially (Abrams et al. 1996; Davidowitz et al. 2003; Berger et al. 2006), which may in part be because these simplified models are easier to analyze mathematically. However, recent studies have indicated that growth trajectories of invertebrates are not well-fit by these simplified growth models (Tammaru and Esperk 2007; Maino and Kearney 2015; Lee et al. 2020). Thus, a critical challenge in studying prey decision making during ontogenic growth is to accurately capture the pattern of the growth trajectory (e.g., linear, exponential, or s-shaped).

Here, we study prey decision making over ontogenic growth by developing a differential equation model that explicitly incorporates size-dependent predation risk and size-specific growth rates. This model allows us to determine the best decision for the prey (forage or hide) depending on the specific conditions and timing of predation. The model assumes that larger prey are equally or more likely to be detected by the predator but are less likely to be successfully killed once detected; this leads to mortality risk which either increases with size or reaches a peak mortality at an intermediate size. Whether foraging under high predation risk is better than hiding depends on the intensity of the risk, the mortality risk while hiding, and the growth benefits of foraging. We will characterize the growth trajectories of juvenile prey using the von Bertalanffy Growth Function (VBGF), which allows great flexibility to capture variation in growth by incorporating size dependence in the terms describing assimilation (acquiring food to gain mass) and catabolism (breaking down stored molecules to make energy) (von Bertalanffy 1951).

To examine how prey decision making under predation risk changes during ontogenic growth, we first develop a general model, which broadly applies to prey with a complex life cycle where juveniles can reduce predation risk by reducing growth and escape predation when they reach a

critical mass and transition to the adult stage. We explore the parameter space for the model to understand how different prey attributes related to growth, predator foraging constraints, and environmental mortality pressures affect the optimal foraging strategy for the prey. The model is applied to a well-studied predator-prey system, that of *Leptinotarsa decemlineata* larvae prey and the predatory *Podisus maculiventris* stink bug. This provides an opportunity to test the model and to understand a anti-predator behavior within this system which could help control the pest population. Specifically, we use the model to explain whether experimental differences in foraging responses of cannibal and non-cannibal larvae might be predicted based on differences in ontogenic size between paired larvae.

Methods

To examine prey optimal responses to predation risk over ontogeny, we developed a system of differential equations to mathematically describe the growth and survival probability of a single prey. Although it is biologically an oversimplification, for computational tractability we assume that the prey is exposed to the focal predator once during growth. When experiencing predation risk, a prey individual will make the decision to either continue to forage or stop foraging. Prey escape predation when the predator leaves or they reaches a critical mass. Figure 1 shows a diagram of the key parts of this model. The probability a prey survives to a critical mass is used as a measure of the fitness of the individual. This is appropriate for species, like many insects and amphibians, that reach maturity at roughly a set size and have similar reproductive productivity as long as they reach maturity. We consider a range of predator visit start times and determine whether foraging or hiding during the predator visit leads to a larger probability the prey survives to the critical size. Using model simulations and a sensitivity analysis, we explore how the function for prey growth (timing and rate of growth) and environmental condition affect the optimal prey behavior in the presence of a predator. For the model, we assume that larger prey are easier to find and stopping foraging activity reduces the probability that the prey is found. The model is then fit to data and parametrized for *L. decemlineata*.

In the following sections we explain the modeling framework, sensitivity analysis, and the experimental test of the model predictions. Table 1 gives a summary description for each parameter, the range for that parameter that was used in the model sensitivity analysis, and the parameter values used to model of the Colorado potato beetle. All modeling and statistical analyses were performed in R (R Core Computing Team 2017) and all R codes are available on github (https://github.com/kmontovan/Montovan-et-al-2022.git).
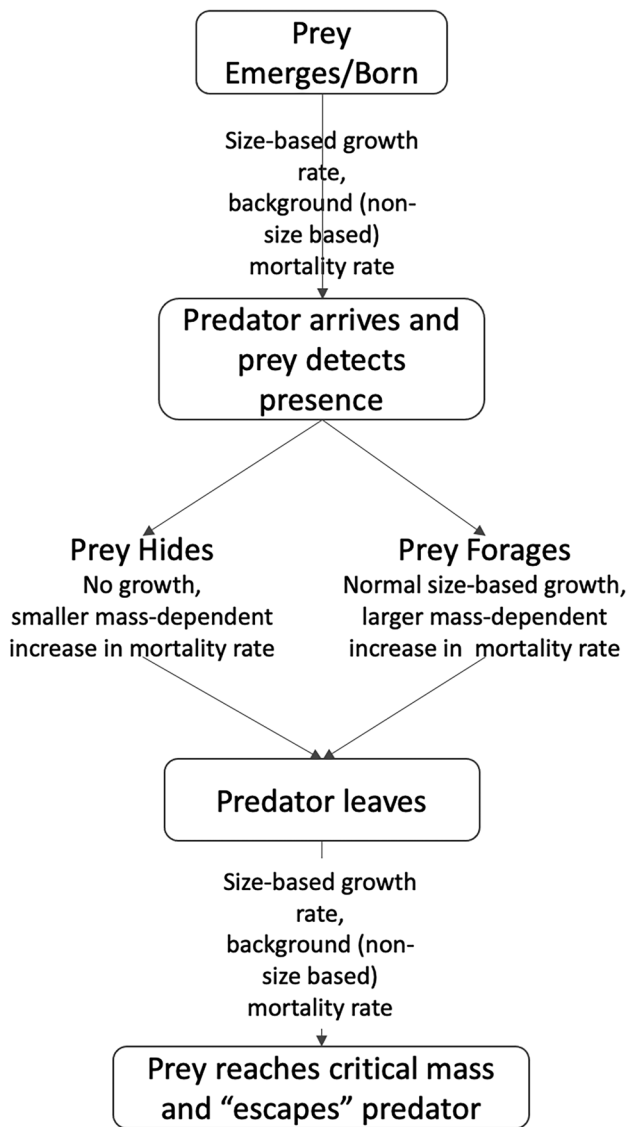
$$x_1'(t) = G(u(t), x_1(t))$$

$$x_2'(t) = \begin{cases} -dx_2(t) & \text{if no predators are present} \\ -dx_2(t) - F(u(t), x_1(t), x_2(t))x_2(t) & \text{if predator is present} \end{cases}$$

Here, $x_1(t)$ is the mass of the prey at time t and $x_2(t)$ is the probability the prey survives to time t. $G(u, x_1)$ is the growth rate of the prey, $F(u, x_1, x_2)$ is the additional rate of mortality from the focal predator, and d is the background mortality rate (independent of the predator of interest). Growth happens when the prey is foraging ($u(t) = 1$) and stops when the prey stops eating to hide ($u(t) = 0$). This is reasonable for many species. Because feeding is dangerous (Bernays 1997) and reducing feeding is not always an option, organisms often stop feeding (and growing) when a predator is present (Lima and Dill 1990; Losey and Denno 1998; Verdolin 2006). When there is no predator present the best action is for the prey to forage, so we will set $u = 1$ when the predator is not nearby and determine the best strategy (forage or hide) only for the window of time when the predator is present. The initial conditions are assumed to be $x_1(0) = m_0$ and $x_2(0) = 1$.

Prey growth

We use a slightly modified von Bertalanffy Growth Function (VBGF) with no growth when the prey is hiding ($u(t) = 0$).

$$x_1'(t) = u(t)(Hx_1(t)^A - Kx_1(t)^B) \tag{1}$$

where the H is the coefficient for assimilation of energy/mass, K is the coefficient for catabolism of existing energy reserves, and A and B control the type of size dependence for the assimilation and catabolism terms, respectively. When exploring the effects of the growth curve shape on prey behavior, we will consider the VBGF with $B = 1$ which makes the equation for $x_1(t)$ solvable, and calculate H to ensure that the size of maturity (M) happens for continuously foraging prey at time T. This gives

$$H = \frac{K(M^{1-A} - m_0^{1-A}e^{(A-1)KT})}{1 - e^{(A-1)KT}} \tag{2}$$

We include the parameters controlling the shape of the growth curve in the sensitivity analysis and also consider three specific growth curves representing different characteristic growth patterns in more depth. They are a) saturating with the growth rate decreasing with size, b) s-shaped with swiftest growth at intermediate sizes, and c) exponential with growth rate increasing with mass. The growth functions we chose (shown in Fig. 5) for these allow us to explore the extremes and middle behavior of our model.

As part of the case study on the Colorado potato beetle, we fit three potential VBGF sub-models to data: 1) $K = 0$ (B not

Fig. 1 Model diagram capturing key components of the growth, mortality, and interactions between the predator and prey

Model formulation

We formulate a model representing the growth and survival of a single prey and use it to find the optimal foraging function, $u(t)$, which describes when the prey should be foraging to maximize the probability of survival to pupation (which occurs at a set mass M). Mathematically, this is formulated as the following optimization problem.

$$max_{(u,T)}x_2(T)$$

where T satisfies $x_1(T) = M$ and

Table 1 Parameters, descriptions, estimates used for the case study, and ranges used for the general sensitivity analysis. ∗ denotes estimations based on empirical data and is described in Appendix A, other parameters were estimated given what we know about the species. H was computed to make it so a continuously foraging prey would reach size M at time T

	Description of parameter	Value or range for sensitivity analysis	Estimate for Case Study
A	Exponent for positive assimilation term for growth curve	(.6, .99)	1.28*
B	Exponent for negative catabolism term for growth curve	1	1.45*
H	Growth coefficient for assimilation term	Computed	0.96*
K	Growth coefficient for catabolism term	(1, 2.5)	0.41*
b	Non-foraging larval detection rate	(0.001, 0.1)	$0.003 mg^{-1} day^{-1}$
m	Additional detection rate when the larvae is foraging.	(0.001, 0.06)	$0.003 mg^{-1} day^{-1}$
p	The probability that a detected larvae is successfully killed if the larvae is very small.	(0.4, 0.98)	.9
α	The relative fraction of the largest larvae consumed (compared to the smallest).	(0.1, 0.9)	0.5
d	The background proportional death rate of prey (not from focal predator).	(0.015, 0.4)	0.05 *
m_0	The mass of the prey at time $t = 0$	0.634	0.634 mg*
M	The size of the larvae at pupation.	157	157 mg*
T	The time of the larvae reach size M and pupate.	15	15 days*

fit), 2) $B = 1$, 3) H, K, A, and B all unconstrained. The built-in optim function in R (R Core Computing Team 2017) is used to find the parameters A, B, H, K, and m_0 (whichever are not constrained) that minimize the log likelihood function. A full explanation of the methods used are in Appendix A.2. AIC weights were then computed to determine the relative support for each model (Wagenmakers and Farrell 2004).

Predator-related mortality

This model considers a focal predator that is detectable by the prey. This predator brings additional mortality costs on top of the background death rate. The prey can choose to mitigate this risk by stopping foraging and growth. The additional mortality from this predator is computed by multiplying the rate prey are detected by the predator ($g(u, x_1)$ by the fraction of detected prey that are successfully consumed once found ($f(x_1)$).

$$F(u, x_1, x_2) = g(u, x_1)f(x_1) \tag{3}$$

We assume that detection probability increases with prey size, independent of whether the prey is foraging. The simplest model for this would be that the detection rate ($g(u, x_1)$) increases linearly with the mass of the prey (x_1) with foraging activity increasing the per milligram detection rate. Although it is possible that this functional response is nonlinear, in the absence of more empirical support we make the assumption that the response is linear.

$$g(u, x_1) = x_1(mu + b) \tag{4}$$

where b is the baseline detection rate (per mg of prey mass) for non-foraging prey and m is the relative increase in the detection rate (per mg) for foraging prey.

The fraction of detected prey that are successfully consumed, f, may or may not be a function of the size of the prey; predators are frequently but not always more likely to successfully kill small prey and larger prey are often likely to be able to escape or injure the predator. To represent these assumptions, we use a linear function for $f(x_1)$ and explore the effects of α in the sensitivity analysis.

$$f(x_1) = p\left(1 - \frac{1 - \alpha}{M}x_1\right) \tag{5}$$

where p and $\alpha \cdot p$ are the probabilities of being killed by the predator if the prey is small (mass 0) and large (mass $\approx M$), respectively, with $\alpha \in (0, 1)$. The model would also work for $1 < \alpha < 1/p$ but would correspond to larger prey being more likely to be killed than smaller prey.

Combining these pieces to predict the overall mortality risk from the predator ($F(u, x_1, x_2)$), we see that if $0 < \alpha < 1/2$, this mortality risk will reach a peak when the prey has mass $x_1 = \frac{M}{2(1-\alpha)}$, and if $\alpha \geq 1/2$, the predator-related mortality risk will increase with prey size for all of the prey's growth.

Sensitivity analysis

We perform a sensitivity analysis to understand how prey attributes related to growth, predator foraging constraints, and environmental mortality pressures change the optimal foraging strategy for the prey. 1000 randomized parameter sets were generated using Latin Hypercube sampling to efficiently sample the large parameter space for our model (McKay 1992). Parameter values were chosen at equally spaced increments in the parameter ranges listed in Table 1

and rescaled so that each is a percentage of the entire range with 0 for the smallest and 1 for the largest value included in the sensitivity analysis. For each of these, 144 visit start times (larval age: 1 hour old to 12 days old) were considered with a set predator visit length of 3 hours and the optimal behavior our model predicted (forage or hide) was recorded. We looked at two metrics in our sensitivity analysis: the age of the larvae when they first switch from foraging to hiding and the size at which this switch occurs.

Linear regression was then applied to the scaled data with the metric of interest (age or size at strategy switch) as the dependent variable (with a fit intercept for the model). The coefficients for each parameter (or elasticities) are then interpreted. For example, an elasticity value of 0.1 means that increasing the parameter from the bottom to the top of its range would increase the metric by 0.1 on average. A negative elasticity value means that the metric would on average decrease by that amount.

Case study: Model applied to *Leptinotarsa decemlineata*

The Colorado potato beetle (*L. decemlineata*) is a major pest for potato crops around the world and is resistant to most insecticides (Hare 1990). As farmers are looking for effective (and often multifaceted) approaches to managing potato beetle populations, it is helpful to understand the risk-avoidance behaviors the Colorado potato beetle employs in response to natural predators. Both adults and larvae feed on plants and respond to the presence of predators by reducing feeding and adults also reduce oviposition. However, larvae exhibit intraspecific variation in prey responses to predation risk that may be linked to variation in ontogenic size. Specifically, *L. decemlineata* larvae often cannibalize sibling eggs (Collie et al. 2013; Tigreros et al. 2017; Tigreros et al. 2018; Tigreros et al. 2019). Cannibals grow faster and show stronger foraging responses to the risk of predation than non-cannibal siblings (Collie et al. 2013; Tigreros et al. 2017; Tigreros et al. 2018). These differences could be due to cannabilism-related state-differences (nutrition, larger size at younger size, etc.) but could also be due to size differences of the age-matched larvae in the study. We use this modeling approach to explain whether the observed differences in foraging responses of cannibals and non-cannibals to predation might be predicted based on differences in ontogenic size between paired larvae.

The model can be applied to this system because the assumptions of the model are consistent with the growth and predation risks of Colorado potato beetle larvae. The Colorado potato beetle accurately detects the predator stinkbug *Podisus maculiventris* and reduces the risk of predation by not foraging in the presence of predators (Hermann and Thaler 2014). High predation risk can also lead to maternally induced sibling egg cannibalism with 4-day-old cannibal off-spring reducing growth and foraging when exposed to a predator while non-cannibal larvae of the same age do not change their behavior (Tigreros et al. 2017). Cannibal larvae grow more quickly through the first instar than non-cannibal larvae (with cannibals spending roughly one day less in the first instar); the size at the start of each instar and growth in the second instar and beyond are roughly equivalent for cannibal and non-cannibal larvae, with cannibals remaining roughly a day ahead throughout larval growth (Collie et al. 2013). When *L. decemlineata* is large enough, it pupates and is no longer susceptible to predation by *P. maculiventris*.

Experimental methods

All data used for parametrization and experimental validation were collected using laboratory colonies of *L. decemlineata*, which was established using individuals from a population in Ithaca, NY (see Tigreros et al. 2017; Tigreros et al. 2018) and maintain with potato plants, *Solanum tuberosum*. Predatory stink bugs were also maintained in a laboratory colony with potato plants and mealworms as prey. All experiments were conducted in an environmental chamber with photoperiod (18-L : 6-D) and temperatures (23 : 21 °C). For all datasets involving larval mass, weights for larvae are to the nearest $0.1\mu g$ (Mettler AT261 balance; Mettler Toledo, Columbus, OH, USA).

Parameter fitting is described in detail in Appendix A and summarized in Table 1.

Experimental validation for *L. decemlineata*

We tested experimentally whether cannibalism effected the chances of larval survival to predation after controlling for larval size by exposing cannibal and non-cannibal larvae of similar body size to a lethal predator. Egg cannibalism was manipulated as in Tigreros et al. (2017, 2018), by allowing newly hatching larvae to consume a conspecific egg. Cannibals and non-cannibals were kept individually on a potato leaflet until the predation experiment. Cannibal larvae at different times of development were matched with control larvae of similar size. Larvae were weighed and each pair of cannibal and non-cannibal was kept with a lethal predation treatment, as in Tigreros et al. (2017) and the first larvae killed by the predator was recorded.
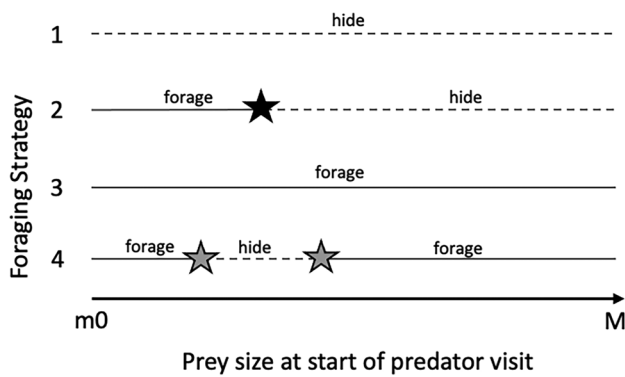
Fig. 2 Diagram showing the four qualitatively different optimal foraging strategies we observed for the model. For strategy two, there is a threshold during ontogenic growth marked by a star in the diagram. If the predator visits when the prey is smaller than that size, the prey should forage while the predator is there, otherwise it should hide until the predator leaves. We call this threshold size the *optimal strategy switching size*. Strategy 4 is rare for the parameter ranges we considered and has two distinct sizes at which the strategy switches

Results

How does prey optimal response change over ontogenic growth?

Over a wide range of parameter space, the general model predicts four qualitatively different optimal responses to a predation risk (see Fig. 2). For two of the possible optimal responses (optimal strategy 1 and 3), prey responses to predation risk were independent of ontogenic growth (size-age of the juvenile exposure to predation). For optimal strategy number 2, prey decision making did change as a function of

ontogenic growth: when experiencing the risk of predation, smaller/younger prey generally do not change their behavior (continue foraging), while larger/older prey hide. For this strategy there is a size/age threshold that we will call the *optimal strategy switching size* (marked by a black star in Fig. 2) which defines the prey's optimal strategy. If the predator visits when the prey is smaller than this size, the prey will continue to forage; if the predator visits when the prey is larger than this size, the prey will hide. A fourth optimal strategy arises more rarely (for roughly 3% of the parameter sets in our sensitivity analysis). In these cases, it is best for the prey to forage when small or large, but hide at a range of intermediate sizes/ages when the predation risks are highest. Figure 3a shows an example of the survival to maturity for hiding (gray) and for foraging (black) over the range of possible predator start times for one parameter set.

How does prey optimal response change with growth rate?

Prey are balancing a trade-off between the benefits of growth and the mortality costs of predation. When growth is drastically decreased or increased this can change the optimal behavior of the prey in the presence of the predator. Slowing growth reduces the benefits and can cause prey to hide, while increasing growth rate can lead prey to forage. One way to look at this is by considering a non-realistic growth curve with a very slow rate of growth and short bursts of rapid growth (Fig. 3b). For the parameters chosen in this example, the prey should forage during growth pulses and hide if the predator visits when growth is slow. Here, the size of the prey is very similar where the prey shifts between strategies and the main difference is the growth rate.
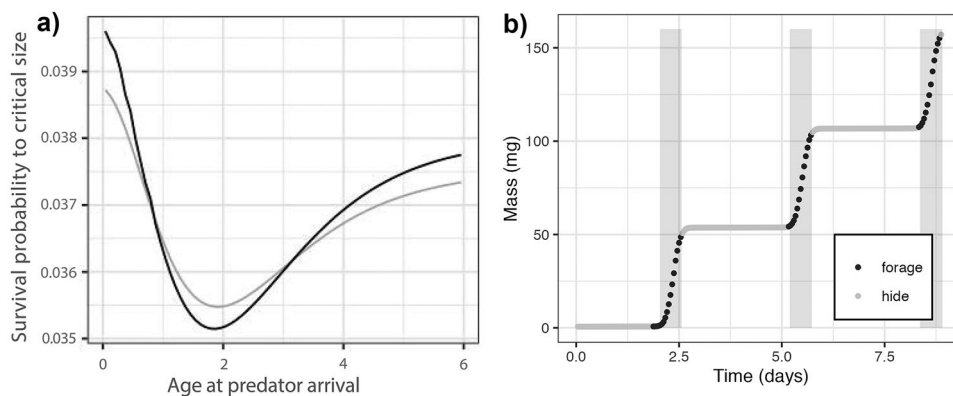

Fig. 3 **a** For optimal strategy 4, the survival probability to the critical size for foraging when the predator is present (black) is less than hiding (gray) for a range of time/sizes at which the predator-related mortality risks are highest. **b** A non-realistic growth curve can be created which shows how the prey strategy depends on the growth rate (for

this example $x_1'(t) = 0.1 + 100 * (sin(t))^{50}$. During periods of slow growth, the prey's best choice is to hide (gray dots), while in pulses of rapid growth (shaded in gray), the prey should continue to forage (black dots)

What parameters most affect the optimal strategy shifting size?

We performed a global sensitivity analysis to assess the relative impact of the parameters related to prey growth, detection by the predator and death (both background and size-dependent predation) on the dependence of the best prey strategy based on the timing of contact with the predator. We considered only the parameter sets where the optimal strategy had at least one switch from foraging to hiding (strategies number 2 or 4) and explored the impact each parameter had on the optimal *strategy switching size*. For optimal strategy 4 which has multiple switching sizes, we considered only the first switch from foraging to hiding. Figure 4 shows the elasticities for several key parameters for the model. Results from the sensitivity analysis show that for strategies 2 and 4, the threshold size where the strategy switches from foraging to hiding is the most sensitive to changes in two parameter related to prey death: the background death rate (*d*) and the detection cost of foraging (*m*). Increasing the background mortality rate increases the average size of the strategy switch and increasing the detection cost for foraging decreases the average size of the switch.

How is the dependency of the trade-off on "ontogenic-size" altered by the shape of the growth curve?

To answer this question, we chose three growth curves (Fig. 5) representing different characteristic growth patterns (a) saturating with the swiftest growth when small, b) s-shaped with swiftest
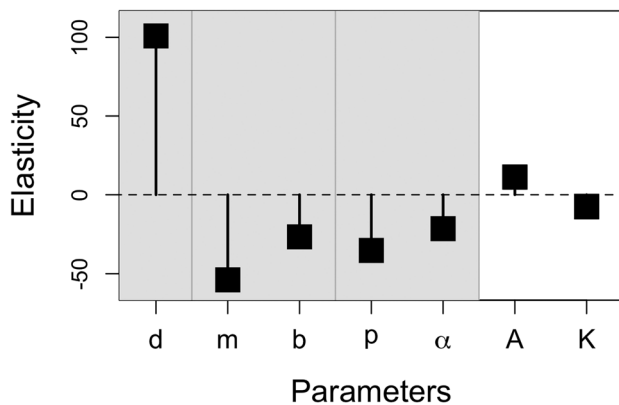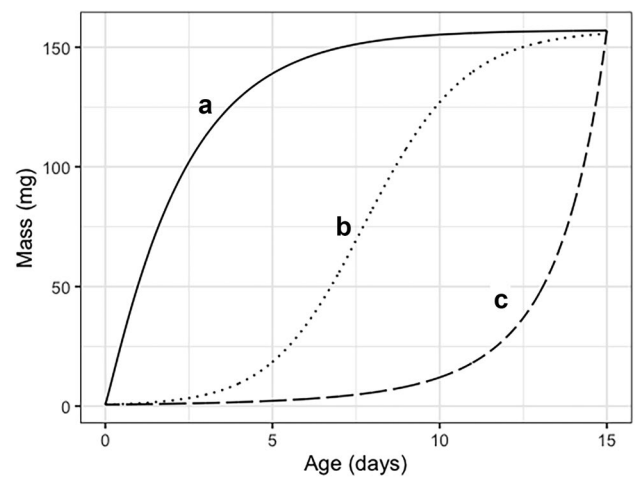
Fig. 5 Three examples of growth curves which capture extremes. **a** is a saturating growth curve with growth slowing as the prey gets larger ($A = 0.1, K = 0.5, H = 47.4, B = 1$). **b** is s-shaped with slow growth when the prey is small and large and faster at intermediate sizes/ages ($A = 1.08, K = 0.03, H = 0.69, B = 1.7$). **c** is close to exponential with growth rate increasing with size throughout growth ($A = 1.2, K = 0.001, H = 0.24, B = 1$)

Fig. 4 Sensitivity analysis of the first *strategy switching size* for parameter sets with at least one switch in strategy. The elasticity is the proportional change in the size when the strategy shifts from hiding to foraging relative to the change in each parameter value (shown as the height of the box and length of the bar above the parameter). A positive elasticity indicates that increases in that parameter lead to, on average, prey continuing to forage in the presence of predators until they weigh more. Parameters *d*, *m*, *b*, *p*, and *α* are related to mortality risks and *A* and *K* control the shape of the growth curve. See Table 1 for explanations of the parameters and the ranges used for this sensitivity analysis

growth at intermediate sizes, and c) exponential with growth rate increasing with mass. For each of these three growth curves, we found the optimal foraging strategy for the prey over plausible ranges of *m* and *d* since the sensitivity analysis indicated that these two parameters had strong effects on the switching size. The rest of the parameters were held constant near the middle of the ranges considered in the sensitivity analysis.

Figure 6 shows the regions in which the qualitatively different strategies occur for each of the growth curves. The s-shaped growth curve (b) represents a sort of middle ground (Fig. 6b). For most of the considered combinations of *m* and *d* the prey has a *strategy switching size* (gray regions). When the prey is small, the mortality costs of foraging are small compared to the benefits of growth. As the prey gets larger, the costs become larger and the benefits decrease to the point where it becomes better for the prey to stop foraging when the predator is present to reduce overall mortality costs. When the prey experiences rapid initial growth that slows as the prey gets larger (growth curve a), the higher growth benefits when it is small, but as it grows, the growth rate decreases. The predicted optimal strategies are shown in Fig. 6a. There is a large region where it is best for the prey to hide regardless of how big it is when the predator visits (white region 1). For growth that is closer to exponential (growth curve c), the prey is small for much of the susceptible period (lower predation risk) and when it does start to get larger (and predation risk increases) it grows quickly which increases the benefits of foraging when larger to grow to the critical size. We see a large region of *m*, *d* parameter space
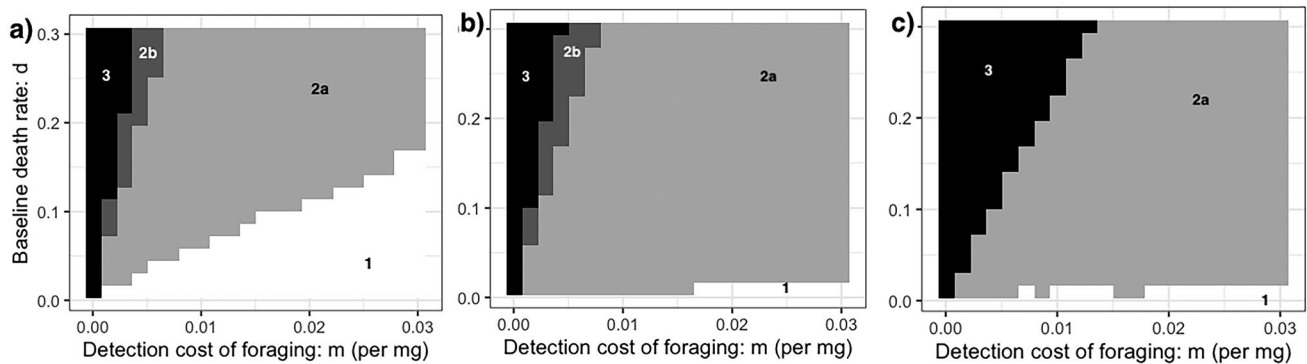
Fig. 6 For the three example growth curves shown in Fig. 6 **a** saturating, **b** s-shaped, and **c** exponential, the optimal strategy and *strategy switching size* were determined over a range of detection costs for foraging (m) and baseline background death rates (d). All other parameters are held constant ($b = 0.0025$, $p = 0.9$, $\alpha = 0.5$, $m_0 = 0.634$ and H calculated so that a continuously foraging prey reaches size $M = 157 mg$ at time $T = 15$). The predator is assumed to visit for 3

hours. We see three distinct optimal strategies which are labeled to match those described in Fig. 2. In regions 1 (white) and 3 (black) the prey should hide and forage, respectively, when the predator visits. In the two grey regions there is a threshold size where the optimal strategy shifts from foraging to hiding. In region 2a (light gray) the *strategy switching size* is less than 50 mg, and in region 2b (dark gray) the *strategy switching size* is greater than 50 mg

(Fig. 6c) where it is best for the prey to forage regardless of its current size (black region 3). The region with larger switch sizes (bigger than 50 mg) also gets so small that it wasn't present for any of the considered combinations of m and d. For the smallest value of d tested, there are also points where as m increases, the best strategy shifts to strategy 1, but also shifts back to strategy 2 a couple of times. There is no stochasticity in the model, so we believe that this is because the survival probability is very similar between both strategies and small errors in the numerical integration are be shifting it one way or the other.

Applying the theory: How does the foraging-risk trade-off change with ontogeny and growth curve shape for the Colorado potato beetle?

What is the right growth curve for the Colorado potato beetle? We fit the VBGF growth function with 1) no catabolism term ($K = 0$), 2) catabolism with exponent set to $B = 1$, and 3) no constraints on any of the parameters to size data for non-cannibal *L. decemlineata* grown in the laboratory (Fig. 7a). Model 3 (black solid line) is the only model that fits growth well throughout larval development because it is the only model that can be parametrized for swifter intermediate growth and slower initial and final growth. The best fit parameters for each of these three models, negative log-likelihood measurements, computed AIC for each model, and the relative likelihood of each model are shown in Table 2. The relative likelihoods based on the AIC values

show overwhelming support for growth model 3 for the Colorado potato beetle.

How does cannibalism change the growth curve? Collie, et al. found that cannibal larvae grow more quickly at the beginning (both in terms of size and stage of development) but after the first instar, growth roughly matched that of their non-cannibal siblings of the same stage of development (Collie et al. 2013). Based on this result, we adjusted the non-cannibal growth curve for cannibal larvae by fitting a parameter which accelerates growth in the first 2.5 days to laboratory data on the growth of cannibal *L. decemlineata* larvae. Other parameters related to the overall shape of the curve were kept the same as for non-cannibals. The best fitting model had cannibals growing 1.19 times faster than non-cannibals during the first 2.5 days. Figure 7b shows the cannibal (black) and non-cannibal (gray dashed) growth curves together with the size data for cannibal larvae (points). This leads cannibals to get about 1/2 a day ahead of non-cannibals if both forage continuously throughout development.

Fitting all of the shape parameters (A, K, B, H, m_0) to the cannibalism data is another way to fit this curve but yields a similar negative log-likelihood (nLL) and involves fitting 5 parameters instead of 1. Comparing the Akaike information criterion (AIC) values leads to a relative likelihood of 99% for the model where non-cannibal growth is adjusted by speeding up growth in the first 2.5 days (nLL = 1037.5, 1 parameter, AIC = 2077, relative likelihood=0.994) compared to the more general model with more variables fit (nLL = 1038.7, 5 parameters, AIC = 2087, relative likelihood = 0.006).
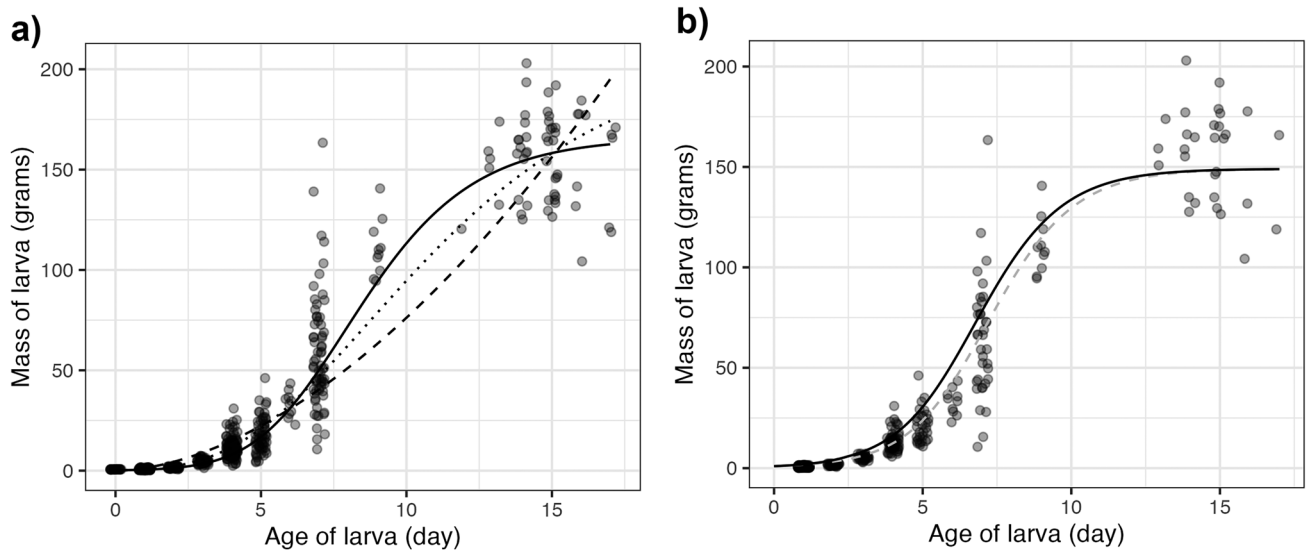
a)

b)

Fig. 7 a Three von Bertalanffy Growth Function sub-models fit to growth data for non-cannibal Colorado potato beetle (dots, jittered and semi-transparent so density is more visible). Model 1 (dashed line) has no catabolism term ($K = 0$). Model 2 (dotted line) has the catabolism term with exponent set to $B = 1$. Model 3 (black solid line) has all parameters fit to the data. Table 2 contains the best-fit parameters for each of these lines, measurement of the fit of the line and AIC model comparison for the four models. **b** The best fitting

growth curve for non-cannibals (gray dashed line here and model 3 in part **a** is adjusted to fit cannibal growth data (dots) by speeding up growth in the first 2.5 days (black line). The best fit model for the cannibals with all growth curve parameters held the same as for non-cannibals has cannibals growing 1.19 times faster for the first 2.5 days. Relaxing these assumptions and fitting all growth parameters did not lead to a better fitting curve for non-cannibals

Model predictions for the foraging-risk trade-off for the Colorado potato beetle cannibal and non-cannibal larvae.

We ran the model once for the cannibal growth curve and once for the non-cannibal growth curve for a range of combinations of background death-rates (d) and detection costs of foraging (m). Cannibals switched strategies from foraging to hiding at larger sizes, with the largest differences in switching size occurring when m was small (Fig. 8a). The cannibals also grew more quickly to the critical mass because of their swifter early growth. Overall, the model predicted that cannibals would have up to a 25% increase in survival probability over non-cannibals with the largest differences occurring when d was large.

Experimental validation of the model Tigreros et al. (2017) observed that when cannibal and non-cannibal Colorado potato beetle larvae were exposed to predators at the same chronological age of 4 days old, non-cannibals continued to

forage and grow while cannibals reduced growth and foraging. We performed a follow-up study to test whether cannibal and non-cannibal larvae would experience the same predation risk when exposed to the predator at the same ontogenic size. Similarly sized *L. decemlineata* larvae pairs (one cannibal and one non-cannibal) were exposing to a non-modified *P. maculiventris* (predator) stink bug and which was killed first was recorded. In 29 of the 56 (51.8%) trials the cannibal was eaten first; cannibals and non-cannibals were equally susceptible to predation ($\chi^2 = 0.07$, $p = 0.79$). The behavior was not recorded but if they exhibited different behaviors they did not result in different survival rates.

Discussion

Several previous models have shown that choices about whether to employ growth-slowing behaviors to reduce predation risk should be expected to shift with prey size under a variety of conditions (Ludwig and Rowe 1990; Werner and

Table 2 Best fit parameters for the growth model for the data we have on Colorado potato beetle Larval growth. Greyed out parameters were predefined and not fit to the data

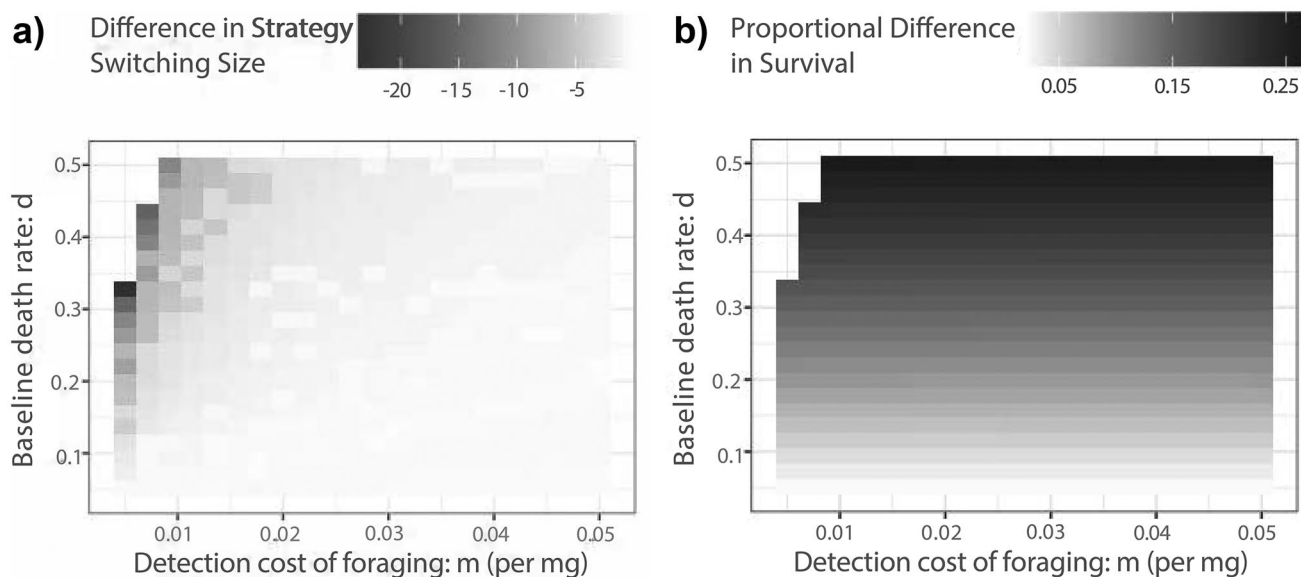| Model	A	B	H	K	m_0	nLL	AIC	Relative Likelihood
1	0.41	NA	2.29	0	$5.5 \cdot 10^{-17}$	1657	3320	<<0.001
2	0.96	1	10.7	8.69	$8.8 \cdot 10^{-7}$	1526	3060	<<0.001
3	1.28	1.45	0.96	0.41	0.67	1510	3030	~1

Fig. 8 Cannibalism in Colorado potato beetles changes the growth curve by increasing early growth. These changes affect the optimal strategy for the larvae with cannibals switching at smaller sizes than non-cannibals (**a**) with the largest differences happening in the darkest gray regions. Cannibals also have a higher chance of survival to the critical size than non-cannibals (**b**). Larger baseline death rates lead to larger survival benefits. Compared to non-cannibals, cannibals have at least 25% higher survival in the darkest gray region of (**b**). For these results, the model was parametrized for Colorado potato beetle (parameters in Table 1 and growth model 3 in Table 2) for cannibals and non-cannibals

Gilliam 1984; Rowe and Ludwig 1991) but little is known about how the timing of rapid growth affects size-dependent behavioral changes in prey. Foraging often increases prey exposure to potential predators, but also helps prey grow more quickly to (potentially) escape predation. Prey are continuously balancing the benefits of foraging and growth with the associated predation risks. Swifter instantaneous growth brings increased growth benefits for foraging so the timing and size dependence of the prey growth rate is important to consider when looking at the optimal prey foraging strategy. We investigate this using a well-established model for growth.

The von Bertalanffy Growth Function (VBGF) is a mechanistic model for growth that has been used for many different species. It is sometimes assumed (especially for insects), that the negative catabolism (energy-use) term can be omitted (Von Bertalanffy 1957; Maino and Kearney 2015). When this term is included, the exponent controlling size dependence is usually assumed to be equal to one and the focus is on determining the right exponent for the positive energy assimilation term (For example: Lee et al. 2020; Renner-Martin et al. 2018; West et al. 2001). These assumptions limit how much growth can slow down as the individual gets larger. Within our case study, our results show that the von Bertalanffy Growth Function with either of these commonly used simplifying assumptions does not fit the growth of Colorado potato beetle larvae well and the more general VBGF

model is needed to capture the growth (according to the AIC which accounts for the increased number of parameters). This points to a need for modelers to investigate more fully the effects of allowing for a wider variety of growth curve shapes on behavior and model outcomes.

While there is ample evidence that both predation risk and growth rates change as a function of prey size, there is little understanding of how these shape prey decision making - to forage or to hide - across ontogenic growth. Our results showed that prey individuals would generally be expected to take risks early in growth but shift to hiding when larger. However, this is dependent on the speed of growth. During periods of swifter growth, the trade-off shifts more toward foraging while slower growth decreases the benefits of foraging. Additionally, our findings indicate that the optimal *strategy switching size* is most sensitive to changes in the background death rate (positively correlated) and the detection risk of foraging (negatively correlated). Higher background mortality leads to switching from foraging to hiding at larger sizes while being more likely to be detected by the predator, while foraging leads to switching to hiding at smaller sizes. In general, experimental validation from the Colorado potato beetle aligned with our model predictions giving additional support for the model.

As is the case in all modeling studies, we made several simplifying assumptions relevant to our investigation as well as to allow for tractability of the results. To the latter point,

we focused our parameter exploration primarily on parameters directly related to growth and mortality and held constant parameters related to overall size and time to maturity. This was necessary so that the model results could be compared across parameter sets. Although we did not exhaustively explore all parameters (for example, initial and final prey size), we focused on those that are most directly related to the foraging-predation trade-off and we therefore anticipate that our qualitative findings would not be impacted. Our analyses provide a baseline assessment of the prey decision making under this foraging-predation trade-off, and future studies may seek to investigate more nuanced aspects of the dynamics. We also assumed that predators were searching in the near vicinity of the prey only once during prey development, and prey choose either to hide or forage for the entire time the predator was there. We believe that the general patterns of foraging when growth is swift enough to overcome the costs of increased predation would apply to cases where a prey is exposed to a predator multiple times. One way we could use our model results to think about the case where a prey is exposed to a nearby predator multiple times during growth would be to look at what happens when the length of a predator visit is extended (to approximate multiple visits in close succession) or to think about additional predator visits as factors increasing the background death rate. In both cases, the model predicts that tradeoff shifts towards foraging. However, investigations into multiple predator visits or strategies which are allowed to change part way through a predator visit might reveal more complex switching behaviors.

More generally, this modeling framework could be used to explore the evolution of specific growth patterns under different size-dependent predation pressures. For example, prey with gape-limited predators sometimes have rapid initial grow to escape predation (Urban 2007; Nowlin et al. 2006), rodents use moon light cues as a proxy for bird predation and stop foraging more on moon-lit nights (Palmer et al. 2017), copepods have daily movement up and down in the water column to decrease predation (Bollens and Stearns 1992), and younger, smaller prey respond more strongly to predators than older, less vulnerable conspecifics (Thaler and Griffin 2008). This modeling framework could be applied to consider how specific predation pressures might lead to the evolution of different prey growth patterns.

Importantly, our model was also verified by applying it to a prey species (the Colorado potato beetle) and its predator (the stink bug). Previously published experimental results show that predator exposure can alter prey behavior with prey sometimes stopping growth to avoid predation. Specifically, it was found that when exposed to a predator, 4-day-old cannibal larvae stop growth while 4-day-old non-cannibal larvae continued to grow as if the predator was not there. We find that cannibalism changes the growth curve by accelerating growth in the first 2.5 days and the model predicts the same behavioral difference because the cannibal larvae are larger (and past the *size switching threshold*) when they reach 4-days old. This leads to an increased survival probability for cannibals to reach the critical size and also a larger optimal *strategy switching size* for cannibals (that is, the size at which prey switch strategies from foraging to hiding) than non-cannibals. This *strategy switching size* will also depend on prey mortality pressures and growth rates. In addition to identifying optimal prey strategies during ontogenic growth, our results also highlight the importance for researchers to carefully consider growth trajectory in addition to size when designing experiments investigating state-dependent risk-aversion, especially when the attribute of interest may cause multiple changes including different rates of growth or size of individuals. These findings suggest ways to optimize the use of predators for control of Colorado potato beetles and other pests. Most biological control agents are released when they can consume the most prey. This research suggests that another avenue is to target predators to the stages of beetles that are most likely to reduce plant feeding and crop damage in response to predator presence.

Supplementary information

The programs used to run the model, fit the parameters, and produce the figures shown in this article have been shared at https://github.com/kmontovan/Montovan-et-al-2022.git.

Appendix A. Parameter estimation for the Colorado potato beetle

A.1 Larval initial and final mass (m_0 and M)

Initial mass is estimated from the masses of 29 individual eggs to be $m_0 = 0.634 \pm 0.009$ mg. The final larval mass at pupation is estimated based on the masses at the time of pupation for 56 larvae reared in the laboratory $M = 157 \pm 2.9$ mg. The masses at pupation were not significantly different between cannibals and non-cannibals so this estimate come from a combination of the masses of both cannibals and non-cannibals. The age of pupation for this dataset was $15 \pm .2$ days for non-cannibals ($n = 26$) and $14.7 \pm .2$ days ($n = 30$) for cannibals.

A.2 Growth parameters (A, B, H, and K)

We consider four submodels of the von Bertalanffy Growth Function (vBGF)

$$dm/dt = Hm^A - Km^B \qquad (6)$$

where m is the mass of the larvae at time t. Model 1 has no catabolism term ($K = 0$), model 2a is constrained to $B = 1$, model 2b has $B = 1$ and $m_0 = 0.634$ mg, and Model 3 has only $m_0 = 0.634$ mg constrained. We use the built-in optim function in R (R Core Computing Team 2017) to find the parameters A, B, H, K, and m_0 (whichever are not constrained) that minimize the log likelihood function (which is equivalent to maximizing the likelihood function) under the assumption that the observations will be normally distributed around the model prediction with a deviance of S (also fit in the model). To eliminate the possibility of the optimization returning negative parameter values outside of the reasonable domain, we log transformed the parameters ($q = log(A), z = log(B), \dots$ which produces positive $A = e^q, B = e^z \dots$ for all $-\infty < q < \infty$ and $-\infty < z < \infty \dots$). The optimization was run 1000 times for starting parameters randomly chosen from a reasonable range. We then assess the range of the parameters estimates for the 100 smallest negative Log Likelihood values to determine if there was an identifiability problem with the model parameters. There is a linear relationship between some of the pairs of parameter estimates but ranges of parameter estimates for the best 10% were within 0.1% of each other so there are not significant identifiability problems. See https://github.com/kmontovan/Montovan-et-al-2022.git for the data and code used to fit these growth curves.

Survival parameter (*d*)

Smaller larvae likely die at a higher rate but most of this mortality happens occurs in the first instar. We make the simplifying assumption that there is a roughly constant background death rate. To estimate d, it is helpful to have an explicit equation for $x_2(t)$ when no predators are present at any point in the life of the larva. Solving for survival as a function of time when no predators are present during growth ($x_2'(t) = -d \cdot x_2$) leads to

$$x_2(t) = c_1 e^{-d \cdot t} \qquad (7)$$

We already assumed that the initial condition is that $x_2(0) = 1$, so $c_1 = 1$. In the lab, the background death for a lava is estimated to be $10/91 = 0.11$ deaths between 4 days old and pupation (which in this study happened on average on day 10.25). In the field the death rate is likely to be significantly higher. We don't know what $x_2(4)$ is so let's set it to be E. Then $x_2(10.25) = .89E$. Plugging these values into equation 7 and solving gives $d \approx 0.019$. We will estimate d to be higher ($d \approx 0.05$) in the field to account for additional sources of mortality not present in the lab. We also consider

a wide range of values for d in the model sensitivity analysis because of the uncertainty in this estimate.

Author contributions All authors contributed to the study conception and design. Data collection was performed by Natasha Tigreros and Jennifer Thaler. Model creation, implementation, and analysis as well as statistical analyses were performed by Kathryn Montovan. The first draft of the manuscript was written by Kathryn Montovan, and all authors commented on previous versions of the manuscript. All three collaborated on the writing and revision of the manuscript and all approve of the current submission.

Data availability Data will be made publicly available for publication.

Code availability R Code is available in github (https://github.com/kmontovan/Montovan-et-al-2022.git).

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflicts of interest/Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

Abrams PA, Leimar O, Nylin S, Wiklund C (1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. Am Nat 147(3):381–395

Barnett C, Bateson M, Rowe C (2007) State-dependent decision making: educated predators strategically trade off the costs and benefits of consuming aposematic prey. Behav Ecol 18(4):645–651

Berger D, Walters R, Gotthard K (2006) What keeps insects small?–size dependent predation on two species of butterfly larvae. Evol Ecol 20(6):575

Bernays E (1997) Feeding by lepidopteran larvae is dangerous. Ecol Entomol 22(1):121–123

Bollens SM, Stearns DE (1992) Predator-induced changes in the diel feeding cycle of a planktonic copepod. J Exp Mar Biol Ecol 156(2):179–186

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7(10):999–1014

Collie K, Kim SJ, Baker MB (2013) Fitness consequences of sibling egg cannibalism by neonates of the Colorado potato beetle *Leptinotarsa decemlineata*. Anim Behav 85(2):329–338. https://doi.org/10.1016/j.anbehav.2012.11.013

Davidowitz G, D'Amico LJ, Nijhout HF (2003) Critical weight in the development of insect body size. Evol Dev 5(2):188–197

Elvidge CK, Ramnarine I, Brown GE (2014) Compensatory foraging in trinidadian guppies: effects of acute and chronic predation threats. Current Zoology 60(3):323–332

Ferrari MC, Chivers DP (2009) Sophisticated early life lessons: threat-sensitive generalization of predator recognition by embryonic amphibians. Behav Ecol 20(6):1295–1298. Retrieved from http://doi.org/10.1093/beheco/arp135. https://academic.oup.com/beheco/article-pdf/20/6/1295/17278740/arp135.pdf

Hare JD (1990) Ecology and management of the Colorado potato beetle. Annu Rev Entomol 35(1):81–100. https://doi.org/10.1146/annurev.en.35.010190.000501

Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Bejder L (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J Anim Ecol 76(5):837–844. Retrieved from https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-2656.2007.01260.x. https://doi.org/10.1111/j.1365-2656.2007.01260.x

Hermann SL, Thaler JS (2014) Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. Oecologia 176(3):669–676. https://doi.org/10.1007/s00442-014-3069-5

Houston AI (2010) Evolutionary models of metabolism, behaviour and personality. Philos Trans R Soc B 365(1560):3969–3975

Karpestam E, Merilaita S, Forsman A (2014) Body size influences differently the detectabilities of colour morphs of cryptic prey. Biol J Lin Soc 113(1):112–122

Kerkhoff A (2012) Modeling metazoan growthand ontogeny. Metabolic Ecology: A Scaling Approach p 48

Lee L, Atkinson D, Hirst AG, Cornell SJ (2020) A new framework for growth curve fitting based on the von bertalanffy growth function. Sci Rep 10(1):1–12

Lima SL (1998) Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27(8):215–290

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68(4):619–640. Retrieved from http://doi.org/10.1139/z90-092

Losey JE, Denno RF (1998) The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. Ecol Entomol 23(1):53–61

Ludwig D, Rowe L (1990) Life-history strategies for energy gain and predator avoidance under time constraints. Am Nat 135(5):686–707

Maino JL, Kearney MR (2015) Testing mechanistic models of growth in insects. Proc R Soc B Biol Sci 282(1819):20151973

Mänd T, Tammaru T, Mappes J (2007) Size dependent predation risk in cryptic and conspicuous insects. Evol Ecol 21(4):485

McKay MD (1992) Latin hypercube sampling as a tool in uncertainty analysis of computer models. In: Proceedings of the 24th conference on Winter simulation, pp 557–564

Moschilla JA, Tomkins JL, Simmons LW (2018) State-dependent changes in risk-taking behaviour as a result of age and residual reproductive value. Anim Behav 142:95–100. Retrieved from https://www.sciencedirect.com/science/article/pii/S0003347218301933730. https://doi.org/10.1016/j.anbehav.2018.06.011

Nelson EH, Matthews CE, Rosenheim JA (2004) Predators reduce prey population growth by inducing changes in prey behavior. Ecology 85(7):1853–1858

Nowlin WH, Drenner RW, Guckenberger KR, Lauden MA, Alonso GT, Fennell JE, Smith JL (2006) Gape limitation, prey size refuges and the top-down impacts of piscivorous largemouth bass in shallow pond ecosystems. Hydrobiologia 563(1):357–369

Palmer M, Fieberg J, Swanson A, Kosmala M, Packer C (2017) A 'dynamic'landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecol Lett 20(11):1364–1373

Pettersson LB, Brönmark C (1993) Trading off safety against food: state dependent habitat choice and foraging in crucian carp. Oecologia 95(3):353–357

R Core Computing Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Renner-Martin K, Brunner N, Kühleitner M, Nowak WG, Scheicher K (2018) On the exponent in the von bertalanffy growth model. PeerJ 6:e4205

Rowe L, Ludwig D (1991) Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72(2):413–427

Rudolf VH (2008) The impact of cannibalism in the prey on predator-prey systems. Ecology 89(11):3116–3127

Stoks R, Swillen I, De Block M (2012) Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in ischnura damselfly larvae. J Anim Ecol 81(5):1034–1040

Tammaru T, Esperk T (2007) Growth allometry of immature insects: larvae do not grow exponentially. Funct Ecol 21(6):1099–1105

Thaler JS, Griffin CA (2008) Relative importance of consumptive and non-consumptive effects of predators on prey and plant damage: the influence of herbivore ontogeny. Entomol Exp Appl 128(1):34–40

Tigreros N, Norris RH, Wang EH, Thaler JS (2017) Maternally induced intraclutch cannibalism: an adaptive response to predation risk? Ecol Lett 20(4):487–494. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12752. https://doi.org/10.1111/ele.12752

Tigreros N, Wang EH, Thaler JS (2018) Prey nutritional state drives divergent behavioural and physiological responses to predation risk. Funct Ecol 32(4):982–989. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2435.13046. https://doi.org/10.1111/1365-2435.13046

Tigreros N, Norris RH, Thaler JS (2019) Maternal effects across life stages: larvae experiencing predation risk increase offspring provisioning. Ecol Entomol 44(6):738–744

Urban MC (2007) The growth-predation risk trade-off under a growing gape-limited predation threat. Ecology 88(10):2587–2597. https://doi.org/10.1890/06-1946.1

Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behav Ecol Sociobiol 60(4):457–464

von Bertalanffy L (1951) Metabolic types and growth types. Am Nat 85(821):111–117

Von Bertalanffy L (1957) Quantitative laws in metabolism and growth. Q Rev Biol 32(3):217–231

Wagenmakers EJ, Farrell S (2004) Aic model selection using akaike weights. Psychon Bull Review 11(1):192–196

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. Nature 413(6856):628–631

Winnie J Jr, Creel S (2017) The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. Food Webs 12:88–94