CHICAGO JOURNALS

The University of Chicago

When to Defend: Antipredator Defenses and the Predation Sequence.

Author(s): Andrew W. Bateman, Matthijs Vos, and Bradley R. Anholt

Source: *The American Naturalist*, Vol. 183, No. 6 (June 2014), pp. 847-855

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/675903>

Accessed: 11/08/2014 10:37

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

NOTE

When to Defend: Antipredator Defenses and the Predation Sequence

Andrew W. Bateman,^{1,*} Matthijs Vos,^{2,3} and Bradley R. Anholt^{1,4}

1. Department of Biology, University of Victoria, PO Box 3020, Victoria, British Columbia V8W 3N5, Canada; 2. Institute of Environmental Sciences (CML), Leiden University, PO Box 9518, 2300 RA Leiden, The Netherlands; 3. Department of Aquatic Ecology, Netherlands Institute of Ecology, Royal Netherlands Academy of Arts and Sciences (NIOO-KNAW), PO Box 50, NL-6700 AB Wageningen, The Netherlands; 4. Bamfield Marine Sciences Centre, PO Box 100, Bamfield, British Columbia V0R 1B0, Canada

Submitted August 10, 2013; Accepted January 8, 2014; Electronically published May 1, 2014

ABSTRACT: Some authors have suggested that prey species stand to benefit most by defending as early as possible during predator-prey encounters, but species in nature employ antipredator defenses at various stages of interactions with their predators. Whether it is generally most advantageous to defend early or late during such encounters is an open theoretical question. We model conditions under which a prey species might evolve early or late defenses in response to predation. Adapting a two-prey, one-predator Rosenzweig-MacArthur system of differential equations, we analyze the effects of modified antipredator defenses (and their associated costs) on the ability of a new prey type to invade the one-prey, one-predator limiting system at equilibrium. We show that the outcome, in terms of invasion potential, is crucially dependent on the ratio of the prey's proportional population growth rate to the cost of predator encounters.

Keywords: defense timing, invasion analysis, predator-prey model, cost/benefit ratio, predation sequence, predation cycle.

Introduction

For a predator to be successful, it must repeatedly complete a set of necessary steps: prey encounter, detection, pursuit, capture, handling, and consumption (collectively called the predation sequence or cycle). Although the details may differ among species, some form of predation sequence is universal in predator-prey interactions. Of course, it is in the interest of prey to avoid consumption, and organisms exhibit a wide array of antipredator defenses that serve to interrupt the predation sequence (reviewed in Edmunds

1974; Endler 1991; Lima and Dill 1990; Richardson and Anholt 2010).

With many possible approaches to defense, it is of interest to consider which antipredator defenses will be favored in a given species (Endler 1991). Fuiman and Margurran (1994) noted that avoiding the notice of a predator is one of the most effective ways to avoid predation, and Endler (1991) asserted that it is most advantageous to defend early in the predation sequence in order to maximize the chance of escape and use energy most efficiently. Organisms, however, employ antipredator defenses throughout the predation sequence, indicating that later defenses are often favored by selection. Brodie et al. (1991) modeled selection on pre-encounter predator-avoidance mechanisms and post-encounter antipredator mechanisms, showing how investment in one type of mechanism could reduce selection on the other, so that species employing one or the other, but not both, might be expected.

Here, we investigate the relative benefits of idealized defenses, employed at different phases of the predation sequence. For simplicity, we consider a predation sequence broken into two parts: pre-attack and post-attack. Prey employ early pre-attack defenses—e.g., camouflage, decreased activity, and warning coloration—and late post-attack defenses—e.g., speed (flight), weaponry or robustness (fight), and noxiousness. We develop a multispecies dynamical model and consider the invasion of an established predator-prey system by a new prey type with altered defense mechanisms, comparing the effectiveness of augmenting early versus late defenses and considering the costs associated with the two classes of defense. Although we discuss attack and ingestion as the two predation phases in the model, the probabilities we use could also refer to another pair of relevant phases in the predation sequence. Using the model, we ask: should we expect prey to evolve to terminate the predation sequence at its onset or evade

* Corresponding author. Present address: Department of Biology/Department of Mathematical and Statistical Sciences, University of Alberta, 632 Central Academic Building, Edmonton, Alberta T6G 2G1, Canada; and Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada; e-mail: andrew.w.bateman@gmail.com.

Am. Nat. 2014. Vol. 183, pp. 847–855. © 2014 by The University of Chicago. 0003-0147/2014/18306-5489\$15.00. All rights reserved.
DOI: 10.1086/675903

Table 1: Description of variables and parameters from the predator-prey model

Symbol	Description
X	Population size of prey type 1
Y	Population size of prey type 2
Z	Population size of predator
a	Encounter rate of predator with prey
P_i	Probability that a predator attacks a prey i individual when encountered
Q_i	Probability that a prey i individual is ingested by a predator after attack
r	Maximal per capita growth rate of prey
K	Carrying capacity of total prey ($X + Y$)
T_a	Attack component of handling time, incurred when prey's early defenses fail
T_m	Manipulation component of handling time, incurred when prey's late defenses fail
ε	Conversion efficiency of prey into predator
d	Natural death rate of predator

capture and consumption once the predation sequence is underway?

Mathematical Models

Consider a predation sequence in which the predator encounters a prey individual, attacks the prey with probability $P(\text{attack}) = P$, and then ingests the prey with probability $P(\text{ingestion}|\text{attack}) = Q$. The probability that the predator attacks and ingests the prey ($P[\text{attack} \cap \text{ingestion}]$) is $P \cdot Q$, the probability that the predator does not attack is $(1 - P)$, and the probability that the predator attacks but is unable to ingest the prey is $P \cdot (1 - Q)$; these are the three mutually exclusive outcomes of the predation sequence we consider.

We define a predator-prey encounter as an event during which prey attack and ingestion are possible; however, encounter may or may not lead to attack, and attack may or may not lead to consumption. When a prey is within a predator's sensory range but the prey avoids attack we consider an encounter to have occurred. We assume that once a prey individual is ingested it is killed, and we ignore the unrealistic cases where P or Q equals zero or one.

Early defense mechanisms decrease the value of P , and late defense mechanisms decrease the value of Q . Prey may possess both types of defense mechanisms, and we assume, in the interest of model simplicity, that each prey individual is able to employ its defenses during the predation sequence, either because the mechanisms are always in place or because the prey is always able to detect the predator in sufficient time.

The Dynamical Model

We use a modified Lotka-Volterra/Rosenzweig-MacArthur two-prey, one-predator system (Lotka 1925; Volterra 1926;

Rosenzweig and MacArthur 1963), similar to those used in many studies of predator-prey dynamics and evolution (e.g., Kretzschmar et al. 1993; Abrams and Matsuda 1997; Vos et al. 2004a, 2004b; Yamauchi and Yamamura 2005; Tien and Ellner 2012). The model incorporates density-dependent prey growth (prey grow below, and decline above, a system carrying capacity) and a Holling type II functional response for the predator (predation rate saturates with increasing prey density; Holling 1959; Rosenzweig and MacArthur 1963). The basic model is represented by the system of differential equations:

$$\frac{dX}{dT} = X \left[r \left(1 - \frac{X + Y}{K} \right) - \frac{aP_x Q_x Z}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} \right] \quad (1a)$$

$$\frac{dY}{dT} = Y \left[r \left(1 - \frac{X + Y}{K} \right) - \frac{aP_y Q_y Z}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} \right] \quad (1b)$$

$$\frac{dZ}{dT} = Z \left[\frac{\varepsilon a(P_x Q_x X + P_y Q_y Y)}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} - d \right] \quad (1c)$$

with symbols defined in table 1.

In the model, X and Y represent two types, or morphs, of the same prey species, with Z their common predator. We are interested in situations where the prey types differ in the effectiveness of their antipredator defenses, but both may use early and late defenses. We assume that all parameters except those related specifically to antipredator defenses are constant across prey types (Abrams and Matsuda 1997; Vance 1978), thus the maximum growth rates, carrying capacities, encounter rates, and handling times are equivalent for both prey. Assuming that the two prey

types experience full niche overlap, we omit a competition coefficient, as its value would be one.

We assume that predators spend a fixed time, T_a , in each attack phase, whether or not the prey is ultimately ingested (Yamauchi and Yamamura 2005), but we assume that a predator must also spend manipulation time, T_m , if the prey is consumed. We assume incremental differences between the two prey types and therefore do not consider prey switching by the predator.

Costs of Defense

We consider possession and usage costs associated with early and late defenses:

Possession Costs. Devotion of resources to morphologies that improve defenses is often reflected in decreased growth rates (e.g., Abrams and Matsuda 1997; Preisser et al. 2005; Ramos-Jiliberto et al. 2007). For prey i , let the proportional cost of early defense be C_{Egi} and the proportional cost of late defense be C_{Lgi} . The fraction of the maximum growth rate maintained when prey i possesses defenses is $1 - C_{Egi} - C_{Lgi}$. The growth rate becomes $r \cdot (1 - C_{Egi} - C_{Lgi})$.

Usage Costs. Usage costs are incurred by prey that implement defenses. Early defenses (e.g., crypsis, predator avoidance) likely involve reduced energy intake (Lima and Dill 1990; Werner and Anholt 1993), while late defenses (e.g., fight, flight) likely involve energy expenditure. Both defenses would, as a result, lead to a reduction in the amount of energy available to prey for growth and reproduction. Energetic equivalents for antipredator behavior (e.g., Abrahams and Dill 1989) have been measured, and the costs appear widespread (e.g., Preisser et al. 2005; Van Buskirk 2000; Verdolin 2006), although the costs of early and late defenses can be difficult to separate empirically. Defenses employed late in the predation sequence may also incur substantial risk of injury (Lima and Dill 1990). In our model, the costs of defense implementation are reflected in a decreased per capita rate of increase for the prey type that incurs them and are considered relative to the cost of a single prey death in the population. Only when prey escape consumption are associated defense-usage costs reflected in the model. Although ingested prey may have paid physiological usage costs, these costs would have been subsumed by the death of the individual. We consider the per-unit prey encounter rate, adjusted for handling time, from the predators' functional response (Case 2000):

$$\frac{aZ}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)}. \quad (2)$$

Quantity (2) is the rate at which an individual prey encounters predators. A fraction, $P_i \cdot Q_i$, of the time, the prey is attacked and consumed; $(1 - P_i)$, of the time, the prey escapes after paying only an early usage cost, C_{Ei} ; and $P_i \cdot (1 - Q_i)$ of the time, the prey escapes after paying combined early and late usage costs, $C_{ELi} = C_{Ei} + C_{Li}$. Due to the sequential nature of predation and our initial assumptions, prey only employ late defenses once they have employed early defenses (however slight). Both C_{Ei} and C_{Li} are fractional, representing a reduction, relative to the death of one individual, to the rate of change of the appropriate prey population. Thus, the defense-related costs that the prey i population experiences per unit prey are

$$\frac{aZ(1 - P_i)C_{Ei}}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} + \frac{aZP_i(1 - Q_i)C_{ELi}}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)}. \quad (3a)$$

Adding the capture "cost" of death and simplifying, for incorporation in equations (1a)–(1c), (3a) becomes

$$\frac{aZ[P_i Q_i + (1 - P_i)C_{Ei} + P_i(1 - Q_i)C_{ELi}]}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)}. \quad (3b)$$

This can be interpreted as the per-prey change in growth rate due to predators. Of course, a prey type may not rely heavily on early defenses—think of aposematic, toxic prey (Endler 1991)—in which case P_i would be near one, and C_{Ei} would be small (similarly for late defenses); this would constitute a special case of the more general model we describe.

If defenses become too costly, a prey population possessing them will decline to extinction. We therefore make the reasonable assumptions that total possession costs do not exceed one (the costs can reduce the prey growth rate but not change its sign) and that total usage costs cannot exceed one (i.e., the cost of death when predators consume prey).

The model, with costs incorporated, becomes:

$$\frac{dX}{dT} = X \left[r(1 - C_{Egx} - C_{Lgx}) \left(1 - \frac{X + Y}{K} \right) - \frac{aZ[P_x Q_x + (1 - P_x)C_{Ex} + P_x(1 - Q_x)C_{ELx}]}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} \right], \quad (4a)$$

$$\frac{dY}{dT} = Y \left[r(1 - C_{Egy} - C_{Lgy}) \left(1 - \frac{X + Y}{K} \right) - \frac{aZ[P_y Q_y + (1 - P_y)C_{Ey} + P_y(1 - Q_y)C_{ELy}]}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} \right], \quad (4b)$$

$$\frac{dZ}{dT} = Z \left[\frac{\epsilon a(P_x Q_x X + P_y Q_y Y)}{1 + aP_x X(T_a + Q_x T_m) + aP_y Y(T_a + Q_y T_m)} - d \right]. \quad (4c)$$

Analysis

We use the model to compare benefits of early versus late defenses and to weigh associated costs. We analyze the model's behavior in relation to two questions: (1) when one prey type is alone at equilibrium with the predator, what conditions will allow the second prey type to invade the system? (2) When is invasion using one defense strategy favored over invasion using the other? We keep the analysis as general as possible, considering the full range of possible defense effectiveness and cost.

Change of Variables

To clarify analysis, we employ the change of variables (Kretzschmar et al. 1993):

$$\begin{aligned} t &:= rT, \\ x &:= \frac{X}{K}, \\ y &:= \frac{Y}{K}, \\ z &:= \frac{aZ}{r}, \end{aligned} \quad (5a)$$

and change of parameters:

$$\begin{aligned} g_i &:= 1 - C_{Egi} - C_{Lgi}, \\ \mu_i &:= P_i Q_i + (1 - P_i) C_{Ei} + P_i (1 - Q_i) C_{ELi}, \\ h_i &:= a K P_i (T_a + Q_i T_m), \\ \alpha_i &:= \frac{K \epsilon a}{r} P_i Q_i, \\ \delta &:= \frac{d}{r}, \end{aligned} \quad (5b)$$

where g_i is the proportion of the prey species' maximum population growth rate available to prey type i , and μ_i is the expected cost, per unit prey per encounter, of the predators' presence in the system. The ratio of the latter two quantities, g_i/μ_i , relates the proportional population growth rate to predation costs for prey type i . Incorporating these parameters and variables, the model becomes

$$\frac{dx}{dt} = x \left[\frac{g_x(1-x-y) - \mu_x z}{1 + h_x x + h_y y} \right], \quad (6a)$$

$$\frac{dy}{dt} = y \left[\frac{g_y(1-x-y) - \mu_y z}{1 + h_x x + h_y y} \right], \quad (6b)$$

$$\frac{dz}{dt} = z \left[\frac{\alpha_x x + \alpha_y y}{1 + h_x x + h_y y} - \delta \right], \quad (6c)$$

Equilibrium Conditions

To find the equilibrium conditions of the model, we solve for species nullclines: combinations of x , y , and z for which the abundance of one species or type does not change. To do this, we set the derivatives in equations (6) equal to zero and solve the resulting equations:

$$\frac{dx}{dt} = 0 \Rightarrow x = 0 \text{ or } z = \frac{g_x}{\mu_x} (1 - x - y) \times (1 + h_x x + h_y y), \quad (7a)$$

$$\frac{dy}{dt} = 0 \Rightarrow y = 0 \text{ or } z = \frac{g_y}{\mu_y} (1 - x - y) \times (1 + h_x x + h_y y), \quad (7b)$$

$$\frac{dz}{dt} = 0 \Rightarrow z = 0 \text{ or } y = -\frac{\alpha_x - \delta h_x}{\alpha_y - \delta h_y} x + \frac{\delta}{\alpha_y - \delta h_y}. \quad (7c)$$

An absent population does not reproduce and grow, so $x = 0$, $y = 0$, and $z = 0$ are referred to as the trivial nullclines. Where nullclines intersect, no species' abundance changes over time, and we have an equilibrium point of the system.

Because (7a) is a multiple of (7b), the system possesses no isolated three-species equilibrium points in the biologically relevant region (i.e., where all species have positive population sizes). It does possess equilibrium points at which the predator and one prey type coexist, where (7c) and either (7a) or (7b) intersect. Also, if $g_y/\mu_y = g_x/\mu_x$, there is a region of infinitely many three-species equilibrium points, due to the resulting shared prey nullcline ([7a], [7b]). This equilibrium region—a three-dimensional curved surface—occurs at the intersection, if it exists, of the predator nullcline (7c) and the nullcline common to both prey types ([7a], [7b]).

Neutral Types

The condition $g_y/\mu_y = g_x/\mu_x$ is satisfied if the two prey types are identical or if one type's advantage with respect to predation is exactly offset by a decrease in population growth rate due to the associated costs (e.g., De Meester et al. 1995). This corresponds to the situation where the two prey types share the same nullcline (see above) and the system has an equilibrium curve rather than an equilibrium point. When the condition is satisfied, solutions are confined to surfaces of the form $y = ax^b$, where a is a positive real constant and b is g_y/g_x (equivalently, μ_y/μ_x).

To see this, one can take the quotient of (6b) and (6a) and solve the resulting z -independent differential equation for y as a function of x . When $g_y/\mu_y = g_x/\mu_x$, all three species coexist, but trajectories behave as if in two dimensions: the predator dimension and a combined prey dimension, defined by $y = ax^b$.

Invasion Criteria

When the g/μ ratio is not equal for the prey types, solutions are not constrained as above. Without loss of generality, we consider the ecologically relevant x - z equilibrium point (predator and one prey type at nonzero densities). Solution paths near the equilibrium point are described by linear combinations of the eigenvectors associated with the linearization of model (6) about the equilibrium point (Jones et al. 2011; Murray 2002). Linearizing the system about this point (we used Maple; Waterloo Maple), two eigenvectors are restricted to the x - z plane, while the third eigenvector has a component in the y direction. For type y to invade (i.e., follow a solution path with a positive y component) any solution's subcomponent involving this third eigenvector must grow over time. For this to occur, the associated eigenvalue must be positive. In our case, the eigenvalue relevant for invasion is

$$\lambda = (g_y\mu_x - g_x\mu_y) \frac{1 - x^*}{\mu_x}, \quad (8)$$

where x^* is the x position of the equilibrium. Since x^* must be less than 1 for this equilibrium to exist (for $x > 1$, the x nullcline (7a) exists only for negative predator densities), $1 - x^*$ is positive (as is μ_x). Thus, the sign of $g_y\mu_x - g_x\mu_y$ determines the sign of λ . To allow invasion, λ must be positive (solutions must move away from the equilibrium and into the interior of the biologically relevant region), i.e., $g_y\mu_x > g_x\mu_y$ (equivalently $g_y/\mu_y > g_x/\mu_x$). Invasion cannot occur if $g_y/\mu_y < g_x/\mu_x$.

Which Defense?

Early defense, allowing prey to avoid more predation events, would intuitively seem most beneficial. From the probability of capture ($P \cdot Q$), however, each defense has comparable bearing on whether an individual is consumed; ignoring costs and handling time, equal proportional decreases in either P or Q would affect a prey type equally (equal absolute decreases would have most effect on the smaller of P and Q , but the relationship is symmetric).

To gain insight into invasion potential, we must consider the costs relevant to the stability conditions described above. Again, without loss of generality, we explore criteria

for invasion of the x - z system by a mutant prey type (y). Prey type x provides the threshold ratio, $\rho = g_x/\mu_x$, and resulting condition that y must satisfy to remain neutral: $g_y = \rho\mu_y$. Only if g_y is greater than $\rho\mu_y$ will y be able to invade.

For y to invade via an increase in net growth rate, g_y , type y must reduce its defense possession costs. As the model is formulated, equal reductions in early- and late-defense possession costs would produce equal increases in g (see eq. [5b]).

To invade via a decrease in the cost of predation, μ_y , y has more options. Prey type y can reduce its attack or consumption probabilities (P_y and Q_y) or can reduce the associated usage costs (C_{Ey} and C_{Ly}). To compare the effects, we simplify μ_y :

$$\begin{aligned} \mu_y &= P_y Q_y + (1 - P_y) C_{Ey} + P_y (1 - Q_y) (C_{Ey} + C_{Ly}) \\ &= P_y Q_y (1 - C_{Ey} - C_{Ly}) + C_{Ey} + P_y C_{Ly} \end{aligned} \quad (9)$$

and differentiate with respect to the parameters of interest:

$$\frac{\partial \mu_y}{\partial P_y} = Q_y (1 - C_{Ey} - C_{Ly}) + C_{Ly}, \quad (10a)$$

$$\frac{\partial \mu_y}{\partial Q_y} = P_y (1 - C_{Ey} - C_{Ly}), \quad (10b)$$

$$\frac{\partial \mu_y}{\partial C_{Ey}} = 1 - P_y Q_y, \quad (10c)$$

$$\frac{\partial \mu_y}{\partial C_{Ly}} = P_y - P_y Q_y. \quad (10d)$$

We interpret equations (10) in terms of the effectiveness of changes to prey defenses (reflected in the values of P_y and Q_y) and the costs of implementing those defenses (C_{Ey} and C_{Ly}). Comparing equations (10a) and (10b), we see that for changes in P_y to have a greater effect on μ_y than changes in Q_y ,

$$\frac{\partial \mu_y}{\partial P_y} > \frac{\partial \mu_y}{\partial Q_y} \Leftrightarrow P_y < Q_y + C_{Ly} (1 - C_{Ey} - C_{Ly}) \quad (11)$$

(fig. 1). Alternatively,

$$\frac{\partial \mu_y}{\partial P_y} > \frac{\partial \mu_y}{\partial Q_y} \Leftrightarrow C_{Ly} > (P_y - Q_y) (1 - C_{Ey} - C_{Ly}) \quad (12a)$$

$$\Leftrightarrow C_{Ly} > \frac{1 - C_{Ey}}{1 + 1/(P_y - Q_y)}, \quad (12b)$$

assuming ($P_y \neq Q_y$). From equation (12a), when $P_y = Q_y$, changes in P_y will always have a greater effect on μ_y than equal changes in Q_y . We can evaluate the effects of changes in P_y and Q_y more generally by using additional

Figure 1: Parameter regions influencing fitness of a new prey type (y) in a predator-prey model that considers antipredator defenses, employed early against attack or late against ingestion (see text). The figure shows all possible combinations of P_y (the probability that a predator attacks prey) and Q_y (the probability that a predator ingests prey post-attack) for three values of the usage cost of late defenses: $C_{Ly} = 0$ (a), $C_{Ly} = (1 - C_{Ey})/4$ (C_{Ey} is the usage cost of early defenses; b), and $(1 - C_{Ey})/2 < C_{Ly} < 1 - C_{Ey}$ (c). In region i, changes in P_y have greater influence than equal changes in Q_y on y 's ability to invade the established predator-prey system at equilibrium. In region ii, changes in Q_y have greater influence than equal changes in P_y . The line $P_y = Q_y + C_{Ly}/(1 - C_{Ey} - C_{Ly})$ separates i from ii. Panels a, b, and c correspond to C_{Ly} values a, b, and c, respectively, in figure 2. All costs are relative to the cost of prey mortality.

information. We assume that defense usage costs are positive (so that $0 \leq C_{Ly}$), and we have already assumed them to be less than the cost of ingestion by the predator (i.e., 1, so that $1 - C_{Ey} > 0$). Thus, when $P_y < Q_y$, equation (12b) implies that $(1 - C_{Ey})/[1 + 1/(P_y - Q_y)] < 0 \leq C_{Ly}$, so that changes in P_y will have a greater effect on μ_y than equal changes in Q_y . We have also assumed that combined defense usage costs do not exceed the cost of ingestion, so that $C_{Ly} < 1 - C_{Ey}$. When $P_y > Q_y$, this condition, in combination with equation (12b), defines two regions: one in which changes in P_y will have a greater effect on μ_y than equal changes in Q_y ,

$$\frac{1 - C_{Ey}}{1 + 1/(P_y - Q_y)} < C_{Ly} < 1 - C_{Ey}, \quad (13)$$

and one in which changes in Q_y will have a greater effect on μ_y than equal changes in P_y ,

$$0 < C_{Ly} < \frac{1 - C_{Ey}}{1 + 1/(P_y - Q_y)} \quad (14)$$

(fig. 2).

We can also compare the right-hand sides of equations (10c) and (10d) to see that changes in C_{Ey} have a larger effect on μ_y than equal changes in C_{Ly} , regardless of P and Q values (recall, we do not consider the case $P_y = 1$).

Discussion

In a differential equation model describing the population dynamics of two prey types and a specialist predator, evolution of antipredator defenses depends on the prey species' ratio of proportional population growth rate to predation costs (g/μ). For a novel prey type with altered antipredator defenses to invade, its value of g/μ must exceed that of the established prey type.

In the simplified case of two prey types and a generalist predator (constant population size and nonsaturating type I functional response; analysis not shown), the result is analogous: the prey type that maximizes g/μ excludes the other type from the system. This simpler case corresponds to a classical Lotka-Volterra competition model.

In the absence of defense costs, changes in early and late defenses have consistent effects on a new prey type's ability to invade the system. One can see this by setting costs equal to zero in equations (10a) and (10b)—a scenario corresponding to panel a in figure 1. This limiting case is directly analogous to the model considered by Brodie et al. (1991), and by making the appropriate notational changes, results are equivalent (compare eqq. [10a] and [10b] to eqq. (4) and (5) in Brodie et al. 1991). Notably, early antipredator defenses enter into our model in the same way that behavioral predator-avoidance strategies en-

Figure 2: Parameter regions influencing fitness of a new prey type (y) in a predator-prey model that considers antipredator defenses, employed early against attack or late against ingestion (see text). The figure shows all possible combinations of $P_y - Q_y$ (the difference between the probabilities that a predator attacks prey and ingests prey post-attack) and C_{Ly} (the usage cost of late defenses), for any fixed value of C_{Ey} (the usage cost of early defenses). In region i, changes in P_y have greater influence than equal changes in Q_y on y 's ability to invade the established predator-prey system at equilibrium. In region ii, changes in Q_y have greater influence than equal changes in P_y . The curve $C_{Ly} = (1 - C_{Ey})/[1 + 1/(P_y - Q_y)]$ separates i from ii. C_{Ly} values a and b and region c correspond to panels a, b, and c, respectively, in figure 1. All costs are relative to the cost of prey mortality.

ter into their model, validating the claim that our model could be applied to arbitrary early and late stages of predation. Through incorporation of a saturating functional response and defense costs, we have accounted for some of the “variation in predator state (e.g., hunger level) or the existence of fitness costs associated with specific prey survival mechanisms” that Brodie et al. (1991, p. 76) note would affect their results.

Possession costs (influencing g), usage costs (influencing μ), and probabilities of attack and ingestion (P and Q , respectively, also influencing μ) affect invasion in our model. Changes in possession costs of both defense classes have equal effect. Changes in usage costs of early defenses, however, have greater effect than equal changes in usage costs of late defenses (for equal reductions in early and late usage costs, the decrease in early defense costs would increase g/μ the most). This seems reasonable, since early usage costs are always paid, while late usage costs are only paid if early defenses fail. The relative effects of changes in P and Q (i.e., the defense targets themselves) are context dependent. If $P \leq Q$, reductions in P increase invasion ability the most; if $P > Q$, defense usage costs and the differences between P and Q are important (fig. 2). All else being equal, improving early defenses (decreasing P) has the greatest effect over the majority of parameter space. We stress that these results rely on the costs of defense use, rather than effects on the probability of successful predation per se (eq. [10a], [10b]). Improving early defenses is particularly effective because it reduces the chances of paying late-defense usage costs, which, as in the case of escape-related injury, can be considerable (Lima and Dill 1990; Endler 1991).

Consider the following example, based on our model. If, during an encounter, the prey implements its early defense mechanism at a cost of 0.1, and the predator attacks the prey with probability $P = 0.225$ and then ingests the prey with probability $Q = 0.1$, the cost to the prey of its late defense mechanism must be greater than 0.1 for decreases in P to increase its ability to invade or resist invasion more than equal decreases in Q . If the time-of-use cost of late defense is less than 0.1, reductions in Q will have the greater effect.

Defense Constraints

We do not consider constraints on the evolution of particular defenses or constraints on defense costs (or costs that are explicitly functions of defense levels). Such constraints are likely, however, and will depend on evolutionary history and developmental and biophysical limitations (Endler 1991). Environment can also constrain the evolution of prey defensive traits (Merilaita and Tullberg 2005), and predator characteristics are clearly relevant.

Various examples of environmental and physiological constraints have been reported. Stoks et al. (2006) used damselfly (*Lestes viridis*) larvae to show that developmental time constraints limit predator aversion and physiological development. They also found that investment in immune function might reach a minimum threshold, perhaps further constraining early defense behavior. Using a computer simulation, Merilaita and Tullberg (2005) showed that distastefulness and aposematic coloration were most likely to evolve when prey inhabited two dissimilar microhabitats. Without a homogeneous habitat, the prey were less likely to evolve effective cryptic coloration and were more likely to resort to an alternate strategy.

Consider the case of prey evolution via decreased time-of-use defense costs. Equations (10b) and (10c) seems to indicate that reductions in the costs of early defenses should evolve more readily than reductions in the costs of late defenses. Early defenses, though, are often behavioral (e.g., refuge use, activity reduction; Lima and Dill 1990). The associated costs might commonly take the form of reduced food intake, for which a reduction in cost would be inextricably linked to a reduction in the defense effectiveness.

Depending on the relationships between prey traits, growth rate, and predation risk, optimal strategies can take very different forms (Werner and Anholt 1993). Which defensive traits or behaviors are possible, the relationships between their benefits and costs, and the level of protection that any trait can provide will all depend on the system in question.

Population Growth, Relative to the Cost of Predation

The trade-off between predation risk and energy acquisition for growth and development is widespread (Lima and Dill 1990; Van Buskirk 2000; Preisser et al. 2005; Verdolin 2006). Here, we have shown that the ratio of proportional population growth (accounting for the possession costs of defenses) to costs incurred during predation events, g/μ , determines prey fitness, insofar as a prey type with a g/μ ratio higher than that of an established type is able to invade our model predator-prey system at equilibrium. We considered not only the direct numerical effects of successful predation but also the costs associated with defensive morphological or behavioral traits.

We showed that, when g/μ is equal for two prey types, neither type gains a permanent advantage over the other (De Meester et al. 1995 provide a possible empirical example). Under these conditions, population bottlenecks and genetic drift come into play. Stochastic disturbances may shift a system involving neutrally adapted prey types, ultimately leading to the extinction of one type (Vance 1978). Alternatively, if the two neutral types remain in the

system long enough, changing environmental conditions or predator traits could, at some point, give one prey type an advantage over the other.

The g/μ ratio provides an intuitive criterion by which to predict invasion in real systems. In empirical settings, however, modifications to our proposed model might be necessary, depending on the requirements of cost accounting in particular systems. In reality, therefore, an altered criterion might result.

Connecting Models to Data

The costs of behavioral and phenotypic defenses can be difficult to measure in the field and in the lab (Van Buskirk 2000; Lind and Cresswell 2005). To make general progress, we should link “the theoretical concepts of evolutionary biologists to the empirical data typically collected by behavioral ecologists” (Ajie et al. 2007, p. 267). Gathering data on multiple traits, behaviors, and fitness responses in concert, and using energy- and time-budget equivalencies (Lind and Cresswell 2005) or path analysis (Ajie et al. 2007) to tease apart the relationships have been suggested as fruitful approaches. Such work likely relies on intimate knowledge of natural systems, as afforded by classical natural history (Lind and Cresswell 2005).

On a smaller scale, it may be possible to test our model using carefully designed mesocosm experiments. Data on dynamics of an appropriate predator-prey system, at various levels of real and perceived (e.g., through chemical predator cues; Boersma et al. 1998; Van Buskirk 2000; Cotton et al. 2004) predation could be used for parameterization. Predation dynamics (the most relevant component of our model) would be easiest to study, but investigating prey dynamics without predation and under perceived predation threat would facilitate disentanglement of growth and functional response (3b) parameters. Such an approach would require a prey species possessing early and late defenses, with at least two types differing in defense effectiveness. Predictions based on g/μ , or a comparable criterion, could be subsequently tested with prey-invasion trials.

A promising model system for such experiments would be clonal strains of *Daphnia*, possessing decoupled early and late defenses, paired with fish or invertebrate predators (De Meester et al. 1995; Boersma et al. 1998). It would be possible to establish plankton-tower mesocosms (De Meester et al. 1995) containing prey with contrasting defense/cost combinations and predators varying in their abilities to overcome prey defenses. Methods for determining mortality rates and defense costs in *Daphnia* are well established, making model parameterization and prediction of outcomes feasible.

Assuming defense costs can be measured, it also might

be possible to evaluate indirectly the larger-scale predictions from our model. If late-defense usage costs are low, our model suggests that species will tend to evolve into early- or late-defense specialists (defense compensation consistent with Brodie et al. 1991), since ineffective early defenses would result in selection for better late defenses, and vice versa (fig. 1a). As late-defense usage costs increase (perhaps as these defenses become better developed), however, early defenses may evolve more readily for a greater range of defense combinations (fig. 1b, 1c; consistent with Endler 1991; Fuiman and Magurran 1994). In the latter case, we might expect prey that already possess late defenses to also evolve early defenses, leading to defense cospecialization.

For example, studies of marine snails (*Gibbula*, *Osilinus*, and *Littorina* spp.: Cotton et al. 2004) and dragonfly (*Leucorrhinia* spp.) larvae (Mikolajewski and Johansson 2004) displaying early behavioral and late morphological defenses match the above predictions regarding compensation/cospecialization. For the snails, late defenses (altered shell morphology) likely carry low time-of-use costs, and species show compensatory defense patterns (Cotton et al. 2004). For the dragonfly nymphs, late defenses (abdominal spines) may be more costly (as defense implementation requires partial ingestion, likely associated with injury), and the *Leucorrhinia* genus shows some degree of cospecialization (Mikolajewski and Johansson 2004).

Early or Late Defense?

We return to our original question: as prey, is it better to interrupt predation early or late in the predation sequence? Incorporating costs and searching for a successful invasion strategy, we see that there is no universal answer. Reducing the usage costs of early defense is more beneficial than reducing the usage costs of late defense, but the relative benefits of changes to the defense strategies themselves are context dependent.

It is worth noting that the conclusions we draw relate to prey at risk from a single predator species. We would naturally expect predictions to be more complicated when multiple predators are involved; defense mechanisms effective against one predator may be useless against another, and some defenses may act in different phases of predation sequences with different predators.

Which defense strategy will ultimately enable evolutionary invasion by a new prey type depends on the prey's existing defenses, their associated costs, and physiological and environmental constraints. We conclude that there exists no exclusive ecological or evolutionary advantage to defending early in the predation sequence. The widespread existence of early and late defenses in nature is a testament to this.

Acknowledgments

Thanks to E. D. Brodie III, J. L. Bronstein, M. Fraker, B. W. Kooi, J. Van Buskirk, and an anonymous reviewer for many helpful suggestions and to R. Edwards for input during model analysis. Funding was provided by the Canada Research Chair program, a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to B.A., and an NSERC Undergraduate Student Research Award to A.B.

Literature Cited

- Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999–1007.
- Abrams, P. A., and H. Matsuda. 1997. Prey adaptation as a cause of predator-prey cycles. *Evolution* 1742–1750.
- Ajje, B. C., L. M. Pintor, J. Watters, J. L. Kerby, J. I. Hammond, and A. Sih. 2007. A framework for determining the fitness consequences of antipredator behavior. *Behavioral Ecology* 18:267–270.
- Boersma, M., P. Spaak, and L. De Meester. 1998. Predator-mediated plasticity in morphology, life history, and behavior of *Daphnia*: the uncoupling of responses. *American Naturalist* 152:237–248.
- Brodie, E. D., Jr., D. Formanowicz Jr., and E. D. Brodie III. 1991. Predator avoidance and antipredator mechanisms: distinct pathways to survival. *Ethology Ecology and Evolution* 3:73–77.
- Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York.
- Cotton, P. A., S. D. Rundle, and K. E. Smith. 2004. Trait compensation in marine gastropods: shell shape, avoidance behavior, and susceptibility to predation. *Ecology* 85:1581–1584.
- De Meester, L., L. Weider, and R. Tollrian. 1995. Alternative antipredator defenses and genetic polymorphism in a pelagic predator-prey system. *Nature* 378:483–485.
- Edmunds, M. 1974. Defence in animals: a survey of antipredator defences. Longman, Burnt Mill, Harlow, Essex.
- Endler, J. A. 1991. Interactions between predators and prey. Pages 169–196 in J. R. Krebs, and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell, Oxford.
- Fuiman, L. A., and A. E. Magurran. 1994. Development of predator defences in fishes. *Reviews in Fish Biology and Fisheries* 4:145–183.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91:385–398.
- Jones, D. S., M. Plank, and B. Sleeman. 2011. Differential equations and mathematical biology. CRC, Boca Raton, FL.
- Kretzschmar, M., R. Nisbet, and E. McCauley. 1993. A predator-prey model for zooplankton grazing on competing algal populations. *Theoretical Population Biology* 44:32–66.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* 16:945–956.
- Lotka, A. J. 1925. Elements of physical biology. Williams & Wilkins, Baltimore.
- Merilaita, S., and B. S. Tullberg. 2005. Constrained camouflage facilitates the evolution of conspicuous warning coloration. *Evolution* 59:38–45.
- Mikolajewski, D. J., and F. Johansson. 2004. Morphological and behavioral defenses in dragonfly larvae: trait compensation and co-specialization. *Behavioral Ecology* 15:614–620.
- Murray, J. D. 2002. Mathematical biology. Vol. 2. Springer, Berlin.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? the effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- Ramos-Jiliberto, R., E. Frodden, and A. Aránguiz-Acuña. 2007. Pre-encounter versus post-encounter inducible defenses in predator-prey model systems. *Ecological Modelling* 200:99–108.
- Richardson, J. M. L., and B. R. Anholt. 2010. Morphological defenses against enemies. In M. D. Breed, and J. Moore, eds. *Encyclopedia of animal behavior*. Academic Press, Elsevier, Dordrecht.
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.
- Stoks, R., M. D. Block, S. Slos, W. V. Doorslaer, and J. Rolff. 2006. Time constraints mediate predator-induced plasticity in immune function, condition, and life history. *Ecology* 87:809–815.
- Tien, R. J., and S. P. Ellner. 2012. Variable cost of prey defense and coevolution in predator-prey systems. *Ecological Monographs* 82: 491–504.
- Van Buskirk, J. 2000. The costs of an inducible defense in anuran larvae. *Ecology* 81:2813–2821.
- Vance, R. R. 1978. Predation and resource partitioning in one predator–two prey model communities. *American Naturalist* 112:797–813.
- Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60:457–464.
- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558–560.
- Vos, M., B. W. Kooi, D. L. DeAngelis, and W. M. Mooij. 2004a. Inducible defences and the paradox of enrichment. *Oikos* 105: 471–480.
- Vos, M., A. M. Verschoor, B. W. Kooi, F. L. Wäckers, D. L. DeAngelis, and W. M. Mooij. 2004b. Inducible defenses and trophic structure. *Ecology* 85:2783–2794.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.
- Yamauchi, A., and N. Yamamura. 2005. Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology* 86:2513–2524.

Associate Editor: Edmund D. Brodie III
Editor: Judith L. Bronstein