Evolution of Forager Responses to Inducible Defenses

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1 Introduction

Inducible defenses are phenotypic expressions of a defensive trait which occur preferentially or exclusively in the presence of predators (Adler and Harvell, 1990; Harvell, 1990). The defenses take a wide variety of forms, including morphological changes, behavioral avoidance, changes in life-history and accumulation of allelo-chemicals. These selectively deployed inducible defenses give the prey a wider array of options than non-selectively deployed constitutive defenses; tactics that would be prohibitively costly if adopted continuously may be easily affordable if they are invoked only when needed. Inducible defenses provide a mechanism through which specialization can partially insulate prey from predation which in turn provides a subset of predators with an opportunity to specialize in overcoming the prey defense. Inducible defenses thus have the potential to alter both the short-term dynamics and long-term evolution of predator-prey systems (Harvell, 1990).

Most theoretical and empirical investigations of inducible defenses have focused on identifying the conditions favoring the evolution of inducibility by the prey species, generally in comparison with constitutive defenses. Inducible defenses are thought to evolve under two general scenarios: "cost-benefit" and "moving target." The cost-benefit model requires unpredictable variation in predation risk, a fitness cost of employing the defense unnecessarily, and the availability of non-fatal predictive cues of future attack (Lively, 1986; Edelstein-Keshet and Rauscher, 1989; Harvell, 1990; Clark and Harvell, 1992; Riessen, 1992). The prey trade off the risk of deploying the defense too late or not at all when attacked against the cost of the defense in an unpredictable world with ambiguous cues.

The trade-off in the "moving target" scenario does not depend on a cost of defense, but instead on an array of predator types which respond differently to different prey phenotypes (Karban and Myers, 1989, Adler and Karban, 1994). In this case, prey that are attacked while deploying one type of defense are induced to switch to another defense. By switching defenses, prey attempt to find an effective deterrent to their particular attacker by trial-and-error. Furthermore, such switching may make prey different from their neighbors, reducing their risk from predators specializing in the locally predominant defense phenotype.

These evolutionary scenarios focus on the strategy set available to the prey, but say little about inducible defenses from a predator's point of view. How might a predator evolve a foraging strategy to best contend with the array of defensive strategies it confronts? Predator responses to inducibly-defended prey can include physiological responses, such as detoxification or sequestration of defensive compounds, behavioral responses, such as foraging movement strategies (Lima and Dill, 1990), and adjustments in life-history characteristics. In many ways, these are precisely the options available to the prey. As responses to other organisms, inducible defenses always exist in an environment with the potential for coevolution, whether it be tightly-coupled or diffuse (Futuyma and Slatkin, 1983; Levin *et al*, 1990).

Some form of information transfer is essential to inducible defenses (Harvell, 1990). At a minimum, as in the moving target model, prey must be able to recognize that some sort of attack is occurring before succumbing. In many aquatic systems, prey pick up a cue of their predators before attack begins, and can prepare a specific response. The production of cues by predators and the type and level of response by prey are traits under selection as much as the quality of the defense or its avoidance. This aspect of the interaction has also received little attention from empiricists or theorists, even with the spate of interest in signaling and signal selection (Guilford, 1995). The related question of whether prey should signal their level of defense, however, has been recently studied with game theoretic models (Augner, 1994).

In this chapter, we present a framework for simultaneously analyzing the evolutionary perspectives of the prey and the predator. We discuss this framework in general terms, and then work out a simplified concrete example demonstrating the potential for coevolution of foraging, signaling and signal response. We predict the strategies that might result from evolution by looking for evolutionarily stable strategies (ESS's) for the species separately and simultaneously (Maynard Smith, 1982). Finally, we look for cases in which there is no ESS, where evolution can maintain a diversity of predator and/or prey strategies (Ellner and Hairston, 1994).

Our overall aim is to call attention to three aspects of inducible defense systems generally overlooked by empiricists and theorists: predator behavior, predator evolution, and the evolution of cues or signals. We develop a modeling framework to address these issues, and use it to demonstrate the possibility of complicated and interesting evolutionary dynamics in even a simple scenario. The framework points toward several promising empirical angles for addressing overlooked issues.

2 A framework for predator-prey dynamics with inducible defenses

In this section we present our general framework for thinking about evolution in inducible defense systems. First we summarize the factors affecting evolution of inducible defenses from the more familiar point of view of the prey (Harvell, 1990). Next, we summarize the factors affecting responses of inducible defenses from the predator's point of view, considering both foraging strategy and signal production. We show graphically how the various dynamical terms might affect populations of prey. These graphs provide the framework for the more quantitative study of the evolution of prey foraging and signal behavior.

2.1 Inducible defenses from the prey's perspective

Our view of the predator-prey population dynamics in an inducible defense system is summarized in Figure 1. The prey habitat is divided into a large number of discrete patches. The state of each patch is specified by the population densities of defended and undefended prey types and whether a predator is present or not. We could further discriminate between patches with different numbers of predators, but here we restrict our attention to patches that are small enough and predator densities low enough that we can neglect patches with more than one predator.

We now consider the dynamical factors that change patch states. These dynamics are dependent on whether a predator is present or absent (Figure

1). Consider a patch at the instant a predator arrives. The patch changes in state from "recovery" to "attack" (i.e., from the right to the left box along the leftward pointing arrow). While under attack, the predator is consuming the prey, possibly with a preference for the undefended phenotype. Simultaneously, the undefended prey phenotype is responding to cues of the predator's presence by deploying the defense. Both consumption and deployment reduce the quality of the patch for the predator. At some point, the predator leaves, dies, matures or otherwise stops foraging.

When the patch is abandoned (moving back to the right box along the rightward pointing arrow), prey in the patch no longer suffer predation, and the cue disappears. The prey population can recover, possibly with a growth advantage for the undefended phenotype. Defended prey may revert over time to the undefended state. This recovery continues until the next predator attack, at which time the cycle starts again. The frequency with which a patch is found in various stages of the cycle, and the number of defended and undefended prey present at each stage determines the selective regime experienced by the prey. This frequency distribution depends in part on the number of predators and the strategy they are employing.

The strategic choice to be made by the prey in this model is the rate at which they respond to predator cue. The fitness of a prey strategy depends on the strategies, as well as on the density, of other prey within the patch. We will compute the evolutionarily favored prey strategy by making quantitative assumptions about the dynamics, computing the resulting state distribution, and looking for a single response rate that, if adopted by most of the population, would exclude any alternative response rates (an ESS).

2.2 Inducible defenses from the predator's perspective

The predator's experience of this inducible system is summarized in Figure 1b. A predator attacking a patch consumes prey until the patch becomes unfavorable, either through depletion of prey or through conversion of prey into the unpalatable defended type. After it abandons the patch it must spend time searching for a new patch. Because the predator does not eat while searching, travel time is costly, and the wise predator does not abandon its patch before it becomes unfavorable enough to justify paying that cost. What does "unfavorable" mean? The state or quality at which the predator should abandon the patch depends on how good it expects the next patch will be. A succinct and quantitative way to express the patch quality at which the predator should depart is provided by the Marginal Value Theorem (Charnov, 1986, Stephens and Krebs, 1986). This theorem states that the optimal time to leave a patch occurs when the predator's rate of return on the patch is equal to the average rate of return it would get by leaving

In addition to abandonment, there is another element to the predator's strategy: the cue. While a predator is in a patch, prey that have not yet been consumed can detect its presence, perhaps through odors or some other non-fatal, short-range signal. We assume that the strength of the predator's signal is under selection. If the predator could reduce its signal without paying a cost, it would do so. However, we expect that suppressing the cue would be costly in most inducible defense systems. There could be a metabolic cost in not emitting an odor or an efficiency cost of being visually inconspicuous. Alternatively, what the prey use as a cue could have other roles as a signal for the predators. For example, prey might use a predator's reproductive pheromone as a cue. The predator could not reduce or change its signal without directly reducing its own fitness. We here consider the simpler scenario in which there is an energy cost to reducing the emission of cues.

Given choices of the predator foraging and cue production strategies and the prey cue response strategy determine the structure of the prey state distribution, and consequently, the fitness accruing to the predator. The predator's fitness depends both on the strategy and abundance of other predators.

3 Describing the evolutionary dynamics

We have found phase plane diagrams to be a convenient way to conceptualize these dynamics (Figure 2). In these plots, the horizontal axis is the population density of undefended prey in a patch, and the vertical axis is the population density of defended prey. From the perspective of a predator, this provides a complete description of the state of the patch. The vectors reflect in which direction and how quickly these densities change under the influence of the different dynamical terms.

Growth and mortality. Figure 2a illustrates prey demography. Reproduction of prey tends to increase the density of prey (move the state towards the right and top). In the presence of a cost, the undefended phenotype has a reproductive advantage over the defended phenotype, so the arrows are bigger when undefended prey are abundant. In this example, we have also assumed a carrying capacity for prey within a patch.

Predation. Figure 2b shows how predation moves the patch to lower densities (back towards the origin). If there is some advantage to being defended, predation on defended prey will be lower than on undefended prey. In this plot, we have assumed that there is no predation at all on defended prey. Therefore, the arrows point straight to the left. There is also some functional response on the part of the predator to prey density. We have assumed that the predator consumes undefended prey in proportion to their numbers.

Deployment of defense and reversion to undefended state. The transition of undefended to defended phenotypes and back does not create or destroy any prey; it is simply an exchange of one type for the other. The vectors representing these processes always point along a diagonal. Figure 2c shows how the population switches from undefended to defended in response to attack by a predator and figure 2d shows how the population switches from defended to undefended in response to absence of the predator.

Patch state distributions. Typically, a patch under attack will move along the deployment arrows (figure 2c) together with the growth and mortality arrow (figure 2a) and the predation arrows (figure 2b), decreasing in quality until the predator is compelled to abandon it. When the predator is gone, the patch follows the growth and mortality arrows (figure 2a) and reversion arrows (figure 2d) until it is once again attacked.

These dynamics provide the information needed to compute optimal predator foraging strategies and ESS predator signal levels. The environment that a predator experiences is described by the patch state distribution, the distribution of densities of defended and undefended prey that it encounters. This distribution is in turn a function of many factors. The environment determines the growth and mortality of prey. Predator strategy and population density determine how long the prey are subject to predation, and how long they have to recover between attacks. Prey strategies determine the dynamics of patch quality from the perspective of the predator.

4 Models

Our models are designed to compute ESS levels of predator cue (or signal) production and prey cue (or signal) response. The analysis proceeds in four steps.

1. Solve the population dynamic equations for a single prey type faced by a single type of predator.
2. Derive the fitness of predators that use an optimal departure time strategy computed with optimal foraging theory.
3. Find the ESS of predator signal level as a function of various parameters.
4. Use the prey population dynamic equations to compute the prey ESS signal response.

For those uninterested in the mathematics, this section formalizes the models presented in figures 1 and 2, and makes simplifying assumptions to make the calculations tractable. Sample results from the model are presented in the next section.

4.1 The dynamical equations for the prey

Prey can be in two discrete states, defended and undefended, and in two discrete environments, with and without a predator (Figure 1). Our basic equations track the population dynamics of the two types of prey in each environment (Figure 2). We assume throughout that only one predator is present in a patch at any one time.

Let U and D represent the numbers of undefended and defended prey when a predator is present. The dynamics follow

$$\begin{aligned} \frac{dU}{dt} &= -\overset{\text{rate}}{\text{eaten}} \pm \text{other births and deaths} \\ \frac{dD}{dt} &= -\overset{\text{rate}}{\text{eaten}} + \overset{\text{rate of switching}}{\text{from undefended}} \end{aligned} \tag{1}$$

Similarly, let $\tilde{U}$ and $\tilde{D}$ represent the numbers of undefended and defended prey when no predator is present. The dynamics follow

$$\begin{aligned} \frac{d\tilde{U}}{dt} &= \overset{\text{rate of switching}}{\text{to defended}} \pm \text{births and deaths} \\ \frac{d\tilde{D}}{dt} &= \overset{\text{rate of switching}}{\text{to undefended}}\ . \end{aligned} \tag{2}$$

We assume that prey switch to the defended state only when under attack, and switch back only between attacks. All births are into the undefended state.

During predation, the various components of the model are parameterized as follows (see table 1 for a list of variables and parameters):

$$\begin{aligned} \text{undefended prey eaten} &= c_u \lambda U \\ \text{defended prey eaten} &= c_d \lambda D \\ \text{rate of switching to defended} &= \epsilon \sigma U \\ \text{births and deaths} &= (\beta_u U + \beta_d D) g(U + D). \end{aligned}$$

The function g describes the density dependence in the population. Between

Table 1: The prey variables and parameters

symbol	meaning
U	undefended prey population in the absence of predators
D	defended prey population in the absence of predators
$\tilde{U}$	undefended prey population in the presence of predators
$\tilde{D}$	defended prey population in the presence of predators
ϵ	prey signal response
σ	predator signal level
c_u	eatability of undefended prey
c_d	eatability of defended prey
λ	encounter rate with prey
β_u	reproduction of undefended prey
β_d	reproduction of defended prey
ρ	rate of switching to undefended

predation events, the components are:

$$\begin{aligned} \text{rate of switching to undefended} &= \rho\tilde{D} \\ \text{births and deaths} &= (\beta_u\tilde{U} + \beta_d\tilde{D})g(\tilde{U} + \tilde{D}). \end{aligned}$$

In the cases to be analyzed in detail, we make two simplifying assumptions: defended prey are completely immune to capture ($c_d = 0$), and there are no births and deaths during predation. This second assumption is a valid approximation when the duration of attack is brief relative to the time scale of demographic processes. The dynamics during predation then follow

$$\begin{aligned}\frac{dU}{dt} &= -(\epsilon\sigma + c\lambda)U \\ \frac{dD}{dt} &= \epsilon\sigma U. \qquad (3)\end{aligned}$$

The dynamics without predation are given by

$$\begin{aligned}\frac{d\tilde{U}}{dt} &= (\beta_u\tilde{U} + \beta_d\tilde{D})g(\tilde{U} + \tilde{D}) + \rho\tilde{D} \\ \frac{d\tilde{D}}{dt} &= -\rho\tilde{D}. \qquad (4)\end{aligned}$$

The only non-linear equation is that for $\tilde{U}$. With initial conditions (U_0, D_0), the system of equations with predator present (equation 3) have solution

$$U(t) = U_0 e^{-(\epsilon\sigma + c\lambda)t} \qquad (5)$$

$$D(t) = D_0 + \frac{\epsilon\sigma}{\epsilon\sigma + c\lambda} U_0 \left(1 - e^{-(\epsilon\sigma + c\lambda)t}\right). \qquad (6)$$

With initial conditions (z^*, D^*), the predator-absent equations have solutions

$$\tilde{U}(t) = H(z^*, D^*, t) \qquad (7)$$

$$\tilde{D}(t) = D^* e^{-\rho t} \qquad (8)$$

where H is an as yet unknown non-linear function.

4.2 Fitness and the behavior of predator

The fraction of time the prey spend fending off predators depends on the strategy and number of predators. In particular, the length of a predator visit and the time between visits determines the experience of the prey. In this section, we use the marginal value theorem (Charnov, 1976; Stephens and Krebs, 1986) to derive the optimal time for predators to leave a patch.

Predators should leave a patch when the instantaneous rate of return is equal to the average rate obtained, or

$$\text{instantaneous intake rate} = \frac{\text{average intake during visit}}{\text{average visit time} + \text{travel time}}. \tag{9}$$

In our case,

$$\text{instantaneous intake rate} = \lambda e_u U(t).$$

where e_u represents the food obtained from eating a single undefended prey item (recall that we have assumed no consumption of defended prey). Let z^* represent the undefended prey population present at the optimal departure time. Let $\phi(U)$ represent the probability density function giving the number of undefended prey when a predator encounters a patch, and $t_u(U)$ be the time it takes for that patch to be depleted to the optimal departure level z^*. Then equation 9 translates to

$$\lambda e_u z^* = \frac{\int_{z^*}^{\infty} \left(\int_0^{t_u(u)} \lambda e_u U(t) dt \right) \phi(u) du}{\int_{z^*}^{\infty} t_u(u) \phi(u) du + T} \tag{10}$$

where $U(t)$ represents the population of undefended prey starting from initial condition u. Substituting in the solution for $U(t)$ (equation 5) and simplifying, we find an implicit equation for z^*,

$$(\epsilon\sigma + c\lambda)T = \int_{z^*}^{\infty} \left(\frac{u}{z^*} - 1 - \log(\frac{u}{z^*}) \right) \phi(u) du. \tag{11}$$

How do we find $\phi(u)$, the probability density function of U when predators enter patches? Even if all patches are abandoned with $U = z^*$, they will

Table 2: The predator parameters and variables

symbol	meaning
e_u	food value of undefended prey
e_d	food value of defended prey (assumed to be 0)
T	average travel time between patches
z^*	optimal number of undefended prey upon departure
θ	optimal fraction of undefended prey upon departure
D^*	number of defended prey upon departure
U^*	number of undefended prey upon arrival
t_m	average time between predator visits to a patch
n_p	number of predators per patch
$k(\sigma)$	cost of signal level σ (decreasing)
k_0	marginal cost of reducing signal level σ

differ when next visited depending on the amount of time they have had to recover. In order to simplify the equations, we approximate this distribution of recovery times by the average recovery time t_m. Patches will then be encountered with the same (still unknown) number of undefended prey. Denote this number by U^*. The equation for z^* (equation 11) can be rewritten

$$(\epsilon\sigma + c\lambda)T = \frac{U^*}{z^*} - 1 - \log\left(\frac{U^*}{z^*}\right).$$

This expression involves only the ratio $\frac{z^*}{U^*}$, the fraction of the original undefended prey left when a forager departs, which we define as θ. The fundamental equation 11 for z^* can be rewritten as

$$(\epsilon\sigma + c\lambda)T = \frac{1}{\theta} - 1 - \log\left(\frac{1}{\theta}\right). \tag{12}$$

This equation can be solved numerically for θ, the optimal fraction of undefended prey to leave. We use the equation for $U(t)$ (equation 5) to find how long it takes to reach this level of depletion, solving for the optimal time in the patch t_u as

$$t_u = -\frac{\log(\theta)}{\epsilon\sigma + c\lambda} \tag{13}$$

because patch quality declines exponentially during a visit.

To find the number of undefended prey upon arrival, U^*, we need to find the average time between visits, t_m. The average cycle from starting one visit to starting the next is $t_u + T$ for each predator, so the average time between arrivals at a patch is

$$t_m = \frac{t_u + T}{n_p} \tag{14}$$

where n_p represents the number of predators per patch. As n_p becomes large, the time between visits becomes small. In a more complete analysis, t_m would have an exponential distribution with mean t_m. Preliminary simulations indicate that including this factor does not qualitatively change the results.

We can now use the population dynamics of the prey to write down the equations for z^*. The trick is to follow the dynamics through a full sequence of recovery and predation, requiring that patches end up exactly where they started. If predator leave patches when $U = z^*$ and $D = D^*$, then

$$\begin{aligned}\begin{pmatrix} z^* \\ D^* \end{pmatrix} & \overset{\text{recovery}}{\longrightarrow} \begin{pmatrix} H(z^*, D^*, t_m) \\ D^* e^{-\rho t_m} \end{pmatrix} \\ & \overset{\text{predation}}{\longrightarrow} \begin{pmatrix} \theta H(z^*, D^*, t_m) \\ D^* e^{-\rho t_m} + \frac{\epsilon\sigma}{\epsilon\sigma + c\lambda} H(z^*, D^*, t_m)(1-\theta) \end{pmatrix}. \end{aligned} \tag{15}$$

Recall that $H(z^*, D^*, t)$ gives the solution of the nonlinear recovery equations a function of their initial conditions. Equation 15 gives a pair of simultaneous equations that can be solved numerically for z^* and D^*.

A predator following the optimal departure strategy consumes food at the rate

$$\text{optimal average intake rate} = \lambda e_u z^*.$$

This equation involves three components: the search efficiency or consumption rate of the predator λ, the quality of the food e_u and the quality of the patch z^*. The last component summarizes the patch state distribution. Following the above procedure chooses the value of z^* that maximizes payoff of a strategy in response to itself. This strategy is evolutionarily stable because an invader that differed would have a different θ. Such a strategy would fail to satisfy the marginal value theorem condition (equation 9) and necessarily be inferior.

4.3 Finding the ESS predator signaling level

If it were possible, predators would reduce σ, the amount of signal produced. We envision three reasons why this might not occur or might not appear to occur. First, the predators might indeed always be reducing the amount of particular cues, but prey are simultaneously learning to recognize new cues, much as in some epidemiological situations where a virus constantly alters antigens (Pease, 1987). Second, the prey may capitalize on a cue that predators cannot modify for other reasons, such as a mating pheromone. Finally, reducing cue production might have a direct energetic or foraging efficiency cost for the predators. Because we are unaware of data on this subject, we make the simple assumption that reducing signal level has an energetic cost. In particular, we assume that the payoff is modified as

$$\text{payoff} = \lambda e_u z^* - k(\sigma).$$

$k(\sigma)$ is a decreasing function, indicating it is more costly to producing a **lower** signal of level σ. This equation summarizes the tradeoff for predators. Those with lower levels of signal can maintain a higher value of z^* by evading the prey defense, but must pay a cost to suppress cue production.

Suppose a predator with signal level $\hat{\sigma}$ invades a population of predators with signal level σ. This invader can compute $\hat{\theta}$, the optimal fraction of prey to leave exactly as above. This value will differ from θ (the fraction left by the resident type) because θ depends on the signal level σ (equation 12). If most predators use signal level σ, an invader will encounter patches with $U^* = \frac{z^*}{\theta}$ undefended prey, and will leave when $\frac{\hat{\theta} z^*}{\theta}$ undefended prey remain. Because $\hat{\theta}$ defines the optimal response, the intake rate at departure matches the long-term average. Therefore, the fitness of a type $\hat{\sigma}$ predator invading type σ is

$$W(\hat{\sigma},\sigma)=\lambda e_u\hat{\theta}\frac{z^*}{\theta}-k(\hat{\sigma}). \tag{16}$$

The evolutionarily stable strategy, or ESS, can occur when

$$\frac{\partial W(\hat{\sigma},\sigma)}{\partial\hat{\sigma}}=0 \ \text{ at } \hat{\sigma}=\sigma>0$$

or

$$\frac{\partial W(\hat{\sigma},\sigma)}{\partial\hat{\sigma}}=0 \ \text{ at } \hat{\sigma}=\sigma=0.$$

We can compute the derivative from the implicit formula for θ (equation 12), finding that

$$\begin{aligned}\frac{\partial W(\hat{\sigma},\sigma)}{\partial\hat{\sigma}} &= \lambda e_u\frac{z^*}{\theta}\frac{\partial\hat{\theta}}{\partial\hat{\sigma}}-k'(\sigma)\\ &= \lambda e_u\frac{z^*}{\theta}\frac{\epsilon T\hat{\sigma}^2}{\hat{\sigma}-1}-k'(\sigma).\end{aligned}$$

Solving, a necessary condition for a positive ESS is

$$\frac{\lambda e_u z^*\epsilon T\hat{\sigma}}{\hat{\sigma}-1}=k'(\sigma). \tag{17}$$

The second derivative of W determines whether this critical point defines an ESS. If $k''(\sigma)\leq 0$, the critical point is never an ESS. The ESS must then be at $\sigma=0$ or at the maximum possible value of σ. When the cost function has the form $k(\sigma)=e^{-k_0\sigma}$, the critical point has always been an ESS in the cases we have examined. We use this cost function throughout. The parameter k_0 describes how quickly the cost of suppressing cue decreases when a small amount of cue is produced, and can be thought of as the marginal cost of suppressing the last bit of cue.

4.4 Finding the ESS prey signal response

Prey too face a tradeoff. Those that defend rapidly are protected from predators but may suffer lowered reproduction in the absence of predators. Furthermore, this tradeoff is frequency dependent. A slowly defending prey type could be indirectly helped by rapidly defending types that induce a predator to leave. A rapidly defending prey type could be indirectly helped by slowly defending types that are severely reduced by predation and open up space for growth.

To determine the ESS signal response level ϵ, we must determine the fitness function for prey. Because the prey equations explicitly include population dynamics, we can compute fitness of an invader as its growth rate over a complete cycle of predation and recovery. During predation, the invading prey follow

$$\begin{aligned} \frac{d\hat{U}}{dt} &= -(\hat{\epsilon}\sigma + c\lambda)\hat{U} \\ \frac{d\hat{D}}{dt} &= \hat{\epsilon}\sigma\hat{U} \end{aligned} \tag{18}$$

where $\hat{U}$ and $\hat{D}$ represent the populations of undefended and defended prey of type $\hat{\epsilon}$. These dynamics are coupled to those of the resident type only through the departure time t_u as determined by the predator response to the resident type (equation 13). With initial conditions $(\hat{U}^*, \hat{D}^*)$, the solution at time t_u can be written

$$\hat{U}(t_u) = \hat{U}^* e^{-(\hat{\epsilon}\sigma + c\lambda)t_u} = \theta^p \hat{U}^* \tag{19}$$

$$\hat{D}(t_u) = \hat{D}^* + \frac{\hat{\epsilon}\sigma}{\hat{\epsilon}\sigma + c\lambda}\hat{U}^*(1 - \theta^p) \tag{20}$$

where

$$p = \frac{\hat{\epsilon}\sigma + c\lambda}{\epsilon\sigma + c\lambda}.$$

Between predation events, invading prey obey the equations

$$\begin{aligned} \frac{d\hat{\tilde{U}}}{dt} &= (\beta_u \hat{\tilde{U}} + \beta_d \hat{\tilde{D}}) g(\tilde{U} + \tilde{D}) + \rho \hat{\tilde{D}} \\ \frac{d\hat{\tilde{D}}}{dt} &= -\rho \hat{\tilde{D}} \end{aligned} \tag{21}$$

where $\hat{\tilde{U}}$ and $\hat{\tilde{D}}$ represent populations of undefended and defended prey. These differential equations are linear in $\hat{\tilde{U}}$ and $\hat{\tilde{D}}$, with non-autonomous terms depending on the solutions $\tilde{U}$ and $\tilde{D}$ for the resident type. The solution has the form

$$\hat{\tilde{U}}(t_m) = \hat{H}(\hat{z}^*, \hat{D}^*, t_m) = a\hat{z}^* + b\hat{D}^* \tag{22}$$

$$\hat{\tilde{D}}(t_m) = \hat{D}^* e^{-\rho t_m}, \tag{23}$$

with the constants a and b to be determined later. A full cycle of the dynamics follows the matrix equation

$$\begin{aligned} \begin{pmatrix} \hat{z}^* \\ \hat{D}^* \end{pmatrix} & \xrightarrow{\text{recovery}} \begin{pmatrix} \hat{H}(\hat{z}^*, \hat{D}^*, t_m) \\ \hat{D}^* e^{-\rho t_m} \end{pmatrix} \\ & \xrightarrow{\text{predation}} \begin{pmatrix} \theta^p \hat{H}(\hat{z}^*, \hat{D}^*, t_m) \\ \hat{D}^* e^{-\rho t_m} + \frac{\hat{\epsilon}\sigma}{\hat{\epsilon}\sigma + c\lambda} \hat{H}(\hat{z}^*, \hat{D}^*, t_m)(1 - \theta^p) \end{pmatrix} \\ & = \begin{pmatrix} a\theta^p & b\theta^p \\ \frac{\hat{\epsilon}\sigma}{\hat{\epsilon}\sigma + c\lambda} a(1-\theta^p) & \frac{\hat{\epsilon}\sigma}{\hat{\epsilon}\sigma + c\lambda} b(1-\theta^p) + e^{-\rho t_m} \end{pmatrix} \begin{pmatrix} \hat{z}^* \\ \hat{D}^* \end{pmatrix} \end{aligned} \tag{24}$$

The invader will invade if the leading eigenvalue $\lambda(\hat{\epsilon}, \epsilon)$ of the matrix exceeds 1. The prey ESS signal response level occurs at a point where

$$\frac{\partial \lambda(\hat{\epsilon}, \epsilon)}{\partial \hat{\epsilon}} = 0 \tag{25}$$

when evaluated at $\hat{\epsilon} = \epsilon$, or could be at an endpoint ($\epsilon = 0$ or equal to some maximum possible value ϵ_{max}).

The fitness of an invader depends on the values of a and b, which in turn depend on the unknown solution of the nonlinear equations for $\tilde{U}$ and $\tilde{D}$. One can be computed in terms of the other using the fact that $\lambda(\epsilon, \epsilon) = 1$, and the second must be computed numerically. We find both by simulating the differential equation 21 starting with initial condition $(1, 0)$ to find a and with the initial condition $(0, 1)$ to find b.

Although it is possible to find an analytical formula for the existence of a critical point in equation 25, such points are always minima rather than maxima in the cases we have examined (unless we add an explicit cost for larger ϵ). Therefore, the ESS response is always at $\epsilon = 0$ or $\epsilon = \epsilon_{max}$. Numerically, we find that the ESS is ϵ_{max} when $\sigma > 0$. When $\sigma = 0$, the prey are indifferent to ϵ because there is no cost to responding to a cue that does not exist.

5 Results

5.1 ESS predator signal levels

We begin by varying several parameters and plotting how the ESS signal level strategy of the predators σ responds. Figure 3 shows how signal level responds to the food quality of undefended prey e_u. The predator's fitness increases roughly in proportion to the food value of the prey. The signaling level decreases, however, as the difference between the food values of undefended and defended prey increases (in our model, defended prey have zero food value) and the predators have more to gain by keeping the prey undefended.

Figure 4 shows how signal level responds to ϵ, the level of prey response to the predators' signal. As the prey become more and more adept at deploying the defense in response to the cue, predators are forced to signal less and less. The cost associated with lowered signaling drives the predators' fitness down. When ϵ becomes sufficiently large, predators do best by reducing the signal to zero.

Figure 5 shows how signal level responds to k_0, the marginal cost of reducing signal level. If k_0 is small, only predators that produce a huge amount of signal receive any energetic benefit. When k_0 is large, even a small increase in signal level above zero generates a dramatic reduction in energetic cost. The predator shows two types of ESS strategy in distinct ranges of k_0. For $k_0 < 1$, the marginal cost of signaling is small and predators do not signal at all. For $1 < k_0 < 2$, the ESS signal level increases rapidly, decreasing for large values of k_0 because the cost function saturates. The increase in fitness with larger k_0 results from the fact that predators can avoid cue suppression costs at even a small level of the cue.

Figure 6 shows how signal level responds to λ, the search efficiency or attack rate of the predators. At very low λ, the predators have low energy intake, and the cost of signaling looms large. Therefore, predators are unable to pay the cost of suppressing signal, signal level is high and predator fitness is low. With increasing attack rate, consumption of prey and fitness increase. At the same time, the relative cost of traveling to a new patch increases. It therefore pays for the predator to maintain patch quality by reducing signaling. Eventually, however, consumption rates become so high that undefended prey are consumed before they have time to deploy their defenses, so there is no profit in not signaling. Because all the other predators have realized this too, the world is full of heavily-defended prey, and predator fitness decreases.

These same phenomena are apparent in Figure 7, which shows how signal level responds to n_p, the number of predators. Higher numbers of predators means that the world is populated by more heavily-defended prey in lower quality patches. This pushes predators to remain in patches longer, and to drive the quality in their own patches lower. Low signal levels can be thought of in this context as form of cooperation. Reducing your own signal is costly and will only benefit other individuals. Thus, overcrowding by predators may not only deplete patches, but also reduce the level of cooperative foraging. This sort of depressing feedback has been observed in fisheries (Clark, 1990).

5.2 The lack of a joint ESS

We noted earlier that the best prey response to any positive signal level is a large value of ϵ. Therefore, according to Figure 4, the predators do best by reducing their signal to zero. In this circumstance, the fitness of the prey is independent of ϵ. If there is any cost to signal response, we would expect the response to be rapidly lost. Even without a cost, we would expect this ability to be lost by drift. The predators might then reduce their cost by resuming cue production, leading into another cycle of coevolution.

However, these sort of coevolutionary dynamics can be very subtle (Levin *et al*, 1990). The results depend on the relative time scales of the evolutionary responses by the predators and the prey, and could be affected in interesting ways by any spatial structure creating asynchrony among the populations.

6 Discussion

We have developed graphical and mathematical models to pose questions about three insufficiently studied aspects of inducible defense systems: predator behavior, predator evolution, and the evolution of cues or signals. Our framework includes the elements necessary to address these issues in at least a rudimentary way.

Our preliminary analysis and the modeling framework have shown that these three aspects are important, and that 1) predators should respond behaviorally to inducible defenses, 2) predator signal levels should respond evolutionarily to inducible defenses, and 3) prey signal response should evolve depending on predator strategies. More particularly, we hypothesize that predators should be more stealthy when stalking superior prey (figure 3) or more vigilant prey (figure 4). The response of predators to their cost function can be subtle (figure 5), but the details depend sensitively on the shape of the function. More interestingly, perhaps, we predict that predators do best with an intermediate level of search efficiency (figure 6), but note that this cannot be thought of as an evolutionarily stable strategy because an invader with superior foraging ability will gain a greater individual payoff. However, if predators are constrained to an intermediate search efficiency, a lower signal level is favored. Finally, greater crowding by predators can lead to a lack of cooperation in that higher ESS signal levels are more successful (figure 7). With our assumptions, however, we find no joint predator and prey ESS for signal production and response.

Of course, these results are dependent on the many simplifying assumptions we have made. Our analysis of cues has left out the very important question of unreliable cues or mistakes in identifying cues (Moran, 1992). We suspect that the maximum cue response favored in our preliminary analysis may be an artifact of this omission. In addition, we ignored any temporal or spatial dynamics of the cue, assuming that a patch is instantly and uniformly saturated when a predator arrives. The time it takes to cue to build up or decay is one factor that makes cues less reliable. It would be worthwhile to analyze how different cue diffusion and decay rate constants affect the results.

Our prey have also been simplified in many ways. Their strategic options are restricted to the speed of response to cue, but could realistically include different levels or types of defense. Our models assumed that the defense has the effect of reducing food quality, but it might be more realistic to assume an increase in handling time. The prey in our model are identical, although differences in size or apparency could create important opportunities for predators. The same differences could be important for entire patches. The selective forces acting on predators and prey could be altered by variability in patch size, patch location, or patch apparency.

The predators in this model interact only through their prey, but direct interactions between predators and the potential for defense of patches against other predators can have strong effects on the evolution of signaling. Even without such interactions, such factors as size structure within the predators could produce different abilities to handle defended prey or different interests (larger predators might be more interested in mating than in eating). We can only begin to speculate on the effects of multiple predator species (Levin *et al*, 1977).

Nonetheless, the models point the way toward several measurements that could clarify our thinking about predators and signaling. First, it would be interesting to test whether predators actually use optimal foraging in response to inducible defenses, by manipulating both the density and defense level of prey that they encounter. Second, a basic assumption of the model is that reducing signal levels is costly. As with defenses themselves, testing for costs can be difficult (Baldwin, 1996), but might be possible in those systems where the cue can be identified. In those same systems, it would be valuable to check for natural variability in signal level by predators or signal response level by prey. More speculatively, it would interesting to measure several of variables across patches in the same system: defense level, degree of damage, cue response level and cue production level. Further modeling could seek robust predictions about the relation among these measurements as a function of ecological conditions.

Further consideration of these models might cast light on some larger issues in predator-prey interactions. Our model assumes a fairly tight relationship between predator and prey. Does a signal-mediated interaction between predator and prey favor specialists? Thought of as a signal detection game, what implications do our models have for the evolution of inducibility? Can these systems break down through the evolution of completely unreliable cues?

We hope that our model provides a useful tool for biologists trying to gain an intuitive understanding of how various parameters shape the evolution of predator and prey strategies in inducible defense systems. Intuition, rather than quantitative prediction, is the intent behind abstract models like ours. However, even though our results are not meant to be quantitatively accurate, we could not have approached this problem without a quantitative model because there are too many hidden and intertwined dynamics to guess at the solutions. Furthermore, the model is formulated with independently measurable parameters and could be made quantitatively accurate if those parameters could be measured. In practice, this would prove difficult. Nonetheless, our framework outlines the information needed to make quantitative evolutionary arguments about these systems.

Our basic message is that we cannot assess the potential benefits to prey of deploying inducible defenses under an assumption of constant predator behavior. For the most part, studies of inducible defenses have focused on the prey's strategy set, with the implicit assumption that the predator has no strategic alternatives, or that the predator strategy set changes little or not at all with differences in prey type. Our simple model demonstrates that this point cannot be taken for granted. Coevolution of predator responses to prey defensive strategies can quantitatively and qualitatively change evolutionary outcomes in inducible defense systems. The additional evolutionary perspective of the predator certainly complicates the formulation of models and vastly increases the effort needed to experimentally characterize an inducible predator-prey system. However, the interactive dynamics make these systems yet more interesting and compelling as model ecological and evolutionary systems.

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Figure Legends

Figure 1. Schematic diagrams of the differing evolutionary perspective of prey and predators with respect to inducible defenses.

Figure 2. Predator-prey dynamics and defense deployment represented in phase-plane diagrams. In these plots, a given position represents the state of a patch, i.e., the density of undefended prey (u-axis) and defended prey (d-axis), and whether or not the patch is under attack by a predator. The vectors represent rates at which patches change in state, due to: (a) growth and mortality of undefended and defended prey; (b) predation of undefended and defended prey; (c) deployment of the defense when under attack and (d) reversion to the undefended condition when predators are absent.

Figure 3. ESS predator signal level σ and resulting fitness as a function of the quality of food e_u.

Figure 4. ESS predator signal level σ and resulting fitness as a function of the prey signal response ϵ.

Figure 5. ESS predator signal level σ and resulting fitness as a function of the marginal cost of signal reduction k_0.

Figure 6. ESS predator signal level σ and resulting fitness as a function of the foraging efficiency or attack rate λ.

Figure 7. ESS predator signal level σ and resulting fitness as a function of the number of foragers n_p.

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