Inducible Defenses: Continuous Reaction Norms or Threshold Traits?

Thomas Owens Svennungsen,[1,*] Øistein Haugsten Holen,[1] and Olof Leimar[2]

1. Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway;   2. Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden

ABSTRACT: Phenotypically plastic traits can be expressed as continuous reaction norms or as threshold traits, but little is known about the selective conditions that favor one over the other. We study this question using a model of prey defenses in which prey can induce any level of defense conditional on cues that are informative of local predator density. The model incorporates a trade-off between defense expression and fecundity and feedback between the defense level of prey and predator attack rates. Both continuous reaction norms and threshold traits can emerge as evolutionarily stable solutions of defense induction, and we show that the shape of the trade-off curve plays a key role in determining the outcome. Threshold traits are favored when selection is disruptive. Ecological conditions that favor defense dimorphisms in the absence of cues will favor threshold traits in the presence of slightly informative cues. We caution that continuous reaction norms and threshold traits may result in similar patterns of defense expression at the population level, and we discuss potential pitfalls of inferring reaction norm type from observational data.

Keywords: phenotypic plasticity, conditional strategy, polyphenism, randomizing strategy, environmental cue, invasion boundary.

Introduction

The expression of an antipredatory defense will often be constrained by a trade-off: while a defense ensures an increased probability of survival, it comes at a cost to other components of fitness, leading to reduced growth, reduced reproductive output, and delayed maturation (e.g., Harvell 1990). Inducible defenses offer many of the benefits of constitutive defenses at reduced fitness costs and are prime examples of adaptive phenotypic plasticity (Travis 1994). Examples include the development of protective morphology in water fleas (Krueger and Dodson 1981), bryozoans (Harvell 1984), and rotifers (Stemberger and Gilbert 1984); chemical defenses in plants (reviewed in Karban

and Baldwin 1997); and, more generally, immune responses and predator avoidance behavior. Agents (cues) that can induce defense expression have been identified in several important model systems (Tollrian and Harvell 1999), thereby facilitating experimental study of the ecology and evolution of adaptive phenotypic plasticity.

Inducible defenses can be described in terms of reaction norms (Dodson 1989). Continuous reaction norms show a graded change in response along a continuous gradient of cue intensity, whereas discontinuous reaction norms entail an abrupt shift in response at a point where the intensity of cues crosses some threshold value (David et al. 2004). Traits following the latter type of reaction norm are commonly referred to as "threshold traits" (Roff 1996), "conditional strategies" (Hazel et al. 1990), or "polyphenisms" (Stearns 1989). Continuous and discontinuous reaction norms may reflect different underlying developmental mechanisms and evolutionary constraints (Smith-Gill 1983; West-Eberhard 1989; Schlichting and Pigliucci 1995). When reaction norms are classified as continuous or threshold traits in the empirical literature, it is not always clear whether the classification is motivated by reaction-norm data or by hypotheses of underlying architecture. The idea of a threshold switch between two developmental pathways producing different morphs is simple and attractive, which may explain why data that seem to indicate a continuous reaction norm are sometimes taken as evidence for a threshold trait (as pointed out by, e.g., Eberhard and Gutiérrez [1991] and Tomkins et al. [2005]).

An open question is whether continuous and discontinuous reaction norms also reflect different selective regimes: are there ecological circumstances under which we can expect one type to evolve rather than the other? Inducible defenses provide a suitable context in which to address this general question because they include examples of both types. A well-studied case is that of the acorn barnacle *Chthamalus anisopoma*, populations of

* Corresponding author; e-mail: t.o.svennungsen@bio.uio.no.

which comprise two alternative phenotypes: undefended conic morphs and well-defended bent morphs, where development into the latter is induced by cues associated with a predator snail (Lively 1986*c*; Lively et al. 2000). It has been argued that the abrupt switch from conic to bent morphology has evolved as an adaptation to the two habitat types in which juvenile barnacles may settle: crevices that host a high concentration of predators and surrounding rock that is virtually predator-free (Lively 1986*a*). The apparent absence of intermediate defense levels (i.e., a continuum from conic to fully bent morphs) is thereby ascribed to a lack of habitats with an intermediate risk of attack. The induction of a chemical defense in cotton provides an example of a continuous reaction norm: cotton seedlings produce defensive chemicals in response to spider mite herbivory (Karban and Carey 1984), and their resistance to subsequent mite infestations increases in a gradual and asymptotic fashion with the number of mites per seedling (Karban 1987). There are also inducible defenses that seem less clear-cut: the neckteeth in the water flea *Daphnia pulex*, which are induced in response to kairomones released by predators, are considered a threshold trait by some (Roff 1996) and a continuous reaction norm by others (Tollrian 1993). There is, however, little discussion in the literature on inducible defenses of why a threshold trait should be adaptive in some cases and a continuous reaction norm should be adaptive in others. The reasoning in the case of the acorn barnacles gives the impression that a threshold trait has arisen as a result of selection in discrete environments. Considering the variety of systems suggested to involve threshold traits (Roff 1996) and given that natural environments are rarely truly discrete, it seems unlikely that this provides a general explanation for why a threshold response in defenses should evolve.

Much of the theoretical work on inducible defenses is phrased in terms of threshold traits and focuses on evolutionary maintenance rather than origin (e.g., Lively 1986*a*; Hazel et al. 1990, 2004; Moran 1992). The models typically do not allow for graded environments or continuous defense levels and are thus unsuitable for addressing the question of whether a threshold trait should be favored over a continuous reaction norm. Models that consider both continuous traits and graded environments have been developed to explore reaction norms in other traits (reviewed in DeWitt and Scheiner 2004), although discontinuous (threshold) reaction norms have not been reported to arise in these models (e.g., Houston and Mc-Namara 1992; Kawecki and Stearns 1993; Sasaki and de Jong 1999; Ernande and Dieckmann 2004). While quantitative genetic models have been developed for both continuous reaction norms (Gomulkiewicz and Kirkpatrick 1992) and threshold traits (Falconer and Mackay 1996),

they are perhaps better suited to the exploration of genetic constraints than to predicting when either should evolve.

In this article, we develop a model to explore the circumstances under which an inducible defense will take the form of a threshold trait or a continuous reaction norm. Four features are believed to be essential for the evolution of inducible defenses (Harvell 1990), and the model incorporates all of them in a continuous fashion: the defense is costly to maintain (otherwise a constitutive defense would do), it is effective against predation (otherwise there would be no benefit), the risk of attack is variable (otherwise a constitutive defense would do), and there are cues available to guide induction. The model also considers the interplay between defense level and predation pressure (Adler and Harvell 1990; Adler and Karban 1994; Adler and Grünbaum 1999): high predation pressure may select for an increased level of defense, which may reduce the prey's value as a resource (in terms of lower energetic value, increased handling time, or higher escape rate [e.g., Havel and Dodson 1984; Hammill et al. 2010]), causing consumers to increasingly switch to more profitable resources (Charnov 1976). This in turn will reduce selection on the defense. We use tools from game theory to solve the model for evolutionarily stable reaction norms under the assumption that the defenses are irreversible and are genetically and developmentally unconstrained. To aid intuition, we explore the model in the context of constitutive defenses before we consider defenses that are induced in response to cues. The model is phrased in terms of defended prey and their predators but may also apply to other systems with consumer-resource interactions.

The Model

At the start of their life cycle, prey are dispersed randomly into any of many patches, with each patch hosting a large number of prey. The prey must survive ongoing predation for a period of time within their patch before they eventually reproduce. After clonal reproduction, the offspring disperse and the parent generation dies out. The prey population is regulated by global density-dependent mortality that is independent of the defense trait. Fitness of individual prey is thus proportional to expected reproductive output.

The probability $S(D)$ that a prey animal survives a predator attack is an increasing function of its defense level, D. Formally, we have $0 \leq D$, $0 \leq S(D) < 1$, and $S'(D) > 0$. (Prime symbols indicate derivatives throughout the article.) For simplicity, we assume that prey are left unharmed if they survive an attack—that is, future survival and potential fecundity are not affected. A prey animal that survives will realize a fecundity $F(D)$ that is a decreasing function of its defense level: $F(D) \geq 0$ and

$F'(D) < 0$. The choice of functions S and F combine to characterize the trade-off associated with investment in defense (fig. 1). It will be convenient to describe this trade-off by the parametric curve f that results from plotting the natural logarithm of F against S (fig. 1B). Any level of defense will be represented by a unique point on f, and the slope and second derivative of f at a point corresponding to some defense level D are respectively given by $[\ln F(D)]'/S'(D)$ and $[[\ln F(D)]'/S'(D)]'/S'(D)$. While the slope of f will always be negative, the second derivative will take negative and positive values in concave and convex regions of f, respectively (fig. 1B).

The probability that a prey animal survives until reproduction depends on the number of attacks it might experience, which in turn depends on both the density of predators and the rate at which they launch attacks. We assume that predators are generalists that modify their attack behavior on the basis of experience and that attack behavior changes on a much faster timescale than prey evolution. More specifically, we assume that the rate of attacks initiated on the focal prey species decreases with the overall defense level expressed within the patch. This could be the case if predators increasingly turn toward alternative food when defense levels tend to be high (i.e., prey profitability is low). Accordingly, we let the attack rate in a patch where all prey have induced the same level of defense $\tilde{D}$ (i.e., a monomorphic patch) be given by the function $A(\tilde{D})$, where $A(\tilde{D}) > 0$ and $A'(\tilde{D}) \leq 0$. When multiple defense levels are present in the same patch (mixed patch), we let the attack rate equal the average of the attack rates that would operate in the corresponding monomorphic patches:

$$\overline{A} = \sum_i A(\tilde{D}_i)\rho_i, \tag{1}$$

with the subscript indicating different defense-level morphs and ρ indicating their frequency in the patch ($\sum \rho_i = 1$). For simplicity, we assume that the period of predator learning is very short and that the asymptotic attack rate given by equation (1) is reached immediately. It is important to note that while F and S are functions of the defense level of a focal individual, $\overline{A}$ depends on the composition of defense levels expressed by all the prey within a patch.

We assume that predators search randomly and independently for prey within patches and that predator density remains constant within prey generations. The number of attacks each prey animal must survive before reaching reproductive age is then Poisson distributed. The expected reproductive output of a focal prey that induces defense level D in a patch with predator density P and attack rate $\overline{A}$ is equal to the probability of surviving all attacks, $e^{-(1-S(D))\overline{A}P}$, times fecundity, $F(D)$:
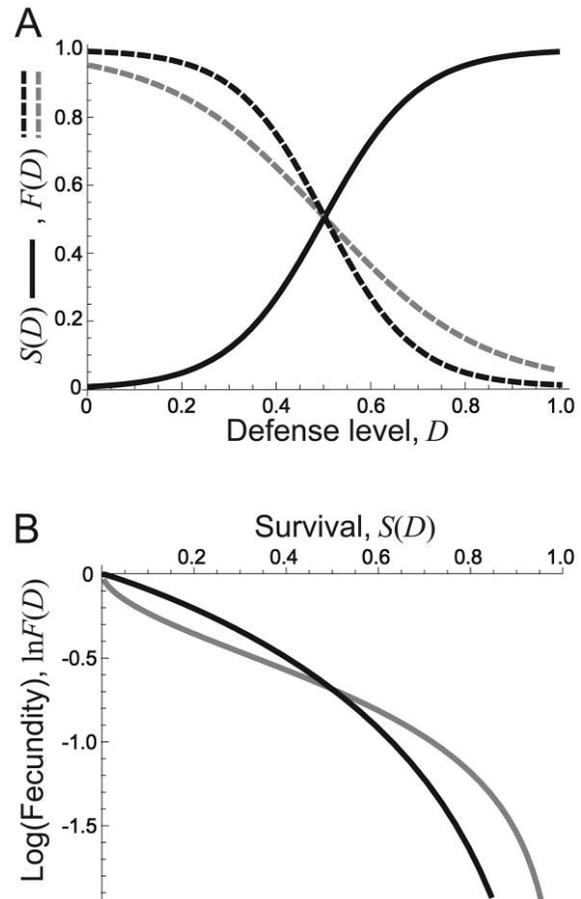
Figure 1: *A*, The dashed lines indicate two examples of a sigmoid relationship between defense level and potential fecundity (normalized); the black line shows $F(D) = (1 + e^{10.5(D-0.5)})^{-1}$, and the gray line shows $F(D) = (1 + e^{6(D-0.5)})^{-1}$. The unbroken line indicates a sigmoid relationship between defense level and the probability of surviving a predator attack, $S(D) = (1 + e^{-10(D-0.5)})^{-1}$. *B*, An everywhere-concave (*black*) and a partly convex (*gray*) trade-off curve resulting from plotting the logarithm of the two fecundity functions in *A* (*black* and *gray*, respectively) against the survival function.

$$W_i(D, \overline{A}) = F(D) \exp\left[-(1 - S(D))\overline{A}P\right]. \tag{2}$$

We incorporate variation in predation by assuming that the density of predators within each patch is drawn from a distribution $\Phi(P)$ with mean $\overline{P}$. This distribution may range from entirely regular (all patches host the same constant predator density) to extremely aggregated (clumped; the majority of patches are virtually predator-free, and the rest tend to include a high density of predators). We use the squared coefficient of variation, $\gamma = \text{variance/mean}^2$, as a measure of predator aggregation under $\Phi(P)$. Increasing γ for a given $\overline{P}$ increases the prevalence of patches with high and low predator density,

which agrees well with a biological interpretation of increased predator aggregation.

The invasion fitness of a rare mutant D that enters a resident population that elicits attack rate $\overline{A}$ is now simply its expected reproductive output averaged over all the predator densities it might experience:

$$W_2(D, \overline{A}) = F(D) \int_0^\infty \exp\left[-(1 - S(D))\overline{A}P\right]\Phi(P)dP. \quad (3)$$

For ease of presentation, we will use $H(t) = \int_0^\infty \exp[tP]\Phi(P)dP$, where $t = -(1 - S(D))\overline{A} < 0$, as shorthand notation for the probability of survival until reproduction averaged over all patches (the integral part of W_2). The function $H(t)$ is the zero term of a mixed Poisson process with mixing distribution $\Phi(P)$, and from the fact that e^{tP} is logconvex in t—and that logconvexity is conserved under mixing (e.g., An 1998)—we have $[\ln H(t)]' > 0$ and $[\ln H(t)]'' \geq 0$. When predator density (P) is constant across patches, W_2 simplifies to W_1.

Constitutive Defenses

We start by deriving results for constitutive defenses, which may occur if there are no cues for predation risk or if prey lack the ability to detect them. The results obtained provide analytical insight into the limiting cases of the full model. We also show that the curvature of the trade-off curve can exclude (nonzero) defense levels from being part of an evolutionarily stable strategy (ESS).

Consider a stable monomorphic resident prey population with defense level $\tilde{D}$ that elicits attack rate $\overline{A} = A(\tilde{D})$. If a mutant strategy has higher fitness than the resident strategy, it can invade. A strategy that cannot be invaded by any mutant constitutes an ESS (Maynard Smith 1982). Two conditions are sufficient to ensure that a strategy D^* in the interior (i.e., $D^* > 0$) is a local ESS. First, the mutant fitness gradient evaluated at D^* must equal 0 (i.e., $(\partial/\partial D)W_2(D, \overline{A})|_{D=\tilde{D}=D^*} = 0$). A strategy satisfying this condition is termed "singular" (Geritz et al. 1998). Second, the function describing mutant invasion fitness must be concave at D^* (i.e., $(\partial^2/\partial D^2)W_2(D, \overline{A})|_{D=\tilde{D}=D^*} < 0$). For an undefended strategy on the lower boundary (i.e., $D^* = 0$), a sufficient condition for local evolutionary stability is that the mutant fitness gradient has a negative slope (i.e., $(\partial/\partial D)W_2(D, \overline{A})|_{D=\tilde{D}=0} < 0$).

These ESS conditions can be rearranged so as to relate directly to the trade-off curve f (section A1 of the appendix in the online edition of the *American Naturalist*). A strategy D^* is evolutionarily singular if the slope of f at D^* equals $-\overline{A}[\ln H(t)]'|_{D=\tilde{D}=D^*}$, that is,

$$\frac{[\ln F(D^*)]'}{S'(D^*)} = -\overline{A}[\ln H(t)]'\Big|_{D=\tilde{D}=D^*}, \quad (4a)$$

and the singular strategy D^* is evolutionarily stable if f is sufficiently concave at this point:

$$\frac{1}{S'(D^*)}\left[\frac{[\ln F(D^*)]'}{S'(D^*)}\right]' < -\overline{A}^2[\ln H(t)]''\Big|_{D=\tilde{D}=D^*}. \quad (4b)$$

A strategy on the boundary (i.e., $D^* = 0$) is an ESS if the slope of f is sufficiently steep (negative) at the boundary:

$$\frac{[\ln F(0)]'}{S'(0)} < -\overline{A}[\ln H(t)]'\Big|_{D=\tilde{D}=0}. \quad (4c)$$

This last result makes intuitive sense: a marginal increase in defense level from 0 will not pay off if it incurs a large loss in fecundity relative to the benefit of increased survival. From condition (4b) we obtain an important result: convex regions of f cannot host an (interior) ESS defense level. This follows from the fact that $H(t)$ is logconvex (i.e., $[\ln H(t)]'' > 0$, as noted above), and thus the right-hand side of condition (4b) is negative regardless of assumptions made about the predator distribution $\Phi(P)$. Convergence stability of a monomorphic ESS is guaranteed if (section A2 of the appendix)

$$[\ln H(t)]' + t[\ln H(t)]'' \geq 0, \text{ for all } t < 0. \quad (5)$$

This holds for several relevant classes of distribution functions $\Phi(P)$, including the gamma and the exponential distributions, and for the special case when all patches have the same density of predators (section A2 of the appendix). Extensive numerical exploration suggests that condition (5) also holds under the lognormal, although we cannot provide a general analytic proof.

A defense-level dimorphism is evolutionarily stable if its two component strategies D_1 and D_2 can be maintained at a stable ecological equilibrium by predation and are also resistant to invasion by mutants at this ecological equilibrium. Under continuous allele frequency dynamics, condition (5) is sufficient to ensure that any ecological equilibrium involving two defense levels must be stable and unique and that such an equilibrium can exist if (and only if) the two defense levels are mutually invasible (section A3 of the appendix). Resistance to mutant invasion and thus evolutionary stability is ensured if both component strategies also satisfy ESS conditions (4a)–(4c). Evolutionarily stable defense dimorphisms are always absolute convergence stable (sensu Leimar 2001; section A4 of the appendix).

To investigate how the shape of the trade-off curve f and the distribution of predators affect ESS defense levels—in particular, the scope for an ESS dimorphism—one

can consider the overall shape of the so-called invasion boundaries (de Mazancourt and Dieckmann 2004; Rueffler et al. 2004). An invasion boundary divides a trait space into regions of mutant traits that may and may not invade a focal resident (monomorphic or dimorphic) population. In our case, this trait space consists of all possible combinations of log fecundity ($\ln F$) and survival probability (S; both taken as free variables unconstrained by the trade-off), and an invasion boundary is a line through this space comprising all combinations of $\ln F$ and S that give the same fitness as individuals of the focal resident population. Since fitness increases with fecundity and survival, all combinations of $\ln F$ and S above the invasion boundary will yield higher fitness than the resident. Thus, for a resident strategy to be resistant to invasion by all (feasible) mutants, it is necessary that its invasion boundary lies above the trade-off curve f at all points except the point corresponding to the resident strategy itself or, in the case of a dimorphic resident, the points corresponding to the strategy's two components (Rueffler et al. 2004). It follows that the invasion boundary of an ESS (component) in the interior must be tangential to f at their point of contact (fig. 2*A*, 2*B*), whereas this need not be the case for an undefended ESS (component). The shape of an ESS's invasion boundary at the points where it touches the trade-off curve f is closely linked to conditions for local evolutionary stability (de Mazancourt and Dieckmann 2004; Rueffler et al. 2004): the slope of the invasion boundary is equal to the right-hand sides of condition (4a) and condition (4c), and for an interior ESS (component) the second derivative is equal to the right-hand side of condition (4b). This provides a graphical interpretation of condition (4b): a singular strategy is evolutionarily stable only if the trade-off curve is more concave than the invasion boundary at their point of tangency.

In the special case where predator density is the same in all patches, invasion boundaries are always linear with a (negative) slope that is proportional to predator density (section A5 of the appendix). If the trade-off curve f is everywhere concave, only monomorphic ESSs can result, since a linear invasion boundary cannot possibly touch f at two points and otherwise be above it (fig. 2*A*). A dimorphic ESS requires that the trade-off curve include a convex region (fig. 2*B*). Because invasion boundaries steepen with predator density, the (monomorphic) ESS under an everywhere-concave trade-off will increase in a continuous fashion as predator density increases (fig. 2*C*). For trade-off curves with convex sections, a slight increase in predator density may result in an abrupt shift in ESS defense levels at the point where an ESS dimorphism appears (fig. 2*D*). The proportion of better-defended prey at ecological equilibrium ($\hat{\rho}$) increases from 0 to 1 over the

interval of predator densities that support an ESS dimorphism.

When predator density varies across patches, the invasion boundaries are strictly concave (section A5 of the appendix). The invasion boundary may then touch the trade-off curve at two points and otherwise be above it also in cases where f does not include a convex region, and everywhere-concave trade-offs may thus support evolutionarily stable dimorphisms (not shown). The defense levels that constitute the dimorphic ESS will differ more when predator density varies over patches than when it is constant, assuming the same trade-off curve (fig. 2*B*).

Numerical examples with variable predator densities are shown in figure 3. Increased predator aggregation tends to decrease the ESS defense level and increase the range of mean predator densities for which the undefended state is an ESS. This latter point makes intuitive biological sense: when predators are more aggregated there will be more patches with low predator densities, and investing in a defense will not pay off as readily. Under the partly convex trade-off curve (fig. 3*B*), there is an abrupt transition from an undefended monomorphic ESS to a dimorphic ESS, and the defended component of a dimorphic ESS increases with predator aggregation. Within the dimorphic region, the equilibrium frequency of the well-defended strategy increases with mean predator density (not shown).

We have presented ESS dimorphisms as a genetic polymorphism maintained by frequency-dependent predation. An alternative possibility is a single randomizing genotype capable of developing into either morph—that is, a genotype that develops into the better-defended morph with some probability ρ and into the less-defended morph with probability $1 - \rho$. The value of ρ is then genetically controlled and will be evolutionarily stable when it equals the corresponding ecological equilibrium $\hat{\rho}$ (section A6 of the appendix). A general discussion of conditions that favor randomizing strategies over genetic polymorphisms has been provided by Leimar (2005).

Reaction Norms of Defense

We next study reaction norm strategies, where defenses are induced in response to the perceived cue intensity. The cues reflect local predator abundance, and by monitoring cues prey obtain a somewhat noisy observation of the predator density in their patch. We represent observations by a continuous random variable that takes values C, and the reaction norm specifies the defense to be induced for each possible observation. We let reaction norms comprise three components $\mathbf{D} = \{D_1(C), D_2(C), \rho(C)\}$, so that for any value of C the reaction norm can specify two alternative defense levels and the probability of inducing either. That is, reaction norms can include randomization be-
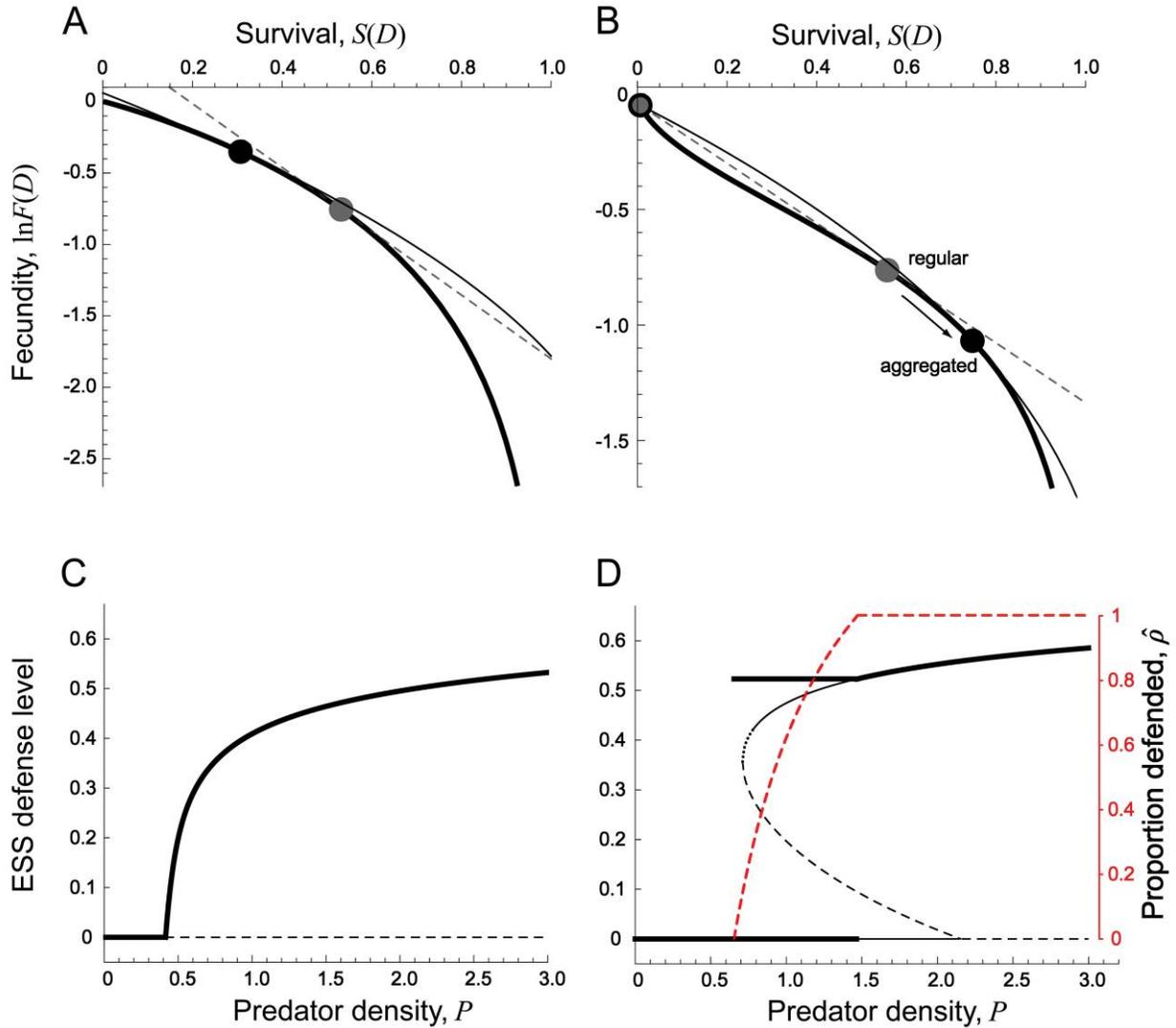
Figure 2: *A, B,* Trade-off curves (*thick black lines*) and invasion boundaries at an evolutionarily stable strategy (ESS) under constant predator density (*dashed gray lines, gray disks*) and at an ESS under variable predator density (*thin black lines, black disks*). The invasion boundary at an ESS is above the trade-off curve at all points other than that corresponding to the ESS. The trade-off curves in *A* and *B* are, respectively, the black and gray trade-off curves in figure 1*B. C, D,* Global ESSs (*thick black lines*) for different (constant) predator densities under the trade-off curves in *A* and *B*, respectively. In the range of predator densities (0.65–1.47) where a dimorphic ESS is supported in *D,* the proportion of well-defended prey increases with predator density (*dashed red line*). Other lines in *C* and *D* signify local ESSs (*thin lines*), evolutionarily unstable repellors (*dashed black lines*), and evolutionary branching points (sensu Geritz et al. 1998; *dotted line*). Other functions/parameters: $A(D) = 2(1 + e^{10(D-0.5)})^{-1}$. Invasion boundaries in *A*: gray, $P = 2.5$; black, $\Phi(P)$ lognormal with $\overline{P} = 2.5$ and $\gamma = 1$. Invasion boundaries in *B*: gray, $P \in (0.65–1.47)$; black, $\Phi(P)$ lognormal with $\overline{P} = 3.5$ and $\gamma = 3$.

tween defense levels: an observation C will induce defense level $D_1(C)$ with probability $1 - \rho(C)$ and $D_2(C)$ with probability $\rho(C)$. It follows that whenever $D_1(C) = D_2(C)$ or $\rho(C) = 0$ or 1, the reaction norm specifies a single defense level; there is no randomization. A straightforward way of discerning a continuous reaction norm from a threshold trait is by plotting $D_1(C)$, $D_2(C)$, and $\rho(C)$ in

the same figure: in the case of a continuous reaction norm, the expressed parts of $D_1(C)$ and $D_2(C)$ will combine to form a single continuous curve.

The observations made in a patch follow a distribution that is conditional on the actual predator density in that patch: $\psi(C|P)$. The effect of cue accuracy on the evolution of reaction norms can then be studied by varying the
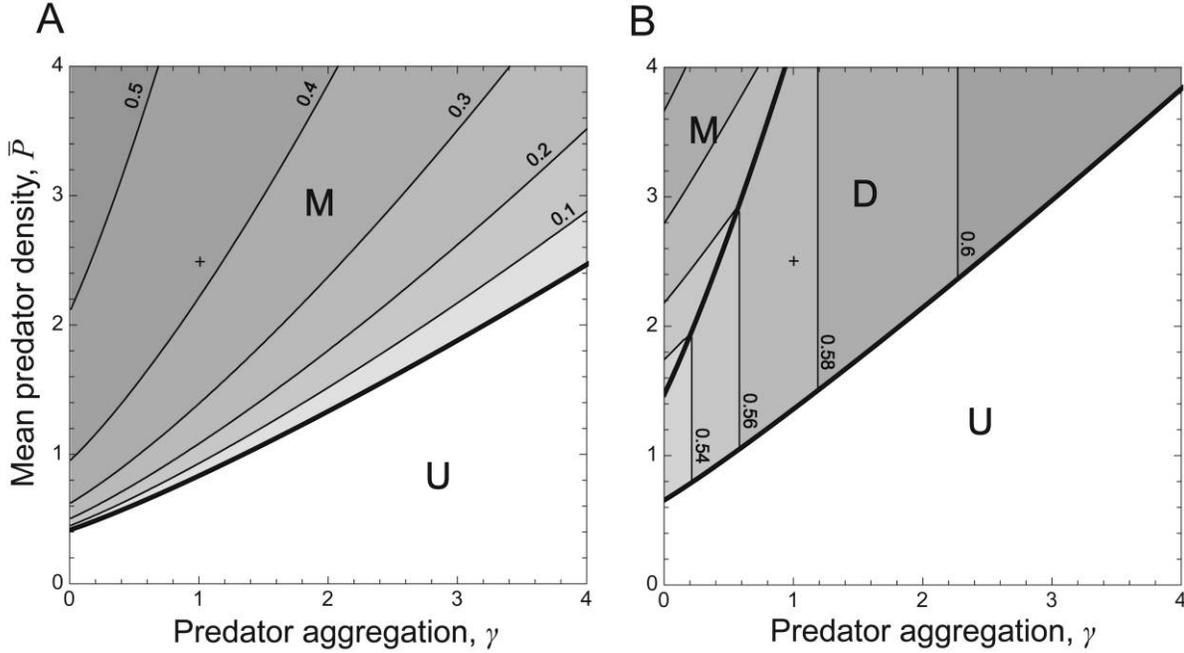
Figure 3: Evolutionarily stable strategy (ESS) levels of defense under different mean predator densities and levels of aggregation when predator densities are lognormally distributed over patches. Regions marked *U*, *M*, and *D* indicate combinations of mean density and aggregation that respectively support only undefended, monomorphic defended, and dimorphic ESSs. All ESS dimorphisms include an undefended component strategy. Contours signify defense levels of monomorphic ESSs or the better-defended component of ESS dimorphisms. *A*, ESSs under the everywhere-concave trade-off curve in figure 2*A*. *B*, ESSs under the partly convex trade-off curve in figure 2*B*. Crosses mark the combination used when illustrating ESS reaction norms under the full model with partly informative cues; *A*(*D*) is as in figure 2.

parameters of this distribution. As long as there is some observation error ($\psi(C|P)$ has nonzero variance), prey within the same patch will make different observations and induce different defense levels even if all prey share the same (nonconstant) reaction norm. In a resident population with reaction norm $\tilde{\mathbf{D}} = \{\tilde{D}_1(C), \tilde{D}_2(C), \tilde{\rho}(C)\}$, the frequencies of the different defense levels in a patch with predator density P will follow from $\psi(C|P)$, and the resulting attack rate will be given by

$$\overline{A}(\tilde{\mathbf{D}}, P) = \int_0^\infty ((1 - \tilde{\rho}(C))A(\tilde{D}_1(C))$$

$$+ \tilde{\rho}(C)A(\tilde{D}_2(C)))\psi(C|P)dC. \tag{6}$$

The probability of a focal prey surviving until reproduction is, as in the previous section, the average of its survival over all the predator densities it may be facing. These densities are now conditional on the observation a focal prey has made within the patch. Having defined a (prior) predator distribution $\Phi(P)$ and a conditional distribution of observations $\psi(C|P)$, the (posterior) distri-

bution of predators conditional on the observation, $\phi(P|C)$, can be derived using Bayes's rule for probability densities:

$$\phi(P|C) = \frac{\Phi(P)\psi(C|P)}{\Psi(C)}, \tag{7}$$

where $\Psi(C) = \int_0^\infty \psi(C|P)\Phi(P)dP$ is the marginal distribution of observations over all patches.

Consider a rare mutant prey that has made an observation C and in response induces the corresponding level of defense D. Its expected reproductive output when the resident population has strategy $\tilde{\mathbf{D}}$ is

$$W_3(D, \tilde{\mathbf{D}}) =$$

$$F(D) \int_0^\infty \exp\left[-(1 - S(D))\overline{A}(\tilde{\mathbf{D}}, P)P\right]\phi(P|C)dP.$$

The full expression for the invasion fitness of a rare mutant reaction norm $\mathbf{D} = \{D_1(C), D_2(C), \rho(C)\}$ is ob-

tained by integrating over the marginal distribution of observations:

$$U(\mathbf{D}, \tilde{\mathbf{D}}) = \int_0^\infty ((1 - \rho(C))W_3(D_1(C), \tilde{\mathbf{D}})$$

$$+ \rho(C)W_3(D_2(C), \tilde{\mathbf{D}}))\Psi(C)dC.$$

With gradual evolution, the defense levels induced under the various observations—that is, each point in the reaction norm—will change in a direction predicted by the local fitness gradient of the resident strategy. For any particular observation C, the gradients at the three components can be obtained by evaluating

$$g_{\tilde{D}_1}(C) = (1 - \tilde{\rho}(C))\frac{\partial}{\partial D_1} W_3(D_1, \tilde{\mathbf{D}})\Big|_{D_1 = \tilde{D}_1(C)},$$

$$g_{\tilde{D}_2}(C) = \tilde{\rho}(C)\frac{\partial}{\partial D_2} W_3(D_2, \tilde{\mathbf{D}})\Big|_{D_2 = \tilde{D}_2(C)}, \qquad (8)$$

$$g_{\tilde{\rho}}(C) = W_3(\tilde{D}_2(C), \tilde{\mathbf{D}}) - W_3(\tilde{D}_1(C), \tilde{\mathbf{D}}).$$

In the case of an ESS, $\mathbf{D}^* = \{D_1^*(C), D_2^*(C), \rho^*(C)\}$, the gradients will be 0 along those parts of the reaction norm that lie in the interior of the strategy space (i.e., $g_{D_i^*}(C) = 0$ where $D_i^*(C) > 0$; $g_{\rho*}(C) = 0$ where $0 < \rho^*(C) < 1$; first-order condition), and the fitness landscape will be locally concave (second-order condition). The gradients will be negative along those parts of the ESS reaction norm that are 0 (i.e., $g_{D_i^*}(C) < 0$ where $D_i^*(C) = 0$; $g_{\rho*}(C) < 0$ where $\rho^*(C) = 0$) and positive at the upper boundary (i.e., $g_{\rho*}(C) > 0$ where $\rho^*(C) = 1$). Of course, whenever $\rho^*(C) = 0$ or $\rho^*(C) = 1$, the value of $D_2^*(C)$ or $D_1^*(C)$ will, respectively, not be expressed, in which case the value (and sign) of the corresponding gradient ($g_{D_2^*}(C)$ or $g_{D_1^*}(C)$) is irrelevant.

Before considering specific examples, we summarize what the analytical results from the section concerning constitutive defenses tell us about ESS reaction norms in general.

Reaction Norms in Two Limiting Cases

We may use the results concerning constitutive defenses to characterize two limiting cases. First, consider the case where observations are made without error. All prey within a patch will then make the same (correct) observation of predator density. The evolutionarily stable level of defense to induce for any particular predator density will equal that of a constitutive ESS under a corresponding constant predator density. To take an example, figure 2C and 2D can (by letting $C = P$) be interpreted as depicting ex-

amples of an ESS reaction norm. In figure 2C the ESS reaction norm is described by a single continuous line, whereas in figure 2D the ESS reaction norm is discontinuous (like a threshold trait) and includes randomization between two defense levels for a range of intermediate predator densities (observations): the bottom thick black line corresponds to $D_1^*(C)$, the top thick black line corresponds to $D_2^*(C)$, and the red dashed line corresponds to $\rho^*(C)$. Second, consider the case where observations are so noisy that they do not provide any information. The conditional distribution of predator densities will then always equal the (prior) distribution $\Phi(P)$, and ESSs can again be identified by the methods given in the section on constitutive defenses. An ESS will then comprise a single defense level or randomization between two distinct defense levels (or, alternatively, a genetic polymorphism).

Reaction Norms When Cues Are Partially Informative

We now explore results between the two extreme ends of the observation-error scale—that is, when reaction norms evolve under partially informative cues. Our analytical results tell us that an evolutionarily stable reaction norm cannot ascribe to any observation a (nonzero) defense level from a convex region of the trade-off curve, since these defense levels must be suboptimal for any possible posterior distribution of predator density (condition [4b]). Such reaction norms would therefore be susceptible to invasion by an otherwise identical reaction norm that ascribes a more beneficial level of defense for the same observation. It follows that continuous reaction norms can be evolutionarily stable only if they are contained within a concave region of the trade-off curve. An evolutionarily stable reaction norm that contains defense levels above and below a convex region of the trade-off curve is necessarily a threshold trait.

Our approach to finding ESS reaction norms is through simulation of adaptive walks. This is done by discretizing the reaction norm into a finite number of points, with increased resolution in regions where the reaction norm is steep or discontinuous. The details of the simulation procedure are provided in section A7 of the appendix.

We assume that observational errors are normally distributed on a log scale with standard deviation $\sigma_{C|P}$ and are centered around the (logarithm of the) true predator density—that is, $\psi(C|P)$ is a lognormal distribution with parameters $\mu_C = \ln P$ and $\sigma_{C|P}$. On an absolute scale, lognormally distributed observational errors are greater for large observations than for small observations, an assumption that has some support from the Weber-Fechner law of psychophysics: the smallest noticeable difference (the error) of perceived stimuli is proportional to the magnitude of the stimuli experienced (in-

tensity of cues). A lognormal distribution is also mathematically tractable: with predator density given by a lognormal distribution $\Phi(P)$ with parameters μ_P and σ_P, the marginal distribution of observations, $\Psi(C)$, is also lognormal with parameters μ_P and $(\sigma_P^2 + \sigma_{C|P}^2)^{1/2}$. Furthermore, it follows from equation (7) that the conditional distribution of predators $\phi(P|C)$ is lognormal too, with parameters $\mu_{P|C} = (\sigma_P^2(\ln C) - \sigma_{C|P}^2\mu_P)/(\sigma_P^2 + \sigma_{C|P}^2)$ and $\sigma_{P|C} = \sigma_P\sigma_{C|P}/(\sigma_P^2 + \sigma_{C|P}^2)^{1/2}$.

ESS reaction norms are shown in the upper panels of figure 4A and 4B. The everywhere-concave trade-off curve (cf. fig. 2A) results in a continuous ESS reaction norm that changes gradually from the ESS reaction norm under perfect information (cf. fig. 2C) to the single level of defense predicted under no information (cf. fig. 3A) as cue accuracy decreases (fig. 4A). If instead the ESS in the absence of information was undefended, the ESS reaction norm would decrease toward 0 as cue accuracy decreased (not shown). The lower row of panels in figure 4A displays, for each ESS reaction norm, the composition of defense levels present under different predator densities. This is what would be recorded by an observer who (thoroughly) sampled patches within the same ESS population.

The partly convex trade-off curve (cf. fig. 2B) results in a threshold trait, and the threshold shifts slightly toward lower values of the cue as cue accuracy decreases (fig. 4B). In this case, the predator distribution supports a dimorphic ESS under no information (cf. fig. 3B). While the ESS reaction norm under perfect information includes a range of predator densities where prey should randomize between two defense levels (fig. 2D), such randomization does not occur under imperfect information; an observation will always correspond to a single level of defense (i.e., $\rho^*(C)$ never takes values between 0 and 1). Other choices of parameters for the distribution of predators could lead to larger shifts in the threshold than in our example. For instance, if the predator distribution supports only a monomorphic well-defended ESS when cues are absent, the threshold in the ESS reaction norm would shift to the left and disappear completely as cue accuracy decreases (not shown). Likewise, if the predator distribution supports only a monomorphic undefended ESS when cues are absent, the threshold would shift to the right until well-defended states were no longer expressed (not shown). The composition of defense levels under different predator densities shifts gradually from that predicted under perfect information to the dimorphic ESS predicted under no information (lower row of panels in fig. 4B).

When observations are very accurate ($\sigma_{C|P}$ is small), the ESS reaction norm may include multiple thresholds (fig. 5A) in the region of predator densities where a randomizing strategy is supported under perfect observations.

Multiple thresholds serve effectively as a randomizing mechanism (see "Discussion"). The number of thresholds incorporated in the ESS increases with observation accuracy (not shown), and the composition of defense levels across patches converges on that predicted under perfect observation (fig. 5B).

Discussion

Our model analysis demonstrates that both continuous reaction norms and threshold traits can emerge as optimal forms of phenotypic plasticity. It has been suggested that threshold traits (polyphenisms) are found mainly in dichotomous or otherwise discrete environments (Lively 1986a; Nijhout 2003). Our analysis, however, shows that a discontinuous environment is not necessary for threshold traits to evolve: they readily emerge even when the ecological factors considered essential to their evolution are treated as continuous variables. Our focus on general rather than specific functional forms should contribute to the generality of our results. The shape of the log fecundity-survival trade-off curve was found to be of great importance: nonzero defense levels lying in a convex region of a trade-off curve are suboptimal under all possible posterior distributions of predators and cannot be part of an optimal reaction norm. An ESS reaction norm encompassing defense levels from both above and below a convex region consequently must entail an abrupt switch from a low level of defense (or no defense) to some high level of defense (as shown in fig. 4B).

The shape of the trade-off curve depends on how the defense trait affects survival probability on the one hand and fecundity on the other. A sigmoid relationship between survival probability and the defense trait seems likely in many cases. Such a relationship emerges if the level of defense that predators can overcome is set by some threshold that varies unimodally around a nonzero mean (due to, e.g., variation in predator size or toxin load); prey survival probability will then increase in a sigmoid fashion according to the cumulative distribution of thresholds in the predator population (Mallet and Joron 1999; Speed and Ruxton 2007). Similarly, if predators assess the defense before accepting or rejecting the prey, perceptual noise will likely lead to a sigmoid relationship between the actual defense level and the probability that the prey is perceived as being too well defended for acceptance (Joron 2003). Less can be said in general about the function linking fecundity to the defense trait. Nevertheless, since a wide range of fecundity functions can combine with a sigmoid survival function to form a partly convex trade-off curve (Svennungsen and Holen 2007), such trade-offs are possible under a wide range of conditions. Qualitative knowledge of the relations need not be enough to determine
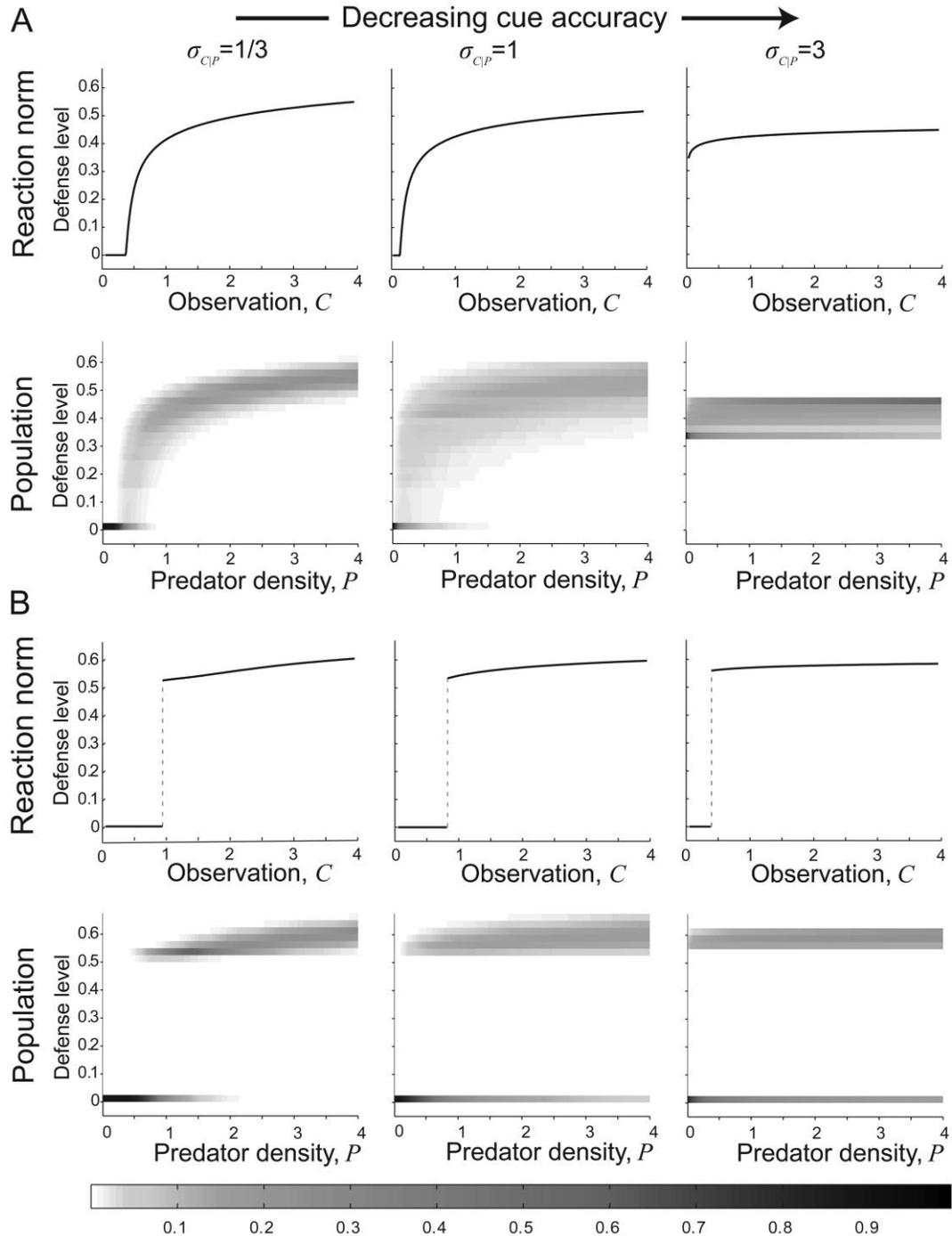
Figure 4: Evolutionarily stable reaction norms and patch composition of defense levels resulting from them, for three levels of cue accuracy. *A*, Continuous reaction norms resulting under the trade-off curve in figure 2*A*. *B*, Threshold reaction norms resulting under the partly convex trade-off curve in figure 2*B*. The upper row of panels in *A* and *B* display reaction norms specifying the level of defense to induce for each observation. The lower row of panels in *A* and *B* display, for each reaction norm, the patch composition of defense levels under the different predator densities. The shade of gray signifies the frequencies of defense levels induced under a given predator density (as indicated by the gray scale bar). Observation errors are assumed to be normally distributed on a log scale, centered around the (logarithm of the) true predator density, with standard deviation $\sigma_{C|P}$ as indicated above each column. Predator densities are assumed to be lognormally distributed over patches with $\overline{P} = 2.5$ and $\gamma = 1$ (cf. crosses in fig. 3); $A(D)$ is as in figures 2 and 3.
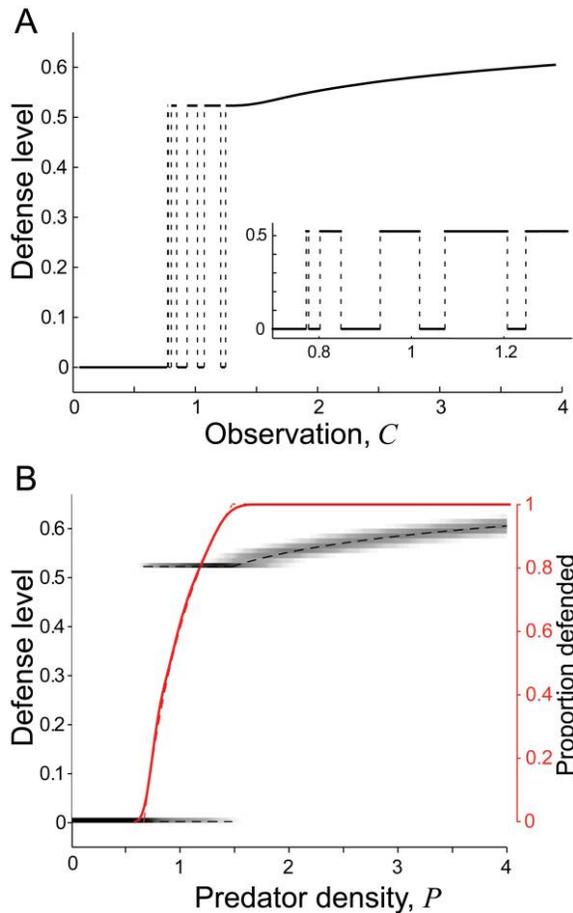
Figure 5: *A*, Evolutionarily stable reaction norm under the partly convex trade-off curve in figure 2*A*. The evolutionarily stable reaction norm includes multiple thresholds (*enlarged inset*) when observations are accurate. *B*, Distribution of defense levels expressed within the different patches and the proportion of defended prey (*unbroken red line*). For comparison, the dashed lines correspond to the ESS under perfectly accurate observations (cf. fig. 2*D*). Note the partly hidden red dashed line. $\sigma_{C|P} = 0.1$; other parameters and functions are as in figure 4.

trade-off shape, though, because survival and fecundity functions that are very similar can combine into qualitatively different trade-off curves (fig. 1). To determine the shape of a trade-off curve, one needs to estimate the relevant traits (e.g., probability of surviving attack and fecundity) for at least three different defense levels. Both survival probability and fecundity can be estimated empirically (e.g., Kerfoot 1977; Dodson 1984; Lively 1986*b*; Hammill et al. 2008). However, it is important to note that, using naturally occurring defense levels, it may not be possible to measure the entire trade-off curve: our model predicts that defense levels in convex sections of the trade-off curve should not be expressed at evolutionary

equilibrium. In fact, the concavity of the invasion boundaries ensures that the measurable part of a trade-off curve must, under the assumptions of our model, form a concave curve at evolutionary equilibrium. A trade-off curve found to be convex would therefore indicate a suboptimal reaction norm; in such a case, a threshold trait would be adaptively favored.

Defense traits may, of course, trade off with traits other than fecundity (e.g., Yin et al. 2011), in which case other properties of the trade-off curve may turn out to be influential for the optimal reaction norm. Theoretical considerations, as outlined by our approach, can provide insight into these cases and into other forms of adaptive plasticity. Pinpointing costs and benefits of horn size and determining how these affect optimal solutions for plasticity might prove informative of factors underlying the large variation in reaction norms found between related species of horned beetles (Emlen et al. 2005). Plasticity may also impose various costs that are directly related to the ability of sensing environmental cues and to the developmental flexibility needed to express different phenotypes (DeWitt et al. 1998; Auld et al. 2010). Whether such costs tend to differ between threshold traits and continuous reaction norms is an open question that could be well worth pursuing.

Determining whether a trait is expressed according to a continuous reaction norm or is a threshold trait must primarily entail close inspection of trait measurement data (Eberhard and Gutiérrez 1991). The reaction norm solutions in our examples, however, reveal that this may not always be straightforward. Multimodal trait distributions and steep sigmoid reaction norms are, for instance, often considered to be indicators of a threshold trait (e.g., Eberhard and Gutiérrez 1991; Moczek and Nijhout 2003; Rowland and Qualls 2005; Rowland and Emlen 2009). As our results show, however, a bimodal trait distribution, both within and across environments, is compatible with both a threshold trait and a steep continuous reaction norm (fig. 4). The expression of horns in the beetle *Onthophagus acuminatus*, which is conditional on body size (which in turn depends on nutritional conditions), illustrates our point (Emlen 1994): a plot of horn length against body size from both a natural and an experimental population of beetles clearly suggests a continuous sigmoid relationship between the two. The sigmoid relationship results in a bimodal distribution of horn lengths at the population level (Emlen 1994). The assertion of a threshold trait in this case (Emlen 2000) and in similar cases seems to rest on an assumption that the expression of intermediate phenotypes around the "threshold" is due to developmental constraints rather than an adaptive response and that the sigmoid reaction norm represents a suboptimal approximation of a discrete threshold trait (Emlen and Nijhout

2000; Rowland and Qualls 2005). However, we have shown that continuous reaction norms that are close to sigmoid may represent optimal and unconstrained plasticity, with intermediate phenotypes being well adapted to the environments in which they are expressed. By themselves, sigmoid reaction norms do not provide evidence of selection against intermediates or of developmental dissociation of trait values (Tomkins and Moczek 2009). Fitness comparisons of extreme and intermediate forms may be a necessary complement to trait measurements in ambiguous cases. Even data with gaps in the distribution of defense levels must be interpreted with some care; a lack of intermediates may be due to sparsely sampled data (Nijhout 2003; Schoeppner and Relyea 2008). This is especially relevant for data originating from observational studies. In some cases, the identification of the inducing cue and experimental trait induction for an appropriate range of cue concentrations may be the only possibility for mapping out the complete reaction norm (Tollrian 1993; Nijhout 2003; Schoeppner and Relyea 2008).

An important prediction from our analysis is that defense-level dimorphisms might be invaded by threshold traits if slightly informative cues are present. Under an evolutionarily stable defense dimorphism, ecological feedback maintains the two morphs at frequencies where they obtain equal fitness when averaged over all patches. Nevertheless, the two morphs will obtain unequal fitness in virtually any patch. A threshold trait in connection to an inaccurate cue will more often produce the more beneficial phenotype in each patch and be able to invade the dimorphism. The low accuracy of the cue will ensure that defense levels from both sides of the threshold will be expressed within most patches, especially in those patches where the presence of both morphs is optimal.

Threshold traits can also be adaptive in cases where cues are very accurate predictors of actual predation risk. However, a reaction norm with a single threshold may perform poorly if defense-level dimorphisms are optimal over a wide range of patches, since prey in the patches far from the threshold will then typically express defense levels from the same side of the threshold, resulting in suboptimal monomorphic patches. One evolutionary solution is then to randomize development between high and low defense levels in those patches where a dimorphism is optimal. Our simulations did not converge on reaction norms with phenotype randomization but rather on a strategy with multiple on-off switches (fig. 5A). These strategies do, however, achieve much the same thing: by spacing the switching points (thresholds) sufficiently close, they ensure that the low variation in the amount of detected cues will suffice for patches to include prey that induce defense levels from either side of a threshold, and fine-tuning the spacing will ensure that the two defense levels are produced

at relative frequencies that are close to optimal (fig. 5B). An optimal reaction norm with multiple switches has been found in a model of environmental sex determination, where it also appeared as a stand-in for a randomizing strategy (Leimar et al. 2004). As discussed in that article, different kinds of strategies at the individual level can sometimes produce a very similar population distribution of phenotypes. Thus, the ESS reaction norm with several switches shown in figure 5A gives rise to nearly the same population distribution of phenotypes as a reaction norm that randomizes correctly (fig. 5B). This means that a randomizing reaction norm is effectively close to the ESS in the sense that selection to modify it would be weak. Leimar et al. (2004) also noted that if constraints allow only for reaction norms with a single threshold, a genetic polymorphism of threshold traits could produce a similar population distribution of phenotypes as an unconstrained ESS reaction norm and would therefore be a conceivable evolutionary outcome. This could also apply to our model of inducible defenses. Although we have not investigated the matter, a population with genetic variation in the location of the threshold could approximate our results for accurate cues and a partly convex trade-off curve.

Our analysis highlights the importance of considering variation in predation pressure when investigating the evolution of defensive traits. We found that disruptive selection leading to threshold traits or genetic defense polymorphisms can arise under a wider range of trade-off curves when predator density varies between patches than when it is constant. The conditions favoring evolutionarily stable defense polymorphisms are thus even wider than previously shown (Svennungsen and Holen 2007). Numerical explorations of the model also revealed that increased aggregation of predators can lead to larger "jumps" in evolutionarily stable threshold traits and a greater difference between the morphs in evolutionarily stable defense polymorphisms. Selection for greater differences in defense level under predator aggregation makes intuitive sense, since increased aggregation increases the likelihood of a more extreme (very few or very high) number of predator encounters.

Genetic variation might underlie some of the variation in defenses in a population. In particular, for environmentally induced defenses there can be genetic variation in the extent and ease with which defenses are induced, as has been found in several studies (e.g., Harvell 1998; Lively et al. 2000; Wiackowski et al. 2003; Hammill et al. 2008). There may be several kinds of explanation for this type of genetic variation, including gene flow between subpopulations with different optimal reaction norms and local frequency-dependent selection. A general perspective on genetic variation in reaction norms is that environmental and genetic cues jointly determine the phenotype

(Leimar et al. 2006; Leimar 2009) and that natural selection can tune an organism's developmental system toward an adaptive response to cues. Although we have not examined the issue of genetic polymorphism in reaction norms, our conclusions with regard to the important role of the shape of the trade-off between survival and fecundity apply quite broadly: the prediction that defense levels from convex regions of a trade-off curve will not be part of an optimal reaction norm should also be valid for situations where genetic variation in the norm is maintained. This suggests that our predictions about the conditions favoring threshold traits versus continuous reaction norms have broad scope.

Acknowledgments

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