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Year: 2007

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DOI: <https://doi.org/10.1086/509939>

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Journal Article

Published Version



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Originally published at:

Steiner, Ulrich Karl; Pfeiffer, Thomas (2007). Optimizing Time and Resource Allocation Trade-Offs for Investment into Morphological and Behavioral Defense. *The American Naturalist*, 169(17206590):118-129.

DOI: <https://doi.org/10.1086/509939>

# Optimizing Time and Resource Allocation Trade-Offs for Investment into Morphological and Behavioral Defense

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Submitted October 20, 2005; Accepted June 14, 2006;  
Electronically published December 7, 2006

Online enhancement: appendix.

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**ABSTRACT:** Prey organisms are confronted with time and resource allocation trade-offs. Time allocation trade-offs partition time, for example, between foraging effort to acquire resources and behavioral defense. Resource allocation trade-offs partition the acquired resources between multiple traits, such as growth or morphological defense. We develop a mathematical model for prey organisms that comprise time and resource allocation trade-offs for multiple defense traits. Fitness is determined by growth and survival during ontogeny. We determine optimal defense strategies for environments that differ in their resource abundance, predation risk, and defense effectiveness. We compare the results with results of simplified models where single defense traits are optimized. Our results indicate that selection acts in favor of integrated traits. The selective advantage of expressing multiple defense traits is most pronounced at intermediate environmental conditions. Optimizing single traits generally leads to a more pronounced response of the defense traits, which implies that studying single traits leads to an overestimation of their response to predation. Behavioral defense and morphological defense compensate for and augment each other depending on predator densities and the effectiveness of the defense mechanisms. In the presence of time constraints, the model shows peak investment into morphological and behavioral defense at intermediate resource levels.

**Keywords:** complex traits, phenotypic plasticity, predator-prey, life-history evolution.

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Am. Nat. 2007. Vol. 169, pp. 118–129. © 2007 by The University of Chicago. 0003-0147/2007/16901-4137\$15.00. All rights reserved.

The evolution of various phenotypes and life histories is determined by selection acting on traits to optimize conflicting demands. Such conflicting demands are often mediated by time and resource allocation trade-offs. Time allocation trade-offs constrain the time for various time-consuming activities, such as mating or courtship activity, foraging effort, or behavioral defense (Lima and Dill 1990; Lima 1998; Angilletta et al. 2003). In many prey organisms, time for foraging is traded off against time spent with activities that reduce predation risk, such as seeking shelter, vigilance, or foraging in less rewarding but safer habitats. All of these activities reduce predation risk and have therefore been referred to as behavioral defense (Lima 1998; DeWitt et al. 1999). Resource allocation trade-offs distribute limited resources between various competing traits, such as growth, maintenance, reproduction, and storage (Herms and Mattson 1992; Perrin and Sibly 1993; Angilletta et al. 2003). In developing prey organisms, a resource allocation trade-off between growth and investment into morphological defense is of particular importance. Behavioral and morphological defenses are often plastic; that is, they are expressed only if a prey senses predation risk (Tollrian and Harvell 1992). Such predator-induced plasticity provides a possibility to assess investment into defense, because predator-exposed individuals can be compared with predator-naïve individuals, as done in many empirical studies (Benard 2004).

Both time and resource allocation trade-offs are not independent of each other. For example, the foraging activity determines the amount of resources that can be invested into morphological defense. On the other hand, the morphological defense of prey organisms determines the predation risk during the time spent on foraging activity (Clark and Harvell 1992; Taylor and Gabriel 1992; Day et al. 2002; Irie and Iwasa 2005). In this study, we use mathematical models to explore time and resource allocation trade-offs that mediate predation risk by studying optimal plastic responses in prey organisms.

Traits such as behavioral and morphological defense are selected to maximize individual fitness (Stearns 1992). The expression of each trait is expected to depend on its costs

and benefits in the current environment. Hence, optimal time and resource allocation strategies are expected to vary among environments. Harsher environmental conditions, such as those with high predator densities or food shortage, are expected to intensify the time and resource allocation trade-off; that is, it is harder to grow and defend at the same time. Low resources are expected to select for high foraging effort, because more time is needed for searching for and harvesting the scarce resources, which are predominantly allocated to essential mechanisms such as maintenance (Clark and Harvell 1992). High predator density is expected to select for better defended individuals, that is, high investment into defense and for reduced foraging effort. Benign environmental conditions (low predator densities and high resources) are expected to relax the time and resource allocation trade-off, and defending, growing, and investing in life-saving mechanisms are easier to accomplish at the same time.

Substantial empirical and theoretical interest has been given to time and resource allocation trade-offs, ranging over a variety of predator-prey systems—such as dragonflies-tadpoles, fish-damselflies, and crayfish-snails—and exploring various environmental effects (McCollum and VanBuskirk 1996; Rundle and Bronmark 2001; Stoks 2001; Altwegg 2002; Benard 2004; Cotton et al. 2004; McPeck 2004). Various theoretical models have been developed in the context of time or resource allocation trade-offs in predator-prey systems (Abrams 1984, 2003; Houston et al. 1993; Werner and Anholt 1993; Yearsley et al. 2002). However, none of the previous theoretical or empirical studies have considered the consequences of the time and resource allocation trade-offs not being independent from one another.

In this article, we develop a model that combines time and resource allocation trade-offs within an optimization framework. First, we calculate the optimal foraging activity in the absence of predation where no morphological and behavioral defense is necessary. Second, we determine the optimal morphological defense under the threat of predation for the constant foraging activity as calculated in the first step. Third, we assume that only foraging activity is optimized under predation, but no morphological defense occurs. Finally, we simultaneously optimize both behavioral and morphological defense in the presence of predation. We examine the predictions of the model for varying predator densities and resource availabilities and for a range of effectiveness of the morphological defense. This approach allows us to compare single-trait optimization with the simultaneous optimization of both morphological and behavioral defense.

By comparing the optimal strategy in the absence of predation with the optimal strategy in the presence of predation, the model allows us to assess the investment

into morphological and behavioral defense. Specifically, the difference in trait expression between the no-predator and the predator environment can be used to define investment into morphological and behavioral defense (Tollrian and Harvell 1992). Most other studies have investigated the response to predation but not the differences in investment, that is, the predator-induced plasticity, which may yield different results (Werner and Anholt 1993).

## The Model

### *Model Background*

We designed the model with growing, immature individuals in mind. We choose this approach for two reasons. First, immature individuals are normally prone to higher predation rates compared with adults and show intensified conflicting demands between growth and defense (Arendt 1997). Second, choosing immature individuals allows us to simplify the model, because we can ignore allocation toward reproduction. We use survival as our surrogate of fitness (Stearns 1992). The initial mass (or initial developmental state) could be the mass (or state) at hatching or birth. The final mass that has to be reached might be the mass at which individuals reach adulthood, overwinter, metamorphose, pupate, or enter the next instar. Once the final mass is reached, prey individuals escape from predation. For simplicity, we assume that there is no variation in final mass; that is, all individuals enter the next stage at the same constant mass. We are aware that this assumption is often not met in nature (Werner 1986). However, we believe that this assumption does not represent a severe restriction for our model. Extensions of the models with variation in mass can easily be made. A detailed discussion is given further below.

The time needed to reach this final mass might often have an impact on fitness and survival. This applies for organisms that face time constraints; that is, they have to reach the next state before the occurrence of seasonal habitat degradation, such as drought, drying of ponds, snow, or freezing, which we refer to as the end of the season. In temperate regions, most insect larvae or metamorphosing vertebrates and other organisms—where being large and early is correlated with high survival probabilities and fitness (Arendt 1997)—are affected by such seasonal degradation of habitats. For some tropical regions or where the habitat stays stable over several generations, a model without time constraints might be more realistic. We incorporate time constraints that account for a gradual increase in fitness cost related to increased time to reach the final mass. We believe that a gradual increase in fitness costs is often biologically more meaningful and reflects the gradual habitat degradation experienced by most organ-

isms more accurately than defining the drying of a pond or the end of the season as a fixed time point, which has been done in some previous studies (Rowe and Ludwig 1991). Survival probabilities toward the end of the season of developing organisms have been shown to decline increasingly (Altwegg and Reyer 2003; Stoks et al., forthcoming). Thus, specifically, if time is constrained or conditions are harsh, it might be beneficial for individuals to enter the next developmental state before the final mass is reached. In this case, the fitness disadvantage due to slow development is mediated by the lower mass of the individuals. Since in our model we use a fixed final mass, we do not account for such variation in final mass. However, in our model, the disadvantage of slower development is mediated by time rather than mass. Therefore, varying the time constraints at constant final mass has a very similar effect to varying final mass at constant time constraints.

#### *Model Implementation*

In our model objective, we maximize survival to final mass, with final mass being equivalent to final state. Survival depends on mortality independent from predation as well as on mortality due to predation. The latter is mediated by foraging activity, size, and morphological defense. In the course of growing, not only the mass but also the morphological defense accumulates, and hence the predation probability changes because mass and defense affect predation probability (McCollum and VanBuskirk 1996; Arendt 1997). In the model, the expression of the morphological defense trait depends on the amount of resources allocated toward morphological defense. We assume a continuous increase of morphological defense, because in most growing and developing organisms, morphological defenses are closely linked to growth. For example, the spines of damselflies, the thickness of a snail shell, the crest of a *Daphnia*, and the tail of a tadpole grow proportionally to the growth of the rest of the body, which is the reason why most studies use size-corrected residuals for assessing morphological defenses (Van Buskirk 2002). In the model, we assume that mortality, and hence survival, is also affected by environmental factors such as predator density and resource availability, as seen in tadpoles (Anholt and Werner 1995, 1998). These effects of environmental conditions are discussed after introducing the model in more detail.

For the model, we use three differential equations to describe mass  $g$ , allocation into morphological defense  $n$ , and the probability of survival  $p$ :

$$\frac{dg}{dt} = (1 - \delta)R_{UP}, \quad (1)$$

$$\frac{dn}{dt} = \delta R_{UP}, \quad (2)$$

$$\frac{dp}{dt} = -mp. \quad (3)$$

Equation (1) describes the growth of an organism, excluding defense traits. Equation (2) describes the dynamics of morphological defense traits. Equation (3) describes the probability of survival  $p$  of an organism experiencing mortality  $m$ . We assume that at the initial state ( $t = 0$ ), the mass is given by the initial mass  $g(t = 0) = g_0$ , the initial morphological defense is  $n(t = 0) = 0$ , and the probability of being alive is  $p(t = 0) = 1$ . The parameter  $\delta$  describes how much of the acquired resources  $R_{UP}$  are invested into morphological defense. This implies that a constant fraction of  $\delta$  of every unit of acquired resource ( $R_{UP}$ ) is converted into morphological defense, while the remaining fraction  $(1 - \delta)$  is converted into biomass for growth.

#### *Resource Uptake*

We assume that resource uptake  $R_{UP}$  depends on the mass  $g$  of an organism, its foraging activity  $\alpha$ , and the resource availability  $R$  in the environment:

$$R_{UP} = \frac{gR\alpha(1 - \alpha)}{1 + R\alpha}. \quad (4)$$

Our assumption that larger individuals ingest more food than small individuals is supported by a linear increase between body size and food ingested shown in damselflies (McPeck et al. 2001). The absolute amount of resources that can potentially be harvested increases linearly with increasing foraging activity and abundance of resources in the environment. However, the term  $1 + R\alpha$  introduces a reduction in the harvesting efficiency with increasing foraging activity and resource abundance due to morphological and physiological constraints. Without such constraints, one could not provide ad lib. food to organisms (Anholt et al. 2000). The term  $1 - \alpha$  introduces a trade-off between time spent for foraging activity and time required for other activities such as resting, processing, and digesting food and implies that the optimal activity cannot exceed 0.5. For simplicity, we do not include terms for maintenance and storage, which are also important parameters in the context of resource allocation trade-offs and would also compete for resources (Stoks et al., forthcoming). We assume that allocation in maintenance and

storage is subsumed under equation (1), allocation toward growth.

### Mortality

Mortality  $m$  is given by the following equation:

$$m = m_b + \frac{\alpha P}{g + (1 + E)n}. \quad (5)$$

Here,  $m_b$  describes a constant predation-independent background mortality. The remaining term describes mortality due to predation. The mortality due to predation is proportional to the foraging activity  $\alpha$ . For example, a high foraging activity increases the encounter rate with sit-and-wait predators, and movement attracts predators (Werner and Anholt 1993). We assume that other time-consuming activities do not increase predation risk. Therefore, allocation of time away from foraging to other activities can be seen as behavioral defense. Mortality due to predation also is proportional to the predator density  $P$ , which enfolds the number of predators in the environment and how dangerous those predators are (Anholt and Werner 1998; Teplitsky et al. 2004). The term  $g + (1 + E)n$  describes the reduction of mortality due to predation as function of mass  $g$  and defense  $n$ . We assume that the mortality decreases with mass  $g$ , because larger individuals are depredated less often, as they, for example, exceed the size limitation of their predators (Arendt 1997). Finally, predation probability decreases with morphological defense  $n$ . The efficiency of the morphological defense  $E$  describes how much more advantageous it is to invest a unit of resource into morphological defense rather than mass. Defenses are often predator specific. A morphological defense such as an increased crest or an increased spine might be effective against an actively hunting gape-limited predator such as a fish, whereas against a non-gape-limited sit-and-wait predator like a dragonfly, it might be ineffective, and another morphological defense such as camouflage or a behavioral defense such as seeking shelter might be more efficient. Such a fine-tuned repertoire of predator-specific induced response might explain—aside from resource limitations—why defenses are not always expressed at their maximum, as shown in various studies (Relyea 2004; Teplitsky et al. 2004). Along a similar line, the morphological defense  $n$  might be more efficient against a sit-and-wait predator, while growing might be the better defense strategy against a gape-limited predator, such as seen in newts, fish, or salamanders feeding on tadpoles (Van Buskirk and Schmidt 2000). Hence, we investigate the variation of efficiency in defense  $E$ .

As described above, many organisms are time constrained in reaching the final mass, for example, by sea-

sonal degradation of the environment (Stoks et al., forthcoming). Larger individuals often show increased survival probabilities over the winter or during other harsh conditions and also have higher prospects of future reproductive output (Arendt 1997; Altwegg and Reyer 2003). Slowly developing and growing individuals might also pay extra fitness costs by delaying reproduction (Arendt 1997). Thus, we include time constraints in our model. We assume that fitness  $w$  is given as

$$w = p(t = t_{\text{final}}) \frac{S^\beta}{S^\beta + t_{\text{final}}^\beta}. \quad (6)$$

The term  $p(t = t_{\text{final}})$  describes the survival until the time  $t_{\text{final}}$  when the final mass is reached. The term  $S^\beta/(S^\beta + t_{\text{final}}^\beta)$  incorporates time constraints; that is, it describes the fitness cost for delaying to reach final mass. It describes a sigmoid relationship with high fitness at the beginning of the season to low fitness after the end of the season. The parameter  $S$  describes the end of the optimal growing season, and  $\beta$  describes how abrupt the end of the optimal growing season takes effect. (For example, if  $\beta$  goes to infinity, the growing season ends at a fixed time  $t = S$ . If final mass is reached before the end of the growing season, there are no fitness costs, while if final mass is reached after the end of the growing season, fitness is 0.) In all simulations, we use moderate transition with  $\beta = 4$ . At the beginning of the growing season ( $t = 0$ ), there is little reduction in fitness with each time step  $t$ ; once an individual approaches the end of the optimal growing season  $S$ , there are high fitness costs. Note that a model without time constraints is nested within equation (6) for  $S$  being infinite.

Equations (1)–(6) allow calculation of the probability of survival from the initial state to the time when the final mass is reached and thereby allow us to calculate fitness  $w$ . We optimize foraging activity  $\alpha$  and allocation of resources into morphological defense  $\delta$  to maximize fitness  $w$ . The model is implemented in the programming language R. We use the functions “optimize” and “optim,” respectively, for the optimization of single and multiple traits (R Core Team 2005).

### Optimizing Activity in the Absence of Predation (Step 1)

In the first step, we determine the optimal activity in the absence of predation ( $\delta = 0$ ,  $\alpha$  is optimized, note  $P = 0$ ). In an environment without predation, there is only a constant background mortality. Therefore, maximizing fitness is equivalent to minimizing the developmental time to the final mass, which is equivalent to maximizing the growth rate  $(1 - \delta)R_{\text{UP}}$ . As can be expected, in the absence of predation, investment into morphological defense at

the cost of a reduced mass is not beneficial. Maximizing the resource uptake  $R_{UP}$  results in an optimal activity of  $\alpha = 1/[1 + (1 + R)^{1/2}]$ . This implies that in the absence of predation, the optimal activity depends only on the availability of resources. Our model predicts a decreasing foraging activity with increasing resource availability, because foraging can be accomplished with less effort searching for food and ingestion of food might be easier when food is abundant. This is in line with most other models and empirical studies (Anholt et al. 2000), although there are models with specific relations between the costs and benefits of activity that may predict other patterns (Norberg 1981; Speakman 1986; Dunbrack and Giguere 1987).

#### *Optimizing Activity in the Presence of Predation (Step 2)*

In the second step, we determine the optimal activity in an environment with predation, given that there is no morphological defense ( $\delta = 0$ ,  $\alpha$  is optimized, note  $P > 0$ ). In this step, predation probability is mediated only by activity and mass. Without morphological defense, the mortality formula (eq. [5]) can be simplified to  $m = m_B + \alpha P/g$ . Again, we use equations (1)–(6) to numerically calculate the fitness at the final mass and determine the optimal activity.

#### *Optimizing Morphological Defense in the Presence of Predation (Step 3)*

In the third step, we determine the optimal morphological defense in an environment with predation, assuming there is no plasticity in activity. Foraging activity  $\alpha$  is the same as determined in step 1; that is, it is fixed at  $1/[1 + (1 + R)^{1/2}]$ , and  $\delta$  is optimized and determines the morphological defense  $n$ . A pattern with only morphological defense but no behavioral defense is shown in larger snails (DeWitt et al. 1999). We use equations (1)–(6) to numerically calculate the fitness at the final mass for any investment into morphological defense. This allows calculation of the optimal investment into morphological defense.

#### *Optimizing Activity and Optimal Morphological Defense in the Presence of Predation (Step 4)*

In step 4, we assume that in contrast to steps 2 and 3, both activity and morphological defense are plastic ( $\alpha$  and  $\delta$  are optimized, note  $P > 0$ ). We thus optimize both activity and morphological defense simultaneously using equations (1)–(6).

The above four steps are explored for their response in fitness, activity, and investment into morphological and behavioral defense (measured as predator-induced plasticity) along a predation and a resource availability gra-

dient. We describe correlations of investment into behavioral and morphological defense in the context of varying predator densities and varying effectiveness of morphological defense. We compare the single-trait optimization settings (steps 2 and 3) with the integrated optimization for both defense traits (step 4). This comparison allows assessment of how phenotypic integration affects the optimal strategy for investment into behavioral and morphological defense in comparison to strategies based on only one defense trait. The investment into behavioral defense is defined as the difference in optimal foraging activities in the absence (step 1) and presence (steps 2 and 4) of predation. Thus, the investment into behavioral defense describes how much time is allocated away from foraging activity in the presence of predation. It is equivalent to predator-induced plasticity of activity and can therefore be determined in experimental systems (Van Buskirk 2000). Furthermore, if studied along an environmental gradient, this definition allows us to disentangle predator-dependent from predator-independent effects: if, along an environmental gradient, the optimal activity changes in both the absence and presence of predation, the difference describes the predation-specific effect. The optimization procedure is always done with the parameters listed in table 1.

## Results

The comparison between the single-trait optimizations (steps 2 and 3) and the integrated-trait optimization (step 4) reveals a general pattern; the single-trait optimizations always show lower fitness (fig. 1A–1C), higher behavioral defense—that is, lower activity (fig. 1D, 1E)—and higher investment into morphological defense (fig. 1F) than the integrated optimization. Fitness differences between the integrated and the single-trait optimizations are stronger at intermediate environmental conditions than at harsh (e.g., low resource, high predation) or benign (e.g., high resource, low predation) conditions (fig. 1A, 1B).

High predator densities decrease fitness (fig. 1A) and select for higher investment in behavioral defense (see fig. 1D) and more investment into morphological defense (fig. A1 in the online edition of the *American Naturalist*). Increased resource availability increases fitness (fig. 1B) and selects for lower activity (fig. 1E) in both the predator-free and predator environment. With increasing resources, investment into morphological and behavioral defense increases when resources are relatively scarce but decreases when resources become abundant. Therefore, investment into defense peaks at intermediate resource availability (figs. 1E, A1).

Increased effectiveness of morphological defense increases fitness in the integrated optimization (step 4) and

**Table 1:** Parameters used in the optimization procedure

Parameter	Parameter description	Value
$g_0$	Initial mass	1
$g(t = t_{\text{final}})$	Final mass	5
$g$	Mass while growing	Equation (1)
$n$	Morphological defense $n(t = 0) = 0$	Equation (2)
$p$	Probability of survival $p(t = 0) = 1$	Equation (3)
$t$	Time	Variable
$m$	Mortality	Equation (5)
$m_B$	Background mortality	.01
$R_{\text{UP}}$	Resource uptake	Equation (4)
$R$	Resources availability	.25–16 (fig. 1B, 1E; figs. A1, A2); 1 (fig. 1A, 1C, 1D, 1F; fig. 2)
$P$	Predator density	.125–8 (fig. 1A, 1D; figs. A1, A2); 1 (fig. 1B, 1C, 1E, 1F); .5–4 (fig. 2)
$\alpha$	Activity	Optimized
$\delta$	Investment into morphological defense	Optimized
$E$	Effectiveness of the morphological defense	2–128 (fig. 1C, 1F); 8 (fig. 1A, 1B, 1D, 1E; figs. A1, A2); 4–32 (fig. 2)
$S$	Season end (time constraints)	30 (figs. 1, 2); 15–120 (figs. A1, A2)
$w$	Fitness	Target of optimization; equation (6)

Note: The exploration of the model was limited to values where the greatest effects were observed. Figures A1 and A2 are available in the online edition of the *American Naturalist*.

morphological defense optimization (step 3; fig. 1F). Interestingly, increasing morphological defense effectiveness selects for investment into morphological defense but against investment into behavioral defense in the integrated optimization (step 4; fig. 2, moving along dashed lines). The selection against behavioral defense occurs mostly at high effectiveness of morphological defense and is an indirect effect of the increased investment into morphological defense, because the decrease in investment into behavioral defense occurs only in the integrated optimization (step 4) but not in the activity optimization (step 2; results not shown). At very high morphological defense effectiveness, investment into morphological defense decreases in the integrated optimization (step 4) and the morphological defense optimization (step 3; fig. 1F). Hence, investment into behavioral and investment into morphological defense are negatively correlated, so that investment into behavioral defense increases to compensate for when the morphological defense is less effective (fig. 2; system shifts along the dashed lines).

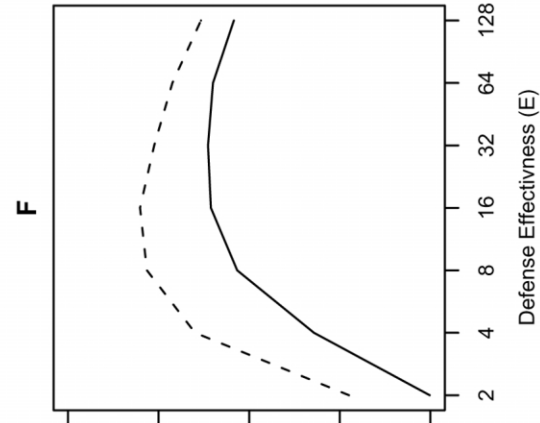
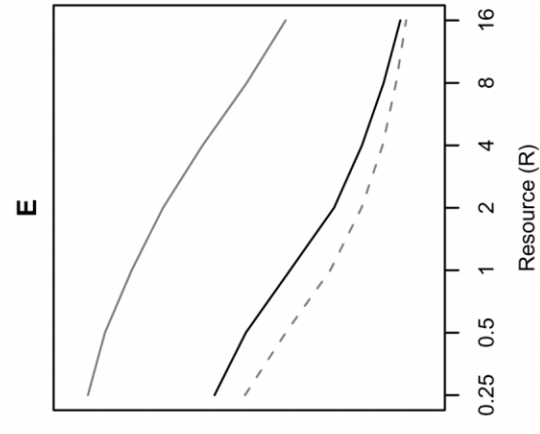
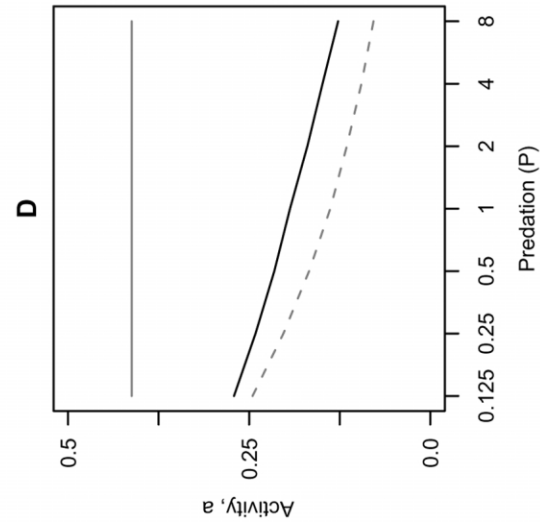
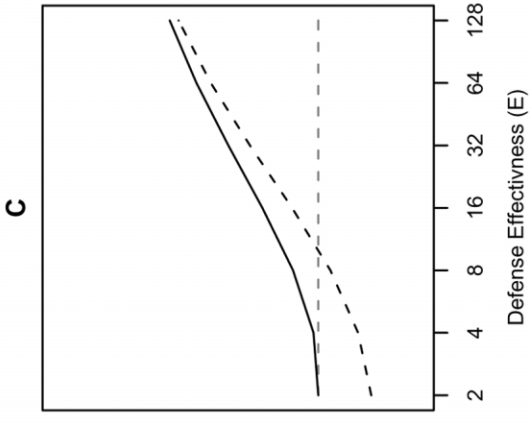
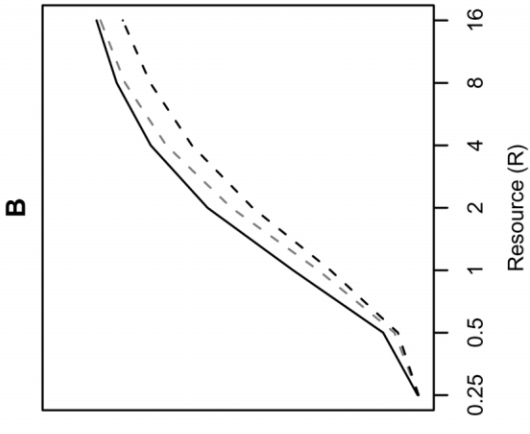
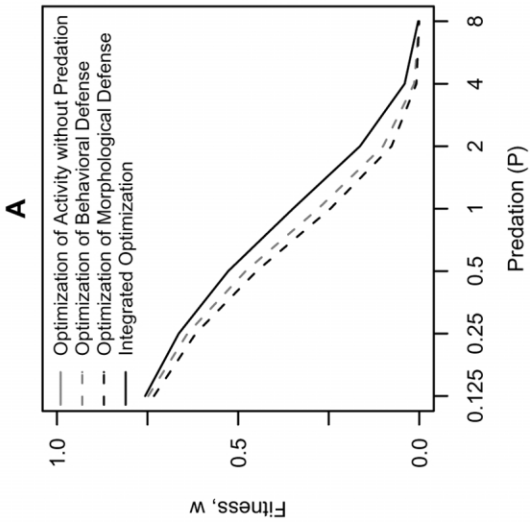
If environments or individuals differ in perceived predation, a positive correlation between investment into behavioral and morphological defense occurs, with larger investment into both kinds of defense in more risky situations (fig. 2; system moves along solid lines). Thus, morphological and behavioral defenses do not necessarily augment each other but can sometimes compensate for each other. The results are robust to various changes in environmental conditions (appendix in the online edition of the *American Naturalist*).

## Discussion

Our results support many previous model predictions derived from optimizing only a single trait. In addition, our model yields a number of results that cannot be derived using single-trait optimization. For example, behavioral and morphological defense compensate or augment each other depending on environmental conditions. Therefore, integrating both behavioral and morphological defense extends our theoretical understanding of compensation and cospecialization of multiple traits.

### *Evolution of Trait Integration*

Selection acts in favor of multiple integrated defense traits. This is demonstrated by the higher fitness in the integrated optimization (fig. 1A–1C), despite less pronounced defense responses compared with the single-trait optimization (fig. 1D–1F). It explains why we commonly see phenotypic integration and the evolution of multiple, integrated defensive traits in nature (Lima 1998). Selection for integrated traits is stronger at intermediate environmental conditions than at harsh (e.g., low resources, high predator densities) or benign conditions (e.g., ad lib. resources, low predator densities), because fitness differences between the integrated-trait and the single-trait optimizations are more pronounced at intermediate environmental conditions (fig. 1A, 1B). This shows that experiments done under ad lib. food might reveal different results than experiments done under more natural con-





ditions, because most organisms do not experience and traits do not evolve under ad lib. food in nature. Tadpoles under predation risk decrease feeding activity and therefore can promote algae growth, which might lead to increased growth rates of predator-exposed tadpoles under natural conditions, whereas predator-naive tadpoles deplete their resource and show reduced growth when resources are limited. Under ad lib. food conditions, naive tadpoles show higher growth rates (Peacor 2002).

An important finding of our model is that integrating more traits simultaneously produces less pronounced response patterns to predation and several environmental gradients than the single-trait optimization. Such a weakening of individual responses can explain why effects predicted by simple models might be hard to detect in empirical or experimental data.

#### *Response along Environmental Gradients*

Most of the changes of investment into morphological and behavioral defenses along the environmental gradients are as expected. When predation risk is high, fitness depends mainly on the defense; therefore, investment into behavioral and morphological defense is high (figs. 1D, A1). Under conditions that drive the optimal life-history strategy toward increased growth (e.g., time constraints; see below), predation has only a minor effect on fitness and on the optimal strategy. Growth rate is the main factor that has to be maximized. Hence, only a little is or can be invested in morphological and behavioral defense, and much is allocated toward growth (fig. A1).

An unexpected result emerges for the investment into morphological and behavioral defense with increasing resources (figs. 1E, A1). We expected that lower resource availability would select for growth and against investment into morphological and behavioral defense. This has been shown in some models that have not assessed investment into defense by predator-induced plasticity (Werner and Anholt 1993). However, in our model, such a pattern is expressed only over a small range of the environmental gradient, when time and resources are limited. Under most conditions, without severe time constraints or at high resource availability, investment into behavioral and morphological defense decreased with increasing resources. This leads to a peak investment into behavioral and mor-

phological defense at intermediate resource availability (fig. A1), which supports predictions of other models (Tuomi et al. 1991; Herms and Mattson 1992). Only at intermediate resource availability does high investment into defense pay off, because resources do not allow a growth rate to flee predation by reaching the final mass quickly, and individuals are exposed to predation for a long time.

Irrespective of predation, there is a decline in foraging activity with increasing resource availability (fig. 1E). This decline leads to a reduction of predation probability and adds to the reduction of predation probability due to investment in behavioral defense (predator-induced plasticity). Investment in behavioral defense peaks at intermediate resource levels. At low resource availability, the optimal foraging activity in the presence of predation declines faster than the optimal foraging activity in the absence of predation. At high resource availability, the optimal foraging activity in the absence of predation declines faster, because optimal foraging activity in the presence of predation is already very low. Several studies showed that tadpoles reduced their activity when resource availability was high (Anholt and Werner 1995; Laurila et al. 1998; Anholt et al. 2000; Babbitt 2001; Peacor 2002; LaFiandra and Babbitt 2004). None of these studies showed a peak investment into behavioral defense at intermediate resources, though there is some empirical evidence in tadpoles for such a peak investment into behavioral defense at intermediate resources (Steiner, forthcoming).

Contrasting the expectations, morphological defense declined with increasing resources when there are no severe time constraints or when resources are abundant (fig. A1). Yet such diminishing investment with increasing resources had been discussed in some plant systems (Myers and Bazely 1991). A likely explanation is that at low resources, individuals are exposed to predation for longer and therefore have to defend themselves better (if there are no time constraints). Morphological defense seems to be the most beneficial defense option under such limited resource conditions. This might indicate that, per unit of mortality reduction, morphological defenses are cheaper than behavioral defenses. When time is constrained, a peak investment into morphological defense occurs at intermediate resource levels; such a peak has been shown in *Daphnia* (Barry 1995).

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**Figure 1:** Fitness at various predator densities (A), resource availabilities (B), and defense effectiveness (C). Activity at various predator densities (D) and resource availabilities (E) and investment into morphological defense at various defense effectiveness (F). Fitness in the integrated optimization is always higher than fitness in the single-trait optimization (A–C). This indicates that it is of advantage to optimize multiple traits. The differences between single-trait and multiple-trait optimization are most pronounced at intermediate environmental conditions (A, B). Investment into behavioral defense is the difference between optimal activity without (solid gray line) and with (solid black line) predation (D, E). The investment into behavioral defense peaks at intermediate resource levels (E). The investment into morphological defense peaks at an intermediate effectiveness of defense (F).

A reason why such peak patterns have rarely been reported in empirical data, even though they might commonly exist, is that most experiments on defenses or reaction norms assessed effects only for two conditions and not along continuous gradients. Hence, these experiments were unable to detect nonlinear patterns (Angilletta et al. 2003). Another explanation why such peaks, which are predicted by our and other models, are hard to detect is that they are more pronounced at intermediate predation risk levels (fig. A1). Many experiments are conducted under high predation risk levels. Empirical data on tadpoles support this explanation for morphological but not behavioral defense (Steiner, forthcoming).

#### *Compensation and Augmenting of Behavioral and Morphological Defense*

Both mechanisms, behavioral and morphological defense, complement each other in different ways depending on environmental conditions by either compensating or augmenting each other (fig. 2). As expected, increased predation risk increases investment into both morphological and behavioral defense. In contrast, increased effectiveness of morphological defense causes increased investment into morphological defense and selects against behavioral defense (fig. 2). Though effectiveness of morphological defense is not directly linked to behavioral defense, the integrated approach we used allows an indirect effect on behavioral defense. The cost-benefit ratio of morphological defense changes positively with increasing effectiveness of the morphological defense, which affects the cost-benefit ratio in behavioral defense negatively. Increased morphological defense allows higher activity, because predation probability can be more efficiently reduced by increased morphological defense than by investing in behavioral defense. Hence, behavioral defense becomes proportionally less effective with increased effectiveness of morphological defense. At low morphological defense effectiveness, predation is mainly or only mediated by activity and not by morphological defense (figs. 1F, 2). When morphological defense becomes more effective, predation is mainly mediated by morphological defense, and activity does not mediate predation strongly (fig. 2). A decline in investment into morphological defense occurs only at very high defense effectiveness (fig. 1F). Such a decline is expected, because little has to be invested in defense to greatly reduce predation probability.

Several empirical studies have shown compensation effects of behavioral and morphological defenses, where morphologically less defended species or individuals exhibit stronger behavioral defense or vice versa (Godin and Clark 1997; DeWitt et al. 1999; Rundle and Bronmark 2001; Cotton et al. 2004; McPeck 2004; Mikolajewski and

Johansson 2004). Unfortunately, these studies do not allow a direct comparison with our model, because these studies do not explore trait integration along environmental gradients as our model does.

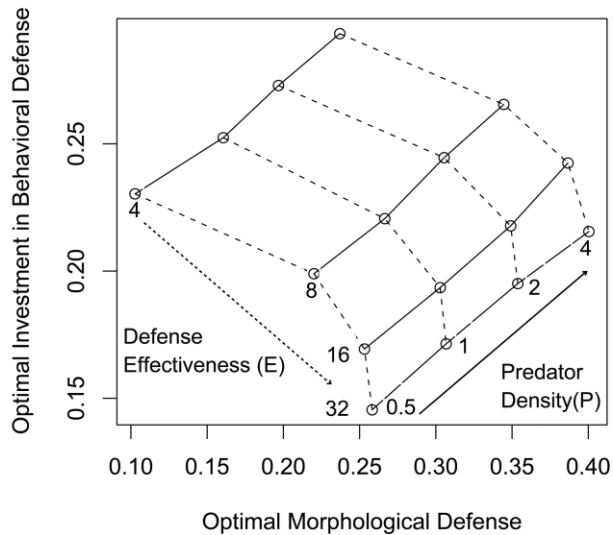
#### *Time Constraints*

Time constraints affect the strategy for mediating predation risk (fig. A1). With increasing time constraints, individuals show reduced fitness (fig. A2 in the online edition of the *American Naturalist*), selection acts more strongly on increased growth, and therefore less investment into behavioral and morphological defense is made (fig. A1). When the growing season is long, the highest investment into morphological and behavioral defense (peak) is at lower resources (fig. A1e, A1f). When time is constrained, the highest investment into morphological and behavioral defense is made at higher resources (fig. A1a, A1b). Under time constraints when resources are scarce, investment into growth is prioritized over defense, because individuals have to invest everything in growth to reach the final mass before the optimal growing season ends. They cannot afford to invest in defense without paying very high fitness costs due to delays in reaching the final mass, which supports empirical evidence in damselflies (Stoks et al., forthcoming).

The differences in the optimal defense strategy in dependence of time constraints has implications for empiricists; laboratory experiments without cues about seasoning or time constraints are expected to produce different results than experiments under more natural conditions. Differences in developmental rate, growth rate, immune defense, and predation risk between time-constrained and unconstrained individuals have been shown in damselflies and tadpoles (Johansson and Rowe 1999; Laurila et al. 2001; Stoks et al., forthcoming). Our model predictions agree with these empirical findings.

#### *Limitations of the Model*

We theoretically explore optimal solutions to simultaneously operating trade-offs. Time and resource allocation trade-offs are widespread in animals, which makes our results applicable to a variety of systems and is not limited to predator-prey systems. However, there are assumptions that limit the model. For the time allocation trade-off, we assume that the defense has to be time consuming, which means that behavioral defenses such as fleeing when under attack or fighting back an attack are likely not very time consuming, but the latter are likely resource consuming and hence have to be traded off against other resource-consuming traits such as growth or morphological defense. Comparing behavioral and morphological or time and resource allocation trade-offs might be problematic, because



**Figure 2:** Correlations among optimized investment into behavioral and morphological defense along a predator density and effectiveness of morphological defense gradient. Each open circle represents an optimal solution for the integrated optimization (step 4) under different predator densities ( $P = 0.5-4$ , system moves along solid lines) and effectiveness of morphological defense ( $E = 4-32$ , system moves along dashed lines).

the time frames might be very different. The behavioral defenses we consider here are all to avoid predator encounters and therefore are expressed not under the actual attack situation, which makes them comparative with morphological defenses (which are likely effective under a current attack, i.e., spines, but are not limited to such situations, i.e., mimicry). Morphological inducible defenses might also differ greatly in their time horizon. The predator induction of a *Daphnia* morph is determined by the environment the mother experiences when the eggs are formed, that is, at least one generation before the organism hatches, whereas morphological defenses in tadpoles (e.g., tail depth) are measurable within 2 days of exposure to predation risk, which is only a small fraction of the whole developmental time. We consider environments with a constant predation risk and not great fluctuations in predator densities over the course of development, which is likely met by many situations, because predators are mostly longer lived than the development time of their prey organisms. We also assume that the trade-offs in juveniles are largely independent from later stages, though this assumption can be relaxed in many cases, because time or final mass is often correlated with subsequent survival and reproduction.

### Implications

Our model has implications for studies on the evolution of trait integration to mediate the impact of predators on

mortality and potentially other fitness-threatening or conflicting factors. The results reveal that prey can alter their defense and efficiency of defense with increasing number of integrated traits. The cost-benefit ratio of investment into defense changes between integrated and single traits, and selection acts in favor of integrated traits. Such changes will likely have implications on the prey and predator population and also on community dynamics by affecting predator-prey interactions. Theoreticians and experimental biologists should be aware of such integrated and interacting traits when exploring environmental gradients, time constraints, and reaction norms in an optimality context. We tried to make our model as simple as possible; hence, we do not call for developing more complicated models, but we would like to alert theoreticians and empiricists to be aware that simplification might lead to alluring expectations of strong effects that will be much weaker when integrating more traits. For instance, our model and its assumptions are in line with a study that showed that faster-growing damselfly species exhibited higher activity and were more vulnerable to predation compared with species showing less growth and less activity and being less vulnerable (McPeck 2004). However, contrary to expectations, the two groups of species that differ in growth showed no difference in feeding or ingestion rates, and the fast growth of the first group was achieved by a higher conversion rate of food in body mass under predation. This shows how important it is to integrate several traits (including behavior, morphology, and physiology) and not to study only atomized traits.

In our study, we mostly referred to optimal strategies of individuals dealing with environmental variation. The individual adaptive responses in defense strategies can be extended to differences in defense strategies at the population or species level. The adaptation of the defense strategy to differences in perceived predation risk, efficiency of defense traits, resource availability, or season length might be genetically fixed or might be plastic. Fixed strategies might be more likely when we compare different species or populations in their natural habitats along environmental gradients. On the other hand, responses might be plastic, and individuals or populations might show fast adaptive responses to environmental gradients or even changes within an individual's life. The time frame of such plastic responses depends greatly on the trait, the organism one is focusing on, and the evolutionary history of the species or population experiencing different environmental conditions.

Our findings can be generalized with some cautions to several allocation trade-offs. Simplification by atomizing behavioral, physiological, or morphological traits of various time and resource allocation trade-offs should have similar problems in underestimating effects mostly at in-

intermediate environmental conditions. We believe that studies that allow the detection of nonlinear responses for more than one environment and for more than a single trait would hold great potential to improve our understanding of the evolution of complex phenotypes and life histories. Studies should be conducted under conditions that are close to natural conditions under which selection acted on traits over evolutionary time frames. We are aware that conducting such experiments will be challenging and time consuming, but we believe that the results of such experiments will reward the effort.

### Acknowledgments

Thanks to B. Anholt and J. Van Buskirk for discussions and helpful comments on the manuscript. Many thanks also to two anonymous reviewers that helped to improve the manuscript. U.K.S. was supported by a Swiss National Science Foundation (31-64991.01) grant to J. Van Buskirk. T.P. would like to thank the Society in Science for financial support.

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Associate Editor: Luc-Alain Giraldeau  
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