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CONCEPTS, REVIEWS AND SYNTHESES

Costs of predator-induced phenotypic plasticity: a graphical model for predicting the contribution of nonconsumptive and consumptive effects of predators on prey

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Abstract Defensive modifications in prey traits that reduce predation risk can also have negative effects on prey fitness. Such nonconsumptive effects (NCEs) of predators are common, often quite strong, and can even dominate the net effect of predators. We develop an intuitive graphical model to identify and explore the conditions promoting strong NCEs. The model illustrates two conditions necessary and sufficient for large NCEs: (1) trait change has a large cost, and (2) the benefit of reduced predation outweighs the costs, such as reduced growth rate. A corollary condition is that potential predation in the absence of trait change must be large. In fact, the sum total of the consumptive effects (CEs) and NCEs may be any value bounded by the magnitude of the predation rate in the absence of the trait change. The model further illustrates how, depending on the effect of increased trait change on resulting costs and benefits, any combination of strong and weak NCEs and CEs is possible. The model can also be used to examine how changes in environmental factors (e.g., refuge safety) or variation among predator–prey systems (e.g., different benefits of a prey trait change) affect NCEs. Results indicate that simple rules of thumb may not apply; factors that increase the cost of trait change or that increase the degree to which an animal changes a trait, can actually cause smaller (rather than larger) NCEs. We provide examples of how this graphical model can provide important insights for empirical studies from two natural systems. Implementation of this approach will improve our understanding of how and when NCEs are expected to dominate the total effect of predators. Further, application of the models will likely promote a better linkage between experimental and theoretical studies of NCEs, and foster synthesis across systems.

Keywords Nonlethal effect · Trait-mediated · Phenotypic plasticity · Nonconsumptive effects · Prey defensive traits

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Introduction

Many species adaptively modify their phenotype to reduce predation risk (Agrawal 2001; Tollrain and Harvell 1999). Such phenotypic responses of prey to predators are common across terrestrial, marine, and freshwater systems (Lima 1998; Tollrain and Harvell 1999; Agrawal 2001) and include shifts in prey behavior (Resetarits and Wilbur 1991), morphology (Dodson and Havel 1988), development (Peckarsky et al. 2002), growth efficiency (McPeek et al. 2001; Trussell et al. 2006a), and physiology (Creel et al. 2007). These prey responses often involve trade-offs, such as reduced growth rate (Abrams 1991a; Werner and Anholt 1993). Therefore, the direct effects of predators on prey extend beyond mortality via consumption. Such

nonconsumptive predator effects (NCEs), where predators directly affect prey fitness through induced changes in prey traits, have been documented for a variety of species and systems (Peacor and Werner 2004a; Creel et al. 2007). A better understanding of NCEs is important because NCEs may be large relative to consumptive predator effects (reviewed in Peacor and Werner 2004a; Preisser et al. 2005); associated changes in predator–prey functional responses could strongly influence population and community dynamics in the short and long term (Abrams 1984, 2010; Bolker et al. 2003; Peacor and Cressler 2012); and NCEs often initiate indirect effects (i.e. trait-mediated indirect effects; sensu Abrams et al. 1996) that can strongly influence community dynamics (Turner and Mittelbach 1990; Wootton 1993; reviewed in Werner and Peacor 2003).

Although there is increasing recognition that NCEs may influence predator and prey dynamics and have indirect effects on communities, little attention has been given to general factors that may affect the relative influence of NCEs versus consumptive effects (CEs). For example, large NCEs have been observed in an anuran system (Peacor and Werner 2001), but it is not known if intrinsic properties of the anuran species studied, their predators, or the pond environment explain why NCEs are large in this system. One notable exception is the work of Schmitz (2008) showing that the magnitude of NCEs on prey depends on the foraging mode of predators (e.g., sit-and-wait vs. active). To understand and predict the influence of NCEs, a general framework is needed to clarify the characteristics of organisms and environments that affect their magnitude. Further, because it is likely that the underlying processes involved in NCEs across systems are analogous, a framework that identifies the similarities and differences between systems will help to synthesize the role of NCEs.

Our objective is to develop a general framework (model) for understanding the conditions that will foster large NCEs and how changes in the system affect their contribution to the net effect of the predator. NCEs are inherently complex because multiple factors simultaneously influence the magnitude of the trait change itself, and how that trait change affects the fitness of the responding prey. To accomplish this goal, we develop a graphical model to help visualize how the processes underlying NCEs interact to shape their magnitude. We describe the model and examine how changes in the costs and benefits of the trait change (due to environmental changes) influence the magnitude of the optimal trait change and the ensuing NCEs and CEs. In so doing, the framework elucidates (1) conditions that foster large trait changes, (2) conditions that foster large NCEs, (3) the relationship between the magnitude of the trait change and the NCE, and (4) relationships between the magnitude of NCEs and CEs.

Materials and methods

General description of the graphical model

We graphically explore the relationship between prey fitness and the magnitude of prey defensive trait change in response to predation risk (Figs. 1, 2). Fitness is decomposed into two broadly defined components: predation rate and growth rate. Growth rate (solid curves) and predation rate (dashed curves) are plotted as a function of trait change (TC). Trait change (on the ordinate) ranges from zero to the maximum value of the trait change that is set to 1 for simplicity. An increased trait change in response to predation risk may represent an increase in the expression of a trait (or a combination of traits), such as an increase in spine length, or refuge use, or a decrease in the expression of a trait, such as reduced swimming speed or time spent foraging. For simplicity, growth rate is normalized to be one at zero trait change. Growth rate operationally encompasses any factors affecting fitness in the absence of the focal predator, including reproduction and mortality caused by disease and predators other than the focal predator. For example, in a simple single predator–single prey model without NCEs, growth rate using our nomenclature would be equal to the growth rate term in a dynamic growth model and the background mortality (if included). Predation rate, i.e. probability of death per unit time, is mortality inflicted by the focal predator.

Decomposing fitness into growth rate and predation rate enables us to explicitly examine the benefits and costs associated with trait changes exhibited in response to predation risk. First, the trait change incurs benefits that occur through a reduction in the predation rate from the predator, e.g., by reducing spatial overlap with the predator or reducing vulnerability due to morphological changes. Therefore, the predation rate curve (hereafter predation curve) declines as a function of the trait change. Second, costs of trait change occur due to inherent tradeoffs associated with trait change. We represent the composite effect of the potential costs to fitness as a negative effect on growth rate, as represented by a decreasing growth rate curve (hereafter, growth curve) as a function of the trait change. Such negative effects that have been measured empirically include a reduction in somatic growth rate due to reduced foraging rates or access to resources (reviewed in Peacor and Werner 2004a), higher susceptibility to other predators (reviewed in Werner and Peacor 2003), reduced mating success (Travers and Sih 1991), stress-induced reduction in fitness (Clinchy et al. 2004), and reduced fecundity due to suboptimal temperatures due to a microhabitat shift (Loose and Dawidowicz 1994).

The magnitudes of NCEs and CEs can be represented directly with the graphical model. The NCE at any given

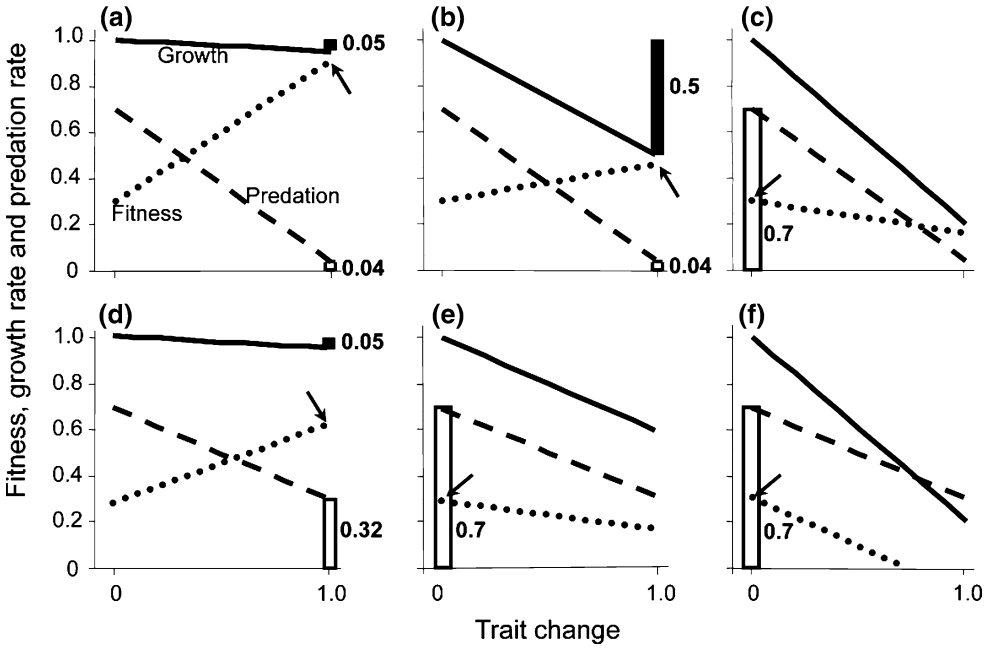
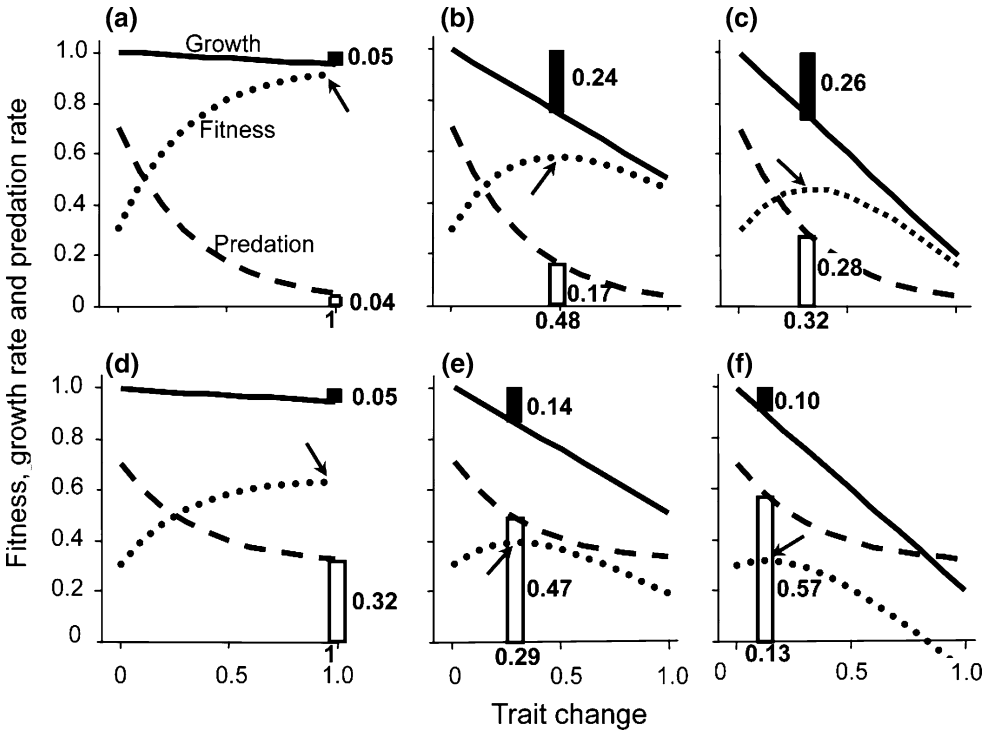


Fig. 1 Graphical framework examining a linear case: a linear decrease in growth rate and predation rate with prey defensive trait change. Growth curves, predation curves, and resultant fitness curves are represented by *solid*, *dashed*, and *dotted lines*, respectively. **a–c** The growth curve is made increasingly steeper representing a higher cost of a trait change to growth rate, whereas the predation curve is unchanged. **d–f** The predation curve is shallower over the same increasing steeper growth curves, representing less benefit of a trait change to reduced predation risk. Fitness is defined as the difference between growth rate and predation rate, with the fitness maximum corresponding to the optimal trait change (indicated by *arrows*).The optimal trait value in the linear case is either 0 (**c**, **e**, **f**) or the maximum value (set to 1; **a**, **b**, **d**). Nonconsumptive effects (NCEs) and consumptive effects (CEs) at the optimal trait change are indicated by *black* and *white bars*, respectively, with *numbers to the right of the bars* representing magnitudes (NCE = 0 if the optimal trait change is zero as in **c**, **e**, and **f**)

Fig. 2 Graphical framework examining a nonlinear case: a linear decrease in growth rate and accelerating decrease in predation rates with trait change. *Lines*, *bars*, and *arrows* as in Fig. 1. For simplicity of comparison, growth rate and predation rate at zero and maximum (TC = 1) trait change are the same as in Fig. 1, and therefore the changes from *left to right* and *top to bottom panels* are identical. **b**, **c**, **e**, **f** The predation curve is initially steeper than the growth curve leading to an increase in fitness with trait change, until an intermediate optimal trait value is reached where the predation curve becomes less steep than the growth curve with increasing trait change. The value of the optimal trait change is indicated below the CE *bar*



trait change is the difference between growth rate in predator absence where the trait change is zero (TC = 0) and growth rate at the trait value expressed in the presence of the predator; i.e. the NCE is the cost of predator presence to prey fitness through reduction in the growth rate. Thus, in the graphical model, the NCE increases with increasing trait change due to a monotonically decreasing growth curve. The CE is simply the magnitude of the predation rate at the given value of trait change. The CE is maximal with no trait change (TC = 0), and declines with increasing defensive trait change. The sum of the CE and NCE is the net negative effect of the predator on prey fitness, which is represented in each panel. Although there is no single defined metric for a "large NCE", we can observe the absolute magnitude of the NCE, which is the reduction in the original growth rate in predator absence, and the relative magnitude of the NCE, which is the proportion of the net effect of the predator constituted by the NCE. Here, we primarily present results on absolute NCEs, and will specify when we are referring to relative NCEs.

We examine two broad types of growth and predation curves, linear (Fig. 1) and nonlinear (Fig. 2). We examine linear curves for two reasons. First, the results of the linear curves yield the same qualitative results as the nonlinear, but analyses with linear curves are easier to interpret and thereby facilitate interpretation of the nonlinear results. Further, the linear curves represent many systems where organisms display on–off responses (reviewed in Kopp and Gabriel 2006), such as fish inducing the production of resting eggs in *Daphnia magna* (Ślusarczyk 1995) and mosquito larvae inducing the free-living ciliate *Lambornella clarkia* to switch to a parasitic life style (Washburn et al. 1988). We examine nonlinear scenarios because they likely represent many natural systems. We examine the nonlinear scenario using a nonlinear predation curve and a linear growth curve yielding fitness optima at intermediate trait values (Fig. 2). We emphasize that results of the nonlinear case are not specific to this particular combination of curvatures. Rather, any combination of curves in which the growth curve changes from being less to more steep than the predation curve with increasing trait change (i.e. the predation curve is more concave than the growth curve) will yield the same results. For simplicity of comparison, the value of growth and predation rates at trait value 0 and 1 are identical in all paired panels in Figs. 1 and 2 (e.g., Figs. 1a, 2a); the only difference between the two figures is therefore the curvature of the predation curve.

We use a series of different combinations of growth and predation curves that enable us to explore basic questions concerning conditions that affect the magnitude of adaptive trait changes and ensuing NCEs. An increasingly steep growth curve is used to represent a gradient of environmental conditions with increasing costs of the trait change (left to right panels in each row in Figs. 1, 2, e.g., Fig. 1a to c). Similarly, a shallower predation curve is used to represent a reduction in the benefit of the trait change through reduced predation rate (top to bottom panels in both figures, e.g., Fig. 2a to d). Note, therefore, that an equivalent trait change is least advantageous from left to right (larger cost due to reduced growth) and top to bottom (smaller reduction in predation risk).

The trait change adopted by the prey will balance the costs and benefits to fitness. In the ecological literature, the value of the "optimal" trait change that maximizes fitness has been represented and examined extensively using a variety of approaches. In general, an equation that describes the fitness or population growth rate of the focal prey species as a function of growth and predation is maximized as a function of the trait in question. Here, we maximize an equation that represents fitness as the difference between growth rate and predation rate (dotted lines in Figs. 1, 2). This optimization approach is routinely used in population dynamic studies (e.g., Abrams 1984; Ives and Dobson 1987; Křivan 2007) to maximize per capita growth rate, which is equivalent to fitness under some conditions (Abrams 1991b).

The effects of modified growth or predation curves on NCEs, as examined here, describes the potential effects of a broad range of biotic and abiotic environmental process. Varying the growth and/or predation curve could represent, for example, (1) different predator–prey pairs, (2) an increase in predator density, (3) the same predator–prey pair in different habitats (when the local environment affects the nature of the growth or predation curve), and (4) prey in different life history stages.

As an example of a trait change depicted in the figures and following analysis, consider the behavioral response of refuge use; the trait-change could represent percent time spent occupying a refuge, from 0 (TC = 0) to a finite percent (e.g., 80 %) of time in which TC = 1. The growth curve will decrease due to costs of increased refuge such as reduced access to resources and decreased growth rate due to a change in an abiotic factor such as temperature. A steeper growth curve (higher cost of trait change as represented by moving from left to right panels in Figs. 1, 2) could represent a change in the system that leads to reduced food levels in the refuge or more deleterious temperature in the refuge. The predation curve will be determined by the protection provided by use of the refuge. A shallower predation curve (as represented by moving from the upper to lower panels in Figs. 1, 2) could then represent a change in the environment (e.g., light levels) that lowers the protective value of the refuge. A shallower predation curve could also represent change in predator behavior, life-history stage, or the predator species, all of which could modify the effectiveness of the refuge.

In summary, the graphical model explicitly represents costs and benefits of a trait change. By varying growth and predation curves, we can examine how different factors that affect the costs and benefits of trait change influence the optimal trait change, and the magnitude of NCEs in predator–prey interactions.

Results

Effects of a steeper growth curve on trait change and NCEs

Fitness will increase, and thus it is adaptive to express a larger trait change, when the benefit due to reduced predation rate outweighs the costs due to reduced growth rate. In our graphical model, in which fitness is equal to the difference between predation rate and growth rate, fitness will therefore increase when the slope of the predation curve is steeper than that of the growth rate curve. Consider linear growth and predation curves as depicted in Fig. 1 in which the predation curve is unchanged, but the growth curve increases in steepness (from left to right panels) representing an increased cost of the trait change. In Fig. 1a, the predation curve is steeper than the growth curve, and it is adaptive (i.e. fitness is higher) to express the trait change. In Fig. 1b, the growth curve though steeper than in Fig. 1a, is still less steep than the predation curve, and therefore fitness increases as in Fig. 1a (but less so) with increasing trait change, and it is also adaptive to express the trait change. In contrast, in Fig. 1c, the growth curve is steeper than the predation curve, and it is therefore not adaptive to express the trait change. Note that if we imagine the steepness of the growth curve gradually increasing, the adaptive trait change "flips" from full trait change (Fig. 1a) to no trait change (Fig. 1c), as found in previous theoretical analyses examining this linear case (Abrams 1982; Werner and Anholt 1993).

Consider next the resultant NCEs over the same gradient of growth curve steepness in the linear case. The initial increase in steepness represented from Fig. 1a to b is accompanied by an increase in the NCE. This is because, even though the optimal trait change is the same (TC = 1), a steeper growth curve is associated with a higher cost of the trait change. However, an even steeper growth curve (Fig. 1c) results in a case where the trait change is no longer adaptive (TC = 0), so the NCE is also zero. A continuous increase in the growth curve steepness would therefore lead to a monotonically increasing value of the NCE until the NCE falls sharply to zero.

In the nonlinear case, the same processes govern the optimal trait change, but an intermediate trait change may be optimal. It is adaptive to express a defensive trait up to the value at which any additional change will incur a higher cost (to growth rate) than benefit (to reduced predation risk). In Fig. 2a, the growth curve is shallower than the predation curve over the entire trait change range, and therefore the full trait change (TC = 1) is optimal. In contrast, in Fig. 2b, the growth curve is initially shallower than the predation curve, and therefore fitness increases, up to a certain point, above which the growth curve is progressively steeper than the predation curve and fitness declines. There is, therefore, an intermediate optimal trait value at TC = 0.48. With an even steeper growth curve (Fig. 2c), the optimal trait change is reached at an even lower trait change magnitude (TC = 0.32).

Next, consider the effect of the increase in the growth curve steepness on the NCE in the nonlinear case. The increase in the steepness of the growth curve from Fig. 2a to b leads to an increase in the NCE (from 0.05 to 0.24) as a consequence of two opposing effects. First, the magnitude of the NCE is higher at any given trait change due to the increased costs directly associated with a steeper growth curve. Second, as described above, the increased growth curve steepness results in a lower optimal trait change, shifting the NCE to a lower value. This negative shift reduces the increase in the NCE substantially from what it would have been if the trait change remained at TC = 1. These two opposing processes can even lead to a net reduction of the magnitude of the NCE with increasing steepness in the growth curve, as exemplified by comparing Fig. 2e to f where the NCE declines from 0.14 to 0.10 as the growth curve becomes steeper. Whether the increase in the steepness of the growth curve increases or decreases, the magnitude of the NCE depends on the magnitude of the growth curve change and the relative curvatures of the growth and predation curves. The opposing two processes in the nonlinear case are the same two processes operating in the linear case that led to an increase in the steepness of the growth curve leading to an increase (Fig. 1a to b) and a decrease (Fig. 1b to c) in the NCE. In the linear case, however, the two processes do not oppose each other as in the nonlinear case, but rather operate separately at different ranges of the trait change. The linear case, therefore, provides a simpler illustration of the two processes that can operate simultaneously in the nonlinear case.

In summary of the analysis of increased steepness of the growth curve:

> An increase in the cost to growth rate of the trait change can lead to a decrease in the optimal trait change. If conditions are such that a full trait change is expressed (Fig. 1a in the linear case or Fig. 2a in nonlinear case), an increase in the cost must be large enough to exceed the steepness in the predation curve, or else the trait will

remained unchanged. Above this threshold level, the trait change will "flip" to zero in the linear case, and decrease monotonically in the nonlinear case.

An increase in the cost to growth rate of the trait change can lead to a stronger or weaker NCE of the predator. This result may seem counterintuitive because one might expect that a change in the environment that makes a trait change more costly to growth should generally lead to stronger NCEs. Our analysis reveals that two opposing processes, which are dependent on the relative curvatures of the growth and predation curve, dictate whether the magnitude of the NCE increases or decreases, both of which are possible outcomes.

Effect of a shallower predation curve on trait change and NCEs

We next examine the effect of shallower predation curves on the trait change and ensuing NCEs. We examined the effects of a change in the predation curve from the perspective of a shallower curve (reduced steepness), because a shallower predation curve is less advantageous to the prey (lowers the benefit of a trait change reducing the predation rate), and therefore is parallel with the previous analysis of increasing the steepness of the growth curve, which is also less advantageous to the prey (increases the cost of the trait change). We illustrate effects by comparing the top row of panels (a–c) to the bottom row of panels (d–f) in Figs. 1 and 2, where both panels in each column have the same growth curves but different predation curves.

In the linear case, a shallower predation curve will reduce the optimal trait change if the decrease in predation curve steepness is great enough to become less steep than the growth curve. This is not the case in comparing Fig. 1a to d, in which it is adaptive to express the full trait expression even with the decreased steepness in the predation curve. However, the trait change "flips" form TC = 1 to TC = 0 with the decrease in the steepness in the predation curve from Fig. 1b to e, both of which have steeper growth curves than those of Fig. 1a and d.

A change in the predation curve only affects the absolute value of the NCE if there is an accompanying change in the optimal trait value (e.g., Fig. 1b to e); however, the relative contribution of the NCE may change greatly even if the optimal trait value does not. For example, in the linear case, reducing the steepness of the predation curve from Fig. 1a to d does not affect the absolute magnitude of the NCE, but there is a large increase in the CE. Thus, in this case, the relative contribution of the NCE to the net effect of the predator declines appreciably.

The effect of a shallower predation curve in the nonlinear case is very similar to that of the linear case, except that, rather than the "flipping" between full and no trait change, and sharp changes in the magnitudes of NCE and CE, more subtle changes occur. For example, a decrease in the steepness of the predation curve (i.e. reduced benefit) from Fig. 2b to e leads to a decrease in the optimal trait change (from 0.48 to 0.29), a reduction in the NCE (from 0.24 to 0.14), and an increase in the CE (from 0.17 to 0.47). All these changes are analogous to those seen for the linear case from Fig. 1b to e, but less dramatic. Note that, in contrast to changes in the steepness of the growth curve that can reduce or increase the absolute magnitude of the NCE, reducing the steepness of the predation curve can only change the NCE in one direction (lower the NCE), because a shallower predation curve has no effect on the NCE (e.g., from Fig. 2a to d) or reduces the absolute magnitude of the NCE (e.g., from Fig. 2b to e, and Fig. 2c to f).

In summary of the analysis of decreased steepness of the predation curve:

A decrease in the benefit to reduced predation of the trait change can lead to a decrease in the optimal trait change. Similar to the effect of the increased growth curve steepness, if initial conditions are such that a full trait change is expressed, a decrease in the cost must be large enough to exceed the steepness in the predation curve, or the trait will remain unchanged. A reduction in the steepness of the predation curve that exceeds this threshold level will cause the trait change to "flip" to zero in the linear case, and decrease monotonically in the nonlinear case.

A decrease in the benefit of the trait change to reduced predation risk can lead to a weaker, but not stronger, NCE of the predator. In contrast to a steeper growth curve, a shallower predation curve can only affect the absolute magnitude of the NCE in one direction by causing a change in the optimal trait value to lower values, and hence weaker NCEs.

Discussion

We developed this graphical model to identify, visually explore, and clarify the multiple processes that influence the magnitude of nonconsumptive predator effects. Graphical models are frequently used in ecology (e.g., Hentschel 1999; Holt et al. 2003) to clarify complex interactions, and to make theory more accessible. For example, much of the clarity of the MacArthur and Wilson theory of island biogeography has been attributed to the graphical model component of the presentation (Brown and Lomolino 1989), which undoubtedly flashes into ecologists' minds when MacArthur and Wilson's ideas are

referenced. As with island biogeography, our model is based on theory that can be represented mathematically (e.g., Abrams 1984; Ives and Dobson 1987; Křivan 2007). Quantitative predictions require mathematical models and will be dependent on model specifics such as the optimization method used. However, the qualitative nature of the relationships (e.g., growth and predation curves) in this graphical model enabled us to make the connections to underlying mechanisms more intuitive and identify counter-intuitive outcomes.

The analysis of the graphical models clarifies two intuitive conditions that are necessary and sufficient for the absolute effect of the NCE to be large:

1. By definition, the growth curve must be steep; i.e. there must be a large cost to fitness via a reduction in growth rate caused by a trait change.
2. The predation curve must be steeper than the growth curve; i.e. benefits of the trait change due to reduced predation must outweigh costs due to reduced growth rate. This condition is necessary for a trait change, which is required for an NCE of any magnitude to occur.

The combination of a steep growth curve and a predation curve that is steeper than the growth curve leads to a corollary condition needed for large NCEs; predation must be large in the absence of the trait change (i.e. at TC = 0). Low predation in the absence of trait change sets a narrow bound on the magnitude of the reduction in growth rate that would allow for the trait change to be adaptive, thereby limiting the second condition above, and the potential magnitude of the NCE. Conversely, if predation is large in the absence of a trait change (i.e. a potentially voracious predator), then the trait change response of the prey can be adaptive even if it incurs a large decrease in growth rate (e.g., Fig. 1b) and hence leads to a large NCE. Therefore, the predation rate in the absence of the trait change (i.e. the maximum potential CE) essentially sets an upper limit on how large the NCE can be in the presence of a trait change.

This graphical model identified and clarified specific conditions that affected the absolute magnitude of the NCE. Whereas defensive trait expression, by definition, is required for NCEs, factors that influence costs and benefits that lead to an increase in trait expression do not necessarily cause an increase in the NCE; increased trait expression may be associated with either an increase (e.g., from Fig. 2f to e) or decrease (e.g., Fig. 2e to d) in the NCE magnitude. We also examined how changes in the relationships between the costs and benefits of trait expression affected the magnitude of NCEs. Factors that reduce the benefit of trait change on predation risk (shallower predation curve) will either have no effect (e.g., Fig. 2a to d) or decrease (e.g., Fig. 2b to f) the magnitude of the NCE. In contrast, a factor that increases the growth costs of a trait change (increased slope of the growth curve) can increase (e.g., Fig. 2a to b), have no effect, or decrease (e.g., Fig. 2e to f) the magnitude of NCEs, depending on the relative influence of two opposing factors; i.e. the increased cost at each trait value and a reduced cost associated with a reduction in the optimum trait change.

Intuitively, one might expect a positive correlation between the absolute magnitudes of CEs and NCEs, e.g., voracious predators that cause large CEs should also cause large NCEs. However, our analyses indicate that the magnitude of the CE and NCE are not necessarily correlated; any combination of large and small CEs and NCEs are possible. For example, we have presented plausible scenarios that illustrate trait expression that leads to a large NCE and CE (Fig. 2c), a large NCE and small CE (Fig. 1b), a small NCE and large CE (Figs. 1d, 2d, f) and a small NCE and CE (Figs. 1a, 2a). In essence, the sum total of the CE and NCE may be any value bounded by the magnitude of the predation rate in the absence of the trait change, and the manner in which this sum total is divided between the NCE and CE is dependent on the form of the growth and predation curves. In addition, the model does make one clear prediction between the magnitude of NCEs and predation risk: NCEs can be large only if the predation rate is large in the absence of a trait change (as described above). However, rather than being correlated to the NCE, predation in the absence of the trait change sets a threshold for the NCE. This is because a trait change associated with either a large (Fig. 1b) or a small (Fig. 1a) cost (i.e. reduction in growth), causing a large and small NCE, respectively, can be adaptive.

We have focused primarily on the absolute magnitude of the CE and NCE, which are proportions of the fitness in the absence of the predator. However, it may be important to describe the relative magnitudes of the CE and NCE in some contexts. For example, even if the absolute value of the NCE is small, the relative contribution of the NCE of a predator can be large or small. Consider the scenario in Fig. 2a, in which the absolute magnitude of the NCE and CE are very small, but their relative contribution is nearly equal; i.e. the NCE constitutes >50 % of the net effect of the predator. In this case, the phenotypic response of the prey to the predator has greatly reduced the net effect of the predator in such a way that both the NCE and CE contribute a high proportion to the net predator effect. In contrast, in Fig. 2d, the absolute value of the NCE is also small, but because of a larger CE, the NCE contributes more negligibly to the net effect of the predator.

This graphical model can be applied to natural systems to examine how changes in environmental factors affect predator–prey interactions within a system or between systems, or to compare different predator–prey pairs. To do

so, estimates must be made of the growth and predation rate curves as a function of the trait change. Quantifying those relationships can be difficult, and the degree of difficulty will vary across systems. Experimental studies typically measure the effect of predator-induced trait change on fitness components more amenable to measurement, such as somatic growth rate or percent survival over a discrete time period. Any negative effect on these fitness components is presumed to have a negative effect on long-term demographic parameters. For example, individual (somatic) growth rate is predicted to have a large effect on the fitness of anuran larvae in ephemeral ponds. In other systems, a well-defined relationship is well established, such as somatic growth rate in early life history stages affecting the fitness of *Daphnia* (Lampert and Trubetskova 1996). Therefore, our graphical model can be applied to experimental systems that measure short-term fitness correlates by, e.g., substituting somatic growth for growth rate in the model. This application of the model can provide a road map for studies that examine the contribution of NCEs in specific natural systems. One can then develop predictions on how different prey or environmental factors (e.g., water clarity that affects predation rates or foraging rates, or increased refuge density) will affect the relative and absolute contribution of the NCE to the net predator effect. Below, we provide examples of applications of these graphical models to examine NCEs in two aquatic systems.

First, we consider the NCEs and CEs of the invasive predatory cladoceran *Bythotrephes* on *Daphnia mendotae* in Lake Michigan (Pangle et al. 2007). The presence of *Bythotrephes* induces *Daphnia* to migrate to deeper water that serves as a refuge from predation. Low light levels in deeper water protect *Daphnia* from this visual predator but also lead to reduced fecundity at colder temperatures. We examined the costs and benefits of this defensive behavior using data from laboratory experiments. The CE is very large in the absence of migration, and migration severely reduces the CE at the cost of a very large NCE, which can account for as much as 90 % of the net effect of *Bythotrephes* during summer lake conditions (Pangle et al. 2007). This case is most closely represented by Fig. 1b, but with an even larger cost (NCE). However, if the temperature gradient is reduced (as occurs in the autumn), the cost of the behavioral response (growth curve slope) is reduced with no influence on the benefit (predation curve slope). This scenario has the same small CE, but the NCE is now small (similar to Fig. 1a). The relative influence of the NCE resulting from the same level of vertical migration is thus strongly dependent on season due to changes in the vertical temperature gradient. The graphical model approach can further be used to explore how competition, other predators, and UV radiation affect the shape of the growth and predation curves, and consequently influence the CEs and NCEs of *Bythotrephes*.

Second, we used the model to predict the optimal expression of defensive traits, as well as the relative consumptive and nonconsumptive effects of two different predators on mayflies in Rocky Mountain streams. *Baetis* mayflies accelerate their larval development in response to chemical cues from brook trout (*Salvelinus fontinalis*), and thereby reduce their risk of aquatic predation by developing faster (Peckarsky et al. 2001). Expression of this trait comes at a fitness cost of $\sim$40 % because mayflies metamorphose at smaller sizes with reduced fecundity in trout streams compared to fishless streams where stoneflies are the top predators (Peckarsky et al. 2002). Brook trout selectively consume larger-bodied *Baetis* (Allan 1978), and the effects of trait change on predation rate can be estimated from previous experiments (McPeek and Peckarsky 1998; McIntosh et al. 2002). In streams with brook trout, the highest fitness is achieved by expressing the trait (accelerated development, similar to Fig. 1b, but with slightly shallower growth and predation curves; Peckarsky et al. 2008). In fishless streams where stoneflies are the top predators, *Baetis* fitness is highest without trait change (similar to Fig. 1e, but with the entire predation curve shifted lower; Peckarsky et al. 2008). Application of the model to this example generated both intuitive and counterintuitive predictions: (1) fitness at optimal trait change is similar for *Baetis* in streams with fish or stoneflies as the top predators, which may explain why those mayflies do not avoid ovipositing in trout streams (Encalada and Peckarsky 2006), and is consistent with previous analyses of probabilities of surviving the larval stage in fish and fishless streams (Peckarsky et al. 2001); (2) relative and absolute NCEs are highest with the more voracious predator (trout), which agrees with previous models (McPeek and Peckarsky 1998); and (3) net effects on *Baetis* fitness by the weaker predator (stoneflies) are due entirely to CEs.

Our analysis examines the direct effects of NCEs and CEs on fitness as defined by the difference in instantaneous growth and predation rates. However, direct effects lead to indirect effects and feedback loops in the system, and therefore the relative influence of NCEs and CEs can change through time even in within-generation studies (Peacor and Werner 2004b). For example, a predator-induced reduction in prey foraging rate can have a direct negative effect on prey growth rate, but also indirect positive effects on prey growth rate (Peacor 2002) through reduced intra- and interspecific competition, and on resource abundance (Peacor and Werner 2004b). Spatial heterogeneity, resource characteristics (e.g., nonlinear growth), prey density, and the competitor density can all influence the magnitude of indirect effects, and thereby affect the sign and magnitude of the net NCE (Relyea

2000; Peacor and Werner 2004b; Turner 2004; Trussell et al. 2006b). In addition, predators may modify hunting strategy in response to changes in prey traits, adding to the complexity of the predator–prey interaction (Hugie 2004). Hence, dynamical models that incorporate indirect effects and feedback loops are needed to describe how the NCEs on instantaneous rates described here are expressed over longer time periods (Bolker et al. 2003; Peacor and Werner 2004b; Abrams 2010; Peacor and Cressler 2012). Further, over longer time scales with feedbacks, interactions between the NCE and CE can arise, such that the net effect of the predator is the sum of not only the NCE and CE but also of an interaction between the two (Peacor and Werner 2001).

As mentioned previously, our model is a graphical representation of previous analytical studies (Abrams 1984; Ives and Dobson 1987; Křivan 2007) of NCEs, in which fitness is expressed as the difference in growth rate. However, this is only one of many different optimization criteria used by theoreticians to describe the fitness consequences of predator–prey interactions. We performed an analogous graphical model using the μ/g approach to optimize fitness, which yielded qualitatively similar results. The well-known μ/g rule (where μ is mortality rate which is analogous to our predation rate, and g is growth rate), which identifies the trait change that maximizes fitness when μ/g is minimized (Gilliam 1982), maximizes fitness over long time scales, rather than the instantaneous measure used here. If μ/g is used to optimize fitness then changes in the ratio of μ/g must be used to represent fitness in the graphical model, rather than the difference. We emphasize that our results can be used to make qualitative predictions; whereas the optimization method most applicable to a given system and problem would need to be applied for more quantitative or specific predictions.

Despite their importance to theory, we know very little about the functional relationships between the costs and benefits associated with trait change as represented in the predation and growth curves (Bolker et al. 2003; Abrams 2010; Peacor and Cressler 2012). An exception is theoretical work by Werner and Anholt (1993), who used basic assumptions of predator and prey movement to develop growth and predation curves to predict predation rate as a function of prey speed (the trait). Theoretical studies on the effect of phenotypic responses on population dynamics have generally assumed functional relationships between growth and predation rates and trait change. In this study, we illustrate how the forms of those relationships are critical to predicting and understanding NCEs, and therefore deserve further empirical attention (Bolker et al. 2003; Peacor and Cressler 2012). We present the graphical model to help guide empirical work, and facilitate comparison across systems and the effects of perturbations within systems.

NCEs are gaining increased attention as an important component of species interactions affecting species abundances. Although details may vary, the same fundamental factors are at play in the diverse systems in which they have been demonstrated. Whereas different species traits and environmental factors will influence the functional form of the growth and predation curves that dictate the magnitude of NCEs, analogous processes determine the magnitude of trait changes and how trait changes can influence the outcome of species interactions. To build a comprehensive understanding of the influence of NCEs and the factors that affect their magnitude, it will be helpful to use common frameworks and language in their description. The graphical model presented here can be used to address this broad need. The model can be applied to a broad range of ecological comparisons, including different species pairs, species characteristics that affect growth rate such as ontogeny or conditions, density of predators, and environmental factors such as temperature and habitat complexity that can affect growth and predation rates. We encourage empiricists to measure or estimate the growth and predation curves used in this framework to provide the much-needed relationships required by ecological theory to explore general implications of NCEs, not only to prey population dynamics but also to food web properties such as stability and resilience.

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