Measuring the population-level consequences of predator-induced prey movement

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ABSTRACT

Questions: (1) What impact does adaptive movement away from areas of high predation risk have on the dynamics of a prey species and its resource? (2) What can experiments that introduce or remove predator cues tell us about the answer to question (1)?

Mathematical methods: These questions are addressed using a two-patch meta-community model in which predators and/or their cues are incorporated into a system consisting of a prey species and its resource. Predators and/or cues may be introduced to one or both patches.

Key assumptions: Prey species move adaptively to maximize their instantaneous rate of increase, but also make some random movement. Predators move randomly or do not move. Resources seldom or never move between patches. Consumer species have saturating functional responses.

Conclusions: (1) Adaptive movement can stabilize or destabilize the dynamics of the tri-trophic system. (2) Monitoring densities in a single patch may give a misleading indication of the global change in densities. (3) Adaptive prey movement in response to predator cues may increase or decrease prey density. (4) Predator introduction may cause an increase or decrease in the size of the prey population. (5) Short-term experiments with local measurements may greatly overestimate the impact of predators on prey and the behavioural component of that impact. (6) The dynamics and interspecific effects in a system with predators and adaptive avoidance by prey cannot in general be deduced from separate experiments with cues alone and with predators in the absence of the cues. (7) Conclusions from recent empirical studies should be reassessed in light of these results.

Keywords: functional response, habitat selection, meta-community, non-consumptive effect, predator–prey interaction, trait-mediated indirect interaction, tri-trophic system.

INTRODUCTION

Beginning close to a quarter of a century ago (Abrams 1984), a series of theoretical papers has suggested that anti-predator behaviour could greatly alter interactions in predator–prey

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systems and in food webs. Recent years have seen the publication of numerous studies designed to measure the consequences for food chain dynamics of anti-predator behaviours by prey (e.g. Schmitz, 1998; Peacor and Werner 2001; for reviews, see Werner and Peacor, 2003; Preisser et al., 2005). However, most theory and some experiments have treated these behavioural effects within a homogeneous system. This article focuses on the case in which the anti-predator behaviour consists of moving away from areas with higher predation risk, a scenario that assumes some spatial structure. The mathematical models presented here show that many potential consequences of such predator avoidance movements are not adequately represented in models of homogeneous systems. In addition, the most commonly used experimental designs for measuring behavioural effects often give misleading results when applied to prey that exhibit adaptive movement away from risk.

The most common method for experimental measurement of the consequences of anti-predator behaviours has been to induce these behaviours in the absence of predators. This method has several general problems (Abrams, 2007b, in press), but it is particularly poorly suited to measuring the population-level consequences of predator-induced movement by prey. Movement away from locations with abundant predators is one of the main methods used by prey to reduce predation risk; such movement was the behavioural variable in 39% of the studies included in Preisser and colleagues' (2005) meta-analysis of demographic consequences of prey defences.

Movement generally has different impacts in an experimental setting, depending on whether the prey are able to leave the area where predators (and/or predator cues) are introduced. In Preisser and colleagues' (2005) meta-analysis, movement was only considered in cases where prey could leave the area in which predator or predator cues were present. In their analysis – and many of the studies it was based upon – movement out of the habitat was assumed to be equivalent to prey mortality in measuring impacts of the anti-predator behaviour on both the prey and resource populations. However, there are several reasons why prey might return to a patch that they had originally left because of high predation risk. Resources might eventually be depleted in the locations to which the prey relocated, and predators might arrive there as well. Resource densities in the location that was initially abandoned are likely to increase over time, making it more attractive even if the predators or their cues persist. Local manipulation of real or perceived predator risk, followed by short-term monitoring of local prey or resource population density, may thus provide a misleading measure of the longer-term, larger-scale consequences of the spatial avoidance of the predator by the prey. This is relevant because studies in which emigration was the anti-predator behaviour yielded the largest average ratio of impacts due to prey behaviour relative to impacts due to consumption by predators of the three behavioural categories considered by Preisser et al. (2005). It is important to determine whether these impacts may have been overestimated due to the limited spatial and/or temporal scale of observations.

Another possible problem arises in interpreting the results of experiments with predator cues applied in a confined area that is large enough for anti-predator movement behaviour to occur within that area. Here predators may change prey movements within the experimental arena in a manner that affects the mean fitness and/or density of prey. For example, Peacor and Werner (2001) observed that small bullfrog tadpoles (*Rana catesbeiana*) restricted the location of their foraging as well as reducing activity level in the presence of caged predators (*Anax junius* dragonfly larvae). When prey aggregate in response to predation risk, the resulting area of high prey density suffers resource depletion. This could eventually

result in the prey aggregation relocating to a part of the experimental arena with more resources, in spite of equal or greater predation risk. In this case again, a short-term response, or one that did not quantify resource density over the entire experimental arena, might produce a misleading measure of the impact of predators on the lower trophic levels.

Movement (dispersal) differs in other ways from non-movement based anti-predator behaviours, such as reduced activity levels, or from non-behavioural forms of phenotypic plasticity, such as induced morphological defences. These other forms of defence usually entail some cost in terms of energy expenditure or reduced reproduction. Although movement may have costs, these need not be present, and movement may also have both short- and long-term benefits. Furthermore, adaptive movement is likely to occur for reasons other than predation risk (e.g. local resource depletion), so that it is not always evident from relatively short-term experiments whether the frequency of movement on a longer time-scale is increased or decreased when predators are added to a system. All of these consider-ations imply that treating movement out of a local area as a measure of the demographic response of prey to predators may greatly exaggerate the actual demographic effect on the population.

The present article will use a model of adaptive movement in a two-patch environment to examine some of the potential consequences of predator avoidance movements for prey population dynamics, and for the dynamics of the prey's resources. In the model, the prey species moves in response to relative food intake rates and mortality risks, so as to increase instantaneous individual fitness. Several aspects of predator impacts on prey and resource populations are addressed. First, the short- and long-term impacts are compared. Second, local and global impacts are compared. Three hypothetical treatments applied to a consumer–resource system that has reached its long-term dynamics are mimicked by the model: (1) adding predators to a consumer–resource system; (2) adding predator cues in the absence of functional predators; and (3) adding functional predators but removing any cues indicating predation risk. The comparison of treatment (1) with the initial consumer–resource dynamics measures the combined impact of predation and the prey's anti-predator movement. Comparing treatment (2) with a control that lacks predators is the usual method for determining the cost of the prey's defence, or the 'non-consumptive effect' of predator on prey (Abrams, 2007b). The difference in resource densities between treatment (2) and the control is usually considered to be the trait-mediated indirect impact of predators on resources. Treatment (1) gives the total (behavioural and consumptive) effect of predators, and treatment (3) provides a measure of the predator's consumptive effect on the prey in the absence of a defensive response. The difference between (3) and (1) is an alternative measure of the extent to which behaviour alters the predator–prey interaction (e.g. Griffin and Thaler, 2006). If the impacts of prey behaviour and consumption were additive, either of these alternatives should yield the same relative impact of behavioural and consumptive effects. However, there are theoretical reasons for not expecting additivity (Okuyama and Bolker, 2007, Abrams, in press), and it has in general not been observed (Peacor and Werner, 2001; Preisser et al., 2005). Nonetheless, additivity was assumed in many of the studies reviewed by Preisser and colleagues (2005).

The traditional assumption (Abrams, 1995; Werner and Peacor, 2003) is that there will be a cost of defence, but that it will be smaller than the mortality due to consumption in the absence of defence. Treatment (2) has frequently been employed to measure this cost (Werner and Peacor, 2003; Bolnick and Preisser, 2005; Preisser et al., 2005). Treatment (3) has been used very rarely because of the difficulty of removing cues or disabling the prey's response without affecting other

aspects of the interaction. This third treatment has been approximated by experimental removal of prey (e.g. Peacor and Werner, 2001; Griffin and Thaler, 2006; Trussell *et al.*, 2006). Another option for implementing treatment (3) is to study similar prey that lack the ability to respond to the cues [as in the comparison of different clones of *Daphnia* by Boeing *et al.* (2005)].

The difference between the impacts of predators in the presence and absence of cues is particularly relevant in an applied context because there are many anthropogenic changes that are capable of reducing the ability of prey to detect or respond to predators (Relyea, 2003). It is desirable to know when this loss of behaviour will have a significant negative effect on prey population size.

MODEL AND ANALYSIS

The population dynamics model

The meta-community model used here was introduced by, and is discussed in more detail in, Abrams (2007a). Although it has just two patches and three trophic levels, the model has too many parameters to explore the entire range of its potential dynamics. The present analysis does not attempt to do so. Rather, specific parameter values are used to illustrate some of the outcomes that can arise when quantifying the population dynamical consequences of adaptive anti-predator movement by the prey.

The system includes a predator species with fixed population sizes P_i in patch i and a prey and resource with respective population sizes N_i and R_i in patch i. The constancy of the predator population is designed to reflect the set-up of most previous experiments used to examine the impact of anti-predator behaviour on population dynamics (see Bolnick and Preisser, 2005; Preisser *et al.*, 2005). When predators are present in each patch, the predator densities are assumed to be equal. This could result if the predator individuals were introduced uniformly across space and do not move between patches, or if predators move randomly between patches. The predator and the prey both have Holling disk equation (Holling, 1959) functional responses, characterized by handling times (H for the prey and T for the predator), and attack rates that may be habitat specific (C_i for the prey's response to resource in patch i, and S_i for the predator's response to prey in patch i). The prey experiences a per capita (non-predatory) death rate D_i in patch i; prey also have a patch-independent efficiency of converting resources to new prey individuals, given by B. The resource is assumed to have logistic growth in each patch with growth parameters K_i and r_i in patch i. Resource individuals may move between patches with a constant but very low per capita rate, m_R. Following Abrams (2000, 2007a), the prey is assumed to move from patch i to patch j with a per capita rate $m_N \exp[\lambda(W_j - W_i)]$, where W_i denotes the instantaneous per capita growth rate of the prey in patch i. [Similar models of movement are used in Ives (1992), Persson and de Roos (2003), and Abrams *et al.* (2007).] The constant λ reflects the prey's ability to measure and respond to the between-patch difference in fitness, and the constant m_N is the 'background' per capita movement probability when both patches confer equal fitness. This function implies that movement is generally adaptive, but movement to the poorer patch always occurs at a low rate. The dynamics of resource and prey in patch i are:

$$\frac{dR_i}{dt} = r_i R_i \left(1 - \frac{R_i}{K_i}\right) - N_i \frac{C_i R_i}{1 + C_i H R_i} - m_R R_i + m_R R_j \tag{1a}$$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \left(\frac{BC_iR_i}{1 + C_iHR_i} - D_i - \frac{S_iP_i}{1 + S_iTN_i} \right)$$

$$- m_N N_i \exp\left(\lambda \left[\frac{BC_jR_j}{1 + C_jHR_j} - D_j - \frac{S_jP_j}{1 + S_jTN_j} - \frac{BC_iR_i}{1 + C_iHR_i} + D_i + \frac{S_iP_i}{1 + S_iTN_i} \right] \right) \quad \text{(1b)}$$

$$+ m_N N_j \exp\left(\lambda \left[-\frac{BC_jR_j}{1 + C_jHR_j} + D_j + \frac{S_jP_j}{1 + S_jTN_j} + \frac{BC_iR_i}{1 + C_iHR_i} - D_i - \frac{S_iP_i}{1 + S_iTN_i} \right] \right)$$

where $i, j = 1, 2$. Numerical integration of this model was carried out using Mathematica 6.0 (Wolfram, 2007).

The most significant feature of the dynamics is the occurrence (for a wide range of parameter values) of cycles in the prey's location (Abrams, 2007a). These cycles are driven by the advantage of being in the habitat with a greater prey density when the predator has a saturating functional response [$T > 0$ in equations (1)]. The resulting aggregation of prey in one patch is often unstable because resources in that patch are eventually depleted, while resources in the other patch recover, eventually favouring a return to that patch. Cycles require a sufficiently large predator population, a moderate predator handling time (T), and a sufficiently high sensitivity (λ) of the prey to fitness differences between patches (Abrams, 2007a). Cycles occur in multi-patch as well as two-patch models (Abrams, 2007a), and were observed much earlier in a related model by Schwinning and Rosenzweig (1990).

The structure of the analysis

The two basic examples differ in whether predators are introduced into one or both patches. The first example (example 1: predators in both patches) is designed to examine the impact of movement within a closed experimental arena. The second (example 2: predators in one patch) is designed to compare local and global impacts of a local predator introduction in a system that allows prey movements into and out of the experimental arena. Within each example I compare two cases that differ in the level of random movement (the parameter m), which is known to have an important effect on system dynamics (Abrams, 2007a).

For each example and movement rate (local or global predator addition; high or low random movement), three potential experimental treatments involving predators and/or predator cues are considered; these are compared with a control that has no predators. As noted above, the three treatments are: (1) predators and (perceived) predator cues; (2) predator cues in the absence of real predators; and (3) predators in the absence of cues to their presence. The comparison of (1) and (2) or (1) and (3) are different methods of determining an effect of the prey's defensive behaviour.

Equations (1) with both P_i set to zero represents the no-predator control. Effects of the predator are measured relative to the prey and resource densities that would occur in this case. The 'predator cue' treatment (treatment B) is equations (1) after removing the predator-loss term ($- S_iP_i/(1 + S_iTN_i)$ within the first set of parentheses in the expression for $\mathrm{d}N_i/\mathrm{d}t$). Anti-predator behaviour can be eliminated (treatment C) by dropping terms containing P_i from the exponential movement functions, but retaining the predation terms in the demographic components of the prey equations. It should be noted that a non-zero predator handling time and an ability of prey to measure predation risk rather than simply predator density are both required for predator cues to have any effect on dynamics when equal amounts of the cues are introduced into two equivalent patches.

Numerical results

Example 1: Predators introduced into both patches and responses measured in both patches

Case 1: High prey movement rate, m_N ("standard" parameter values given in legend to Fig. 1). The parameters used here represent a system in which: (1) prey are relatively efficient exploiters of their resource and have a stable equilibrium with those resources in the absence of predation; (2) predators have significant effects on the prey, and their addition destabilizes the system; (3) prey have a high ability to discriminate between fitness in the two patches; and (4) prey have a high background movement rate ($m_N = 1.0$). Figure 1 shows the time course of the change in resource density (panel A) and prey density (panel B) in each patch following addition of equal numbers of predators to both patches at time zero,
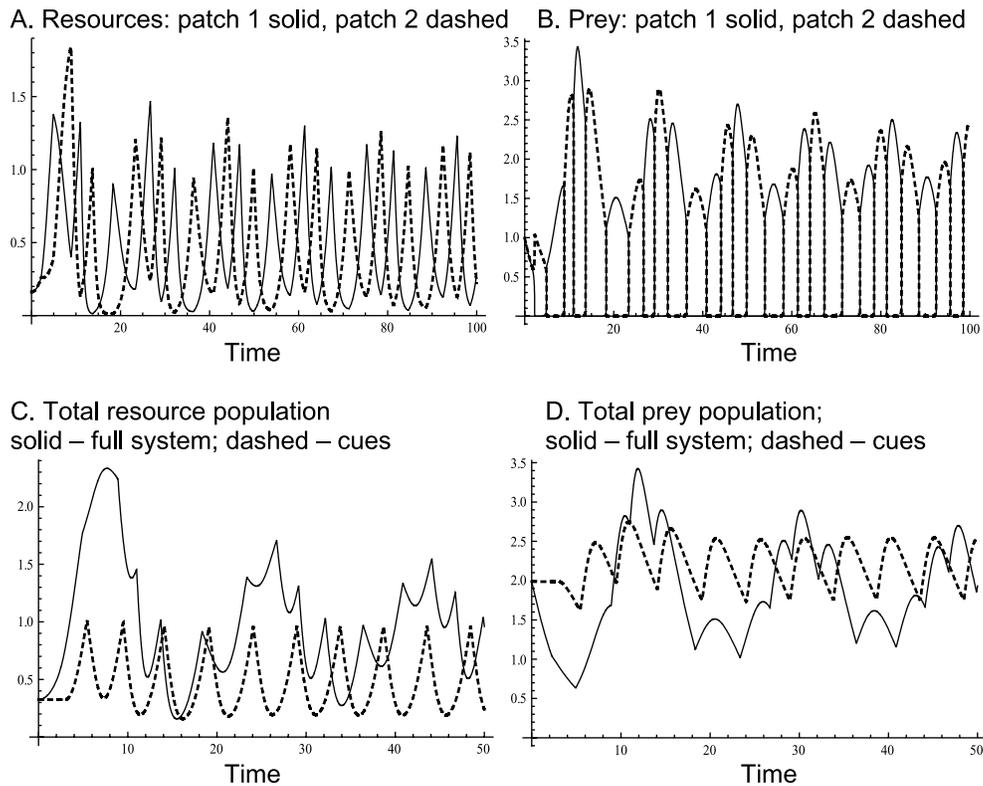

Fig. 1. Prey and resource densities in Example 1, Case 1 of equations (1). Panels (A) and (B) give resource and prey populations in each patch separately for the first 100 time units of the simulation. Panels (C) and (D) give the total resource density and total prey density for the first 50 time units of two treatments; the predators-plus-cue treatment is given by the solid line, and the cue treatment is given by the dashed line. The initial densities in all cases are the equilibrium densities in the absence of predation. The parameter values are: $r_1 = r_2 = 1$; $K_1 = K_2 = 2$; $m_R = 0.01$; $m_N = 1$; $C_1 = C_2 = S_1 = S_2 = 1$; $H = 0.5$; $T = 3$; $D_1 = D_2 = 0.15$; $P_1 = P_2 = 1$; $B = 1$; $\lambda = 10$. These parameters (and those in Fig. 2) imply a generation time for the prey of 6.67 time units (defined as 50% turnover of individuals at equilibrium).

starting with the system close to its consumer–resource equilibrium. The corresponding total densities in both patches are shown by the solid lines in panels C and D. The dashed lines in panels C and D give the time course of total resource and prey populations in a corresponding system in which predator cues are introduced at time zero, but predators are absent. Because the initial densities in panels C and D represent the stable equilibrium in the absence of predation, the differences between the dashed lines and these initial densities represent the non-consumptive effect of predators on prey (panel D) and the trait-mediated indirect impact of predators on resource (panel C). Similarly, the solid lines, which represent the treatment with predators and cues, give the combined impact of consumptive and behavioural effects on both prey and resource.

Experiments that examine the impacts of predator or cues usually do not obtain a time course of population densities, and only quantify effects at a particular termination time. This termination time is usually less than a single prey generation (Preisser et al., 2005), and almost always well before the tens or hundreds of generations that may be required to reach the final dynamics. The lines for the cue effects in panels C and D show that anti-predator movement alone could be seen as having positive or negative effects on the prey and on the resource, depending on when an experiment was terminated. If the experiment illustrated in Fig. 1 were terminated and densities measured at approximately time 28 (panel D), one would conclude that predators benefit prey that have defences, while predator cues alone harm prey.

The third treatment gives the effect of predators in the absence of cues (so there is no behavioural response by the prey). For this system, such a treatment leads to large amplitude prey–resource cycles that are synchronized across patches. Figure 2 illustrates the resulting population dynamics. It is again clear that different termination times will produce different conclusions about the sign of the effect of the predator on both the prey and the resource. Nevertheless, the figure shows that the long-term impact of predators is a significant decrease in the mean prey density and a very large increase in the mean resource density. At the same time, predators also cause much greater temporal variation in densities in both prey and resource than in the system with prey defence (solid line in Figs. 1C, D). The difference between the solid line in Figs. 1C, D and the corresponding lines in Figs. 2A, B can be attributed to the presence of the prey defence in the former but not the latter. This difference is not plotted, but it is clearly different from the dashed lines in Figs. 1C, D, which plot the impact of the defensive behaviour in the absence of predators.

Table 1 summarizes the effects on long-term densities of all three treatments for the system illustrated in Figs. 1 and 2 (predators in both patches; high baseline movement rate). The first two columns of Table 1 give the change in the long-term average densities for the cue-plus-predator and cue treatments after the populations have attained their final

Table 1. Impacts of predator and predator cues on mean prey and resource densities: Example 1, Case 1 (figures give proportional changes in density from the no-predator control; i.e. change divided by initial density)

	Predator and cues	Cues only	Predators without cues
Prey density, N	−0.048	+0.114	−0.3344
Resource density, R	+1.605	+0.4105	+4.959

A. Total resource density relative to control
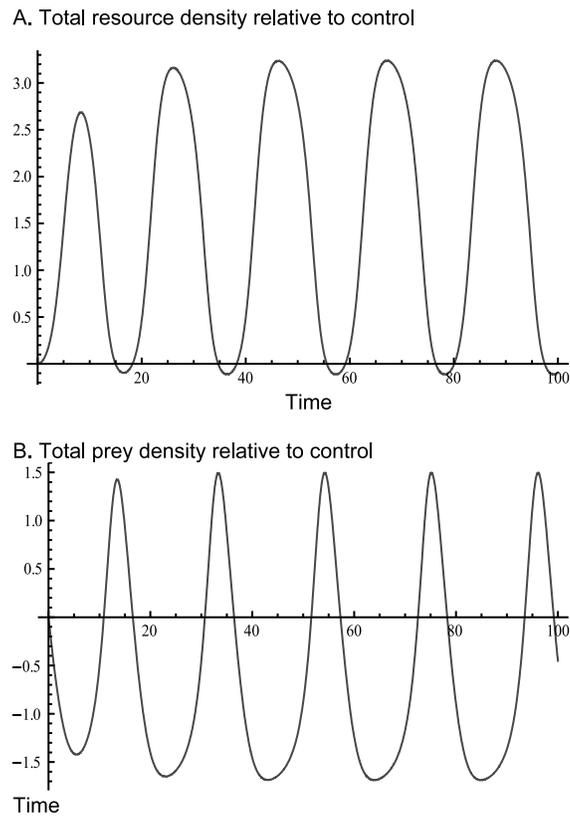

B. Total prey density relative to control

Fig. 2. The dynamics of the system assumed in Fig. 1 under a different treatment (treatment 3) in which predators are present but prey are unable to detect them. The initial densities are the equilibrium densities in the absence of the predator, and the lines describe the summed density over the two patches. Here, unlike Fig. 1, the lines describe the difference between the treatment and control (no-predator) treatments, rather than the absolute densities.

dynamics. When measured over a long period after reaching their final dynamics in the cue-treatments, the mean prey density is 11.5% above the control (predator-free) density, and the mean resource density is 40.2% larger than the control. The relatively small effect on mean prey abundance masks the large impact of behaviour on spatial and temporal variation in population sizes, both of which are driven by the adaptive movement of the prey. Surprisingly, the presence of predators and cues only reduces the mean prey population to 4.8% below its equilibrium in the absence of the predator. This is in large measure because of the 160.5% increase in the long-term mean resource density that occurs in the predator-plus-cue treatment. Finally, predators without cues produce a much larger (−33.4%) decline in the prey and a much larger (+ 495.9%) increase in the resource population than in the system with prey defences. It is clear that no simple additive or multiplicative combination of consumptive (treatment 3) and non-consumptive (treatment 2) effects yields the changes in densities observed with both prey defensive movement and predatory consumption (treatment 1).

Case 2: Low movement rate. This modifies case 1 by a single change – the background movement rate m_N is 0.005 rather than 1.0. In the presence of both predators and perceived cues, the system has anti-phase cycles in which the two patches have identical cycles in density that are 180° out of phase; this pattern is similar to that shown in Figs. 1A,B, but the detailed form of the population trajectories differs considerably. The lower movement rate in this example can also lead to lengthy transient dynamics in which the two patches are synchronized, so it takes much longer for the eventual anti-synchronized dynamics to develop than in case 1. The resulting temporal changes in total prey and resource densities are shown by the solid lines in Fig. 3, where total densities are again displayed relative to the equilibrium with no predators. The mean total resource and prey densities are 1.6556 and 1.5275 respectively. The second treatment has predator cues but no predators, which is represented by the dashed lines in Fig. 3. Because of the lack of actual predation, these
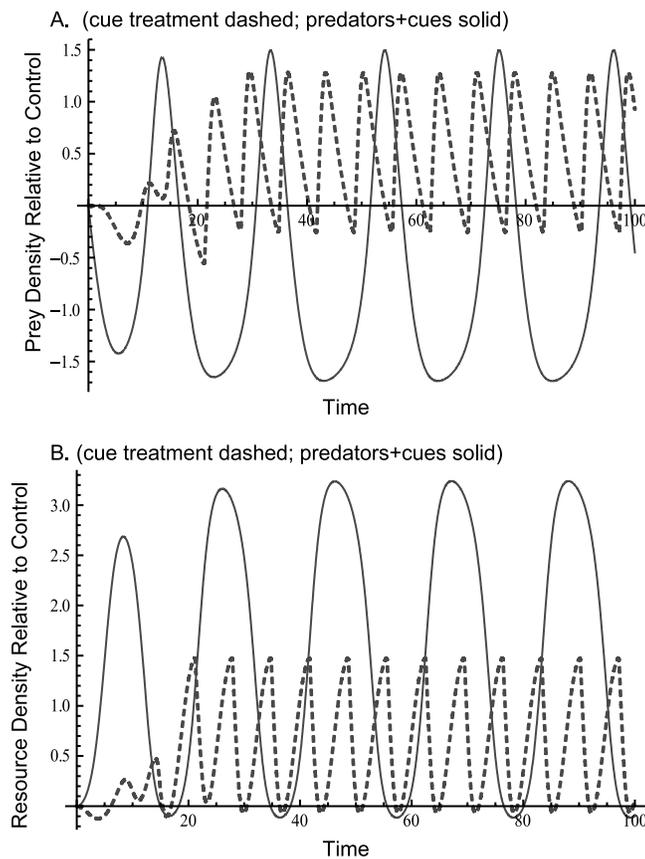

Fig. 3. The temporal change in total prey (A) and resource (B) populations in the system given by Example 1, Case 2 for treatments (1) and (2). Lines give population density minus the equilibrium density in the no-predator control. This system is identical to that in Fig. 1 except that the background prey movement rate is $m = 0.005$. The solid line represents a treatment with predators and cues (treatment 1), while the dashed line is a case with cues only (treatment 2). There is an alternative attractor in the cue treatment, where population densities do not change relative to the no-predator control. This is given by the x-axis in each figure.

cycles differ from those with functional predators, having a relatively higher prey density and relatively lower resource density. The temporal mean total resource density over the course of the cycle is 0.9702 and the temporal mean total prey density is 2.4966. Both of these represent significant increases relative to the system without cues.

If the predator is present, but there are no cues, two alternative attractors exist, each consisting of synchronized cycles in both patches, but the mean prey density is higher and mean resource density is lower in one patch than the other. The prey dynamics in each patch are shown in Fig. 4A, while the resource dynamics are shown in Fig. 4B. The alternative attractor simply has the identity of the patches reversed. The temporal mean of the total density is 1.4214 for the resource and 1.6328 for the prey. Comparing these with the results for predators plus cues shows that the presence of adaptive anti-predator behaviour produces a decrease in the prey density and an increase in the resource density compared with a system in which predators cannot be detected. Paradoxically, predator cues have a large beneficial effect on prey density when the predator is absent, while it has a moderate detrimental effect on prey density when the predator is present.
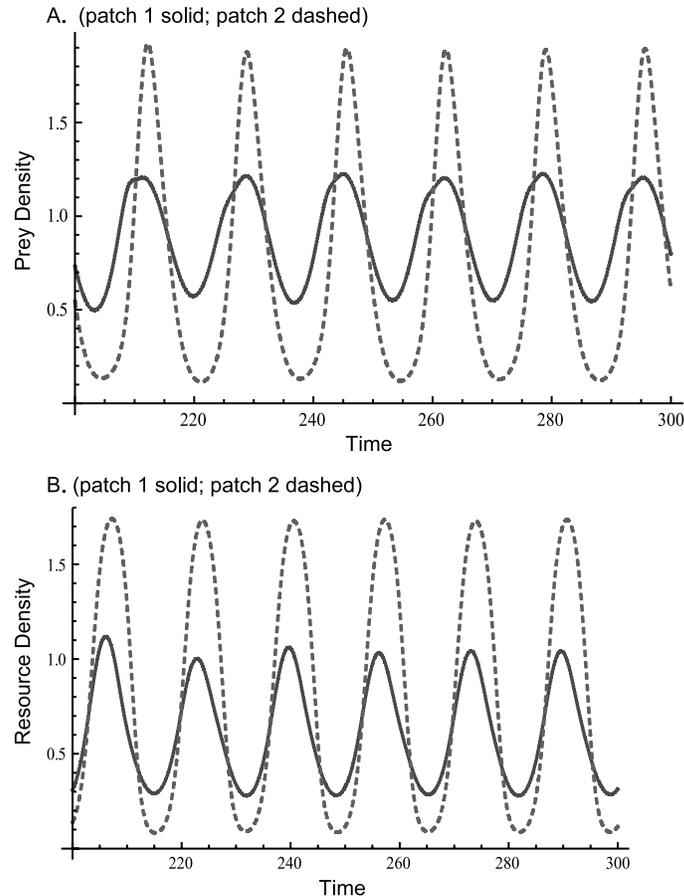

Fig. 4. The temporal changes in prey (A) and resource (B) populations in each patch for treatment (3) (predators but no cues) in the system in Example 1, Case 2. There is an alternative attractor that has identical dynamics with the patch identities of the two populations reversed.

A further reduction in the background movement rate (to $m_N = 0.001$; results not shown) again changes the impact of adaptive prey movement. In the absence of predators, the system has apparently chaotic dynamics, involving large amplitude fluctuations of all prey and resource populations, with each patch having a mean prey density of approximately 0.715 and an approximate mean resource density of 0.865. This is an example of the complex dynamics produced by weak coupling in a two-patch predator–prey system [shown for a similar system with random movement by Jansen (2001)]. Adding predators when there is an adaptive prey response leads to alternative attractors in each of which there is a simple limit cycle with a relatively small amplitude, but prey are virtually absent from one of the two patches. The identity of the 'empty' patch differs between attractors. The average prey density in one patch increases (relative to the no-predator state), while mean prey density in the other patch and total prey density both decrease relative to the no-predator state. Resource density decreases in one patch while increasing in the other patch, and total resource density increases.

Other parameters can produce a range of behavioural effects. If patches are equivalent and the dynamics of the entire system are stable with and without predator cues, then there is no effect of the cues on movement. The interesting interspecific effects in the examples explored here are associated with non-stationary dynamics. Such dynamics occur for a wide range of parameters. Prey aggregation to dilute risk can produce behavioural cycles, and these can interact with population dynamical cycles driven either by the prey's or by the predator's saturating functional response. In Case 1 considered above, values of $\lambda > 2.6$ result in dynamics similar to those shown in Figs. 1 and 2, while values < 2.5 yield perfectly synchronized cycles, in which conditions are equivalent in the two patches, and the ability to detect predator cues has no impact on dynamics.

Some of the important conclusions from these cases involving movement within an experimental area are as follows: (1) by affecting stability, predator avoidance movements can have very large impacts on dynamics and mean densities, in spite of the lack of a direct cost of movement; (2) in some cases, the process of avoiding predators can result in an increase in the prey population in the presence of the predator; (3) the consumptive and non-consumptive effects of predators on population sizes do not combine in any simple additive or multiplicative manner to determine the impact of the predator in the presence of adaptive prey movement; and (4) the presence of cycles means that experiments in which populations are measured at one or a few instants in time are likely to be misleading for long-term impacts.

Example 2: Predators introduced into and constrained to stay in one patch

An alternative scenario that more closely matches most previous experiments assumes that predators and/or cues are introduced into only one of the two patches. Here one might monitor prey and/or resource densities either in patch 1 alone or in both patches; most experiments have only monitored the manipulated patch (reviewed by Preisser *et al.*, 2005). The impact of predator addition to patch 1 under equations (1) may be quantified either by the change in prey and resource densities in patch 1 or by the change in the total densities in the system as a whole. It is again possible to use many different time scales to make this measurement. The effect of the prey's behaviour may be separated from the total effect using a treatment with cues in the absence of predators or using a treatment in which cues are absent, but predators are present. I will only discuss the first of these experimental designs, because it is by far the most commonly used in experiments conducted to date. For

comparison with the previous example, I examine two cases having the same parameters as in Cases 1 and 2 under Example 1. Predator numbers in patch 1 are assumed to be identical to those in the previous example, but predators are absent from patch 2. Thus, the total number of predators is one-half of what it was in Example 1. The two cases considered under this example again differ in the baseline movement rate m. Recall that, regardless of m, this system has a stable prey–resource equilibrium with equal densities in the two patches ($R_i = 0.16216$ and $N_i = 0.99343$).

Case 1: High background movement ($m_N = 1.0$). The dynamics produced in this case are shown for the full-predator and cue-only treatments in Fig. 5, which should be compared with Fig. 1. These systems differ only in the absence of predators from patch 2 in the system shown in Fig. 5. Summary statistics for all three treatments (predators plus cue; cue only; predators without cue) are shown in Table 2, which makes two comparisons: (1) between the short-term and long-term responses and (2) between the local (one-patch) and the global (two-patch) responses. Table 2A shows the impact of predator addition when the prey exhibits adaptive anti-predator movements. The comparison of the figures for $t = 0.1$ with the long-term means shows that the initial local response of N (i.e. N_1) greatly overestimates
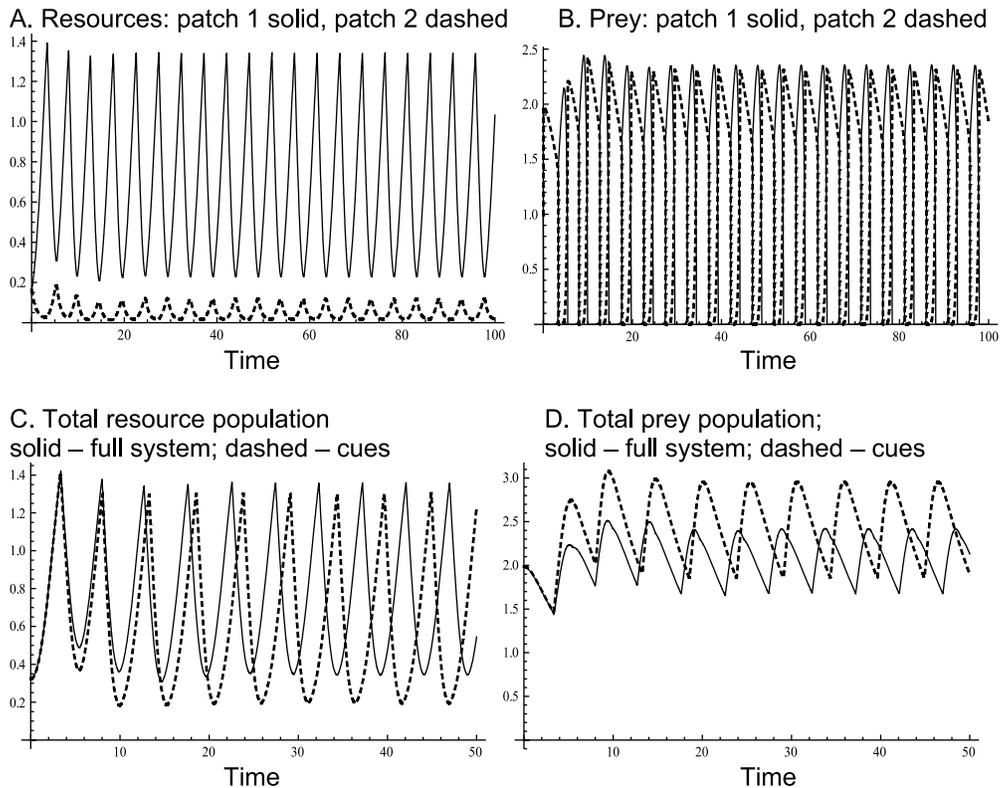

Fig. 5. The temporal dynamics of prey and resource in the system in Example 2, in which predators are only added to one patch. This system is comparable to that in Fig. 1 in all respects except that the predator density in patch 2 is zero. Initial densities of prey and resource are their equilibrium densities in the absence of the predator

Table 2. Responses to predator addition in both patches: Example 2, Case 1

A. Type of dynamics following predator addition with adaptively moving prey: Large amplitude limit cycles in each patch, anti-synchronized between patches

	Response at $t = 0.1$	Long-term mean response
N_1	$\cong -1$	-0.15291
$N_1 + N_2$	-0.0045	$+0.05709$
R_1	$+0.06978$	$+3.2149$
$R_1 + R_2$	$+0.000207$	$+1.26135$

B. Type of dynamics following addition of predator cue alone: Large amplitude limit cycles in each patch, anti-synchronized between patches, with much larger resource density in patch 1

	Response at $t = 0.1$	Long-term mean response
N_1	$\cong -1$	-0.1223
$N_1 + N_2$	-0.000377	$+0.2417$
R_1	$+0.03471$	$+2.5755$
$R_1 + R_2$	$+0.001758$	$+0.8593$

C. Type of dynamics following addition of predators in the absence of cues: Large amplitude limit cycles in each patch, synchronized with similar densities across patches for each species

	Response at $t = 0.1$	Long-term mean response
N_1	-0.02380	-0.1329
$N_1 + N_2$	-0.01256	-0.1290
R_1	$+0.000740$	$+2.1635$
$R_1 + R_2$	$+0.000216$	$+2.1136$

the long-term local response, although both are negative. The initial response of the global N is a decrease, even though the long-term response is an increase. The resource increases for all types of measurements, but the ratio of local to global (in patch 1) is initially two orders of magnitude greater than the final ratio of response magnitudes.

Table 2B shows the impacts of the presence of cues without actual predation. The cues alone produce the same initial rapid and nearly complete emptying of prey from patch 1 as occurs with actual predation (Table 2A). Cues alone produce a significantly larger increase in prey density and a smaller increase in resource density than does the predator. The changes in local and global resource densities produced by the cues alone are more than two-thirds as large as those produced by the predator and cues, suggesting a relatively large behavioural effect.

When predators are present but cues are absent (Table 2C), the change in prey density in patch 1 declines by an amount similar to that produced when the prey avoids the predator. A local measurement would therefore suggest that predator-avoidance behaviour has a

limited impact on prey density. However, the global density is changed from an approximate 6% increase in the presence of adaptive prey avoidance, to an approximate 13% decrease in its absence. The local resource density increases less than with adaptive prey movement, but the global resource density increases by much more.

Table 2 shows that the impact of the predators on both prey and resources attributable to predator avoidance movement behaviour alone is at least comparable to the impact attributable to predation in the absence of such movement. However, it is clear that the impacts of behaviour alone and consumption alone cannot be simply added or multiplied together to obtain the long-term impact on densities when both factors act simultaneously. This is in part because the behavioural effect drastically changes the type of dynamics compared with the system without avoidance behaviour. Not surprisingly, the proportions of the short-term effects attributable to behaviour are very much greater than those due to consumption when the effects are measured on a local level (i.e. in the one patch where predators are present). However, even on a global level, the impact of predator cues on the total prey and resource populations at time 0.1 is comparable in magnitude (although smaller) than the impact of consumption alone. The long-term impact of predators with cues or cues alone on local prey densities is a modest decrease, masking an increase at the level of the entire population. The short-term measurements of the impact of predators with cues or cues alone on the global prey population are negative, although the long-term effects are significantly positive. Impacts of the predator on the resource populations are much greater than the predator's impacts on the prey.

Case 2: $m_N = 0.005$. Table 3 describes the interactions in Case 2. Here, only impacts on long-term temporal mean densities are given. The cues, either alone or in combination with predators, produce the same initial rapid and nearly complete emptying of prey from patch 1 as does actual predation (Table 3A). However, several of the long-term impacts on densities differ considerably from those of Case 1. Most significantly, the equilibrium with predators and cues is a stable point, rather than the cycles seen in Case 1. Somewhat paradoxically, the addition of predators to just one of the two patches produces a much greater decrease in the prey population than does addition of predators to both patches (i.e. Example 1). Addition of predators to just one patch also produces a larger increase in resource density than does addition of predators to both patches. Impacts on the patch containing predators (patch 1) are much greater than impacts on the entire system, with a 98.9% reduction in prey in patch 1.

In the system with cues but no predators, there are two alternative attractors, the first involving anti-synchronized dynamics between the patches, and the second involving synchronized dynamics. Attractor 2 is observed when predators are introduced into an equilibrium consumer–resource system with no predators. Given initial densities of all species that are randomly chosen from a uniform distribution between 0 and 1, attractor 2 arises over 90% of the cases. The identity of the attractor determines whether the cues have a positive or negative effect on the total consumer population, although consumers in patch 1 always decline. In either case, cues alone have a much smaller impact on all of the population densities than do cues and predator together. Compared with Example 1, in which predators were introduced in both patches, the positive effect on total consumer density is smaller.

The results in Table 3C (predators but no cues) are again counterintuitive in that predation combined with adaptive prey movement produces a much larger decline in total

Table 3. Responses to predator addition in both patches: Example 2, Case 2

A. Type of dynamics following predator addition with adaptively moving prey: Stable point

	Long-term mean response
N_1	−0.9890
$N_1 + N_2$	−0.3704
R_1	+11.153
$R_1 + R_2$	+5.581

B. Type of dynamics following addition of predator cue: Two alternative attractors, each with complex cycles; attractor 1 has anti-synchronized patches, attractor 2 has synchronized patches

	Mean response, attractor 1	Mean response, attractor 2
N_1	−0.1981	−0.2965
$N_1 + N_2$	+0.00626	−0.1188
R_1	+2.7276	+3.8356
$R_1 + R_2$	+1.1939	+1.8587

C. Type of dynamics following addition of predators in the absence of cues: Apparently chaotic fluctuations that drift in and out of synchrony over time

	Long-term mean response
N_1	−0.06113
$N_1 + N_2$	−0.00256
R_1	+1.8607
$R_1 + R_2$	+1.1426

prey density than does predation in the absence of any prey-avoidance movements. The smaller impact on resource density from predation in the absence of cues is consistent with the smaller effect on prey density. Nevertheless, the substantial changes in resource densities (compared with a no-predator system) occur in spite of very small changes in the mean consumer population. In the low movement case (2), the impacts on both local and global resource populations due to the cues alone are much greater than those due to consumption alone. In the high movement case (1), this was only true for the patch containing predators or cues.

DISCUSSION

The impact of predators on prey that stems from the prey's anti-predator behaviour has been the object of considerable study. These impacts have been called 'non-consumptive effects' here, although a variety of other terms have been used by other authors (discussed in Abrams, 1995, 2007b; Abrams *et al.*, 1996). In many cases (e.g. Preisser *et al.*, 2005), the non-consumptive effect is assumed to be the result of costs inherent in the defensive behaviour. Although

movement may have measurable costs in natural systems, these need not be significant, and have been assumed to be zero in the model explored here. In spite of this, prey movement in response to predator cues alone results in changes in population densities of both prey and resource that are often comparable in magnitude to those produced by actual consumption by predators in the examples considered here. Adaptive movement also has a major effect on the stability of the entire food chain. Clearly, large non-consumptive effects of predators on prey do not require that the prey's defensive behaviour be inherently costly.

The models for local predator addition analysed here suggest that short-term local measurement of prey density following local addition of predators is likely to greatly overestimate the impact of the predator on prey over a longer time span or a larger spatial scale. The fraction of the prey's density response attributable to adaptive prey behaviour is also likely to be overestimated by such short local experiments. The finding of large non-consumptive effects of predators on prey due to emigration in a recent meta-analysis (Preisser *et al.*, 2005) should be reassessed in light of these theoretical results.

The finding that some pesticides interfere with anti-predator behaviour in anuran larvae (Relyea, 2003) has raised concerns that these species will experience declines in density if such substances are introduced into aquatic systems. While this is certainly possible, and is of great concern, the models presented here suggest that adaptive anti-predator movement may sometimes have little effect on, or may actually decrease, prey population size. Holt (1985) also pointed out that substituting random movement for adaptive movement may result in lower population size of a single species in a patchy habitat.

The examples considered here show that it is not possible to determine the impacts of any one of the three manipulations considered (predators with cues, cues alone, and predators without cues) by any simple formula using the results of the other two manipulations. This has, however, been a common practice in the literature on behavioural effects (reviewed by Bolnick and Preisser, 2005; Preisser *et al.*, 2005). Peacor and Werner (2001) called attention to the non-additivity of impacts on prey due to consumption and due to behavioural responses to the predator's cues, and Okuyama and Bolker (2007) have recently discussed some of the problems in calculating one of these three measures from the other two.

The examples presented illustrate only a small subset of the dynamics that can be produced by the model considered here. These examples do not consider the possibility that predators as well as prey move adaptively. Such predator movements further expand the range of dynamic possibilities. In addition, the model considered here is only one of a huge family of potential models that could be used for adaptive movements in meta-communities (Abrams *et al.*, 2007). Nevertheless, the examples are sufficient to show that adaptive movement of prey can have important population dynamical consequences even when movement itself has no inherent cost. Furthermore, these consequences often cannot be meaningfully quantified using the sorts of cue experiments that dominate the field. A wide variety of counter-intuitive effects result from adaptive movement, including the possibility that greater numbers of predators have smaller impacts on the prey population than do smaller numbers of predators.

In 1994, Sih and Wooster (1994, p. 1206) ended their article on prey movement in streams with the statement that: 'In general, ecologists should profit from more detailed studies of interactions between prey behavior, prey movement, and predator impacts'. This sentiment remains equally valid today.

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REFERENCES

Abrams, P.A. 1984. Foraging time optimization and interactions in food webs. *Am. Nat.*, **124**: 80–96.

Abrams, P.A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *Am. Nat.*, **146**: 112–134.

Abrams, P.A. 2000. The impact of habitat selection on the heterogeneity of resources in varying environments. *Ecology*, **81**: 2902–2913.

Abrams, P.A. 2007a. Habitat choice in predator–prey systems: spatial instability due to interacting adaptive movements. *Am. Nat.*, **169**: 581–594.

Abrams, P.A. 2007b. Defining and measuring the impact of dynamic traits on ecological interactions. *Ecology*, **88**: 2555–2562.

Abrams, P.A. in press. The use of predator-cue experiments to quantify behavioral effects in tri-trophic systems: A theoretical analysis. *Ecology*.

Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D. and Yodzis, P. 1996. The role of indirect effects in food webs. In *Food Webs: Integration of Patterns and Dynamics* (G. Polis and K.O. Winemiller, eds.), pp. 371–395. New York: Chapman & Hall.

Abrams, P.A., Cressman, R. and Krivan, V. 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. *Am. Nat.*, **169**: 505–518.

Boeing, W.J., Wissel, B. and Ramcharan, C.W. 2005. Costs and benefits of *Daphnia* defense against *Chaoborus* in nature. *Can. J. Fish. Aquat. Sci.*, **62**: 1286–1294.

Bolnick, D.I. and Preisser, E.L. 2005. Resource competition modifies the strength of trait-mediated predator–prey interactions: A meta-analysis. *Ecology*, **86**: 2771–2779.

Griffin, C.A.M. and Thaler, J.S. 2006. Insect predators affect plant resistance via density- and trait-mediated indirect interactions. *Ecol. Lett.*, **9**: 338–346.

Holling, C.S. 1959. The characteristics of simple types of predation and parasitism. *Can. Entomol.*, **91**: 385–398.

Holt, R.D. 1985. Population dynamics in 2-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.*, **28**: 181–208.

Ives, A.R. 1992. Continuous time models of host–parasitoid interactions. *Am. Nat.*, **140**: 1–29.

Jansen, V.A.A. 2001. The dynamics of two diffusively coupled predator–prey populations. *Theor. Popul. Biol.*, **59**: 119–131.

Okuyama, T. and Bolker, B.M. 2007. On quantitative measures of indirect interactions. *Ecol. Lett.*, **10**: 264–271.

Peacor, S.D. and Werner, E.E. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Nat. Acad. Sci. USA*, **98**: 3904–3908.

Persson, L. and de Roos, A.M. 2003. Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology*, **84**: 1129–1139.

Preisser, E. L., Bolnick, D. I., and Benard, M. 2005. Scared to death? The effects of intimidation and consumption on predator-prey interactions. *Ecology* **86**: 501–509.

Relyea, R.A. 2003. Predator cues and pesticides: a double dose of danger for amphibians. *Ecol. Appl.*, **13**: 1515–1521.

Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, **151**: 327–342.

Schwinning, S. and Rosenzweig, M.L. 1990. Periodic oscillations in an ideal-free predator–prey distribution. *Oikos*, **59**: 85–91.

Sih, A. and Wooster, D.E. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology*, **75**: 1199–1207.

Trussell, G.C., Ewanchuk, P.J. and Matassa, C.M. 2006. Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecol. Lett.*, **9**: 1245–1252.

Werner, E.E. and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**: 1083–1100.

Wolfram, S. 2007. *Mathematica 6.0*. Champaign, IL: Wolfram Research.