*Evolutionary Ecology* 1996, **10**, 13–28

# Effects of predator-specific defence on biodiversity and community complexity in two-trophic-level communities

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## Summary

Antipredator strategies employed by prey may be specific (effective against only one type of predator) or non-specific (effective against all predators). To examine the effects of the specificity of antipredator behaviour on biodiversity and community complexity, we analyse mathematical models including both evolutionary and population dynamics of a system including multiple prey species and multiple predator species. The models assume that all predator species change in their prey choice and all prey species have evolutionary change in their antipredator effort in evolution. The traits of each species change in an adaptive manner, whose rate is proportional to the slope of their fitness function. We calculate community complexity, resource-overlap between predators, an index of biodiversity and other properties of the co-evolutionarily stable community for two cases: (1) all prey species have non-specific antipredator behaviour and (2) all prey species have predator-specific defence. Predator-specificity in defence increases community complexity, resource-overlap between predators, the total abundance of predators and the ratio of predator to prey abundance. Specific defence also decreases the number of isolated subwebs within the entire foodweb.

*Keywords*: co-evolution; exploitative mutualism; anti-predator behaviour; co-evolutionarily stable state; community structure

## Introduction

The structure of a foodweb is defined by its predator-prey links. The predator-prey links are in turn determined by the predators' traits influencing their choice of prey and the prey's antipredator traits (efforts). In general, the predators' choice behaviours change with prey densities and antipredator efforts in a way that increases the predators' fitnesses. The antipredator efforts of prey also change in a direction that increases prey's fitness; this direction depends on the predators' densities and choice-related traits. Thus, foodweb structure should be understandable based on a co-evolutionary process involving both prey and predator traits, including behaviour.

The specificity of the prey's defence against predators is one of the more important determinants of co-evolution. Antipredator traits that are effective against all predator species represent non-specific defence and traits that are effective against only one predator species represent perfectly-specific defence. Specificity is a continuous property; many traits will be maximally effective against one predator, but partially effective against others. As Lima (1992)

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has noted, little is known about the specificity of defensive behaviours. Clearly, some defences are effective against a wide variety of predators. For example, lack of movement is effective against a variety of visual predators that use movement to detect prey and the chemical defences of plants are often effective against a wide variety of herbivores. However, there are many cases in which a high degree of specificity has been shown or is likely.

Specificity of defence can be the result of adaptive habitat selection by prey when different predators are found in different locations. Avoiding locations where one predator is common may either not affect or even increase the risk of predation by other predator species. For example, fish that avoid bird predation by avoiding shallow water increase their susceptibility to piscivorous fish (Power, 1984; Heads, 1985; Schlosser, 1988), rodents that avoid avian predators by foraging close to bushes increase their susceptibility to snakes (Kotler *et al.* 1993) and mayflies foraging on the tops of rocks become available to fish predators, but if they switch their foraging area to the bottoms of rocks, they become available to stoneflies (Soluk and Collins, 1988). Similarly, small fish (darters) that gain refuge from large piscivores in shelters increase their susceptibility to crayfish (Rahel and Stein, 1988). Specificity arises when different predators search for their prey at different times, e.g. day and night. Specificity can also arise when different predators use different sensory modalities; cryptic coloration does not protect against predators that locate prey by tactile or olfactory cues (Endler, 1986). When different predators use different attacking methods, defence against one may not protect against others (Hori, 1987, 1993; Lima, 1992). Hori (1987) has noted that fish in Lake Tanganyika have such specific attacking methods. Savino and Stein (1989) discussed different tactics used by bluegill sunfish against predatory bass and pike. Fitzgibbon and Fanshawe (1988) noted that Thomson's gazelles use a stotting as an antipredator strategy against coursing predators, but not against ambush predators. Seyfarth *et al.* (1980) documented different alarm calls and different subsequent reactions by vervet monkeys faced with three different types of predators. We expect that complete specificity of defence for every single predator species may be rare in environments with many predators. Nevertheless, it is important to understand the case of complete specificity if we are to understand the potential effects of defence specificity on community structure. This is the goal of the present article.

We have investigated the implications of defence specificity for community structure in two previous papers. Matsuda *et al.* (1994) investigated a two-trophic-level community with at most two species per level. That article assumed that different prey species are located in different patches or found by different search techniques, so that a given predator cannot search for both prey species simultaneously (prey-specific searching). Both species of predators were assumed to adjust their choice behaviours (foraging location or search method) to maximize their food intake rate. Both prey were assumed to adjust their antipredator behaviour to maximize their individual fitness. The analysis derived conditions for a co-evolutionarily stable state (CSS) of the community, defined as a state where each species occupies a stable maximum of individual fitness. That study showed that predator-specific defence results in foodwebs with more predator–prey links than does non-specific defence.

In a related work, Matsuda *et al.* (1993) considered a two-predator–one-prey system in which the densities of two predator species were assumed to be constant, but both prey density and the antipredator effort of the prey could change with time. That study showed that the fitness of one predator species may increase as the density of the other predator species increases, as a result of adaptive predator-specific defence by the prey. We call such a relationship between predators 'exploitative mutualism'. Each predator species also depletes the prey population; the effects of predators on each other's equilibrium densities may thus be competitive or mutualistic. However, in all cases, the specificity of the prey's defence diminishes competition between the predators and facilitates their co-existence.

In this paper, we extend these previous works in several ways. First, we include explicit dynamic models for both population densities and behavioural traits (prey choices and antipredator efforts). Secondly, we consider larger communities, with up to ten species on each trophic level. These two changes allow us to investigate the effect of defensive specificity on community properties that depend on species abundance, to investigate more directly the role of the prey's defensive specificity on predator co-existence. As in Matsuda *et al.* (1994), we assume that traits within a species change in a way that increases individual fitness. This adaptive change may be the result of evolution by natural selection or the result of behavioural plasticity. The direction of adaptive change in traits is that which increases individual fitness; the rate of change in trait values is assumed to increase with the marginal individual fitness (the derivative of individual fitness with respect to its trait value, evaluated at the mean trait value) and to decrease as trait values approach their maximum or minimum possible values. The per capita rate of change in population density of each species is an increasing function of its population-mean fitness. When there are both multiple traits within a species and constraints relating the trait values, we use Lagrange-multiplier methods to find the CSS; these methods have been explained by Lloyd and Venable (1992).

## A model for non-specific defence

Suppose there are $S_1$ species of prey and $S_2$ species of predators. The population density of predator species $k$ is denoted by $y_k$ and the population density of prey species $i$ is denoted by $x_i$. We assume that the choice and defence behaviors, denoted $f$ and $v$, can both be scaled so that they take on values between zero and one. If search behaviour is prey-specific, a predator can only search for one prey type at a time; in this case, the search effort by predator $k$ for prey $i$ can be denoted $f_{ki}$ ($0 \leq f_{ki} \leq 1$); this can be considered to be the proportion of predator $k$'s available time that it spends searching for prey $i$. In this section we assume that a prey species is capable of being vigilant or otherwise reducing attacks by all predator species simultaneously (non-specific defence). Its total antipredator effort is denoted $v_i$; this variable is again scaled to have a maximum of one. There are assumed to be costs of increased antipredator effort. Animals often reduce or eliminate foraging while watching for predators (Lima and Dill, 1990). Although we will discuss the model in terms of animal prey, it may also be relevant to plants; some defensive chemicals confer generalized protection while others are more specific. Furthermore, plants must divert energy or resources from reproduction or growth to increase defensive compounds or structures (Berenbaum *et al.*, 1986). In both plants and animals, the cost to the prey species $i$ can be considered to be a reduction in its own effort devoted to resource acquisition, $f_i$. Here we make the simple assumption that $f_i = 1 - v_i$.

The changes in population densities of prey $i$ and predator $k$ are given by

$$\frac{dx_i}{dt} = F_i x_i \tag{1a}$$

and

$$\frac{dy_k}{dt} = G_k y_k \tag{1b}$$

where $F_i$ and $G_k$, respectively, denote the population-mean fitnesses of prey $i$ and predator $k$; $t$ is time. If reproduction occurs at discrete intervals rather than continuously, these functions should be considered to represent the logarithms of the expected number of descendants produced per parent per unit time. We ignore any cooperative or interference effects involved in predation and antipredator behaviours. Such effects would have to be included to understand the co-evolution of most animals that form groups for the purpose of either defence or predation (Hamilton, 1971; Clark and Mangel, 1986; Packer and Abrams, 1990).

The fitness of prey $i$ ($F_i$) is the sum of three components: (1) the benefit of foraging or resource acquisition, (2) the cost due to predation and (3) a cost due to the negative effects of increased density on other aspects of fitness, such as competition for habitats or mates. We assume that $F_i$ depends on the population density of prey $i$ ($X_i$), the population densities ($y_k$) of all predators $k$ which attack prey $i$, the prey's antipredator effort ($v_i$) and the choice behaviours ($f_{ji}$) of all relevant predator species $j$. The fitness of predator $k$ ($G_k$) depends on its own population density ($y_k$), the population densities of all prey types ($x_j$) which it exploits and the relevant antipredator efforts ($v_j$) and predator's choice ($f_{kj}$). The following expressions give simple functional forms for these two fitnesses:

$$F_i = \mathrm{B}[(1-\upsilon_i)r_i] - \sum_{j=1}^{S_2} (1-\upsilon_i)e_{ij}f_{ji}y_j - (c_i + \mathrm{a}_i\mathrm{x}_i) \tag{2}$$

$$G_k = \mathrm{B}\left[\sum_{j=1}^{S_2} (1-\upsilon_j)e_{jk}f_{kj}x_j\right] - (d_k + \mathrm{b}_k\mathrm{y}_k) \tag{3}$$

where $B(z)$ is a function describing the fitness benefits of food consumption (generally reproduction). Here we assume that $B(z) = \sqrt{z}$, which reflects the fact that the use of food becomes inefficient when very large amounts are processed (Matsuda *et al.*, 1994). The definitions of the other parameters are as follows: $r_i$ is the abundance of resources used by prey $i$, $e_{ij}$ is the maximum encounter rate of predator $j$ and prey $i$, $a_i$ ($b_k$) is the per capita effect of prey $i$'s (predator $k$'s) population density on prey (predator) fitness and $c_i$ ($d_k$) is the density-independent mortality rate of prey $i$ (predator $k$). Because we assume that predators require negligible time to handle prey, the analysis of the model is simplified considerably. In general, prey–predator systems are likely to have stable equilibria when the predator does not spend a significant amount of time recognizing (Hughes, 1979), pursuing (Anholt *et al.*, 1987) or catching and ingesting prey items (Holling, 1966). If handling time is negligible, the prey's fitness is intraspecifically frequency independent (Abrams, 1989; Matsuda and Abrams, 1994) and the predator's feeding rate is a linear function of prey densities (Matsuda and Namba, 1991). Frequency independence implies that the derivative of population-mean fitness with respect to population-mean strategy is identical to the derivative of individual fitness with respect to individual strategy, evaluated at the population mean.

Given densities of all prey and predator species, $x_i$ and $y_k$, the co-evolutionarily stable state (CSS) for the predators' prey choice and the prey's antipredator effort, $f_{ki}$ and $v_i$, is here defined as a state in which a small change in any trait value (prey choice and antipredator effort) of any species does not increase its individual fitness. At a CSS, the antipredator effort of each prey species that has a positive equilibrium density must satisfy the following conditions:

$$\partial F_i/\partial \upsilon_i < 0 \text{ if } \upsilon_i^* = 0 \tag{4a}$$

$$\partial F_i/\partial \upsilon_i = 0 \text{ if } 0 < \upsilon_i^* < 1 \tag{4b}$$

and

$$\partial F_i/\partial \upsilon_i > 0 \text{ if } \upsilon_i{}^* = 1 \tag{4c}$$

where asterisks mean the trait value at a CSS. The last case, Equation 4c, cannot arise in this model because it implies that the prey does not consume any of its resources and therefore cannot have a positive equilibrium density.

Finding a CSS represents a constrained optimization problem, which can be solved by forming Lagrangian functions (see Lloyd and Venable, 1992) and finding the extrema of the Lagrangians. In this case, the predators' functions have the form

$$\Gamma_k = G_k - \gamma_k(\Sigma_j f_{kj} - 1) \tag{5}$$

where $\gamma_k$ is the Lagrange multiplier. The Lagrange multiplier technique allows constrained variables such as $f_{kj}$ to be treated as independent arguments. At a CSS, the $f_{ki}{}^*$ for each predator $k$ that can exist ($y_k{}^* > 0$) satisfies the following conditions:

$$\partial \Gamma_k/\partial f_{ki} = \partial G_k/\partial f_{ki} - \gamma_k < 0 \text{ if } f_{ki}{}^* = 0 \tag{6a}$$

$$\partial \Gamma_k/\partial f_{ki} = \partial G_k/\partial f_{ki} - \gamma_k = 0 \text{ if } 0 \leq f_{ki}{}^* \; 5 \; 1 \tag{6b}$$

If $f_{ki}{}^* = 1$ for a particular prey species $i$, then $f_{kj}{}^* = 0$ for all other prey species.

To obtain a CSS numerically, we use the following dynamic model for the prey's antipredator behaviour:

$$\frac{d\upsilon_i}{dt} = \kappa(1-\upsilon_i)\upsilon_i \frac{\partial F_i}{\partial \upsilon_i} \tag{7}$$

where κ is a positive constant (see Equation 8a below for the corresponding equation for the predator). The right-hand side of Equation 7 is zero at trait values that represent fitness maxima, i.e. if $\partial F_i/\partial v_i = 0$ for an intermediate trait value $v_i{}^*$ or if $\partial F_i/\partial v_i < 0$ for $v_i{}^* = 0$. Equilibria of Equation 7 must satisfy the CSS condition Equation 4. Equation 7 is designed to mimic the features of evolution of a quantitative trait that is constrained to have values between 0 and 1; the rate of change of the trait increases with the slope of the fitness function, $F_i$, for a given genetic variance. The rate of evolution also increases with the additive genetic variance, which must approach zero as the trait approaches 0 or 1. This is reflected in the factor $v_i(1 - v_i)$ in Equation 7. The dynamics here are analogous to those of a one-locus, two-allele genetic model, in which the change of gene frequency $g$ is described by $\Delta g = g(1-g)(\partial W/\partial g)/2$, where $W$ is the population-mean fitness. This model is also likely to approximate the dynamics of behavioural plasticity, although the constant, κ, is much larger for behavioural plasticity than for evolutionary change (Abrams *et al.*, 1993).

The same logic used for Equation 7 leads to the following model for the dynamics of evolution of prey choice in the predator:

$$\frac{df_{ki}}{dt} = \kappa f_{ki}\left(\frac{\partial G_k}{\partial f_{ki}} - \tilde{\gamma}_k\right) \tag{8a}$$

where

$$\tilde{\gamma}_k = \sum_{j=1}^{S_2} f_{kj} \frac{\partial G_k}{\partial f_{kj}} \tag{8b}$$

The sum of the foraging efforts must again be unity, i.e. ${}_j f_{kj} = 1$. The right-hand side of Equation 8a disappears at the maxima of the constrained fitness function, i.e. at foraging efforts where $\partial G_k/\partial f_{ki} = \tilde{\gamma}_k$ for $0 < f_{ki}^* \leq 1$ or $\partial G_k/\partial f_{ki} < \tilde{\gamma}_k$ for $f_{ki}^* = 0$. If the number of prey species is given by $S_1 = 2$, this model will have the same mathematical form as Equation 7. More generally, this equation takes into account the relationship between foraging efforts imposed by the constraint that efforts sum to unity; this means that the rate of change of a given effort depends on the fitness effects of other efforts. The quantity on the right-hand side of Equation 8a represents the mean marginal fitness of predator *k*. An equation analogous to Equation 8a was derived by Eigen and Schuster (1977) in their analysis of hypercycles.

We numerically obtained CSSs by simulation of the population dynamic Equation (1) using fitness functions (Equations 2 and 3) and trait dynamics (Equations 7 and 8a); the stable equilibria of these simulations represent CSSs. We examined two-prey–two-predator systems based on 1000 computer simulations: $(S_1 = S_2 = 2)$, $r_i = 1$, $a_i = 0.1$, $b_k = 0.1$, $c_i = 0$ and $d_k = 1$ for $i = 1, 2$, $k = 1, 2$ and $e_{ik}$ was randomly chosen between 0 and 1. We also examined ten-predator–ten-prey systems from 100 computer simulations: $(S_1 = S_2 = 10)$, $a_i = 0.1$, $b_k = 0.1$, $c_i = 0$ and $d_k = 1$ for $i = 1, 2$, $k = 1, 2$ and $r_i$ and $e_{ik}$ were randomly chosen between 0 and 1.

We assumed that the benefit of feeding is proportional to the square root of the feeding rate in our initial simulations of Equations 2 and 3. To examine how our results are affected by this assumption, we repeated the simulations using the Monod function, $B(z) = \beta z/(q + \beta z)$ in Equations 2 and 3 for two-prey–two-predator systems. The equilibrium point does not vary with the evolutionary rate coefficient, $\kappa$ in Equations 7 and 8a; thus we have used $\kappa = 1$ for most of the simulations reported here. In theory, the values of $\kappa$ for different species may affect the stability of the equilibrium point, but unstable equilibria seem to be rare for the range of parameter values we have simulated, regardless of $\kappa$ (see below).

## A model for predator-specific defence

If a particular antipredator behaviour is effective against only one predator species (perfectly-specific defence) and if each prey species has a distinct antipredator behaviour for each predator species, we denote the antipredator effort of prey *i* against predator *k* by $v_{ik}$. If antipredator behaviour against a particular predator is partly effective against another predator (partly-specific defence), the effective protection against predator *k* by prey *i* is represented by $v_{ik} + \sigma \sum_j v_{ij}$, where $\sigma$ means the specificity of antipredator behaviour $(0 \leq \sigma \leq 1)$. We assume that all of the possible antipredator behaviours preclude foraging by the prey. This means that the prey as well as the predator is characterized by a foraging effort, *f*. There is a trade-off between total antipredator effort and foraging effort, $f_i$, within the prey species; $0 \leq v_{ik} \leq 1$ and $\sum_k v_{ik} + f_i = 1$. Using similar assumptions about the shapes of fitness components as in Equations 2 and 3, the fitnesses of prey *i*, $F_i$ and predator *k*, $G_k$, are

$$F_i = \mathrm{B}(f_i r_i) - \sum_{j=1}^{S_2} (1 - \upsilon_{\mathrm{ij}} - \sigma \sum_{k \neq \mathrm{k}} \upsilon_{\mathrm{ik}}) e_{ij} f_{ji} y_j - (c_i + \mathrm{a_i x_i}) \tag{9}$$

$$G_k = \mathrm{B}\left[ \sum_{j=1}^{S_2} (1 - \upsilon_{\mathrm{jk}} - \sigma \sum_{l \neq \mathrm{k}} \upsilon_{\mathrm{jl}}) e_{jk} f_{kj} x_j \right] - (d_k + \mathrm{b_k y_k}) \tag{10}$$

where we assume in the simulations that $B(z) = \sqrt{z}$. The co-evolutionarily stable antipredator efforts follow from the conditions

$$\partial \Phi_i/\partial \upsilon_{\mathrm{ik}} < 0 \text{ if } \upsilon_{\mathrm{ik}}^* = 0 \tag{11a}$$

$$\partial \Phi_i/\partial \upsilon_{\mathrm{ik}} = 0 \text{ if } 0 < \upsilon_{\mathrm{ik}}^* < 1 \tag{11b}$$

$$\partial\Phi_i/\partial \mathrm{f_i} = 0 \text{ if } 0 \# f_i^* \# 1 \tag{11c}$$

$$\partial\Phi_i/\partial \mathrm{f_i} > 0 \text{ if } f_i^* = 1 \tag{11d}$$

where

$$\sum_{j=1}^{S_2}{}_i = \mathrm{F_i} - \phi_\mathrm{i}(\Sigma_k \upsilon_\mathrm{ik} + \mathrm{f_i} - 1) \tag{12}$$

$\phi_i$ is a Lagrange multiplier. The co-evolutionarily stable prey choice is again derived from Equations 6a–b. To numerically obtain a CSS, we use the following dynamic equations with Equations 1a and 1b:

$$\frac{\mathrm{d}\upsilon_{ik}}{\mathrm{d}t} = \kappa\upsilon_{ik}\left(\frac{\partial F_i}{\partial\upsilon_{ik}} - \tilde{\phi}_i\right) \tag{13a}$$

$$\frac{df_i}{dt} = \kappa f_i\left(\frac{\partial F_i}{\partial \mathrm{f_i}} - \tilde{\phi}_i\right) \tag{13b}$$

$$\frac{\mathrm{d}f_{ki}}{\mathrm{d}t} = \kappa f_{ki}\left(\frac{\partial G_k}{\partial \mathrm{f_{ki}}} - \tilde{\gamma}_k\right) \tag{13c}$$

where

$$\tilde{\phi}_i = f_i\frac{\partial F_i}{\partial f_i} + \sum_{j=1}^{S_2} \upsilon_{ij}\frac{\partial F_i}{\partial \upsilon_\mathrm{ij}} \tag{14a}$$

$$\tilde{\gamma}_k = \sum_{j=1}^{S_1} f_{kj}\frac{\partial G_k}{\partial \mathrm{f_{kj}}} \tag{14b}$$

The equilibrium of this dynamic system (Equations 13 and 14) satisfies the CSS Equations 11a-c and 6a-b. In the simulations, we set a lower limit (0.001) for every trait ($v$ and $f$) and density ($x$ and $y$) even when the time derivative is negative. This prevents traits or species from being eliminated by transient dynamical responses or round-off error. However, when a variable was not greater than this lower limit at equilibrium, this trait or population was classified as extinct.

We examined 1000 computer simulations of two-prey-two-predator systems for perfectly-specific defence ($\sigma = 0$) and partly-specific defence ($\sigma = 0.5$) with the same parameter values as in the case of non-specific defence. We also examined ten-prey-ten-predator systems using 100 different simulations, again with the same values of parameters as in the case of non-specific defence.

We examined 1000 simulations of two-prey-two-predator systems with no defence, non-specific defence, partly-specific defence and perfectly-specific defence using the square-root function and the Monod function for the feeding-benefit relationship. We also examined simulations of predator-prey systems initially containing 8, 12, 16 and 20 species (100 simulations of each case under non-specific defence and under perfectly-specific defence); these simulations assumed that $B(z) = \sqrt{z}$.

## Results

In the above model communities, prey never go extinct because all predators have prey-specific searching behaviour. This means that they ignore prey which are rare. Some predators may go

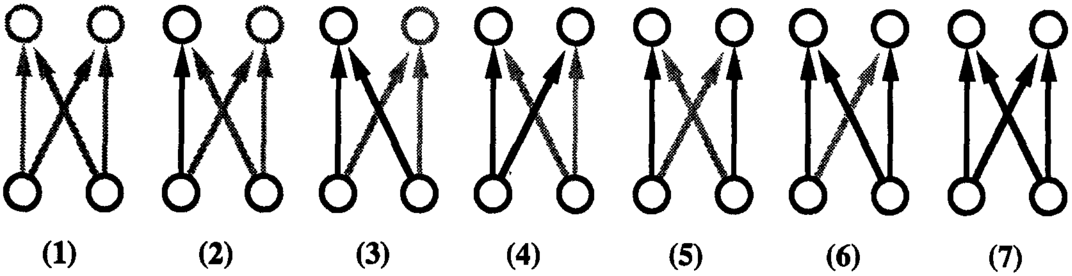

Figure 1. Possible foodwebs in two-predator-two-prey systems. The upper and lower circles represent predator and prey species. Dark arrows represent actual links from prey to predators. Grey circles and arrows are extinct predator species and links.

Table 1. Resultant foodwebs of two-predator-two-prey systems from 1000 computer simulations of each case

| Defence | (1) | (2) | (3) | (4) | (5) | (6) | (7) | $p(\pm\ \mathrm{sd})$ |
|---|---|---|---|---|---|---|---|---|
| $B(z)=\sqrt{z}$ | | | | | | | | |
| No defence | 0 | 48 | 135 | 32 | 491 | 294 | 0 | 0.273 + 0.383 |
| Non-specific defence | 0 | 36 | 202 | 16 | 500 | 245 | 0 | 0.194 + 0.314 |
| Partly-specific ($\sigma$ = 0.5) | 0 | 31 | 153 | 20 | 221 | 489(1) | 86 | 0.453 + 0.353 |
| Perfectly specified ($\sigma$ = 0) | 0 | 22 | 100 | 35 | 138 | 542(10) | 163 | 0.551 + 0.332 |
| $B(z)=\beta z/(q+\beta z)$, where $\beta=2, q=1$ | | | | | | | | |
| No defence | 0 | 52 | 119 | 29 | 498 | 302 | 0 | 0.265 + 0.375 |
| Non-specific defence | 0 | 38 | 175 | 21 | 497 | 269 | 0 | 0.214 + 0.324 |
| Partly-specific ($\sigma$ = 0.5) | 0 | 31 | 141 | 20 | 243 | 477 | 88 | 0.491 + 0.358 |
| Perfectly-specific ($\sigma$ = 0) | 0 | 25 | 95 | 29 | 159 | 543(8) | 149 | 0.537 + 0.338 |

Pianka's niche overlap index $p$ was averaged over cases (4)-(7) with ± sd. Food webs are categorized into seven configurations which are defined in Fig. 1. Numbers between parentheses are the number of webs that had not attained a stable equilibrium at the end of simulation ($t$ = 5000).

extinct if their encounter and mortality rates ($e_{ik}$ and $d_k$) result in a disadvantage relative to other predators (Matsuda and Namba, 1989). At a CSS in a two-prey-two-predator system, there are seven possible configurations of foodwebs at equilibrium which are shown in Fig. 1: (1) no predators persist, (2) only one predator persists and it uses a single prey species, (3) one predator persists, but uses two prey, (4) two predator species co-exist each using the same unique prey species, (5) two predators co-exist, each using a different unique prey species, (6) two predators co-exist, one of which uses only a single prey while the other uses both prey species and (7) two predators co-exist, both of which use both prey. In the case of non-specific defence, Foodweb 7 is impossible because the sum of numbers of predators and prey must be larger than the number of links at a CSS (Matsuda and Namba, 1991; Matsuda *et al.*, 1994).

Partly-specific defence had an intermediate effect between non-specific and perfectly-specific defence as shown in Table 1. The number of parameter sets that results in foodweb Equation 7 for partly-specific defence was approximately half as many as the number for perfectly-specific defence. There were no significant differences based on the form of the reproductive rate function, *B*.

There were only minor differences between no defence and non-specific defence. In both of these cases, the availability of a prey to all of its predators is characterized by a single variable,

$x_i$ or $(1\text{-}v_i)x_i$. In contrast, the availability of a prey with specific defence is characterized by a different value for each predator; $(1\text{-}v_{ik})x_i$ for predator $k$. This causes major differences in community structure between specific and non-specific defence. Foodweb 3 occurred more frequently in the case of non-specific defence than in the case with no defence. This seems to be at least partly due to generalized defensive behaviour tending to convert Foodweb 6 to configuration Foodweb 3. The prey that is fed upon by both predators in Foodweb 6 adopts high levels of defence, which can cause extinction of the more specialized predator, changing Foodweb 6 to Foodweb 3.

In general, the dynamic system we have modelled may have more than one CSS, and an equilibrium may not be dynamically stable. However, general theory (May, 1973) suggests that the equilibria of the population dynamic system will be dynamically stable if the intraspecific density effects $a_i$ and $b_k$ are sufficiently large. If no predator species has a negative effect of its density on its own per capita growth rate ($b_k = 0$), the number of predator species that uses a given prey species is at most one. In addition, the number of predator-prey links in the community cannot be more than the number of prey species (Armstrong and McGehee, 1980; Matsuda and Namba, 1989), given that the system approaches a dynamically stable equilibrium and all predators have prey-specific searching. The assumption of no predator density-dependence would probably have resulted in significantly simpler communities. We obtained a stable equilibrium for almost every set of randomly chosen parameter values shown in Table 1. Specific defence was much more likely to result in the two most highly connected Foodwebs 6 and 7. This is reflected in the higher value of Pianka's niche overlap index, $p$, here calculated as $p = (f_{11}f_{21} + f_{12}f_{22})/\ [(f_{11}{}^2 + f_{12}{}^2)(f_{21}{}^2 + f_{22}{}^2)]$. In the majority of cases involving non-specific defence there was no interaction between the two predators at equilibrium, either because they did not overlap in prey use or because one predator had become extinct. In contrast, interaction between the predators was present in approximately 70% of the predator-specific defence. We did not determine what fraction of the cases of predator-prey interaction involved competitive or mutualistic effects (Matsuda *et al.*, 1993).

The results shown in Table 1 were consistent in almost all ten 100-run subsets of the entire set of 1000 simulations for each parameter comparison. Although we did not examine other ranges of parameter values, it is unlikely that the qualitative comparison of specific and non-specific defence would be changed significantly. The qualitative differences have a simple, intuitive explanation that is independent of parameter values. Other parameters would produce some quantitative differences in the form of Table 1. For example, it is clear that relatively high rates of density independent mortality, $d$, among the predators would increase the frequency of occurrence of Foodweb 1.

These results should be compared with those in Matsuda *et al.* (1994), who considered a model in which there was no density dependence and in which population densities of the species were fixed at values that were randomly chosen for each simulation. The assumption of fixed densities in the previous article eliminates the possibility of exclusion of one predator by another (Foodwebs 1–3 in Fig. 1). In both the previous work and this one, approximately half of all the simulations with non-specific defence resulted in a web with Foodweb 5 in Fig. 1.

In systems that start with ten prey and ten predators, the CSS foodweb has at most ten predator species and at most 100 links. However, there must always be fewer than 20 links in the case of non-specific defence according to the necessary conditions for a CSS presented above. Table 2 shows some of the properties of the equilibrium foodwebs from our 100 simulations of ten-prey-ten-predator systems with non-specific and predator-specific defence. The table gives values of the following community parameters at the CSS, averaged over all 100 simulations: (1) the number of persisting predator species (denoted by $S_2{}^*$), (2) the number of actual links ($L^*$), (3)

Table 2. Several properties of the resultant foodwebs of ten-predator-ten-prey systems from 100 computer simulations of each case (mean + ± sd)

| Indices | Non-specific defence | Specific defence | Pairwise difference |
|---|---|---|---|
| Number of predator species ($S_2$*) | 9.11 ± 0.74 | 9.64 ± 0.52 | −0.53 ± 0.69(0, 43) |
| Number of links ($L$*) | 13.8 ± 1.64 | 17.0 ± 2.16 | −3.22 ± 2.00(3, 92) |
| Connectance ($C$) | 0.15 ± 0.02 | 0.18 ± 0.02 | −0.03 ± 0.02(10, 84) |
| Diversity index of predators ($D$) | 7.61 ± 0.79 | 8.31 ± 0.72 | −0.70 ± 0.38(3, 97) |
| Total abundance of predators | 5.19 ± 0.74 | 8.66 ± 1.43 | −3.47 ± 0.71(0, 100) |
| Predator-to-prey abundance | 0.22 ± 0.01 | 0.31 ± 0.04 | −0.09 ± 0.03(0, 100) |
| Number of isolated subwebs | 5.30 ± 1.40 | 3.62 ± 1.54 | +1.68 ± 1.59(79, 8) |

The mean and ± sd of the pairwise difference between the two cases are shown. The numbers in parentheses, respectively, give the numbers of webs for which non-specific defence resulted in a larger and a smaller index than did perfectly-specific defence. See the text for detail.

the connectance (defined by $L^*/S_1S_2^*$, where $L^*$ is the number of actual links at a CSS; this means the ratio of actual links to possible links between species present at equilibrium); (4) Simpson's index of diversity for predator species [$D = (\Sigma_k y_k{}^{*2})/(\Sigma_k y_k{}^{*2})$], (5) the total abundance of predators ($\Sigma_k y_k{}^{*2}$), (6) the ratio of total predator abundance to total prey abundance ($\Sigma_k y_k{}^{*2}/\Sigma_i x_i{}^*$ and (7) the number of isolated subwebs (see below).

The indices varied with the values of the randomly chosen parameters. Some of the indices had considerable overlap in distribution between the two types of defence. However, all of the differences between community indices for specific and non-specific defence in Table 2 were statistically significant from pairwise tests. There was no overlap between the two distributions for the total abundance of predators and the ratio of predator to prey abundance. There was a slight overlap between the two distributions for the number of links and diversity index. Predator-specific defence significantly increased community complexity (evaluated by $L^*$, $C$ or $S_2^*$), as shown in Table 2. The intuitive reason for this is the same as that given for simpler models in Matsuda *et al.* (1994). When defence is predator-specific, rare predators are likely to have a fitness advantage, because prey do not defend against them. This tends to prevent predators from going extinct and it preserves feeding links which would disappear if the predator became extinct. In the case of predator-specific defence, a prey is likely to experience a larger total predation pressure than in the case of non-specific defence, because the prey cannot defend against all predator species simultaneously. Although the total abundance of all predator species may depend on parameter values such as intraspecific density effects ($a_i$ and $b_k$), the ratio of predator to prey abundance for the case of predator-specific defence was likely to be larger than for the case of non-specific defence. This is a consequence of the greater mean success of predators in multispecies communities when there is predator-specific defence. These results could change if we assumed that non-specific defence was less effective than specific defence.

Figure 2 is a typical example of CSSs in two systems having identical parameter values, but one having non-specific (Equation 2a) and the other having predator-specific (Equation 2b) defence. In Fig. 2(a), predators 4 went extinct, while all predators co-existed in Fig. 2(b). The number of actual links in Fig. 2(a) is 14, which is smaller than the 18 links in Fig. 2(b). We did not count links to extinct predators as actual links. All of the links (except that connecting prey 10 to extinct predator 4) that are present in Fig. 2(a) are also present in Fig. 2(b). Connectance $C$ in Fig. 2(a) is 0.16, which is smaller than the $C$ for Fig. 2(b), which is 0.18. The foodweb in Fig. 2(a) is divided into five isolated subwebs of consisting of the following sets of predator

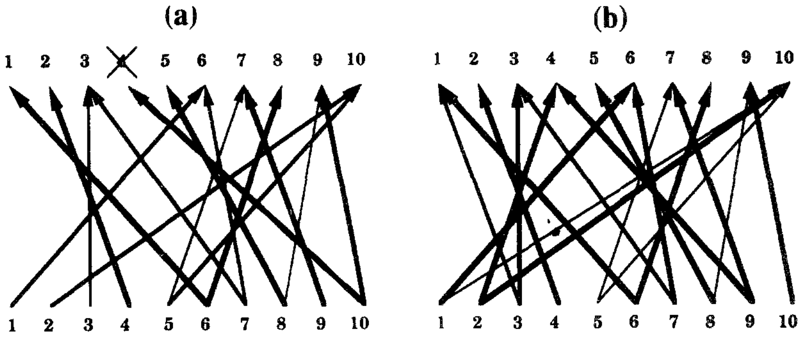

Figure 2. Resultant foodwebs of 10-prey-10-predator system in the cases of (a) non-specific defense and (b) predator specific defense with the same parameter values. The upper and lower numbers respectively represent predator and prey species. The width of an arrow indicates the magnitude of $\log[f_{ki}(1 - v_{ik})]$. See the text for detail.

species: (1, 8), (2), (3, 6), (5, 9) and (7, 10). On the other hand, the foodweb in Fig. 2(b) is divided into three subwebs: (1, 3, 6, 7, 8, 10), (2) and (5, 9). Although we showed the prey choice of extinct predators in Fig. 2(a), it would be difficult to observe the adaptive prey choice of extinct predators in a real community. A rare or extinct predator uses only one prey species at a CSS in both non-specific and specific defence. This is because no prey species exerts vigilance against a rare predator species and the predator will therefore only consume that prey species which it can capture most rapidly. Because the predator is rare, it does not depress the density of this prey and it is therefore not adaptive for the predator to broaden its diet. Thus, in our model, which assumes predators have prey-specific searching, specialization is a consequence of rarity, rather than the reverse.

If there is a non-specific search and no handling time and no evolutionary trade-offs between capture rates, the correlation between rarity and specialization may not occur at the level of biological species. However, it is still likely to occur at the level of trophic species. Biological species that can be searched for simutaneously will be a single trophic species.

We investigated the number of links of foodwebs at CSSs starting with 8, 12, 16 and 20 species ($S_1 = S_2$ are, respectively, equal to 4, 6, 8 and 10). We examined 100 simulations for each case. The number of links ($L^*$) increased proportionately with the number of species ($S^* = S_1^* + S_2^*$) both for non-specific defence ($L^* \approx 0.703S^*$, sum of squared errors = 559) and specific defence ($L^* \approx 0.825S^*$, sum of squared errors = 1307) as shown in Fig. 3.

There is currently a debate regarding the relationship between the number of links and the number of species in a foodweb. Cohen *et al.* (1990), using foodwebs culled from the literature, found the relationship to be directly proportional, as in Fig. 3. However, more detailed, longer-term studies suggest that the number of links increases disproportionately with the number of species (Martinez, 1991; Polis, 1991). Our models seems to be more consistent with the observations of Cohen *et al.* (1990). However, this consistency may be a result of some of our simplifying assumptions. It is possible that our models would predict a non-linear link-species relationship if environmental variability or endogenously driven cycles were present; in these cases some links may be present only temporarily. It may be that the studies of Polis (1991) and Martinez (1991) differ from those reviewed in Cohen *et al.* (1990) by the inclusion of more such variable links. It is also possible that inclusion of more trophic levels, omnivory, non-specific

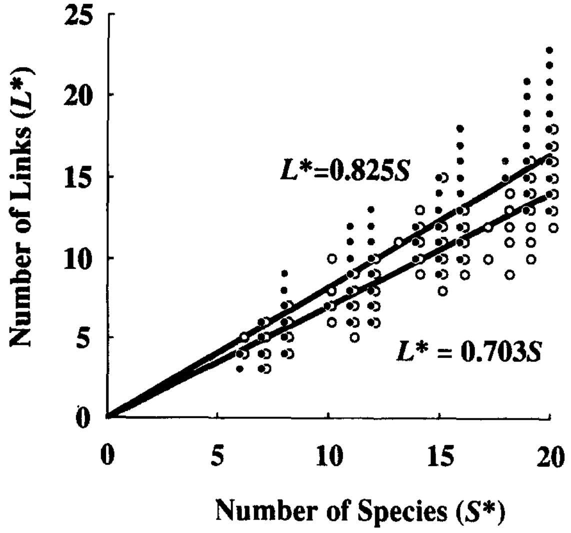

Figure 3. The number of species versus the number of links of CSS's starting with 8, 12, 16 and 20 species. Open and closed circles respectively represent CSS's for non-specific and specific defense. Lines represent regression lines for these cases.

searching by predator or other factors would change our predicted link-species relationship to a non-linear one, even in the absence of variability.

The results of this analysis qualitatively support those of earlier analyses (Matsuda *et al.*, 1993, 1994) using simpler models. Predator-specific defence by prey promotes both community complexity and the co-existence of predator species. However, it is clear that there are a number of other effects of the specificity of defence beyond these simple generalizations. More specific defence allows greater overlap in resource use between predators and is likely to result in higher predator biomass. Community complexity is usually evaluated by the number of links and the number of species in a community and our results suggest that there will be greater connectance in communities with specific defence. However, connectance treats all feeding links as equivalent, regardless of their strength. For example, the connectance of a two-prey-two-predator system with $f_{11} = f_{22} = 0.9$ and $f_{12} = f_{21} = 0.1$ is the same as the connectance of a system with $f_{ki} = 0.5$ for any $i$ and $k$. Because the niche overlap between predators in the former system is much smaller than the overlap in the latter system, the former system is much more likely to result in the co-existence of predators than is the latter if the antipredator behaviour is non-specific. To incorporate this variance in the strengths of the actual capture rates per unit prey density into the connectance, we define a new index of community complexity, which we call 'effective connectance':

$$C^* = \frac{1}{S_1 S_2^*} \times \sum_{k=1}^{S_2^*} \frac{1}{\sum_{i=1}^{S_1} q_{ki}^2} \tag{15a}$$

where

$$q_{ki} = \frac{e_{ik} f_{ki}^*(1-\upsilon_{ik}^*)}{\sum_{j=1}^{S_1} e_{jk} f_{kj}^*(1-\upsilon_{jk}^*)} \tag{15b}$$

This coincides with the connectance when the links that are present are equal in strength [$e_{ik}f_{ki}^*(1-u_{ik}^*) = e_{jk}f_{kj}^*(1-u_{jk}^*)$ if predator $k$ uses prey $i$ and $j$]. The quantity $q_{ki}$ represents relative preference of predator $k$ to prey $i$. The mean (± sd) values of $C^*$ for the case of non-specific defence and predator-specific defence were, respectively, 0.13 (± 0.01) and 0.15 (± 0.01). The difference in $C^*$ between non-specific and specific defence is smaller than the difference in $C$. This suggests that there was greater similarity in the strengths of feeding links in the case of specific defence than in the case of non-specific defence.

One of our assumptions is that there is no limit to the number of defensive tactics and the predators' search strategies are equally prey-specific regardless of the number of prey in the community. There is likely to be a finite range of prey defences. Predators' search strategies are likely to become less specific as the number of prey increases. This will lead to an increase in the number of biological species per trophic species as the species number increases. This does not affect the conclusions of Cohen *et al.* (1990) for trophic species. However, Matsuda and Namba (1991) predicted that the number of links per trophic species will increase linearly with the number of biological species. This means that the number of links per biological species will increase faster than linearly with species number. It is easier to misidentify a trophic species than a biological species. The number of errors is likely to increase as the number of biological species per trophic species increases. This is another possible reason for the differences between the results of Cohen *et al.* (1990) and those of Polis (1991) and Martinez (1991).

## Discussion

It is certainly true that many antipredator traits and behaviours in nature are at least partially effective against more than one type of predator. However, our simulations of partly-specific defence (Table 1) indicate that it has many of the same qualitative effects on community structure as does perfectly-specific defence. It is quite common for different predators to be restricted to different habitats (e.g. Power, 1984; Heads, 1985; Rahel and Stein, 1988; Schlosser, 1988; Kotler *et al.*, 1993), which should lead to some specificity of defensive behaviour among mobile prey that are able to detect predation risk. Unfortunately, relatively little is known about the specificity of defence in larger communities compared to simpler communities. Hori's (1987, 1993) examples of highly predator-specific defence in a very species-rich community (Lake Tanganyika) is consistent with the findings of our models, that greater defensive specificity allows greater complexity.

The simulations shown in Tables 1 and 2 assumed that there was a strong negative intraspecific effect of density on fitness in both prey and predator species; this increases the likelihood of dynamic stability. However, negative density effects in theory do not ensure that the equilibrium will be dynamically stable, because trait values can fluctuate even when population densities are kept constant. The stability of the equilibrium point depends on the dynamics of the co-evolutionary process and parameter values of $\kappa$ in Equations 7 and 8a. We also examined $\kappa \gg 1$, which is appropriate for adaptive change in behavioural traits. These traits typically change much faster than do population densities. The frequency of unstable systems with $\kappa = 100$ was slightly different from the frequency shown in Table 1 ($\kappa = 1$). However, the frequencies were still very low. Nevertheless, the exact conditions producing cycles have not been derived and cycles may be more common in the general case when different species have different rates of adaptive change.

The simultaneous attempts by both predator and prey to maximize fitness by habitat selection behaviour has been shown to be capable of producing a permanent oscillation in such behaviours (Schwinning and Rosenzweig, 1990). In this case, the predator's habitat selection represents choice and the prey's habitat selection represents defence. In Schwinning and Rosenzweig's (1990) model, the same predator species can exploit prey in both habitats at equilibrium, while in our model, use of different antipredator behaviours (analogous to selection of different habitats) means that the prey will be exploited by different predator species. Cycles seem to arise in Schwinning and Rosenzweig's (1990) model because of the time lag involved in each species' response to the other's change in distribution. In fact, a polymorphism in jaw asymmetry of a scale-eating fish in Lake Tanganyika seems to be maintained by prey-specific defence. The frequency of different predator phenotypes oscillates with the period of several years (Hori, 1993; Takahashi and Hori, 1994). Schwinning and Rosenzweig (1990) found that cycles were most likely when there was no cost to the process of habitat shift. Although our multispecies models ignore costs to choice and defence strategies, we consider not only trade-off between vigilance against two predators but also trade-off between vigilance and foraging effort of prey. The presence of trade-off between antipredator effort and another behaviour could stabilize the ideal free distribution.

Our results here are similar in some ways to those of Frank (1994a, b), who has studied hos-parasite co-evolution with population dynamics. He also finds that co-evolution promotes diversity provided that the consumers (parasites in his models) vary in their inherent abilities to attack different food species (hosts).

The relationship between community complexity and the stability of population dynamics has been of interest to ecologists at least since Elton's (1958) book. Models based on randomly constructed community matrices suggested a negative relationship between complexity (either connectance or number of species) and stability (May, 1972, 1973). Some limitations of this analysis have been explored by DeAngelis (1975, 1980) and Haydon (1994). Haydon's (1994) recent work stresses that increasing relationships between stability (defined as return time) and complexity often occur in models when there is sufficient between-species variability in the strength of intraspecific density dependence. However, this relationship apparently has not been investigated for models in which community structure is constructed from co-evolutionary change as is true here. Future work will consider the effects of co-evolutionary change in prey choice and antipredator effort on the complexity-stability relationship.

## Acknowledgements

We thank Dr Y. Nishida for suggesting the concept of the number of subwebs. We also thank Drs Y. Iwasa and L. Oksanen who is a reviewer for valuable comments on our earlier manuscript. This work was supported in part by a Japan Ministry of Education, Science and Culture Grant-in-aid for Priority areas (no. 319) to M.H., grant-in-aid for Encouragement of Young Scientists (no. 06740581) to H.M. and grants from the National Science Foundation (BSR 8918646 and IBN 9202342) to P.A.A.

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