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Game theory as a conceptual framework for managing insect pests

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For over 100 years it has been recognized that insect pests evolve resistance to chemical pesticides. More recently, managers have advocated restrained use of pesticides, crop rotation, the use of multiple pesticides, and pesticide-free sanctuaries as resistance management practices. Game theory provides a conceptual framework for combining the resistance strategies of the insects and the control strategies of the pest manager into a unified conceptual and modelling framework. Game theory can contrast an ecologically enlightened application of pesticides with an evolutionarily enlightened one. In the former case the manager only considers ecological consequences whereas the latter anticipates the evolutionary response of the pests. Broader applications of this game theory approach include anti-biotic resistance, fisheries management and therapy resistance in cancer.

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Introduction

Game theory is the field of mathematics devoted to solving conflicts of interest between two or more players. It solves problems where your best action (strategy) depends upon the strategies of others. In nature, game theory is particularly suited for understanding adaptations emerging from evolution by natural selection [1•]. "The deer flees and the wolf pursues" [2] succinctly describes games between predators and prey. The evolution of pesticide resistance represents a special and economically crucial case of predator–prey games. Here, we illustrate how classical game theory and evolutionary game theory can be conjoined to produce bioeconomic games of pesticide resistance. Game theory and pest management thus become part of integrated pest management [3,4].

The evolution of biocide resistance marks the most dramatic, damaging and rapid manifestations of natural selection. Examples of rapid evolution in response to humans attempts to chemically control pests include herbicide resistance [5–8], antiobiotic resistance (*e.g.*, MRSA [9]), drug resistance by parasites (*e.g.*, malaria, [10,11]), and at the most personal level, the evolution of therapy resistance in human cancers [12,13]. Here we shall focus on the use of pesticides to control insect damage to agricultural crops, but the concepts and models can be extended to these other examples of disease and pest control.

We shall review the problem of pesticide resistance as a bio-economic game. The game has insect players that may evolve pesticide resistance, and the farmers in addition to the manufacturers and regulators represent players with economic and social interests. Such games can consider human health and environmental consequences of pesticides, and they can be added as costs and externalities. With the aim of sharing the contexts of pesticide games, we shall introduce a simple model for illustrating concepts. We shall emphasize the comparison between ecologically versus evolutionarily enlightened [14] approaches to pesticide applications [15•]. Throughout, we shall discuss parallels in such systems as fisheries management [16], anti-biotic resistance in infectious diseases [17•], and therapy resistance in cancer [18]. In conclusion, we advocate greater use of game theory in developing *resistance management practices* [19].

Pesticide management as game

The interacting players in the game can be diverse and include society at large, regulators, biocide manufacturers, seed companies breeders, the birds or spiders that consume the pest, and of course, the farmers and the insect pest [20]. The insects and other species within the ecosystem find themselves in an *eco-evolutionary game* where ecological dynamics occur through changes in population size and evolutionary dynamics involve heritable changes in the species. In an evolutionary game the individuals (players come and go through births and deaths), their strategies are inherited, and their payoffs take the form of increased survivorship and breeding [21]. The solution to such games are often *evolutionarily stable*

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strategies (ESS) [22]. An ESS is a strategy (or coexisting set of strategies) that when common cannot be invaded by any rare alternative strategies.

The farmers or other human players engage in a more traditional, classical game. They choose rather than inherit their strategies, and payoffs take the form of monetary and/or utility rewards. Furthermore, the human players can anticipate and plan for the responses of other players [23]. Players in evolutionary games can never evolve a response to something that has not yet happened. The solution to classical games can be the *Nash Solution* [24]. This is a no regret strategy. When all players are at a Nash solution no individual player can benefit from unilaterally changing his/her strategy.

As humans we can anticipate the evolutionary consequence of our actions on nature. Yet in managing, we often do not anticipate but merely respond to the evolutionary changes we cause. And so it is with much of pest management. We respond to the ecological costs and benefits of our biocides without regard to their evolutionary consequences. We shall call this *ecologically enlightened management*. Game theory explains the temptation to simply be ecologically enlightened stewards. Game theory is also ideal for anticipating and incorporating the eco-evolutionary dynamics that we cause. When both the population and evolutionary dynamics of the species of interest are incorporated into human decision making we shall refer to this as *evolutionarily enlightened management* (sensu [25]).

To keep things simple, we will view pesticides as a game of the farmers versus the insect pests. The game may take a general form of:

$$G(u,m,N) = F(u,N) - \mu(u,m) \qquad (1)$$

$$\Pi(u,m,N) = Y(u,N) - cm \qquad (2)$$

where G is the per capita growth rate of the insect pest and Π is the net profit to the farmers. The per capita growth rate of the insects is the difference between their growth rate in the absence of pesticides, F, and the mortality rate induced by the application of pesticides, μ. The farmers' net profit is the difference between the crop harvest, Y, and the cost of the pesticides. Each of these are functions of the resistance strategy of the insects, u, the rate at which pesticides are applied, m, and the density of insects, N.

We can assume that the insect's per capita growth rate, F, in the absence of pesticide declines with insect density, N, and that their resistance strategy, u: $\partial F/\partial N < 0$ and $\partial F/\partial u < 0$ represent negative density-dependence from competition and the cost of resistance, respectively. The insect's mortality rate from the pesticide declines with their resistance strategy ($\partial\mu/\partial u < 0$) and increases with the dosage of pesticide ($\partial\mu/\partial m > 0$). In this formulation the population growth rate of the insects is given by $\frac{dN}{dt} = NG(u,m,N)$. See Table 1 for more details regarding the model assumptions.

Crop yield will decline with the density of insects ($\partial Y/\partial N < 0$) and it may decline directly with the resistance strategy of the insects if this renders the insects less efficient foragers (an additional cost of resistance; $\partial Y/\partial u > 0$). The cost of pesticides is simply the product of their cost, c, and the rate at which pesticides are applied, m.

In the absence of pesticide, or under some critical level of pesticide, the optimal level of pesticide resistance for the insects will be $u^* = 0$. As applications of pesticide increase, the optimal level of resistance will also increase.

Table 1

Model basics

Pests' perspective			
Dynamics of pests' density *N*	$\dot{N} = \dfrac{dN}{dt} = NG(u,m,N)$		
Fitness generating function	$G(u,m,N) = r\frac{(1-u)K-N}{K} - \frac{m}{k+bu}$		
Optimal level of pesticide resistance *u**	$u^* = \mathbf{arg}\max_u G(u,m,N) = \sqrt{\frac{m}{rb}} - \frac{k}{b}$		
Equilibrium density of pests *N**	$N^* = K(1-u) - \frac{mK}{(k+bu)r}$		
Farmer's perspective			
Net profit of the farmer *Π*	$\Pi(m,N,Y) = Y\left(1 - aN^2\right) - cm - \gamma$		
	Ecologically enlightened pest control	Evolutionarily enlightened pest control	Neither
$\frac{\partial\Pi}{\partial m}$	$-2aYN\frac{\partial N}{\partial m} - c$	$-2aYN\left[\frac{\partial N}{\partial m} + \frac{\partial N}{\partial u}\frac{\partial u}{\partial m}\right] - c$	$-2aYN - c$
$\frac{\partial N^*}{\partial m}$	$-\frac{K}{r(k+bu)}$	$-K\frac{\partial u}{\partial m} - \frac{rK(k+bu) - bmrK\frac{\partial u}{\partial m}}{r(k+bu)^2}$	n.a.

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