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Reconstructing past population processes with general equilibrium models: House mice in Kern County, California, 1926–1927

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ABSTRACT

Reconstructing past ecosystem conditions is helpful in addressing a range of basic and applied questions, but difficult because of a lack of inferential or modeling approaches. Here, we demonstrate the use of a general equilibrium ecosystem model (GEEM) to investigate ecological conditions surrounding a population eruption of the house mouse (*Mus musculus*) in Kern County, California in the 1920s, arguably the most dramatic mammalian population eruption reported for North America. Our application of GEEM to this ecosystem allowed us to evaluate the plausibility of reported population densities of house mice that were extreme, even in comparison with values for the same species introduced in Australia, and to examine alternative hypothetical community interactions and their effects on populations. The modeled ecosystem included vegetation, native small rodents and introduced house mice as herbivores, and mammalian predators. Individual plants and animals behaved as net energy optimizers, with net energy directed to reproduction. Optimizing predators determined the biomass taken from prey, and prey, through feeding choices, determined their vulnerability to predators. Model inputs incorporated the competitive superiority of house mice to native small rodents, the time of arrival of house mice in the area, and the timing and intensity of predator removal. Without an invasion of house mice, human removal of predators was predicted to minimally affect native small rodents. Without human removal of predators, invading house mouse populations were predicted to attain high, oscillating densities by the 1920s that stabilized at lower densities by the 1930s, with native small rodents persisting in the area. With near-complete human removal of predators and with house mice present, native small rodents were predicted to go nearly extinct, and house mice to attain densities similar to those reported. The predicted lag between the introduction and eruption of house mice approximated reported values. Predation on native and introduced rodents was predicted to allow both rodent groups to coexist, whereas near-complete removal of predators caused native small rodents to approach extinction during the house mouse eruption, consistent with empirical studies. GEEM appears to be a useful tool for reconstructing past ecosystem conditions and trophic interactions.

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1. Introduction

Reconstructing past ecosystem conditions is important to a range of basic and applied ecological questions. It allows us to understand the functioning of systems no longer available for empirical study, and to gain insights into ecological events too rare or brief for field investigation. Although various modeling approaches allow retrospective investigation of population, energetic, or biomass processes (Cox et al., 2002), few models allow linkages among these currencies (Tews et al., 2006). Here we report on the use of general equilibrium models, which allow linkages among all three currencies, to investigate a brief, dramatic population eruption of the house mouse (*Mus musculus*) in Kern County, California in 1926–1927.

General equilibrium modeling was arguably the most important advance in economics in the 20th century (Sandler, 2001). Its purpose is to predict important variables in an economic system that result from the interactions of numerous consumers and firms, all of which are assumed to optimize some objective function. An economic system is adaptive in that individual consumers and firms respond to changes in the important variables, yet it is their aggregated behaviors that determine these variables. The general equilibrium approach also has been used to derive general functional forms for species dynamics (Christiaans et al., 2007; Eichner and Pethig, 2006). The general equilibrium ecosystem model (GEEM) is an appropriately modified version of an economic general equilibrium model applied to adaptive ecosystems (Tschirhart, 2000). Consumers and firms are replaced by individual plants and animals, and each individual is assumed to behave as if it is optimizing net energy intake, which is channeled into maintenance and reproduction. Including reproduction means that GEEM, unlike most economic general equilibrium models, is dynamic, an example of what Nisbet et al. (2000) described as a model linking individual processes to those at higher organizational levels.

GEEM has been applied to several ecosystems with or without connections to economies. These include a 13-species marine system in the Bering Sea, where commercial fishing affects both native trophic interactions and economic activity (Finnoff and Tschirhart, 2003; Tschirhart, 2004). It also has been used to model the impacts of agricultural runoff into a North Carolina estuary (Finnoff and Tschirhart, in press), and the impacts of invasive plant species in a Great Plains grazing system (Finnoff et al., 2007).

Here, we use GEEM to model population dynamics and flows of biomass and energy in an ecosystem that included vegetation, native small rodents as herbivores, and predators, and which was subject both to the introduction of house mice and removal of predators by humans. Our case study is from an historic eruption of the house mouse in California in the 1920s, arguably the most dramatic mammalian population eruption reported for North America (Pearson, 1963). Such eruptions of house mice have been reported from other regions (Singleton and Redhead, 1990); Australia in particular has a history of them. Certain environmental features (Singleton et al., 2005) are common. First, eruptions tend to occur in grain-producing areas with typically mild winters. Second, they tend to be associated with unusual rainfall and food supply conditions (Brown and Singleton, 1999). Third, they are aperiodic and their amplitudes unpredictable, but they can reach absolute densities of >2000 mice ha^{-1}.

We were interested in applying GEEM to the Kern County ecosystem of the 1920s because it presents an especially challenging test of the general equilibrium approach, given the extreme population attributes described in the historical record. For example, reported population densities of house mice were higher by a factor of 6 than those typical of “major plagues” in Australia (Singleton et al., 2005). Are such densities plausible, given the other ecosystem conditions present in Kern County at the time? And, given the estimated time that the house mouse invaded the ecosystem, and that humans began eliminating predators, are the predicted times of dramatic population behaviors consistent with the historical record? Further, what insights can GEEM provide on the interactions of species introductions, predator removal, and native species persistence?

2. The Kern County mouse eruption

On 10 January 1927, the Museum of Vertebrate Zoology, University of California was notified of a rodent eruption in Kern County, California characterized by “...highway[s] plastered with dead mice, and millions of them alive chasing across the highway...” E. Raymond Hall investigated the report and found that the rodents were house mice (*Mus musculus*). The latest outbreak had followed two others that began in November 1926. The affected area was about 27 km in diameter and centered on the dry bed of Buena Vista Lake. The areas north and south of the lake were reported as barren hills with little human habitation. East of the lake and in the lakebed itself, the land was cultivated in barley, wheat, milo, and cotton. The crops were thought to provide food and shelter for the mice, but after the autumn harvest and sheep grazing, little food and shelter remained and the mice began an outward migration from the lakebed.

Hall (1927) estimated exceedingly high densities of mice; in the densest areas he found 20.6 small rodents m^{-2} (205,700 [2805 kg] ha^{-1}, 5000 ha^{-1} over hundreds of km^2). These values are so high as to strain ecological creduity; they exceed those in “major plagues” in Australia by a factor of 6, and the highest values reported from Australia by a factor of 2 (Singleton et al., 2005). About 15% of the mice were the much larger-bodied California vole (*Microtus californicus*), found mostly in crowded burrows, whereas the house mice were virtually everywhere. The farmers and businesses in the area spread poisons and in one barn killed 1818 kg of mice in 1 day.

The mouse control campaign began in late January, 1927, when Stanley Piper from the Bureau of Biological Survey arrived to battle against an estimated >10^8 mice (Piper, 1928). Eschewing the flute approach used by the Pied Piper of Hamelin, this Piper used a crew of 25 men to lace 36,000 kg of alfalfa with strychnine. By the end of February victory was declared against what was labeled the worst rodent infestation in U.S. history, although no data allow evaluation of the efficacy of the eradication effort.