

Interspecific Competition and Pests:  
Managing the Impact of Feral Pigs on the Foxes of Santa Cruz Island

Richard T. Melstrom  
rtmelstrom@salisbury.edu

Abstract

This paper presents a model of pest impacts in a multispecies framework. Strong detrimental relationships often form between pest populations and other biota, damaging ecosystem services and reducing social welfare. Under these circumstances, optimal pest management must account for the interactions between pests and other species. The bioeconomic model of competition developed in this manuscript is illustrated using the case of feral pigs (*Sus scrofa*) on Santa Cruz Island, California. The presence of the pigs, an introduced species, resulted in the near extirpation of the native island fox (*Urocyon littoralis*) before managers intervened and removed the pigs from the island. The application shows that an optimal removal program for an established pest will initially require overculling the pest relative to the equilibrium level. For the foxes of Santa Cruz Island, the results indicate that strict permanent control of the pig population is the appropriate long run policy.

Keywords: Exotic species, invasive species, pests, bioeconomics, control, multispecies system, feral pigs, island foxes, Channel Islands

JEL Codes: C61, Q20, Q57

## 1. Introduction

Pests, both indigenous and exotic, are a form of biological pollution that significantly harms social welfare. Their impacts include billions of dollars in lost marketable goods and control costs as well as biodiversity loss. It is estimated that more than half of all endangered species are at risk due to competition with or predation by nonindigenous species (Pimentel et al., 2005) and, furthermore, some indigenous species have also been implicated in endangering other native wildlife (DeCesare et al., 2010). A major policy goal in natural resource management is the restoration of habitat conditions and wildlife in high-valued ecosystems impacted by invasives (NISC, 2008). Physical removal or harvesting of pests and harmful invasives is a key method in managing these adverse impacts (Olson, 2006).

A large portion of the pest control literature analyzes damage mitigation policies using dynamic bioeconomic models. This approach is useful because pests are biological resources although it also complicates the analysis (Burnett et al., 2008). Perhaps for this reason, most of the literature limits the bioeconomic model to the pest species itself and explores innovations in control programs. These models have been used to study problems with insects (Ceddia et al., 2009), weeds (Pannell, 1990; Eiswaerth and van Kooten, 2002; Burnett et al., 2006) and invasive species (Zivin et al., 2000; Eiswaerth and Johnson, 2002; Burnett et al., 2008), as well as generic pest control policies such as eradication (Olson and Roy, 2008).

An important consideration in the control of a pest is its interaction with other wildlife (Barbier, 2001; Eppink and van den Bergh, 2007). When these interactions significantly impact ecosystem functions, efficient management strategies must account for the secondary species effects from managing pests and invasives (Zavaleta et al., 2001). Ignoring these interactions means ignoring spillover effects, which can result in inefficient pest control policies. This was

recognized early by Feder and Regev (1975), who showed that when pest control applications harm the predator of a pest, myopic decision making can actually increase pest damages.

Subsequent work has investigated other situations in which the pest is a predator (Settle et al., 2002; Settle and Shogren, 2002), prey (Harper and Zilberman, 1989; Fenichel et al., 2010), competitor (Barbier, 2001; Frésard and Boncoeur, 2006) and parasite (Sims et al., 2010).<sup>1</sup>

However, most of this research has focused on pests that generate market damages rather than those that have significant nonmarket impacts.

This paper is concerned with the situation of an exotic pest competing with valuable native wildlife. The theoretical multispecies model is akin to that of Barbier (2001) and Frésard and Boncoeur (2006) who also analyze a pest engaged in interspecific competition, although there are key differences. First, the native wildlife is valued through its existence rather than through some commercial or recreational activity, e.g. harvests. The paper therefore builds on prior work by analyzing ecosystem interactions involving an exotic species and nonmarket impacts. Second, because there is no incentive to harvest the valued wildlife the system is managed only through predator removal. Optimal control theory is used to solve for the removal policy that maximizes social welfare over time.

The optimal removal policy is illustrated for the case of the endangered island fox (*Urocyon litoralis*) and feral pig (*Sus scrofa*) on Santa Cruz Island, California. Although exotic species were long recognized for causing widespread damage to the natural resources of the island (NPS, 2002), the pigs' impact on fox survival became a special concern in the late 1990s

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<sup>1</sup> Several other papers do not analyze multispecies pest control specifically but study related problems. In regards to pest management, Skonhofs and Olaussen (2005) study pest harvesting strategies to improve the value of a metapopulation system, Finnoff and Tschirhart (2005) model plant competition to help identify successful invasive plant species, and Gutierrez and Regev (2005) model a multiple-trophic level system to show how species maximize their adaptedness over time, which can result in local extinctions for other species. For a review of multispecies bioeconomic modeling in general, see Tschirhart (2009).

when the fox population fell to extremely low levels (Coonan, 2003). Pig removal was a dominant issue until an extermination program was successfully carried out in 2006. This paper examines the optimal pig removal strategy where pig damages are a function of the fox population. The results suggest that a considerable and permanent reduction in the pig population is desirable, although eradication appears suboptimal for fox conservation per se. The results of this numerical application show that an optimal removal program for an established pest will generally require initially overculling the pest relative to the equilibrium population in order to jumpstart recovery of the ecosystem.

## 2. Multispecies bioeconomic model

The model should capture the feedbacks between a pest and the flora and fauna within an ecosystem. To keep the analysis tractable, the affected flora and fauna is modeled as a single stock  $f$ . This stock could be viewed as the biomass for all wildlife in an ecosystem, the biomass of a keystone species or the population of a charismatic species. The pest stock is notated by  $p$ . The biological interaction between the pest and affected wildlife consists of a pair of impacts that determines whether the relationship is one of amensalism, competition or predation. This paper focuses on the competitive case, i.e. that a pest negatively impacts the stock of wildlife and vice-versa. The dynamics of the two stocks are therefore modeled as the two equations

$$(1) \quad \frac{df}{dt} = g(f) - m(f, p)$$

$$(2) \quad \frac{dp}{dt} = q(p) - n(f, p) - h(t)$$

where  $g(\cdot)$  is the natural growth of  $f$ ,  $q(\cdot)$  is the natural growth of  $p$ ,  $m(\cdot)$  is the reduction in growth of  $f$  due to competition with the pest and  $n(\cdot)$  is the corresponding reduction in  $p$  from

competition. The final term in eq. (2) is the reduction in the growth of the pest due to management, which is modeled as a harvest rate.

A manager wants to maximize the net benefits of the multispecies system or, in other words, minimize the damages from the pest plus control costs. The pest creates social damages by reducing  $f$  and its ecosystem service value, which is denoted by  $V(f)$ , where  $V_f > 0$  and  $V_{ff} < 0$ . The cost of pest control—specifically, pest removal—is defined as  $c(p)h(t)$ . The term  $c(p)$  is the per-unit cost of removing a pest, where  $c_p < 0$  and  $c_{pp} > 0$ . Removal costs are increasing and convex because it becomes increasingly costly to find and trap pests as the population of pests diminishes (Horan and Melstrom, 2011). The management objective is to

$$(3) \quad \max_{h(t)} SNB = \int_0^{\infty} [V(f) - c(p)h(t)] e^{-\rho t} dt$$

subject to (1), (2),  $0 \leq h(t) \leq h_{\max}$ ,  $f(0) = f_0$ ,  $p(0) = p_0$

where  $\rho$  is the discount rate. The current value Hamiltonian for problem (3) is

$$(4) \quad H = V(f) - c(p)h(t) + \lambda_f(t)[g(f) - m(f, p)] + \lambda_p(t)[q(p) - n(f, p) - h(t)]$$

where  $\lambda_f(t)$  and  $\lambda_p(t)$  are the adjoint or co-state variables (Clark, 1976).

The solution to problem (3) involves choosing  $h$  to maximize  $H$ . The marginal impact of  $h(t)$  on  $H$  is

$$(5) \quad \frac{\partial H}{\partial h} = -c(p) - \lambda_p(t)$$

The right-hand side (RHS) of eq. (5) includes the marginal costs of removal,  $-c(p)$ , and the marginal intertemporal benefit of culling a pest,  $-\lambda_p(t)$  (the pest co-state will be negative). It is optimal to set  $h = 0$  when eq. (5) is negative and  $h = h_{\max}$  when eq. (5) is positive. The singular value for  $h$ ,  $h_{SV}$ , is optimal when eq. (5) is zero. That is,  $h_{SV}$  requires

$$(6) \quad \lambda_p(t) = -c(p)$$

which suggests that the pest should only be removed when it has negative value. Assuming the optimal equilibrium strategy does not occur at  $h = 0$  or  $h = h_{max}$ , then eq. (6) is a necessary condition for a solution.

A solution must also satisfy two adjoint equations:

$$(7) \quad \frac{d\lambda_f}{dt} = \rho\lambda_f(t) - V_f - \lambda_f(t)[g_f - m_f] + \lambda_p(t)n_f$$

$$(8) \quad \frac{d\lambda_p}{dt} = \rho\lambda_p(t) + c_p h(t) + \lambda_f(t)m_p - \lambda_p(t)[q_p - n_p]$$

Eqs. (7) and (8) show how the co-states should evolve over time. If pest removal proceeds optimally, then eq. (7) says that  $\lambda_f(t)$  will vary depending on its own current value, the discount rate, marginal value of  $f$ , the marginal net growth of  $f$ , the pest co-state and marginal effect of  $f$  on pest growth. Likewise, eq. (8) says that  $\lambda_p(t)$  will vary depending on its own current value, the discount rate, the marginal cost of removal with respect to  $p$ , the removal rate, the valued wildlife co-state, the marginal effect of  $p$  on wildlife growth and the marginal net growth of  $p$ .

Focusing on the interior solution, the optimal pest control strategy is determined by using eqs. (6), (7) and (8). The singular solution for  $h$  is found by taking the time derivative of eq. (6) to get

$$(9) \quad \frac{d\lambda_p}{dt} = -c_p \cdot \frac{dp}{dt} = -c_p [q(p) - n(f, p) - h(t)]$$

The expressions for  $\lambda_p(t)$  and  $d\lambda_p/dt$  from eqs. (6) and (9), respectively, should be inserted into eq. (8). This yields the following:

$$(10) \quad \lambda_f(t) = \frac{c(p)[\rho + n_p - q_p] - c_p [q(p) - n(f, p)]}{m_p}$$

The numerator of eq. (10) consists of a positive term minus a negative term. The denominator is positive. The complete expression equates the co-state for  $f$  with the marginal cost of pest

management divided by the marginal effect of the pest on  $f$ . In effect, eq. (10) says that the manager should only invest more resources into pest control if society places greater value on  $f$ .

An explicit equation for  $h_{SV}$  is found using eqs. (7) and (10). Taking the time derivative of eq. (10) yields

$$(11) \quad \begin{aligned} \frac{d\lambda_f}{dt} &= \frac{\partial\lambda_f(t)}{\partial f} \cdot \frac{df}{dt} + \frac{\partial\lambda_f(t)}{\partial p} \cdot \frac{dp}{dt} \\ &= \frac{\partial\lambda_f(t)}{\partial f} \cdot [g(f) - m(f, p)] + \frac{\partial\lambda_f(t)}{\partial p} \cdot [q(p) - n(f, p) - h(t)] \end{aligned}$$

Inserting this expression into eq. (7) yields the following:

$$(12) \quad h_{SV}(f, p) = q(p) - n(f, p) + \frac{V_f + \lambda_f [g_f - m_f - \rho] - \lambda_p n_f + \partial\lambda_f / \partial f \cdot [g(f) - m(f, p)]}{\partial\lambda_f / \partial p}$$

where the time notation is dropped for conciseness. From eq. (12), the singular value of  $h$  is a feedback rule that depends on the values of  $f$  and  $p$ .

The feedback control  $h_{SV}(f, p)$  will be combined with a bang-bang control to create the optimal pest control strategy. Why would a bang-bang control alone not be optimal here? The answer lies in the characteristics of the management problem, which involves managing a multispecies system with only a single control. The objective of pest removal is to recover one or several impaired wildlife species. Intuitively, a bang-bang control is too crude a method to optimally guide several populations. Note that this means the equilibrium strategy is not reached via a quick adjustment (i.e. a most-rapid-approach-path). Instead, the optimal pest control strategy will use a bang-bang control to reach some path through  $f$ - $p$  space defined by  $h_{SV}(f, p)$ . This path, which implies sluggish adjustment, is the preferred route to equilibrium because  $h$  directly affects only one state so optimally managing the entire system requires gradual adjustments in the control.

The problem of pest removal and wildlife recovery is examined numerically in the next section. A case study is used to illustrate the value of two different approaches to a solution. The first analyzes optimal ecosystem management, in which the populations of the pest and its competitor slowly adjust to equilibrium under the ideal pest control strategy. The second considers a pest control strategy that immediately adjusts the pest population to the equilibrium level.

### 3. Empirical illustration

#### 3.1. California Channel Islands foxes and feral pigs

A useful example of an ecosystem pest problem can be found on the California Channel Islands. This group of islands, located off the coast of the southwestern United States, is home to a large number of unique, endemic species. One of these species is the island fox (*Urocyon littoralis*), the smallest canid of North America and a descendent of the gray fox (*Urocyon cinereoargenteus*) (Roemer, 2004). The island fox has been subject to several mortality pressures brought about by human-induced landscape changes, including the introduction of feral pigs (*Sus scrofa*) in the nineteenth century. The fox-pig dynamic observed on Santa Cruz Island in particular provides the case study used in this paper.

A form of apparent competition developed between the foxes and feral pigs of Santa Cruz Island (Roemer et al., 2001). Feral pigs do not compete with foxes over food resources, but they can act as an abundant food source for predators that, in turn, overexploit native species, such as the island fox. Numerous endangered species problems are linked to this form of competition (DeCesare et al., 2010). In the 1990s, the large pig population allowed golden eagles to colonize Santa Cruz Island from the mainland. The presence of the eagles facilitated apparent competition



and drove the fox onto the U.S. endangered species list. This effect is illustrated in Figure 1, which is parameterized for the numerical model in the following section. In the figure, there are two pairs of  $df/dt = 0$  and  $dp/dt = 0$  isoclines representing the thresholds for changes in  $f$  and  $p$ , respectively, before and after the onset of apparent competition. When there is no competitive interaction ( $m = n = 0$ ) the fox and pig populations are near their carrying capacities at point A. With apparent competition the two populations fall to point B. Note that  $df_1/dt = 0$  and  $dp_1/dt = 0$  do not intersect, which suggests that the pigs will eventually drive foxes to extinction.

Recovering the fox population required an intensive ecosystem management program. The presence of the pigs caused the fox population on Santa Cruz Island to fall from about 1,500 to fewer than 100. The recovery program included eagle translocation early on, but eagles from the mainland and other islands could replace the removed birds (Roemer et al., 2001). It was therefore determined conserving the fox required feral pig control (Roemer et al., 2002; Coonan, 2003). In 2005, the U.S. National Park Service and the Nature Conservancy, which owns most of Santa Cruz Island, implemented a pig removal program. Within a year over 5000 pigs were removed and the species was successfully eliminated from the island (Griggs, 2007). The fox population has subsequently rebounded to a healthy level (estimated 734 +/-254 in 2008; Morrison, 2011).

### 3.2. Equations and parameters

Explicit functional forms are necessary to numerically illustrate a solution. The biological functions adopted here are consistent with those used in prior work (e.g. Kar and Chaudhuri, 2003; Burnett et al., 2006). Fox growth is modeled as  $g(f) = r_f(1-f/k_f)f$  with the competitive effect  $m(f,p) = \mu \cdot f \cdot p$ , where  $r_f$  is the intrinsic growth rate of foxes,  $k_f$  is the carrying capacity for foxes and  $\mu$  is a parameter accounting for apparent competition. Pig growth is modeled as  $q(p) =$

$r_p \cdot (1-p/k_p) \cdot p$  with the competitive effect  $n(f,p) = \eta \cdot (f + \delta) \cdot p$ , where  $r_p$  is the intrinsic growth rate of pigs,  $k_p$  is the carrying capacity for pigs,  $\eta$  is parameter accounting for apparent competition and  $\delta$  accounts for the mortality from eagles when  $f \rightarrow 0$ .

The biological parameter values are based upon work from published sources. The foxes' intrinsic growth rate,  $r_f$ , is 0.32 and carrying capacity,  $k_f$ , is 1544 (Roemer et al., 2002). The pigs' intrinsic growth rate,  $r_p$ , is 0.78 and carrying capacity,  $k_p$ , is 15189 (Roemer et al., 2002). The competitive effect on foxes,  $\mu$ , is 0.000066 so that the system (1)-(2) when left unmanaged predicts that a population of about 133 foxes remains 15 years after the onset of apparent competition (Roemer et al., 2002). The parameter  $\delta$  is selected such that 5000 pigs would be left if foxes went extinct (Roemer et al., 2001), i.e.  $0 = 0.78 \cdot (1 - 5000/15189) - \eta \cdot \delta \cdot 5000$ , which implies that  $\delta = 0.523/\eta$ . The parameter  $\eta$  is 0.000013 so that the model predicts there are 5036 pigs 15 years after eagles arrive and enable apparent competition, which is the number observed during the eradication effort (Griggs, 2007).

The nature of the economic benefits of the foxes is unknown, but given  $V_f > 0$  and  $V_{ff} < 0$  it seems reasonable to use  $V(f) = v \cdot \ln(1+f)$ , where  $v$  is a parameter. The island fox appears to be a charismatic species with substantial existence value. There are no published studies of the economic benefits of these foxes, so a value for  $v$  is determined using benefits transfer where  $v = (\text{aggregate WTP}_{\text{canids}})/\ln(1+k_f)$ . Chambers and Whitehead (2003) calculate the willingness to pay (WTP) for the Minnesota gray wolf (*Canis lupus*) preservation at \$21.49 per household with a 95% confidence interval of (10.66, 32.32). This WTP is multiplied by 1.14 to get \$24.50 (12.15, 36.84) in 2006 dollars. Assume that only California residents benefit from island foxes. There were about 12.29 million households in California in 2006, which suggests that lump-sum WTP

for fox preservation is \$264.11 million. Using a discount rate of 5% to annualize benefits, aggregate WTP is \$13205605, which suggests that  $v$  is 1798448.

The form of the removal cost function is based on a style used in the literature because the true function is unknown. The marginal cost of removal is  $c(p) = c/p$  where  $c$  is a parameter. It is known that pig eradication required removal of 5036 pigs and cost about \$5 million (Griggs, 2007). Assuming that eradication occurs when  $p \leq 1$ , the parameter  $c$  can be determined by the

formula  $\int_1^{5036} [c/p] dp = 5000000 \Rightarrow c \ln(5036) = 5000000$ , which indicates that  $c$  is 586554.

### 3.3. Pest control

First consider optimal ecosystem management. This is the strategy that maximizes the value from the fox-pig ecosystem by recognizing that the economic damages from the pigs arise from their impact on the valuable foxes. There are three types of strategies that could be optimal: no management, immediate pig eradication or the control of an endemic pig population through indefinite pig removal. The first yields *SNB* of \$155 million (with the foxes going extinct). The second yields *SNB* of \$234 million (assuming pigs go extinct once culled to  $p \leq 1$ ).

The third candidate strategy, optimal pig control strategy, involves several phases. Figure 2 presents these phases in a state-space diagram. The local dynamics of the system, determined by the singular control  $h_{SV}(f,p)$ , are indicated by phase arrows. The  $dp/dt|_{h_{SV}(f,p)} = 0$  isocline intersects the  $df/dt = 0$  isocline at point B, a saddle point equilibrium in the singular solution for  $h$ . To reach equilibrium there is a saddle path, labeled *SP* in the figure. This path is a switching curve that indicates it is optimal to set  $h = h_{\max}$  when the system lies to the right of the curve and  $h = 0$  when the system lies to the left of the curve. The first phase of the pig removal strategy involves culling a large number of pigs to move the system to *SP* because the system begins

somewhere to the right of point A. The second phase begins once the system reaches  $SP$  and engages  $h = h_{SV}(f,p)$  to proceed along the saddle path toward equilibrium. The third and final phase of pig removal occurs once the system reach equilibrium, which requires removing pigs indefinitely to maintain a small pig population and a large fox population. This yields  $SNB$  of \$238.4 million, so this strategy is first-best.

The optimal pig control strategy involves over-culling the pig population relative to the equilibrium level to jumpstart fox recovery. In the first years following the initial cull, the pig population is small and few pigs should be removed. The foxes recover more quickly than the pigs, although it gradually becomes necessary to intensify the rate of pig removal as the system approaches equilibrium. The time path for the system is presented in Figure 3(a).

Now consider a plausible alternative control strategy. Rather than initially overshooting the equilibrium, a manager may choose to cull just enough pigs to reach the desired equilibrium level. This is consistent with a most-rapid-approach-path (MRAP) to equilibrium. However, continuing to equilibrium still requires varying  $h$  over time because changes in the fox population impact the net growth of the pigs. To stabilize the pig population after the initial cull,  $h$  must be slightly higher than the equilibrium level but can be gradually reduced as the foxes recover. The time path of the system for this strategy is presented in Figure 3(b). This strategy yields  $SNB$  of \$238.3 million, which is nearly the same value as the optimal strategy.

The near-equivalence between the  $SNB$  of the optimal and alternative pig control strategies arises because the tradeoffs between the two strategies are rather minor. Both strategies involve a large initial cull and the steady recovery of foxes within about the same period of time. The chief difference lies in the first years of the removal program. The optimal strategy uses a larger initial cull to reduce the rate pigs must be removed in the next few years and allow foxes

to recover a little faster. Of course, the larger initial cull increases management costs in itself. Overall, this leaves the alternative control strategy nearly as good as the optimal strategy.

### 3.4. Sensitivity analysis of economic parameters

There was some uncertainty in the choice of economic parameters. In particular, the economic value of the foxes was determined through benefits transfer and the discount rate was assumed. So consider a sensitivity analysis to study how changing these parameters affects the results (Table 1). First, the 95% confidence interval bounds on the WTP estimate reported in Chambers and Whitehead (2003) were used to derive alternative benefit estimates for the foxes. A smaller benefit estimate reduces the steady state population of foxes and vice versa, although the proportional population change relative to the benchmark is small. On the other hand, a smaller benefit estimate increases the steady state number of pigs and vice versa, and the proportional change relative to the benchmark is quite large—an 88% increase in the first case. Although not illustrated, the optimal pig control strategy used here follows the same pattern as the benchmark case in Figure 3(a), in which the pig population is first driven to a low level and then allowed to recover somewhat as the fox population improves.

Next, consider a change to the discount rate. Relative to the benchmark, a smaller discount rate makes pig removal more worthwhile and yields a larger steady state fox population and a lower steady state pig population. As with changes in the benefit estimate of the foxes, variations in the discount rate have a greater relative influence on the pig population than on the fox population. Nevertheless, these changes do not alter the overall structure of the optimal pig control strategy.

The alternative management strategy proposed in the previous section is also analyzed in the sensitivity analysis. The *SNB* from these simulations are reported in the last column of Table 1. Although it necessarily remains suboptimal, it is clear that this control strategy does not result in significant foregone economic values.

#### 4. Discussion and conclusion

This paper examined the tradeoffs involved in controlling a pest that negatively impacts ecosystem services. The objective of pest control is to reduce lost ecosystem service values, but the source of these values cannot be taken for granted. Removing a pest will not immediately replace lost values because ecosystems are dynamic and it takes time for wildlife to recover. Furthermore, management will have indirect effects on the pest because the pest is itself impacted by other species. As a control program proceeds over time, interspecies competition as well as predation can exert negative impacts on a pest, which may help reduce the magnitude and costs of a control program.

Application of the model to the feral pig problem on Santa Catalina Island provides insights in managing an ecosystem pest problem. The optimal pest control program initially over-culled the long-run managed pig population but still left the species endemic, albeit with a small population relative to the unmanaged level. This containment strategy allowed the fox population to nearly reach carrying capacity in equilibrium. Additional modeling simulations suggested that the economic value of the fox (or pig removal costs) would have to be substantially larger (smaller) before eradication would be optimal, although compared with the outcome of no management eradication greatly increased the economic value of the system.

However, eradication may have become the optimal policy had the application included the pigs' impacts on the other (largely nonuse-valued) ecosystem services on Santa Cruz Island.

The paper analyzed an alternative pest control strategy that involved rapidly adjusting the pig population to the ideal equilibrium level. Although sub-optimal, this strategy yielded economic values that were approximately the same as the optimal pig control strategy, which suggests that when the optimal management strategy is unknown rapid adjustment to the preferred equilibrium may be nearly as good. This numerical finding reinforces Clark's (1976) remark that in the case of selective harvesting "if many feasible approach paths are available, do not be concerned if the ideal path is not apparent" (p. 323). These simpler strategies may be particularly useful in resolving more complex ecosystem management problems.

In conclusion, a removal strategy can be used to recover wildlife populations damaged by a pest or invasive species. Of course, the optimal removal strategy is significantly determined by the value of the impaired resource, which is not well known for many ecosystem management problems. The results of this paper suggest that careful identification of ecosystem service values for use in determining the equilibrium management policy may be of significantly greater practical importance than the type of removal strategy used to get to the desired equilibrium.

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6. Figures and tables

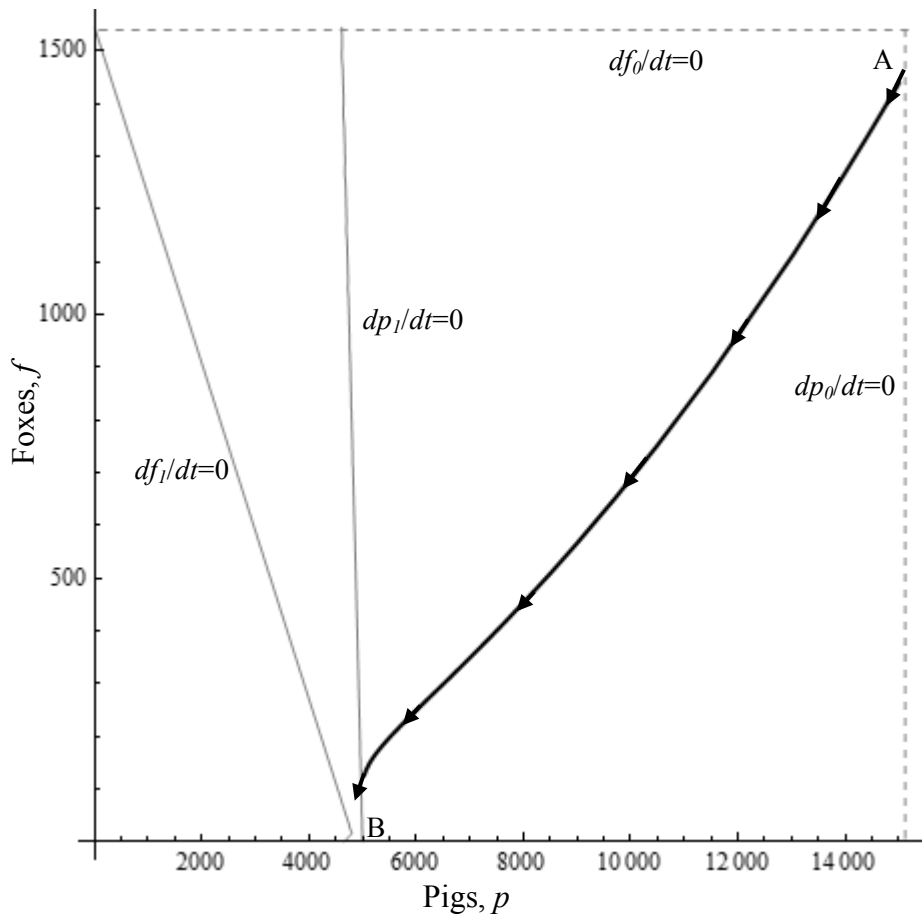


Figure 1. The decline in the fox and pig populations at the onset of apparent competition. Before competitive interaction the system lies near point A, at the intersection of the dashed nullclines  $di_0/dt$  for  $i = f, p$ . Once the species begin to compete the nullclines shift to the solid lines  $di_i/dt$  for  $i = f, p$  and the system proceeds along the bolded trajectory to point B.

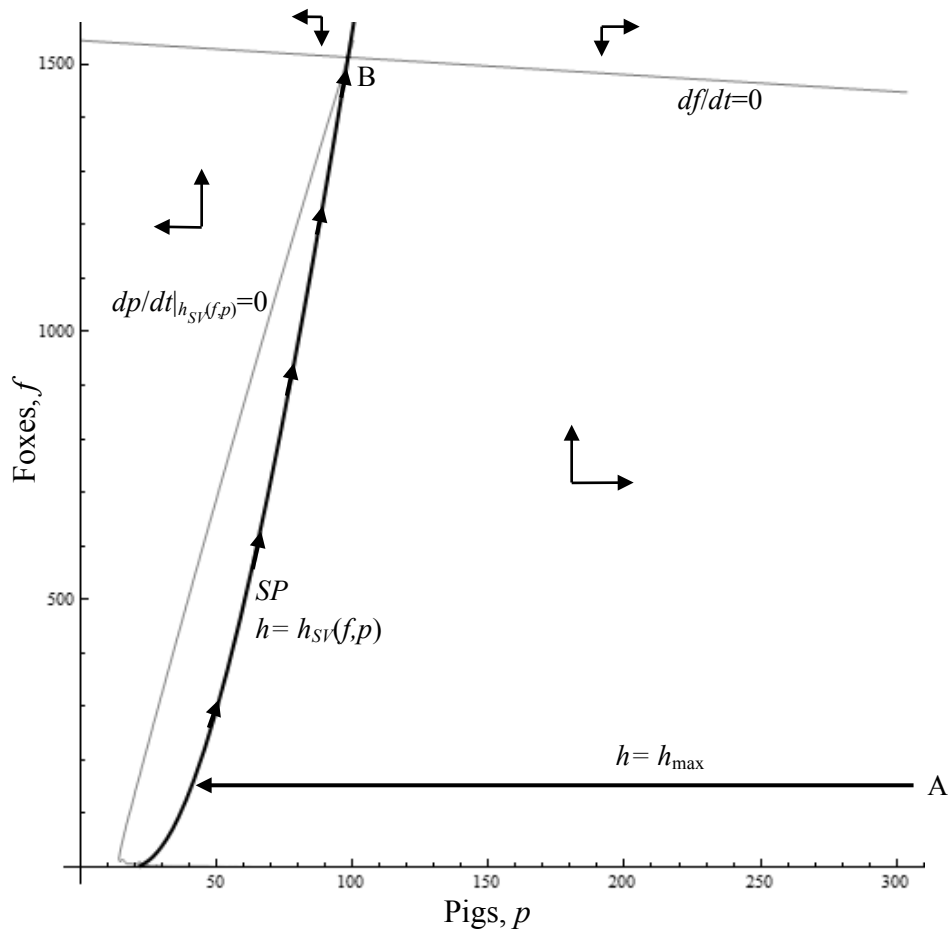


Figure 2. State-space diagram of the solution to the pig removal strategy. Note the change in scale from Figure 1.

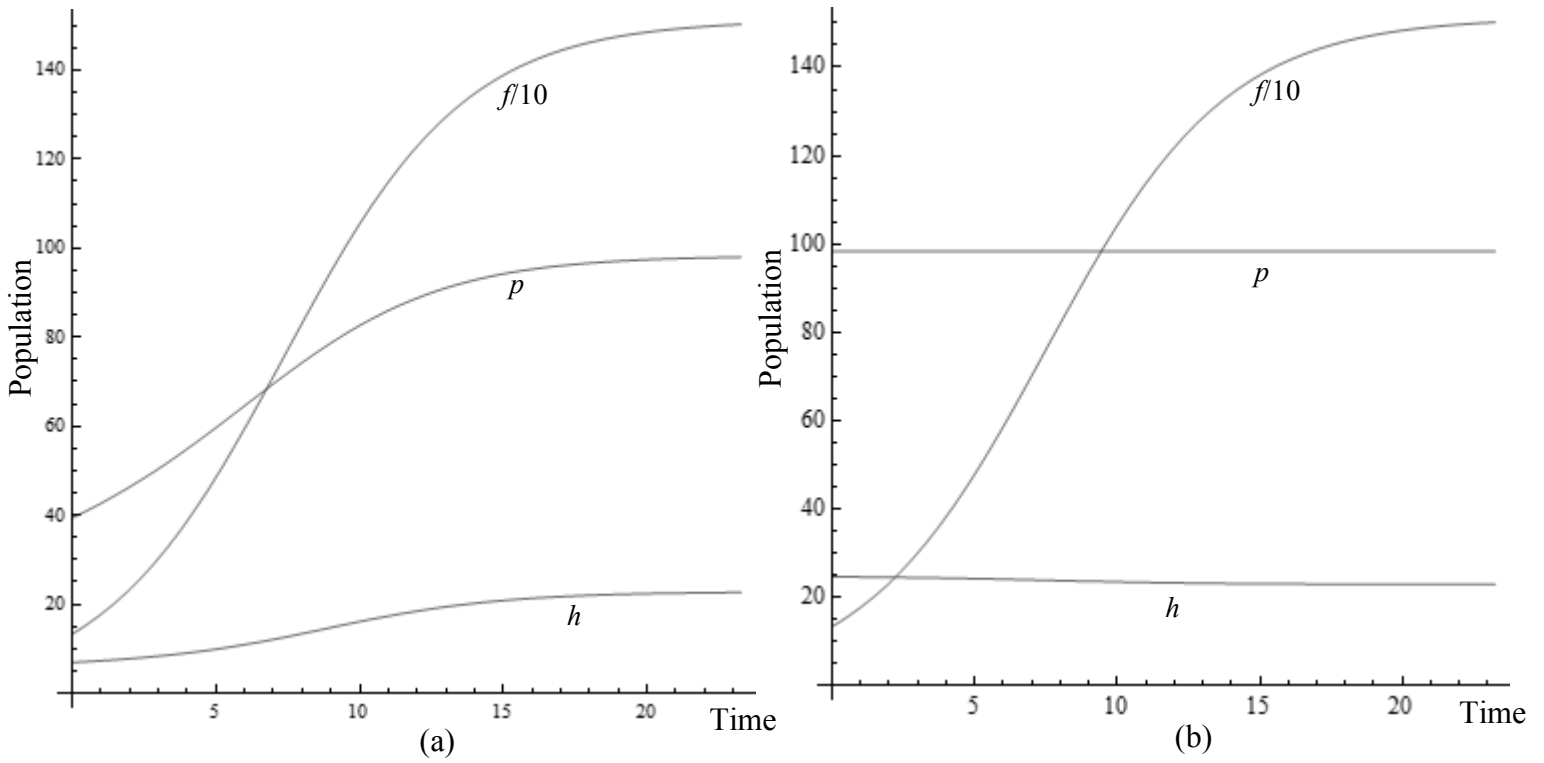


Figure 3. Time-paths of  $f$ ,  $p$  and  $h$  for a removal strategy that uses a feedback control (a) and a removal strategy that attempts a most-rapid-approach-path (MRAP) to equilibrium (b).

Table 1. Simulation results

Model scenario	Parameter change	$f^a$	$p^a$	<i>SNB</i> of optimal removal strategy <sup>b</sup>	<i>SNB</i> of alternative removal strategy <sup>b</sup>
Benchmark	N/A	1513	98	238.4	238.3
Fox WTP/household reduced to \$12.15	$v = 1016805$	1485	184	132.6	132.5
Fox WTP/household increased to \$36.84	$v = 3082053$	1526	56	412.4	412.4
Discount rate halved	$\rho = 0.025$	1529	46	497.3	497.2
Discount rate doubled	$\rho = 0.10$	1473	222	111.4	111.3

<sup>a</sup>Steady state populations.

<sup>b</sup>Benefits are in millions of dollars.