Exotic species become a problem when they involve significant harm, either to humans or the natural environment. Many experts believe that these exotic invaders contribute to the extinction of native species around the globe (Wilcove et al.). Exotic species disrupt both natural and human functions in many ecological systems, including terrestrial, freshwater and marine, animal, plant, and microbe (Williamson). Rational choice theory provides one framework to better understand the complex interactions and feedbacks between human behavior and natural processes, and to assess the efficiency of alternative policy options aimed at eliminating exotics. Economics helps us understand the human drivers of the problem of native-exotic species, and the potential risks these conflicts impose on society (Perrings, Williamson, and Dalmazzone).

This paper discusses the necessary components for an integrated economic-biological assessment of an ecosystem with an exotic species. Our work combines the economic approach of constrained optimization in which the biological constraints of the ecosystem are used both to create a fully functioning model and to constrain the productivity in the economic model; humans maximize total benefits of the ecosystem, including ecological products, given budget limitations and biological constraints of the ecosystem (see Crocker and Tschirhart). We first take the reader through a generic economic system-ecosystem model highlighting the research process for economists. We discuss a predator-prey model with an exotic predator, ecological services from the two species, and finally human intervention into the ecosystem. We apply the model to a specific problem—the introduction of exotic lake trout into Yellowstone Lake, which pose a risk to the native cutthroat trout. We discuss whether the integration of the economics with the ecosystem yields different results than treating the two systems as separate; estimate the optimal policy path, comparing it to current policy; and examine whether hyperbolic discounting induces different policy conclusions.

Modeling Native-Exotic Interactions

We first sketch out a general native-exotic model that has two species competing for survival. A predator-prey model is one type of model, but the two species do not have to compete directly for survival. Direct competition exists through a predator-prey relationship, but indirect competition also exists through use of the same territory and competition for the same food source. The direct and indirect competition results in an inverse relationship between the population of one species and the population of the competing species. We use state equations to track the population of both species. The equations of motion for each species are $\dot{A} = \hat{A}(A, B, Z)$ and $\dot{B} = \hat{B}(B, A, Z)$, in which $A$ is the state equation for the population of species $a$; $B$ is the state equation for the population of species $b$; and $Z$ is the outside effort to affect the species population through management of the ecosystem.

These species are an integral part in deriving ecosystem services. Humans gain benefits from the population of either one or both species. The state equations for species define the household production function in the production of ecosystem services, $C = C(A, B, T_e)$, where $C$ is the level of services derived from the ecosystem, and $T_e$ is time spent by humans generating services. The services depend on both species $A$ and $B$, since larger populations...
lead to more species interactions and more ecosystem services. These ecosystem services include consumptive uses such as harvesting the species, partially consumptive uses such as catch and release programs in which some species die inadvertently, and nonconsumptive uses such as wildlife viewing.

Humans have another option at their disposal—spending their time generating services away from the two species. This time generates a vector of other goods, say a composite good, \( D \), produced as \( D = D(T_d, Y) \), in which \( T_d \) is the amount of time spent by humans generating this nonspecies composite good, and \( Y \) is the outside effort that affects the productivity. These services do not depend on the two species, rather they depend on the productivity of the nonspecies good.

A collective agency also has partial control over both the species populations and the productivity of the nonspecies good, through \( Z \) and \( Y \). The agency sets its policy to maximize the net benefits of humans given its fixed budget. The agency can spend money increasing the productivity of the nonspecies good (\( Y = M_d \)), or it can spend money aiding one or both of the species in the park (\( Z = M_s \)), given its fixed budget (\( M_t \)). The agency’s budgetary constraint is \( M_d + M_s = M_t \). The agency spends its fixed budget on one of two activities, and is presumed to be unable to increase its fixed budget. Here the productivity of the nonspecies good is also a function of \( M_d \), and the species population(s) is a function of \( M_s \). The agency increases the productivity of ecosystem services derived from species and increases the productivity of nonspecies production. The agency divides the fixed budget such that the marginal gains to the nonspecies production equal the marginal gains to the species production.

This general model can be applied to many different ecosystem contexts. We apply the approach to a native-exotic species conflict in Yellowstone. Lake trout (Salvelinus namaycush) are an exotic predator of the native cutthroat trout (Oncorhynchus clarki bouvieri) that inhabit Yellowstone Lake. Figure 1

![Diagram of integrated model of Yellowstone Lake](http://ajae.oxfordjournals.org/)

**Figure 1. Diagram of integrated model of Yellowstone Lake**
illustrates the overall model. Now consider the specifics. The ecosystem model is a predator-prey relationship between lake trout and cutthroat trout, in which other species like grizzly bears and eagles also prey on cutthroat trout.

The equation of motion for lake trout is

$$\dot{LT} = L^{\tau} (LT, CT, h_{lt}, m_{lt})$$

where \(dL^{\tau} / dLT > 0, dL^{\tau} / dCT > 0, dL^{\tau} / dh_{lt} < 0, dL^{\tau} / dm_{lt} < 0\), and \(m_{lt}\) is the amount of money spent by the National Park Service to control the lake trout population. The equation of motion for cutthroat trout is

$$\dot{CT} = C^{\tau} (CT, LT, h_{ct})$$

where \(dC^{\tau} / dCT > 0, dC^{\tau} / dLT < 0, dC^{\tau} / dh_{ct} < 0\), since an increase in the predatory population of lake trout leads to more cutthroat trout caught by lake trout, while a larger population of cutthroat trout leads to larger spawning and more human harvest decreases the cutthroat trout population. State equations are also used for other species in the park that feed on cutthroat trout, birds of prey, \(B\) (e.g., eagles, osprey, and white pelicans), and grizzly bears, \(G\). People gain utility from viewing them through the use of sight functions similar to the harvest functions for lake trout and cutthroat trout. These state equations play an important role in determining success of the fishermen who come to catch cutthroat trout, and as a guide of ecosystem health for park managers who are in charge of managing the ecosystem.

Humans interact with the Yellowstone Lake ecosystem daily. Fishermen travel to Yellowstone Lake to catch cutthroat trout. Humans impact the ecosystem by reducing the population of cutthroat trout, which can impact species who prey on cutthroat trout. We capture the direct impact on a species population by linking species population to the human catch through harvest functions. The cutthroat trout population is tracked by the state equation, \(CT\). Larger populations of cutthroat trout lead to a higher success rate for fishermen, \(h_{ct} = h_{ct} (CT, T_f)\). The human harvest of cutthroat trout, \(h_{ct}\), depends on the population of cutthroat trout, \(CT\), and the amount of time spent fishing by the visitor, \(T_f\), where \(dh_{ct} / dCT > 0, dh_{ct} / dT_f > 0\). Assume fishermen fishing for cutthroat trout also inadvertently catch lake trout, \(h_{lt} = h_{lt} (LT, T_f)\). The human harvest of lake trout, \(h_{lt}\), depends on the population of lake trout, \(LT\), and the time spent fishing, \(T_f\), where \(dh_{lt} / dLT > 0, dh_{lt} / dT_f > 0\).

National Park Service managers must determine how to allocate the park’s limited budget and how to manage the visitors to the park. Park managers have a fixed budget, which is spent on two activities—netting lake trout or improving the park public good, \(X\). The public good is denoted by the state equation, \(\dot{X} = X(X, m_x)\). The budget spent improving the park public good is \(m_x\), the budget spent killing lake trout is \(m_{lt}\), and the total available budget is \(m_t\), where \(m_t = m_x + m_{lt}\).

Assume visitors fish or enjoy the park public good or do both. Assume visitors are myopic in that they either do not care about the utility of future visitors or do not know exactly how their actions alter the ecosystem. The visitor maximizes utility

$$\max \ U(h_{ct}(CT, T_f), h_{lt}(LT, T_f), \ S_g(G, T_f, T_x), \ S_b(B, T_f, T_x), \ S_x(X, T_x))$$

subject to

$$T_f + T_x = T_t$$

Note that species populations do not directly induce utility, rather utility is derived from the consumption or encounter with one of the species. Species populations are a measure of productivity, for example, larger species populations lead to a higher number of encounters. The average visitor equates marginal utility across activities to the shadow value of time to solve for \(T_f^*\) and \(T_x^*\), which show the optimal amount of time spent by the average visitor for both activities as a function of the population of each species in the ecosystem and the state of the nonlake public good (\(CT, LT, B, G, X\)).

These functions are used as visitor reaction functions for the park manager’s allocation decisions as a social planner. Park managers maximize the discounted stream of intergenerational utility of future visitors to the park by allocating resources to harvest lake trout or to improving roads to increase access to the park public good. Given \(\{m_{lt}, m_x\}\) are control variables, their dynamic optimization problem is

$$\max \ \int_0^T U(h_{ct}(T_f, CT), h_{lt}(T_f, LT), \ S_g(G, T_f, T_x), \ S_b(B, T_f, T_x, G), \ S_x(X, m_x))e^{-rt} dt$$

subject to

$$C T = \dot{C} T (CT, LT, B, G, h_{ct})$$

$$L T = \dot{L} T (LT, h_{lt}, m_{lt}, CT)$$

$$B = \dot{B} (B, CT) = 0$$

$$\dot{X} = X(X, m_x)$$

$$m_{lt} + m_x = m_t.$$
Solving the optimal control model yields functions determining the optimal allocation of money between the two activities at the disposal of the NPS managers, \( m^*_{lt}(t) \) and \( m^*_{x}(t) \). The park manager equates the marginal benefits from spending a dollar killing lake trout to the marginal benefits from spending a dollar improving roads in the park. The information from \( T^*_{lt} \) and \( T^*_{x} \), and \( m^*_{lt}(t) \) and \( m^*_{x}(t) \) capture how visitors to the park allocate their time across the two activities, and how the park managers allocate their budget between the two available options.

**Simulation Results**

We use this information to simulate the integrated ecological-economic model of Yellowstone Lake so that we can address three specific questions. Consider each in turn. First, does the integration of the economic system and the ecosystem lead to different policy results than treating the two systems as separate? We address this question by considering three scenarios, each with and without feedbacks between the economic and ecological systems (Settle, Crocker, and Shogren). The best-case scenario eliminates lake trout immediately and without cost. The worst-case scenario exists when lake trout are left alone without any interference from the Park Service; lake trout and cutthroat trout are left to reach their own steady-state equilibrium. The policy scenario has the National Park Service reducing the risk to cutthroat trout by gill netting lake trout, assuming the Service’s current level of expenditures is continuous and perpetual.

We use the population of cutthroat trout as a yardstick. If the population of cutthroat trout differs with and without feedbacks, the accounting of feedbacks between the two systems can provide a better understanding of the behavior of both systems. Figure 2 summarizes the results for each scenario. Under the best-case scenario without feedbacks, the steady-state population of cutthroat trout is about 2.7 million. With feedbacks, the steady-state population is about 3.4 million. The difference arises from fishermen’s behaviors. Without feedback, fishermen continue to fish as before, putting constant pressure on the cutthroat. With feedback, fishermen adapt by fishing less and visiting other attractions more. Reduced human pressure on the cutthroat allows its population to increase by an amount greater than with constant fishing pressure. The resulting population of cutthroat trout is therefore greater with feedback from human adaptation. The results are similar for the policy scenario. The worst-case scenario, however, generates distinctly different results. As people shift time away from fishing as the cutthroat trout population declines and the lake trout population increases, the incidental catch for fishermen of lake trout also declines. Now a no-feedback model suggests a healthier outcome than might exist—almost 1 million cutthroat trout versus zero cutthroat once feedbacks are considered.

The second question we consider is while assessing what conditions must exist for the current policy to be optimal, how does the optimal policy path compare to the current policy? Here we find a troubling result from a species protection perspective—a small difference between the present value of net benefits between the best- and worst-case scenarios exists, which suggests gillnetting policy is inefficient (Settle and Shogren, 2002a). The policy implication is the managers should not spend limited resources killing lake trout since the average visitor cares more about protecting road quality than protecting cutthroat trout (optimal fixed budget = $0). A few strong assumptions created this result. First, only use values for cutthroat trout were included—visitors received benefit only if they caught cutthroat.
trout, and received no benefit from their existence. This assumption was relaxed by allowing for a small existence value of $1 per visitor. Second, a 5% constant discount rate was used which implies the benefits of the lake trout control program were discounted toward zero since the cutthroat trout population was similar for the first twenty to twenty-five years with or without the control program. Now, with these two changes, the optimal fixed budget is $5,000. One can create favorable conditions for a large-scale lake trout control program by assuming a 1% discount rate; a $20 existence value; existence values take the form of a pseudo-existence value; and the threshold for the pseudo-existence value on cutthroat trout is 1,800,000. Under these assumptions of the representative visitor, one finds significantly large fixed budgets that are optimal (optimal fixed budget = $169,000).

The third question we consider is whether applying hyperbolic discounting leads to different policy conclusions than does using constant discounting? We compare the results of hyperbolic and constant discounting to determine whether the choice of discounting matters from an economic perspective. We define the PV wedge as the difference in net present value between the best- and worst-case scenarios (Settle and Shogren, 2002b). Several results emerge from this analysis (see table 1). Hyperbolic discounting increases the size of the PV wedge compared with constant discounting using the same initial discount rate. Constant discounting uses a fixed discount rate, whereas hyperbolic discounting begins with an initial discount rate and reduces it over time. Assuming constant discounting and hyperbolic discounting have the same initial discount rate, hyperbolic discounting implies the economic value of future events will not be discounted toward zero as quickly. Hyperbolic discounting leads to a greater present value for the project, which in this case implies a larger discounted stream of utility from Yellowstone National Park. The policy implications are the following. If maintaining a viable population of cutthroat trout is the central goal of park managers, or if park visitors are more interested in maintaining viable species populations than in seeing the core attractions, the fixed budget spent controlling lake trout should be as large as necessary to keep cutthroat trout populations viable. But if the central goal is not to maintain viable populations of cutthroat trout, few resources would be spent controlling lake trout.

The use of hyperbolic discounting is not without its problems. As has been pointed out in the literature, using hyperbolic discounting leads to time inconsistent policy conclusions (see Strotz, Albrecht and Weber, Heal). Consider a policy that must be implemented today, but might be reconsidered in the future. If we use current information and hyperbolic discounting to determine the optimal policy path, and then recompute the optimal policy path at an arbitrary point in the future, the two policy paths would be different. We do this to determine the degree of time inconsistency to address the question of whether these policy paths are close to each other or are they distinctly different. We find that time inconsistency does exist, but for some cases it is approaching zero (Settle and Shogren, 2002b). In cases in which the optimal fixed budget is zero, the recalibration in twenty-five years results in an almost identical zero fixed budget. At the other extreme, when optimal fixed budgets are large enough to maintain a viable population of cutthroat trout, the recalibration once again results in almost identical fixed budgets. But for cases in between these two extremes time inconsistency is substantial. These results illustrate that the conditions that tempt one to use hyperbolic discounting are exactly the same conditions under which time inconsistency is large. This implies the conditions for using hyperbolic discounting are the same for those in which we might choose to alter our decisions in the future.

<table>
<thead>
<tr>
<th>Type of Discounting</th>
<th>Size of PV Wedge</th>
<th>Size of PV Wedge as a Percentage of Total Park Value</th>
<th>Optimal Fixed Lake Trout Control Budget</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant discounting</td>
<td>$7,900</td>
<td>0.01%</td>
<td>$75</td>
</tr>
<tr>
<td>Hyperbolic discounting</td>
<td>$33,772,000</td>
<td>6.42%</td>
<td>$3,000</td>
</tr>
</tbody>
</table>
Concluding Remarks

We conclude by considering a possible extension that would capture how native-exotic conflicts in Yellowstone Lake links with the greater Yellowstone ecosystem. With lake trout in the lake, cutthroat trout populations will decline; some fisheries biologists even suggest an 80–90% decline of catchable-size cutthroat trout, from 2.5 million to 250,000 (Kaeding, Boltz, and Carty). Our simulations suggest that if lake trout are left unchecked, the cutthroat trout population might be eliminated from Yellowstone Lake. While these cases are extreme, it points to some broader implications across the greater Yellowstone ecosystem. Our exotic-native trout species conflict rests on the presumption that the populations of the extraordinarily charismatic grizzly bear will not decline due to lake trout inhabiting Yellowstone Lake. Though correct, the number of grizzly bears that come to Yellowstone Lake to feed is a function of the cutthroat trout spawning in the nearly 120 tributaries feeding the lake. Small fluctuations in the cutthroat trout population are normal and would likely have no effect on grizzly bear populations seen around Yellowstone Lake, but an extreme change to the population of cutthroat trout would affect grizzly bears coming to streams in the spring to catch cutthroat trout. This holds because lake trout do not replace cutthroat trout in the diet of grizzly bears since lake trout spawn in the lake instead of in the streams. Given that fewer cutthroat trout could imply fewer grizzly bears feeding around Yellowstone Lake, a next step in the research process is to extend the basic ecosystem model to include the possibility of fluctuations in the grizzly bear population and the impacts that change would have on the populations of both cutthroat trout and lake trout. A similar tactic could be used for the other forty-plus mammals and birds that also consume the cutthroat trout in Yellowstone Lake.

References