Managing Excessive Predation in a Predator-Prey Setting:

The Case of Piping Plovers

Richard T. Melstrom

melstrom@msu.edu

Richard D. Horan

horan@msu.edu

Michigan State University

Department of Agricultural, Food and Resource Economics

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Abstract: Ecosystems involve interspecies interactions that can be influenced by human interventions. Prior work shows interventions that ignore these interactions cause efficiency-reducing ecosystem externalities. We show inefficiencies may also be attributable to nature, via interspecies interactions generating excessive competition or predation. Ecosystem management therefore may involve correcting both ecological and economic inefficiencies. We explore ecosystem management to correct ecological inefficiencies from predation. The inefficiencies are shown to be akin to anthropogenic externalities arising when humans harvest resources under open access conditions, and so the solution is to "regulate" predators. Viewing the ecological inefficiencies in this manner facilitates the choice of controls. We examine predator removal and predator exclosures that shelter prey from predation. Using a numerical example of the Great Lakes Piping Plover, an endangered bird, and Merlins, a falcon that predates on plovers, we find using predator exclosures can yield a win-win outcome that increases both prey and predator populations.

Key Words: bioeconomics, wildlife management, endangered species, open access, predator control, predator removal, exclosures, Piping Plovers, Merlins

1.   Introduction

Ecosystems generally involve many complex interspecies interactions, including resource competition (Brock and Xepapadeas 2002; Tilman et al. 2005), mutualisms (Wacker 1999), and predator-prey relations (Ragozin and Brown 1985; Crocker and Tschirhart 1992; Ströbele and Wacker 1995; Hoekstra and van den Bergh 2005; Horan et al. 2011). Prior work has shown human interventions may influence these stock-dependent interactions, so that management or exploitation of one species that does not account for interspecies interactions will generate spillover effects impacting other valued species. That is, human interventions may cause efficiency-reducing ecosystem externalities (Crocker and Tschirhart 1992).

Inefficiencies arising when humans do not intervene may be driven by species interactions. For instance, suppose people value greater species abundances, and no private incentives exist to intervene (i.e., assume harvests are not valued and habitat modification is prohibitively costly). Absent species interactions, each species would equilibrate at its carrying capacity, and this would be efficient: "nature's objective" of maximum species abundances coincides with human objectives. The distribution of species abundances is likely to be inefficient, however, if species interactions reduce the abundance of one or more valued species. These inefficiencies, arising because "nature's objectives" are altered by the interactions and hence diverge from human objectives (Brock and Xepapadeas 2002), are attributable to nature. This means ecosystem management may involve correcting both ecological and economic sources of inefficiencies.

We explore ecosystem management to correct ecological inefficiencies. A key result is that recognizing the sources of ecological inefficiencies can help ecosystem managers select the right controls. Prior work on ecosystem management has focused primarily on setting the levels of controls to optimally account for interspecies interactions (Brock and Xepapadeas 2002; Ragozin

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and Brown 1985; Ströbele and Wacker 1995; Hoekstra and van den Bergh 2005; Crocker and Tschirhart 1992), with minimal discussion of which controls (e.g., harvest controls versus habitat interventions) promote greater efficiency. The selection of controls is not a trivial matter, however, especially for complex ecological systems (Horan et al. 2011).

We examine the selection of controls, and their optimal levels, by extending concepts from the joint-determination literature that seeks to more fully integrate economic and ecological systems (Tschirhart 2000, 2009; Brock and Xepapadeas 2002). An important strain of this literature anthropomorphizes species "behavior" to provide an economic interpretation for various ecological relations (Tschirhart 2000, 2009; Brock and Xepapadeas 2002; Tilman et al. 2005).[1] We expand on these concepts by showing how an individual animal's "behavior" creates externalities affecting conspecifics. For instance, predation creates externalities analogous to the anthropogenic externalities arising when humans harvest open access resources: individual predators over-predate, reducing future prey stocks and thereby also reducing future predator fertility.[2] Humans valuing one or more of these species are also affected. That interspecies interactions create externalities implies some species must be "regulated" to improve efficiency. The literature on resource regulation can guide control choices to address various "types" of externalities (e.g., overharvesting). To this end, we show how specific ecosystem controls may be akin to particular regulatory instruments capable of correcting the relevant externalities.

The concepts are illustrated by a problem of conserving an existence-valued prey and predator species, where harvest values do not arise for either predator or prey (in contrast to

[1] For instance, Tschirhart (2000; 2009) describes interspecies interactions as economic transactions involving energy flows among the interacting species, with the species "behaving" as if they were optimizing some biological objective (see also Brock and Xepapadeas 2002). Brock and Xepapadeas (2002) and Tilman et al. (2005) describe interspecies competition as being analogous to mechanistic resource competition among myopic humans. While not adopting an anthropomorphic perspective, Hoekstra and van den Bergh (2005), Ströbele and Wacker (1995), and Horan et al. (2011) explore problems where humans and (myopic) predators compete for the same prey.
[2] This is analogous to, though opposite of, the notion that open access resources can be interpreted as a predator-prey model in which humans are the predator (Ragozin and Brown 1985).

virtually all the bioeconomic work on multi-species problems). This problem allows us to focus

on managing externalities arising entirely from ecological sources. Moreover, the conservation

of species that are threatened due to interspecies interactions, rather than overharvesting, is

increasingly important (MEA 2005; Soulé et al. 2005). In particular, the multi-trophic nature of

ecosystems is a key factor in species conservation (Soulé et al. 2005).[3]

As indicated above, describing un-managed predation as open access harvesting facilitates

control choices and yields insight into their optimal values. License fees and harvest quotas can

efficiently manage standard open access problems analogous to the type we study here, and we

find two controls can "regulate" predator-prey interactions in an analogous manner: predator

removal to reduce predator numbers, and predator exclosures to reduce predation per predator.

Although the analogy is helpful, two complexities arise relative to conventional open access

problems. First, predators may be valued directly, implying a potential conflict between efforts to

conserve predators and to reduce over-predation. We find efficient predator controls increase

both stocks when certain ecological conditions cause the interests of nature and society to

coincide. This win-win outcome is akin to the standard result that efficient regulations

simultaneously enhance economic welfare in the harvest sector and increase resource stocks. A

second complexity is that investing in predator controls to regulate predator behavior generates

real costs, whereas bioeconomic models generally assume negligible transactions costs from

regulation. Together, these two complexities affect the optimal mix of controls for predator

management relative to the conventional open access setting. In particular, we find an exclosure-

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[3] DeCesare et al. (2009) document the decline of over a dozen species from predation. Examples include predation by the Golden Eagle (*Aquila chrysaetos*) on the Island Fox (*Urocyon littoralis*) on the Channel Islands (Roemer et al. 2002), predation by gulls and falcons on the Piping Plover (*Charadrius melodus*), and predation by the Caspian tern (*Hydroprogne caspia*) on the endangered Snake River salmon (Antolos et al. 2005). A related issue is that interspecies competition can threaten predators. An example is the Bard Owl (*Strix varia*) displacing the Northern Spotted Owl (*Strix occidentalis caurina*) (Kelly et al. 2003).

only strategy is optimal in some settings. Mathematically, this result is of interest because exclosures are non-targeted so as to affect both species (in contrast to targeted predator controls).

Our analysis is applied to the case of the Great Lakes subpopulation of the Piping Plover, a small North American shorebird. In the mid-1980s there were only 28 Great Lakes plovers (Haig and Oring 1985). Since then the species has benefited from intensive management efforts, including productivity monitoring, predator exclosures, electrified fencing, predator removal, nest translocation, habitat enhancement, seasonal access closures and educational outreach (Gratto-Trevor and Abbott 2011). A significant portion of the birds' historical habitat is also now protected from development. However, the Great Lakes plover remains troubled by heavy loss rates to predators, especially small falcons known as Merlins (*Falco columbarius*) (V. Cavalieri, personal communication). This has led to the use of the predator exclosures for protection. Predator exclosures are wire-mesh cages placed over the plovers' nests. The cages have gaps large enough for plovers to exit and enter through, but small enough to stop predators. Alternatively, managers can, and have in the past, adopted a predator removal policy.

In section 2, we develop the ecological plover-falcon model with predator removal and predator exclosures. A bioeconomic model of this problem is presented in section 3, and the economic-ecological tradeoffs arising in an optimal management regime are assessed. Numerical results are derived in section 4 for the Great Lakes Piping Plover. The final section concludes.

2.   Ecology

2.1   Model with no controls

Consider an ecosystem composed of falcons and their prey, the plovers. The falcon population, denoted *Y*, changes over time according to

(1) $\quad \dot{Y} = g(X,Y)Y - \delta Y = (\sigma(\hat{Y} - Y) + \alpha\beta X - \delta)Y$,

where $g(\cdot)$ is falcon per-capita fertility, X is the plover stock, and $\delta > 0$ is the falcon mortality rate. The right-hand-side (RHS) term $\sigma(\hat{Y} - Y)$ is per capita growth absent plover predation, where σ and $\hat{Y}$ are parameters. This growth, reflecting predation of other species, yields a carrying capacity of $\hat{Y} - \delta/\sigma > 0$ absent plover predation. The term βX is each falcon's plover predation, where β is a catchability parameter. Parameter α converts captured plovers into new predators.

Growth of the plovers is described by

(2) $\quad \dot{X} = rX(1 - X/k) - \beta XY$.

The first RHS term is net plover growth prior to falcon predation, where r is the intrinsic growth rate and k is the carrying capacity absent predation. The second RHS term is falcon predation.

2.2   Predation as an open access problem: ecosystem externalities and control measures

The predator-prey dynamics (1)-(2) are analogous to an open-access resource extraction problem with sluggish entry and exit (e.g. Smith 1968): (2) is the equation of motion for the harvested resource and (1) is the equation of motion for entry and exit of the harvesters. Under the entry-exit interpretation for (1), the net fertility relation $g(X,Y) - \delta$ is the predator's welfare measure analogous to per capita rents, where $g(\cdot)$ is the return to predation and δ is a fixed survival cost.[4] Specifically, in the relation $g(\cdot)$, $\alpha\beta X$ is analogous to total revenue from harvesting plovers, $\sigma\hat{Y}$ is net revenue from harvesting other species, and $-\sigma Y$ is a congestion externality related to predation on other resources.

The predator-prey dynamics embed two ecosystem externalities that overly deplete prey

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[4] Likewise, evolutionary investments myopically maximize net fertility in evolution models (Rice 2004).

stocks in the same way that resource stocks are overly depleted in conventional open access

problems: (i) individual predators, each harvesting at the constant level βX, harvest too much

because they have no incentive to preserve plovers, and (ii) too many predators enter the system,

over depleting the prey stock and causing congestion. This latter effect arises as, just like profit-

motivated firms, falcons enter (i.e., are born into) the system until rents are driven to zero.

Viewing the conservation problem as an externality problem yields insight into the types of

controls to consider. Specifically, we know these types of over-harvesting externalities can be

corrected in conventional settings using harvest taxes (to correct both externalities) or a

combination of harvest quotas (correcting excess harvests) and entry restrictions or license fees

(correcting excess entry). The key is to identify wildlife controls that perform similar functions.

We can identify two such controls: falcon removal and predator exclosures.[5] Define falcon

removal by hY, where h is the removal rate. The second control, predator exclosures, excludes a

portion of prey habitat from predators.[6] Managers use this control to shield a proportion, p, of

plovers from falcons while leaving the remainder susceptible to predation. With these controls,

the falcon-plover dynamics (1)-(2) become

(3) $\dot{X} = rX(1 - X/k) - \beta XY(1 - p).$

(4) $\dot{Y} = (\sigma(\hat{Y} - Y) + \alpha\beta X(1 - p) - \delta - h)Y$

It is apparent from system (3)-(4) that p works like a quota and h works like a license fee. Just

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[5] Removal of plovers is not considered, since reducing the plover stock harms both species and it is assumed (a) the presence of stock-dependent benefits (existence values) for both species, and (b) there are no positive use values for either species (see section 3.1). With these assumptions, it would never be optimal to remove plovers.

[6] Predator exclosures often fence off area(s) the prey frequents. In the case of Piping Plovers the areas fenced in are the birds' nests. Gaps in the fencing material are sizeable enough to allow the plovers to move in and out of the exclosure but are inaccessible to predators like Merlins. Electrified fences have been used to this purpose for decades (Mayer and Ryan 1991). Practically speaking, exclosures are best suited against ground-based predators, although over-hanging lines can shield against avian predators and nets might be used in an aquatic environment. Evidence indicates fencing off terrestrial areas is effective in limiting the movements of predators (Moseby and Read 2006) and reducing predation (Lokemoen et al. 1882; Mayer and Ryan 1991; Bennett et al. 2009).

like quotas, exclosures reduce each falcon's predation from βX to $\beta X(1-p)$, reducing predation

returns and leaving more plovers *in situ*.[7] Predator removal is analogous to a lump-sum license

fee on harvesters, in that it reduces net returns by increasing the survival cost. The result is that h

slows entry and speeds exit of falcons, the same as a license fee.

System (3)-(4) is analogous to a special class of open access problems where there are no

variable production costs, so that an individual harvester's scale of production is not a concern.

In this class of problems, and assuming a traditional setting where the manager costlessly

implements regulations to maximize discounted rents from a single renewable resource, only one

control – a quota or a license fee – is needed to achieve the efficient outcome. This is the case for

(3)-(4) when $\sigma = 0$ (i.e., a single-species model with no congestion externalities) and there are no

transactions costs of regulation (see Appendix A). The use of both instruments is efficient when

$\sigma > 0$, implying a congestion externality. These results also hold when social welfare is defined

as discounted stock-dependent (existence) values rather than resource rents, although there will

be greater marginal incentives to use exclosures when Y is valued directly (Appendix A).

These results suggest that two controls may optimally manage both populations in the

predator-prey model. However, the predator-prey model differs from traditional open access

models in an important way that could impact this result. Specifically, the controls are not

implemented costlessly, as shown in the bioeconomic model in section 3. The relative costs of

the controls, viewed as transactions costs under the open access analogy, will influence the

relative magnitude(s) of the control(s) – including whether more than one control is optimal.

The steady state of system (3)-(4) is examined to gain insight into the ecological impacts of

these controls, with a particular focus on the impacts to the predator population as over-predation

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[7] Control p may also look like a harvest tax in (4). However, taxes do not affect prey dynamics (3), whereas p does.

is reduced. For simplicity, our analysis here assumes constant values for the controls p and h (this is relaxed in the bioeconomic analysis below). The steady state populations of X and Y, X^* and Y^*, are solved by setting (3) and (4) equal to zero:

$$(5) \qquad X^* = Max\left(\frac{k\sigma[r - \beta(1-p)(\hat{Y} - [h+\delta]/\sigma)]}{k\alpha\beta^2(1-p)^2 + r\sigma}, 0\right) = Max\left(\frac{k\sigma[r - \beta(1-p)Y^*|_{X\to 0}]}{k\alpha\beta^2(1-p)^2 + r\sigma}, 0\right)$$

$$(6) \qquad Y^* = \frac{r\sigma[\hat{Y} - (h+\delta)/\sigma + k\alpha\beta(1-p)/\sigma]}{k\alpha\beta^2(1-p)^2 + r\sigma} = \frac{r\sigma Y^*|_{X\to k}}{k\alpha\beta^2(1-p)^2 + r\sigma}$$

where $Y^*|_{X\to 0} = \hat{Y} - [h+\delta]/\sigma$ is the equilibrium predator population that would emerge in the special case where $X\to 0$, and $Y^*|_{X\to k}$ is the equilibrium predator population that would emerge in the special case where $X\to k$. Equation (5) indicates $X^* > 0$ when the prey's intrinsic growth rate exceeds the predation pressure that occurs as $X\to 0$. In what follows we assume $X^* > 0$.

Taking derivatives of X^* and Y^*, we find predator removal (h) unambiguously increases the equilibrium prey population but decreases the equilibrium predator population

$$(7) \qquad \partial X^*/\partial h = k\beta(1-p)/[k\alpha\beta^2(1-p)^2 + r\sigma] > 0$$

$$(8) \qquad \partial Y^*/\partial h = -R/[k\alpha\beta^2(1-p)^2 + r\sigma] < 0$$

Predator exclosures (p) increase the long-run prey stock, but the effect on predators is ambiguous:

$$(9) \qquad \partial X^*/\partial p = [k\sigma[\beta Y^*|_{X\to 0}] + 2k\alpha\beta^2(1-p)X^*]/[k\alpha\beta^2(1-p)^2 + r\sigma] > 0$$

$$(10) \qquad \begin{aligned} \frac{\partial Y^*}{\partial p} &= \frac{[k\alpha\beta^2(1-p)^2 + r\sigma]r\sigma[\partial Y^*|_{X\to k}/\partial p] + 2k\alpha\beta^2(1-p)r\sigma[Y^*|_{X\to k}]}{[k\alpha\beta^2(1-p)^2 + r\sigma]^2} \\ &= \frac{[2\beta(1-p)Y^* - r][k\alpha\beta]}{[k\alpha\beta^2(1-p)^2 + r\sigma]} = \frac{[(r - 2rX^*/k)][k\alpha\beta]}{[k\alpha\beta^2(1-p)^2 + r\sigma]} \end{aligned}$$

where the final equality in (10) stems from the steady state condition for X: $r(1 - X^*/k) = \beta(1-p)Y^*$.

Relation (10) indicates predator exclosures increase Y^* when $r > 2rX^*/k$, which occurs when X^*

$<X^{MSY}$ (where X^{MSY} is the plover population supporting the maximum sustainable yield of plovers to falcons). [8] When $X^* < X^{MSY}$, an increase in p increases both the plover stock and the yield to falcons, increasing the falcon stock. The interests of society and the falcon population coincide (qualitatively) in this case, so that regulating predation increases plover and falcon stocks. In contrast, the plover yield and the falcon stock decline for larger values of p when $X^* > X^{MSY}$.

These results echo Sanchirico and Wilen's (2001) findings that prohibiting harvests in part of a fishery (i.e., creating a reserve) can generate a "double payoff" of more fish and larger harvests. The size of the reserve and non-reserve are fixed in their model, but they show that a double payoff is possible if the dispersal rate between the reserve and open-access zone is not too small relative to the growth rate of the reserve stock. In our model, investing in exclosures is equivalent to reserve creation, and managers have control over the rate prey are consumed, which is akin to Sanchirico and Wilen's dispersal rate (in our case, dispersal is of plovers becoming falcon prey). Thus, the conclusion is similar: if the rate of predation is not reduced too much (i.e. the dispersal rate remains high enough), managers can achieve a double payoff.

Unlike Sanchirico and Wilen, whose marine reserve is costlessly established, predator controls have real economic costs. This increases the pertinence of the present model to open access problems, enriching the current understanding of open access resource regulation. This is because regulation of open access harvesting actually requires compliance and enforcement costs (Anderson 1989). These control costs are considered in the following bioeconomic section.

3. Bioeconomics

3.1 The social planner's problem

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[8] This is likely the case for systems where predation significantly increases prey extinction risks, as there is evidence predators harvest their prey below MSY (see Beddington et al. 1978; Taylor 1981; Seip 1991).

Suppose society derives nonuse (existence) values from the stock of each species. These values take the form $B_X(X) + B_Y(Y)$, where B_i is increasing and concave in the stock of species $i = X,Y$. Harvests do not generate positive use values for either species.

Conservation efforts are costly.[9] Predator removal costs take the Schaefer form (Clark 2005), $c_h hY/Y = c_h h$, where c_h is a parameter. Exclosure costs take the form, $c_p p/(1-p)$, where c_p is a parameter. These costs are increasing and convex in p, as it becomes increasingly costly to find and protect remaining unprotected plovers as the proportion of exclosure protection increases. The exclosure cost function ensures $p = 1$ is suboptimal as this implies infinite costs.

The social planner's problem is to maximize discounted social net benefits, denoted *SNB*:

$$\max_{h,p} \quad SNB = \int_0^\infty \left(B_X(X) + B_Y(Y) - c_h h - c_p p/(1-p)\right)e^{-\rho t} dt$$
$$s.t. \ (3),(4) \quad X(0) = X_0, \ Y(0) = Y_0, \ p \in [0,1], \ h \geq 0,$$

where ρ is the discount rate. Although the problem's ecology is analogous to open access dynamics, *SNB* differs in two ways from welfare in traditional open access problems: (i) falcon-related benefits depend on the stock, not on rents (net fertility), and (ii) there are real costs to implementing predator controls, whereas implementation of license fees and quotas in open access regulatory settings is generally assumed to be costless.

The current value Hamiltonian for the planner's problem is

(11) $\quad H(X,Y,h,p,\lambda_X,\lambda_X) = B_X(X) + B_Y(Y) - c_h h - c_p p/(1-p) + \lambda_X \dot{X} + \lambda_Y \dot{Y}$,

where λ_X and λ_Y are the costates for plovers and falcons, respectively. The Lagrangean is $L = H + \mu p$, where μ is the Langrangian multiplier for the lower-bound constraint on p. Other constraints

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[9] Costs associated with the negative social perceptions of predator removal (i.e., a disutility associated with predator removal h) are not modeled. For Plovers, there is evidence people are willing to support predator removal (Messmer et al. 1999), suggesting any social costs associated with predator removal are probably negligible in this case.

are treated implicitly. In what follows, the superscript * denotes an optimal trajectory.

The Lagrangean is linear in h, yielding a linear control problem in this variable. Accordingly, the optimality condition for h is (Clark, 2005)

$$(12) \quad \frac{\partial L}{\partial h} = -c_h - \lambda_Y Y = 0 \quad \begin{array}{lll} > 0 & \textit{iff} & h^* \to \infty \\ \textit{iff} & h^* = h_{sv} \\ < 0 & \textit{iff} & h^* = 0 \end{array} .$$

Condition (12) states that h is used as an impulse control when $\partial L/\partial h > 0$. Alternatively, no predator removal should occur if $\partial L/\partial h < 0$. The singular solution, h_{sv}, is optimally adopted when $\partial L/\partial h = 0$. The relation $\sigma(Y,\lambda_Y) = -c_h - \lambda_Y Y$ is known as the switching function (Clark, 2005), as this function determines when h optimally switches from one extreme to the other. Note that $\lambda_Y = -c_h/Y < 0$ when $\sigma(Y,\lambda_Y) = 0$. Thus, when h follows a singular (interior) solution, the shadow price of the predator is negative—i.e., the falcons are a nuisance. This is intuitive: managers only remove predators when the marginal predator has negative value. In contrast, if λ_Y is positive and large, so that the marginal predator is valued, $\sigma(Y,\lambda_Y) < 0$ and no predators are removed.

The necessary (Kuhn-Tucker) conditions related to p are

$$(13) \quad \partial L / \partial p = -c_p /(1-p)^2 + (\lambda_X - \alpha\lambda_Y)\beta XY + \mu = 0 \Rightarrow p^*$$

$$(14) \quad \partial L / \partial \mu \geq 0; \quad \mu[\partial L / \partial \mu] = 0.$$

The shadow price of plovers, λ_X, is always positive because $B_X > 0$ and plovers do not detrimentally affect falcons. When $\mu > 0$, then $p^* = 0$. This is optimal when $-c_p/(1-p) + (\lambda_X - \alpha\lambda_Y)\beta XY < 0$, which occurs when the net marginal cost of falcon predation on plovers, $\lambda_X - \alpha\lambda_Y$, is sufficiently small—i.e., society derives little welfare from protecting a plover from predation. An interior trajectory for p is followed when $\mu = 0$, which can only occur when $\lambda_X - \alpha\lambda_Y > 0$. This latter condition implies that $p > 0$ does not require $\lambda_Y < 0$, as was required for $h > 0$. Rather,

exclosures could be optimal in cases when the marginal falcon is valued positively. Therefore, while $\lambda_Y > 0$ implies $h^* = 0$, it does not mean that predator management in general is undesirable.

Two adjoint conditions, $\dot{\lambda}_i = \rho\lambda_i - \partial L / \partial i$ $(i=X,Y)$, are also necessary. We write these conditions in golden rule form (Clark 2005). The golden rule condition for the plover stock is

(15) $\rho = r(1 - 2X/K) + (B'_X/\lambda_X) + (\dot{\lambda}_X/\lambda_X) - (\lambda_X - \alpha\lambda_Y)(1-p)\beta Y/\lambda_X$.

This relation equates the rate of return that could be earned elsewhere, ρ, to the net rate of return from conserving plovers (the RHS of (15)). The first RHS term is the marginal growth of plovers prior to falcon predation. The second RHS term is the marginal existence benefit of plovers. The third RHS term represents the capital gain or loss from changes in the plover stock. Finally, when $\lambda_X - \alpha\lambda_Y > 0$ ($\lambda_X - \alpha\lambda_Y < 0$), the fourth RHS term is the net marginal cost (benefit) of greater falcon predation in response to more plovers. When $\lambda_X - \alpha\lambda_Y > 0$, these costs are declining in p. Alternatively, when $\lambda_X - \alpha\lambda_Y < 0$ it must be that $\mu > 0$ and so $p = 0$.

The golden rule condition for conserving the falcons is

(16) $\rho = \left[\sigma(\hat{Y} - 2Y) - \delta - h\right] + (B'_Y/\lambda_Y) + (\dot{\lambda}_Y/\lambda_Y) - (\lambda_X - \alpha\lambda_Y)(1-p)\beta X/\lambda_Y$.

When $\lambda_Y > 0$, the interpretation of (16) is similar to (15): the rate of return ρ is equated to the net return to falcon conservation. The first RHS term in (16) is the marginal growth of falcons prior to predation on plovers. Note that, from (12), $h^* = 0$ when $\lambda_Y > 0$ and so the rate of return to falcon conservation is not influenced by predator removal. The second RHS term is the marginal existence value of falcons. The third RHS term is the capital gain or loss. Finally, when $\lambda_X - \alpha\lambda_Y > 0$ ($\lambda_X - \alpha\lambda_Y < 0$), the final RHS term is the net marginal cost (benefit) of greater predation on plovers in response to more falcons. When $\lambda_X - \alpha\lambda_Y > 0$, these costs are declining in p, so that a larger p increases the return to conserving falcons. Alternatively, when $\lambda_X - \alpha\lambda_Y$

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< 0 it must be that $\mu > 0$ and so $p = 0$. These results and those for (15) indicate that, when $\lambda_Y > 0$,

it is only optimal to use exclosures when these increase the rate of return on both stocks.

The interpretation of (16) changes when $\lambda_Y < 0$. In that case, ρ represents the opportunity

cost of pulling resources from elsewhere in the economy and using them to manage falcons as a

nuisance. The RHS represents the rate of return to controlling nuisance falcons. This rate of

return is increasing in the marginal growth of falcons prior to predation on plovers (the first RHS

term). The second RHS term indicates the rate of return to nuisance control is decreasing in

marginal existence values for falcons. The capital gain/loss term changes in sign when $\lambda_Y < 0$.

Finally, consider the fourth RHS term. With $\lambda_Y < 0$, then $\lambda_X - \alpha\lambda_Y > 0$ and the rate of return to

nuisance control is increasing in response to greater falcon predation on plovers at the margin.

Note that both predator removal, h, and predator exclosures, p, reduce the rate of return to

nuisance control, suggesting there are diminishing returns to managing nuisance falcons.

3.2 Candidate management strategies

Conditions (12) – (14) imply the solution could be interior, in which $h^* = h_{SV}$ and $p^* > 0$, or a

corner, in which one control is constrained while the other is free. Some combinations involving

corner solutions can be discarded as candidate long-run strategies. For instance, $h \to \infty$ cannot

persist for more than an instant or else $Y \to 0$ and removal costs become infinite; however, $h \to$

∞ can be used as an impulse control to move to a particular long-run trajectory. Also, $p = 1$ was

ruled out as either a short-run or long-run solution. Finally, corner solutions with either $h = 0$ or

$p = 0$ can be part of the long-run optimal trajectory, or they can be used to move the system to

such a trajectory. The remainder of this section focuses on each of four strategies that can hold

for a period of time: (A) no management ($h = p = 0$), (B) predator removal and exclosures ($h = h_{SV}$,

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$0 < p < 1$), (C) predator removal only ($h = h_{sv}$, $p = 0$), and (D) exclosure only ($h = 0$, $0 < p < 1$).

3.2.1   Strategy A: *No management ($h = p = 0$)*

The no-management strategy yields the system (1)-(2). It is currently believed that following this strategy indefinitely will lead to plover extinction. In fact, our numerical analaysis below is parameterized as such (also see Appendix B). However, if falcons were eradicated prior to following the no-management strategy, then the no-management strategy would yield $X \rightarrow K$. Numerically, it is not possible to eradicate falcons in finite time when removal is defined as a rate, although a sufficient reduction in the population may be interpreted as eradication.

3.2.2   Strategy B: *Predator removal and exclosures ($h = h_{sv}$, $0 < p < 1$)*

To derive this candidate solution, we first set $\partial L/\partial h = 0$ in (12) to obtain

(17) $\lambda_Y(Y) = -c_h/Y \Rightarrow \dot{\lambda}_Y = -\lambda_Y \dot{Y}/Y$,

Next, substitute (17) into (16) and solve for λ_X:

(18) $\lambda_X(X,Y,p) = [B'_Y + (c_h/Y)(\rho + \sigma Y)]/[\beta(1-p)X]$.

Then use (13), with $\mu = 0$, to derive the following expression,

(19) $c_p/(1-p)^2 - (\lambda_X(X,Y,p) - \alpha\lambda_Y(Y))\beta XY = 0$,

which implicitly defines the feedback relation $p = p^B(X,Y)$. Substituting $p^B(X,Y)$ into (18) yields

$\lambda_X(X,Y,p(X,Y)) = \Phi(X,Y)$. Take the time derivative of Φ, $\dot{\Phi} = (\partial\Phi/\partial X)\dot{X} + (\partial\Phi/\partial Y)\dot{Y}$,

and substitute $\dot{\Phi}$ and Φ into (15) to derive the feedback relation $h_{sv} = h^B(X,Y)$. Strategy B's

dynamics are determined by substituting $p^B(X,Y)$ and $h^B(X,Y)$ into system (3)-(4).

3.2.3   Strategy C: *Predator removal only ($h = h_{sv}$, $p = 0$)*

To find the optimal trajectory in this case, set $\partial L/\partial h = 0$ in (12) and solve for λ_Y and $\dot{\lambda}_Y$ as in

(17). Then substitute these relations into (16) to derive

(20) $\lambda_X(X,Y) = [B'_Y + (c_h/Y)(\rho + \sigma Y)]/[\beta X]$

which is just (18) with $p = 0$. Note that for $p = 0$ to be optimal, it must be that $\lambda_X(X,Y) - \alpha\lambda_Y(X,Y)$

$< c_p/\beta XY$; assume this is the case. Take the time derivative of (20), $d\lambda_X(X,Y)/dt$, and

substitute this relation and $\lambda_X(X,Y)$ into (15) to solve for $h_{sv} = h^C(X,Y)$. The dynamics for strategy

C are determined by substituting $p = 0$ and the feedback solution $h^C(X,Y)$ into system (3)-(4).

3.2.4   Strategy D: Predator exclosures only ($h = 0$, $0 < p < 1$)

For this case, we use (13) to write p in terms of λ_X and λ_Y:

(21) $p = 1 - \sqrt{c_p/[(\lambda_X - \alpha\lambda_Y)\beta XY]}$,

so that $p = p(X,Y,\lambda_X,\lambda_Y)$. From (13), note that $0 < p^* < 1$ only if $\lambda_X - \alpha\lambda_Y > c_p/\beta XY$. To find λ_X and

λ_Y one solves the adjoint conditions associated with (15) and (16). An analytical solution is not

possible, so the solution must be determined numerically. Actually, in this case the optimal

management regime will be governed by four differential equations, $\dot{\lambda}_X$, $\dot{\lambda}_Y$, $\dot{X}$, $\dot{Y}$ (from (3)-(4)

and (15)-(16), with $h = 0$ and $p = p^*$), rather than just $\dot{X}$ and $\dot{Y}$, as in cases A, B and C. As the

two costates only affect the system through p, it is possible to describe the numerical solution

(see the next section) in three dimensions as moving through (X,Y,p)-space, with $\dot{p} =$

$dp(X,Y,\lambda_X,\lambda_Y)/dt$. Note that $X(0)$ and $Y(0)$ are given, whereas $\lambda_X(0)$ and $\lambda_Y(0)$ – and hence $p(0)$

– are optimally determined. Hence, the solution effectively involves choosing $p(0)$ to place the

system on the optimal trajectory (i.e., a three-dimensional saddle path), given the initial values of

the state variables X and Y. The system then optimally follows the trajectory as determined by

the differential system. This is akin to a traditional resource management problem involving a

single management choice (e.g., harvests) and a single species.

4.   Numerical Example

Strategies A-D are each candidate predator control regimes. A particular strategy may be a long-run optimum, or it may be pursued temporarily until it becomes optimal to transition to another strategy. The complete solution therefore may be a combination of strategies, with switches between two or more trajectories defined by strategies A-D. Whether a switch occurs depends on the switching curve for h and the Kuhn-Tucker condition for p. It is not possible to determine the optimal trajectory analytically. The precise nature of the solution will depend on the model parameters. A numerical example is now considered to illustrate possible solutions.

4.1   Application

Piping Plovers are divided into three distinct subpopulations that nest on the Atlantic coast, the Great Lakes and the Great Plains. Their nesting habitat consists primarily of beaches that have been subjected to significant development and recreational use. Hunting in the early 1900s considerably reduced Piping Plover numbers, while beach use in the mid-1900s renewed these declines. Recent recovery efforts have led to partial recovery and the IUCN upgrading the species from Threatened to Near Threatened. However, the Great Lakes subpopulation (residing mostly in Michigan), which is our focus, remains precariously small (IUCN 2010) and is officially endangered under the Endangered Species Act (Gratto-Trevor and Abbott 2011).

Predation is now a significant limiting factor to recovery (Rimmer and Deblinger 1990). Population modeling predicts the Great Lakes Piping Plover will go extinct within the next century if predation rates are not reduced (Plissner and Haig 2000; Wemmer et al. 2001). The federal recovery plan for plovers outlines emergency anti-extirpation methods (USFWS 2003),

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including predator removal and protective nest exclosures (Gratto-Trevor and Abbott 2011). We

examine these approaches, as studies indicate they can be successful (Mayer and Ryan 1991;

Struthers and Ryan 2005). Piping Plover managers use protective exclosures as the primary anti-

predator tool, while predator removal is used only marginally.[10]

The plover predator of most concern is the Merlin, a small falcon (V. Cavalieri, personal

communication). Merlins have been consistently observed predating on plover adults and chicks.

These falcons are protected as a threatened species under the Endangered Species Act of the

State of Michigan (MNFI 2011). Their current population in Michigan is unknown, but their

numbers have been increasing in recent years (V. Cavalieri, personal communication). Although

these falcons may roam between areas of plover habitat and the rest of the state, we assume a

fixed subpopulation hunting in the vicinity of plover habitat, to keep the model tractable.

Economic and ecological parameter values for the benchmark scenario of our numerical

analysis are listed in Table I, with calibration of the model described in Appendix B. Functional

forms for the model have already been described, with the exception of existence values. We

assume $B_i(i) = V_i \ln(i+1)$, where V_i is a parameter ($i = X,Y$).

4.2   Results for the benchmark scenario

We determine the optimal solution by examining each candidate strategy, A-D, in turn. The

numerical solutions were derived using Mathematica 7.0 (Wolfram 2008).

4.2.1   Strategy A: No management (h = 0, p = 0)

The phase plane for strategy A is presented in Figure 1. The $\dot{X} = 0$ and $\dot{Y} = 0$ isoclines do not

intersect in the positive orthant, indicating there is no equilibrium in which both species co-exist.

The phase arrows indicate plover extinction is a globally stable outcome if strategy A is

maintained without a switch to an alternative strategy. Despite this outcome, strategy A remains

a candidate long-run strategy, because nothing in the formulation of the social planner's problem

precludes plover extinction as a feasible equilibrium. If this strategy is chosen from the start,

plovers go extinct, falcons attain an equilibrium population of 195, and $SNB = \$724$ million.

4.2.2   Strategy B: Predator removal and exclosures ($h = h_{SV}$, $0 < p < 1$)

The phase plane for this case is presented in Figure 2. The phase arrows indicate the direction of

potential trajectories. By definition, all possible trajectories are switching curves for h since

$\sigma(Y,\lambda_Y) = 0$ along each trajectory. Once on such a trajectory, there is no reason to switch off

unless the trajectory enters some space where $h_{SV}(X,Y)$ becomes infeasible. This is indicated by

the $h_{SV} = 0$ boundary: above this curve, $h_{SV}(X,Y) < 0$, and the singular solution is infeasible, while

below the curve $h_{SV}(X,Y) > 0$. A similar logic holds for p, although a $p^*(X,Y) = 0$ boundary is not

drawn because at this scale it is not distinguishable from the X-axis: above this curve, $p^*(X,Y) > 0$.

The phase dynamics are governed by the saddle point equilibrium at the intersection of the

isoclines. This equilibrium, and the portion of the saddle path that converges to this outcome, lie

above the $h_{SV} = 0$ boundary and are therefore infeasible. The only feasible trajectories are those

that exist below the $h_{SV} = 0$ boundary. Trajectories that start below the boundary and then

intersect the boundary can only be followed in the short-run, with strategy D then being pursued

immediately upon reaching the boundary. All other trajectories that start below the boundary

eventually intersect the X-axis, resulting in a long-run equilibrium of $Y \to 0$, $X \to K$. Extinction

of Merlins can only be attained, however, if $h \to \infty$, implying infinite predator removal costs.[11]

So these paths, and strategy B, can be discarded as candidates for the long-run optimal trajectory.

4.2.3 Strategy C: Predator removal only ($h = h_{SV}$, $p = 0$)

Figure 3 presents the phase plane for strategy C. The dynamics are governed by the saddle point

equilibrium at the intersection of the isoclines. Unlike strategy B, the equilibrium and saddle path

of strategy C lie below the $h_{SV} = 0$ boundary. However, the saddle path and virtually all

trajectories in the state space lie above the $p^*(X,Y) = 0$ boundary (lying minimally north of the X-

axis), indicating that some positive level of p is optimal. This contradicts the formulation of

strategy C, so that this strategy is sub-optimal.

4.2.4 Strategy D: Predator exclosures only ($h = 0$, $0 < p < 1$)

Finally, consider strategy D, which is illustrated by the three-dimensional system presented in

Figure 4. Although the solution for this strategy is characterized by a dynamic system in

$(X,Y,\lambda_X,\lambda_Y)$-space, it is possible to graphically represent the solution in (X,Y,p)-space, as

described earlier in section 3.2.4. The $\dot{X} = 0$ and $\dot{Y} = 0$ isoplanes are illustrated in Figure 4.

However, to ease visualization, the $\dot{p} = 0$ isoplane is not depicted. The isoplanes intersect at a

conditionally stable steady state equilibrium. In Figure 4, this equilibrium is where the saddle

path intersects the $\dot{X} = 0$ and $\dot{Y} = 0$ isoplanes. The initial state, (X_0,Y_0), illustrated by a vertical

line in Figure 4, has a unique saddle path. Indeed, there will be different paths for different initial

states. The optimal strategy is to choose $p(0)$ to put the system on the saddle path and follow it to

the equilibrium. Since this path does not cross a switching curve for h, where $\sigma(Y,\lambda_Y) = 0$, it is

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[11] In fact, $Y = 1$ before $h \to \infty$, which is effectively eradication. One could assume eradication is achieved when a strategy B trajectory leads to $Y = 1$ (so that further control is unnecessary), but this is also found to be suboptimal.

optimal to remain on the path indefinitely. Choosing the initial p to start the system on some other path leads to either $p \to 1$ and infinite costs (which cannot be optimal), $\sigma(Y, \lambda_Y) = 0$ (and a switch to strategy B, which is found to be not optimal), or $p \to 0$ (and a switch to strategy A). The last case, which involves an eventual switch to strategy A, merely delays extinction. Therefore, the only feasible long-run strategy D management program is to select $p(0)$ to place the system on the saddle path and then follow the path to the steady state. Along this path, the plover population increases from 126 to 260, and the falcon population increases slightly from 195 to 197. We do not illustrate $p^*(t)$, as this value changes little over time, monotonically declining from approximately 0.901 to 0.886.

Numerically, strategy D yields $SNB = \$993$ million, which exceeds the value of strategy A. Compared to the no-management scenario A, strategy D yields a win-win outcome in that there are more plovers and falcons. In this case, the interests of society and falcons coincide, so that predator control improves both social welfare and the "welfare" of falcons. The result is that strategy D (exclosure-only) is the optimal management strategy overall. Note that the use of a single control differs from the traditional open access case described earlier, where we indicated two controls were optimal. There are two reasons for this difference: in the current setting, (i) predator removal involves real costs, and (ii) predators are valued directly, so that predator removal implies an additional social cost.

4.3   Sensitivity Analysis

A parameter sensitivity analysis (Table II) yields further insights. We first examine the role of Merlin existence values. Richardson and Loomis' (2009) results, which were used to calibrate $B_Y(Y)$, are based on the assumption that the public considers the Merlins to be at risk. While

Merlins are officially threatened in Michigan, the IUCN (2010) lists Merlins as a species of Least Concern and so the public may not consider them at risk. Suppose $V_Y = \frac{1}{2} \cdot V_{Y0}$ (where '0' denotes a benchmark value). In this case a win-win outcome yielding more falcons confers fewer benefits, implying fewer incentives to use exclosures. Indeed, strategy B is optimal in this case, with p slightly reduced and h slightly positive, resulting in a small increase in plovers and a 20 percent decrease in falcons (all relative to the benchmark).[12] Moreover, falcons decline compared to no-management. This makes sense: when falcons are valued less there is less opportunity cost to removing them, so predator removal is more likely to be optimal.

If the existence value of falcons is eliminated altogether, so that $V_Y = 0 \cdot V_{Y0}$, then the optimal solution involves even greater substitution of predator removal for exclosures. Specifically, it is optimal in this case to follow strategy C ($h = h_{SV}$, $p = 0$), so that the optimal set of controls is opposite that of the benchmark scenario. This was implied in the simple open access model discussed in section 2.2, where it was noted that predator removal (a license fee) was less likely to be optimal when predators had existence value (stock-dependent values). Note that the steady state $Y < 1$, so the optimal strategy is essentially one of falcon eradication.

The next scenario increases the plover carrying capacity, $k = 2 \cdot k_0$. It is still optimal to follow strategy D. At equilibrium, the rate of exclosures is slightly less ($p = 0.84$) than in the benchmark scenario, although the equilibrium plover population is now twice as high ($X^* = 519$) and there are more falcons ($Y^* = 199$). Fewer exclosures are optimal because the larger carrying capacity, which yields more plover growth, implies predation has a smaller marginal cost (i.e., $\lambda_X - \alpha\lambda_Y$ is smaller, though still positive) relative to the benchmark case.

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[12] The optimal long run trajectory is a movement along the saddle path to equilibrium. The system initially lies above this path, where $\sigma(Y,\lambda_y) > 0$, and it is optimal to use an impulse harvest until the system reaches the path, when $\sigma(Y,\lambda_y) = 0$. Then, the control $h = h_{SV}$ is followed and the system proceeds along the saddle path to equilibrium.

The next two scenarios, $\hat{Y} = \frac{1}{2} \cdot \hat{Y}_0$ and $r = 2 \cdot r_0$, favor plovers so that plovers do not go extinct in the no-management scenario. Nevertheless, strategy D remains optimal in both cases. The primary quantitative changes from the benchmark are that a smaller $\hat{Y}$ significantly reduces the equilibrium falcon stock, while a larger r slightly increases the equilibrium number of plovers. Also, neither scenario yields a win-win outcome for the falcons. This is because the interests of falcons and society are less likely to coincide when plovers are not at risk of extinction. On the other hand, predator control can still be optimal even without extinction risks.

The last two scenarios increase the cost of the exclosure control, with $c = 2 \cdot c_{p0}$ and $c = 3 \cdot c_{p0}$. Once exclosure costs are high enough, the optimal management strategy switches to strategy B, with a lower p and a small, positive h. The equilibrium involves fewer falcons and plovers relative to the benchmark. Thus, as costs become excessive it becomes too expensive to regulate (control predation), so externalities (excessive predation) persist.

5. Conclusion

We have analyzed how predator-prey relations create ecosystem externalities that are akin to the externalities from anthropogenic overharvesting of valuable resources, and how management can correct these externalities. Using this perspective, we find that predator removal and predator exclosures are analogous to license fees and harvest quotas, which are capable of correcting the relevant externalities in a standard open access system. Just as management of human hunters can benefit both humans and the exploited resource stock, we find management of predators can lead to a win-win situation in which both the prey and predator stocks increase. This is particularly true when over-predation would otherwise lead to prey extinction.

Although this win-win outcome has analogies in open access management, an important

difference in the present context is that predator controls are costly, in contrast to the usual assumption that regulation of open access hunters is costless. These costs have implications for the choice of controls. Existence values related to the predator may also influence the optimal choice of controls, in contrast to existing analyses of open access problems involving humans. In the Great Lakes Piping Plover and Merlin application, an exclosure-only policy is found to be optimal when there are existence values for the predator population. The result arises, in part, because exclosures generate a win-win outcome in which regulation increases both wildlife populations. However, if predator existence values are sufficiently small or if the costs of exclosures are excessive, some predator removal optimally substitutes for exclosures and a win-win outcome may fail to materialize.

Our numerical results have implications for managing open access resources, by showing how the optimal mix of regulatory instruments could be influenced by two types of values that are often ignored: regulatory transactions costs, and non-market values related to the regulated industry. In particular, these latter values may arise for industries that become sentimentalized, such as with Maine's "lobster culture" (Daniel et al. 2008). The inclusion of these values results in the optimal management strategy being parameter dependent and therefore a numerical issue.

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Appendix A

The main text described how the equation of motion for the predators, (4), is analogous to an entry-exit condition for resource harvesters in a regulated open access setting. Here, we set up and analyze the problem in such a setting, treating Y as harvesters, X as the resource, p as a proportional reduction in the harvest (i.e., a quota), and h as a licensing fee. As with traditional regulated open access models, we assume harvesters and resource managers both value the economic rents from harvesting activities. Managers may also have non-market (existence) values associated with the prey species, but not generally with harvesters of the prey. Denote non-market (existence) values associated with the prey by $B_X(X)$. Finally, we make the typical assumption that regulations (i.e., h and p) are implemented costlessly.

Given these assumptions, the planner maximizes the present value of economic (after-tax) rents, prey existence values, and tax receipts, subject to (3)-(4). The current-value Hamiltonian is

(A1) $H == [(\sigma(\hat{Y} - Y) + \alpha\beta X(1 - p) - \delta)Y][1 + \lambda_Y] + B_X(X) + \lambda_X \dot{X} - \lambda_Y hY$.

Note the licensing fee h does not appear in the bracketed term in (A1) since h is a transfer payment and not a true cost. As H is linear in h and p, the optimality condition for h is given by (12) with $c_h = 0$, and the optimality condition for p is

$$(A2) \quad \frac{\partial H}{\partial p} = (\lambda_X - \alpha[1 + \lambda_Y])\beta XY = 0 \quad \begin{array}{ll} > 0 & iff \quad p^* = 1 \\ iff & p^* = p_{sv} \\ < 0 & iff \quad p^* = 0 \end{array} ,$$

The following adjoint equations are also necessary

$$(A3) \quad \dot{\lambda}_X = \rho\lambda_X - \alpha\beta(1-p)Y[1+\lambda_Y] - \lambda_X[r(1-2X/k) - \beta Y(1-p)] - B'_X ,$$

$$(A4) \quad \dot{\lambda}_Y = \rho\lambda_Y - (\sigma(\hat{Y} - 2Y) + \alpha\beta X(1-p) - \delta)[1+\lambda_Y] + \lambda_X X\beta(1-p) + \lambda_Y h .$$

Consider whether both controls are used simultaneously. As $h^* \to \infty$ can only hold for an instant, we focus on the singular solution for h. From (12) with $c_h = 0$, this requires $\lambda_Y = \dot{\lambda}_Y = 0$. With $\lambda_Y = 0$, (A2) implies $\lambda_X \geq \alpha$ must hold for $p^* > 0$. Consider the singular solution for p (given h is also singular), so that $\lambda_X = \alpha$ and $\dot{\lambda}_X = 0$. Insert these values into (A3)-(A4):

$$(A5) \quad X^* = k[B_X/\alpha + r - \rho]/[2r] ,$$

$$(A6) \quad Y^* = (\hat{Y} - \delta/\sigma)/2 .$$

The solution in (A5)-(A6) is a fixed (steady state) point, and so h^* and p^* are found by setting (3) and (4) equal to zero and setting $X = X^*$ and $Y = Y^*$. The two controls are used together: h^* addresses the congestion externality to maintain Y at the level that maximizes returns from "other resources" (implicit via $\sigma\hat{Y}$), while p^* ensures X is harvested efficiently. Note only one control would be optimal if not for the "other resource". That is, a double singular solution does not exist when $\sigma = 0$, which is seen in that Y^* in (A6) becomes undefined when we set $\sigma = 0$. It is also easy to show that $h^* = h_{sv}$, $p^* = 1$ is not an optimal solution when $\sigma = 0$. Rather, only a single

control is required when $\sigma = 0$. This is because harvests, $\beta(1-p)XY$, may be managed via p or by changing Y (via h), with neither control implying a different opportunity cost.[13]

A single control is also optimal when social welfare is instead defined as discounted stock-dependent (existence) values, even when $\sigma > 0$, because in this case there is no reason for a second control to manage rents from the "other resource". Defining the existence value for harvesters by the increasing, concave function $B_Y(Y)$, the current-value Hamiltonian becomes

(A7) $H = B_X(X) + B_Y(Y) + \lambda_X \dot{X} + \lambda_Y \dot{Y}$.

The optimality conditions for the controls are now (12), with $c_h = 0$, and

(A8) $\dfrac{\partial H}{\partial p} = (\lambda_X - \alpha \lambda_Y)\beta XY = 0$ $\begin{array}{lll} >0 & iff & p^* = 1 \\ iff & p^* = p_{sv}, \\ <0 & iff & p^* = 0 \end{array}$

Consider whether both controls are used simultaneously, again focusing on the singular solution for h. From (12), $h^* = h_{sv}$ requires $\lambda_Y = 0$, and hence $\dot{\lambda}_Y = 0$. With $\lambda_Y = 0$, (A8) implies $\lambda_X \geq 0$ for $p^* > 0$. As $\lambda_X = 0$ will never arise for an optimally managed resource, a singular value for p is ruled out. The only option for a positive p is thus $p^* = 1$. To see if this can be optimal, consider the adjoint condition for Y for our proposed solution of $p^* = 1$, $\lambda_Y = 0$, and $\dot{\lambda}_Y = 0$:

(A9) $\dot{\lambda}_Y = \rho\lambda_Y - B_Y' - \lambda_Y\left(\sigma(\hat{Y} - 2Y) + \alpha\beta X(1 - p) - \delta - h\right) + \lambda_X X\beta(1 - p) = -B_Y' = 0$

Given that $B_Y' > 0$, expression (A9) represents a contradiction. Hence, using both controls to manage the system (for more than an instant) is sub-optimal.

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[13] Although h is ineffective in situations where the optimal strategy would be to let Y increase, the linear nature of the problem implies a most rapid approach path (i.e., $h = p = 0$) would be optimal in such instances.

Appendix B

*Intrinsic growth rate***: *r***.** No published sources present a Piping Plover intrinsic growth rate. Courchamp *et al.* (2000) use a value of 0.2 for the Macquarie Parakeet, which went extinct due to predation. Similarities between the Macquarie Parakeet and the Piping Plover also extend to food preferences and size. Like the plover, the parakeet's habitat was near the shore and they fed on invertebrates. The parakeet was small, too, although somewhat larger than the plover (30cm vs 20cm in length). Due to this likeness, the value of 0.2 is used for the Piping Plovers.

    *Carrying capacity***: *k*.** Plissner and Haig (2000) use $k = 300$ for the Great Lakes plover population, which is the value managers believe the current habitat can support (USFWSb 2009).

    *Initial values***: X_0, Y_0.** The U.S. Fish and Wildlife Service (USFWSb 2009) estimated the Great Lakes population of Piping Plovers in 2009 at 126 individuals. The initial value for the predator population was set at its carrying capacity, that is, $Y_0 = \hat{Y} - \delta/\sigma$.

    *Other Merlin ecological parameters***: $\hat{Y}$, β, α, σ and δ.** These values were not directly available due to a lack of published data. We chose values based on reasonable assumptions and simulations that reflect current knowledge of Merlins. The particulars are described below. The sensitivity analysis in section 4.3 examines the impact of various parameter choices on results.

    We begin by specifying the Merlin carrying capacity when $X = 0$: $\hat{Y} - \delta/\sigma$. Doolittle and Balding's (1995) reported sightings in Michigan, Minnesota and Wisconsin imply a population density of 0.29 Merlins/mile^2. We focus on habitat in Michigan because most of the Great Lakes Piping Plovers nest in Michigan (Sleeping Bear Dunes National Park alone contains about one third of all nesting pairs in the Great Lakes, S. Jennings, personal communication). Suitable Merlin habitat in Michigan comprises about 7100 square miles (pine forests), so that if the Merlin population has recovered from historical lows in the 1960s at an average annual rate of

3.3% (Niven et al. 2004) the Michigan Merlin population would be 3900 in 2012. Only a fraction of the total Merlin population actually lives near Piping Plover habitat. A precise estimate of this fraction is not available. However, based on the relative size of Merlin and plover habitats, we assume five percent of the Merlin population, or 195 Merlins, resides in territory that overlaps with Piping Plover habitat. We take this value to be the Merlin carrying capacity when $X = 0$.

Next, we specify the intrinsic growth rate for Merlins: $\hat{Y}\sigma - \delta$. Tanner (1975) estimates the maximum fertility of the European Sparrow Hawk, a similarly-sized predatory bird, to be 0.363. We adopt this value for the intrinsic growth rate of Merlins.

The third piece of information we use for calibration is that plovers are small and occupy only a fraction of the Merlin diet, so the Merlin population benefits marginally (a small increase in fertility) from plover predation (V. Cavalieri, personal communication). This implies $\alpha\beta X_0 Y_0$ should be small, i.e. equivalent to only a few Merlins. We select parameters so that $\alpha\beta X_0 Y_0 \approx 3$.

Along with the conditions for carrying capacity ($\hat{Y} - \delta/\sigma = 195$), the intrinsic growth rate ($\hat{Y}\sigma - \delta \approx .363$), and sustenance ($\alpha\beta X_0 Y_0 \approx 3$), the final two parameters are set to satisfy a condition related to plover extinction. Specifically, Plissner and Haig (2000) and Wemmer et al. (2001) predict extinction of Plovers within 100 years if nothing is done. Assuming Merlins are the primary driver of extinction, we select parameters so that a numerical simulation of (1)-(2) (using Mathematica 7.0, Wolfram 2008) satisfies the extinction conditions and the other conditions. The combination of $\hat{Y}$, β, α, σ and δ finally selected (Table I) yielded approximately 195 Merlins and one Piping Plover by year 100 in the simulation, as well as $\hat{Y}\sigma - \delta = 0.365$ and $\alpha\beta X_0 Y_0 = 3.686$, closely satisfying each calibration condition listed above.

Benefit values: V_X, V_Y. For species i ($i=X,Y$), we calibrate V_i using Richardson and Loomis' (RL's) (2009) *aggregate* willingness to pay (WTP) estimates (i.e.,WTP/ household times

households) for a percentage increase in i: $W_i(\%\Delta_i)$, where $\%\Delta_i = (i - i_0)/i_0$. $W_i(\%\Delta_i)$ is related to

$B_i(i)$ by $W_i(\%\Delta_i) = B_i(i) - B_i(i_0) \approx (V_i/100)\%\Delta_i \approx V_i \times \ln([1+i]/[1+i_0])$, where $V_i = i_0 B_i'(i_0)$. Hence,

W_i is consistent with our logarithmic relation $B_i(i) = V_i \ln(1+i)$. Using the first approximation

above, we calibrate $V_i = 100 \times W(\%\Delta_{i1})/\%\Delta_{i1}$, where $\%\Delta_{i1} = i_0/[i_1 - i_0]$ is an independent variable

in RL's model. For each species, we follow RL's example and assume $\%\Delta_{i1}=100$. We then

calculate $W(\%\Delta_{i1})$ by assuming 0.35 million households (i.e., $\approx$ the population of northern

Michigan), and that the other independent variables of RL's model take the following values: the

survey response rate equals 100%; the species in question is a non-charismatic bird; the sample

means of the RL data were used for the fraction of the survey done by mail, 0.851, and the

fraction of respondents who were visitors, 0.231. Finally, we multiply V_Y by 0.2 since only some

Merlins in northern Michigan overlap with plovers (we previously assumed a 5% overlap of

Merlins and plover habitat in *all* of Michigan; now we only consider northern Michigan).

Cost of predator removal: c_h. The federal recovery plan for the Piping Plover estimates the

cost of predator control (task # 1.222 in USFWS, 2003) to be \$35,000, with the disclaimer that

"Final costs contingent on areas and numbers of predators." Assuming this cost is adequate for

removing one quarter of the predator stock, we calculate $c_h h = c_h/4 = 35{,}000 \Rightarrow c_h = 140{,}000$.

Cost of predator exclosures: c_p. For locating Piping Plover nests and identifying critical

habitat, the recovery plan estimates a total cost of \$319,000 (i.e., the sum of the costs for task #s

1.12, 1.16, 1.17, 1.18, 1.21, 1.221, 1.223, 1.31, 1.341, 4.1 in USFWS 2003). These figures are

adequate for protecting 75% of the Great Lakes Piping Plovers (Gratto-Trevor and Abbott, 2011)

and correspond closely to estimates provided by the National Park Service (S. Jennings, personal

communication). This implies $c_p p_0/(1-p_0) = 3c_p = 319{,}000 \Rightarrow c_p = 106{,}333.33$.

Tables and Figures

Table I. Benchmark parameter values.

Parameter	Value
r	0.2
k	300
$\hat{Y}$	248
X_0	126
Y_0	195
α	0.125
β	0.0012
σ	0.001875
δ	0.1
V_X	7,936,958
V_Y	1,587,392
c_h	140,000
c_s	106,333.33
ρ	0.05

Table II. Simulation results.

Scenario		Optimal management			No management	
	Strategy	$(X^\infty, Y^\infty)^a$	(h^∞, p^∞)	SNB^b	(X^∞, Y^∞)	SNB^b
Benchmark scenario	D	(260, 197)	(0.00, 0.89)	10.00	(0, 195)	7.27
Alternative parameters						
$V_Y = \frac{1}{2} \cdot V_{Y_0}$	B	(264, 157)	(0.08, 0.87)	9.21	(0, 195)	6.43
$V_Y = 0 \cdot V_{Y_0}$	C	(300, <1)	(0.41, 0.00)	8.71	(0, 195)	5.59
$K = 2 \cdot K_0$	D	(519, 199)	(0.00, 0.89)	10.08	(0, 195)	7.63
$\hat{Y} = \frac{1}{2} \cdot \hat{Y}_0$	D	(274, 75)	(0.00, 0.81)	9.89	(151, 83)	9.10
$r = 2 \cdot r_0$	D	(273, 198)	(0.00, 0.85)	10.03	(116, 204)	9.29
$c_p = 2 \cdot c_{p0}$	D	(245, 198)	(0.00, 0.84)	9.91	(0, 195)	7.27
$c_p = 3 \cdot c_{p0}$	B	(236, 183)	(0.03, 0.80)	9.80	(0, 195)	7.27

[a] The superscript ∞ denotes the equilibrium value.
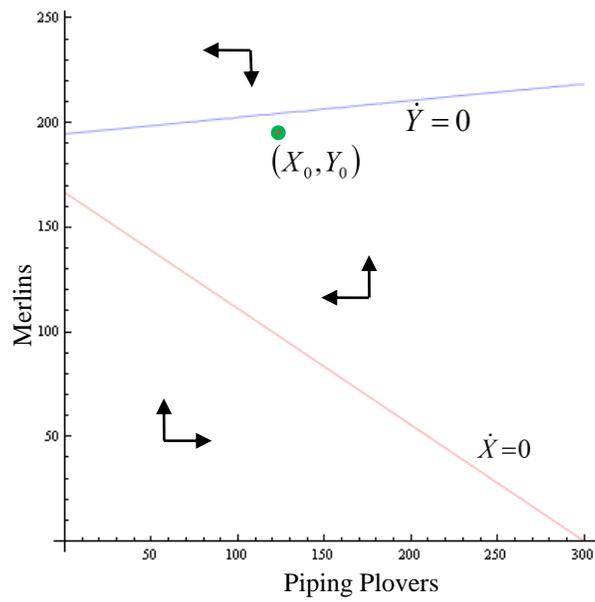[b] All economic values are in US\$ $\times 10^8$.

Figure 1. Phase diagram of strategy A ($h = 0$, $p = 0$) in the benchmark scenario.
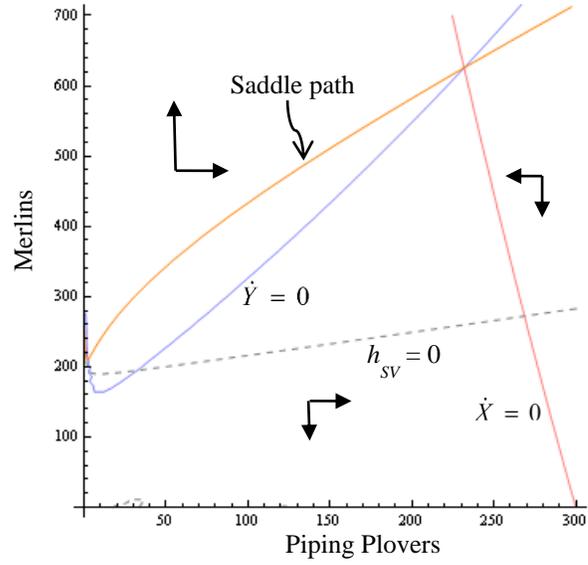
Figure 2. Phase diagram of strategy B ($h = h_{SV}$, $0 < p < 1$) in the benchmark scenario. The dashed

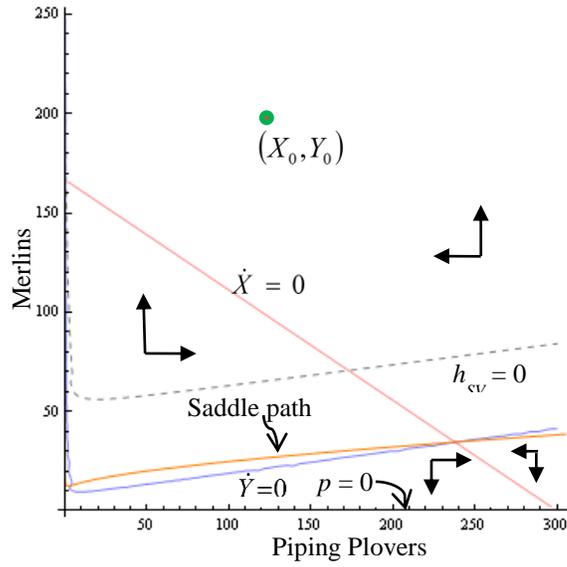line marks the $h_{SV} = 0$ threshold. Above this line $h_{SV} < 0$ and below the line $h_{SV} > 0$.

Figure 3. Phase diagram of strategy C ($h = h_{SV}$, $p = 0$) in the benchmark scenario. The dashed line marks the $h_{SV} = 0$ threshold. Above this line $h_{SV} < 0$ and below the line $h_{SV} > 0$. Running close to the X-axis is the p = 0 threshold. Above this line $p > 0$ and below the line $p = 0$
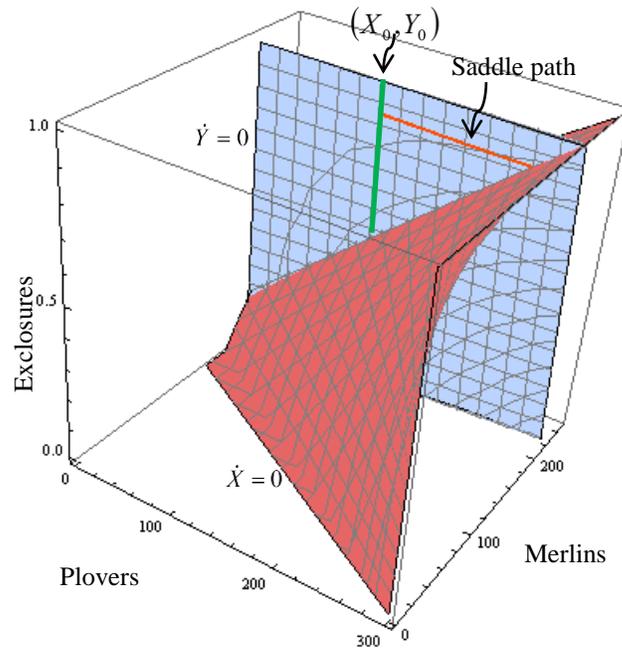
Figure 4. Graph of strategy D ($h = 0$, $0 < p < 1$) in the benchmark scenario.