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Melstrom, Richard and Horan, Richard

Salisbury University, Michigan State University

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Interspecies Management and Land Use Strategies to Protect Endangered Species

Richard T. Melstrom
Department of Economics and Finance
Department of Environmental Studies
Salisbury University

Richard D. Horan
Department of Agricultural, Food and Resource Economics
Michigan State University

Running title: Interspecies Management and Land Use Strategies

Corresponding Author: Richard T. Melstrom
Department of Economics and Finance
Salisbury University
Purdue Hall
1101 Camden Avenue
Salisbury, MD 21801-6860
rtmelstrom@salisbury.edu

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Abstract

We consider an ecosystem management problem where managers can use habitat creation and predator removal to conserve an endangered species. Predator removal may become particularly important in the face of habitat loss, and ecosystem management strategies that ignore the influence of habitat are likely to be inefficient. Using a bioeconomic model, we show that the marginal impact of prey habitat on predators is a key factor in determining the substitutability or complementarity of habitat and removal controls. Applying the model to the case of the endangered Atlantic-Gaspésie Woodland Caribou (*rangifer tarandus caribou*), we find that the first-best strategy involves extensive caribou habitat protection and a large predator cull initially, and then substituting habitat investments for predator removal as both populations begin to recover, suggesting that habitat protection and predator removal are effectively substitute controls.

Interspecies Management and Land Use Strategies to Protect Endangered Species

Introduction

Habitat loss is widely seen as the primary driver of biodiversity decline (Wilcove et al. 1998; MEA 2005), with the lack of suitable habitat having left many species “conservation reliant” (Scott et al. 2005). Species that are conservation reliant require continuous, species-specific intervention that usually involves the control of predators, parasites and competitors. Scott et al. (2010) find that 66% of the recovery plans for species listed under the U.S. Endangered Species Act call for such controls.

Managing species interactions is particularly important in the face of habitat loss (Scott 2010). The growing literature on ecosystem management focuses on population controls (harvests) to manage species interactions (Tschirhart 2009). This work has shown the need to adjust harvest levels to account for the effects of stock-dependent species interactions (Brock and Xepapadeas 2002), including predator-prey relations (Ragozin and Brown 1985; Ströbele and Wacker 1995) and species competition (Chaudhuri 1986). However, prior work does not simultaneously address the issue of habitat loss, which can also affect species interactions (Moon et al. 2010).

Wildlife management strategies that ignore the influence of, and indeed the management of, habitat are likely to be inefficient. Some prior bioeconomic work has examined habitat management to reduce exploitative competition (e.g. when humans develop land that is otherwise used by species as habitat), but not in the context of species interactions such as an endangered species subject to predation (e.g. Swallow 1990; Sanchirico and Springborn 2011;

Bednar-Friedl et al. 2012).¹

We examine optimal investments in predator controls and habitat provision, given that habitat affects the interacting species in different ways. Specifically, we analyze a problem where protecting the habitat of an endangered prey species may either benefit or adversely affect the predator population. The marginal impact of prey habitat on predators is shown to be a key factor in determining the biotechnical substitutability or complementarity of the controls. However, similarly-defined bioeconomic relationships are shown to depend additionally on economic considerations. Our numerical results suggest both controls, applied as bioeconomic substitutes, are generally optimal in the long run, although a single control may be optimal in the short run.

Our analysis is motivated by the conservation of Atlantic-Gaspésie Woodland Caribou (*rangifer tarandus caribou*), the only remaining herd of woodland caribou living south of the St. Lawrence River. This population has been largely extirpated from the southern portion of its range due to human encroachment and habitat loss, and it now resides almost entirely within the Parc National de la Gaspésie, Quebec, established in 1937 to protect caribou habitat. Because caribou are sensitive to human activity (Recover Plan 2006), recreational activities in the park are highly regulated to minimize human interference with the caribou (PNG 2011). Still, the caribou population has fallen from about 750 in the 1950s to 270 in 1983, and then to 140 in 2001. It is now clear that predation is a major limiting factor (Boisjoly et al. 2010). The Gaspésie

¹ Swallow (1990) and Sanchirico and Springborn (2011) study human-animal land use conflict as a development problem. Development generates economic rents but reduces habitat and the returns from a harvestable resource, and may ultimately drive the harvested resource to extinction. Bednar-Friedl et al. (2012) study land use conflicts in the context of a park management problem. The park's value increases with visits, but visitors damage the habitat of an existence-valued endangered species. To aid the endangered species, Bednar-Friedl et al. consider visitor controls, habitat restoration and population enhancements, and they find optimal ecosystem management involves at least some reduction in visits.

Woodland Caribou Recovery Plan has made predator control a priority, which has been shown to improve caribou survival (Mosnier et al. 2003). In 1999, measures were also taken to create caribou habitat outside the park boundaries. Applying the bioeconomic model to the case of the caribou, we find that the first-best strategy involves culling a large number of predators and establishing a large reserve initially, and then substituting reserve investments for predator removal as both populations begin to recover, suggesting that habitat protection and predator removal are effectively substitute controls.

Ecological Model

Our analytical model is based on the problem of conserving an endangered prey species at risk from predation and habitat loss. Assume total land area, denoted L , is divided into two uses: a share of land, s , is managed as a conservation reserve for endangered prey (with the total reserve area being sL), while the remaining share, $(1 - s)$, is managed for human use. We treat s as a control, so that managers can instantaneously change the size of the reserve. This may be a reasonable approximation for some species, including the Gaspé caribou, when the land remains in a fairly natural state under both alternative land uses (e.g., non-reserve land is managed for activities like recreation, not development).²

Denote the prey population by C and the predator population by P . Prey dynamics take the form of a Lotka-Volterra equation, modified to account for the land allocation³

² Instantaneous adjustment in habitat will be inaccurate for forms of habitat loss that are destructive to the land and require many years to rehabilitate (i.e. “grow back”). In such cases, it would be more appropriate to model land in a conservation reserve as a state variable that can only change gradually over time.

³ A carrying capacity that is specified independently of the particular predator-prey interactions being modeled represents a constraint on population growth that is implied by a limiting resource, which is generally food, space, or some other resource (e.g., other prey, in the case of predators; Larkin 1966) (Tanner 1975). The mathematical specification of carrying capacity does not depend on which resource is limiting (Tanner 1975). We model carrying

$$(1) \quad \dot{C} = C[r_C(\alpha_C + \beta_C s - C) - \gamma P]$$

The first term in brackets is per capita growth prior to predation, where r_C is a growth parameter, α_C is the carrying capacity absent predation and any reserve, and β_C is a parameter measuring how the carrying capacity increases when more land is allocated to the reserve (Hannesson 1983). The final term in brackets captures the effect of predation, which follows a Holling Type I functional response in which γ is a catchability parameter.

Predator population dynamics take an analogous form:

$$(2) \quad \dot{P} = P[r_P(\alpha_P + \beta_P s - P) + \gamma C - h].$$

The first term in brackets is density-dependent predator growth before consumption of the endangered prey (Ives and Murray 1997). This term implies predators do not rely solely on the endangered prey (Larkin 1966).⁴ The predator carrying capacity, before endangered prey consumption, is implicitly determined by the availability of other prey as determined by land use (Boisjoly et al. 2010). If other prey are more abundant on the conservation reserve set aside for the endangered prey, then $\beta_P > 0$. This need not be the case, however, as some predator species thrive on land in human use so that $\beta_P < 0$.⁵ Henceforth, to avoid confusion between the endangered prey and other prey, we simply refer to the endangered prey as “prey” while other

capacity to be a linear function of space (habitat area), both for predators and prey, which represents a first-order approximation of the true relation. Defining carrying capacity as a function of space is reasonable, as more space in a “good” habitat generally represents both more cover and a greater food supply (e.g. more plant material for herbivores; more “other” [i.e. non-caribou] prey for predators). Bulte and Horan (2003) adopt a similar growth equation incorporating a habitat effect for a single species model.

⁴ See Hannesson (1983), Ragozin and Brown (1985), and Brown et al. (2005) for bioeconomic applications making this assumption.

⁵ It is well documented that foxes, raccoons and other small mammalian predators have higher densities in human land-use areas (Riley et al. 1998), reducing bird and amphibian populations (Engeman et al. 2010). Other examples include black bears benefiting from roadside forage (Rogers and Allen 1987), birds of prey exploiting schools of salmon near hydroelectric dams (Engeman et al. 2009), parasitic cowbirds thriving in residential areas (Borgmann and Morrison 2010) and coyotes adapting to human-disturbed environments (Markovchick-Nicholls et al. 2008).

prey are only referenced indirectly via the carrying capacity variables. The second term in brackets, γC , is the rate of predation on the endangered prey. Finally, h is the rate predators are removed by managers.

Although both species may be valued, consider how management promotes prey conservation. From (1) and (2), a larger h enhances prey conservation by reducing the number of predators and hence predation. The impact of the reserve on prey conservation is less clear. A larger s increases \dot{C} , but the effect on \dot{P} – and hence on future predation – depends on the sign of β_P . The reserve reduces future predation when $\beta_P < 0$, but may increase it when $\beta_P > 0$. In the latter case, the net effect of s on prey conservation depends on ecological relations. This result can be seen by examining long-run outcomes.

Consider the steady state values of C and P , denoted C^* and P^* . These are derived as the solution to $\dot{C} = \dot{P} = 0$: $C^* = r_P(\gamma h + r_C(\alpha_C + \beta_C s) - \gamma(\alpha_P + \beta_P s)) / (r_C r_P + \gamma^2)$ and

$P^* = r_C(-h + r_P(\alpha_P + \beta_P s) + \gamma(\alpha_C + \beta_C s)) / (r_C r_P + \gamma^2)$. The marginal impact of s on C^* is

$$(3) \quad \partial C^* / \partial s = r_P(r_C \beta_C - \gamma \beta_P) / (r_C r_P + \gamma^2).$$

Relation (3) is positive, so that s and h are biotechnical substitutes for prey conservation, when (i) $\beta_P < 0$, or (ii) $\beta_P > 0$ and $(r_C \beta_C) / (\gamma \beta_P) > 1$. In case (i), the reserve reduces predator productivity, benefitting prey. In case (ii), the term $(r_C \beta_C) / (\gamma \beta_P)$ measures how well the prey can withstand predation pressure on reserve land, which is related to the prey population's *biotechnical productivity* (Clark 2005).⁶ When condition (ii) holds, the larger reserve increases the ability of

⁶ Specifically, $r_C \beta_C$ is the increase in the prey's growth for a marginal increase in s , while $\gamma \beta_P$ is the increase in predation for a marginal increase in s . Hence, our measure of biotechnical productivity of prey is defined as a ratio of the growth rate to the predation mortality rate. Somewhat analogously, Clark (2005) measures biotechnical productivity as the ratio of a species' intrinsic growth to the catchability rate associated with predation by humans.

the prey to withstand predation pressure. These results arise even though $\partial P^*/\partial s = r_C(\gamma\beta_C + r_P\beta_P)/(r_C r_P + \gamma^2)$ may be positive. Specifically, $\partial P^*/\partial s > 0$ when $\beta_P > 0$, and also in the case of $\beta_P < 0$ when the negative habitat effect on predators is outweighed by the positive effect of more prey, i.e. when $(\gamma\beta_C)/(-r_P\beta_P) > 1$.

The sign of (3) is negative when $\beta_P > 0$ and the reserve reduces the ability of the prey population to withstand predation, i.e. when $(r_C\beta_C)/(\gamma\beta_P) < 1$. The two controls are biotechnical complements in this case, in the sense that investments in the reserve must be accompanied by increased predator controls to offset conservation risks.

Similar tradeoffs arise away from the steady state. Consider the concern that the endangered species is at risk of extinction. Extinction occurs when $\dot{C}/C < 0$ as $C \rightarrow 0$ and $P \rightarrow P^*|_{C \rightarrow 0} = (\alpha_P + \beta_P s) - h/r_P$. This extinction condition is written

$$(4) \quad (r_C\alpha_C - \gamma\alpha_P) + s(r_C\beta_C - \gamma\beta_P) + \gamma h/r_P < 0$$

We assume $r_C\alpha_C < \gamma\alpha_P$, so that the prey go extinct absent the reserve or predator harvests ($s=h=0$). This makes the prey conservation reliant, a common wildlife management problem (Scott et al. 2005). As above, condition (4) indicates that s and h are biotechnical substitutes in preventing prey extinction when (i) $\beta_P < 0$, or (ii) $\beta_P > 0$ and $(r_C\beta_C)/(\gamma\beta_P) > 1$, and they are biotechnical complements when $\beta_P > 0$ and $(r_C\beta_C)/(\gamma\beta_P) < 1$.

Bioeconomic Model

Economic objectives

Suppose each species generates stock-dependent non-market benefits, or existence values.

Denote existence values by $u_i \ln(i)$ (for $i=C,P$), where $u_i > 0$ is a parameter. This specification implies infinite marginal benefits from preventing extinction of species i . Thus, some investment in prey conservation is optimal, given that prey are conservation reliant. For simplicity, assume neither species has harvest value, which is consistent with our numerical example and has little bearing on the general insights obtained below.

Conservation measures are costly. Predator removal costs take the Schaefer form (Clark 2005), $c_h h$, where $c_h > 0$ is a parameter.⁷ To maintain habitat in a conservation reserve society foregoes the returns from using land for human activities. Conservation reserve costs take the quadratic form (a second-order approximation to any convex cost function) $c_{R1} Ls + c_{R2} (Ls)^2 = c_{s1} s + c_{s2} s^2$, where $c_{s1} = c_{R1} L > 0$ and $c_{s2} = c_{R2} L^2 > 0$ are parameters. Convex costs arise because the reserve initially displaces only economically marginal activities, but eventually encroaches on increasingly beneficial land.

A manager wishing to maximize the present value of net benefits would solve

$$(5) \quad \max_{h,s} \int_0^{\infty} [u_C \ln(C) + u_P \ln(P) - c_h h - (c_{s1} + c_{s2} s)s] e^{-\rho t}$$

subject to (1), (2), $0 \leq h$, $0 \leq s \leq 1$, $C(0) = C_0$, $P(0) = P_0$

where ρ is the discount rate. The Hamiltonian associated with problem (5) is⁸

$$(6) \quad H = u_C \ln(C) + u_P \ln(P) - c_h h - (c_{s1} + c_{s2} s)s + \lambda_C \dot{C} + \lambda_P \dot{P},$$

where λ_i is the co-state variable for species i ($i = C, P$). Note that $\lambda_C > 0$ because the prey are only valued (they do not inflict social costs), whereas λ_P may be positive or negative since

⁷ Recall, h is the removal rate. Schaefer costs are typically written as $c_h Q/P$, where Q is total removal (Clark 2005). Given $Q = hP$, removal costs equal $c_h h$, as in the text.

⁸ The constraints on h and s are addressed implicitly below.

predators have existence values but also generate ecological damages via predation.

Necessary Conditions

As the Hamiltonian is linear in h , the optimal choice of h , denoted h^* , must satisfy

$$(7) \quad \frac{\partial H}{\partial h} = -c_h - \lambda_p P = 0 \quad \begin{array}{l} > 0 \quad \text{iff} \quad h^* \rightarrow \infty \\ < 0 \quad \text{iff} \quad h^* = 0 \end{array} \quad \text{iff} \quad h^* = h_{SV},$$

where h_{SV} is the singular solution for h . Condition (7) indicates $h^* = h_{SV}$, is optimal when $-\lambda_p = c_h/P$. An impulse control for h is optimal when $-\lambda_p > c_h/P$, and $h^* = 0$ is optimal when $-\lambda_p < c_h/P$. These results indicate it is only optimal to remove the predator when it has negative value, i.e. it is a nuisance.⁹

The optimal choice of s , denoted s^* , is positive when:

$$(8) \quad \partial H / \partial s = 0 \Rightarrow c_{s1} + 2c_{s2}s = \lambda_c r_C \beta_C C + \lambda_p r_p \beta_p P.$$

First order condition (8) equates the marginal cost of increasing the share of reserve land with the marginal net ecological benefits of this larger share. There is optimally no reserve ($s^* = 0$) if the marginal net ecological benefits are less than c_{s1} .

The marginal benefit of predator removal, $-\lambda_p P$, is critical to deriving both h^* and s^* .

From condition (7), $h^* > 0$ requires $-\lambda_p P > 0$, with the incentives for h being larger the larger is $-\lambda_p P$. If $-\lambda_p P > 0$ and $\beta_p < 0$, then the final term in condition (8) is positive and the incentives to use both controls are larger. Alternatively, there may be incentives to use only removal when $-\lambda_p P > 0$ and $\beta_p > 0$, or to use only reserve investments when $-\lambda_p P < 0$ and $\beta_p > 0$ (although this

⁹ Predator removal with $\lambda_p > 0$ could be optimal if the predator had harvest value.

latter case is ruled out as a long-run outcome when $(r_C/\gamma)(\beta_C/\beta_P) < 1$ because equation (4) implies extinction of the prey). Finally, the likelihood that neither control is optimal is increased when $-\lambda_P P < 0$ and $\beta_P < 0$ (although this case is ruled out as a long run outcome since prey are conservation reliant).

Whether both controls are used and how they vary with each other cannot be determined solely from conditions (7) and (8). The reason is that the tradeoffs in system (7)-(8) depend on the values of the co-states, which are determined jointly with the controls. The co-states evolve according to two adjoint conditions that can be expressed in “golden rule” form for species i ($i = C, P$) as $\rho = \dot{\lambda}_i / \lambda_i + (\partial H / \partial i) / \lambda_i$.

The golden rule condition for the prey is

$$(9) \quad \rho = \dot{\lambda}_C / \lambda_C + u_C / (\lambda_C C) + r_C (\alpha_C + \beta_C S - 2C) - (\lambda_C - \lambda_P) \gamma P / \lambda_C,$$

which equates the discount rate, ρ , to the net rate of return from conserving prey (the right hand side, or RHS). The first three RHS terms, respectively, are the capital gain or loss from changes in the prey stock, the marginal existence value of prey (normalized by λ_C), and the marginal growth in prey before predation. The final RHS term is the normalized net cost of one more prey to predation, assuming $\lambda_C - \lambda_P > 0$, or the net benefit of one more prey to predation if $\lambda_C - \lambda_P < 0$.

The golden rule condition for the predators is

$$(10) \quad \rho = \dot{\lambda}_P / \lambda_P - u_P / (-\lambda_P P) + [r_P (\alpha_P + \beta_P S - 2P) - h] + (\lambda_C - \lambda_P) \gamma C / (-\lambda_P),$$

which has an interpretation analogous to condition (9) when $\lambda_P > 0$. The interpretation of (10) changes when $\lambda_P < 0$. In that case, the golden rule condition equates the opportunity cost of capital, ρ , with the rate of return to controlling the nuisance predator – which equals the rate of

loss due to the predator. The first RHS term is the capital gain or loss from changes in the predator stock, the second term is the marginal existence value of the predator, the third term, in brackets, is the growth in predators (prior to predation of the endangered prey) and the final term, which is positive when $\lambda_p < 0$, is the normalized net cost of predation, as predation reduces the prey and increases predators.

Determining whether and to what extent s and h are used requires jointly solving the conditions (7)-(10) to derive feedback relations for s and h . We now turn to this issue.

Optimal Management Strategies

The optimal management strategy may be an interior solution, a corner solution or a combination of the two. We can rule out several strategies as possible long-run solutions, although they may be short-run solutions implemented en route to a long-run strategy. These include a strategy of maximum predator removal, $h \rightarrow \infty$, as doing so implies predator extinction and infinite removal costs, and a strategy of no conservation reserve and no predator removal ($s = h = 0$), as this leads to extinction and infinite marginal existence values for the prey. The remaining, long-run candidate strategies are: a dual control strategy with both a conservation reserve and predator removal ($s^* > 0, h^* = h_{SV}$), a predator removal-only strategy in which there is no reserve ($s = 0, h^* = h_{SV}$) and a reserve-only strategy in which there is no predator removal ($s^* > 0, h^* = 0$).¹⁰

Insight into the candidate strategies is obtained by examining the dual control strategy, as determined by (7)-(10) with $\partial H/\partial h = \partial H/\partial s = 0$. From (7), $\partial H/\partial h = 0$ yields

$$(11) \quad \lambda_p(P) = -c_h/P$$

¹⁰ A long-run solution could involve a cyclical series of switches among the candidate strategies, with the switches governed by (7)-(8). We do not find such a strategy is optimal in our numerical example.

which indicates predators are managed as a nuisance species. Take the time derivative of (11),

$\dot{\lambda}_P = (c_h / P^2) \dot{P}$, and substitute this expression and (11) into (10) to obtain

$$(12) \quad \lambda_C(C, P) = [u_P / P - \lambda_P(P)(\rho + r_P P)] / (\gamma C) = [u_P / P + (c_h / P)(\rho + r_P P)] / (\gamma C).$$

Condition (12) stems from equating the marginal ecological cost of predation (the LHS, multiplied by predation per predator, γC), or equivalently the marginal ecological benefits of reduced predation, with the marginal costs of investing in nuisance control (the RHS numerator, which is equivalently the marginal benefit of allowing more predators by forgoing predator removal). Relation (12) indicates that prey must be more highly valued when society is willing to give up more benefits to control predators as a nuisance.

It is now possible to derive feedback rules for the two controls. First, substitute $\lambda_C(C, P) = \lambda_C$ and $d\lambda_C(C, P)/dt = \dot{\lambda}_C$ into (9) and solve for

$$(13) \quad h_{SV}(C, P, s^*) = r_P \beta_P s^* + r_P \alpha_P + \rho + (r_C + \gamma)C + \Omega P.$$

where $\Omega = [c_h(r_C r_P + \gamma^2)C - (r_P u_P + u_C \gamma)] / [u_P + \rho c_h]$. Relation (13) indicates the choice of h conditional on s^* . Next, we derive the feedback rule for s , denoted $s^*(P)$, by substituting $\lambda_C(C, P)$ and $\lambda_P(P)$ into (8) and solving for

$$(14) \quad s^*(P) = \frac{\lambda_C(C, P)r_C \beta_C C - c_h r_P \beta_P - c_{s1}}{2c_{s2}},$$

where the term $\lambda_C(C, P)C$ is independent of C , from relation (12). Now, the feedback rule $s^*(P)$ can be substituted into $h_{SV}(C, P, s^*)$ to derive

$$(15) \quad h_{SV}(C, P) = h_{SV}(C, P, s^*(P)).$$

Feedback rules (14) and (15) are only valid when they are applied jointly and both yield positive values, and they may only be valid along a particular locus of values for C and P (i.e. a

particular singular arc). Consider when the reserve is utilized, $s^*(P) > 0$, given that $h_{SV} > 0$. Let $\Psi = c_h r_P \beta_P [r_C \beta_C / (\beta_P \gamma) - 1] - c_{s1}$ be the marginal net value of enhanced biotechnical productivity from habitat provision. $s^*(P)$ is always positive when $\Psi > 0$, which requires s and h are biotechnical substitutes and c_{s1} is sufficiently small. If $\Psi < 0$ (so c_{s1} is large or s and h are biotechnical complements), then $s^*(P) > 0$ requires

$$(16) \quad P < \hat{P} = [u_P + \rho c_h] r_C \beta_C / [-\gamma \Psi]$$

If condition (16) is not satisfied, then predation (rather than habitat) is the limiting factor for endangered prey from an economic perspective: society is better off focusing its resources on predator removal so as to quickly reduce the predator population. This could imply following a predator removal-only strategy indefinitely or until (16) is satisfied.

Predator removal is used, $h_{SV}(C, P) > 0$, given that the reserve is also used, when:

$$(17) \quad C > \hat{C} = \left(2c_{s2} \gamma [r_P u_P + u_C \gamma] P^2 - r_C r_P \beta_C \beta_P (u_P + c_h \rho)^2 - [u_P + c_h \rho] [c_h r_P^2 \beta_P (r_C \beta_C - \beta_P \gamma) + \gamma (-c_{s1} r_P \beta_P + 2c_{s2} [r_P \alpha_P + \rho])] P \right) / \Lambda$$

where $\Lambda = 2c_{s2} \gamma P [(r_C + \gamma)(u_P + c_h \rho) + c_h (r_C r_P + \gamma^2) P] > 0$. The case of $C < \hat{C}$ implies that habitat availability (rather than predation) becomes the limiting factor from an economic perspective: society is better off investing in a reserve to support the prey.

Conditions (16) and (17) essentially bound the lengths of potential singular arcs.

Consider whether certain trajectories can be ruled out as optimal solutions. That is, over the state space for which $h_{SV}(C, P)$ and $s^*(P)$ are positive, are there combinations of states for which the feedback rules (14) and (15) produce a sub-optimal trajectory, implying that a single control is optimal at these states? It is useful to rule out as many sub-optimal trajectories as possible, since substituting $h_{SV}(C, P)$ and $s^*(P)$ into (1) and (2) yields an infinite number of possible trajectories,

depending on the initial state. Such identification is really a numerical issue, and in our numerical example we find only two trajectories, or separatrices to a saddle point steady state, are optimal. Together, these separatrices define a unique singular arc, or saddle path, denoted $C(P)$. All other dual control trajectories lead to outcomes that fail to satisfy the necessary conditions in the long run. For initial states not on $C(P)$, either the predator removal-only strategy or the reserve-only strategy must be followed. These strategies, which can be used to move the system to $C(P)$, are discussed in Appendix A. We proceed by assuming $C(P)$ is unique.

Changes in Controls Along the Saddle Path

We now examine how the controls jointly respond to changes in the state variables along the saddle path. If both controls move in the same direction ($dh_{SV} / ds^* > 0$) in response to state changes, then we say the controls are bioeconomic complements. If the controls move in opposite directions ($dh_{SV} / ds^* < 0$), we say they are bioeconomic substitutes.¹¹

We derive dh_{SV} / ds^* by totally differentiating each feedback rule and dividing:

$$(18) \quad \frac{dh_{SV}}{ds^*} = \frac{(\partial h_{SV} / \partial C)C'(P) + (\partial h_{SV} / \partial P)}{(ds^* / dP)} = \Theta_{CP}C'(P) + \frac{\Omega}{(ds^* / dP)} + r_P\beta_P,$$

¹¹ Traditionally, choices are characterized as economic substitutes or complements based on cross-price effects. Noting that $C(P)$ will depend on the cost parameters, we can derive $dh_{SV}/dc_{si} = r_P\beta_P(ds^*/dc_{si}) + ([r_C + \gamma] + [c_h P(r_C r_P + \gamma^2)]/[u_P + \rho c_h])(dC/dc_{si})$ ($i = 1, 2$). With $ds^*/dc_{si} < 0$, the first RHS term is the opposite of the sign of β_P . As it is likely that $dC/dc_{si} < 0$ (i.e., for a given P , there is less prey conservation when habitat is more costly), the second RHS term is negative. Hence, predator removal is an economic complement for habitat when $\beta_P > 0$, and it will only be an economic substitute when $\beta_P < 0$ and sufficiently small. We can also derive $ds^*/dc_h = (\rho + r_P P)r_c\beta_C/(2c_{s2}\gamma P) - r_P\beta_P/(2c_{s2})$. The first RHS term is positive, while the second is opposite the sign of β_P . Hence, habitat is an economic substitute for predator removal when $\beta_P < 0$, and it will only be an economic complement when $\beta_P > 0$ and sufficiently large. As the control cost parameters are fixed, we examine cross-price effects in our numerical sensitivity analysis.

where $\Theta_{CP} = \frac{r_C + \gamma}{(ds^*/dP)} < 0$, $\frac{ds^*}{dP} = \frac{1}{2c_{s2}} \left[- \left(\frac{u_P + \rho c_h}{\gamma P^2} \right) r_C \beta_C \right] < 0$, and Ω is as defined in (13).

Relation (18) indicates how the optimal mix of controls changes along $C(P)$ in response to a marginal increase in P . As $ds^*/dP < 0$, the sign of (18) is determined by the sign of dh_{SV}/dP : the controls will be bioeconomic substitutes when $dh_{SV}/dP > 0$, and they will be bioeconomic complements when $dh_{SV}/dP < 0$. The sign of dh_{SV}/dP depends on three factors, as represented by the three RHS terms in (18). The first RHS term reflects movement along the C dimension: holding P fixed, a larger prey population implies more predator controls, and so $\Theta_{CP} < 0$. The sign of the first RHS term is therefore of the opposite sign as $C'(P)$, which is the slope of the saddle path. If both states are moving in the same (opposite) direction along an optimal path, then this first RHS term promotes using the controls as bioeconomic substitutes (complements).

The second RHS term in (18) reflects movement along the P dimension. The sign of this term is opposite the sign of Ω . It is possible to show that $\Omega < 0$ when $\dot{P} \geq 0$ along the saddle path: holding C fixed, fewer predator controls are used if it is optimal to allow P to increase. Hence, the second RHS term is positive when $\dot{P} \geq 0$ along the saddle path, in which case a larger (smaller) value of this term promotes using the controls as bioeconomic complements (substitutes).

Finally, the third RHS term represents the conditional response of predator removal to changes in habitat investments, from (13). This term is of the same sign as β_P . This suggests the controls are more likely to be bioeconomic substitutes when $\beta_P < 0$ or bioeconomic complements

when $\beta_P > 0$, which is roughly in accordance with the biotechnical productivity results.¹²

The sign of (18), which clearly depends on different factors than those determining the biotechnical relation between controls, is ambiguous. In our numerical example below, $C'(P) > 0$ and $\beta_P < 0$. Our analytical results above suggest the controls are more likely to be substitutes in this setting, and that is what we find numerically.

Numerical Example: Gaspésie Woodland Caribou

We further explore the analytical results with a numerical model of Gaspésie Woodland Caribou conservation. This population is currently at risk due to a small extant population, habitat loss, and predation. It is well documented that managed land is poor habitat for the Gaspésie caribou, who prefer the Parc National de la Gaspésie's conservation reserve (Ouellet et al. 1996; Mosnier et al. 2003). This suggests $\alpha_C \approx 0$ and $\beta_C > 0$.¹³ However, the carrying capacity for predators may be greater on managed land than on the reserve, suggesting $\alpha_P > 0$ and $\beta_P < 0$ (Boisjoly et al. 2010).¹⁴ There are two major species of caribou predators: coyote and black bear (Recovery Plan 2006). We model these two predators as a single population, which is a common and reasonable approach to maintaining model tractability (Sokol-Hessner and Schmitz 2002). As the hunting level necessary to reduce predator populations may be intense (Mosnier et al. 2003) and private incentives for hunting are small, a publicly-driven predator control regime is considered

¹² It should be noted that dC/dP also depends on β_P , with the marginal impact being ambiguous.

¹³ Adjacent to the park are wildlife management zones and privately-owned lands where recreational and forestry activities are allowed. These activities are regulated to promote sustainable ecosystem practices, although sustainable timber harvesting may still adversely affect caribou (Stone et al. 2008). Hunting and fishing are permitted in these zones, which restrain caribou habitat outside Parc National de la Gaspésie.

¹⁴ St-Laurent et al. (2009) also discuss how caribou predators benefit from managed land. Specifically, regenerating forests are rich in berries and small prey, benefiting bears and coyotes. Dumps of hunting by-products also provide additional sustenance for coyote predators of caribou (Mosnier et al. 2008).

necessary to caribou conservation, which may require different harvesting techniques specific to the predator species (Recovery Plan 2006).

Benchmark Scenario

Benchmark parameter values are listed in Table 1, with the derivations provided in Appendix B. Numerical solutions were derived using Mathematica 7.0 (Wolfram 2008).

The optimal solution is determined by studying the three long-run strategies. The predator removal-only strategy can be discarded as a long-run optimum since Gaspé caribou are believed to have difficulty surviving on managed land, so $s > 0$ is required to sustain caribou (Ouellet et al. 1996). This leaves the conservation reserve-only strategy and dual control strategy as the feasible candidate long-run strategies.

We find the conservation reserve-only strategy ($s > 0, h = 0$) does have a unique, interior steady state of $C^* = 206, P^* = 253$ and $s^* = 0.59$. However, a contradiction arises when the optimality condition for h is evaluated at this equilibrium: $\partial H/\partial h > 0$, which means setting $h > 0$ would increase social net benefits. The conservation reserve-only strategy also has a unique, stable steady state of $C^* = 389, P^* = 258$ at the corner solution of $h = 0$ and $s = 1$, but here a contradiction arises as $\partial H/\partial s < 0$. These results indicate the reserve-only strategy is suboptimal as a long-run solution, which means only the dual control strategy has the potential to yield a long-run optimum.

The phase plane for the dual control strategy is illustrated in Figure 1. Stability analysis indicates the equilibrium point A (where $\dot{C} = \dot{P} = 0$), with $C^* = 213, P^* = 114$, and control levels $h^* = 0.33$ and $s^* = 0.53$, is a saddle point. The saddle path, $C(P)$, terminates at the dashed curve

$h_{SV}(C,P) = 0$, which defines the predator removal threshold (17).¹⁵ The dual control strategy is infeasible below the $h_{SV}(C,P) = 0$ curve, as $h_{SV}(C,P) < 0$ in this region. Moreover, as we have already indicated that only the dual control strategy may yield a long-run optimum, any dual control trajectory that crosses the $h_{SV}(C,P) = 0$ threshold is suboptimal. The only dual control trajectory that does not cross the $h_{SV}(C,P) = 0$ threshold is $C(P)$, and so this is the optimal long-run path.

As $C(P)$ represents the unique singular solution for h , it also represents the switching curve for h , conditional on $s^* > 0$. For initial states right of $C(P)$, the optimal solution is to use an impulse control of $h \rightarrow \infty$ to implement a jump to $C(P)$ (i.e. a most rapid approach path). For initial states left of $C(P)$, the optimal solution is to set $h = 0$ and implement the reserve-only strategy ($s > 0, h = 0$) that moves the system to $C(P)$ while satisfying smooth pasting conditions for the reserve size at the point of intersection.

Figure 2 illustrates the overall solution. The portion of the curve S to the right of point T represents $C(P)$, with point T being the $h_{SV}(C,P) = 0$ threshold. The portion of S below point T represents the unique reserve-only trajectory that intersects $C(P)$ at the $h_{SV}(C,P) = 0$ threshold. Combining these two segments, curve S effectively serves as the complete switching curve: an impulse removal control is used right of S and the reserve-only strategy is used left of S , with the associated trajectories following the phase arrows.

The initial state is point B at $(P(0)=270, C(0)=140)$. An impulse control moves the system horizontally to S , followed by movement to steady state point A . The same is true for other initial points below S (with only one such trajectory moving directly to A). For initial states

¹⁵ Note that $s^*(P) > 0$ throughout the relevant region of the state space where $h_{SV}(C,P) > 0$.

left of S , such as point Z , a reserve-only strategy that moves the system more gradually to S is initially optimal (with only one trajectory left of S leading directly to A). As described earlier, the reserve-only strategy involves slower adjustment because habitat costs are nonlinear in s and because s directly affects both states: efforts to alter one state impact the other state, creating ecological adjustment costs. The short-run reserve-only path eventually intersects S . Numerical analysis indicates economic welfare is increased by abandoning the reserve-only strategy at S , and then proceeding along S to point A .

Figure 3 illustrates the optimal time paths of the controls along S after the jump from point B . The initial large reduction in predator numbers, coupled with large initial habitat investments, jump-start caribou recovery. After these initial investments, however, the increases in caribou begin to slow. As habitat is expensive to maintain, the optimal strategy begins to substitute from habitat controls to harvest controls. Increasing the rate of predator removal is necessary because predator numbers are allowed to increase as the size of the reserve declines. A similar, initial overinvestment in habitat, followed by substitution of predator controls for habitat, would also arise starting at a point left of S (e.g. such as point Z in Figure 2). The substitution of predator removal for habitat is as predicted by equation (18), given that that S is upward sloping and $\beta_P < 0$.

The optimal long-run caribou population of 213 is about 22 percent larger than the Gaspésie Woodland Caribou managers' goal of 175 caribou. This outcome is attained under a regime similar to that proposed by managers: reduce the predator population and preserve caribou habitat. However, the optimal long-run conservation reserve, $s^* \times L = 1192.5 \text{ km}^2$, exceeds the 1092 km^2 in the current reserve and adjacent conservation zones. Moreover, we find the optimal strategy involves a large reserve initially (1540.1 km^2) and then a gradual decline to

1192.5 km². This suggests managers should invest in more habitat protection via temporary conservation zones as an efficient way to quickly build up the caribou population. The results also indicate continuous, indefinite predator removal is optimal, in contrast to historical strategies of periodic predator culls.¹⁶ Once a large reserve is established and a large portion of predators is culled, the dual control strategy suggests predator removal should gradually substitute for a smaller reserve.

Our path of conservation reserve creation is qualitatively similar to Sanchirico and Springborn's (2011) findings that it is optimal to initially restore more habitat than is optimal in the long run, in order to achieve a faster rate of recovery of the endangered species. Our analysis suggests this result is robust in situations involving predation.

Sensitivity Analysis

We now investigate the sensitivity of the benchmark results to changes in parameters used to calibrate the numerical model. Steady state results are presented in Table 2. Each scenario is defined by the indicated parameter change relative to the benchmark value.¹⁷ A general observation is that the benchmark result of using the dual control strategy is robust to parameter

¹⁶ Periodic culls can be optimal when there are substantial fixed costs in using a control (Clark 2005). The model here assumes no fixed costs in running a predator removal strategy. It is not clear if Gaspésie Woodland Caribou managers face substantial fixed costs in organizing predator control.

¹⁷ As indicated in Appendix B, some parameters in the benchmark scenario are specified while others are calibrated based on the specified parameters. In particular, the choice of β_P affects calibration of r_P and α_P , while the choice of α_C affects calibration of r_C . Our sensitivity analysis results in Table 2 hold r_P , α_P , and r_C fixed at their benchmark values – that is, these parameters are not re-calibrated as we examine changes in β_P and α_C in Table 2. If we did re-calibrate all relevant parameters, then the only change in scenario 1's results in Table 2 would be a smaller equilibrium $h^* = 0.38$. Recalibration under scenarios 2 and 3 would yield a smaller value of r_C . Scenario 2 would exhibit more caribou and fewer predators, $C^* = 262$ and $P^* = 62$, greater reliance on predator removal and less reliance on habitat controls, $h^* = 0.56$ and $s^* = 0.17$, and less surplus (PVSNB = \$3,949 mln). Qualitatively similar changes would arise under scenario 3: $C^* = 397$ and $P^* = 81$, $h^* = 0.61$ and $s^* = 0$, and PVSNB = \$4,572 mln, although this now represents a case where dual control is no longer optimal (note that a smaller r_C means condition (16) is less likely to hold).

changes. Although not illustrated for each case (to conserve space), the qualitative results of Figure 2 hold for each scenario as well.

Scenarios 1 – 6 examine changes in biological parameters. Scenario 1 assumes $\beta_P = 0$, representing an improvement in the suitability of the reserve as habitat for predators, putting caribou at more risk from predation. The equilibrium stock and habitat levels change only slightly from the benchmark, as the ecological effects of the increase in β_P are optimally offset by increasing the predator harvest rate by forty-five percent.¹⁸ The controls remain biotechnical and bioeconomic substitutes in this case. If we were to further increase β_P , say to $\beta_P = -1.5\beta_{P0}$ (not reported in Table 2), then the controls would become bioeconomic complements – with values of both s and h increasing over time until they attain their steady state levels – even though they remain biotechnical substitutes (the controls become biotechnical complements for $\beta_P \geq -10.8\beta_{P0}$).

Scenarios 2 and 3 assume managed land provides some caribou habitat. When managed land can support caribou densities at 50% of reserve land densities, the need for predator controls and habitat is diminished, but the dual control strategy remains optimal. This suggests the optimality of the dual control strategy does not hinge on our benchmark value of $\alpha_C = 0$.

Scenario 3 indicates that doubling α_C relative to the scenario 2 value, so that caribou are equally supported by either habitat, begins to produce the opposite effect: harvest controls increase slightly whereas habitat investment is reduced to a low level to provide a bit of predator control, since $\beta_P < 0$. That s^* remains positive is consistent with condition (16), which is independent of

¹⁸ The changes in stock and habitat levels are only detectable at the first decimal level. Both stocks are smaller relative to the benchmark case, and investment in the reserve also declines, as is predicted by (14).

α_C . Scenario 4 reduces the predator growth parameter, diminishing the incentives for caribou conservation, although only the rate of predator removal is significantly affected. The final two biological scenarios alter the predation rate: a greater (lesser) predation rate yields more (less) predator removal.

Scenarios 7 – 11 examine changes in economic parameters. When the cost of conservation reserve land increases, it is optimal to shift resources out of reserve creation, although the larger non-reserve area enhances predator growth so that more resources are optimally allocated to predator removal. Analogously, habitat substitutes for predator removal when predator removal costs are increased.¹⁹

The remaining scenarios examine the role of existence values. When the existence value of the predator declines, it is optimal to increase predator removal and decrease the reserve relative to the benchmark. These results reflect the substitution of predator removal for habitat as a means for controlling predation: the use of predator controls is increased when there is less value to conserving predators, and the resulting decline in the predator stock means there are fewer incentives to invest in the reserve. Qualitatively opposite changes occur when the existence value of the predator increases. Finally, scenarios 10 – 11 explore the effects of a change in the existence value of caribou. A decline in this value reduces the return from caribou conservation, optimally reducing all caribou conservation investments. The opposite occurs for a larger existence value.

¹⁹ We do not report a scenario for an increased cost of predator removal because the difference from the benchmark results is small; nevertheless, the effect is reduced investment in predator removal and greater investment in the reserve. Therefore, given $\beta_{P0} < 0$, the controls are *economic* substitutes for each other in the traditional sense. These results are consistent with the results in footnote 11.

Conclusion

The importance of predation is often heightened when the prey species has experienced habitat loss. In such situations, it seems intuitive that attempts to conserve an endangered prey species should include investments in both predator controls and habitat provision. But an important consideration is how the expanded habitat will affect predators.

We have examined optimal investments in predator controls and the provision of prey habitat when this habitat provision may either benefit or adversely affect the productivity of the predator population. The impact of habitat on the predator species is shown to be important ecologically in determining whether the controls are biotechnical substitutes or complements for prey conservation. However, this ecological impact plays less of a role in determining whether investments in the two controls move together (bioeconomic complements) or in opposition (bioeconomic substitutes) along an optimal path, as economic factors matter and may play a stronger role.

In the Gaspésie Woodland Caribou example, habitat investments that benefit caribou may simultaneously hurt predator productivity. This dual impact increases the value of habitat controls, so that it becomes optimal to invest more in habitat provision the larger are the adverse impacts to predators. In all cases analyzed, predator removal is also used as part of an optimal long-run conservation strategy, although the optimal mix of investments is state-dependent and therefore changes over time. For instance, given the current large predator population and depleted caribou levels, we find large initial investments in both predator removal and habitat creation are optimal to kick-start the recovery of the caribou population. Then, once the caribou population has recovered somewhat, some predator removal is substituted for habitat protection. That is, some initial habitat protection is only temporary to facilitate the recovery efforts.

Alternatively, if both predator and caribou levels were initially small, so that habitat were more of a limiting factor for caribou, then it may be optimal to initially invest only in habitat provision. Then, once caribou – and predators – have rebounded, both controls are optimally applied. Again, the result here is that some initial habitat protection is only temporary to facilitate the recovery effort. The results for any initial predator population level indicate that the controls are bioeconomic substitutes, i.e. over time predator removal substitutes for habitat provision as the population levels rebound.

Our benchmark results suggest the current Gaspésie Woodland Caribou management plan could be improved. Caribou managers are now largely focused on predator research and removal (Recovery Plan 2006). Our results indicate a major predator cull is indeed optimal now. We also find that a much larger conservation reserve should initially be available, although some habitat may be returned to human use after the caribou population has sufficiently recovered.

Sensitivity analysis indicates our result that both controls are optimally utilized in the long run is fairly robust, at least for conservation-reliant prey. Additionally, our result that habitat provision and predator removal are bioeconomic substitutes is robust to changes in the parameter measuring the marginal impact of habitat on predator productivity. We do find, however, that the two controls are bioeconomic complements for a large range of parameter values for which the controls remain biotechnical substitutes. This result indicates that ecological relations alone cannot adequately inform how the mix of controls optimally changes over time.

Appendix A: Partial Control Strategies

Predator removal-only strategy ($s = 0, h^* = h_{SV}$)

This candidate strategy is found by solving (9), (10) and $\partial H/\partial h = 0$ in (7). This system yields $\lambda_p(P)$ as defined in (11), and $\lambda_c(C,P)$ as defined in (12). Take the time derivative of (12), $d\lambda_c(C,P)/dt$, and substitute this and $\lambda_c(C,P)$ into (9) to solve for $h_{SV}(C,P,0)$. This is equivalent to the relation in (13), except that s is now set equal to zero. For this strategy, the optimal trajectory is determined by (1) and (2) substituting $h = h_{SV}(C,P,0)$ and $s = 0$.

Conservation reserve-only strategy ($s > 0, h^* = 0$)

This candidate strategy is determined by solving (8)-(10). In principle, condition (8) could be used to solve for $s(C,P,\lambda_c,\lambda_p)$. However, it is not possible to then use (9) and (10) to obtain a state-dependent feedback rule for s of the form $s(C,P)$. The reason is that the problem is nonlinear in s , and the standard solution to nonlinear control problems is a differential equation, rather than a feedback rule, for the control. Further complicating matters here is that s simultaneously affects both state variables, effectively implying additional adjustment costs as s cannot control either state very efficiently.

We therefore pursue an alternative approach. First, solve (8) for one of the co-states, say λ_p , to yield $\lambda_p(C,P,s,\lambda_c)$. Next, take the time derivative of this expression to obtain a differential equation of the form $\dot{s} = F(C,P,s,\lambda_c)$, which may be solved jointly with (9) and the ecological system (1)-(2) to yield the optimal trajectory.

Appendix B: Parameter Values

Total land: L . The Parc National de la Gaspésie conservation reserve is currently 802 km² (Mosnier et al. 2003). There are calls to add a 214 km² park enlargement and a 1234 km² buffer zone; expansion beyond this 2250 km² area would encroach on land that has been more intensively logged and could not feasibly support caribou for some time (Cadieux and Guay 2010). This suggests a maximum reserve of 2250 km². While predators can survive on managed land outside of the 2250 km² area, such animals are likely to be part of a separate population than those residing inside within the area. Indeed, predators outside the 2250 km² area are unlikely to interact with caribou inside the reserve, as a minority of coyotes are transitory (with a range of ~2600 km²; Mosnier et al. 2008). Hence, we only model predators and caribou that interact within a total area of $L = 2250$ km².

Caribou carrying capacity from managed land: α_c . Land managed for human use is generally unsuitable habitat for caribou. The small fraction of caribou (~17%) that travel outside the park remain near the park and in land with reserve-like (“conservation zones”) protection (Mosnier et al. 2008; Recovery Plan 2006). This implies $\alpha_c = 0$.

Caribou carrying capacity from conservation reserve land: β_c . Courtois and Ouellet (2007) use a carrying capacity of 20 caribou per 100 km². This implies $\beta_c = 0.2L$.

Caribou growth parameter: r_c . Courtois and Ouellet (2007) construct a predator-prey model of wolves and Gaspésie Woodland Caribou. They use logistic growth with an intrinsic growth rate of 0.245 for caribou. We adopt a sigmoid growth function similar to that of Courtois and Ouellet (although their model is nonlinear in caribou carrying capacity, while it is linear here). Intrinsic growth in our model, given the initial land use $s_0 = 802/L$, is $r_c(\alpha_c + \beta_c s_0) = r_c$

×160.4. Equating this to 0.245 yields $r_C = 0.0015$.

Caribou predation rate: γ . We calibrate γ so that the model yields a reasonable steady state when $s = s_0$ and $h = 0$. The steady state C and P under these conditions are unknown. We assume a steady state of $C = 96$, which is the smallest recorded caribou population (St. Laurent et al. 2009) and, due to a lack of other estimates, a steady state $P = 270$, which is the extant number of predators (Mosnier et al. 2003). Equation (1) then implies $\gamma = 0.00036$.

Predator growth parameters: r_P , α_P and β_P . These parameters are calibrated by simultaneously solving three relations. First, Tanner (1975) suggests an intrinsic growth rate of 0.5 for wolves, which we use because there is a lack of published data for coyote and wolves are physiologically similar to coyotes (black bears likely have a smaller growth rate but coyotes compose most of the predators around the park. In any case, the robustness of the growth rate examined via sensitivity analysis). Intrinsic growth in our model, given the initial land use s_0 , is $r_P[\alpha_P + \beta_P s_0]$. Setting this equal to 0.5 yields $r_P = 0.5/[\alpha_P + \beta_P s_0]$. As predators prefer managed lands, we assume $\beta_P = -\alpha_P/2$. Finally, we calibrate α_P to ensure the steady state described above ($C = 96$ and $P = 270$ when $h = 0$ and $s_0 = 0.356$) exists. In a steady state, equation (2) implies $[0.5/(\alpha_P - \alpha_P(0.356)/2)] \times [\alpha_P - \alpha_P(0.356)/2 - 270] - 0.00036 \times 96 = 0 \Rightarrow \alpha_P = 353$. In turn, we can solve for $\beta_P = -176.5$ and $r_C = 0.0017$. These values imply approximate densities of 14 predators/100 km² on managed land and 7 predators/100 km² in a reserve, which are within observed bounds for coyotes (Patterson and Messier 2001) and black bears (Rogers and Allen 1987).

Value of caribou and predators: u_C , u_P . Published estimates of household annual willingness to pay, in 2005 dollars (all dollars are in U.S currency), for a population of woodland

caribou (\$44.71) and a population of coyotes (\$5.49) come from Martín-Lopez et al. (2008); we are not aware of a published nonmarket, nonuse value for black bears, which may differ substantially from coyote and would therefore affect the computation of predator existence values. We take the number of households to be those in the provinces of Quebec (3.16 million, given a population of 7.9 million and an average Canadian household size of 2.5) and New Brunswick (0.3 million, given a population of 0.75 million). Given the total of 3.46 million households and converting monetary values to 2012 dollars using an inflation factor of 1.17, then, $u_C \ln(140) = 3,460,000 \times 44.71 \times 1.17 \Rightarrow u_C = 36,766,035$, and $u_P \ln(270) = 3,460,000 \times 5.49 \times 1.17 \Rightarrow u_P = 3,986,302$.

Cost of predator removal: c_h . An average coyote hunt costs \$17,200 (1983 dollars) and yields a 26.33% population reduction (Smith et al. 1986). Adjusting to 2012 dollars using an inflation factor of 2.303, this implies $c_h \times 0.2633 = 17,200 \times 2.303 \Rightarrow c_h = 150,433$.

Cost of conservation reserve: c_{R1} , c_{R2} . The opportunity cost of placing land into the reserve is the foregone benefits of activities such as timber and hunting. To our knowledge, there are no reports on the value land in the area. Instead, at the current reserve size, we assume the annual benefit of one more hectare of managed land is \$250 (or \$25000/km²), which from an internet search of real estate on the Gaspé peninsula is within the range of market values for forested land. This implies $c_{R1} + 2c_{R2}s_0L = c_{R1} + 2c_{R2} \times 802 = 25000$. We also assume a cost elasticity of 1.25, yielding $25000/[c_{R1} + c_{R2}s_0L] = 1.25$. These conditions imply $c_{R1} = 15000$ and $c_{R2} = 6.23$.

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Tables and Figures

Table 1. Parameter values

| Parameter | Interpretation (units) | Value |
|------------|--------------------------------------------------------------------------------------------------------------------------------|------------|
| L | Available land area (km ²) | 2250 |
| r_C | Caribou growth parameter (rate/animal) | 0.0015 |
| r_P | Predator growth parameter (rate/animal) | 0.0017 |
| α_C | Caribou carrying capacity on managed land (animals) | 0 |
| α_P | Predator carrying capacity on managed land (animals) | 353 |
| β_C | Increase in caribou carrying capacity for a marginal increase in the proportion of land in the conservation reserve (animals) | 450 |
| β_P | Increase in predator carrying capacity for a marginal increase in the proportion of land in the conservation reserve (animals) | -176.5 |
| γ | Predation rate | 0.00036 |
| u_C | Benefits of caribou parameter (US\$) | 36,766,035 |
| u_P | Benefits of predator parameter (US\$) | 3,986,302 |
| c_h | Predator removal cost parameter(US\$) | 150,433 |
| c_{R1} | Reserve cost parameter(US\$) | 15000 |
| c_{R2} | Reserve cost parameter(US\$) | 6.23 |
| ρ | Discount rate | 0.05 |

Table 2. Sensitivity Analysis

| Scenario | Optimal Strategy | Equilibrium Stocks (C^*, P^*) | Equilibrium Controls (h^*, s^*) | PVSNB (in millions \$) |
|------------------------------------------------------------------|------------------|-----------------------------------|-------------------------------------|------------------------|
| Benchmark | Dual Control | (213, 114) | (0.33, 0.53) | 3,735 |
| 1. $\beta_P = \beta_{P0} \cdot 0$ | Dual Control | (213, 114) | (0.48, 0.53) | 3,735 |
| 2. $\alpha_C = \beta_{C0} \cdot 0.5$ | Dual Control | (301, 155) | (0.37, 0.25) | 4,325 |
| 3. $\alpha_C = \beta_{C0}$ | Dual Control | (420, 211) | (0.38, 0.04) | 4,764 |
| 4. $r_P = r_{P0} \cdot 0.75$ | Dual Control | (213, 114) | (0.26, 0.53) | 3,735 |
| 5. $\gamma = \gamma_0 \cdot 0.5$ | Dual Control | (213, 230) | (0.09, 0.53) | 3,791 |
| 6. $\gamma = \gamma_0 \cdot 1.5$ | Dual Control | (213, 76) | (0.43, 0.53) | 3,701 |
| 7. $c_{R1} = c_{R10} \cdot 1.5,$ $c_{R2} = c_{R20} \cdot 1.5$ | Dual Control | (156, 87) | (0.39, 0.39) | 3,509 |
| 8. $u_P = u_{P0} \cdot 0.5$ | Dual Control | (217, 68) | (0.43, 0.51) | 3,556 |
| 9. $u_P = u_{P0} \cdot 1.5$ | Dual Control | (209, 168) | (0.23, 0.55) | 3,931 |
| 10. $u_C = u_{C0} \cdot 0.75$ | Dual Control | (118, 141) | (0.31, 0.34) | 1,864 |
| 11. $u_C = u_{C0} \cdot 1.25$ | Dual Control | (288, 99) | (0.33, 0.69) | 5,749 |

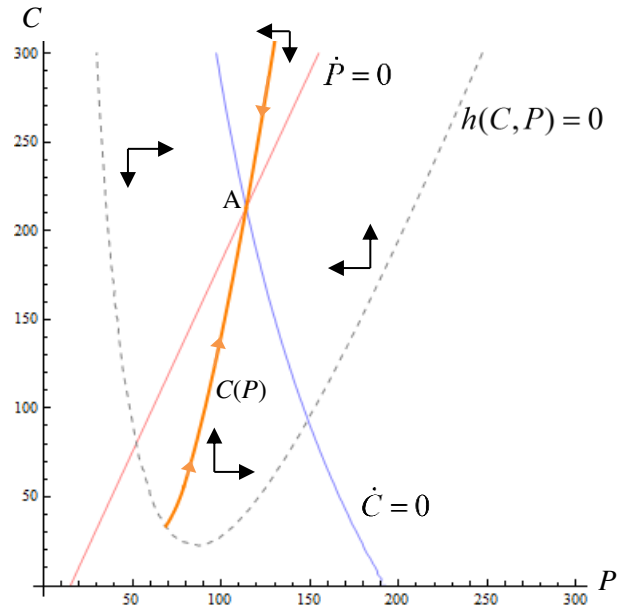


Figure 1. Phase plane for the dual control strategy ($s^* > 0, h^* = h_{SV}$).

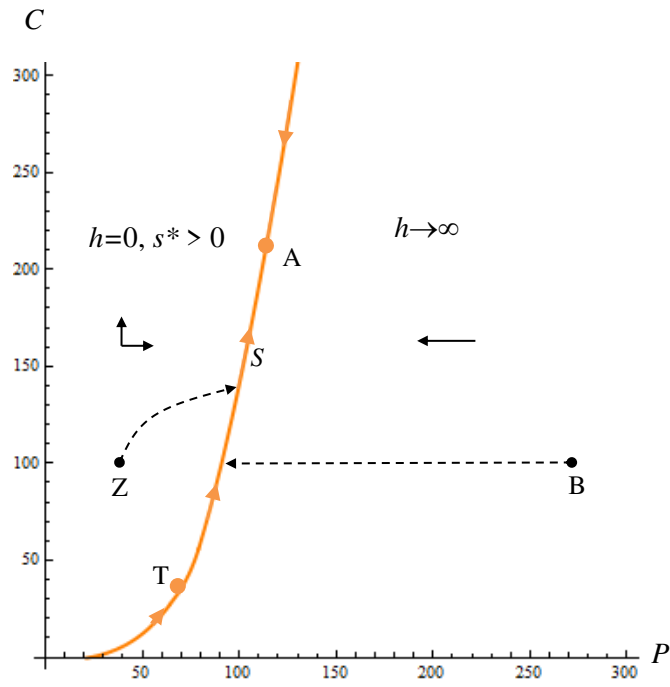


Figure 2. Feedback control diagram for the benchmark case. The optimal solution involves moving to curve S as quickly as possible and then proceeding to A . S is a switching curve that divides the state space between regions where it is optimal to follow the strategy $h \rightarrow \infty$ or $h = 0$, $s^* > 0$, en route to S . Once on S , the system will follow the strategy $h = 0$ and $s^* > 0$ along the portion to the left of T and the strategy $h = h_{SV}$ and $s^* > 0$ along the portion to the right of T .

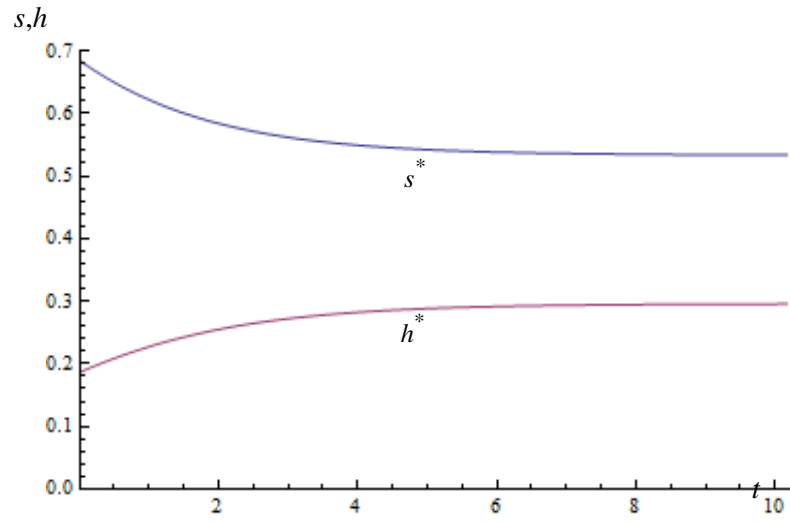


Figure 3. Time path of the proportion of predators removed and the proportion of land in the conservation reserve size, under the optimal management strategy.