Optimal control of native predators

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ABSTRACT

We apply decision theory in a structured decision-making framework to evaluate how control of raccoons (*Procyon lotor*), a native predator, can promote the conservation of a declining population of American Oystercatchers (*Haematopus palliatus*) on the Outer Banks of North Carolina. Our management objective was to maintain Oystercatcher productivity above a level deemed necessary for population recovery while minimizing raccoon removal. We evaluated several scenarios including no raccoon removal, and applied an adaptive optimization algorithm to account for parameter uncertainty. We show how adaptive optimization can be used to account for uncertainties about how raccoon control may affect Oystercatcher productivity. Adaptive management can reduce this type of uncertainty and is particularly well suited for addressing controversial management issues such as native predator control. The case study also offers several insights that may be relevant to the optimal control of other native predators. First, we found that stage-specific removal policies (e.g., yearling versus adult raccoon removals) were most efficient if the reproductive values among stage classes were very different. Second, we found that the optimal control of raccoons would result in higher Oystercatcher productivity than the minimum levels recommended for this species. Third, we found that removing more raccoons initially minimized the total number of removals necessary to meet long term management objectives. Finally, if for logistical reasons managers cannot sustain a removal program by removing a minimum number of raccoons annually, managers may run the risk of creating an ecological trap for Oystercatchers.

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1. Introduction

High predation rates can be a serious problem for many protected species and managers may seek to eradicate or control predators that threaten protected prey populations (Courchamp et al., 2003; Meckstroth and Miles, 2005; Baxter et al., 2008). However, predator removal programs can be controversial and have demonstrated only mixed success (Côté and Sutherland, 1997). They have been criticized as ineffective, costly, requiring unsustainable effort, lacking specificity for the target predator, and increasingly, are viewed negatively by the public (Goodrich and Buskirk, 1995). Unfortunately, many predator removal programs have used an *ad hoc* approach when removing individuals, with little prior knowledge or consideration of impacts on either the predators themselves, the target prey, or the scope of the unintended consequences to other species in the system.

Although alien predators are considered more dangerous than native predators in the decline and extinction of prey species (Salo et al., 2007), the impact of native predators on prey can also be significant under certain conditions (e.g., meso-predator release, subsidized predators [Crooks and Soulé, 1999; Gommper and Vanak, 2008]). Indeed, anthropogenic influences can result in an increase in food availability and cover, thereby increasing predator carrying capacity. Also, the effects of predation can be magnified if the abundance of prey species is reduced due to overharvest, pollution, competition from introduced species, or habitat loss or fragmentation.

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Prey species often do not have adequate time to adapt to such abrupt system changes. In the case of predator–prey interactions, a number of indigenous, generalist predators have recently become overabundant, posing a severe threat to some prey species (Garrott et al., 1993). Under these circumstances, predator control may be an appropriate and necessary management action.

Predator control is not a panacea, however, and science-based predictions of the potential efficacy of predator control, as well as the effects on other species in the system, are needed to conduct defensible management, which is especially critical in light of the controversial nature of these programs (Sinclair et al., 1998). Control of a native species can be especially problematic and often results in unintended consequences for established relationships or interactions among species (Goodrich and Buskirk, 1995). If predator control programs are not carefully implemented, removal actions can actually favor the spread of or increase the abundance of the predator (Sih et al., 1985; Abrams, 2009). A review of studies involving manipulation of predator populations showed that a sizeable proportion of studies (40%) exhibited some type of unexpected response (e.g., increase in population size and predatory effect of a species that was formerly competitively excluded by the predator targeted for removal; Sih et al., 1985) through unintended pathways (Pimm, 1991; Bergstrom et al., 2009).

Structured decision-making (SDM) provides a promising framework to help resolve controversial management problems by: (1) clearly identifying the objectives; (2) adding transparency to the decision process (e.g., Martin et al., 2009); (3) including stakeholders in the decision process (e.g., recreation groups); (4) developing explicit predictions of system response to control actions that can be checked against monitoring data; and (5) identifying decisions that are optimal with respect to the management objectives and the current knowledge of the system (and account for important sources of uncertainty, Williams et al., 2002).

Here we illustrate this approach by focusing on the control of raccoons (*Procyon lotor*) to protect American Oystercatcher (*Haematopus palliatus*) populations in coastal North Carolina, as a case study in the application of SDM to predator control programs. We emphasize the importance of carefully identifying an objective function that simultaneously captures several management goals, in this case increased nesting success of the prey species and viability of the predator species. We also investigate the value of selectively controlling predators of different age classes, as opposed to removing predators non-selectively. Finally, we consider adaptive management (Walters, 1986; Johnson et al., 1997; Williams et al., 2002) as a special case of SDM, in which management decision-making is iterated over time, and monitoring data are used to update understanding of system behavior and knowledge of the system state, to allow for long-term optimal decision-making.

2. Methods

2.1. Study area

Cape Lookout and the barrier islands between Beaufort and Ocracoke Inlets comprise the southern portion of the Outer Banks, along the central coast of North Carolina. Our work was confined to South Core Banks (SCB), one of four barrier islands that comprise Cape Lookout National Seashore (CLNS), a unit of the U.S. National Park Service.

2.2. Data sources

We used a combination of information collected locally along with data reported in the scientific literature to develop our Oys-

tercatcher and raccoon population models. Specifically, we used estimates of raccoon abundance obtained using mark-resight data (A. Waldstein, T. Simons, and A. O'Connell, unpublished data). Estimates of Oystercatcher reproductive success were derived from ten years of productivity monitoring on the Outer Banks of North Carolina (Simons and Schulte, 2009).

2.3. Management objectives

The objective established by CLNS managers was to minimize the number of raccoons to be removed while maintaining productivity of Oystercatchers above a specified threshold (i.e., utility threshold, Martin et al., 2009). Because the raccoon is a native species, managers also did not wish to eradicate it from SCB, wanting instead to keep the number of raccoons above a specified minimum value. The utility threshold for Oystercatcher productivity was set at 0.35 chicks fledged per breeding pair per year. This value was determined by estimating the minimum level of reproductive success needed to maintain the population based on population modeling of Oystercatcher populations in North Carolina (Schulte, 2010). The utility threshold for raccoons was set at 25 female raccoons (i.e., 50 individuals total assuming 1:1 sex ratio) which should be high enough to guard against risks of extinction associated with demographic stochasticity (Morris and Doak, 2002). We note that the model that we used to model raccoon abundance was a typical single sex model (see Section 2.4.1), that is, we only considered the female component of the raccoon population. Therefore, when we refer to raccoons we mean the number of females.

We worked with managers to translate their three objectives (i.e., meet Oystercatcher productivity threshold, minimize removals, meet raccoon population threshold) into a combined utility function:

$$U_t = \left(N_t^{R[\text{TOT}]} - d_t^{R[\text{TOT}]}\right) \times \alpha_t \times \beta_t \tag{1}$$

where U_t is the utility value at time t, and is a function of the total number of raccoons at time t ($N_t^{R[\text{TOT}]}$) and the total number of raccoons removed at time t ($d_t^{R[\text{TOT}]}$, which correspond to the management action). The terms α_t and β_t are penalty factors at time t. Indeed, α_t is:

$$\alpha_t = \begin{cases} \frac{E\left(P_{t+1}^{\text{OYS}}\right)}{0.35}, & E\left(P_{t+1}^{\text{OYS}}\right) < 0.35 \\ 1, & E\left(P_{t+1}^{\text{OYS}}\right) \geqslant 0.35 \end{cases} \tag{2}$$

Eq. (2) indicates that if the expected Oystercatcher productivity after the action is implemented, $E\left(P_{t+1}^{\text{OYS}}\right)$, is <0.35, then α_t is $\frac{E\left(P_{t+1}^{\text{OYS}}\right)}{0.35}$ (i.e., the return is devalued proportionally, Kendall, 2001); otherwise it is 1. The term β_t is a penalty factor relating to the objective of maintaining raccoon abundance above some desired level:

$$\beta_t = \begin{cases} 0, & E\left(N_{t+1}^{R[\text{TOT}]}\right) < 25 \\ 1, & E\left(N_{t+1}^{R[\text{TOT}]}\right) \geqslant 25 \end{cases} \tag{3}$$

Hence, Eq. (3) indicates that if the expected number of raccoons after the action is implemented (i.e., $E\left(N_{t+1}^{R[\text{TOT}]}\right)$) is less than 25, then β_t is 0 (i.e., that action is completely devalued); otherwise it is 1. In order to meet the Seashore's management objectives, we used an optimization method (see next section) to find the decision that maximizes:

$$\sum_{t=0}^{t=T} U_t \tag{4}$$

where T is a specified time horizon. Note that the utility function to be maximized includes the term $\left(N_t^{R[\text{TOT}]} - d_t^{R[\text{TOT}]}\right)$, which

corresponds to the number of raccoons not removed (maximizing this expression can be viewed as an equivalent to minimizing the number of raccoons to be removed).

2.4. System models

We developed system models that projected the consequences of raccoon removal on raccoon abundance as well as the effect of raccoon abundance on the productivity of Oystercatchers (i.e., the models predicted the outcomes of management with respect to the objectives). Our model of system behavior assumed the following sequence of events: monitoring to estimate raccoon abundance occurred in September, removal of raccoons occurred thereafter in September, and raccoon parturition occurred in May.

2.4.1. Modeling the raccoon population

Abundance of adults at the time of the monitoring in year $t + 1$ was described by:

$$N_{t+1}^{R[A]} = \left(N_t^{R[A]} - d_t^{R[A]}\right)S_{12}^{R[A]} + \left(N_t^{R[Y]} - d_t^{R[Y]}\right)S_{12}^{R[Y]} \tag{5}$$

where $N_t^{R[x]}$ is the population size of raccoons (R) at time t, for age class x (A: adults [>12 months]; Y: yearlings [>4 to 12 months]; N: nestlings [1–4 months]); $d_t^{R[x]}$ is the number of raccoons to be removed at time t, for age class x; $S_j^{R[x]}$ is the survival probability of raccoons for j months, for age class x. As explained earlier, this model was a single sex model; thus, when we refer to raccoons we mean the number of females. Abundance of yearlings was:

$$N_{t+1}^{R[Y]} = \left(N_t^{R[A]} - d_t^{R[A]}\right)S_8^{R[A]}f_t^{R[A]}S_4^{R[N]} + \left(N_t^{R[Y]} - d_t^{R[Y]}\right)S_8^{R[Y]}f_t^{R[Y]}S_4^{R[N]} \tag{6}$$

where $f_t^{R[x]}$ is the annual fecundity of raccoons at time t for age class x. We defined annual fecundity as the average number of nestling females produced per adult or yearling female (Caswell, 2001). This quantity is equal to the number of females produced per adult breeding female multiplied by the probability that a female will breed.

The proportion of yearlings in the population at time t was:

$$a_t^{R[\text{TOT}]} = \frac{N_t^{R[Y]}}{N_t^{R[Y]} + N_t^{R[A]}} \tag{7}$$

Our model considered the total number of female raccoons to remove in a given September $\left(d_t^{R[\text{TOT}]}\right)$ as the decision variable (see also variation of this for selective, or age-specific removals described in Section 2.5). The number of adult females removed in the model for any value of $d_t^{R[\text{TOT}]}$ was computed as:

$$d_t^{R[A]} = d_t^{R[\text{TOT}]}\left(1 - a_t^{R[\text{TOT}]}\right) \tag{8}$$

whereas for the yearlings it was:

$$d_t^{R[Y]} = d_t^{R[\text{TOT}]} - d_t^{R[A]} \tag{9}$$

We assumed a density-dependent effect on fecundity of adult raccoons. We modeled this effect as a log linear relationship between fecundity and the total number of raccoons in May, $N_{t+1}^{R[\text{May}]}$:

$$f_t^{R[A]} = e^{\left(\beta_0 + \beta_1 N_t^{R[\text{May}]}\right)} \tag{10}$$

where $N_t^{R[\text{May}]}$ is the total number of raccoons in May just before parturition:

$$N_{t+1}^{R[\text{May}]} = \left(N_t^{R[A]} - d_t^{R[A]}\right)S_8^{R[A]} + \left(N_t^{R[Y]} - d_t^{R[Y]}\right)S_8^{R[Y]} \tag{11}$$

We fitted Eq. (10) to two empirical points to estimate parameters β_0 (0.77) and β_1 (−0.007) and to model the effect of density dependence on fecundity (see Appendix A for details on how to de-

rive these parameters, and for a complete list of the parameter values used in the model). We did not consider an Allee effect (Morris and Doak, 2002) in this analysis.

We assumed that yearlings are less likely to reproduce successfully than adults:

$$f_t^{R[Y]} = \gamma f_t^{R[A]} \tag{12}$$

where $0 < \gamma < 1$ (see Appendix A for details on computation of γ).

2.4.2. Modeling the effect of raccoon abundance on productivity of Oystercatchers

Productivity of Oystercatchers $\left(P_t^{\text{OYS}}\right)$ was defined as the number of fledglings per breeding pair. We constructed a model that assumed a log linear relationship between P_t^{OYS} and the total number of raccoons in May:

$$P_t^{\text{OYS}} = e^{\left(\beta_2 + \beta_3 N_t^{R[\text{May}]}\right)} \tag{13}$$

We used nesting data collected on Oystercatchers from 1999 to 2007 to estimate β_2 (−0.598) and β_3 (−0.008) and to establish the relationship between raccoon abundance and Oystercatcher productivity (details on how we derived these parameters are presented in Appendix B). Although we have used the best available information about the system under study, we recognize that there are uncertainties associated with the parameters used in the models. However, our structured decision-making approach is particularly well suited to deal with high levels of uncertainty (Williams et al., 2002). In addition, managers generally cannot wait until better parameter estimates become available before making their decisions (note that doing nothing is in fact a decision, e.g., Martin et al., 2009). The approach that we describe in the following sections allows for the identification of decisions that are optimal with respect to the objectives, given the current knowledge of the system and associated uncertainties (e.g., Williams et al., 2002; Martin et al., 2009).

2.5. Optimization and simulations

2.5.1. Analysis based on best available parameter values

We used stochastic dynamic programming (Bellman, 1957; Williams et al., 2002) to find the sequence of decisions that are optimal with respect to our objective, given our model of the system and associated uncertainties. We approximated the decision problem for an infinite time horizon via backward iteration dynamic programming, by iterating through time steps until a stable policy was maintained for 15 time periods, with a maximum of 100 time periods (Martin et al., 2009). We used program Adaptive Stochastic Dynamic Programming (ASDP) Version 3.2 for the optimization (Lubow, 2001).

We used simulation to evaluate the consequences, with respect to the objectives, of following the optimal policies for several scenarios. In particular, we were interested in examining the consequences of potential management actions (i.e., removal of raccoons) on the productivity of Oystercatchers, the number of raccoons removed, and the number of raccoons remaining in the population. We compared the average and cumulative number of raccoons to be removed over an "infinite" time frame (approximated by looking at simulations over a period of 10,000 time steps).

The analysis based on best available parameter values (i.e., as described in Appendix A) was stochastic. We refer to this analysis as stochastic because the model included some environmental stochasticity by accounting for the process variance of survival rates. This is in contrast with the exploratory analyses described below, which were all deterministic. In addition, the removal strategy for the stochastic analysis was to remove raccoons

without consideration of their age. In this case, the decision alternatives were various levels of $d_t^{R[\text{TOT}]}$ (see Eq. (8) and (9)). We named this strategy the "non-selective" removal method.

2.5.2. Exploratory analyses

Because we wanted to gain insights on the optimal control of native predators we also conducted some exploratory analyses to gain insight into general features of the predator removal problem independent of particular parameter values estimated for our study system or constraints that we imposed on the optimization and simulation exercises described above. All of the exploratory analyses were based on deterministic models (i.e., constant values for raccoon survival). This is because it was easier to illustrate general points with the deterministic analyses. First, we compared the optimization results under two removal strategies. The first strategy was the deterministic equivalent of the stochastic analysis described in the previous section (the only difference was that the vital rates were held constant); and was also referred to as the "non-selective removal" strategy. The second removal strategy consisted of selectively removing adults and yearlings; we called this strategy the "selective" removal method. Here, the decision variables to optimize were $d_t^{R[A]}$ (number of adults removed at t) and $d_t^{R[Y]}$ (number of yearling removed at t). The system model for the selective removal was the same as the one for the non-selective removal except that we excluded Eqs. (7)–(9) from the model. This is because the selective removal involved two decision variables: $d_t^{R[A]}$ and $d_t^{R[Y]}$, whereas the non-selective removal included only one decision variable in the optimization: $d_t^{R[\text{TOT}]}$. Indeed, with the non-selective removal strategy, the optimal decision given the state of the system (i.e, how many adults and yearling were present in the population at the time of the decision) was just one number: $d_t^{R[\text{TOT}]}$; therefore, we had to derive values of $d_t^{R[A]}$ and $d_t^{R[Y]}$ based on $d_t^{R[\text{TOT}]}$ and $a_t^{R[\text{TOT}]}$ (Eqs .(7)–(9)). In contrast, with the selective removal the optimal decision given the state of the system consisted of two numbers: one for $d_t^{R[A]}$ and another for $d_t^{R[Y]}$. In other words, with the selective removal the values of $d_t^{R[A]}$ and $d_t^{R[Y]}$ were directly obtained from the optimization and therefore did not need to be derived (unlike with the non-selective removal strategy, see Eqs. (7)–(9)). The maximum number of raccoons that could be removed at any time step was set at 50 raccoons (i.e., $d_t^{R[\text{TOT}]} \leqslant 50$) in the case of the non-selective removal; and $d_t^{R[A]} \leqslant 25$ and $d_t^{R[Y]} \leqslant 25$ in the case of selective removal), to reflect budgetary and logistical constraints.

Second, we compared scenarios with two levels of reproductive values. We predicted that the selective removal approach would lead to more efficient policies when there was a large difference in reproductive values between yearlings and adults. To evaluate this prediction we considered models in which we increased the difference in reproductive values between yearlings and adults by reducing yearling survival by 20%, increasing adult survival by 20%, and reducing γ (Eq. (12)) to 0.01 instead of the estimated value of 0.64 (see Appendix A). Hereafter we refer to these as exploratory models that assumed a large difference in reproductive values. In contrast, models that were based on the most realistic parameter values (see Appendix A) assumed a small difference in reproductive values (the difference in reproductive values is reported in the Results).

Third, we wanted to explore the short term and long term benefits of raccoon removal at various levels of potential effort. To do this, we considered two additional removal scenarios, one where the maximum number of female raccoons that could be removed annually was 16; and one where up to 50 female raccoons could be removed. We also identified the minimum number of female raccoons that needed to be removed annually to maintain the Oystercatcher productivity above 0.35.

Finally, we calculated a yield curve (Runge et al., 2009) for the deterministic version of the raccoon model (Eqs. (5)–(12)) by finding the equilibrium population size and removal for a range of fixed removal rates.

2.5.3. Adaptive optimization

In the case of the non-adaptive optimization (i.e., the optimizations presented above) we only considered one model. However, to account for both model and parameter uncertainty, we considered multiple models and used adaptive optimization (Williams et al., 2002). In this case, we considered two models, one assuming a strong effect of raccoons on Oystercatcher productivity (the parameterization of this model was based on empirical data and corresponds to the model described above). The second model assumed no effect of raccoons on Oystercatcher productivity (where Oystercatcher productivity was set to the average value for the period 1997–2007: 0.25, see Appendix B). When multiple models were considered, a passive adaptive optimization algorithm (Kendall, 2001; Williams et al., 2002) was used to account for model uncertainty. In this case model uncertainty is reflected as a difference in parameter values (i.e., parameter uncertainty), as opposed to a difference in model structure. However, adaptive optimization can help address both types of uncertainty. Adaptive updating can then be implemented to reduce model uncertainty over time (Williams et al., 2002).

The weights of the models $(p_i(t))$ were updated by applying Bayes' Theorem (Williams et al., 2002, see also Martin et al., 2009):

$$p_i(t+1) = \frac{p_i(t) \times P_i(x_{t+1}|x_t, d_t)}{\sum_{i=1}^{n} p_i(t) \times P_i(x_{t+1}|x_t, d_t)} \qquad (14)$$

where $P_i(x_{t+1}|x_t, d_t)$ is the probability of the observed state at $t + 1$ under model i, given that the system was in state x_t at time t (i.e., abundance of raccoons at t) and that decision d_t (e.g., number of raccoons to remove at t) was implemented.

3. Results

3.1. Analysis based on best available parameter values

For the raccoon model built with the best available parameter values (stochastic version), the optimal strategy for non-selective removal shows that when the number of female raccoons is below the threshold value (25), few raccoons are removed (Fig. 1). As the number of female raccoons increases, more raccoons should be removed. Fig. 2 illustrates the consequences of following the optimal
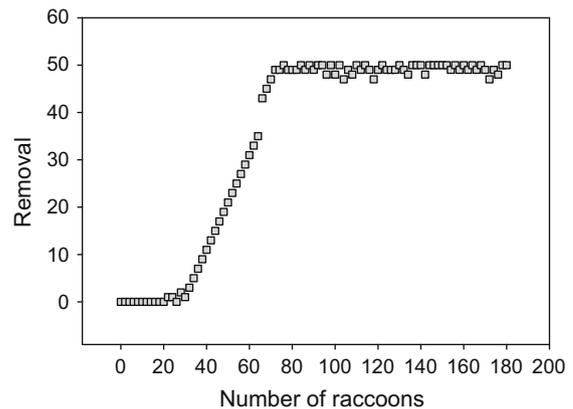

Fig. 1. Optimal state-dependent strategy for non-selective removal. The horizontal axis corresponds to the number of female raccoons $\left(N_t^{R[\text{TOT}]}\right)$. The gray squares correspond to the optimal number of females to remove $\left(d_t^{R[\text{TOT}]}\right)$. For example, if there are 60 females in a given year, the optimal decision would be to remove 31 females during that same year. These results are for the model that uses the best available parameter estimates and accounts for environmental stochasticity.
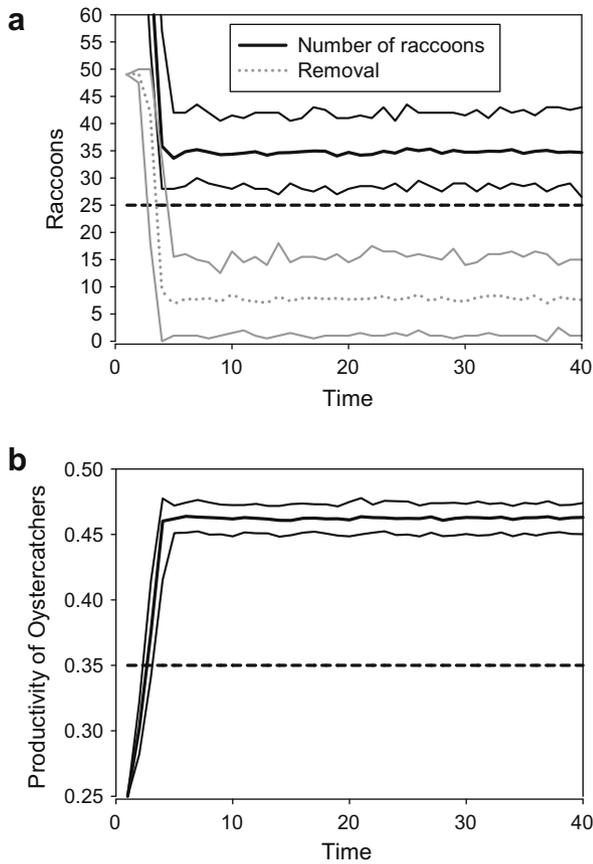
Fig. 2. Simulation of the optimal removal policies (i.e., optimal number of females to remove, doted gray line ($d_t^{R[\mathrm{TOT}]}$, a) on raccoons (thick black line, a) and American Oystercatchers productivity (b). The thin lines correspond to the 97.5 and 2.5 percentiles. This illustrative figure is based on 100 simulations. Initial abundance of raccoons in September was 143, and initial Oystercatcher productivity was 0.25. The dashed lines correspond to the utility thresholds for raccoons (a) and Oystercatcher productivity (P_t^{OYS}, b).

of Oystercatchers also remained substantially higher than the specified utility threshold for Oystercatcher productivity (Fig. 2).

3.2. Exploratory analyses

The average annual removal of female raccoons over a period of 10,000 iterations was always smaller for the selective removal than for the non-selective removal, and the difference increased when the difference in reproductive values between adults and yearlings was larger (Table 1). As explained in Section 2, the model that considered a large difference in reproductive values assumed a larger difference in survival between adult and yearling raccoons and a smaller value of γ (Eq. (12)). For both selective and non-selective removal, average productivity remained substantially higher than the utility threshold for Oystercatcher productivity (Fig. 2).

In our deterministic analyses (i.e., parameters were assumed to be fixed), we found that if it was not possible to remove a maximum of 13 female raccoons annually ($d_t^{R[\mathrm{TOT}]} \leqslant 13$), Oystercatcher productivity could not be maintained above 0.35. This is because it is necessary to be able to remove more than the maximum sustained yield for a short period of time to drive the population size to the left side of the yield curve; and only if the population is held at these lower levels can Oystercatcher productivity be maintained at desired levels. If up to 16 female raccoons could be removed at a time ($d_t^{R[\mathrm{TOT}]} \leqslant 16$), it was possible to reach the desired equilibrium point on the left shoulder of the yield curve, but the cumulative removal over 30 years was considerably higher (489 female raccoons and it would take 14 years to reach the desired value of Oystercatcher productivity of 0.35) than if up to 50 raccoons could be removed annually (391 raccoons and it would only take 2 years).

Based on the yield curves for the raccoon model built from the best available parameter values (but with a deterministic version of the model, that is, with constant values of vital rates), the carrying capacity (the equilibrium population size in the absence of removal) was 168 females, and the maximum sustained removal of 12.9 female raccoons occurred at a non-selective harvest rate of 14.7% and an equilibrium population size of 87 females (Fig. 3). For the exploratory raccoon model with the large difference in reproductive values, the carrying capacity was 222 females, and the maximum sustained yield of 12.2 females occurred at a non-selective harvest rate of 11.2% and an equilibrium population size of 110 females (Fig. 3).

3.3. Adaptive optimization

When equal weights were initially assigned to our two models (one where raccoons affected Oystercatcher productivity and one

strategy on the number of raccoons, the number of raccoons to be removed, and Oystercatcher productivity. Initial raccoon abundance in September was set to 143 raccoons for all simulations (i.e., the current best estimate of population size in September). The optimal policy when $N_t^{R[\mathrm{TOT}]} \geqslant 143$ was $d_t^{R[\mathrm{TOT}]} = 50$ (i.e. the maximum removal policy). After five time steps, $N_t^{R[\mathrm{TOT}]} < 44$ and $d_t^{R[\mathrm{TOT}]} < 18$. The 2.5 percentiles remained above the utility threshold for raccoon abundance for the rest of the time frame (Fig. 2). The productivity

Table 1
Summary of simulation results for selective (i.e., raccoons are removed according to their age) and non-selective removal of raccoons (i.e., raccoons are removed irrespective of their age). We also considered scenarios in which there were large and small differences in reproductive values (RV) between yearlings and adults. The utility corresponds to the utility value described in Eq. (4).

Model	Average removal ($t = 10^5$)	Average number of raccoons ($t = 10^5$)	Cumulative utility ($t = 10^5$)	Average Oystercatcher productivity ($t = 10^5$)
Not selective/small difference in RV	7.7	34[d]/19[e]/15[f]	412,993	0.465
Not selective/large difference in RV	6.98	35[d]/21[e]/14[f]	425,465	0.459
Selective/small difference in RV	7.41[a]/7.24[b]/0.17[c]	35.6[d]/20.4[e]/15.2[f]	423,106	0.458
Selective /large difference in RV	5.45[a]/5.45[b]/0.00[c]	34.3[d]/21.3[e]/13[f]	439,296	0.455

[a] Total number of female raccoons removed at t $\left(r_t^{R[\mathrm{TOT}]}\right)$.

[b] Number of female adult raccoons removed at t $\left(r_t^{R[A]}\right)$.

[c] Number of female yearlings removed at t $\left(r_t^{R[Y]}\right)$.

[d] Total number of female raccoons at t $\left(N_t^{R[\mathrm{TOT}]}\right)$.

[e] Number of adult females at $t\left(N_t^{R[A]}\right)$.

[f] Number of yearling females at t $\left(N_t^{R[Y]}\right)$.
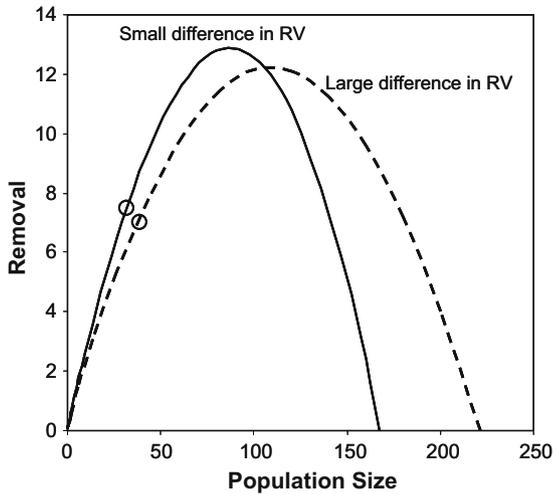
Fig. 3. Yield curves for the deterministic raccoon models. The curves show that the sustained removal rate associated with a particular equilibrium population size of female raccoons for the model using the best available parameter estimates (small difference in reproductive value (RV)) and the exploratory model with a large difference in reproductive values. The open circles are the equilibria sought by the optimal strategies.

where raccoons had no effect), the optimal $d_t^{R[TOT]}$ was 50 on the first iteration of the simulation (if $N_{t=1}^{R[TOT]}$ = 143, which correspond to the number of female raccoons in September), no matter which model was the "true" model (Fig. 4a). However, the adaptive process allowed us to discriminate between the two models after a few iterations of the process the two model weights accumulated

toward the true model (Fig. 4d). If the true model was the one that predicted no effect of raccoons on Oystercatcher productivity (solid lines, Fig. 4a–d), then no raccoons were removed after the second iteration. If the true model was the one that assumed a strong effect of raccoons on Oystercatchers (dashed lines, Fig. 4a–d), then the average number of raccoons to be removed was 10 over a period of 40 years (Fig. 4a). Note that the rate of learning was faster when the true model was the one that assumed a strong effect of raccoons (Fig. 4d).

4. Discussion

4.1. Optimal control of raccoons

The SDM approach that we describe to address the optimal control of native predators can be used to satisfy several competing objectives. In our case study, we were able to identify optimal policies that minimized the removal of raccoons while satisfying two utility thresholds: maintaining Oystercatcher productivity above a specified level deemed necessary for its recovery (Schulte, 2010), and also maintaining raccoon abundance above a level acceptable to Seashore managers. One major benefit of this approach is that it is well suited for making decisions when facing large uncertainties (e.g., Williams et al., 2002). With our specific example, we showed how to address environmental stochasticity (Figs. 1, 2 and 4) and parameter uncertainty (see adaptive optimization, Fig. 4). In order to illustrate some specific points more clearly we then used deterministic analyses (Fig. 3 and Table 1).

Based on our stochastic analysis (i.e., with a model that included some environmental stochasticity) we found that the optimal control of raccoons would result in Oystercatcher
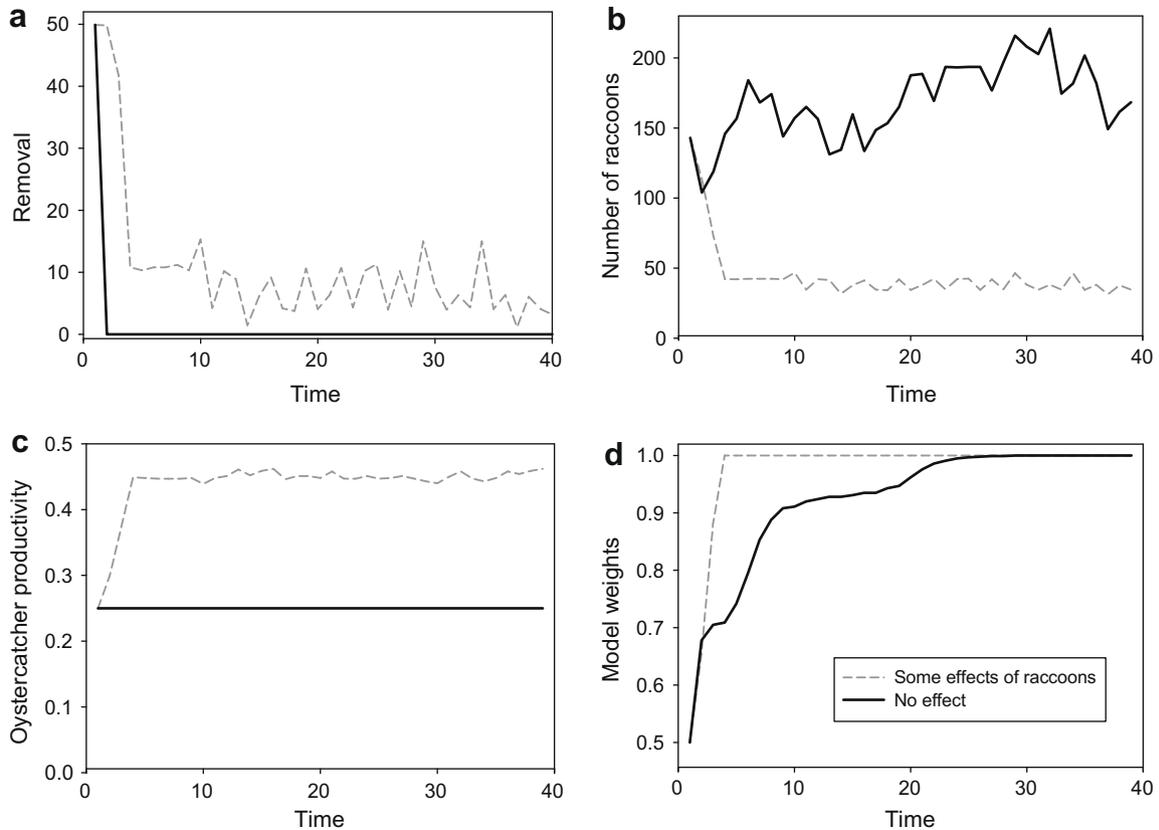
Fig. 4. Simulation of the optimal removal policies ($d_t^{R[TOT]}$, a) obtained from an adaptive optimization on the number of female raccoons ($N_t^{R[TOT]}$, b), and Oystercatcher productivity (c). The initial weights for the two models were set at 0.5 (d). We conducted two simulations, one in which the true model was the model that predicted a strong effect of raccoons on Oystercatcher productivity (P_t^{OYS}, dashed lines); the second simulation assumed the no effect model to be the true model (solid lines).

productivity that remains significantly higher than the specified utility threshold of 0.35 (Fig. 2 and Table 1). This result can be explained in the context of the theory of sustainable exploitation (e.g., Runge et al., 2004, 2009). Indeed, the annual removal is substantially reduced at a lower raccoon abundance (Figs. 1 and 3). Over the long term, the optimal strategy seeks to hold the raccoon population on the left shoulder of the yield curve, at a population size well below where sustainable take is maximized (Fig. 3). Therefore, the optimal policy leads to removals that keep the raccoon population near the specified utility threshold (i.e., 25 females, Fig. 2), which also coincides with high Oystercatcher productivity. Thus, in order to reduce the cumulative number of raccoons that need to be removed over a period of 30 years, it is preferable to initially remove a number of raccoons large enough to bring the population close to the utility threshold. This number may be large if the initial population is substantially higher than the utility threshold. Yet, this strategy leads to a lower cumulative removal of raccoons than a strategy that would remove fewer raccoons over a longer time period. For instance, if the maximum number of raccoons that can be removed in any one year is 16, the cumulative removal over 40 years led to considerably higher removal (489 raccoons and 14 years to reach the desired value of Oystercatcher productivity of 0.35) than if up to 50 raccoons could be removed (391 raccoons and only 2 years; based on our results from a deterministic model). In fact, if for practical reasons (e.g., annual budgetary constraints) managers cannot commit to a minimum number of raccoon removals annually (13 raccoons in our example assuming a deterministic model), the removal program would be unable to keep Oystercatcher productivity above 0.35. These results emphasize the value of applying SDM tools before implementing such controversial management actions. Ideally, this process can help to identify decisions that are optimal with respect to the management objectives. But it may also help managers realize when they do not have the resources to meet their intended objectives. If that were the case, managers may need to consider different management actions, or revise their objectives. This analysis also shows that if managers decide to control the population of raccoons on SCB they would make a commitment over a long time period to meet the current management objectives. Otherwise, they may run the risk of creating an ecological trap for Oystercatchers (Schlaepfer et al., 2002). For example at a lower density of raccoons (due to control effort) Oystercatchers from other breeding areas may be attracted to SCB; however, if the control of raccoons stops abruptly the breeding success of these "new" Oystercatchers may be drastically reduced because of a rapid increase in raccoon density (due to the interruption of the control program).

The policies based on selective removal led primarily to the removal of adults. The difference in the proportion of adults versus yearlings removed increased if we assumed a greater difference in reproductive value between yearlings and adults (Table 1). We found that when the reproductive values differed greatly among age classes, the selective removal was more efficient (i.e., fewer animals could be removed while still meeting Oystercatcher productivity and raccoon abundance objectives) than the non-selective removal. Thus, even though the difference in policies was negligible given the particular parameter values in our system (Table 1), selective removal should still be considered in the evaluation process of other predator control programs, especially where the reproductive values of the different age classes vary substantially. For example, we found that when the difference in reproductive values was large, the selective removal approach lead to an average of 5.45 raccoons removed per year compared to an average of 6.98 raccoons under the non-selective removal. Over a period of 40 years this difference could lead to a cumulative difference of approximately 60 raccoons.

4.2. Adaptive optimization

One additional benefit of the SDM approach to managing the control of native predators is that it is well suited for the implementation of adaptive management. Adaptive management can be used to reduce model uncertainty resulting in more effective management in the future (e.g., Walters, 1986; Kendall, 2001; Williams et al., 2002; Martin et al., 2009). For example, we considered two competing models to assess the effect of raccoon abundance on nest success of Oystercatchers. One model assumed a substantial effect of raccoon abundance on nest success of Oystercatchers (this first model was based on historical data, see Methods) whereas the second model assumed no effect of raccoon abundance on Oystercatcher productivity (additional models could be considered if warranted). By simulating the policies from the passive optimization algorithm, we found that if equal weights were given to each of the two models on the first iteration, and if the "true" model is the "no effect model", 50 raccoons would be removed in the first iteration but no raccoons would be removed thereafter (Fig. 4a). This is because the adaptive process allows for the identification of the decision model that represents the best approximation of reality (Fig. 4d). Even in the absence of learning, the implementation of a passive adaptive optimization algorithm is useful to account for the uncertainty associated with the parameters in the model. For instance, if there are large uncertainties about the model parameters, as was the case with the raccoon Oystercatcher problem, these uncertainties can be accounted for with a passive adaptive optimization algorithm (Fig. 4). Accounting for large parameter uncertainty in decision-making is an important problem (e.g., Regan et al., 2005), because, generally decision makers cannot afford to postpone decisions until better estimates can be obtained (especially, because doing nothing is in fact a decision).

5. Conclusions

The decision analysis that we presented focused on two species: Oystercatchers and raccoons. This analysis would be well suited if Seashore managers were interested in controlling raccoons to specifically promote the recovery of Oystercatchers or if they believed that Oystercatchers can be viewed as an indicator species (i.e., a species whose protection would be a good predictor of the protection of other species of interest). This decision-making framework can be expanded to include additional prey species based on the needs of managers and the ecological functioning of the system. For example, additional utility thresholds could be included for sea turtles and the Piping Plover (*Charadrius melodus*), which are other nesting species of concern along the southeast coast. Concerns about the potential release of alternative predators such as ghost crabs could be incorporated, by including models that assume a negative effect of crabs on sea turtle nest success (Barton and Roth, 2008). However, including additional species would considerably increase the dimensionality of the problem and therefore alternative optimization methods could be necessary (e.g., reinforcement learning; Fonnesbeck, 2005). Nevertheless simpler models provide initial insights and come at a lower cost. Thus, before undertaking a full analysis of a large management issue, it may be wise to focus on a key subset of the problem to ensure that the objectives can be attained through the actions considered. In our application we have shown that, based on our current knowledge of the system, control of raccoons could promote the recovery of Oystercatchers. We have also provided managers with a quantitative assessment of the effort (in terms of trapping) that would be necessary to reach the stated objectives (Figs. 1 and 2). Managers can then decide if expanding the decision framework to more species would be appropriate to meet their objectives.

The SDM framework that we described provides several benefits for dealing with the control of native predators in protected areas. It provides a rigorous and transparent framework for addressing controversial management issues. It is transparent in the sense that decision makers must be explicit about their objectives and rigorous due to a foundation in decision theory and models of system behavior that are based on the best scientific information available and also account for uncertainty in that information. (Williams et al., 2002; Martin et al., 2009). These characteristics make the SDM process well suited for guiding decision-making under the National Environmental Policy Act (NEPA) (Thrower, 2006). Finally, the adaptive component of this approach allows for the incorporation of new relevant information to improve management decisions in the future (Williams et al., 2002).

Acknowledgements

Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.04.023.

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