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To exclose nests or not: structured decision making for the conservation of a threatened species

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Abstract. Decisions regarding endangered species recovery often face sparse data and multiple sources of uncertainty about the effects of management. Structured decision making (SDM) provides a framework for assembling knowledge and expert opinion and evaluating the tradeoffs between different objectives while formally incorporating uncertainty. The Atlantic Coast piping plover provides an illustrative case for the utility of SDM in endangered species management because its population growth is simple to model, most populations are monitored, decision alternatives are well defined, and many managers are open to recovery recommendations. We built a model to evaluate the decision to use nest exclosures to protect piping plover eggs from predators, where the objective was to maximize λ and the tradeoff was between nest survival and adult survival. The latter can be reduced by exclosures. We used a novel mixed multinomial logistic exposure model to predict daily nest fates and incorporated the results into a stochastic projection matrix that included renesting after nest failure, and adult mortality associated with abandonment. In our test data set (n = 329 nests from 28 sites over four years), the mean nest survival over 34 days was markedly higher for exclosed nests (0.76 ± 0.03 SE) than for unexclosed nests (0.37 ± 0.07). Abandonment rates were also higher for exclosed nests (0.092 ± 0.017) than for unexclosed nests (0.045 ± 0.017), but the difference was not statistically significant and the loss rate to "other sources" (mostly predators) was much lower for exclosed nests (0.15 ± 0.03) than for unexclosed nests (0.58 ± 0.07). Population growth rate (λ) was clearly improved by exclosure use at the sites with high background nest loss rates, but λ was still <1 with exclosure use. Where the background nest loss rates were low, the decision to use exclosures was ambiguous, and λ could benefit from reducing uncertainty in vital rates. Our process demonstrated that geographic and temporal variation in nest mortality determines whether exclosures will be useful in attaining positive population growth rates and that other management options must be considered where the background nest mortality rates are high.

Key words: endangered species; nest exclosures; nest survival; piping plover; population model; structured decision making.

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Introduction

Management of endangered species often must proceed despite the significant uncertainty in abundance and vital rates and in how threats or limiting factors impact those quantities (Regan et al. 2005). Key sources of uncertainty affecting the wildlife management include environmental stochasticity, partial observability (including measurement and sampling errors), partial controllability (factors outside of the manager's control affect the population), and structural or model uncertainty (Williams et al. 2002, Martin et al. 2009). Failing to address and acknowledge uncertainty creates a false sense of confidence in the desired outcome (Marcot et al. 2012). Alternatively, mischaracterizing uncertainty can erode confidence in successful actions. Finally, not addressing uncertainty can enable successful challenges from stakeholders dissatisfied with the decision (e.g., Mansfield and Haas 2006). Even evidence presented as "best available science" can be insufficient in preventing inconsistency in the implementation of listing and recovery procedures (Doremus 2004, Woods and Morey 2008).

Structured decision making (SDM) provides a systematic process for organizing information about management actions in the face of uncertainty, focusing on the value of different actions for one or more biological, economic, and social/political objectives (Ralls and Starfield 1995, Gregory and Keeney 2002, Martin et al. 2009). Agencies around the globe use SDM for threatened and endangered species management, including recovery planning for endangered fish populations (Gregory and Long 2009, Gregory et al. 2013), prioritization of recovery planning in New Zealand (Joseph et al. 2009), mitigating bycatch effects on dolphins (Conroy et al. 2008), and managing the indirect effects of commercial fisheries on migratory birds (McGowan et al. 2011). In all these cases, managers and stakeholders created a transparent structure showing how the objectives they value change under different alternative actions. This structure directly connects the "best available science" to stakeholder values, reducing the risk of inconsistent implementation.

Decision problems for endangered species often require predicting the size of the population in the future, given a set of alternatives (Runge 2011). The primary objective is usually increased probability of persistence, which is a function of growth rate (λ), abundance, and stochasticity in vital rates (McGowan 2013). These quantities vary in time and space, and in response to management actions, and our ability to precisely predict these changes is not perfect.

For the federally threatened Atlantic Coast population of the piping plover (*Charadrius melodus*), a beach-nesting shorebird, nest exclosure cages have been used for over two decades as a means to prevent the depredation of eggs and to increase λ (USFWS 1996, Cohen et al. 2009, Maslo and Lockwood 2009). However, even with intense monitoring during the years that exclosures have been used, uncertainty remains regarding their effect on λ, due to a potential tradeoff between nest survival and adult survival. The question of exclosure use for piping plover recovery provides an excellent case for the use of SDM in science-based management of endangered species (McGowan 2013). The Atlantic Coast population has several characteristics that simplify the modeling and decision-making process. First, the population is large enough that maximizing growth rate can be considered the main objective at a regional (although not necessarily local) level, although the recovery abundance goal has not yet been met (USFWS 2012). This species is recovering through the management of threats, including predation, that are pervasive and persistent, and active conservation is likely to be needed in perpetuity even after delisting (Hecht and Melvin 2009). Second, piping plover population ecology is fairly simple to model: monogamy, little delay to sexual maturity, typically one brood of young produced per year, and high breeding site fidelity (Elliott-Smith and Haig 2004). Moreover, the demography of piping plovers has been well studied, and there currently exists a suite of management options to exercise (Loegering 1992, Melvin and Gibbs 1996, Calvert et al. 2006, Cohen et al. 2006, Hecht and Melvin 2009).

Piping plovers nest in a shallow scrape on the ground in open or sparsely vegetated zones of beaches and interdune areas, and they rely on crypsis, early detection of predators, and parental distraction displays to prevent egg predation (Elliott-Smith and Haig 2004). These evolved defenses are inadequate for sustainable nest

survival in the face of introduced predators, such as feral cats (*Felis sylvestris*), and human-subsidized populations of predators, such as crows (*Corvus* spp.) and red foxes (*Vulpes vulpes*) (Cohen et al. 2009). Several early trials reported improved nest survival using exclosure cages (Rimmer and Deblinger 1990, Melvin et al. 1992), and by 1993, exclosures were deployed in every state and at least three Canadian provinces in the plovers' Atlantic Coast breeding range (U.S. Fish and Wildlife Service 1996). Nest exclosures have been subsequently demonstrated to provide substantial improvement in nest survival for piping plovers and other ground-nesting shorebirds (Hardy and Colwell 2008, Cohen et al. 2009, Maslo and Lockwood 2009, Dinsmore et al. 2014). However, problems associated with exclosures included nest abandonment, adult mortalities, and depredation of multiple exclosed nests at a site within a very short period of time (Vaske et al. 1994, Murphy et al. 2003, Neuman et al. 2004, Maslo and Lockwood 2009, Barber et al. 2010). Recently, evidence that apparent nest abandonment represents breeding season mortality in Great Lakes piping plovers (Roche et al. 2010) further shifted the perception of demographic risk associated with exclosure use. Population projection analysis determined that exclosure use could lead to a population decline due to adult mortality for piping plovers, at abandonment rates seen in Atlantic Canada (Calvert and Taylor 2011) and the related snowy plover (*Charadrius nivosus*) (Watts et al. 2012). However, estimates of exclosure-related adult mortality have been difficult to determine in the Atlantic Coast population where few birds are marked.

Allocating resources in the most effective possible manner is critical for recovery of the piping plover given that over $3 million is spent annually on conservation on the Atlantic Coast (Hecht and Melvin 2009). Thus, reducing uncertainty regarding the contribution of nest exclosures to population growth is an urgent need. A decision process with the sole objective of maximizing λ would allow for a rational approach to the use of exclosures, where the alternatives are simply to use the technique or not. Our objective was to perform a decision analysis on exclosure use for Atlantic Coast piping plovers, with the objective of maximizing growth rate, given a tradeoff between adult survival and hatching success. Our results will provide the basis for a standardized regional approach to making decisions on exclosure use for piping plovers and could serve as a template for using SDM for related ground-nesting species.

Materials and Methods

We defined our decision problem and discussed objectives and possible alternative actions in a series of conference calls prior to our week-long workshop. During those calls, we also identified information needs, including nest fate data and expert opinion on the probability that a nest abandonment represented adult mortality, as the latter data are lacking for the Atlantic Coast. Prior to the workshop, we developed a nest survival model from nest monitoring data gathered across the breeding range. During the workshop, plover biologists and managers worked with population modeling coaches to refine a projection model for piping plovers that could incorporate the potential positive and negative effects of nest exclosures. For this decision analysis, we used a series of statistical models to evaluate how the population growth rate (λ) would be affected by placing predator exclosures on piping plover nests. We used a modified version of the population projection model of Calvert et al. (2006) and Calvert and Taylor (2011) to predict long-term expected population growth as a function of survival and reproduction parameters. To estimate the parameters within the population projection model, we modeled hatching success and adult mortality assuming multiple nesting attempts per season following the nest failure. The components of hatching success (daily estimates of nest survival, nest abandonment, and other nest losses) were estimated with a mixed multinomial logistic exposure model, an extension of the binomial logistic exposure model (Shaffer et al. 2004). Data to inform this statistical model were collected from nesting sites throughout the northeastern United States. Piping plover biologists contributed nest monitoring data collected at 28 nesting beaches distributed among Maine, Massachusetts, Rhode Island, and New Jersey in 2009–2012. Each row in the database contained a single day's check for one piping plover nest and included the date, the site, whether the nest had an exclosure on that day (1) or not (0), and the nest's status (alive or source of loss).

For one unknown parameter, the probability that nest abandonment represents one or more adult mortalities (m), we used the four-point method of expert elicitation (Speirs-Bridge et al. 2010) and the modified Delphi method (Kuhnert et al. 2010). We asked the panel to provide, of 20 abandoned nests, the lowest realistic number of nests that would be abandoned as a result of adult mortality, the greatest realistic number of nests abandoned because of adult mortality, their best guess of the number of nests abandoned because of adult mortality, and their confidence (50–100%) that the true value falls within the range provided. We then asked the panel to consider 20 nests that were abandoned because of adult mortality and provide the same four points of information (lowest, highest, best guess, and confidence) for the number of these nests in which both the male and female of the breeding pair were depredated. We also asked the panel to provide their rationale for their elicited values. This information was used to generate a discussion about the individual responses. The ranges and estimates of confidence that each panelist provided were used to standardize all responses to an 80% confidence interval, assuming that the logit-transformed intervals followed a normal distribution, which provided a range of estimates of m for the population model. The best guess values and standardized 80% CIs were averaged across panelists and transformed into a probability range to use in the model.

Population projection matrix

We used a hatching population projection matrix similar to that of Calvert et al. (2006) and Calvert and Taylor (2011), simplified to two stage classes, to predict the long-term expected population growth (λ) as a function of survival and reproduction parameters. The two stages were juvenile (hatch year) female piping plovers and adult (after hatch year) female plovers. Matrix entries were parameterized assuming a population census as taking place just after hatching but before fledging:

$$\boldsymbol{A} = \begin{bmatrix} \phi_j^w f y_s H2E & \phi_a y_a H2E \\ \phi_j^w f & \phi_a \end{bmatrix} \quad (1)$$

where ϕ_j^w is the survival probability of juveniles from time of fledging in year t (hatch year) to time of census in year $t + 1$, f is the probability of survival from hatching to fledging ($\phi_j^w f$ = annual survival of juveniles), y_s is the probability of breeding for second-year plovers (i.e., their first breeding attempt), y_a is the probability of breeding for all other age classes, $2E$ is the mean number of female eggs hatched from a nest (where E is the proportion of eggs that hatch, given that at least one egg in the nest hatches, and assuming that the total of four eggs are laid with an equal primary sex ratio), H is the probability of hatching a nest during the nesting season, and ϕ_a is survival from census in year t to census in $t + 1$ for all adult plovers (aged >1 yr). Emigration and immigration can be discounted for the purposes of assessing the effect of exclosures on the population growth rate of a local population, as long as exclosures do not affect the rates of emigration and immigration. The long-term expected growth rate (λ) is the leading (maximum) eigenvalue of A.

Effects of multiple nesting attempts

To relate the estimated abandonment and hatching probabilities of individual nests to abandonment and hatching probabilities for each female over all nesting attempts in a season, we created the models of hatching and abandonment-related mortality that included the effects of renesting (Fig. 1). If we let a be the probability of abandonment of an individual nest, o be the probability of failure due to all other causes, and m be the probability of death after an observation of abandonment, then the probability of hatching is $h = 1 - (a + o)$ and the probability of the adult being alive after an abandonment is observed is $a(1 - m)$ (Fig. 1).

Although an extreme case of five nesting attempts by a banded female piping plover has been documented (MacIvor 1990), our model considered a maximum of three possible renesting attempts, based on a sharp decline in the probability of renesting in the second half of the breeding season (Cohen et al. 2009). The total hatching probability for a female over all nesting attempts is as follows:

$$\begin{aligned} H = h + r_2[oh + a(1-m)h + o\left[or_3 + a(1-m)r_3h\right] \\ + a(1-m)\left[oh + a(1-m)r_3h\right)] \end{aligned} \quad (2)$$

where $h = 1-(o + a)$ is the probability of hatching for a single nest attempt and r_i is the probability of nesting on the ith attempt ($r_1 = y_s$ for second-year females and $r_1 = y_t$ for third-year females).

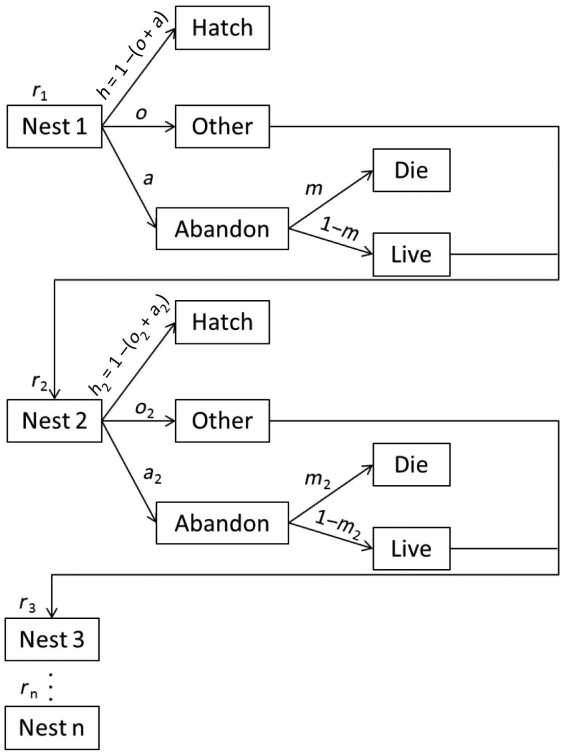

Fig. 1. Nest fate diagram for piping plovers describing the estimation of the probabilities of hatching and abandonment-related mortality, taking into account renesting throughout the breeding season.

Similarly, we calculated the probability that abandonment indicates female mortality over all nest attempts as

$$M = r_1\left[\mathrm{am} + a(1-m)r_2\left[\mathrm{am} + a(1-m)r_3\mathrm{am}\right]\right] \quad (3)$$

where r_1 is defined as above for second- and third-year females. We related M to annual survival by decomposing annual survival into breeding and nonbreeding components.

$$\phi_\mathrm{a} = \phi^b\phi_\mathrm{a}^w. \quad (4)$$

We assumed that mortality is equally distributed among months of the year and that $\phi^b = \sqrt[6]{\phi_\mathrm{a}}$, as the nesting part of the breeding season lasts approximately 2 months, and that breeding season survival is identical between second- and third-year females (as data are not available to empirically estimate breeding season survival). We decomposed breeding season survival into a component for abandonment in the absence of exclosures and a component encompassing all other sources of mortality

$$\phi^b = \phi_0\phi_{M(x=0)} \quad (5)$$

where $\phi_{M(x=0)} = 1 - M(x=0)$, such that M is a function of exclosure use, $x = 0$ is no exclosure use, and $x = 1$ is exclosure use. The parameters a, o, and h, as well as the function H, are also functions of exclosure use, the effect being determined from the statistical analysis described below. With these definitions, $\phi_0 = \phi b/\phi_{M(x=0)}$ serves as a scaling factor to determine the proportion of breeding survival that is due to mortality sources other than those that might lead to a nest being classified as abandoned. From this baseline, breeding season survival with exclosure use ($x = 1$) is calculated as follows:

$$\phi^b(x=1) = \phi_0\phi_{M(x=1)} \quad (6)$$

The annual survival for adults with exclosure use is as follows:

$$\phi_\mathrm{a}(x=1) = \phi_0\phi_{M(x=1)}\phi_\mathrm{a}^w \quad (7)$$

and the annual survival for juveniles (recalling that our model begins in the posthatch period and thus includes exposure to exclosures in their first breeding season) becomes

$$\phi_j(x=1) = \phi_0\phi_{M(x=1)}\frac{\phi_j^w f}{\phi^b} = \frac{\phi_0\phi_{M(x=1)}\phi_j^w f}{\phi_0\phi_{M(x=0)}} = \frac{\phi_{M(x=1)}\phi_j^w f}{\phi_{M(x=0)}}. \quad (8)$$

Statistical analysis of exclosure effect

We developed a mixed multinomial logistic exposure model using Proc NLMixed (SAS Institute, Cary, North Carolina, USA) to estimate the daily probabilities of survival, abandonment, and "other" nest losses (i.e., predation, flooding) as a function of exclosure presence as a fixed effect and "site by year" (hereafter "siteyear") as a random effect:

$$y_{ij} \sim \mathrm{multinomial}(p(t_j)_{ij}^s, p(t_j)_{ij}^a, p(t_j)_{ij}^o, n)$$

where nests are indexed $i = 1, \ldots, N$, each nest is observed over intervals indexed $j = 1, \ldots, M_i$, and the interval is t days long. For each nest and interval, $y_{ij} = 1$ if nest i survived interval j, 2 if nest

i was abandoned in interval j, and 3 if nest i was lost to other causes in interval j. The probabilities of an event of type c (either s = survived, a = abandoned, or o = other) are $p(t_j)^c_{ij}$, and there is $n = 1$ trial per nest check. These probabilities apply across an interval of t days in length.

To determine the effects of exclosures and site-year on these probabilities, we calculated linear predictors for daily abandonment rate (η_a) and daily other loss rate (η_o) as:

$$\begin{aligned}\eta^a_{ij} &= \beta^a_0 + \beta^a_1 X_{ij} \\ \eta^o_{ijk} &= \beta^o_0 + \beta^o_1 X_{ij} + u_k, u_k \sim N(0,\sigma^2)\end{aligned} \quad (9)$$

where $\beta_{c,l}$ are regression coefficients for each cause c. We set $X = 1$ if a nest had an exclosure during the interval and 0 otherwise, and u_k is the random effect for site-by-year combination k. For a nest check interval of one day,

$$\begin{aligned}p(t=1)^s_{ijk} &= \frac{1}{1+e^{\eta^a_{ij}}+e^{\eta^o_{ijk}}} \\ p(t=1)^a_{ijk} &= \frac{e^{\eta^a_{ij}}}{1+e^{\eta^a_{ij}}+e^{\eta^o_{ijk}}} \\ p(t=1)^o_{ijk} &= \frac{e^{\eta^o_{ijk}}}{1+e^{\eta^a_{ij}}+e^{\eta^o_{ijk}}}.\end{aligned} \quad (10)$$

which is the standard multinomial logit function. For intervals of length i (Heisey and Fuller 1985),

$$\begin{aligned}p(t=i)^s_{ijk} &= \left(p\,(t=1)^s_{ijk}\right)^t \\ p(t=i)^a_{ijk} &= \frac{p(t=1)^a_{ijk}}{1-p(t=1)^s_{ijk}}\left(1-\left(p(t=1)^s_{ijk}\right)^t\right) \\ p(t=i)^o_{ijk} &= \frac{p(t=1)^o_{ijk}}{1-p(t=1)^s_{ijk}}\left(1-\left(p(t=1)^s_{ijk}\right)^t\right)\end{aligned} \quad (11)$$

The model therefore estimates daily survival and partitions daily mortality into sources: the probabilities of hatching, abandonment, and "other" nest loss for a single 34-d nest attempt (7 d for egg-laying plus 27 d of incubation) are $h = p(t=34)^s_{ijk}$, $a = p(t=34)^a_{ijk}$, and $o = p(t=34)^o_{ijk}$, respectively (Fig. 1).

Uncertainty in the decision analysis

With the models described above, we calculated the expected population growth rate at a local site with and without exclosure use. However, there are several important sources of uncertainty. First, each of the parameters used in the model had some level of estimation error, usually reported as a standard error for the parameter. In addition, the mixed-effect models we used to estimate the effects of exclosures on hatching success estimated the amount of variation in baseline (without exclosures) hatching success among different sites and years. This environmental heterogeneity is superimposed on the effects of estimation error. We recognize that this environmental heterogeneity itself is an estimate with an unknown amount of error. We assumed that exploring estimation error would itself account for some of the uncertainty in environmental variation. However, we did include the environmental variation itself in our simulation, as described below. We addressed the effects of estimation error with a 10,000-iteration Monte Carlo simulation to calculate a distribution of λ conditional on the estimation error in our parameters. This procedure was performed for different degrees of hatching success ranging from good (two standard deviations above the mean) to bad (two standard deviations below the mean). We then estimated the sensitivity of the population growth rate to each of the model parameters. We also calculated the upper limit of how much additional population growth could be realized by improving information about the population parameters.

Bootstrap simulation of population growth rate

We simulated the variation in expected growth rate (λ) related to parametric uncertainty by conducting bootstrap resampling from the sampling distribution of parameters. For parameters for which there was no estimate of the parametric uncertainty, we assumed a coefficient of variation of 10% (Franklin et al. 2002) although we considered the sensitivity of our results to this choice. We examined the sensitivity of the decision to variation in f by repeating the bootstrap at lower ($f = 0.2$) and higher ($f = 0.6$) mean values. For the parameter estimates associated with abandonment and nest loss, we sampled each parameter from a multivariate normal distribution with the estimated mean and sample covariance matrix from the nest survival statistical analysis. Our analysis does not account for parametric uncertainty in the random effect variance.

Table 1. Parameters, definitions, and statistical distributions (mean and coefficient of variation [CV]) used in the predictive model for piping plover population growth rate (λ).

Parameter	Definition	Mean	CV†	Source for mean
E	The proportion of eggs that hatch in a nest that survives to hatch	0.94	0.00‡	Informal expert opinion
ϕ_a	Annual adult survival	0.74	0.10	Calvert et al. (2006)
ϕ_j^w	Juvenile survival from fledging in year t to nest hatching in time $t + 1$	0.52	0.10	Informal expert opinion
f	Probability of fledging	0.40	0.06	Informal expert opinion
y_s	Probability of breeding as a second-year bird	0.68	0.10	Gratto-Trevor et al. (2010)
y_a	Probability of breeding as an after the second-year bird	0.99	0.00‡	Melvin and Gibbs (1996)
r_2	Probability of a second nest attempt	0.70	0.10	Cohen et al. (2009)
r_3	Probability of a third nest attempt	0.70	0.10	Informal expert opinion
m	Probability of adult female mortality given the nest abandonment	0.39§	1.04	Formal expert elicitation

Note: All parameters were simulated from a normal distribution on the log odds scale, unless otherwise noted.
† Coefficient of variation on the log odds scale. With the exception of the CV for f, these were all based on expert opinion, and a value of 10% was used as a default.
‡ Parameter fixed at a single value for the Monte Carlo analysis.
§ One-half the value of the elicited adult mortality given the abandonment.

Sensitivity analysis

We performed a prospective sensitivity analysis (Caswell 2000) of population growth rate for each of the probabilities listed in Table 1 and for the probabilities associated with daily nest abandonment and nest loss to other sources. To maximize the interpretability of the results, we conducted all sensitivity calculations for probability parameters on the probability scale. We calculated the sensitivity and elasticity of each parameter for each realization of the bootstrap parameter samples and then a standardized regression coefficient between the bootstrapped samples of population growth rate and of parameters.

Because sensitivity and elasticity are based on derivatives, they are referred to as a "local" analysis and the results only apply at the set of parameter values used to calculate the derivative. Therefore, we also used a simulation and regression approach to sensitivity that regressed population growth rate against the standardized (mean = 0, standard deviation = 1.0) values of the bootstrap sample of parameters. This gives a sensitivity measure that applies across the full range of parameter values (an "average slope" across the variance in the parameters) and evaluates the importance of the parameter relative to the uncertainty in the parameter of interest. For example, a regression slope estimated at 0.1 means that population growth rate increases 0.1 for 1 standard deviation unit increase in the parameter. Because we have standardized the parameters, a small regression coefficient can be due to either a small sensitivity or a small range of uncertainty about the parameter.

We conducted the analysis at two different levels. First, we conducted the analysis on the matrix entries in A (Eq. 1). The survival and hatching entries in A are influenced by a set of lower-level parameters as defined in Eqs. 2–11 and estimated in the statistical analysis described above. Therefore, we also conducted the sensitivity analysis on these lower-level parameters in a separate analysis, but otherwise identical to above. Here, we transformed the cumulative log odds-scale parameters to the probability scale and expressed the exclosure effects on abandonment and nest loss as a change in probability; Δa and Δo are the difference in probability due to exclosure use for abandonment and nest loss, respectively.

Value of information

We calculated the expected value of perfect information (EVPI) from the bootstrap samples of growth rate (λ). EVPI is an estimate of the maximum value that could be gained by learning about the true parameter values (Williams et al. 2011). We calculated the difference between making a decision based on knowing exactly what λ is and making the decision based on the value of λ averaged over all estimation errors.

EVPI for growth rate with n bootstrap samples was calculated as follows:

$$\mathrm{EVPI}(\lambda) = \frac{1}{n}\sum_i \max[\lambda(\theta_i|x=0), \lambda(\theta_i, x=1)] - \max\left[\frac{\sum_i \lambda(\theta_i|x=0)}{n}, \frac{\sum_i \lambda(\theta_i, x=1)}{n}\right]. \quad (12)$$

The first term in the summation chooses the decision x that maximizes λ for each bootstrap replicate (i.e., under perfect information), while the second term makes the decision only by selecting the decision that gives the greatest average λ. The units of EVPI are expected improvement in λ given that the best decision is made. For example, an EVPI of 0.01 means that the annual growth rate could be improved by an average of 1% per year with perfect knowledge of the system. We calculated EVPI assuming the particular values for the random effect of hatching success (low, average, and high, described above), which only evaluates the value of improving the baseline life history rates. We also calculated EVPI without assuming a value of the random effect. This evaluates the value of determining the baseline nest loss rate for a particular site in addition to improving the life history rates.

Results

Participants identified "whether or not to use exclosures on a particular nesting beach" as the focal problem for the workshop. This was a deliberate simplification of the larger issue designed to get the discussion moving and focus our analytical efforts appropriately. Although many SDM applications examine the tradeoffs among multiple objectives, participants chose to focus on a single objective, maximizing the population growth rate λ, because that effectively synthesizes responses of different vital rates to the management action. In addition, λ was the target of previous analyses of the effects of exclosures, allowing for the direct comparisons among studies. There was a substantial discussion about whether or not to include monetary cost of management actions in the analysis. The group chose to leave cost out of the analysis at the present time because agencies' variable costs for exclosure use are relatively small in the context of overall monitoring and management, but it was discussed that they might want to revisit this tradeoff if contributions to λ were also small. Thus, the primary benefit of the SDM approach was in how uncertainties about the outcomes were identified, quantified, and then used to evaluate the choice at hand.

The best guess of most experts was that a nest abandonment implied a single adult mortality 60–70% of the time, although one expert thought it was much lower (Table 2). Most of the experts believed that on the high end, an abandonment implied the death of both adults in <70% of cases (Table 2) and the average "high" opinion was 78%, although one expert did not believe that abandonment was commonly an indicator of mortality (Table 2).

Daily and 34-d interval survival rates of piping plovers were lower for unexclosed nests than for exclosed nests, owing mostly to greater loss to "other sources" (likely predators) for unexclosed nests (Table 3). Abandonment rates were greater for exclosed nests than for unexclosed nests, but the difference was not statistically significant, based on the large overlap in the confidence intervals of the estimates (Table 3). The standard deviation of the random effect of site-year ($s_{(siteyear)}$) was 0.98 ± 0.31 SE.

For our test data set, we found that when unexclosed hatching success was average or low, exclosure use resulted in a greater population growth rate for all fledging probabilities examined (f = 0.2, 0.4, 0.6) than leaving all nests unexclosed, assuming that 78% of nest abandonments represent an adult mortality or 39% represent the adult female mortality (Fig. 2). When unexclosed hatching success was high, exclosure use resulted in a slightly lower value of λ under all estimates of fledging success, but the difference was very slight. Exclosures improve λ when the fledge rates are low (f = 0.2), but the population declines regardless of exclosure use (Fig. 2). Although exclosures have a positive effect on λ in a below-average year and site, λ is generally <1 regardless of the decision. In addition, λ is <1 regardless of exclosure use and average unexclosed nest success if the average fledging rates are low. Use of a smaller guess at the coefficient of variation in vital rates than the 10% we used would give us more confidence in our decisions because the standard errors of our estimates would be lower, but the decision would not change. Use of a larger guess

Table 2. Estimates of the number of nests, of 20 abandoned nests, abandoned because of mortality of at least one plover in the nesting pair and the number of nests, of 20 nests that were abandoned because of predation, in which both members of the breeding pair were depredated, elicited from piping plover biologists and managers.

		Four-point elicitation				Std. 80% CI	
Probability	Expert	Low	High	Best	Confidence (%)	Low	High
1 mortality	A	5	20	14	90	5.3	18.7
	B	0	7	2	75	0.4	7.5
	C	6	17	12	75	5.3	17.3
	D	6	16	13	85	8.1	16.7
	E	11	18	13	75	7.6	17.0
	F	5	15	12	75	6.1	16.7
2 mortalities	A	1	20	5	100	1.0	20.0†
	B	0	2	0	75	0.5	2.1
	C	1	5	2	55	0.5	6.9
	D	1	3	1	85	0.6	1.7
	E	1	5	2	75	0.8	4.7
	F	1	3	1	60	0.4	2.3

Note: Numbers represent the experts' lowest realistic estimate (low), highest realistic estimate (high), best guess (best), confidence that the true value is within the range elicited, and standardized 80% confidence intervals.

† This expert's confidence meant that the standardized range exceeded the possible limits of the parameter.

would decrease our confidence in our decision for the average site and year (random effect = 0), but would not affect our decision when the background nest loss rates are very high or very low.

For the parameters of the matrix entries in A, the population growth rate was most sensitive to adult survival (ϕ_a), followed by fledging probability (f) and then juvenile survival (ϕ_j^{w}) and hatching probability (H) (Table 4). When expressed as elasticities, adult survival was most important followed by the average egg production ($2E$), nest success probability (H), and fledging probability (f), which all had equal elasticities (Table 4). In terms of the standardized regression coefficient, adult survival (ϕ_a) and nest success (H) were most important (Table 4). For lower-level parameters (as defined in Eqs. 2–11 and estimated in the statistical analysis), the population growth rate was most sensitive to the exclosure effect on nest abandonment, but when expressed as an elasticity or the standardized regression coefficient, the background probability of nest loss was most important but there was a considerable uncertainty across the bootstrap distribution for elasticities. The standardized

Table 3. Estimated daily and 34-d interval rates and 95% confidence bounds (CB) of survival, abandonment, and loss to other sources (e.g., predators and flooding) for 343 piping plover nests (248 exclosed on at least 1 d) on the Atlantic Coast (28 sites from Maine, Massachusetts, Rhode Island, and New Jersey) in 2009–2012.

Nest status	Parameter (probability)	Estimate	SE	L 95% CB	U 95% CB
Exclosed	Daily Survival	0.992	0.001	0.990	0.994
	Daily Abandonment	0.003	0.001	0.002	0.004
	Daily Other Loss	0.005	0.001	0.003	0.007
	Interval Survival	0.759	0.030	0.698	0.820
	Interval Abandonment	0.092	0.017	0.058	0.127
	Interval Other Loss	0.149	0.028	0.094	0.204
Unexclosed	Daily Survival	0.971	0.005	0.961	0.981
	Daily Abandonment	0.002	0.001	0.001	0.004
	Daily Other Loss	0.027	0.005	0.017	0.037
	Interval Survival	0.371	0.065	0.240	0.501
	Interval Abandonment	0.045	0.017	0.012	0.079
	Interval Other Loss	0.584	0.068	0.448	0.720

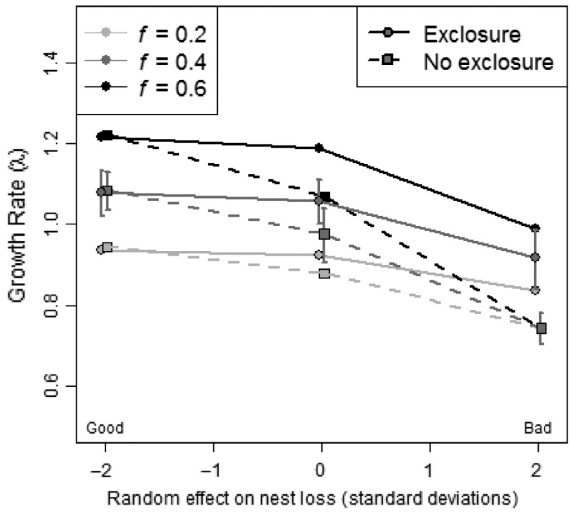

Fig. 2. Expected population growth rate (λ) of piping plovers as a function of exclosure use, fledging probability (f), and standard deviation of the random effect for hatching success. Error bars show the 95% bootstrap interval for all parametric uncertainties and are only given for intermediate fledging probability ($f = 0.4$) to reduce clutter.

regression coefficient for nest loss was similar to that for the most important higher-level parameters of adult survival and hatching probability.

The EVPI increased with the increasing nest success (Table 5). Under low nest success, there was virtually no improvement in growth rate associated with the perfect knowledge of the system. For the average nest success, EVPI was still quite low, with an expected improvement in annual growth rate of less than 1% for all values of f. Under scenarios of high nest success, there was an expected improvement of 1.1–1.4% in the annual growth rate associated with the perfect knowledge of the system (Table 5). When the baseline nest success was unknown, there was likewise an expected improvement of 1.1–1.4% associated with the perfect knowledge of the system (Table 5).

Discussion

Our results do not support the conclusions of Calvert et al. (2006), which imply that managing for increased nest success alone would be an ineffective way to increase the population growth rate, even though our elasticity results were nearly the same as theirs. However, Calvert et al. (2006) did not directly compare population growth rates between exclosed and unexclosed sites, but considered the reproductive outputs averaged across entire regions and variable use of exclosures. The sensitivity and elasticity analyses used consider only small changes in single matrix parameters (the partial derivative of λ with respect to the matrix entry). However, adding exclosures to nests leads to large changes in

Table 4. Sensitivity analysis for plover population growth rate simulation (10,000 iterations).

Parameters	Sensitivity			Elasticity			Std. regression coefficient
	Median	Q2.5	Q97.5	Median	Q2.5	Q97.5	
E	0.23	0.17	0.29	0.22	0.17	0.26	NA†
ϕ_a	1.02	1.01	1.03	0.78	0.74	0.83	0.021
ϕ_j^w	0.41	0.30	0.50	0.22	0.17	0.26	0.001
f	0.54	0.39	0.67	0.22	0.17	0.26	0.003
y_s	0.06	0.03	0.08	0.04	0.02	0.06	0.001
y_t	0.18	0.14	0.21	0.18	0.15	0.21	NA†
H	0.35	0.33	0.36	0.22	0.17	0.26	0.03
r_2	0.06	0.04	0.07	0.04	0.03	0.05	0.002
r_3	0.007	0.004	0.010	0.005	0.003	0.009	0.001
m	−0.03	−0.06	−0.003	−0.02	−0.05	−0.002	−0.001
P_a	−9.58	−11.74	−5.57	−0.02	−0.05	−0.01	−0.006
ΔP_a	−18.28	−22.09	−8.00	−0.02	−0.05	0.03	<−0.001
P_o	−3.52	−4.05	−2.99	−0.10	−0.16	0.06	−0.025
ΔP_o	−3.26	−3.89	−2.73	0.07	0.04	0.12	<−0.001

Notes: All analyses were conducted on the probability scale (not the cumulative log odds scale) for the parameter and at the mean across sites and years (random effect = 0). Median, 2.5th percentile (Q2.5), and 97.5th percentile (Q97.5) values of the simulations are shown. Parameters are defined in the text and in Table 1.

† Parameters fixed at a single value for the bootstrap sampling.

Table 5. The expected value of perfect information (EVPI) for maximizing plover population growth rate under the decision to use or not use exclosures.

Random effect for nest failure	Mean fledging probability	EVPI
−2 (high nest success)	0.6	0.014
	0.4	0.012
	0.2	0.011
0 (average nest success)	0.6	<0.001
	0.4	<0.001
	0.2	0.002
2 (low nest success)	0.6	<0.001
	0.4	<0.001
	0.2	<0.001
Unknown (averaged across sites)	0.6	0.014
	0.4	0.012
	0.2	0.011

multiple life history rates, making the actual outcome of management difficult to predict from the standard sensitivity and elasticity calculations (Hodgson and Townley 2004). The present model also has high sensitivity and elasticity for adult survival compared with nest success, but the changes in nest success were large enough to offset the decreases in adult survival caused by exclosures in our test data set.

If the nest abandonment rates were higher than the 9% observed in our test data set, the decision outcome may have been different. Maslo and Lockwood (2009) reported the abandonment rates of 7% and 19% in unexclosed and exclosed nests, respectively, in a 10-yr study in New Jersey. Cohen et al. (2009) found the abandonment rates to be 5.6% and 8.6% for unexclosed nests and exclosed nests, respectively, at one site in New York over 12 years, but at an adjacent site, the rates were 9.3% and 29.8%. If certain locations in certain years have much higher abandonment rates than our test data set, the optimal decision might change if it is assumed that the abandonment often represents adult mortality. Larson et al. (2003) concluded that the expanded use of predator exclosures would be sufficient to meet recovery goals for the Great Plains population of piping plovers, but they did not account for the potential negative effects of exclosures on adult survival. Thus, the variation in nest survival and abandonment among sites and years emerged as the key uncertainty that needs to be addressed in the future, in that the baseline nest loss rates affected our optimal decision.

Although λ was sensitive to uncertainty in fledging probability, the nest exclosure decision was not. Additional management strategies to improve chick survival, such as predator removal (USDA 2006, NPS 2007, Cohen et al. 2009), might be necessary to achieve an increasing population in some sites in some years, but according to our results, this should not affect the decision to exclose unless predator removal also makes the baseline nest survival very high. However, we did not model an effect of exclosures on fledging rate, and at some sites, predators may wait at exclosures for chicks to emerge (M. Hake, National Park Service, *personal communication*; C. Davis, New Jersey DEP, *personal observation*). If that phenomenon were found to be common, the decision could be changed by negative effects of exclosures on fledging rate. Furthermore, various refinements to our model were suggested by workshop participants as ways to implement the management recommendations adaptively. These included assessing the importance of density dependence in population growth at the local scale, which might imply using endpoints besides λ such as persistence (McGowan 2013), and examining the effect of ecological correlates on exclosure effectiveness, such as vegetation density around nests and the presence of colonial nesting birds in piping plover breeding areas.

Remaining uncertainties about the effects of exclosure use on life history rates and spatiotemporal variation in predation rates suggest that an adaptive management approach (Williams et al. 2009) to piping plover recovery is warranted. Adaptive management seeks to reduce uncertainties in the predicted outcomes of management actions by studying the results of those management actions. Williams et al. (2009) provided a series of diagnostic questions for identifying adaptive management opportunities. The decision to use exclosures is an "iterated decision" that is made repeatedly at different sites and in consecutive years, creating the opportunity to learn from the results of past choices. The uncertainties that affect the decision are "reducible," in the sense that studying the outcomes for particular nests and fledglings will allow us to estimate the effects of management and shrink the uncertainties surrounding those estimates. Managers already collect data on daily nest and fledgling survival, the very quantities needed to reduce

uncertainty about the effects of management actions. All that is needed is an effort to actually use that information to effectively inform decisions at a local scale. Finally, the commitment to use that information is already in place. Agencies are already taking these actions annually and expect to continue to do so in perpetuity.

Despite the use of a limited data set and uncertainties in demographic rates, our decision process led to a clear choice among alternatives depending upon the random effect in our model. We demonstrated the utility of SDM for the management of a terrestrial endangered species. By gathering a team of mathematical modelers and wildlife biologists who manage piping plovers across their U.S. Atlantic Coast range, we tapped a broad range of perspectives and experiences to address a shared, well-defined problem and objective. Through this exercise, piping plover management practitioners were able to test their preworkshop beliefs about the relative benefits and risks of exclosures based on the literature highlighting the sensitivity of population growth to even small declines in adult survival rates (Melvin and Gibbs 1996, Calvert et al. 2006, Brault 2007, Calvert and Taylor 2011). Early on in the decision analysis workshop, it became clear to the coaching team that this demographic tradeoff was what made the decision nebulous for local biologists and managers. The most important part of the decision analysis workshop was modifying an accepted life history model of the species so that it could assess this demographic tradeoff directly using the parameters estimated from participants' data and expert opinions, rather than making the tradeoff in an ad hoc manner. Through the application of the model to our test data set, we were able to examine our assumptions, evaluate competing hypotheses, and begin developing a model for further exploration of decisions that we make many times annually and that have real conservation implications.

The use of population models or other structured processes to inform value-based decisions is increasingly becoming a part of the management of species of conservation concern. Drechsler (2000) used a population modeling approach to evaluate several management scenarios for the orange-bellied parrot (*Neophema chrysogaster*), with recommendations for incorporating costs into the decision analysis. VanderWerf et al. (2006) used probabilistic decision trees with demographic data and expert opinion on the likelihood of management success to evaluate several management options for a critically endangered Hawaiian forest bird, the po'ouli (*Melamprosops phaeosoma*). Martin et al. (2010) used SDM to evaluate native predator control to improve the productivity of the beach-nesting American oystercatcher (*Haematopus palliatus*) while minimizing the impact of management on the predator population. All of these cases provide examples of using SDM to transparently make a decision using the best available knowledge. In our own case, we evaluated a simplified decision, to use exclosures to protect piping plover nests or not, because of deep uncertainty among managers as to the benefit of the method and because currently many sites exclose all nests or none. Participants were somewhat surprised at the outcome strongly favoring the use of exclosures, a result that is leading to a longer-term effort to refine the decision problem to focus on site- or year-specific ecological conditions under which exclosures are more likely to be deleterious or might be beneficial for some nests at a site, but not others. The importance of baseline nest survival rates to the decision is also leading to efforts to understand among- and within-season patterns of nest survival at a range of sites.

Our multinomial logistic exposure model and our life history-based decision model could be adapted to address the management actions, such as exclosure use, that affect competing risks to nests and adults of other shorebirds of conservation concern. Nest exclosures reduced the predation of killdeer nests (*C. vociferous*) by gulls (*Larus* spp.), but not by mammals, a result that was attributed partly to design of the exclosures (Nol and Brooks 1982). Failure of exclosures to accomplish their main purpose of reducing nest predation is an obvious problem, but reducing uncertainty in exclosure design parameters is easily accomplished. Dinsmore et al. (2014) found that nest survival rates for the closely related snowy plover (*C. nivosus*) benefited from exclosures or predator removal, but that using both provided little added value for nest survival. Mayer and Ryan (1991) found that electric fencing of breeding areas greatly improved nest and chick survival at sites in the Great Plains. Unpublished accounts of attempts to use this method on the

Atlantic Coast indicate that the maintenance needs are high in the dynamic coastal environment. However, without some management action to address chick survival, exclosures alone might not benefit productivity and may reduce adult survival. Isaksson et al. (2007) found that nest exclosures improved the hatching rates for nests of northern lapwings (*Vanellus vanellus*) and common redshanks (*Tringa totanus*). Nest abandonment rates were slightly higher for exclosed than for unexclosed nests for lapwings, and redshanks experienced higher adult mortality at exclosures, which was attributed to a delay in adults getting up and leaving the nest as predators approached. Our method allows these issues to be integrated into a single model. These species have some significant differences in life history and natural history traits from piping plovers, but such differences can be readily addressed with reparameterization of the population projection matrix and the renesting process models.

Runge (2011) identified several misconceptions about the use of SDM and adaptive management for endangered species, including the requirement for a large-scale problem, high costs, and the unacceptably high risks of experimental approaches to management. The decision about whether to use exclosures will be made by local site managers. Therefore in our case, the decision problem was local in scale, even though the potential tradeoff between adult mortality and nest survival was perceived across a large portion of the piping plover's geographic range and our results will affect decisions made over a similarly large area. Our process has identified remaining uncertainties and has created a framework by which the costs and risks of further experimental management can be better understood prior to the implementation of adaptive management. Moreover, inaction itself has been identified as a potential risk in natural resource management (Parma 1998), and our results suggest that in some circumstances, not using exclosures due to concerns over adult mortality may be the wrong decision if maximizing the growth rate is the objective.

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