

Balancing Demographic Benefits and Risks of Using Predator Exclosures on U.S. Atlantic Coast Piping Plover Nests

A Case Study from the Structured Decision Making Workshop

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Decision Problem

Every year, shorebird biologists and beach managers decide whether to use wire cages (i.e., exclosures) to reduce predator access to nests of approximately 1,500 pairs of U.S. Atlantic Coast piping plovers (*Charadrius melodus*). Although these decisions must be consistent with written authorizations from the State wildlife agencies, discretion to deploy exclosures is often conferred on experienced local biologists who factor current conditions at more than 250 sites into decisions about whether to use exclosures in site- or nest-specific situations. There is an ongoing debate over how effectively predator exclosures increase productivity, as well as their potential negative effects on survival of breeding adults. The goal of this decision analysis was to maximize piping plover population growth rates by providing local biologists with a decision framework to determine, on a yearly, site-, and nest-specific basis, when to erect predator exclosures.

Background

Managers conducted the first trials of wire fences to prevent predation of piping plover nests on the Atlantic Coast in 1987, when seven exclosures were used at four sites (USFWS 1996). Rimmer and Deblinger (1990) found that 24 of 26 nests (92%) protected by exclosures hatched

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at least one egg, while only six of 24 (25%) unenclosed nests hatched at a Massachusetts site over four years. Melvin et al. (1992) reported 90% (26/29) hatching of enclosed nests versus 17% (4/24) hatching of unenclosed nests at six sites on Outer Cape Cod, Massachusetts. By 1993, enclosures were deployed in every state and at least three Canadian provinces in the plovers' Atlantic Coast breeding range (USFWS 1996).

However, there were reports of local problems associated with enclosures including nest abandonment, adult mortalities and depredation of multiple enclosed nests at a site within a very short period of time (Vaske et al. 1994, USFWS 1996). As a result, guidelines for the use of predator enclosures (USFWS 1996, Appendix F) recognized that they were not appropriate for use in all situations. Accordingly, the guidelines included procedures for pre-use evaluation, design and construction, post-construction monitoring of incubating adult piping plovers and nests, removal of enclosures where potential risks are observed, and prompt reporting of potential problems.

Implicit in the decision to use enclosures are assumptions regarding hatching success, fledging success, and effects on survival of breeding adults. Frequent monitoring inherent to intensive management of plovers on beaches where heavy public recreational activity is also accommodated (Hecht and Melvin 2009b) facilitates accurate estimates of hatching and fledging rates. However, estimates of enclosure-related adult mortality are difficult to determine in a population where few birds are marked. Biologists managing piping plovers recognized the serious implications of adult mortality incidents associated with enclosed nests in light of the sensitivity of extinction risk to small declines in adult plover survival rates (Melvin and Gibbs 1996, Calvert et al. 2006, Brault 2007).

Studies of other piping plover populations and species fed a growing awareness of the demographic risks of nest enclosures (e.g., Johnson and Oring 2002, Murphy et al. 2003, Neuman et al. 2004). Nonetheless, most of the 70+ federal, state, and local government agencies and private organizations implementing piping plover conservation on the U.S. Atlantic Coast believed that predator enclosures were a valuable recovery tool through at least the late 2000s. Between 1986 and 2008, the Atlantic Coast piping plover population estimate increased 234%, from approximately 790 pairs to an estimated 1,849 pairs in 2008, and the U.S. portion of the population almost tripled, from approximately 550 pairs to an estimated 1,596 pairs (USFWS 2009). Hecht and Melvin (2009a) noted significant, positive relationships between productivity and population growth in the subsequent year for each of the three U.S. recovery units (New England, New York-New Jersey, and Southern). In addition, many periods of rapid regional growth in abundance of breeding pairs also coincided with widespread use of enclosures in those areas. Substantially higher hatching rates were observed for enclosed nests than unenclosed nests in most areas. For example, observed nest success (% of nests that hatched ≥ 1 egg) for the 62% of 6,044 nests enclosed in Massachusetts in 1992-2003 was 75%, versus 42% for unenclosed nests (S. Melvin, MassWildlife, pers. comm. 2013). Similarly, Maslo and Lockwood (2009) reported a 43% increase in hatching success for enclosed vs. unenclosed nests.

The overall perception of benefits versus risks associated with enclosures began to shift in the late 2000s (USFWS 2009). Cohen et al. (2009) found that enclosures improved nest survival, but not overall reproductive output on Westhampton Island, New York study sites, a result echoed

by studies of other plover species (e.g., Neuman et al. 2004). Managers reported episodes of systematic harassment of incubating piping plovers (primarily by foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), American crows (*Corvus brachyrhynchos*), and fish crows (*Corvus ossifragus*)), elevated rates of nest abandonment, and incidents of adult mortalities associated with enclosed piping plover nests on the Atlantic Coast (Mostello and Melvin 2002, Melvin and Mostello 2003) and on the Northern Great Plains (Murphy et al. 2003). For many years, however, these concerns were somewhat tempered by the beliefs that enclosures may increase detectability of adult mortalities and abandonments compared with unenclosed nests, and that most adults that abandon nests survive to renest, either later in the same breeding season or in a future year. Recently, however, evidence that apparent nest abandonment is usually evidence of breeding-season mortality in Great Lakes piping plovers (Roche et al. 2010) further shifted the perception of demographic risk associated with enclosure use. There was also an emerging (although untested) concern that rates of abandonment, depredation of eggs, and depredation of breeding adults at enclosed nests may be increasing, perhaps as a result of “smart” predators learning to exploit enclosures or a density-dependent effect of increasing piping plover abundance.

The perception that the benefit of increased nest success from enclosures could be outweighed by increases in adult mortality arises from 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). These papers used age structured matrix projection models, and carried out sensitivity and elasticity analyses to identify matrix entries with large effects on population growth rates (Caswell 2000). The conclusion in all cases is that a change in the annual survival of adult birds has the largest effect on population growth (λ), and a larger improvement in nest success is required to compensate for a given decrease in adult survival.

As a result of these shifts in perceived risks to the population, managers’ use of enclosures declined at some locations, while remaining common in other areas along the Atlantic Coast. For example, the percentage of nests enclosed at the Cape Cod National Seashore in Massachusetts declined from 82% in 1992-1994 (average nesting pairs = 70) to 55% in 2002-2004 (average nesting pairs = 89 pairs), and enclosure use was completely suspended in 2012 and 2013 (average nesting pairs = 92) (Cape Cod National Seashore annual reports; M. Hake, Cape Cod National Seashore, pers. comm., 2014). A moratorium on enclosures was also instituted in Eastern Canada starting in 2012 (J. Rock, Canadian Wildlife Service, pers. comm. 2013). By contrast, Assateague National Seashore deployed enclosures on 79% of nests at the in 2010-2012 (average nesting pairs = 40) and Maine used enclosures on 80% of nests in 2010-2012 (average nesting pairs = 35).

As use of enclosures declined, managers increased use of other methods (e.g., selective predator removal activities) at many sites throughout the U.S. Atlantic Coast range (e.g., USDA 2006, NPS 2007, Cohen et al. 2009). However, given the magnitude of continuing (and perhaps intensifying) predation threats, recovery cooperators wanted a systematic analysis of enclosure risks and benefits.

The goal of this case study was to explore methods for assessing the overall demographic benefits and risk of the decision to deploy enclosures at a site. If environmental factors that increase benefits and/or decrease risks can be identified, then the overall contribution of

exclosures can be increased.

Decision Structure

Objectives

We discussed several potential fundamental objectives (which reflect the ends we are trying to achieve) to measure the value of deploying exclosures at a site. Ecologically, the fundamental objective was to maximize λ , the population growth rate, estimated using an age structured matrix projection model. The means objectives that contribute to attainment of this fundamental objective were to maximize hatching success and minimize adult mortality. λ provides a single measure that appropriately trades off these vital rates of concern against each other. When λ is greater than 1, a local population is contributing to population growth, while if λ is less than 1 the local population is a sink that can only persist with continued immigration.

In addition to ecological concerns, we identified other values (potential fundamental objectives) that might be considered in determining whether to use predator exclosures. These included minimizing resources used (cost), with means objectives of minimizing man-hours and minimizing expenditures for materials. The group also discussed ideas related to minimizing confrontation with the public and landowners, but this was acknowledged to be a bigger concern arising when predator removal techniques are considered rather than exclosure use.

Alternatives

During the workshop, we focused on the two extreme alternatives of 1) never using exclosures, or 2) always using exclosures. These two alternatives represent the full range of possibilities. In the future, we could evaluate more nuanced alternatives that take into account covariates that influence the effectiveness of predator exclosures as a management technique for individual sites or even nests. The predictive model will be modified as more data become available to evaluate additional alternatives such as:

- Use exclosures except when vegetation and/or topography obstruct the incubating plover's view of approaching real or perceived predators
- Use exclosures at some infrequent interval (e.g., not more than one in every three or five years) at a given site or region
- Use exclosures when specified egg predators are present (e.g., determined from some index such as tracks)
- Use exclosures except when specified predators of adult plovers are present
- Use exclosures unless the site experiences high levels of weather related adult mortality in exclosures
- Use exclosures at sites in a restricted range of latitudes
- Use exclosures when least tern (*Sternula antillarum*) are (or are not) nesting nearby

Consequences and Tradeoffs

Although the benefits of closures to hatching success are well documented, there is considerable uncertainty about the effects of closures on adult mortality. As a result the bulk of our prototyping efforts focused on connecting the effects of closures to population growth rates using statistical models to estimate closure effects, and an age structured population model to explicitly trade off decreases in adult survival with improvements in hatching success. The primary tradeoff to be made involves two demographic rates, and life history theory tells us how that tradeoff works. There was no need to elicit weights for these objectives or carry out other multi-criteria analyses to select the best alternative. Whichever alternative provides the highest value of λ is the one that should be selected, although the presence of uncertainty about parameter values makes the comparison more complicated if the effect of closures is small. Tradeoffs between increases in λ and other fundamental objectives such as resource costs could be made, but participants were much less concerned with expending resources if the benefits of taking action were positive, and therefore elected to defer that objective in the prototype model.

Decision Analysis

Predictive Model of Consequences

We used a population projection model similar to that of Calvert et al. (2006) and Calvert and Taylor (2011), simplified to two age classes, to predict long term expected population growth (λ) as a function of survival and reproduction parameters. If we define the column vector N_t as the number of juvenile (hatch year) female piping plovers and the number of adult (after hatch year) female plovers and define the population census as taking place just after hatching but before fledging, the number of plovers in the next year is $N_{t+1} = AN_t$ with

$$A = \begin{bmatrix} \phi_j^w f y_s H 2E & \phi_a y_a H 2E \\ \phi_j^w f & \phi_a \end{bmatrix} \quad (1)$$

where ϕ_j^w is the survival probability of juveniles from time of fledging in year t (their 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 4 total eggs are laid with an equal primary sex ratio), H is the probability 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 (ages > 1). However, emigration and immigration can be discounted for the purposes of assessing the effect of closures on the population growth rate of a local population, as long as closures do not affect the rates of emigration and immigration. The long term expected growth rate (λ) is the leading (maximum) eigenvalue of A .

We assumed that closures positively affect hatching probability (H) and negatively affect survival parameters (ϕ_j^w and ϕ_a) through mortalities during nesting that were recorded as nest abandonments. We estimated the effect on H with a statistical analysis of nesting data, described

below. We also looked for the effect of enclosures on survival from hatching to fledging (f) but did not find a statistically significant effect of enclosures with the data available (results not shown). We elicited the probability that an abandonment represents one or more adult mortalities from workshop participants with relevant expertise (described below), because there are no data to estimate this probability. The estimates of Roche et al. (2010) could have influenced our experts.

We needed to consider potential effects of re-nesting in order to relate estimated abandonment and hatching probabilities of individual nests to abandonment and hatching probabilities for each female over all nesting attempts in a season (Figure 1). If we let a be the probability of an individual nest becoming abandoned, o be the probability of all other failed nest fates, 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 $a(1 - m)$ (Figure 1). Although an extreme case of five nesting attempts by a banded female piping plover has been documented (MacIvor 1990), our prototype model considered a maximum of three possible nesting attempts such that the total hatching probability for a female over all nesting attempts is

$$H = h + r_2 [oh + a(1 - m)h + o[or_3 + a(1 - m)r_3h] + a(1 - m)[oh + a(1 - m)r_3h] \quad (2)$$

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 i^{th} attempt ($r_1 = y_s$ for second-year females and $r_1 = y_t$ for third-year females). See Table 1 for parameter values used in our base-line model.

Similarly, we calculated the probability of abandonment-associated mortality over all nest attempts as

$$M = r_1 [am + a(1 - m)r_2 [am + a(1 - m)r_3am]] \quad (3)$$

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

$$\phi_a = \phi^b \phi_a^w \quad (4)$$

and assuming that $\phi^b = \sqrt[\epsilon]{\phi_a}$, to reflect that most nest abandonment occurs during the months of May and June, and that breeding season survival is identical between second- and third-year females (since data are not available to empirically estimate breeding season survival). We then further decomposed breeding season survival into components due to abandonment in the absence of enclosures and a component due to 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 enclosure use, $x=0$ is no enclosure use, and $x=1$ is enclosure use. [Note that the parameters a , o , and h , as well as the function H are also functions of enclosure 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 enclosure use ($x=1$) is calculated as

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

and the annual survival for adults with enclosure use becomes

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

and the annual survival for juveniles 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 Enclosure Effect

It has long been recognized that estimating the effects of ecological and management variables on nest survival requires the days of nest exposure to hazards in a statistical model (Mayfield 1961, 1975, Shaffer 2004). Exposure must be accounted for because some nests are likely to have been created then lost without being discovered by researchers, such that raw estimates of “surviving nests” / “nests found” will be biased high. Thus, modern techniques such as logistic exposure models extend logistic (binary) regression to estimate daily survival, and extrapolate it to the entire nesting span. Etersson et al. (2007) developed an extension of binary logistic exposure that uses a Markov Chain model (MCEstimate) to estimate probabilities that nests will be in a particular state (e.g., “alive”, “eaten by predator”, “abandoned”) as a function of variables of interest, and corrects for exposure time. However, publicly available versions of MCEstimate do not allow for time-varying covariates of survival (e.g., erecting enclosures partway through incubation such that early on, the nest is not protected), and does not allow for random effects. Thus, for this exercise we developed a mixed multinomial logistic exposure model using Proc NLMixed (SAS Institute 2004). We used it to estimate daily probabilities of survival, abandonment, and “other” nest losses (i.e., predation, flooding) as a function of enclosure presence (fixed effect) and “site by year” (hereafter “siteyear”) random effect, using data on the fate of 343 nests at 28 sites from Maine, Massachusetts, Rhode Island, and New Jersey, between 2009-2012. We estimate that this sample constitutes <3% of piping plover nests on the Atlantic Coast during these 4 years. The statistical model used in the workshop was:

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

Where Nests are indexed $i = 1, \dots, N$, each nest is observed over intervals indexed $j = 1, \dots, M_i$, and the interval is t days long. For each nest and interval the observation is $y_{ij} = 1$ 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 are $p(t)^c_{ij}$, and there is only $n = 1$ trial per nest check. The t indicates that these probabilities apply across an interval of t days in length.

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

$$\begin{aligned} \eta_{ij}^a &= \beta_0^a + \beta_1^a X_{ij} \\ \eta_{ijk}^o &= \beta_0^o + \beta_1^o X_{ij} + u_k, u_k \sim N(0, \sigma^2) \end{aligned} \quad (9)$$

Where $\beta_{c,t}$ are regression coefficients for each cause c . $X = 1$ if a nest was enclosed 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 1 day

$$\begin{aligned} p(t=1)_{ijk}^s &= \frac{1}{1 + e^{\eta_{ij}^a} + e^{\eta_{ijk}^o}} \\ p(t=1)_{ijk}^a &= \frac{e^{\eta_{ij}^a}}{1 + e^{\eta_{ij}^a} + e^{\eta_{ijk}^o}} \\ p(t=1)_{ijk}^o &= \frac{e^{\eta_{ijk}^o}}{1 + e^{\eta_{ij}^a} + e^{\eta_{ijk}^o}} \end{aligned} \quad (10)$$

which is the standard multinomial logit function. For intervals of length t

$$\begin{aligned} p(t)_{ijk}^s &= \left(p(t=1)_{ijk}^s \right)^t \\ p(t)_{ijk}^a &= p(t=1)_{ijk}^a \sum_{l=1}^{t-1} \left(p(t=1)_{ijk}^s \right)^l \\ p(t)_{ijk}^o &= p(t=1)_{ijk}^o \sum_{l=1}^{t-1} \left(p(t=1)_{ijk}^s \right)^l \end{aligned} \quad (11)$$

The model therefore estimates daily survival, and partitions daily mortality into sources. The probability of hatching, abandonment, and “other” nest loss for a single 34-day nest attempt (7 days for egg-laying plus 27 days incubation), $h = p(t=34)_{ijk}^s$, $a = p(t=34)_{ijk}^a$, and $o = p(t=34)_{ijk}^o$, respectively (Figure 1). The standard deviation of the random effect of siteyear ($S_{(\text{siteyear})}$) was 0.98 ± 0.31 SE. Daily and 34-day interval survival rates were lower for unenclosed nests than enclosed nests, owing mostly to higher loss to “other sources” (likely predators) for unenclosed nests (Table 2). Abandonment rates were higher for enclosed nests than unenclosed nests, but the difference was not statistically significant, based on large overlap in the confidence intervals of the estimates (Table 2).

Expert Elicitation of Mortality

Data were not available to estimate m , the probability of adult mortality given nest abandonment. Therefore, we elicited the expert opinion of the panel of piping plover experts involved in the workshop to obtain an estimate of this parameter. We used the four-point interval elicitation procedure (Speirs-Bridge et al. 2010) and the modified Delphi method (Kuhnert et al. 2010). We asked the panel to provide, out of 20 abandoned nests, the lowest realistic number of nests that would be abandoned as a result of adult predation, the greatest realistic number of nests abandoned because of adult predation, their best guess of the number of nests abandoned because of adult predation, 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 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 during the workshop 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 (Table 3). The best guess values and standardized 80% CIs were averaged across panelists and transformed into a probability range to use in the model (Table 1).

Uncertainty

With the models described above we calculated the expected population growth rate at a local site with and without enclosure use. However there are several important sources of uncertainty. First, each of the parameters used in the model has some level of estimation error, usually reported as a standard error for the parameter. In addition, the mixed models we used to estimate the effects of enclosures on hatching success estimated the amount of variation in baseline (without enclosures) hatching success between different sites and years. This environmental heterogeneity is superimposed on the effects of estimation error. We addressed the effects of estimation error using a Monte Carlo approach to calculate a distribution of λ conditional on the estimation error in our parameters. We did this for different degrees of hatching success ranging from good (2 standard deviations above the mean) to bad (2 standard deviations below the mean). 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 variation in expected growth rate (λ) due to parametric uncertainty by conducting bootstrap re-sampling from the sampling distribution of parameters. For parameters where we had no estimate of the parametric uncertainty, we assumed a coefficient of variation of 10% (Table 1). 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 estimated mean and sample covariance matrix from the nest survival statistical analysis (Table 2). Thus, our analysis does not account for parametric uncertainty in the random effect variance. We used 10,000 bootstrap samples. Results of the bootstrap are shown in Figure 2. For our limited test data set, we found that when unenclosed hatching success was average or low, enclosure use resulted in a greater population growth rate for all fledging probabilities examined than leaving all nests unenclosed. When unenclosed hatching success was high, enclosure use resulted in a slightly lower value of λ under all estimates of fledging success, but the difference was very slight. The benefit gained from enclosures does decrease when fledging success rates are low. In addition, although enclosures have a positive effect on λ in a below average year and site, λ is generally less than 1 regardless of the decision. In addition, λ is less than 1 regardless of enclosure use and average unenclosed nest success if average fledging rates are low. This indicates that sites with below average unenclosed nest success and/or low fledging success are population sinks in the years analyzed.

Sensitivity Analysis

We performed a prospective sensitivity analysis (Caswell 2000) of population growth rate for each of the probabilities listed in Table 1 and on the probabilities associated with daily nest abandonment and nest loss. To maximize 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 30,000 bootstrap parameter samples and then a standardized regression coefficient between the bootstrapped sample of population growth rate and the bootstrapped sample of parameters. The bootstrapping sample is described above. Sensitivity is defined as the partial derivative of population growth rate with respect to the parameter of interest. Sensitivity measures the absolute change in λ as a parameter is changed. Elasticity is the sensitivity multiplied by the ratio of population growth (λ) to the parameter value (θ), $\lambda/\theta * \partial\lambda/\partial\theta$. Elasticity measures the proportional change in population growth rate for a proportional change in the parameter. For example, an elasticity value of 1 means that at the value of the parameter, an increase in the parameter value of 1% will result in an 1% increase in population growth rate. Values less than 1.0 mean that population growth rate will increase less than the proportional increase in the parameter. For example, an elasticity of 0.1 means that population growth will only increase by 0.1% for the example above. Because sensitivity and elasticity are based on derivatives, they are referred to as a “local” analysis and 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 zero, standard deviation equal to 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 one 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 parameters of the matrix entries in A (equation 1). The survival and hatching entries in A are influenced by a set of lower-level parameters as defined in Equations 2–11 and estimated in the statistical analysis describe above. Therefore, we also conducted the sensitivity analysis on these lower-level parameters in a separate analysis, otherwise identical to above. Here we transformed the cumulative log odds-scale parameters to the probability scale and expressed the enclosure effects on abandonment and nest loss as a change in probability; Δa and Δo are the difference in probability due to enclosure use for abandonment and nest loss, respectively. Code is given in the attached supplement.

For the higher level parameters, population growth rate was most sensitive to adult survival, followed by fledging probability and then juvenile survival and hatching probability (Table 4). When expressed as elasticities, adult survival was most important followed by average egg production ($2E$), nest success probability (H), and fledging probability (f), which all had equal elasticities. These elasticities are essentially identical to those reported in Calvert and Taylor (2011). In terms of the standardized regression coefficient, adult survival and nest success (H) were most important. For lower-level parameters, population growth rate was most sensitive to the enclosure effect on nest abandonment, but when expressed as an elasticity or the standardized regression coefficient, the background probability of nest loss was most important. The standardized regression coefficient for nest loss was similar to that for the most important higher-level parameters of adult survival and hatching probability.

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 calculate 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 error. EVPI for growth rate with n bootstrap samples is calculated as

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

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 highest average λ . The units of EVPI are the expected improvement in λ given that the best decision is made. For example, an EVPI of 0.01 means that annual growth rate could be improved by an average of 1% per year with perfect knowledge of the system. We calculated EVPI assuming particular values for the random effect of hatching success, so this analysis only evaluates the value of improving baseline life history rates.

For the bootstrap samples described above, the EVPI for growth rate under three levels of mean fledging success and three values of the random effect of hatching success is given in Table 5. The EVPI increased with increasing nest success. Under low nest success, there was virtually no improvement in growth rate associated with perfect knowledge of the system. For 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 . Even under scenarios of high nest success, there was expected improvement of 1.0 – 1.3% in annual growth rate associated with perfect knowledge of the system.

Discussion

During the workshop, we developed a decision framework that begins to answer the question of when and where to use exclosures on piping plover nests. We evaluated the two extreme alternatives of exclosure use for piping plover nests – exclose all nests or exclose none of the nests. The choice to focus on these two alternatives was made because of time and data constraints for the workshop. We focused on developing models that evaluate the consequences of exclosure use on the fundamental objective of maximizing piping plover population growth rate (λ). We then evaluated how robust the decision was to uncertainty in key parameters.

Contrary to most participants' expectations, the use of exclosures resulted in greater piping plover population growth rates than leaving nests unexclosed, except in scenarios in which hatching success was very good relative to an average year and site. In this latter case, the two alternatives produced approximately equivalent results. Population growth rate was sensitive to fledging success rate, but in all cases, the decision of whether or not to use exclosures was not sensitive to changes in this rate. In this preliminary evaluation of the extreme alternatives of exclosing all nests or exclosing none of the nests, exclosure use is beneficial when baseline

hatching success is average or poorer. In cases in which baseline hatching success is good, the objectives related to cost would become more important, as decision makers might weight cost of deploying exclosures more highly if there is nothing to be gained from using them.

Understanding site and year specific factors that lead to the large variation in hatching success is very important for deciding whether or not to use exclosures. The potential gain in population growth rate from studying piping plover life history to improve estimates of parameters such as probability of renesting generally is very small ($EVPI < 0.01$ in most cases), while being able to predict if hatching success at a site is worse than average could potentially increase growth rate by 0.1 or even more depending on fledgling success.

Value of Decision Structuring

This workshop explored how a structured decision approach could be used by shorebird managers to evaluate the demographic trade-offs of predator exclosures. By gathering a team of biologists and modelers from across the U.S. Atlantic piping plover range, we tapped a broad range of perspectives and experiences to address a shared, well-defined problem and objective. We also had fun doing it! Through this exercise, the piping plover management practitioners were able to test their pre-workshop beliefs about the relative benefits and risks of exclosures that were based on 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 prototyping process it became clear to the coaching team that this demographic tradeoff was what made the decision difficult and contentious among local biologists and managers. The most important part of the decision workshop was modifying an accepted life history model of the species so that it could assess this demographic tradeoff directly using 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.

Why did the prototype model contradict the conclusions of previous modeling exercises about the value of exclosures? Calvert et al. (2006) did not directly compare population growth rates between exclosed and unexclosed sites, but considered reproductive outputs averaged across entire regions and variable use of exclosures. The sensitivity and elasticity analyses used considered 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 multiple life history rates, and thus the actual outcome of management is difficult to predict from standard sensitivity and elasticity calculations (Hodgson and Townley 2004). The present model also has high sensitivity and elasticity for adult survival compared to nest success, but the improvements in nest success are large enough to offset decreases in adult survival caused by exclosures.

Calvert and Taylor (2011) did directly compare population growth rates with and without exclosures, and found that under all conditions populations were declining; exclosures were either not helpful or actively harmful depending on how the effect of exclosures on adult survival were calculated. Direct comparison of our parameters with theirs is difficult because we

calculated the effects of exclosures differently. However, we did observe large variation in nest survival and abandonment across years and sites, so it is entirely consistent to find that exclosures are not helpful at sites and in years other than those used in the present study. Our next steps are to continue exploring model refinements, plan for acquisition of additional data to expand the model, and look for a funding source to support that effort. Our goal is to add data to the model (including more geographic areas and years) so that analyses can be conducted on a more local (or regional) basis. We hope to test hypotheses regarding what environmental factors affect the overall benefits of exclosures.

We presented our findings to 85 attendees of the biennial piping plover and least tern workshop in early February 2014. The prototype model and preliminary results were well-received, and we plan to bring more people (critical thinking and data) into the process to improve and expand the model. We believe that the structured decision making workshop demonstrated a very promising approach to better decisions about using exclosures. The model still requires biologists on-the-ground to assess the factors influencing risks and benefits, and we are very optimistic that application of a fully developed model to a larger data set has potential to help biologists make better choices about exclosure use.

Recommendations

The nest survival estimates have considerable room for refinement. The prototype model only includes random effects of site/year in baseline abandonment rates, but variation among sites and years in effects of exclosures would also be of interest. Given that much of the inter-annual variation in nest survival is within sites, or at least groups of local sites, rather than coast-wide, it may be useful to test the random effect of year within sites, which would require longer-term datasets from each site. Since the December 2013 structured decision making workshop, we have developed a Bayesian version of the model in WinBUGS that models site and year, and their interaction, as separate random effects. Potential covariates that could be included as fixed effects on nest success and as interactions with the exclosure effect (i.e., weather variables, predator communities and abundance, vegetation, time in the season – see also the *Alternatives* section, above) were suggested before and after the February 2014 plover-tern workshop. The nature of logistic exposure models allows for the modeling of different management strategies that vary by days into nest phenology, such as placement or removal of exclosures partway through incubation, and it may be interesting to test some of these scenarios and their effects on nest survival and λ . Inclusion of spatial autocorrelation among nests or sites was also suggested at the plover-tern workshop as a way to control for non-independence among nests in close proximity to each other.

Acknowledgements

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Figures

Figure 1. Nest fate diagram describing the estimation of the probabilities of hatching and abandonment-related mortality, taking into account re-nesting throughout the breeding season.

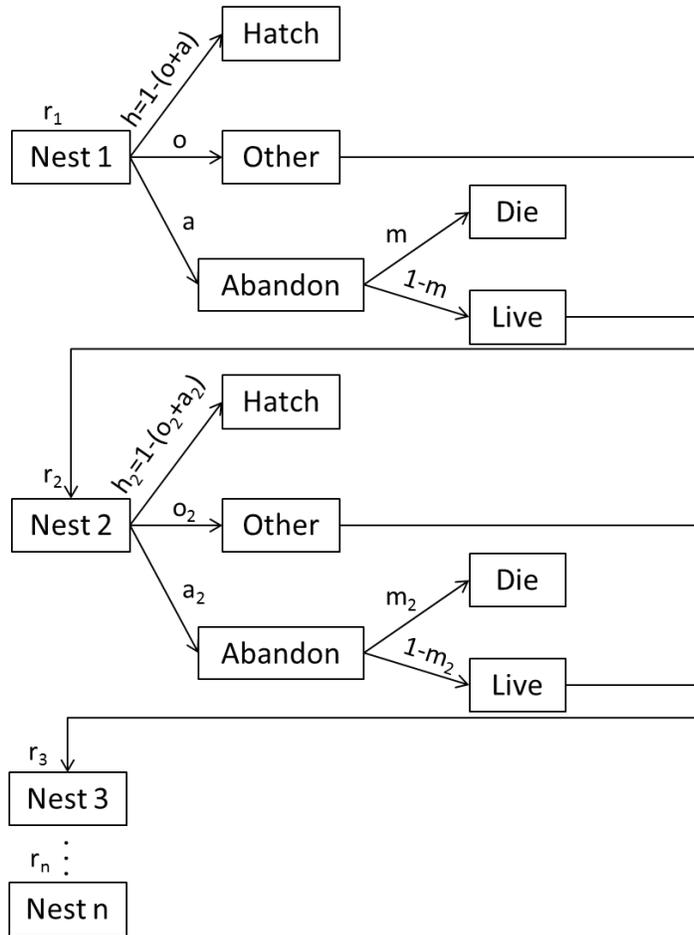
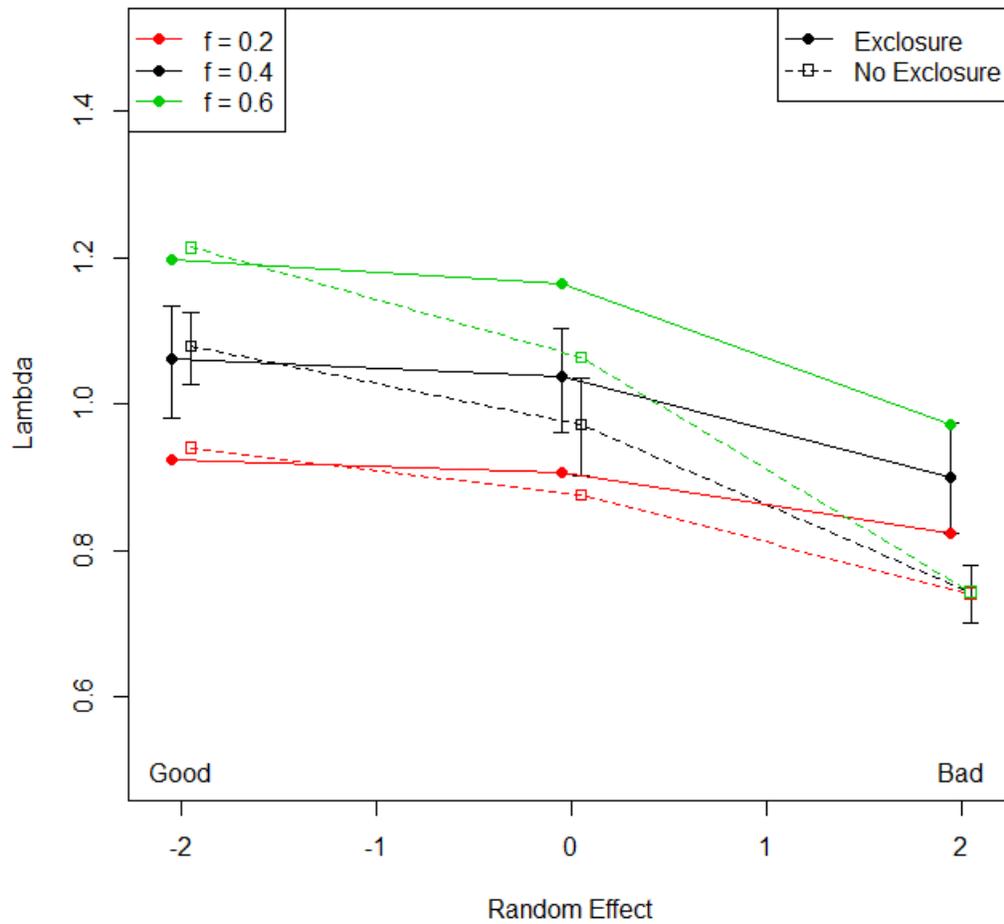


Figure 2. Expected population growth rate (λ) as a function of exclosure use, fledging probability (f), and standard deviation of the random effect for hatching success. Error bars show the 95% bootstrap interval for all parametric uncertainty, and are only given for intermediate fledging probability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



Tables

Table 1. Parameters (other than nest success and abandonment rates, Table 2), definitions, and statistical distributions (mean and coefficient of variation [C.V.]) used in the predictive model for piping plover population growth rate (λ). All parameters were simulated from a normal distribution on the log odds scale, unless otherwise noted.

Parameter	Definition	Mean	C.V. ¹	Source
E	Probability of an egg hatching, given that the nest hatches	0.94	0 ²	Informal expert opinion
ϕ_a	Annual adult survival	0.74	0.1	Calvert et al. 2006
ϕ_j^w	Juvenile survival from fledging in the first year of life at year t to hatching a nest as a second-year bird in year $t+1$	0.53	0.1	Informal expert opinion
f	Probability of fledging	0.4	0.06	Data analysis, this paper
y_s	Probability of breeding as a second-year bird	0.68	0.1	Informal expert opinion
y_t	Probability of breeding after the second year	0.9999	0 ²	Melvin and Gibbs 1996
r_2	Probability of re-nest after failure of first nest	0.7	0.1	Informal expert opinion
r_3	Probability of re-nest after failure of second nest	0.7	0.1	Informal expert opinion
m	Probability of adult mortality given that a nest was classified as abandoned	0.75	1.59	Formal expert elicitation

¹Coefficient of variation on the log odds scale.

²Parameter fixed at a single value for the Monte Carlo analysis.

Table 2. Estimated daily and 34-day 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 one day) on the Atlantic Coast (28 sites from Maine, Massachusetts, Rhode Island, and New Jersey), 2009-2012.

Nest Status	Parameter (Probability)	Estimate	Std.	L 95% CB	U 95% CB
			Error		
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

Table 3. Estimates of the number of nests, out of 20 abandoned nests, abandoned because of mortality of at least one plover in the nesting pair, and the number of nests, out 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. 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.

Expert	Low	Four-point elicitation			Confidence (%)	Standardized 80% CI	
		High	Best	Low		High	
<i>P(1 or more mortalities / Abandonment)</i>							
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	
<i>P(2 mortalities / At least 1 mortality)</i>							
A	1	20	5	100	1	20 ¹	
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	

¹This expert's confidence meant that the standardized range exceeded the possible limits of the parameter.

Table 4. Results of a sensitivity analysis for plover population growth rate are shown. Sensitivity is the partial derivative of population growth rate with respect to the parameter. Elasticity is based on the partial derivative and measures the proportional change in population growth rate with a proportional change in the parameter. The standardized regression coefficient is the partial regression coefficient of population growth rate from a model that included as predictors 30,000 random samples from the distribution described in Table 1. The standardized regression coefficient measures the importance of the parameter for determining population growth relative to the uncertainty in the parameter (i.e., the change in population growth rate for 1 standard deviation of the parameter). 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). Shown are the median values over the bootstrapped samples, and in parentheses are the 5th and 95th quantiles over the samples. For definition of parameters see Table 1 and text. The two greatest values, rounded to one decimal place, are given in bold for the higher level parameters, and for the lower level parameters, only the greatest value is in bold.

Parameter	Sensitivity	Elasticity	Standardized Regression Coefficient
Higher level			
E^l	0.23 (0.17, 0.29)	0.22 (0.17, 0.27)	NA ¹
ϕ_a	1.02 (1.01, 1.03)	0.78 (0.73, 0.83)	0.021
ϕ_j^w	0.41 (0.30, 0.52)	0.22 (0.17, 0.27)	0.001
f	0.54 (0.39, 0.69)	0.22 (0.17, 0.27)	0.003
y_s	0.06 (0.03, 0.09)	0.04 (0.02, 0.06)	0.001
y_t^l	0.18 (0.14, 0.22)	0.18 (0.15, 0.21)	NA ¹
H	0.35 (0.33, 0.36)	0.22 (0.17, 0.27)	0.03
Lower level ²			
r_2	0.05 (0.03, 0.07)	0.03 (0.02, 0.05)	0.003
r_3	0.005 (0.002, 0.011)	0.004 (0.002, 0.008)	0.001
m	-0.06 (-0.11, -0.008)	-0.04 (-0.10, -0.002)	-0.003
a	0.06 (0.002, 0.22)	0.002 (0.0001, 0.01)	-0.013
Δa	-30 (-39, -8)	-0.03 (-0.09, 0.04)	$\pm 10^{-4}$
o	-3.1 (-4.0, -2.2)	-0.09 (-0.15, -0.05)	-0.025
Δo	-2.6 (-3.9, -1.7)	0.06 (0.03, 0.11)	<-0.001

¹ Parameter fixed at a single value for the bootstrap sampling.

² Sensitivity analysis also included matrix entries, except H , which is determined by lower level parameters.

Table 5. The expected value of perfect information (EVPI)¹ for maximizing plover population growth rate under the decision to use or not use exclosures.

Random Effect of nest success	Mean Fledging Probability	EVPI
-2 (high nest success)	0.6	0.013
	0.4	0.011
	0.2	0.010
0 (average nest success)	0.6	0.001
	0.4	0.002
	0.2	0.006
2 (low nest success)	0.6	<0.001
	0.4	<0.001
	0.2	<0.001

¹ EVPI is an estimate of the maximum value that could be gained by learning about the true parameter value, calculated as 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 error.

Supplemental Material: R code used in analysis for calculating growth rate, Monte Carlo sampling, EVPI, and the sensitivity analysis.

```
##Piping Plover Demographic model for SDM workshop, NCTC December 10-13, 2013
## Code for "The Beast"
## Developed by Erik Osnas
## Modified 1-22-2014
## Modified 3-26-2014:
## (1) added sensitivity analysis,
## (2)found mistake in exclosure effect on juv survival = was calculed in Amat function but not
included in matrix from Amat
## (3) attempted to improve code style and readability
#####
#####
logodds=function(x){log(x/(1-x))}
invlogit=function(x){exp(x)/(1+exp(x))}
icumlogit=function(x=NA){ #x is list of cumlogistic parameters
  p=list()
  xx=lapply(x, sum)
  for(i in 1:length(x)){p[i]=exp(xx[[i]])/(1+sum(exp(unlist(xx))))}
  return(p) #list with same elements as x but now probabilities
}
cumodds=function(x){ #x is a list of probabilities, the output from icumlogit
  b=list()
  xx=1-sum(unlist(x))
  bb=-log(xx)
  for(i in 1:length(x)){b[i] = log(x[[i]])+bb}
  return(b)
}
require(MASS)
lambda=function(T){ #find and return leading eigenvalue
  lam = max(Mod(eigen(T)$values))
  return(lam)
}
pval=function(x,val=1.0){length(x[x>val])/length(x)}
#Function to transform daily nest success to nesting interval success
# parameter list x must be the same as x for function Amat
nest=function(x=NA, period=34, exclose=0, ran.eff=0){
  a.daily=invlogit(x$ab[1:2]%%c(1,exclose))
  o.daily=invlogit(x$ot[1:2]%%c(1,exclose)+ran.eff)
  no.x.p <- c(1-a.daily-o.daily,a.daily,o.daily)
  no.x.p <- no.x.p/sum(no.x.p)
  ss <- no.x.p[1]^(0:(period-1))
  return(
    c(h = no.x.p[1]^period,
```

```

    a = sum(ss*no.x.p[2]),
    o = sum(ss*no.x.p[3]))
}

Amat=function(x=NA, exclose=1, ran.eff=0){
  #calculate hatching for no exclosure
  no.np <- nest(x=x, exclose=0, ran.eff=ran.eff)
  #calculate hatching for exclosures
  yes.np <- nest(x=x, exclose=exclose, ran.eff=ran.eff)
  p=lapply(x, invlogit)
  with(p, {
    h.tilda = with(as.list(yes.np), {(h + (o*r2*h + a*(1-m)*r2*h) + o*r2*(o*r3*h + a*(1-
m)*r3*h) + a*(1-m)*r2*(o*r3*h+a*(1-m)*r3*h))})
    phi.m.tilda = with(as.list(no.np), {1 - c(y.s, y.t)*(a*m+a*(1-m)*r2*(a*m+a*(1-
m)*r3*a*m))})
    phi.m.tilda.ex = with(as.list(yes.np), {1 - c(y.s, y.t)*(a*m+a*(1-m)*r2*(a*m+a*(1-
m)*r3*a*m))})
    phi.b=(phi.a)^(1/6)
    phi.0=phi.b/phi.m.tilda
    phi.breed.ex = phi.0*phi.m.tilda.ex
    phi.adult=phi.breed.ex[2]*(phi.a)^(5/6)
    phi.juv=phi.breed.ex[1]*(phi.jw*f)^(5/6)
    matrix(c(phi.juv*f*y.s*2*E*h.tilda,phi.juv,phi.adult*y.t*2*E*h.tilda,phi.adult), 2,2)
  })
}

#####
#####
## Function to calculate Value of Information
evpi=function(x,y){
  ##First value under certainty
  vuc=mean(apply(data.frame(x,y),1,max))
  ##Second, value at mean
  emv=max(c(mean(x),mean(y)))
  evpi=vuc - emv
  return(list(evpi,vuc,emv))}
#####
#####

#####
#####
## Functions to calculate sensitivity and elasticity
## sens0 is sensitivity on low-level parameters in Amat, parms[1:6], h.tilda.
## used numerical derivative of max(eigen(Amat)$values) = numerical eigen value, does not
use derivative of Amat and left and right eigen vectors
## sen1 is on cumlogodds scale

```

```

##      sensity on cumlogodds is hard to interpret so ...
## sens2 is on probability scale, with daily nest effects ab = loss due to abandonment, ot=loss
## due to other,
##      enclosure effect is defined as probability difference, see below
## exclose is an indicator for enclosure use
## ran.eff is the value (in unit of standard deviation) of the random effect, default is ran.eff=0,
## the mean
sens0=function(parms=NA){ #sensitive of Amat based base on higher-level parameters,
  parms[1:6, h.tilda] on probability scale
  require("numDeriv")
  lam=function(x){
    Amat = with(as.list(x),
  {matrix(c(phi.jw*f*y.s*2*E*h.tilda,phi.jw*f,phi.a*y.t*2*E*h.tilda,phi.a), 2,2)})
    return(lambda(Amat))
  }
  xx=as.list(nest(parms))
  h.tilda =with(parms, {with(xx,
    {(h + (o*r2*h + a*(1-m)*r2*h) + o*r2*(o*r3*h + a*(1-m)*r3*h) + a*(1-
m)*r2*(o*r3*h+a*(1-m)*r3*h)}}))
  pars=c(invlogit(unlist(parms[1:6])),h.tilda=h.tilda)
  sen <- grad(lam, x=pars)
  names(sen) <- names(pars)
  ela=sen*(pars/lam(pars))
  names(ela) <- names(pars)
  return(list(sensitivity=sen,elasticity=ela,parameters=pars, lambda=lam(pars)))
}
sens1=function(parms=NA, exclose=1, ran.eff=0){
  require("numDeriv")
  lam=function(vec.pars=NA, exclose=0, ran.eff=0){ #named vector, names must
correspond to list Amat, last four entries are ab[1], ab[2], ot[1], ot[2]
  list.par=as.list(vec.pars[1:9])
  list.par$ab=c(vec.pars[10:11])
  list.par$ot=c(vec.pars[12], vec.pars[13])
  M=Amat(x=list.par, exclose=exclose, ran.eff=ran.eff)
  return(lambda(M))
}
  pars=unlist(parms)[1:13]
  sen <- grad(lam, x=pars, exclose=exclose, ran.eff=ran.eff)
  names(sen) <- names(pars)
  ela=sen*(pars/lam(pars))
  names(ela) <- names(pars)
  return(list(sensitivity=sen,elasticity=ela,parameters=pars, lambda=lam(pars)))
}
sens2=function(parms=NA, exclose=1, ran.eff=0){
  require("numDeriv")

```

```

lam=function(vec.pars=NA, exclose=0, ran.eff=0){      #named vector, names must
correspond to list Amat, last four entries are ab[1], ab[2], ot[1], ot[2]
  list.par=as.list(logodds(vec.pars[1:9]))
  bb0=cumodds(list(vec.pars[10],vec.pars[12]))
  bb1=cumodds(list(sum(vec.pars[10:11]),sum(vec.pars[12:13])))
  list.par$ab=c(bb0[[1]],bb1[[1]]-bb0[[1]])
  list.par$ot=c(bb0[[2]],bb1[[2]]-bb0[[2]])
  M=Amat(x=list.par, exclose=exclose, ran.eff=ran.eff)
  return(lambda(M))
}
aa0=icumlogit(list(parms$ab[-2],parms$ot[-2]))
aa1=icumlogit(list(parms$ab,parms$ot))
bb=c(aa0[[1]],aa1[[1]]-aa0[[1]],aa0[[2]],aa1[[2]]-aa0[[2]])
pars=c(invlogit(unlist(parms)[1:9]),bb)
names(pars) <- names(unlist(parms))
sen <- grad(lam, x=pars, exclose=exclose, ran.eff=ran.eff)
names(sen) <- names(pars)
ela=sen*(pars/lam(pars))
names(ela) <- names(pars)
return(list(sensitivity=sen,elasticity=ela,parameters=pars, lambda=lam(pars)))
}

###
#####
#####
##Build loop through parameters
##Background parameters
parms=list(
  #FOR NO EXCLOSURE
  E =logodds(0.9375),          #logodds of p, where p is pr(eggs hatched), expected
number of hatchs is 4*logodds(p)
  phi.a = logodds(0.74),      #adult survival, NO EXCLOSURE
  phi.jw = logodds(0.53),#juvenile survival post-fledge to next 1 year old
  f = logodds(0.4),          #suival from hatch to fledge
  y.s = logodds(0.68),       #probability second-year bird nests
  y.t = logodds(0.9999),     #probability third-year bird nests
  r2 = logodds(0.7),         # renest second attempt
  r3 = logodds(0.7),         # renesting third nest
  m = logodds(0.75),         # pr(adult mortality after abandonment)
  ab = c(-6.1465, 0.3785),   # pr(nest fate = abandoned), log odds scale
  ot = c(-3.5814, -1.7006)   # pr(nest fate = other), logodds scale
)
sd.parms=list(
  #sd of parmaters on logodds scale
  E =0,                      #logodds of p, where p is pr(eggs hatched), expected number of hatchs is
4*logodds(p)
  phi.a = abs(logodds(0.74)*0.1), #adult survival, NO EXCLOSURE
  phi.jw = abs(logodds(0.53)*0.1),#juvenile survival post-fledge to next 1 year old

```

```

f = abs(logodds(0.4)*0.06),          #suival from hatch to fledge
y.s = abs(logodds(0.68)*0.1),      #probability second-year bird nests
y.t = 0,                            #probability third-year bird nests
r2 = abs(logodds(0.7)*0.1),        # renest second attempt
r3 = abs(logodds(0.7)*0.1),        # renesting third nest
m = abs(logodds(0.75)*1.59),       # pr(adult mortality after abondonment)
sigma.ab=matrix(c(0.1432,-0.1432,-0.1432,0.1818),2,2), #Covariance matrix
sigma.ot=matrix(c(0.0357,-0.0125,-0.0125,0.0295),2,2), #Covariance matrix
sd.re = 0.9829
)

Num=30000
results=array(NA, dim=c(3,2,3,Num))
fledge = c(0.2,0.4,0.6)
exclosure = c(0,1)
raneff = c(-2, 0, 2)
for(ii in 1:length(fledge)){
  for(jj in 1:2){
    for(kk in 1:length(raneff)){

lam=rep(NA,Num)
for(i in 1:Num){
samples=list(
  E = rnorm(1,parms$E,sd.parms$E),
  phi.a = rnorm(1,parms$phi.a,sd.parms$phi.a),
  phi.jw = rnorm(1,parms$phi.jw,sd.parms$phi.jw),
  f = rnorm(1,logodds(fledge[ii]),abs(logodds(fledge[ii])*0.06)),          #suival from hatch
to fledge
  y.s = rnorm(1,parms$y.s,sd.parms$y.s), #probability second-year bird nests
  y.t = rnorm(1,parms$y.t,sd.parms$y.t), #probability third-year bird nests
  r2 = rnorm(1,parms$r2,sd.parms$r2),          # renest second attempt
  r3 = rnorm(1,parms$r3,sd.parms$r3),          # renesting third nest
  m = rnorm(1,parms$m,sd.parms$m),          # pr(adult mortality after abondonment)
  ab = mvrnorm(1, mu=c(parms$ab[1], parms$ab[2]), Sigma=sd.parms$sigma.ab),
  ot = mvrnorm(1, mu=c(parms$ot[1], parms$ot[2]), Sigma=sd.parms$sigma.ot),
  raneff = rnorm(1,0,sd.parms$sd.re)
)

A=Amat(x=samples, exclose=exclosure[jj], ran.eff=raneff[kk]*sd.parms$sd.re)
lam[i]=lambda(A)
}
results[ii,jj,kk,]=lam
}}}}

###Plot histograms

```

```

hist(results[2,2,2,], xlim=c(0.75,1.25), xlab="Lambda", main="Average site and year",
col=gray(0.5))
hist(results[2,1,2,], density=20, add=TRUE)
text(x=0.75,y=230, adj=0, paste("Pr(Lambda>1)= ",round(pval(results[2,1,2,],4)))
text(x=1.05,y=200, adj=0, paste("Pr(Lambda>1)= ",round(pval(results[2,2,2,],4)))
legend("topright", legend=c("Exclosure", "No Exclosure"), pch=c(22,22), pt.bg=c(gray(0.5),0),
pt.cex=2)

#make plot
x11()
ci.lam=apply(results,c(1,2,3), quantile, probs=c(0.025, 0.5, 0.975))
x=c(-2,0,2)
f=2 #fledge = 0.4
plot(x-0.05,ci.lam[2,f,2,], pch=16, col=1, xlab="Random Effect", ylab="Lambda", xlim=c(-2.1,
2.1), ylim=c(0.5,1.5))
lines(x-0.05,ci.lam[2,f,2,], col=1)
arrows(x0=x-0.05,x1=x-0.05,y0=ci.lam[1,f,2,],y1=ci.lam[3,f,2,], code=3, length=0.05, angle=90)
points(x+0.05,ci.lam[2,f,1,], pch=22, col=1)
lines(x+0.05,ci.lam[2,f,1,], lty=2, col=1)
arrows(x0=x+0.05,x1=x+0.05,y0=ci.lam[1,f,1,],y1=ci.lam[3,f,1,], code=3, length=0.05,
angle=90)
legend("topright", legend=c("Exclosure", "No Exclosure"), pch=c(16,22), lty=c(1,2))
text(x=-2,y=0.5, label="Good")
text(x=2,y=0.5, label="Bad")
f=1 #fledge = 0.2
points(x-0.05,ci.lam[2,f,2,], pch=16, col=2)
lines(x-0.05,ci.lam[2,f,2,], col=2)
#arrows(x0=x-0.05,x1=x-0.05,y0=ci.lam[1,f,2,],y1=ci.lam[3,f,2,], code=3, length=0.05,
angle=90)
points(x+0.05,ci.lam[2,f,1,], pch=22, col=2)
lines(x+0.05,ci.lam[2,f,1,], lty=2, col=2)
#arrows(x0=x+0.05,x1=x+0.05,y0=ci.lam[1,f,1,],y1=ci.lam[3,f,1,], code=3, length=0.05,
angle=90)
f=3 #fledge = 0.6
points(x-0.05,ci.lam[2,f,2,], pch=16, col=3)
lines(x-0.05,ci.lam[2,f,2,], col=3)
#arrows(x0=x-0.05,x1=x-0.05,y0=ci.lam[1,f,2,],y1=ci.lam[3,f,2,], code=3, length=0.05,
angle=90)
points(x+0.05,ci.lam[2,f,1,], pch=22, col=3)
lines(x+0.05,ci.lam[2,f,1,], lty=2, col=3)
#arrows(x0=x+0.05,x1=x+0.05,y0=ci.lam[1,f,1,],y1=ci.lam[3,f,1,], code=3, length=0.05,
angle=90)
legend("topleft", legend=c("f = 0.2", "f = 0.4", "f = 0.6"), pch=rep(16,3), lty=c(1,1,1),
col=c(2,1,3))

##Calculate EVPI

```

```

voi=matrix(NA, 3,3)
for(ii in 1:length(fledge)){
  for(kk in 1:length(raneff)){
    voi[ii,kk]=evpi(x=results[ii,1,kk,], y=results[ii,2,kk,])[[1]]
  }
}
voi

##Calculate sensitivity on bootstrapped samples
Num=30000
d.sen0=array(NA, dim=c(3,Num,7),
dimnames=list(NULL,NULL,c(names(unlist(parms)[1:6]),"H")))
d.lam0=numeric()
#d.sen2=array(NA, dim=c(3,Num,13), dimnames=list(NULL,NULL,c(names(unlist(parms))))))
#d.lam2=numeric()
for(i in 1:Num){
samples=list(
  E = rnorm(1,parms$E,sd.parms$E),
  phi.a = rnorm(1,parms$phi.a,sd.parms$phi.a),
  phi.jw = rnorm(1,parms$phi.jw,sd.parms$phi.jw),
  f = rnorm(1,parms$f,abs(parms$f*0.06)), #suivival from hatch to fledge
  y.s = rnorm(1,parms$y.s,sd.parms$y.s), #probability second-year bird nests
  y.t = rnorm(1,parms$y.t,sd.parms$y.t), #probability third-year bird nests
  r2 = rnorm(1,parms$r2,sd.parms$r2), # renest second attempt
  r3 = rnorm(1,parms$r3,sd.parms$r3), # reneesting third nest
  m = rnorm(1,parms$m,sd.parms$m), # pr(adult mortality after abandonment)
  ab = mvrnorm(1, mu=c(parms$ab[1], parms$ab[2]), Sigma=sd.parms$sigma.ab),
  ot = mvrnorm(1, mu=c(parms$ot[1], parms$ot[2]), Sigma=sd.parms$sigma.ot)
)
sen0=sens0(parms=samples)
sen2=sens2(parms=samples)
for(j in 1:3){
  d.sen0[j,i,1:7]=sen0[[j]]
  d.lam0[i]=sen0[[4]]
  #d.sen2[j,i,1:13]=sen2[[j]]
  #d.lam2[i]=sen2[[4]]
}
d.sen=d.sen0
d.lam=d.lam0
ci.sen=apply(d.sen,c(1,3), quantile, probs=c(0.025, 0.5, 0.975))
ci.lam=quantile(d.lam, probs=c(0.025, 0.5, 0.975))

##look at regression-based sensitivity, should be same as derivative-based sensitivity if response
is linear
dat=data.frame(lam=d.lam, d.sen[3,,])
lm(lam~phi.a+phi.jw+f+y.s+H, data=dat) #E and y.t do not vary, and h and o are colinear
#standarized covariates,

```

```

st.dat=(d.sen[3,,-
matrix(apply(d.sen[3,,2,mean),Num,dim(d.sen)[3],byrow=TRUE))/matrix(apply(d.sen[3,,2,sd
),Num,dim(d.sen)[3],byrow=TRUE)
dat2=data.frame(lam=d.lam, st.dat)
lm(lam~phi.a+phi.jw+f+y.s+H, data=dat2)

d.sen=d.sen2
d.lam=d.lam2
ci.sen=apply(d.sen,c(1,3), quantile, probs=c(0.025, 0.5, 0.975))
ci.lam=quantile(d.lam, probs=c(0.025, 0.5, 0.975))

##look at regression-based sensitivity, should be same as derivative-based sensitivity if response
is linear
dat=data.frame(lam=d.lam, d.sen[3,,])
lm(lam~phi.a+phi.jw+f+y.s+r2+r3+m+ab1+ab2+ot1+ot2, data=dat)      #E and y.t do not
vary, and h and o are colinear
#standarized covariates,
st.dat=(d.sen[3,,-
matrix(apply(d.sen[3,,2,mean),Num,dim(d.sen)[3],byrow=TRUE))/matrix(apply(d.sen[3,,2,sd
),Num,dim(d.sen)[3],byrow=TRUE)
dat2=data.frame(lam=d.lam, st.dat)
lm(lam~phi.a+phi.jw+f+y.s+r2+r3+m+ab1+ab2+ot1+ot2, data=dat2)

#####
##Calculate EVPI with random effect variation
##but fixed mean fledging rate, only sampling variation here, no random effect variation
##seems r.e. of f should be highly correlated to r.e. for nest success
Num=10000
results2=array(NA, dim=c(3,2,Num))
fledge = c(0.2,0.4,0.6)
exclosure = c(0,1)
for(ii in 1:length(fledge)){
  for(jj in 1:2){

lam=rep(NA,Num)
for(i in 1:Num){
samples=list(
  E = rnorm(1,parms$E,sd.parms$E),
  phi.a = rnorm(1,parms$phi.a,sd.parms$phi.a),
  phi.jw = rnorm(1,parms$phi.jw,sd.parms$phi.jw),
  f = rnorm(1,logodds(fledge[ii]),abs(logodds(fledge[ii])*0.06)),      #suivival from hatch
to fledge
  y.s = rnorm(1,parms$y.s,sd.parms$y.s), #probability second-year bird nests
  y.t = rnorm(1,parms$y.t,sd.parms$y.t), #probability third-year bird nests
  r2 = rnorm(1,parms$r2,sd.parms$r2),      # renest second attempt

```

```

r3 = rnorm(1,parms$r3,sd.parms$r3),          # renesting third nest
m = rnorm(1,parms$m,sd.parms$m),           # pr(adult mortality after abandonment)
ab = mvrnorm(1, mu=c(parms$ab[1], parms$ab[2]), Sigma=sd.parms$sigma.ab),
ot = mvrnorm(1, mu=c(parms$ot[1], parms$ot[2]), Sigma=sd.parms$sigma.ot),
raneff = rnorm(1,0,sd.parms$sd.re)
)

A=Amat(x=samples, exclose=exclosure[jj], ran.eff=samples$raneff)
lam[i]=lambda(A)
}
results2[ii,jj,]=lam
}}
voi=rep(NA, 3)
for(ii in 1:length(fledge)){
  voi[ii]=evpi(x=results2[ii,1,], y=results2[ii,2,])[[1]]
}
voi
##Plot histograms
hist(results2[2,2,], xlim=c(0.5,1.5), xlab="Lambda", main="Average site and year",
col=gray(0.5))
hist(results2[2,1,], density=20, add=TRUE)
text(x=0.75,y=230, adj=0, paste("Pr(Lambda>1)= ",round(pval(results2[2,1,],4)))
text(x=1.05,y=200, adj=0, paste("Pr(Lambda>1)= ",round(pval(results2[2,2,],4)))
legend("topright", legend=c("Exclosure", "No Exclosure"), pch=c(22,22), pt.bg=c(gray(0.5),0),
pt.cex=2)

```