A modeling methodology to evaluate the efficacy of predator exclosures versus predator control

O. C. Stringham[1] & O. J. Robinson[1,2]

1 Graduate Program in Ecology and Evolution, Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA
2 School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, USA

Correspondence

Oliver C. Stringham, Graduate Program in Ecology and Evolution, Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08902, USA.
Email: oliverstringham@gmail.com

Abstract

Predation is seen as the most important source of mortality for many endangered species, including the piping plover. However, predation can be managed through lethal methods, birth control or by excluding predators from nests. Nevertheless, managing a predator population in order to protect a threatened prey population has uncertain outcomes making the monetary expenditures required to manage predators less appealing. We developed a methodology that utilizes a stochastic coupled predator–prey population viability analysis to determine the efficacy of using predator exclosures to protect piping plover nests versus using lethal or birth control measures for one of its principal predators, the red fox. We found that implementing predator exclosures led to slightly higher final abundances of plovers compared with the lethal or birth control of foxes. Moreover, the joint effort of predator control and predator exclosures resulted in considerably higher final plover abundance compared with either option alone. Additionally, there may be situations where certain demographic data about a predator population, such as the population size and age distribution, is not known to the manager. We evaluated the effect these demographics had on the predator control management option chosen. We found that the efficacy of different management options change depending on the starting demographics of the fox population. We emphasize the implementation of this type of model when managing a predator for the sake of prey in order to make informed management decisions that could save money while ensuring better protection of endangered species.

Introduction

Exotic predators, as well as the release of native mesopredators, are a serious threat to the persistence of vulnerable prey species and have contributed to the decline, extirpation and extinction of numerous prey populations (Fritts & Rodda, 1998; Crooks & Soulé, 1999; Blackburn et al., 2004; Salo et al., 2007; Holt et al., 2008; Prugh et al., 2009; Ritchie & Johnson, 2009). While removal of predators makes intuitive sense to increase prey populations, it has had variable outcomes when applied. Several studies have found that the removal of predators was successful at increasing their avian prey (e.g. Tapper, Potts & Brockless, 1996; Harding, Doak & Albertson, 2001), including a meta-analysis of 83 published papers (Smith et al., 2010). In contrast, several other studies found predator removal to be ineffective (e.g. Keedwell, Maloney & Murray, 2002; Bodey et al., 2011; Moseby & Hill, 2011; Walsh et al., 2012). Birth control as a management technique can similarly have variable outcomes (e.g. Caughley, Pech & Grice, 1992; Pech

et al., 1997; Twigg et al., 2000; Saunders, Gentle & Dickman, 2010).

Besides management of prey through predator removal/birth control, sometimes, management can reduce predation rates, with varying degrees of success, by building predator exclosures (e.g. LaGrange et al., 1995; Estelle, Mabee & Farmer, 1996; Murphy et al., 2003; Neuman et al., 2004; Ivan & Murphy, 2005; Maslo & Lockwood, 2009; Smith et al., 2013; Dinsmore et al., 2014). From a wildlife conservation and management perspective, it is beneficial to be able to determine the efficacy of both types of predator management independently, as well as conjointly, in relation to prey abundance and persistence, before management is enacted.

The management of predators is often quantitatively determined using population models such as population viability analysis (PVA; e.g. Harding et al., 2001). Often, PVAs utilize vital rate matrices and population vectors to project population change into the future (Reed et al., 2002). While the need to manage predators for the sake of

prey is widespread, few studies have modeled the predator–prey interaction explicitly (Sabo, 2008).

Robinson, Fefferman & Lockwood (2013) recently introduced a relatively simple way to model predator–prey interactions linked via a functional response in a coupled stochastic population model. This model explores how management of a predator population will affect prey abundance and persistence, through the use of perturbation analysis on specified vital rate(s). Here, we develop a modeling methodology to determine the efficacy of predator control and predator exclosures for piping plovers (*Charadrius melodus*) nesting along the New Jersey shore.

The piping plover is a small shorebird that inhabits oceanic beaches and barrier islands and is endangered in the state of New Jersey with 121 nesting pairs as of 2012 (Pover & Davis, 2012). They nest on bare sand and face threats from predators such as the red fox (*Vulpes vulpes*), other mammals and human activities (Maslo & Lockwood, 2009; Doherty & Heath, 2011; Pover & Davis, 2012). The establishment of predator exclosures has been successful at increasing nest success (Larson, Ryan & Murphy, 2002; Maslo & Lockwood, 2009). But, state and federal managers also utilize lethal control of foxes, via culling adults and den fumigation, on barrier beaches near piping plover nesting grounds.

We utilize the predator–prey population model in Robinson *et al.* (2013) to simulate realistic changes in predator and prey vital rates that accompany lethal control and/or predator exclosures. We then determine the efficacy of each management option, independently and conjointly, by comparing the persistence and abundance of the final piping plover population. In addition, we perform a separate analysis to demonstrate the possible effects that a decrease in adult survival accompanied with the use of predator exclosures can have on plover viability.

We also explore, when predator management for the sake of prey is needed, how an initial unknown predator population size and age distribution will affect the management option chosen as most efficient. This question can yield important information about the relationship between different predator demographics and the type of management needed to ensure the persistence of their native prey. These parameters have been shown to affect the management option chosen in a single-species PVA (Reed, Fefferman & Averill-Murray, 2009) and for that reason we investigate if it has similar results for a predator–prey multispecies PVA.

Materials and methods

Coupled predator–prey model

Following Robinson *et al.* (2013), we created a coupled predator–prey model based on piping plover and red fox life stage information. The red fox female-based, age-structured, post-breeding census, vital rate matrix, with a projection interval of 1 year, was defined as:

$$A_C = \begin{matrix} F_1 & F_2 & F_3 & F_4 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & S_4 \end{matrix} \qquad (1a)$$

where F and S are the fecundity and the 1-year survival, respectively, of specified age classes for red foxes (C), with subscripts 1, 2, 3 and 4 that correspond to the first, second, third and fourth age classes, respectively. For the piping plover, we utilized a stage-structured, post-breeding census, vital rate matrix, with a projection interval of 2 months defined as:

$$A_N = \begin{matrix} 0 & 0 & 0 & 0 & 0 & F_{juv} & 0 & 0 & 0 & 0 & 0 & F_{ad} \\ S_{nest} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{juv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{juv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{juv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{juv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{juv} & 0 & 0 & 0 & 0 & 0 & S_{ad} \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{ad} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{ad} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{ad} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{ad} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{ad} & 0 \end{matrix}$$
$$(1b)$$

where F and S are the fecundity and the 2-month survival of specified stages with subscripts nest, juv and ad, that correspond to the nest, juvenile and adult stage class of the piping plover (N), respectively.

We projected the piping plover matrix six times to simulate 1 year, with one projection given by:

$$\bar{N}_{(t_{m+2})} = A_N \times \bar{N}_{t_m} \qquad (2a)$$

where m represents a given numerical value for a month and t represents a given year. We allowed the red fox matrix to project once, which simulated 1 year, given by:

$$\bar{C}_{(t+1)} = A_C \times \bar{C}_t \qquad (2b)$$

$\bar{N}_{t_m}$ and $\bar{C}_t$ are the female population vectors that represent the number of piping plovers and red foxes of each stage/age class at the specified time. We started the model directly after the plover breeding season and thus placed the number of juveniles in the second row of the population vector and number of adults in the eighth row. We allowed the model to continue 10 years, which is considered to be an appropriate time frame, in relation to the generation times of plovers and foxes, to enable a rapid managerial response (Wilcox, 1959; Ables, 1975).

The red fox, a generalist predator, interacted with the piping plover population via a type-III functional response

(Holling, 1959; Pech *et al.*, 1992) according to the following equations:

$$N_{\text{nest}_{t_{m+2}}} - [C_4 + C_3 + C_2 + P_{\text{eat}} + (C_1)] \left(\frac{k_2 N^2_{\text{nest}_{t_m}}}{D_2^2 + N^2_{\text{nest}_{t_m}}} \right) = N_{\text{nest}_{\text{remain}}}$$

(3a)

$$N_{\text{juv}_{t_{m+2}}} - [C_4 + C_3 + C_2 + P_{\text{eat}} + (C_1)] \left(\frac{k_2 N^2_{\text{juv}_{t_m}}}{D_2^2 + N^2_{\text{juv}_{t_m}}} \right) = N_{\text{juv}_{\text{remain}}}$$

(3b)

$$N_{\text{ad}_{t_{m+2}}} - [C_4 + C_3 + C_2 + P_{\text{eat}} + (C_1)] \left(\frac{k_3 N^2_{\text{ad}_{t_m}}}{D_3^2 + N^2_{\text{ad}_{t_m}}} \right) = N_{\text{ad}_{\text{remain}}}$$

(3c)

P_{eat} is the percentage of plovers eaten by the first age class of foxes relative to the older age classes, k is the maximum feeding rate (also defined as $1/h$, where h is handling time) for foxes feeding on plovers of the specified age class. D is the half saturation constant, which is the point at which the feeding rate is half the maximum (also defined as $1/\alpha h$ where α is the capture efficiency).

We multiplied the functional response by the total number of predators feeding on prey to determine the number of prey in each class consumed. We subtracted this from N_{nest}, N_{juv} and N_{ad} to obtain the number of prey remaining in each stage after the predation event. The values $N_{\text{nest}_{\text{remain}}}$, $N_{\text{juv}_{\text{remain}}}$ and $N_{\text{ad}_{\text{remain}}}$ are the number of newborn, juvenile and adult piping plovers remaining after the predation event, which occurred once per year and coincided with the breeding season for the piping plover. We used this population vector to project the plover population into the next time step.

We ran 5000 realizations for each model scenario. In each realization, we drew the values for fecundity and survival from a normal and beta distribution, respectively, to address the variation in vital rate values that occurs between years. We defined the probability of extinction as the number of realizations the piping plover population reached zero divided by the total number of realizations performed. When analyzing the results of the model, we only considered plover adults, N_{ad}, in the final population size.

Parameter estimation

All parameters used in the model and their values are listed in Table 1. We calculated the red fox vital rates and coefficients of variation by taking the sample size-weighted averages of eight different studies on red foxes (Englund, 1970; Pils & Martin, 1978; Harris, 1979; Nelson & Chapman, 1982; Harris & Smith, 1987; Marlow *et al.*, 2000; McIlroy, Saunders & Hinds, 2001; Saunders *et al.*, 2002; data compiled by Devenish-Nelson *et al.*, 2013). We considered fecundity to be maternity (number of female kits born; equal sex ratio assumed) multiplied by the survival of the specified age class reproducing (Devenish-Nelson *et al.*, 2013). We included a fecundity value for the first age class because female foxes are able to reproduce at around 10 months old (Englund, 1970). For functional response parameter estimation and values, refer to Supporting Information Appendix S1.

For piping plovers, we considered the survival probability of an individual in the nest stage, S_{nest}, to be the product of survival of eggs to hatchlings and survival of hatchlings to fledglings (Mayfield, 1961), which is a duration of approximately 2 months. Juvenile and adult plover survival reflected the Atlantic coast population vital rates, which was provided from the literature (Melvin & Gibbs, 1994; Plissner & Haig, 2000). As the juvenile stage lasts 10 months (from fledgling to adult), we evaluated the fifth root of juvenile survival to obtain the 2-month juvenile survival, S_{juv} (equal to the projection interval). Similarly, we evaluated the sixth root of the 1-year adult survival, to obtain the 2-month adult survival, S_{ad}. We considered fecundity to be maternity (number of female eggs produced; equal sex ratio assumed) multiplied by the survival probability of the specified stage reproducing and assumed that juveniles reproduced at half the maternity of adults.

Table 1 List of parameter values and their coefficients of variation (CV)

Red fox				Piping plover			
Parameter	Value[a]	CV	Source	Parameter	Value[a]	CV	Source
F_1	0.506	0.092	a–h	F_{ad}	1.275	0.512	k
F_2	0.876	0.111	a–h	F_{juv}	0.417	0.512	k
F_3	1.422	0.124	a–h	S_{nest}[bc]	0.226	0.122	l, j
F_4	0.976	0.126	a–h		0.279	0.077	l, j
S_1	0.404	0.049	a–h	S_{juv}[b]	0.865	0.209	m, n
S_2	0.532	0.063	a–h	S_{ad}[b]	0.951	0.109	m, n
S_3	0.576	0.073	a–h	Initial N_{juv}	44	–	i
S_4	0.536	0.066	a–h	Initial N_{ad}	121	–	i

[a]See methods for calculation. [b]Represents 2 month survival probability. [c]Value used depends on model scenario; (a) Saunders *et al.* (2002); (b) McIlroy *et al.* (2001); (c) Marlow *et al.* (2000); (d) Harris & Smith (1987); (e) Harris, 1979; (f) Englund (1970); (g) Pils & Martin (1978); (h) Nelson & Chapman (1982); (i) Pover & Davis (2012); (j) T. Pover, Conserve Wildlife Foundation of NJ, pers. comm.; (k) Burger (1987); (l) Maslo & Lockwood (2009); (m) Melvin & Gibbs (1994); (n) Plissner & Haig (2000).

No reliable source for the number of foxes and their age distribution for New Jersey beaches could be found in the literature or from government organizations. However, as an initial assumption, we set the current fox population to be at a stable age distribution (SAD). Lethal control of foxes takes two forms: den fumigation, which results in fewer newborns (first age class) and shooting or lethal baiting, which results in fewer adults (second, third and fourth age class) (Saunders et al., 2010). Also, sterilization targets adults, but results in fewer newborn foxes. Therefore, if practiced by managers, den fumigation and/or sterilization may skew the age distribution towards having more adults compared with a SAD. Thus, to properly explore the effects of a different initial age distribution on the management option chosen, we also tested an adult biased distribution (ABD). We calculated a low and high estimate of 26 and 47 female foxes (equal sex ratio assumed), respectively, for the initial population size of foxes (for procedure, refer to Supporting Information Appendix S2).

Model implementation

In place of sensitivity or elasticity analysis, we utilized a vital rate sensitivity analysis (VRSA; Fefferman & Reed, 2006) in order to determine the efficiency each management option. Unlike VRSA, sensitivity/elasticity analysis conventionally assume a stable age distribution (Citta & Mills, 1999; Heppell, Caswell & Crowder, 2000), which is unlikely to be the case for populations where one or more age class is being actively managed (Koons et al., 2005). In addition, VRSA can apply any incremental change to vital rates, is valid over short periods of management, and can be used to compare the effects management options that target more than one vital rate, all of which are not possible in a sensitivity/ elasticity analysis (Fefferman & Reed, 2006).

We increased piping plover S_{nest}, the survival probability of an individual in the nest age stage, to simulate an increase in the use predator exclosures. Currently, 75% of plover nests have predator exclosures (T. Pover, Conserve Wildlife Foundation of NJ, pers. comm.), which we considered the model baseline. We modeled an increase to 95% of plover nests exclosed, where a linear relationship between exclosures and survival was assumed.

We examined five different predator management options: (1) sterilization, simulated by a decrease in fox fecundity (F_1, F_2, F_3, F_4); (2) culling/removal of newborns, simulated by a decrease in newborn fox survival (S_1); (3) culling/removal of adults, simulated by a decrease in adult fox survival (S_2, S_3, S_4); (4) culling/removal of newborns and adults, simulated by a decrease in all fox survival (S_1, S_2, S_3, S_4); and (5) a 'do nothing' (baseline) management option. We assumed that for each management option, the vital rate(s) managed for did not alter the value of non-target vital rates. We allowed multiple vital rates to be simultaneously reduced because, aside from the first age class, it is difficult to distinguish between the adult age classes of foxes and therefore will be targeted indiscriminately by managers. We accomplished this simulation by perturbing each vital rate(s) corresponding to the management actions above by 50% in each time step, except for the 'do nothing' management option where we did not change any vital rates. We stress that this degree of perturbation is not universally constant for all predator populations and may need to be adjusted depending on factors such as the population size, area and costs. Given the small population size of foxes in this system (see earlier), restrictive target area of inhabitance (shoreline of New Jersey) and availability of money for management (implied from existence of current management methods), we conclude that 50% perturbation is a conservative estimate for this system.

We evaluated the efficacy of predator exclosures versus predator management by allowing the model to run with increased plover S_{nest} and no change to fox vital rates. Then, we ran the model to examine the five different predator management options without change to plover S_{nest}. We compared the option that resulted in the highest plover persistence/abundance with the results from the increase in predator exclosures to determine the degree to which each was effective (Fig. 1). To evaluate the efficacy of both predator control and exclosures in conjunction, we ran the model with increased plover S_{nest} and implemented the five different predator management options. To evaluate the effects of a decrease in adult survival that may accompany the use of predator exclosures, we decreased plover S_{ad} by 8% during the breeding season (Barber et al., 2010) and increased plover S_{nest}. We tested these scenarios with an initial fox population at high density and SAD.

To evaluate if an unknown initial predator population size and age distribution will affect the management option chosen as the most effective, we developed four different scenarios by varying two different initial parameters: fox population size and age distribution (Fig. 2). Scenarios with an initial SAD represent a predator population that is near
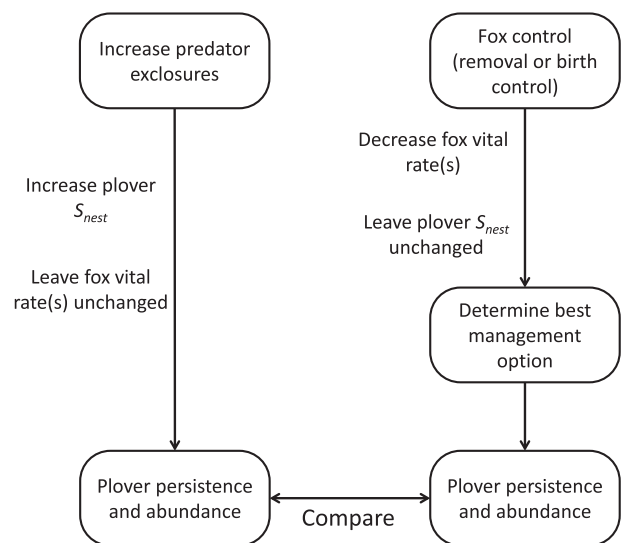
Figure 1 Schematic diagram of methodology used to determine the efficacy of increasing predator exclosures versus red fox control.
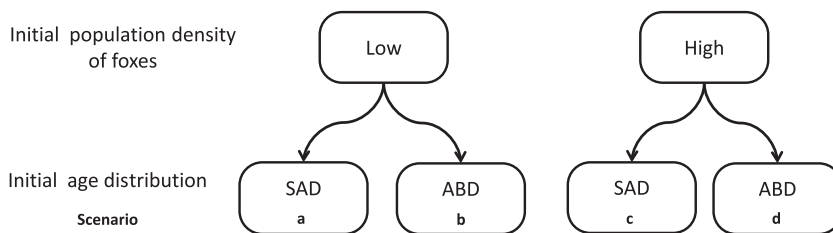
Figure 2 Schematic diagram of model scenarios used to explore the effect initial red fox population size and age distribution have on the management option chosen. SAD refers to a stable age distribution while ABD refers to an adult biased distribution. For the ABD we used a ratio of 0:0.15:0.75:0.10 and for the SAD we used a ratio of 0.61:0.25:0.07:0.07.
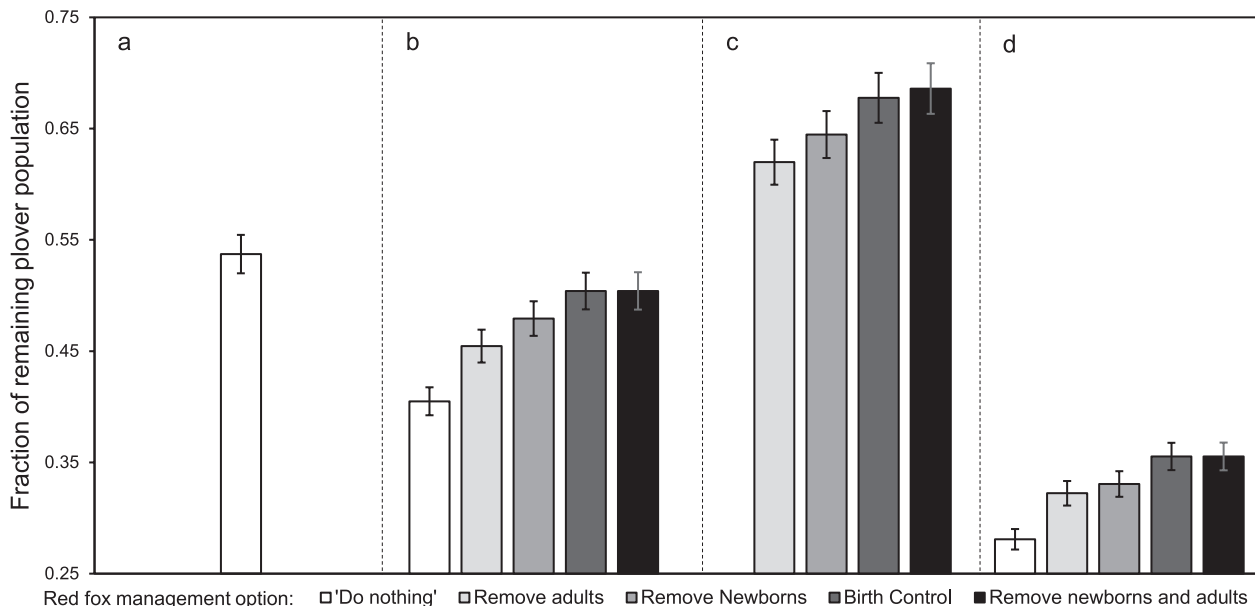
Figure 3 Comparison of increased predator exclosures and red fox control on plover abundance. (a) Simulation of an increase predator exclosures (b) simulation of predator control (c) simulation of both an increase in predator exclosures and use of predator control and (d) simulation of a decrease in adult plover survival accompanied with an increase in predator exclosures. In mentioned fox management options, vital rate(s) were reduced by 50%, except for 'Do nothing' where no vital rates were decreased. Increasing the use of predator exclosures was modeled as a 19% increase in S_{nest} for plovers. Decreasing adult survival that may accompany predator exclosures was modeled as an 8% decrease in S_{ad} during the breeding season. Error bars represent 95% confidence interval around the mean value.

equilibrium in terms of deaths and birth rates across age groups, while scenarios with an initial ABD represent a predator population where there are far fewer young age classes than older ones because of the effects of age-specific culling or drops in fecundity because of the effects of sterilization.

We defined the most effective fox management option to be the one that resulted in the highest final plover abundance. In addition, we evaluated if sub-best management options differed in their efficacy compared with the best management option for each scenario by calculating the percent error between the final plover abundance of sub-best management options and the best management option. All calculations were performed using the software package MATLAB (Mathworks, 2013).

Results

For all scenarios, piping plover probability of extinction over 10 years was < 1%. Despite this low probability of extinction, all model scenarios resulted in a decline in plover abundance even when management was implemented (Fig. 3). Therefore, we focused on the final adult population size as a basis of comparison.

The efficacy of increased predator exclosures was slightly higher compared with the effects of predator control (Fig. 3a and 3b). Increasing predator exclosures resulted in plover abundance that was, on average, 55% of their initial abundance (Fig. 3a). Removal of newborns and adults resulted in 52% of the initial number of plovers while sterilization resulted in 51%. The sub-best management predator
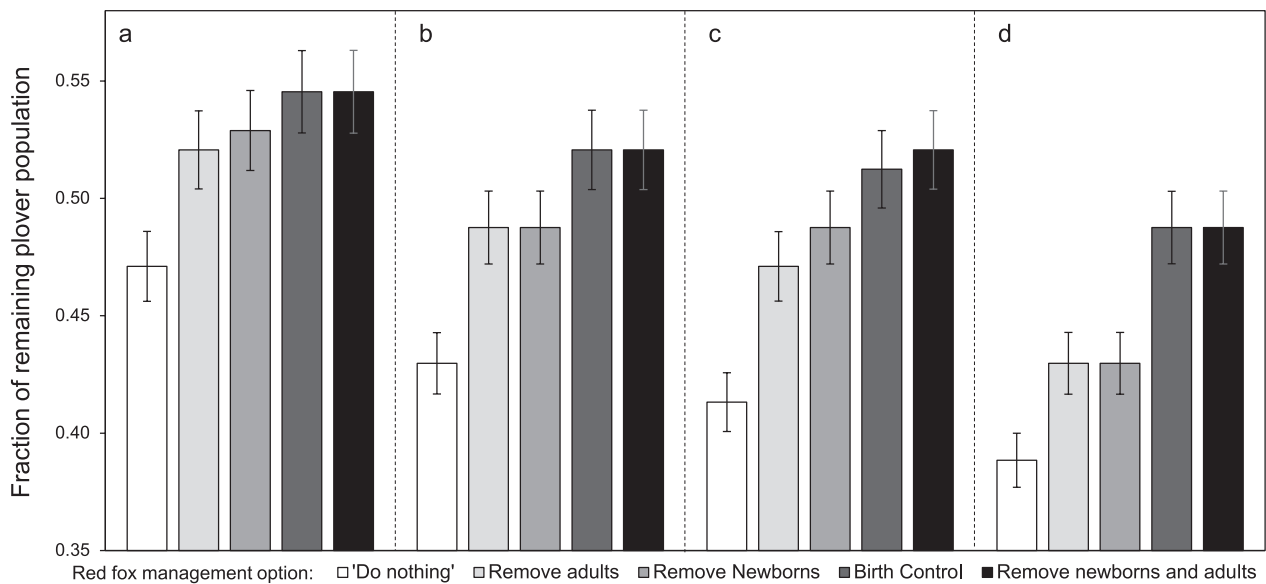
Figure 4 Final adult piping plover population size from different model scenarios. (a) Initial low red fox density at a stable age distribution (SAD); (b) initial low red fox density at an adult biased distribution (ABD); (c) initial high red fox density at SAD; and (d) initial high red fox density at ABD. Error bars represent 95% confidence interval around the mean value.

control options were: removal of newborns (49% of the initial number of plovers), removal of adults (47% of the initial number of plovers) and lastly the 'do nothing' option (41% of the initial number of plovers; Fig. 3b). The efficacy of both predator control and predator exclosures together resulted in substantially higher final plover abundances compared with either option alone, where the best predator control option was to remove newborns and adults. This resulted in 70% of the initial number of plover (Fig. 3c).

The efficacy of increased predator exclosures was substantially reduced when accompanied with a decrease in adult plover survival. This resulted in a maximum of 36% of the initial number of plovers (Fig. 3d), which is lower final population size compared with the baseline of not increasing predator exclosures and no predator control.

For all model scenarios, starting age distribution and fox density did not alter the choice of most efficient fox management option, which was to either remove or sterilize newborns and adults (Fig. 4). The efficacy of sub-best management options relative to the most efficient option varied depending on the scenario. With an initial SAD and low fox density, removing newborns resulted in a 3% lower plover population relative to the best management option. On the other hand, in the scenario with an initial ABD and high fox density, removing newborns resulted in a 12% lower plover population compared with the best management option (Fig. 5). A similar result was seen with the third best option to remove adults. Here the plover population difference was lower by 4–12% relative to the best management option.

Discussion

Given the high monetary and ethical costs of implementing any predator management program in order to protect prey

species from extinction, it is vital to have a tool that managers can use to quantify, visualize and compare outcomes of their actions. Here, we use a coupled predator–prey model to explore whether increasing the use of predator exclosures for the conservation of the endangered piping plover or controlling its main predator, the red fox, results in a higher abundance/persistence for the piping plover. We found increasing nest survival, via predator exclosures, results in slightly higher final plover abundance compared with removing adult and newborn foxes or reducing their fecundity. In addition, the joint effort of predator control and predator exclosures resulted in substantially higher final plover abundance compared with either option alone. The resulting decision that a manager may take would likely hinge on the associated ethical or monetary costs associated with each option.

In practice, the eradication of a predator poses additional management challenges because it may not completely alleviate predation pressure on a threatened prey species. Such a scenario occurs when there are compensatory shifts in predator dynamics, where other predator species take the place of the one removed (Ellis-Felege *et al.*, 2012). Our model assumes that no compensatory shifts occur. This assumption is open to criticism in relation to predators on piping plovers in New Jersey as many other predator species inhabit these beaches and they may compensate for the loss of foxes via either numerical rises in abundance or their increased use of plovers as prey items. If compensation were to occur, these results may not be accurate.

There is also indication that while nest exclosures increase nest success, they also can decrease adult survival. This has been observed in several different shorebird species (Neuman *et al.*, 2004; Isaksson, Wallander & Larsson,
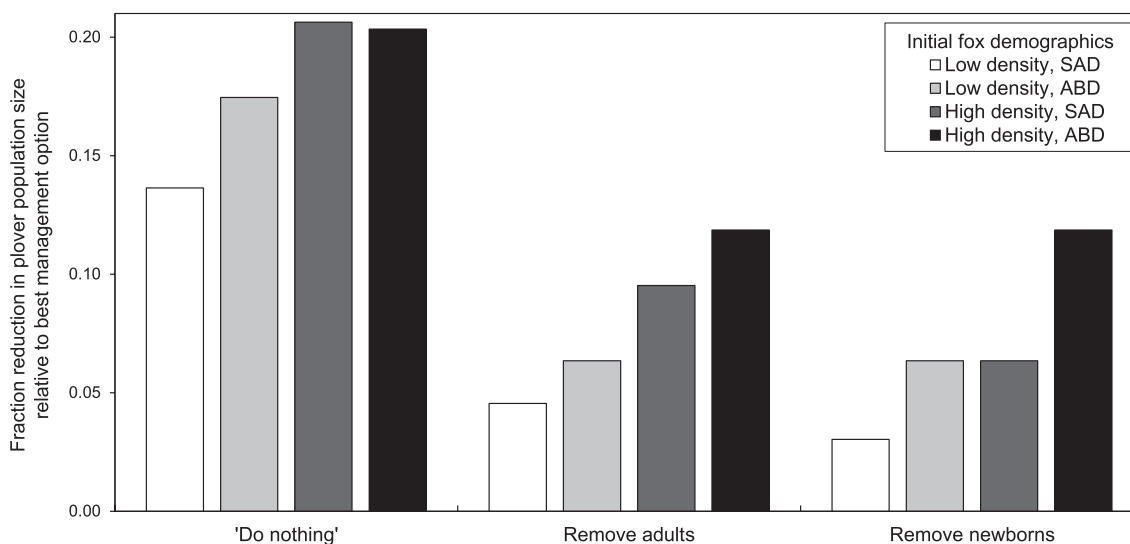
Figure 5 A comparison of the efficiency of sub-best predator management options to the best option. Fraction reduction in plover population size relative to best management option was calculated from the relative error between the best management option and each given sub-best management option.

2007), including a piping plover population at Prince Edward Island, Canada (Barber *et al.*, 2010). We stress that this is not known to happen for the piping plover studied in New Jersey. However, as an illustration about the importance of this type of feedback, we modeled an increase in predator exclosures and an 8% decrease in adult plover survival (Barber *et al.*, 2010). This revealed that using predator exclosures results in a lower abundance of plovers compared with the baseline of not increasing predator exclosures and doing nothing to the predator population. Therefore, it is very important for future models and wildlife managers to better understand the relationship between usage of exclosures and adult survival in the prey population they manage. Additionally, for other systems, the management of one vital rate, for either predator or prey, may affect another vital rate differently than a decrease in adult survival. Our model is flexible to these feedbacks and can incorporate them if deemed necessary.

Wildlife managers will sometimes encounter monetary constraints that may prevent the theoretically most effective management strategy from being implemented (e.g. Engeman *et al.*, 2003; Pascal *et al.*, 2008). In our system, piping plovers benefit from both predator exclosures and predator control, yet a rough estimate places culling red foxes at approximately 13 times more expensive then constructing, installing and maintaining predator exclosures, over a 10-year period (V. Turner, US Fish and Wildlife, pers. comm.). Because of this constraint, it is important to realize that optimal results from models may not be practical to implement.

There may be situations where certain demographic data about a predator population, such as the population size and age distribution, is not known to the manager. This type of information is shown to change the most effective management decision in single-species PVA. Here, we test if this information changes the management decision chosen for a predator species in an explicit predator–prey model. We found that throughout all model scenarios, the most effective fox management option (to remove adults and newborns or sterilization) remained the same. However, the efficacy of other management options in relation to the best option differed depending on the scenario. In situations like this, a manager may choose to opt out of the best management option if the second or third best is almost as effective, but is less costly or presents fewer ethical quandaries. In addition, sometimes the most effective management option may not be possible because of monetary, political or social reasons. Therefore, it is important to understand the outcomes of sub-best management options if the best option is not attainable.

Our results showed that the efficiency of the sub-best management option, to remove newborn foxes, relative to the best management option was diminished when different initial fox demographics were modeled. This possibility highlights the importance of a manager knowing basic demographic information about the predator population they are trying to control. With the simple knowledge of approximate population size and age distribution, the type of model we produce here can help managers make informed decisions about how to manage endangered prey through predator control. Therefore, we urge that managers obtain information about the predator population size and age distribution before acting. As shown here and in other studies (Fefferman & Reed, 2006; Reed *et al.*, 2009; Robinson *et al.*, 2013), these factors provide necessary information for making management decisions.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Methods – estimation of functional response parameters.

Appendix S2. Methods – estimation of initial population size of foxes.