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ABSTRACT

Listing a species under the Endangered Species Act (ESA) and developing a recovery plan requires U.S. Fish and Wildlife Service to establish specific and measurable criteria for delisting. Generally, species are listed because they face (or are perceived to face) elevated risk of extinction due to issues such as habitat loss, invasive species, or other factors. Recovery plans identify recovery criteria that reduce extinction risk to an acceptable level. It logically follows that the recovery criteria, the defined conditions for removing a species from ESA protections, need to be closely related to extinction risk. Extinction probability is a population parameter estimated with a model that uses current demographic information to project the population into the future over a number of replicates, calculating the proportion of replicated populations that go extinct. We simulated extinction probabilities of piping plovers in the Great Plains and estimated the relationship between extinction probability and various demographic parameters. We tested the fit of regression models linking initial abundance, productivity, or population growth rate to extinction risk, and then, using the regression parameter estimates, determined the conditions required to reduce extinction probability to some pre-defined acceptable threshold. Binomial regression models with mean population growth rate and the natural log of initial abundance were the best predictors of extinction probability 50 years into the future. For example, based on our regression models, an initial abundance of approximately 2400 females with an expected mean population growth rate of 1.0 will limit extinction risk for piping plovers in the Great Plains to less than 0.048. Our method provides a straightforward way of developing specific and measurable recovery criteria linked directly to the core issue of extinction risk.

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1. Introduction

The central part of any recovery planning process for endangered or threatened species is to establish criteria for recovery. Under the various endangered species protection laws (e.g., the US Endangered Species Act, the Canadian Species at Risk Act, etc.) the reason endangered species are protected is because of some elevated risk of extinction. When that risk of extinction is somehow reduced, the species is considered recovered and therefore taken off the protected species list (delisted; 16 U.S.C. 1531 et seq.). It logically follows that recovery criteria for a species should somehow be related to eliminating or greatly reducing the risk of extinction (Goodman, 2002). Setting recovery criteria

is a decision in which, minimizing, eliminating or reducing the probability of extinction for the protected species is the fundamental objective of endangered species protection and recovery efforts. However extinction probability itself is not empirically measurable and therefore recovery criteria serve as the means objectives or measurable attributes of the extinction probability fundamental objective. A rational process would first identify a tolerable level of extinction risk for a species, and then use some process to identify measurable quantities that effectively represent extinction risk. Structured decision making (SDM) is an increasingly applied decision analytical approach to complex natural resource decision making and may be well suited to endangered species management (Gregory and Keeney, 2002; Gregory and Long, 2009; McGowan, 2013). In SDM it is imperative to first establish fundamental objectives and then select measurable attributes of those fundamentals that are unambiguous, understandable,

comprehensive, direct, and measurable (Keeney and Gregory, 2005; McGowan, 2013) to improve both the decision making transparency and the likelihood of achieving the fundamental objectives. The measurable attributes of extinction probability should address each of those five criteria; indeed, a thorough structured decision making process to set recovery criteria for a protected species would use the criteria established by Keeney and Gregory (2005) as objectives and also consider other fundamental objectives such as monitoring costs and efficiency. Setting recovery criteria would be a decision process that selects the best measurable attributes that maximizes the precision of the relationship to extinction probability but also minimizes costs and inefficiency.

Extinction probability is derived from a model that projects current conditions into the future, replicates that projection under demographic and environmental stochasticity with ecological and statistical uncertainty, and calculates the proportion of replicates that went extinct (Beissenger and Westphal, 1998; Morris and Doak, 2002). Population projection models (conceptual or quantitative, implicit or explicit) are key components of any effort to manage a species or population (Starfield, 1997). Making effective management decisions requires the ability to make formal predictions about the probable effects of management choices (Starfield, 1997). Measuring extinction probability is impossible with field data alone. However, models that predict extinction can be used to develop surrogate metrics that represent measures of extinction risk. Observation error associated with measuring attributes of recovery criteria further complicates the setting of recovery criteria. Inaccurate measurement could inhibit our ability to detect whether a species is recovered or has gone extinct; it could result in premature or delayed delisting. Recovery criteria should in some way account for imperfect detection either by only using metrics that can be accurately measured or by accounting for observational uncertainty of measurable attributes when setting the recovery criteria.

Piping plovers are a protected species under the U.S. Endangered Species Act (ESA) and the Canadian Species at Risk Act (SARA). Piping plovers are a small, widely distributed, migratory shorebird (Elliott-Smith and Haig, 2004). In the United States there are three separately listed populations, the Atlantic Coast (Threatened), the Great Lakes (Endangered), and the Great Plains (Threatened; U.S. Fish and Wildlife Service, 1985). Piping plovers are listed as endangered throughout Canada (Environment Canada, 2012). In 2010 the U.S. Fish and Wildlife Service (USFWS) convened a new recovery team and initiated an effort to revise the recovery plan for piping plovers in the Great Plains. The previous recovery plan for the Great Plains population was written in 1988 (USFWS, 1988) and new data and research suggested the recovery plan may need to be redrafted. The Great Plains breeding population spends the non-breeding season mainly on beaches, coastal sand flats and marshes of the Gulf Coast in the United States and Mexico (Elliott-Smith and Haig, 2004; Gratto-Trevor et al., 2012). During the breeding season, birds nest on the ground in sand and gravel substrates on river sandbars, reservoir beaches and alkali wetlands (Prindiville Gaines and Ryan, 1988; Lefer et al., 2008; Anteau et al., 2012) from Manitoba, Canada, to eastern Montana and south to Nebraska, Colorado, and rarely in northeastern Kansas, USA (Elliott-Smith and Haig, 2004).

In this paper we present an SDM-rooted, transparent process that uses population projection models and regression analysis of simulated data to directly link recovery criteria (e.g., population abundance targets, demographic parameter targets) to the probability of extinction. Our primary objective is to frame the process of setting recovery criteria as a decision in which the fundamental objective is to maximize the precision of the relationship of the metric to extinction probability. To aid in that framing we present a process for establishing and evaluating the link between

measurable attributes of a population and extinction probability using simulation models and regression analysis of the simulated data. We developed a population projection model for piping plovers in the Great Plains to inform and support the recovery planning process and to link piping plover abundance and other demographic parameters to extinction probability. The model builds on previously published models (Ryan et al., 1993; Plissner and Haig, 2000; Larson et al., 2002; McGowan and Ryan, 2009) and incorporates existing data and expert opinion (i.e., consultation with the recovery team) of population dynamics and meta-population structure in the Great Plains. We used the model to predict the necessary starting population size, spatial distribution, and population growth rate needed to reduce the probability of extinction to a prescribed level. We also assessed how observation error and imprecision can affect recovery criteria. The end result is a set of tables describing the sets of conditions (combinations of initial population size and expected population growth rate) that achieve recovery (reduced extinction risk), akin to an optimal decision table (Williams et al., 2002), under perfect and imperfect observability. Though population viability models have been used in developing recovery criteria previously (e.g., Schultz and Hammond, 2003), to our knowledge, creating a decision table based on varied initial conditions and expected demographic rates is a novel approach for establishing recovery criteria. Furthermore, while extinction probability has been linked to initial population conditions and input demographic parameters (e.g., Lande and Orzack, 1988), establishing the measurable attributes of recovery criteria directly quantitatively linked to extinction probability has rarely, if ever, been carried out. Here, we are presenting a method to utilize these relationships in the decision making contexts of establishing recovery criteria and delisting a species.

2. Methods

All projection models and analyses of simulated data were developed and executed in program R (R core development team, 2011). Our process was initiated through consultation with the piping plover Northern Great Plains recovery team, which consisted of representatives from State or Federal wildlife or management (e.g., Nebraska Game and Parks Commission, the U.S. Army Corps of Engineers) agencies. The team provided species and management expertise and we relied on their input to ensure that the model we developed was ecologically and management relevant.

The model we developed included spatial structure that divided the northern Great Plains into four breeding/management regions: Southern Rivers (primarily the Platte River and Missouri River in southern South Dakota and along the Nebraska-South Dakota border), Northern Rivers (the Missouri River and its constructed reservoirs in central South Dakota north through North Dakota and Montana), alkali wetlands (i.e., along the Missouri Coteau in North Dakota and Montana), and Prairie Canada (all river, reservoir and wetland habitats in Prairie Canada; Fig. 1). The model included limited exchange of individuals between the breeding regions and can be considered a meta-population model (Hanski, 1994). These divisions of the breeding range were supported by the available banding data (see below) from multiple studies in the Great Plains. In addition to reflecting suspected regional boundaries between breeding populations, these sub-population units would likely have differing reproductive rates, different limiting factors, and would therefore require potentially different management strategies. That is, the management actions could be differentially effective among regions given the variation in ecological and physical processes.
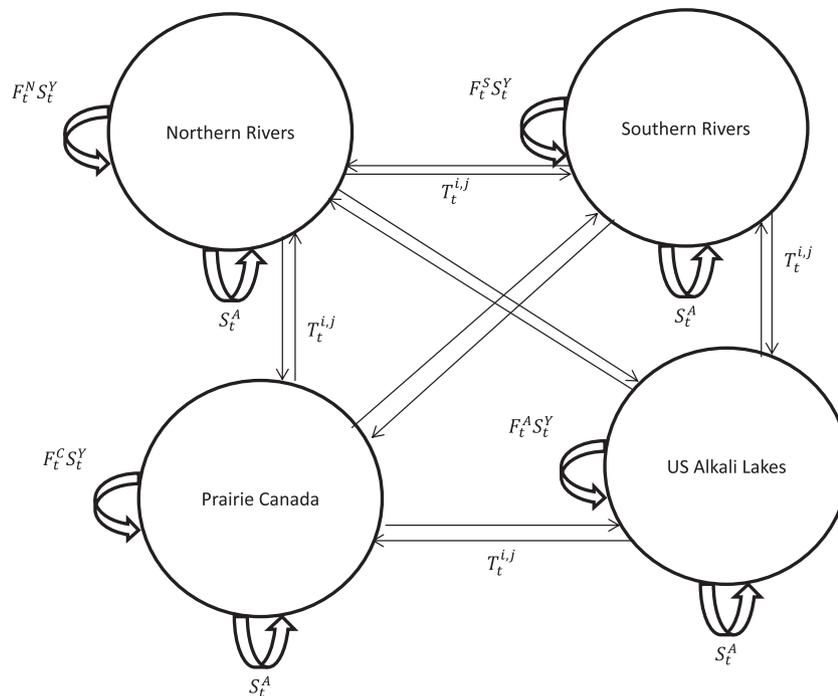
Fig. 1. Conceptual diagram of the Great Plains piping plover meta-population dynamics, showing regional divisions, transition rates between regions and annual intraregional dynamics where S^A is the annual survival rate of adults, F is the annual fecundity rate in region i (female fledglings produced per breeding female) and S^Y is the juvenile (first winter) annual survival rate, the super script j indicates any one of the three subpopulations in the model available for immigration or emigration and T is the annual transition rate from region i to j (emigration) or j to i (immigration).

The projection equations for the population were crafted as algebraic expressions and the simulation program had one equation for each region. The equations were composed of a recruitment term, a survival term, and immigration/emigration terms where annually a small, random percentage of the sub-population could depart each region and move to another region as follows:

$$N_{t+1}^i = (N_t^i S_t^A) + (N_t^i F_t^i S_t^Y) - \sum((N_t^i S_t^A) + (N_t^i F_t^i S_t^Y))T_t^{ij} + \sum((N_t^j S_t^A) + (N_t^j F_t^j S_t^Y))T_t^{ji}$$

where N^i is the population size in region i, S^A is the annual survival rate of adults, F^i is the annual fecundity rate in region i (female fledglings produced per breeding female) and S^Y is the juvenile (first winter) annual survival rate. The subscript t indicates the year. The super script j indicates any one of the three subpopulations in the model available for immigration or emigration and T is the annual transition rate from region i to j (emigration) or j to i (immigration). Following McGowan and Ryan (2009), our model assumes that annual adult and juvenile survival does not vary by region but that fecundity does. Analyses distinguishing survival rate by region in the Great Plains have not been conducted/completed, but survival estimates from the Atlantic Coast population suggest that far northern breeding birds (e.g., Nova Scotia) may have lower survival than more southern birds, at least for juveniles (Calvert et al., 2006; Hecht and Melvin, 2009). Without conclusive analyses to support regional survival differences in the Great Plains (Cohen and Gratto-Trevor, 2011, D. Catlin unpublished data), we decided to keep survival consistent among regions. Overall mean adult survival was set at 0.78 (SE = 0.03) and was based on unpublished (D. Catlin, unpublished data) and published estimates (Larson et al., 2000; Cohen and Gratto-Trevor, 2011; Roche et al., 2010). Overall mean juvenile survival was set at 0.52 (SE = 0.12) and was based on unpublished analyses of mark recapture data (D. Catlin, unpublished data) and is similar to published values from Saskatchewan at 0.57 (SE 0.05; Cohen and Gratto-Trevor, 2011). Survival rates

were modeled as beta-distributed random variables in the simulation model.

Productivity estimates for each region were based on the best available published estimates or the best available data. The southern rivers region had an estimated 0.77 (SE = 0.24) female fledglings per pair, derived from nest survival, chick survival, clutch size and renesting rate data (D. Catlin, unpublished data) using a Noon and Sauer (1992) approach for estimating fecundity (McGowan and Ryan, 2009). The estimates for southern rivers might be artificially elevated due to recent intensive habitat management by the U.S. Army Corps of Engineers in the area where the data originated (Catlin, 2009). If that investment and effort are not perpetuated, the fecundity levels in the Southern Rivers would likely decline to levels similar to other riverine habitats in the Northern Great Plains. Shaffer et al. (2013) reported that birds produced 0.32 (SE = 0.27) female fledglings per breeding female in the northern rivers region during a three year study. McGowan and Ryan (2009) reported that annual fecundity estimates from alkali wetland habitats were highly variable, but averaged approximately 0.60 (SE = 0.47) female fledglings per female. For the Canadian provinces we used 0.52 (SE = 0.40) females per female, based on unpublished data (C. Gratto-Trevor, unpublished data) and estimates incorporated into the McGowan and Ryan (2009) population model. Fecundity parameters in each region were modeled as lognormally distributed random variables; the parameters for modeling the log-normal distribution were derived using the delta method to convert the means and standard errors (Morris and Doak, 2002; McGowan et al., 2011b).

Mean transition rates between breeding regions were assumed to be low. We have scant evidence of birds moving between regions from several multi-year banding studies that have been conducted. Movement data from mark-recapture studies in the Great Plains indicate that long distance dispersal (e.g. from Nebraska to North Dakota) occurs infrequently (D. Catlin, unpublished data, C. Gratto-Trevor, unpublished data, Roche et al.,

2012) for adults and immature birds/first time breeders. Less than two percent of birds banded in a multi-year mark-recapture study in Saskatchewan were ever observed in another region, although these are largely incidental resight data and do not reflect directed efforts to study and sample interregional movement. For purposes here we assumed the total emigration rate from each region was 0.02. We divided that rate equally among the other regions (i.e. the immigration rate into any one region from another averaged 0.0066 (SE 0.02) of the population in the origin region in the previous year). We modeled these transition parameters as beta-distributed random variables. We used the method-of-moments calculations to derive the beta distribution scale and shape parameters from the mean and standard error (see Morris and Doak, 2002 for details).

The model included a simple ceiling type density dependence function that reduced productivity in a region to zero if the population in that region exceeded a threshold of 6000 individuals. There are limited published assessments of density dependence in this population, but some data do indicate density-dependent reproductive success occurs on the nesting beach/island scale (M. Ryan unpublished data, Catlin, 2009; Anteau et al., 2014). It seems logical that there must be some limiting effect of habitat availability on population growth and abundance. McGowan et al. (2011a) published a model with density-dependent juvenile survival, but the density dependent function was generic and not empirically based. The McGowan et al. (2011a) model was developed to demonstrate the interaction of density dependence and incidental take, not to serve as a management model for plovers in the Great Plains. Here we used a common approach of setting a maximum ceiling for the population without speculating on the details or functional form of the density-dependent function, similar to McGowan and Ryan (2009).

The two primary model outputs were mean expected population growth rate and the probability of extinction in year 50. Calculating population growth was simply a matter of dividing current population size by the population size in the previous year:

$$\lambda_t^i = \frac{N_t^i}{N_{t-1}^i},$$

where λ was the population growth rate for the ith management region, N was the population size and t was the time step. Population growth was calculated for each time step and the geometric mean of λ was calculated for each replicate. We also calculated the mean population growth rate across replicates to obtain the overall expected mean population growth rate.

We calculated regional quasi-extinction probability using a Boolean-logic function that recorded a "one" if the population was less than 50 individuals and a "0" if the population was greater than 50 individuals for each year in each region for each replicate. Quasi-extinction thresholds are frequently used in population modeling as surrogates of true extinction to account for the complexities of demographic stochasticity in a mathematically simple way. Similarly, for the entire Great Plains population, we set a quasi-extinction (hereafter extinction) threshold of 100 individuals. At the end of each simulation, we summed the number of extinction events for each year and divided by the number of replicates. We tracked extinction every year but for the post-simulation analyses (see below) we looked only at the number of replicates where the population was extinct at year 50 to allow regions to be recolonized naturally by dispersal events from other regions. At the regional level, this is not the same as a cumulative extinction probability for each region, but more analogous to a single year probability of extinction 50 years into the future. The state of the system 50 years into the future is the end result of 50 years of stochastic events, including previous extinction and colonization

and thus our tracking of regional extinction incorporates the accumulation of those stochastic events. The overall population estimate of extinction probability is equivalent to a cumulative extinction probability because our model does not allow for recolonization from outside the Great Plains.

2.1. Uncertainty

There is a great deal of uncertainty embedded in our model. Several of the parameters had no empirical estimates, were based on limited data, or inferred from studies not directly estimating the parameter of interest. Even the parameters that are empirically estimated (e.g. survival or productivity) are subject to sampling variation causing parametric uncertainty. The individuals that are captured and studied and even the years that a study took place can influence the mean estimates of demographic parameters and the estimates of annual variation in those parameters (McGowan et al., 2011b). Parametric uncertainty due to sampling variance can have large effects on model predictions and those effects should be incorporated into population projection models, especially when modeling in a management context (McGowan et al., 2011b). We followed the recommendations of McGowan et al. (2011b) for incorporating parametric uncertainty into our model for survival, fecundity and regional transition parameters. We sampled mean values for each parameter in each replicate of the population projection (sampling variability). The standard deviation of survival due to sampling variation was 0.03, and for fecundity it was 0.2 for all regions. The mean values for each replicate were then used to create new statistical distributions to select parameter values for each year in that replicate projection, mimicking temporal variability in annual demographic rates. Annual variation in survival was drawn from a beta distribution with mean selected in the out replication loop and a standard deviation of 0.001 for adults and 0.012 for immature birds. The standard deviation for fecundity to incorporate annual variation varied from replicate to replicate and was generated in the outer replication loop. This hierarchical approach allows the model to include both parametric uncertainty and temporal variability into the projections and assessment of extinction probability.

Our model also allowed us to include observation uncertainty on abundance and population growth outputs. Our ability to assess population status and management effectiveness is partly dependent on our ability to observe the population accurately. However, piping plovers are difficult to count given their cryptic coloration, elusive behavior and the vastness of some breeding areas (e.g., shorelines of large reservoirs). Models, on the other hand, predict precisely the expected number of individuals in the population given survival and productivity, and estimates of future abundance or extinction risk are derived from those precise predictions. Our application of model-based prediction of extinction probability, as it relates back to population size and population growth rate, assumes highly accurate or near perfect ability to detect and count a population through monitoring programs. Recovery criteria based on those model predictions may lead to premature or delayed delisting of a species due to imperfect monitoring and population status assessment. Temporal and parametric uncertainty accounts for variability in parameter estimates or stochastic variation in the environment, but does not account for imperfect monitoring of a population. To incorporate imperfect detection, we included a post-projection randomized adjustment to number of birds in the population and subsequently to population growth. We took the actual number of breeding birds from the simulation and the number of offspring produced in each year and multiplied each by a uniform random number between 0.5 and 1.1. Our uniform random distribution multiplier allows for both over and undercounting of individuals in any region in any year but the

distribution is skewed towards undercounting because one study supported frequent and significant undercounting for current monitoring efforts in the Northern Rivers region and consistent but less significant undercounting in the Southern Rivers region (Shaffer et al., 2013). We recorded the actual and the adjusted abundances and population growth rates separately and used the two to assess the effect of monitoring error on predicting extinction probability.

2.2. Parameter sensitivity simulations

We used the model to predict extinction risk region by region and for the whole population at 50 years if current demographics and management effort continues for the next 50 years. Initial population size and regional distributions were set to reflect the 2006 international "census" (2331 total females with 0.28 in southern rivers, 0.16 in northern rivers, 0.20 in alkali wetlands, and 0.37 in Prairie Canada) and the demographic parameters were set at the baseline levels described above. We tested the sensitivity of extinction risk to changes in the density-dependent ceiling and to the magnitude of inter-regional movement parameters, the two sets of model parameters with the least amount of empirical support. In one scenario we increased the density-dependent ceiling from 6000 per region to 10,000 per region. In a separate simulation, restoring the ceiling to 6000, we increased the immigration rates between regions from 0.0066 annually to 0.012 annually uniformly across regions.

2.3. Simulating extinction risk related to initial conditions

We ran simulations to identify the minimum population size and population growth rates required to reduce extinction risk to an acceptably low threshold. This set of simulations input random starting values for initial population abundance, regional distribution of the population and overall mean values for fecundity and survival. We used three hierarchical looping functions, where overall means for survival and fecundity and initial population size were selected in the outer loop, replicate means for survival and fecundity were selected and sampling variance applied in the second level loop, and temporal variability was applied in the inner loop (the annual loop; Fig. 2). In the outer loop, initial population size was drawn from a uniform random distribution bounded by 1000 and 10,000, mean fecundity was drawn from a uniform random distribution bounded between 0.2 and 1.2 females produced per breeding female, adult survival was drawn from a uniform distribution bounded by 0.65 and 0.85, and first year survival was drawn from a uniform distribution bounded by 0.35 and 0.65. The range of survival and fecundity values represent the full range of published or reported values for piping plovers in the Great Plains. The regional distribution parameters were also drawn from a uniform random distribution and the four parameters were set to sum to one. We ran 1000 replicates under these conditions to generate 1000 extinction probabilities and expected population growth rates, one for each starting scenario. Under each of the 1000 different initial conditions, we replicated the population 1000 time in the secondary loop, 50 years into the future in the annual loop (Fig. 2). Each extinction probability output from the model was the proportion of the 1000 secondary replicates that went extinct in 50 years. With those input and output data, we evaluated a set of candidate binomial regression models (glm models in R where the family equaled "binomial" and weights were set to the number of replicates) to investigate the relationship between extinction probability (the response variable) and initial population size, population growth rate, mean fecundity, mean adult survival, and mean first year survival (the predictor variables; abundance covariates were input as raw values or log transformed values in different competing models) for both the actual and adjusted data output from the simulations. This regression analysis was done at the Great Plains population level as well as separately for each regional population. We used AIC model selection to compare and select the best model to describe variation in extinction risk in each region due to those independent variables (i.e., the model with the lowest AIC score and highest model weight was considered best and if additional models fell within 2.0 AIC units of the best model we relied on multi-model inference; Burnham and Anderson, 2002) Model fit of the top model was assessed using an X^2 comparing the top model to a global model (Crawley, 2007). We used the regression parameter estimates from that model to populate a decision table that described the population size and predicted population growth combinations required to achieve the pre-determined acceptable extinction risk threshold. We argue that the decision table can serve as a delisting criterion for the population (i.e., the "decision" is whether to delist).

3. Results

Under current conditions with low inter-regional transition probabilities and a low density-dependent ceiling, the mean population growth rate was 1.001 (SD = 0.029), extinction probability was 0.033 and median abundance at 50 years was 11,379 (2.5 percentile = 63, 97.5 percentile = 24,858) females for the entire Great Plains population. The southern rivers region, where intensive habitat management has occurred in recent years had the lowest extinction probability (0.043) and seemed to insulate the overall population from extinction risk. Extinction probability in the other three regions exceeded 6% at 50 years (Fig. 3). Increasing the density dependent ceiling from 6000 birds in each region to 10,000 birds in each region did not greatly change overall extinction risk (from 0.043 to 0.030) but did increase the predicted median abundance over time (from ~13,100 to ~21,600 at 50 years) for the whole Great Plains population. That same pattern was observed in each of the individual regions. Increasing the interregional transition probabilities resulted in a slight decrease in extinction risk for the entire Great Plains population (0.043 with low transition rate, 0.031 with higher transition rates), and very little change in the total abundance (11,379 with low transition rate, 12,383 with higher transition rates). Region by region there was very little change in extinction risk and all regions exhibited increases in median abundance at 50 years when the transition probability between regions was doubled.

The best regression model to explain variability in extinction risk under perfect observability for the whole Great Plains population had the natural log of population size (b = −1.032; SE = 0.006) and the mean population growth rate over 50 years (b = −47.09; SE = 0.130) as covariates ($intercept$ = 52.114, SE = 0.156, AIC = 22,519, ΔAIC = 0.00, w = 1.00; Table 1). That same model structure garnered all the AIC weight at the whole population scale and for each of the four population/management regions, therefore our results and discussion focus on the whole population scale for simplicity and brevity. Under an expected population growth of 1.0 and a minimum extinction threshold of 0.05, a total initial population of approximately 2400 females is required (Table 2). Whereas, a minimum extinction threshold of 0.01 and an expected population growth of 1.00 requires a total initial population of >5600 females (Table 2). While the top model only included population growth and initial population size, population growth rate may not be easily measured in the field. It may be more useful to use other, more empirically based metrics such as fecundity (Table 3). If the purpose is to establish useful measurable attributes of the fundamental objectives (i.e., eliminating or reducing extinction
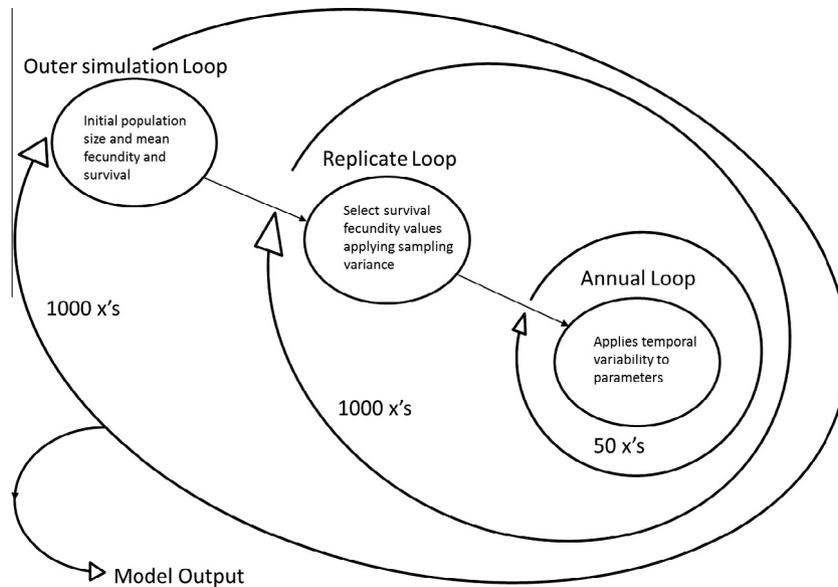
Fig. 2. Hierarchical loop structure of the simulation demonstrating how our model selected initial values and overall means in the outer loop, applied sampling variance in the replicate loop, and applied temporal variation in the annual loop.
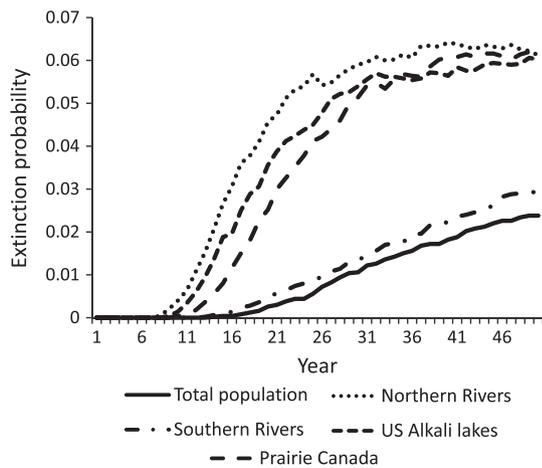

Fig. 3. Probability of extinction of piping plovers for the entire Great Plains population and by individual management region (Southern Rivers, Northern Rivers, US Alkali Lakes and Prairie Canada) as estimated by a meta-population model in each of 50 years.

risk; e.g., Keeney and Gregory, 2005) using the top AIC model for inference may be unnecessary; it may be prudent to limit the candidate metrics in the regression analysis to only those that are easily measurable for a specific species; the metrics included in this model comparison essentially become the alternatives in a recovery criteria decision analysis. A minimum extinction threshold of 0.05 requires a mean fecundity (female chick produced per female) of 0.80 and an initial population of approximately 5400 females (Table 3). Each regression parameter has an associated variance and it may be important to represent this uncertainty in the output of the analysis. One approach would be to calculate the 95% C.I. of each regression parameter, then build additional extinction probability tables for the upper (Table 4) and lower bound (Table 5), or any other relevant and useful percentile of expected variation.

When the observation model was applied to model output data, accounting for imperfect observations of the population, the strongest regression model in the AIC analyses for the whole Great Plains population had log of counted initial population size ($b = -1.03$; SE = 0.007) and expected population growth rate ($b = -46.7$; SE = 0.129) as covariates in the regression. The top model for the adjusted output data was the same model as the perfect detection output but with different regression parameter estimates (*intercept* = 52.6, SE = 0.156). That same model structure garnered all the AIC weight in each of the four population/management regions when the observation model was applied to the data.

Table 1
Candidate models and AIC results (scores, ranks and weights) for regression models to explain variation in extinction probability and identify the best variables for setting recovery criteria.

Model	AIC	ΔAIC	w
Ln(initial population size) + λ	22519.95	0	1
Initial population size + λ + Proportion in Region 1	24964.77	2444.82	0
Initial population size + λ	24968.37	2448.42	0
Ln(initial population size) + Adult Survival + Immature Survival	39103.29	137811.6	0
λ	46376.67	23856.72	0
Adult Survival + Juvenile Survival + Fecundity	47239.61	24719.66	0
Adult Survival + Juvenile Survival	106064.66	83544.71	0
Ln(initial population size) + Fecundity	145176.38	122656.43	0
Initial population size + Proportion in Region 1	200347.42	177827.47	0
Ln(initial population size)	200446.06	177926.11	0
Initial population size	200647.5	178127.55	0

Table 2
Expected extinction probability at 50 years into the future under mean population growth rate and starting population size combinations with perfect observability of the population.

Starting population size	Average population growth					
	0.97	0.98	0.99	1	1.01	1.02
2000	0.196	0.132	0.087	0.056	0.036	0.023
2200	0.181	0.121	0.079	0.051	0.033	0.021
2400	0.168	0.112	0.073	0.047	0.030	0.019
2600	0.157	0.104	0.068	0.043	0.028	0.017
2800	0.147	0.097	0.063	0.040	0.026	0.016
3000	0.138	0.091	0.059	0.038	0.024	0.015
3200	0.131	0.086	0.055	0.035	0.022	0.014
3400	0.124	0.081	0.052	0.033	0.021	0.013
3600	0.117	0.077	0.049	0.031	0.020	0.012
3800	0.112	0.073	0.047	0.030	0.019	0.012
4000	0.107	0.069	0.044	0.028	0.018	0.011
4200	0.102	0.066	0.042	0.027	0.017	0.011
4400	0.098	0.063	0.040	0.026	0.016	0.010
4600	0.094	0.061	0.039	0.025	0.015	0.010
4800	0.090	0.058	0.037	0.024	0.015	0.009
5000	0.087	0.056	0.036	0.023	0.014	0.009
5200	0.083	0.054	0.034	0.022	0.014	0.009
5400	0.081	0.052	0.033	0.021	0.013	0.008
5600	0.078	0.050	0.032	0.020	0.013	0.008

Table 3
Expected extinction probability at 50 years into the future under mean fecundity rate and starting population size combinations.

Starting population size	Average fecundity					
	0.6	0.7	0.8	0.9	1	1.1
2000	0.123	0.086	0.060	0.041	0.028	0.019
2200	0.122	0.085	0.059	0.040	0.027	0.018
2400	0.120	0.084	0.058	0.039	0.027	0.018
2600	0.118	0.083	0.057	0.039	0.026	0.018
2800	0.117	0.082	0.056	0.038	0.026	0.018
3000	0.116	0.081	0.056	0.038	0.026	0.017
3200	0.115	0.080	0.055	0.038	0.025	0.017
3400	0.114	0.079	0.054	0.037	0.025	0.017
3600	0.113	0.078	0.054	0.037	0.025	0.017
3800	0.112	0.078	0.053	0.036	0.025	0.017
4000	0.111	0.077	0.053	0.036	0.024	0.017
4200	0.110	0.076	0.052	0.036	0.024	0.016
4400	0.109	0.076	0.052	0.036	0.024	0.016
4600	0.108	0.075	0.052	0.035	0.024	0.016
4800	0.107	0.075	0.051	0.035	0.024	0.016
5000	0.107	0.074	0.051	0.035	0.024	0.016
5200	0.106	0.074	0.051	0.034	0.023	0.016
5400	0.105	0.073	0.050	0.034	0.023	0.016
5600	0.105	0.073	0.050	0.034	0.023	0.016

Table 4
Upper bound of the 95% confidence interval of the expected extinction probability at 50 years into the future under mean population growth rate and starting population size combinations with perfect observability of the population (generated using the upper bound of the regression model parameters to predict extinction probability).

Starting population size	Average population growth					
	0.97	0.98	0.99	1	1.01	1.02
2000	0.319	0.227	0.155	0.103	0.067	0.043
2200	0.298	0.210	0.143	0.094	0.061	0.039
2400	0.280	0.196	0.132	0.087	0.056	0.036
2600	0.264	0.183	0.123	0.081	0.052	0.033
2800	0.250	0.172	0.115	0.075	0.049	0.031
3000	0.237	0.162	0.108	0.071	0.045	0.029
3200	0.225	0.154	0.102	0.066	0.043	0.027
3400	0.214	0.146	0.097	0.063	0.040	0.026
3600	0.205	0.139	0.092	0.059	0.038	0.024
3800	0.196	0.132	0.087	0.056	0.036	0.023
4000	0.188	0.126	0.083	0.054	0.034	0.022
4200	0.180	0.121	0.079	0.051	0.033	0.021
4400	0.173	0.116	0.076	0.049	0.031	0.020
4600	0.167	0.112	0.073	0.047	0.030	0.019
4800	0.161	0.107	0.070	0.045	0.029	0.018
5000	0.156	0.103	0.067	0.043	0.028	0.017
5200	0.150	0.100	0.065	0.042	0.026	0.017
5400	0.145	0.096	0.063	0.040	0.025	0.016
5600	0.141	0.093	0.060	0.039	0.025	0.016

Table 5
Lower bound of the 95% confidence interval of the expected extinction probability at 50 years into the future under mean population growth rate and starting population size combinations with perfect observability of the population (generated using the upper bound of the regression model parameters to predict extinction probability).

Starting population size	Average population growth					
	0.97	0.98	0.99	1	1.01	1.02
2000	0.113	0.073	0.047	0.030	0.019	0.012
2200	0.103	0.067	0.043	0.027	0.017	0.011
2400	0.095	0.062	0.039	0.025	0.016	0.010
2600	0.088	0.057	0.036	0.023	0.014	0.009
2800	0.082	0.053	0.034	0.021	0.013	0.008
3000	0.077	0.049	0.031	0.020	0.012	0.008
3200	0.072	0.046	0.029	0.018	0.012	0.007
3400	0.068	0.044	0.028	0.017	0.011	0.007
3600	0.064	0.041	0.026	0.016	0.010	0.006
3800	0.061	0.039	0.025	0.015	0.010	0.006
4000	0.058	0.037	0.023	0.015	0.009	0.006
4200	0.055	0.035	0.022	0.014	0.009	0.005
4400	0.053	0.034	0.021	0.013	0.008	0.005
4600	0.051	0.032	0.020	0.013	0.008	0.005
4800	0.049	0.031	0.019	0.012	0.008	0.005
5000	0.047	0.030	0.019	0.012	0.007	0.005
5200	0.045	0.028	0.018	0.011	0.007	0.004
5400	0.043	0.027	0.017	0.011	0.007	0.004
5600	0.042	0.026	0.017	0.010	0.006	0.004

Again, required population size was dependent on the desired level of extinction probability and the desired population growth rate. Under all starting population size and growth rate combinations, the estimated extinction probability was 7.9% greater when observation error was applied compared to perfect detection. Under an expected population growth of 1.0 and a minimum extinction threshold of 0.05, a total initial population of approximately 5600 females is required (Table 6). Whereas, a minimum extinction threshold of 0.01 and an expected population growth of 1.00 requires a total initial population much greater 5600 females (Table 6). Alternatively, a population growth rate of 1.01 and an initial population size of 3600 females would achieve a minimum extinction threshold of 0.05 (Table 6). The numeric value of the regression parameter estimates are not substantially different when using the observation adjusted model from the perfect observation model but the recovery criteria using the same extinction risk threshold would be much larger.

4. Discussion

In our model, under the baseline scenario, mean population growth rates and projected abundance were higher, and extinction probabilities were much lower than in previous efforts to model this population (Ryan et al., 1993; Plissner and Haig, 2000; Larson et al., 2002; McGowan and Ryan, 2009). We expect that this is primarily due to three factors that distinguished our model from previous efforts. In recent years, due in large part to intensive habitat and predator exclusionary management, reproductive success has greatly increased in the northern Great Plains, especially in the "Southern Rivers" region where the USACE has invested tremendous effort in habitat creation projects (Catlin, 2009; Catlin et al., 2011). These increased reproductive success rates led to increased population growth and decreased extinction probability, but habitat and predator management may need to be maintained over time in order for these population growth and extinction

Table 6
Expected extinction probability at 50 years into the future under mean population growth rate and starting population size combinations with imperfect observability of the population.

Starting population size	Average population growth					
	0.97	0.98	0.99	1	1.01	1.02
2000	0.373	0.272	0.190	0.128	0.084	0.055
2200	0.350	0.253	0.175	0.117	0.077	0.050
2400	0.330	0.236	0.162	0.108	0.071	0.046
2600	0.312	0.222	0.151	0.101	0.066	0.042
2800	0.296	0.209	0.142	0.094	0.061	0.039
3000	0.281	0.197	0.133	0.088	0.057	0.037
3200	0.268	0.187	0.126	0.083	0.054	0.034
3400	0.256	0.177	0.119	0.078	0.050	0.032
3600	0.245	0.169	0.113	0.074	0.048	0.030
3800	0.235	0.161	0.108	0.070	0.045	0.029
4000	0.225	0.154	0.103	0.067	0.043	0.027
4200	0.217	0.148	0.098	0.064	0.041	0.026
4400	0.208	0.142	0.094	0.061	0.039	0.025
4600	0.201	0.136	0.090	0.058	0.037	0.024
4800	0.194	0.131	0.086	0.056	0.036	0.023
5000	0.188	0.126	0.083	0.054	0.034	0.022
5200	0.181	0.122	0.080	0.052	0.033	0.021
5400	0.176	0.118	0.077	0.050	0.032	0.020
5600	0.170	0.114	0.075	0.048	0.031	0.019

probability predictions to come to fruition. We also used updated and improved estimates of annual survival for adults and juvenile birds (Catlin, 2009; Roche et al., 2010; Cohen and Gratto-Trevor, 2011) and the mean estimates of survival were somewhat higher than estimates used in previous models (Root et al., 1992; Larson et al., 2000). Given that population growth and extinction probability are highly sensitive to annual survival rates (Ryan et al., 1993; Larson et al., 2002) using higher survival rates in our model led to more stable and optimistic population projections. Finally, we expect that the meta-population structure insulated the overall population from extinction because the probability of concurrent extinction in all four subpopulations was low.

Extinction probability exhibited low sensitivity to the modeled density-dependent ceiling for each regional population and to transition rates between regions. It is possible that despite doubling the rate of transition among regions, the transition rates we used in our simulations were still too small to generate large changes in extinction probability. Transition probability of individuals moving among management regions has been indirectly studied for approximately 10 years. While extensive mark-recapture and resighting studies have taken place in the Northern Great Plains, those studies were focused on estimating survival and other demographic parameters, not interregional movement probabilities. In those studies few instances of inter-regional movement were observed and therefore we assumed, based on those data, that transition rates were low. Opportunity for interregional movement is probably greatest between Northern Rivers and U.S. Alkali Lakes, given their proximity to one another. Emerging data (Shaffer, unpublished data) may indicate that movement rates between at least some regions may be much higher than we assumed. Mid-way through the 2013 breeding season, no fewer than 8 adult plovers captured and marked from nests in Northern Rivers Region had been resighted within the Alkali Lakes Region despite limited resighting effort in the Alkali Lakes (U.S. Geological Survey, unpublished data). We tested the sensitivity of extinction probability to transitions rates that were quite low, but still within the realm of possibility given the observed data; a posteriori simulations with mean transition rates set to 0.13 showed an increase in extinction probability to 0.083 for the entire Great Plains population; the insulating effect of regional structure on population viability is potentially lessened by increased connectivity. It may be prudent to further evaluate transition rates among regions to more accurately parameterize a meta-population model.

We used our model to demonstrate the effect of observation error in the field on conditions required for recovery. In our case, field-based counting error led to undercounting, on average, of individuals in the population, which therefore led to a substantial inflation of the required population size for delisting given a specific extinction probability and a desire for stationary populations (population growth equal to 1.00; Tables 1 and 2). For piping plovers in the northern Great Plains, counting error undoubtedly occurs as this is a species whose primary strategy for survival and reproduction is to not be seen (Elliott-Smith and Haig, 2004). We accessed one study (Shaffer et al., 2013) that indicated a significant monitoring program in the Northern Rivers and Southern Rivers management regions typically undercounted. We applied that error to all management units in our model but more specific measurement error could be empirically evaluated to more accurately reflect counting error in each of the regions in our model. We are not arguing that our specific observation error is the best approach for all wildlife species or even for piping plovers, but rather trying to demonstrate how observation error can affect model predictions and management decisions, in this case setting recovery criteria. Given the potentially massive effect of observation error on the recovery criterion, and the possible risk involved with prematurely or delayed delisting, careful and detailed region specific assessment of observation error processes and effects may be warranted Great Plains for piping plovers, and generally may be important for other species in other contexts. Regardless of specific implications for piping plovers, our purpose here was to explore the effect of potential counting error on recovery criteria, and our simulations and analysis indicate that measurement error may be important to consider when establishing delisting criteria.

We have presented a logical and transparent method for establishing recovery criteria that integrates the best available science on a given species and a simulation based approach. While some understanding of population dynamics is required to implement our method, McGowan and Ryan (2010) demonstrate that developing a useful model for endangered species decision making may not be as data limited or challenging as some might predict. We acknowledge previously documented limitations to specificity of results from population viability analyses (e.g. McCarthy et al., 2003) and suggest that, with improved accounting of parametric uncertainty (e.g., McGowan et al., 2011b), limited projection horizons (e.g., less than 50 year projections) and frequent model updating and reassessment of results, viability models can be useful in the context we presented.

The regression results and inferential capacity of this analysis may be sensitive to the simulation conditions set up in the model. We tried to explore a wide variety of scenarios by drawing replicate values from uniform distributions in which the upper and lower bounds spanned the range of estimated demographic parameters for this population to generate highly variable parameter combinations (i.e., initial population size, fecundity and survival) to fully explore the parameter and subsequent decision space. Selecting an appropriate range of input values can greatly affect the regression analysis and the ranges deserve careful consideration. We recommend using a very large range because interpolating within the bounds of a regression model is more defendable than extrapolating beyond the bounds. Further, the regression model precision and predictive power would be highly related to the number of replicates in the simulation model, i.e., 10,000 replicates would likely return greatly reduced regression model uncertainty than a 100 replicate simulation. In this analysis, there should be a balance between presenting a false sense of certainty by using too many replicates versus presenting so much uncertainty with too few replicates that decision making is impeded. Furthermore, users of our approach could apply additional layers of risk aversion to listed species by using the lower

bound or some other percentile of the regression parameters which would likely increase the recovery thresholds (i.e., higher population requirements, population growth rates or fecundity), but also reduce the risk of premature delisting. It may be possible and sufficient, with some demographic parameters, like fecundity, to forego the regression step of this analysis and build a decision table directly by simulating multiple scenarios and parameter combinations. However, the regression approach presents a generalized approach where any measurable attribute of the population that can be incorporated into the simulation model can be used to set recovery criteria that are directly linked to extinction probability. Furthermore, the regression modeling step allows recovery planners to concurrently evaluate the predictive power and the utility of multiple demographic parameters as measurable attributes of extinction probability through model selection (or some other model comparison technique). Under this approach, decision makers could evaluate multiple candidate measurable attributes in terms of their utility and precision for predicting extinction probability using regression and model selection to compare competing models of the simulation data.

With our model and regression analysis we can quantify the extinction probability for any given starting population size and expected population growth rate for the modeled species. Conceivably, this type of analysis and table could be done for any measurable population parameter. If certain parameters are difficult to measure, such as adult survival or population growth rate, the analysis could be limited to quantities that are measurable with precision. We demonstrated that even though population growth and initial abundance were the best predictors of extinction probability, a similar table could be constructed for mean fecundity. Though fecundity was not heavily supported as a covariate of extinction probability in the model selection analysis, the regression model had a adequate fit to the data according to the X^2 goodness of fit test and seems to adequately describe variation in extinction probability ($p < 0.001$) to potentially be a useful predictor and measurable attribute for extinction probability. The trade-off faced by recovery planners is that fecundity seems to be a lower quality predictor or extinction probability, but maybe more accurately and easily measured than population growth rate.

The result of this regression-based approach is similar (in practice, not mathematically) to a state dependent optimization output table that identifies the optimal action under any state of the managed system. With our approach, a recovery team could select, a priori, an acceptable extinction risk for the protected species and subsequently use our regression-based analysis of projection data to identify combinations of expected population growth and population size (or other demographic parameters) that constitute recovery for the species/population; that is, the conditions where extinction probability is acceptably low to warrant de-listing. The recovery team could then set delisting criteria and manage the population accordingly to achieve the target population growth rate and population size (or other demographic parameters) as surrogate measures of the fundamental objective of avoiding or reducing extinction risk. The regression-based approach allows recovery planners to present and evaluate sets of recovery criteria using alterative combinations of parameters that meet the a priori extinction risk threshold. For example, de-listing may be allowable at lower abundance if higher population growth rates or fecundities are expected, as long as the extinction risk threshold is likely to be met according to the model predictions.

To our knowledge this is a unique approach to establishing recovery criteria for an endangered or protected species. One in which an acceptable level of risk to that species persistence is first identified through discussion of risk tolerance. The conditions required to achieve that acceptable level of risk are then identified through simulation modeling and regression analysis. We recognize

that extinction probability has been previously linked to starting population size or population growth rate (e.g., Lande and Orzack, 1988), but here we present an approach that explicitly and transparently incorporates this relationship into the process of establishing recovery criteria. Historically recovery targets for listed species were typically set by setting some abundance threshold higher than current without any explicit link to extinction risk (e.g., USFWS, 1988; Schemske et al., 1994; Elphick et al., 2001; Neel and Che-Castaldo ,2013). Some recovery plans in more recent years have use population models to assess species status and even to link recovery criteria to population growth rate (Goodman, 2002; USFWS, 2001, 2012) and a rare few have centered on extinction probability (USFWS, 2002). Under our projection modeling and regression based approach, the attributes of recovery are specific, measurable and directly related to extinction probability. The measurable criteria are also scientific and transparently derived but the core objective, the acceptable level of extinction risk to a species, is a matter of societal value and risk tolerance and the objective is open for reasoned debate. This framework, a priori selecting an acceptable extinction risk and then using a projection model to link measurable attributes of the population to extinction risk and identify the conditions for delisting trough analysis of simulation output, could be applied to any endangered population for which a model could be constructed. From species to species the primary differences will be model structure and the range of input values for the replicate simulations; however we envision application for birds, mammals, reptiles, invertebrates and protected flora. The real limiting factor is the ability to identify an acceptable extinction risk then build a model to output extinction probability.

References

Anteau, M.J., Shaffer, T.L., Sherfy, M.H., Sovada, M.A., Stucker, J.H., Wiltermuth, M.T., 2012. Nest survival of piping plovers at a dynamic reservoir indicates an ecological trap for a threatened population. Oecologia 170, 1167–1179.

Anteau, M.J., Wiltermuth, M.T., Sherfy, M.H., Shaffer, T.L., Pearse, A.T., 2014. The role of landscape features and density dependence in growth and fledging rates of Piping Plovers in North Dakota, USA. Condor 116, 195–204.

Beissenger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manag. 62, 821–841.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, second ed. Springer-Verlag, New York.

Calvert, A.M., Amirault, D.J., Shaffer, F., Elliot, R., Hanson, A., McKnight, J., Taylor, P.D., 2006. Population assessment of an endangered shorebird: the Piping Plover (*Charadrius melodus melodus*) in Eastern Canada. Avian Conserv. Ecol. 1, 4 (online).

Catlin, D.H., 2009. Population dynamics of piping plovers (*Charadrius melodus*) on the Missouri River Doctoral dissertation. Virginia Polytechnic Institute and State University.

Catlin, D.H., Fraser, J.D., Felio, J.H., Cohen, J.B., 2011. Piping plover habitat selection and nest success on natural, managed, and engineered sandbars. J. Wildl. Manage. 75, 305–310.

Cohen, J.B., Gratto-Trevor, C.L., 2011. Survival, site fidelity, and population dynamics of Piping Plovers in Saskatchewan. J. Field Ornithol. 82, 372–394.

Crawley, M.J., 2007. The R Book. John Wiley & Sons, Ltd., West Sussex, England.

Elliott-Smith, E., Haig, S.M., 2004. Piping plover (*Charadrius melodus*). In: Poole, A. (Ed.), The Birds of North America Online. Ithaca, Cornell Lab of Ornithology. doi: http://dx.doi.org/10.2173/bna.2. <http://bna.birds.cornell.edu/bna/species/002>.

Elphick, C.L., Reed, M.J., Bonta, J.M., 2001. Correlates of population recovery goals in endangered birds. Conserv. Biol. 15, 1285–1291.

Environment Canada, 2012. Recovery Strategy for the Piping Plover (*Charadrius melodus melodus*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. v + 29pp.

Goodman, D., 2002. Predictive Bayesian population viability analysis: a logic for listing criteria, delisting criteria and recovery plans. In: Beissinger, S.R., McCullough, D.R. (Eds.), Population Viability Analysis. The University of Chicago Press, Chicago, USA.

Gratto-Trevor, C.L., Amirault-Langlais, D., Catlin, D., Cuthbert, F., Fraser, J., Maddock, S., Roche, E., Schaffer, F., 2012. Connectivity in Piping Plovers: do breeding populations have distinct winter distributions? J. Wildl. Manag. 76, 348–355.

Gregory, R.S., Keeney, R.L., 2002. Making smarter environmental management decisions. J. Am. Water Resour. Assoc. 38, 1601–1612.

Gregory, R.S., Long, G., 2009. Using structured decision making to help implement a precautionary approach to endangered species management. Risk Anal. 29, 518–532.

Hanski, I., 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63, 151–162.

Hecht, A., Melvin, S.M., 2009. Population trends of Atlantic coast piping plovers, 1986–2006. Waterbirds 32, 64–72.

Keeney, R.L., Gregory, R.S., 2005. Selecting attributes to measure the achievement of objectives. Oper. Res. 53, 1–11.

Lande, R., Orzack, H.S., 1988. Extinction dynamics of age-structured populations in a fluctuating environment. Proc. Natl. Acad. Sci. USA 85, 7418–7421.

Larson, M.A., Ryan, M.R., Root, B.G., 2000. Piping plover survival in the Great Plains: an updated analysis. J. Field Ornithol. 71, 721–729.

Larson, M.A., Ryan, M.R., Murphy, R.K., 2002. Population viability of piping plovers: effects of predator exclusion. J. Wildl. Manag. 66, 361–371.

LeFer, D., Fraser, J.D., Kruse, C.D., 2008. Piping plover chick foraging, growth, and survival in the Great Plains. J. Wildl. Manag. 72, 682–687.

McCarthy, M.A., Andelman, S.J., Possingham, H.J., 2003. Reliability of relative predictions in population viability analysis. Conserv. Biol. 17, 982–989.

McGowan, C.P., 2013. A structured approach to incidental take decision making. Environ. Manage. 51, 241–250.

McGowan, C.P., Ryan, M.R., 2009. A quantitative framework to evaluate incidental take and endangered species population viability. Biol. Conserv. 142, 3128–3136.

McGowan, C.P., Ryan, M.R., 2010. Arguments for using population models in incidental take assessments for endangered species. J. Fish Wildl. Manag. 1, 183–188.

McGowan, C.P., Runge, M.C., Larson, M.A., 2011a. Incorporating parametric uncertainty into population viability analysis models. Biol. Conserv. 144, 1400–1408.

McGowan, C.P., Ryan, M.R., Runge, M.C., Millspaugh, J.J., Cochrane, J.F., 2011b. The role of demographic compensation theory in incidental take assessments for endangered species. Biol. Conserv. 144, 730–737.

Morris, W., Doak, D., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, MA, USA.

Neel, M.C., Che-Castaldo, J.P., 2013. Predicting recovery criteria for threatened and endangered plant species on the basis of past abundances and biological traits. Conserv. Biol. 27, 385–397.

Noon, B.R., Sauer, J.R., 1992. Population models for passerine birds: structure, parameterization and analysis. In: McCullough, D.R., Barrett, R.H. (Eds.), Wildlife 2001: Populations. Elsevier Applied Science, London, pp. 441–464.

Plissner, J.H., Haig, S.M., 2000. Viability of piping plover *Charadrius melodus* metapopulations. Biol. Conserv. 92, 163–173.

Prindiville Gaines, E.P., Ryan, M.R., 1988. Piping plover habitat use and reproductive success in North Dakota. J. Wildl. Manag. 52, 266–273.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roche, E.A., Cohen, J.B., Catlin, D.H., Amirault-Langlais, D.L., Cuthbert, F.J., Gratto-Trevor, C.L., Fraser, J.D., 2010. Range-wide piping plover survival: correlated patterns and temporal declines. J. Wildl. Manag. 74, 1784–1791.

Roche, E.A., Gratto-Trevor, C.L., Goossen, J.P., White, C.L., 2012. Flooding affects dispersal decisions in Piping Plovers (*Charadrius melodus*) in prairie Canada. Auk 129, 296–306.

Root, B.G., Ryan, M.R., Mayer, P.M., 1992. Piping plover survival in the Great Plains. J. Field Ornithol. 63, 10–15.

Ryan, M.R., Root, B.G., Mayer, P.M., 1993. Status of piping plovers in the Great Plains of North America: a demographic simulation model. Conserv. Biol. 7, 581–585.

Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M., Bishop, J.G., 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75, 584–606.

Schultz, C.B., Hammond, P.C., 2003. Using population viability analysis to develop recovery criteria for endangered insects: case study of the fender's blue butterfly. Conserv. Biol. 17, 1372–1385.

Shaffer, T.L., Sherfy, M.H., Anteau, M.J., Stucker, J.H., Sovada, M.A., Roche, E.A., Wiltermuth, M.T., Buhl, T.K., Dovichin, C.M., 2013. Accuracy of the Missouri River Least Tern and Piping Plover Monitoring Program—Considerations for the future: U.S. Geological Survey Open-File Report 2013-1176, 74p., with 4 appendixes. <http://pubs.usgs.gov/of/2013/1176/>.

Starfield, A.M., 1997. A pragmatic approach to modeling for wildlife management. J. Wildl. Manag. 61, 261–270.

US Fish and Wildlife Service, 1985. Determination of endangered and threatened status for the Piping Plover. Fed. Reg. 50 (238), 50720–50734.

US Fish and Wildlife Service, 1988. Great Lakes and Northern Great Plains piping plover recovery plan. U.S. Fish and Wildlife Service, Twin Cities, MN, 160pp.

U.S. Fish and Wildlife Service, 2001. Florida Manatee Recovery Plan, (*Trichechus manatus latirostris*), third Revision. U.S. Fish and Wildlife Service. Atlanta, Georgia, 144pp. + appendices.

U.S. Fish and Wildlife Service, 2002. Steller's Eider Recovery Plan. Fairbanks, Alaska.

U.S. Fish and Wildlife Service, 2012. Final Recovery Plan for the Mexican Spotted Owl (*Strix occidentalis lucida*), first Revision. U.S. Fish and Wildlife Service. Albuquerque, New Mexico, USA, 413pp.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press, New York.