Calvert, A. M., D. L. Amirault, F. Shaffer, R. Elliot, A. Hanson, J. McKnight, and P. D. Taylor. 2006. Population assessment of an endangered shorebird: the Piping Plover (*Charadrius melodus melodus*) in eastern Canada. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* **1**(3): 4. [online] URL: http://www.ace-eco.org/vol1/iss3/art4/

Research Papers

Population Assessment of an Endangered Shorebird: the Piping Plover (*Charadrius melodus melodus*) in Eastern Canada

Statut démographique d'un oiseau de rivage en voie de disparition : le Pluvier siffleur (*Charadrius melodus melodus*) de l'est du Canada

Anna M. Calvert[1], *Diane L. Amirault*[2], *François Shaffer*[3], *Richard Elliot*[2], *Alan Hanson*[2], *Julie McKnight*[2], *and Philip D. Taylor*[4]

ABSTRACT. Small, at-risk populations are those for which accurate demographic information is most crucial to conservation and recovery, but also where data collection is constrained by logistical challenges and small sample sizes. Migratory animals in particular may experience a wide range of threats to survival and reproduction throughout each annual cycle, and identification of life stages most critical to persistence may be especially difficult for these populations. The endangered eastern Canadian breeding population of Piping Plover (*Charadrius melodus melodus*) was estimated at only 444 adults in 2005, and extensive effort has been invested in conservation activities, reproductive monitoring, and marking of individual birds, providing a comprehensive data set on population dynamics since 1998. We used these data to build a matrix projection model for two Piping Plover population segments that nest in eastern Canada in order to estimate both deterministic and stochastic rates of population growth (λ_d and λ_s, respectively). Annual population censuses suggested moderate growth in abundance between 1998–2003, but vital rate estimates indicated that this temporary growth may be replaced by declines in the long term, both in southern Nova Scotia ($\lambda_d = 1.0043$, $\lambda_s = 0.9263$) and in the Gulf of St. Lawrence ($\lambda_d = 0.9651$, $\lambda_s = 0.8214$). Nonetheless, confidence intervals on λ estimates were relatively wide, highlighting remaining uncertainty in future population trajectories. Differences in projected growth between regions appear to be driven by low estimated juvenile post-fledging survival in the Gulf, but threats to juveniles of both population segments following departure from nesting beaches remain unidentified. Similarly, λ in both population segments was particularly sensitive to changes in adult survival as expected for most migratory birds, but very little is understood about the threats to Piping Plover survival during migration and overwintering. Consequently, we suggest that future recovery efforts for these and other vulnerable migrants should quantify and manage the largely unknown sources of both adult and juvenile mortality during non-breeding seasons while maintaining current levels of nesting habitat protection.

RÉSUMÉ. Les petites populations en péril sont celles pour lesquelles il est essentiel de posséder des données démographiques exactes aux fins de la conservation et du rétablissement, mais également celles où la collecte de données est limitée par des défis logistiques et la petite taille des échantillons. Les animaux migrateurs en particulier peuvent être affectés par un large éventail de menaces pour leur survie et leur reproduction tout au long de chaque cycle annuel et il peut s'avérer particulièrement difficile de déterminer quels stades de vie sont les plus cruciaux pour la persistance de ces populations. En 2005, la population reproductrice du Pluvier siffleur (*Charadrius melodus melodus*) de l'est du Canada, qui est en voie de disparition, était estimée à 444 adultes seulement. Des efforts soutenus ont été déployés en activités de conservation, de suivi de la reproduction et de marquage d'individus, ce qui a permis de recueillir un ensemble de données détaillées sur la dynamique de la population depuis 1998. Nous avons utilisé ces

[1]Department of Biology, Dalhousie University, [2]Canadian Wildlife Service, Atlantic Region, [3]Canadian Wildlife Service, Quebec Region, [4]Biology Department, Acadia University

Sponsored by the Society of Canadian Ornithologists and Bird Studies Canada

Parrainée par la Société des ornithologistes du Canada et Études d'oiseaux Canada

données pour établir un modèle matriciel de projection pour deux segments de la population nicheuse de Pluviers siffleurs de l'est du Canada afin d'estimer les taux de croissance déterministe et stochastique de la population (λ_d et λ_s, respectivement). Des recensements annuels de la population ont suggéré une croissance modérée de l'abondance entre 1998–2003, mais les estimations des paramètres vitaux ont indiqué que cette croissance temporaire pourrait être remplacée par des déclins à long terme, tant dans le sud de la Nouvelle-Écosse (λ_d = 1.0043, λ_s = 0.9263) que dans le golfe du Saint-Laurent (λ_d = 0.9651, λ_s = 0.8214). Néanmoins, les intervalles de confiance des estimations de λ étaient relativement grands, mettant en relief l'incertitude qui subsiste quant à l'évolution future de la population. Les différences entre les taux de croissance obtenus à l'aide du modèle pour chaque région semblent être liées à une faible taux de survie estimé pour les jeunes à l'envol dans le golfe, mais les menaces qui pèsent sur les jeunes des deux segments de la population après leur départ des plages de nidification demeurent inconnus. De même, la valeur de λ dans les deux segments de la population était particulièrement sensible aux changements du taux de survie des adultes, comme il faut s'y attendre pour la majorité des oiseaux migrateurs, mais on ne sait que peu de choses sur les menaces à la survie du Pluvier siffleur pendant la migration et la période d'hivernage. Par conséquent, nous proposons que les efforts qui seront déployés en vue du rétablissement de cette population et de celles d'autres migrateurs vulnérables visent à quantifier et à gérer les causes largement inconnues de la mortalité chez les adultes et les jeunes en dehors de la saison de reproduction, tout en maintenant les niveaux actuels de protection de l'habitat de nidification.

Key Words: *conservation; endangered population; matrix model; migration; non-breeding survival; recovery; sensitivity*

INTRODUCTION

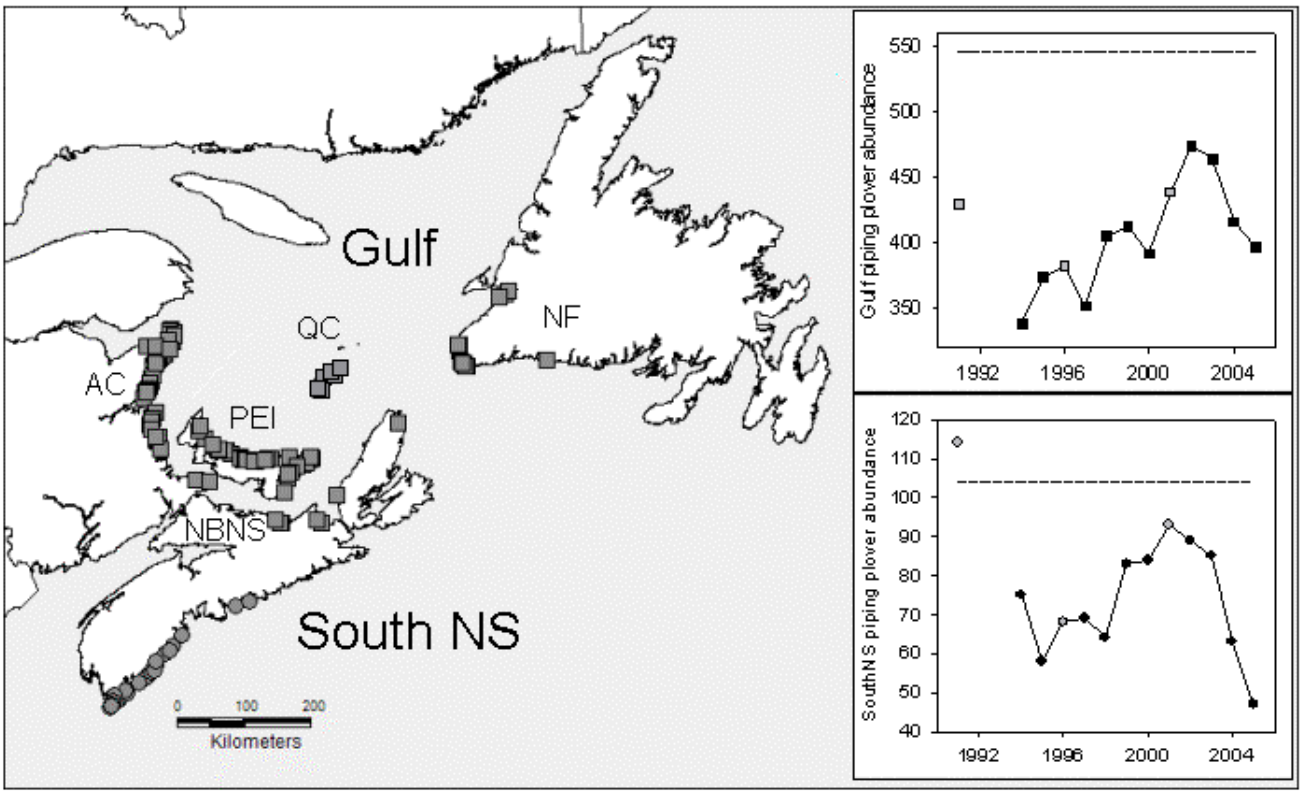
To assess current and future threats facing wildlife populations, we need to understand the relative importance of population vital rates to overall persistence and to past variation in abundance. For small, endangered populations in particular, such knowledge is critical to the wise investment of conservation resources (Beissinger and Westphal 1998, Caswell 2000). However, given that these populations are by definition composed of very few individuals, estimation of demographic parameters is often constrained by limited data. The few endangered plants or animals for which there exist comprehensive demographic data may, therefore, contribute insight into broader issues surrounding the protection of small, at-risk populations.

Ideally, the management of small populations will begin with estimates of demographic parameters (survivorship, recruitment, dispersal) and an understanding of the factors that influence them. Critical habitat protection is a key element of conservation programs, but for most species, basic relationships between habitat and population parameters are unknown. Many migratory shorebirds, for example, rely year round on fragile beaches for breeding, migration, and wintering. They may face habitat-related risks to their reproduction (Patterson et al. 1991, Goss-Custard et al. 1995, Espie et al. 1996, 1998, Knetter et al. 2002) and survival (Burger 1994, Durell et al. 1997, Goldin and Regosin 1998), yet the demographic impacts of specific disturbances are rarely quantified (Larson et al. 2002).

The Piping Plover (*Charadrius melodus*) is a well-studied but highly vulnerable species whose conservation demands detailed demographic assessment. Several North American Piping Plover populations have shown strong declines in recent years (Haig et al. 2005), and the eastern Canadian population (*C. m. melodus*) dropped to as few as 422 birds in 1996 (Amirault 2005). It was identified as "Endangered" under Canada's Species at Risk Act (SARA) in 2001. Although there has been considerable effort invested in protecting nesting habitat (e.g., Haig 1992, Larson et al. 2003, Goossen et al. 2002, Amirault 2005), Piping Plover populations remain at low levels across the continent and have shown limited growth in recent years (Fig. 1; Amirault 2005, Haig et al. 2005).

As with many migratory species (e.g., Goss-Custard et al. 1995, Cuthbert et al. 2001), Piping Plover conservation initiatives have focused primarily on

Fig. 1. Location of beaches used by eastern Canada Piping Plovers breeding in the Gulf of St. Lawrence (squares) and South Nova Scotia (circles) from 1998 to 2003, with associated population abundance trends between 1991 and 2005 as indicated by the standardized annual population survey (black) and international census (gray) data (see Amirault 2005). Recovery goals for each population segment are also noted (dashed lines; Amirault 2006). Regions within the Gulf population segment are: AC (Acadian peninsula, northern New Brunswick), NBNS (southern New Brunswick and northern Nova Scotia), NF (Newfoundland), PEI (Prince Edward Island), and QC (Magdalen Islands, Quebec).



improving productivity and survival during the breeding season, with little consideration of hazards over the rest of the annual cycle. Plovers nesting in eastern Canada spend the winter in the southeast United States and the Caribbean, but threats to migration and overwinter survival or related habitat conservation concerns during non-breeding seasons remain largely unknown, despite demonstrated risks in other wintering populations (Nicholls and Baldassarre 1990, Drake et al. 2001). Moreover, in addition to direct impacts on annual survival, non-breeding habitat conditions can affect the fitness of migrants and their subsequent reproductive success (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004), further highlighting the need for protection of critical habitat beyond the breeding season (e.g. Crouse et al. 1987, Wilson 2003).

To enhance the recovery of endangered migratory populations, wildlife managers need to understand the relative importance of breeding vs. non-breeding seasons to annual population growth, and consequently which vital rates might be the most realistic targets for investment of conservation resources. We hypothesized that if population dynamics of eastern Canadian Piping Plovers have been largely influenced by recent conservation efforts on breeding grounds aimed at increasing productivity, then we should observe similar dynamics in both breeding population segments identified in this region. Alternatively, different dynamics might be detected if productivity differed greatly between the two breeding areas despite conservation efforts, or if non-breeding events were strongly affecting population dynamics. The objectives of this study were therefore to (1) estimate current vital rates for both segments of the eastern Canada population of Piping Plovers based on demographic data collected from 1998 to 2003; (2) develop a projection model for both segments of this population to assess the long-term expected population trajectory relative to observed changes in current abundance; and (3) estimate the sensitivity and elasticity of the long-term population growth rate (λ) to changes in variable population parameters in order to facilitate the planning of future conservation efforts.

METHODS

Study Population

In eastern Canada, Piping Plovers nest at relatively low densities on beaches scattered throughout the provinces of Nova Scotia (NS), New Brunswick, Prince Edward Island, Newfoundland, and the Magdalen Islands of Quebec (Fig. 1). Although there is some dispersal of birds among most of these regions, there have been no observations of exchange between marked birds nesting in southern NS and those in the Gulf of St. Lawrence (Amirault 2006); nesting habitats in southern NS may also be distinct (Flemming et al. 1992). Consequently, we separated plovers nesting throughout the Gulf of St. Lawrence (hereafter the "Gulf") from those nesting in southern NS (hereafter "South NS") for all analyses, considering these to be two separate population segments. There is also little evidence of any substantial exchange of marked birds between the eastern Canada population and breeders on the Atlantic Coast of the USA (Amirault 2006; but see Haig and Oring 1988a), so for the purposes of the population modeling, we treated Canadian birds as demographically isolated.

Breeding season data included detailed monitoring of reproductive success and marking of adult and juvenile birds with individually coded metal leg bands (see Amirault [2005], Amirault et al. [2006a] for data collection details). Methods were similar for both population segments, with the exception of somewhat reduced re-observation effort due to logistical constraints in two regions of the Gulf (Acadian Peninsula in New Brunswick, and Newfoundland; D. L. Amirault, personal observation); recapture and recruitment rates in that region were thus modeled separately from other Gulf regions (see below). We estimated all population parameters from the initiation of banding (1998 for the Gulf, 1999 for South NS) until the end of the breeding season in 2003.

A standardized international Piping Plover census was conducted in 1991, 1996, and 2001 (Amirault 2005, Haig et al. 2005), and an annual regional census began in eastern Canada in 1994. Beaches with pairs or single birds that were located at the beginning of each year were visited regularly throughout the breeding season to follow the success of nesting birds, as well as to monitor nest-protection efforts. Multiple visits to each beach allowed confirmation of numbers of birds and their productivity; consequently, annual census counts have been shown to be highly accurate (D. L. Amirault, unpublished data). Moreover, Piping Plovers nest in fairly linear and discrete habitat along eastern Canada beaches, and the census included all potential nesting-habitat beaches, thereby minimizing the probability that any breeding birds would be missed. These census data suggest that, after declines in the early 1990s, both population segments increased steadily from 1998 to 2003, at rates of 2.8% and 5.7% per year (assuming exponential growth) in the Gulf and South NS, respectively (Fig. 1). However, substantial decreases have occurred in both regions since 2003, and as of 2005, the total abundance (n = 444) remained well below the stated recovery target (n = 650; Amirault 2006).

Population Model Structure

Piping Plovers may begin to breed as second-year (SY) birds, and all are assumed to breed by their fourth summer (4Y; Haig 1992, D. L. Amirault, unpublished data). Therefore, the model included three age classes (1, 2, 3^+). Projection model time periods often begin before breeding ("pre-breeding census") for simplicity of calculations, particularly relating to estimates of stochastic growth (Cooch et al. 2003). However, because the population census occurred during or after the reproductive season, we built a post-breeding birth-pulse deterministic population matrix model, with birds counted at ages just over the year mark, e.g., hatch-year birds (HY) are ~1 month old, SY birds are ~1.1 years old, third-year birds (TY) are ~2.1 years old. Consequently, when we project forward one full year, HY birds (age class 1) would have the chance to reproduce within that first projection year, as SY birds; similarly, birds that were SY (age class 2) at census could breed as TY birds within the next interval (Fig. 2). Age class 3^+ applied to all birds aged TY or older at the time of the census.

We defined S_1 as "juvenile survival" (the probability that a HY bird survives the next 12-month period), and assumed that after their first year, plovers experience no variation in survival, meaning that $S_2 = S_{3+}$ = "adult survival" (the probability that a SY or older bird survives the next 12-month period). Because marking of HY birds occurred when chicks were still hatchlings, S_1 included the combined probability of fledging and surviving the next 12 months (see Table 1). The fertility values F_1, F_2, and F_{3+} represented the reproductive contribution of HY, SY, or TY^+ birds, respectively, within the next 12 months: these included the probabilities of surviving to the next year, breeding, the average number of eggs produced, and the chance that eggs survive to be counted as HY birds in the next census. We modeled only females and assumed a 1:1 sex ratio at hatching, and therefore, divided fertility values by two. Population parameters are defined in Table 1, and the projection matrix is shown in Eq. 1.

$$A = \begin{bmatrix} F_1 & F_2 & F_{3+} \\ S_1 & 0 & 0 \\ 0 & S_2 & S_{3+} \end{bmatrix} = \begin{bmatrix} \Phi_J^w f \cdot y_S Eh/2 & \Phi_A \cdot y_T Eh/2 & \Phi_A \cdot Eh/2 \\ \Phi_J^w f & 0 & 0 \\ 0 & \Phi_A & \Phi_A \end{bmatrix} \quad (1)$$

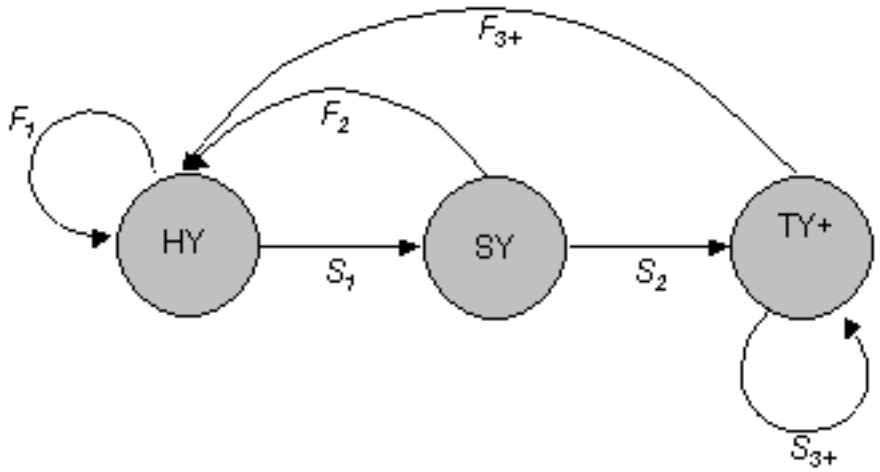
(Note that $\Phi_J^w = \Phi_J f$, meaning that $\Phi_J^w f$ in the above matrix could be replaced by Φ_J)

Estimation of Survival and Dispersal Probabilities

Annual survival probabilities were estimated using live-recapture models in program MARK (White and Burnham 1999), based on birds marked at breeding grounds and re-observed or recaptured (hereafter, "recaptured") in subsequent breeding seasons. Birds were banded in the Gulf from 1998–2002 and recaptured from 1999–2003, whereas South NS birds were banded from 1999–2002 and recaptured from 2000–2003 (see Amirault et al. 2006a for details). Although observations were made at all known potential breeding sites within eastern Canada, emigration to unknown sites or to other regions might not have been detected and could be confounded with mortality. As a consequence, survival estimates represented "local survival," the combined probability that a bird survived and returned to a monitored potential breeding site within eastern Canada the following year. However, because both natal and breeding dispersal may be high in Piping Plovers (Haig and Oring 1988c), for Gulf birds we used multi-strata models (Brownie et al. 1993, Schwarz et al. 1993) to separate region-specific mortality from dispersal to other regions within the Gulf population segment. These models permitted simultaneous estimation of survival and movement among the five Gulf regions: AC (Acadian peninsula, northern New Brunswick), NBNS (southern New Brunswick and northern Nova Scotia), NF (Newfoundland), PEI (Prince Edward Island), and QC (Magdalen Islands, Quebec). Movement probabilities were assumed to depend only on the region in which an individual was captured at the beginning of an annual interval, and not on previous history. A total of 191 marked individuals in South NS (134 HY, 57 AHY) and 688 individuals in the Gulf (425 HY, 263 AHY) provided the encounter histories for the live-recapture data sets.

For each population segment, we developed an a priori set of candidate models that allowed apparent survival rate (Φ) and recapture probability (p) to

Fig. 2. Post-breeding, birth-pulse life-cycle diagram for the Piping Plover, where S_i represents the probability that a bird of age class i survives the 12 months following census to age class i+1, and F_i represents the probability that a bird of age class i (HY, SY or TY+) survives to the following summer, recruits to the breeding population (as part of age class i+1), and breeds successfully (i.e., the number of female offspring per female parent).



vary with time (Φ_t, p_t), age group (Φ_{a2}, p_{a2}: juveniles [banded as HY] vs. adults [banded as AHY]), or region (Φ_r, p_r). Similarly, movement probabilities within the Gulf (ψ) could vary with time (ψ_t), age group (ψ_{a2}) or region of origin (ψ_r). Each parameter could alternatively be constant across time, region, and age group ($\Phi.$, $p.$, $\psi.$), and interactive effects of time, age, and/or region were also modeled. Sexes were pooled, as preliminary analyses indicated no sex differences in survival or recapture probabilities for either segment.

We tested the fit of the most general model for each population segment ($\{\Phi_{a2*t}\ \mathbf{p}_{a2*t}\}$ for South NS, $\{\Phi_{a2*t*r}\ \mathbf{p}_{a2*t*r}\ \Psi_{a2*r}\}$ for Gulf) using bootstrap goodness-of-fit tests (Efron 1979) implemented in MARK, to obtain a variance inflation factor c-hat (Lebreton et al. 1992). This value was used to correct for overdispersion in our data by adjusting the deviance in the calculation of each model's information-theory criterion ($QAIC_c$: quasi-likelihood Akaike Information Criterion, corrected for sample size; Burnham and Anderson 2002). We used $QAIC_c$ to select the best model (i.e., the smallest $QAIC_c$ value) for parameter estimation, and $QAIC_c$ weights ($\omega QAIC_c$) to evaluate importance of particular factors. We built a total of 29 models for the South NS data set, and 39 models for the Gulf.

Estimation of Reproductive Parameters

We defined recruitment rate (y) as the age-specific probability that a bird returned to a breeding beach and established a nest. Although some known-age birds (i.e., those banded as HY) were captured again as breeders, recapture probability (p) was often low (see Results) and, therefore, the ages of first recapture did not represent the actual age-specific recruitment rates. Instead, birds not seen again until their third or fourth year may actually have been breeding before first recapture. Using time-invariant estimates of adult recapture probability for each population segment, we adjusted these proportions of age-at-first-recapture by the

Table 1. Component parameters for the eastern Canada Piping Plover projection matrix model, and estimates for each breeding population segment (South NS: southern Nova Scotia; Gulf: Gulf of St. Lawrence); see text for details of parameter estimation.

Parameter	*Notation*	*Definition*	*South NS*	*Gulf*
Adult survival	Φ_A	SY^+ bird survival 1 yr after census	0.7324	0.7331
Juvenile survival (from hatch)	Φ_J	HY bird survival 1 yr after census	0.3279	0.2395
Fledging success	f	Probability hatchling survives to fledge	0.6171	0.7014
Juvenile survival (post-fledge)	$\Phi_J^w = \Phi_J/f$	HY bird survival from fledge to 1 yr old	0.5314	0.3415
Second-year recruitment	y_S	Probability that SY bird builds nest	0.8095	0.8504
Third-year recruitment	y_T	Probability that TY bird builds nest	0.9910	0.9823
Number of eggs laid	E	Mean number eggs laid per nest	3.8065	3.9389
Hatching success	h	Probability that an egg hatches	0.4603	0.5120

probability of having been present but not seen (i.e., [1-p] for birds first seen as TY, [1-p]^2 for birds first seen as 4Y) to obtain age-specific recruitment rates (y_S and y_T for SY, TY, respectively) for each population segment. Given that most Piping Plovers breed as SY birds (Haig and Elliott-Smith 2004), we assumed all 4Y and older birds (age class 3^+) to be breeders.

Beach census data were used to estimate nesting parameters, and parameters were estimated separately for each population segment. The average clutch size laid per female (E), was estimated as the mean number of eggs per nest, based on nest visits during incubation. Hatching probability (h) was calculated as the mean ratio between the number of eggs hatched and the number of eggs laid for all nests where both quantities were known. Similarly, fledging probability (f) was calculated as the mean ratio of the number of fledglings to the number of eggs hatched for all nests where both quantities were known. See Amirault (2005) for further details on beach census methods.

Population Growth, Retrospective and Prospective Analyses

Programs MATLAB 6.5 (MathWorks 2002) and ULM 4.0 (Legendre and Clobert 1995) were used to calculate the following information for each population segment based on Eq. 1: long-term expected growth rates (λ); sensitivities and elasticities of each matrix element and of each population parameter (absolute and proportional changes in λ resulting from changes in parameter values); stable age distributions (the expected proportion of the population belonging to each age class once the long-term growth rate λ is reached); and age-specific reproductive values (the relative contribution of each age class to the production of juveniles; Caswell 2001).

The short time period of data collection prevented separation of process error from observation error (Link and Nichols 1994, Gould and Nichols 1998) and thus the variance associated with parameter estimates reflected total error. Total variance was estimated directly in MARK for Φ, directly from the data for E, h and f, and indirectly for y from the formula (Lande 1988, Caswell 2001). Consequently, we modeled population dynamics both deterministically and stochastically, where deterministic λ (λ_d) and

stochastic λ (λ_s) were taken to represent maximal and minimal possible values of λ, respectively (i.e., due to under- and over-estimation of process error; Caswell 2001). We estimated λ_s as the mean growth rate from 1000 Monte Carlo 50-year simulations in ULM, where the mean and total estimated variance for each parameter were used to define stochastic parameter distributions; all parameters were assigned beta distributions (values restricted to interval 0–1) with the exception of *E* (normal distribution). Nevertheless, we used λ_d and associated matrix characteristics for assessment of past population growth, differences between population segments, and vital rate perturbation analyses. Confidence limits on λ_d estimates were derived from a retrospective analysis of the contribution of individual parameter variation to past growth (Caswell 2000, 2001). This allowed separation of past vital rate variability from future sensitivity of λ to vital rates, a distinction that can be particularly important to future manipulation of vital rates (Cooch et al. 2001).

In order to compare the dynamics of the two regional population segments, we used a life table response experiment (Caswell 2001) to determine the relative contributions of each matrix element to the overall difference in λ_d. One matrix served as a control (Gulf) and one as a treatment (South NS) to contrast both the value difference and the sensitivity of each matrix element, based on an "averaged matrix" where all matrix element values were calculated as the mean of the corresponding values of the matrices being compared (i.e., the Gulf and South NS matrices; Caswell 2001). The resulting values indicated the absolute difference in magnitude between equivalent parameters in the two population segments, as well as their contributions (positive or negative) to the difference in estimated λ_d.

In the draft recovery strategy for Piping Plovers (Amirault 2006), provincial recovery goals were set in terms of the desired number of breeding pairs relative to abundance in the 2005 population estimate. For South NS (comprising ~80% of the total NS population), a ~126% increase in abundance (from 23 to 52 pairs) would be required to attain the stated recovery goal, and for the Gulf, a ~44% increase (from 190 to 273 pairs; Amirault 2006). Therefore, we determined the λ_d value required to reach these abundance goals within 5 or 10 years, and the parameter perturbations that would be necessary to reach these λ_d values, assuming that parameter values could be altered instantaneously (i.e., without time delay for adjustment); see Appendix for calculation details.

RESULTS

Parameter Estimates

The bootstrap goodness-of-fit test for South NS mark-recapture models suggested a good fit of the most general model $\{\Phi_{a2*t}\ \mathbf{p}_{a2*t}\}$ to the data (c^=1.038). The weight of evidence ($\omega QAIC_c$=0.307) for the best-fit model $\{\Phi_{a2}\ \mathbf{p}_t\}$ was more than double that of the next closest model, and pointed to age-dependent survival and temporal variation in recapture probability (Table 2). Mean annual apparent survival probabilities for adults and juveniles were estimated from this model as $\Phi_{A(South\ NS)}$ =0.7324 (SE=0.0665) and $\Phi_{J(South\ NS)}$ =0.3279 (SE=0.0624), respectively.

The bootstrap test for multi-state mark-recapture models in the Gulf also suggested a good fit of the most general model $\{\Phi_{a2*t*r}\ \mathbf{p}_{a2*t*r}\ \Psi_{a2*r}\}$ to the data (c^=1.058). The best-fit model $\{\Phi_{a2*t}\ \mathbf{p}_{a2*(AC,NF:others)}\ \Psi_{a2*r}\}$ had very strong support ($\omega QAIC_c$=0.982), and suggested age- and time-dependent survival, age- and region-specific recapture probability (with AC and NF differing from the other regions), and movement probabilities varying with age and region of origin (Table 2). Age-specific, time- and region-invariant survival estimates (Φ_{a2}) were used for deterministic projections, giving $\Phi_{A(Gulf)}$=0.7331 (SE=0.0381) and $\Phi_{J(Gulf)}$ =0.2395 (SE=0.0376). A model allowing for age-group and regional variation in survival, recapture, and movement probabilities $\{\Phi_{a2*r}\ \mathbf{p}_{a2*r}\ \Psi_{a2*r}\}$ received little support (ωQAICc <0.001).

The best-fit models with time-invariant recapture gave adult recapture probability estimates of 44% for South NS (model $\{\Phi_{a2}\ \mathbf{p}.\}$) and 55% for most of the Gulf (model $\{\Phi_{a2*t}\ p_{a2*(AC,NF:others)}\ \Psi_{a2*r}\}$; but 23% for birds in AC and NF). Of all birds banded in their hatch year and subsequently recaptured, the proportions recaptured for the first time as SY, TY, and 4Y birds were 0.61, 0.32, and 0.07 for South NS, and 0.77, 0.09, and 0.14 for the Gulf, respectively. The age-specific recruitment rates (SY and TY^+) estimated with the recapture probability adjustment, as well as estimates of the mean number of eggs laid and hatching and fledging probabilities, are shown in Table 1, and the resulting projection

Table 2. The five best-fit models and the most general model (in bold) representing apparent survival (Φ), recapture (p) and movement (Ψ: Gulf only) probabilities for Piping Plovers nesting in southern Nova Scotia 1999 to 2002, and in the Gulf of St. Lawrence 1998–2002, as estimated with capture-recapture models in program MARK (multi-state models for the Gulf). Each model is shown with its deviance, number of parameters, difference in QAICc value from the best model (ΔQAICc) and relative QAICc weight (ωQAICc), using overdispersion values of South NS c-hat = 1.038 and Gulf c-hat = 1.058. Subscripts following the parameter indicate the variation: constant (.), time-variant (t), region-variant (r, where all regions differ, Gulf only), age-variant (a2, where juveniles take on adult rates after their first year), age-time interaction (a2*t), age-region interaction (a2*r), an additive age and time effect (a2+t), or regionally grouped (e.g., AC,NF:others indicates that the Acadian peninsula and Newfoundland were constrained to be equal, whereas Nova Scotia/New Brunswick, PEI, and Quebec were all constrained to be equal to one another but different from Acadia and Newfoundland). Differential variation between adults and juveniles is indicated by subscripts A and J.

Model	*# Parameters*	*Deviance*	$\Delta QAIC_c$	$\omega QAIC_c$
South NS				
$\Phi_{a2}\, p_{t}$	6	38.33	0.00	0.307
$\Phi_{a2}\, p_{a2+t}$	7	37.84	1.64	0.135
$\Phi_{a2}\, p_{AtJ.}$	7	38.25	2.04	0.110
$\Phi_{a2+t}\, p_{t}$	8	36.26	2.26	0.099
$\Phi_{a2}\, p_{.}$	3	47.33	2.42	0.092
$\Phi_{a2*t}\, p_{a2*t}$	**14**	**33.96**	**13.26**	**<0.001**
Gulf				
$\Phi_{a2*t}\, p_{a2*(AC,NF:others)}\, \Psi_{a2*r}$	54	254.46	0.00	0.982
$\Phi_{a2*t}\, p_{a2*r}\, \Psi_{a2*r}$	60	249.45	9.14	0.010
$\Phi_{a2}\, p_{a2*(AC,NF:others)}\, \Psi_{a2*r}$	46	282.73	9.79	0.007
$\Phi_{a2}\, p_{a2*r}\, \Psi_{a2*r}$	52	276.14	17.01	<0.001
$\Phi_{a2*t}\, p_{a2}\, \Psi_{a2*r}$	52	277.76	18.64	<0.001
$\Phi_{a2*t*r}\, p_{a2*t*r}\, \Psi_{a2*r}$	**134**	**171.38**	**129.10**	**<0.001**

matrices for each regional population segment are shown in Eqs. 2 and 3.

$$A_{SouthNS} = \begin{bmatrix} 0.2325 & 0.6359 & 0.6416 \\ 0.3279 & 0 & 0 \\ 0 & 0.7324 & 0.7324 \end{bmatrix} \quad (2)$$

$$A_{Gulf} = \begin{bmatrix} 0.2054 & 0.7261 & 0.7392 \\ 0.2395 & 0 & 0 \\ 0 & 0.7331 & 0.7331 \end{bmatrix} \quad (3)$$

Population Growth

Estimated λ_d, stable age distributions and age-specific reproductive values from deterministic models for each population segment are shown in Table 3. These estimates suggested that Piping Plovers in the Gulf were decreasing at about 3.6%/year (λ_d = 0.9651), and that South NS plovers were just maintaining stability in abundance (λ_d = 1.0043). The retrospective analysis (Caswell 2000, 2001, Cooch et al. 2001) indicated high variance in λ_d for both population segments, driven mainly by variation in adult apparent survival and hatching success (Table 4). Based on these values, the standard error on South NS λ_d was estimated at 0.1265, giving 95% confidence limits on λ_d = 1.0043 of (0.7563 to 1.2523); for the Gulf, the standard error was 0.0701, with 95% confidence limits on λ_d = 0.9651 of (0.8277 to 1.1025). Therefore, although the point estimates of λ_d suggested a fairly large difference in deterministic growth between the two population segments, the confidence interval overlap showed that there is also a high probability that the long-term growth rates were not in fact different. Moreover, although the point estimates of λ suggested a discrepancy in population trends inferred from the census (growth between 1998–2003) and the models (long-term decline), confidence intervals on λ_d included the census-derived estimates for both population segments.

Deterministic growth rates λ_d were viewed as the maximal potential rates, whereas stochastic rates were considered the lower limit, given that total variance (and not just process variance; Table 4) was used to estimate vital rate variability. Indeed, our estimates of stochastic growth rates (λ_s = 0.9263 for South NS, λ_s = 0.8214 for the Gulf) were substantially lower than λ_d, although again consistent in the direction of differences between the two population segments. These estimates provide further support for long-term declines in Piping Plover abundance in both South NS and the Gulf.

For both population segments, stable age distributions were similar (close to 50% HY, less than 15% SY), and SY and TY^+ birds contributed the most to reproductive value. In addition, elasticity estimates for both the Gulf and South NS suggest that, of all vital rates, adult apparent survival had proportionally a much stronger impact on λ_d than juvenile apparent survival or reproductive parameters, and that age-specific breeding probabilities had the least impact (Table 3).

The "life table response experiment" (Caswell 2001) suggested that, although F_2 and F_3 were higher in the Gulf than South NS, it was the higher S_1 estimate in South NS that resulted in the greater λ estimate for that population segment (Fig. 3). Thus, if the Gulf population segment is indeed experiencing a more rapid decline than South NS, as suggested by our λ_d and λ_s estimates as well as by beach census numbers, important differences in juvenile apparent survival could explain most of this divergence in population trends.

There was evidence that neither population segment may yet have reached its long-term trajectory. Census counts (Amirault 2005) do not distinguish between SY and TY^+ Piping Plovers, but relative proportions of fledgling vs. adult birds from the population census and productivity estimates suggest that the proportion of HY birds in both regional population segments was variable from 1998–2003 and consistently lower than in the projected stable age distribution. In the Gulf, the proportion of fledglings at the end of the breeding season ranged between 0.311 and 0.400 (mean 0.355), below the 0.492 expected based on the long-

Table 3. Deterministic growth rate estimates, stable age distribution, age-specific reproductive values, sensitivities, and elasticities for southern Nova Scotia and Gulf of St Lawrence population segments of Piping Plovers in eastern Canada, 1998–2003.

	South NS (λ_d = 1.0043)		**Gulf (λ_d = 0.9651)**	
Parameter	*Sensitivity*	*Elasticity*	*Sensitivity*	*Elasticity*
Φ_A	1.0140	0.7398	1.0090	0.7666
Φ_J	0.7970	0.2602	0.9404	0.2334
f	0.4235	0.2602	0.3212	0.2334
$\Phi_J{}^w = \Phi_J/f$	0.4918	0.2602	0.6596	0.2334
y_S	0.0748	0.0603	0.0564	0.0497
y_T	0.0545	0.0538	0.0428	0.0436
E	0.0687	0.2602	0.0572	0.2334
h	0.5678	0.2602	0.4400	0.2334
Age Class	*Stable Age Distribution*	*Reproductive Contribution*	*Stable Age Distribution*	*Reproductive Contribution*
Hatch-year (HY)	0.4533	0.1750	0.4921	0.1359
Second-year (SY)	0.1480	0.4120	0.1221	0.4311
Third-year or older (TY^+)	0.3986	0.4130	0.3858	0.4330

term growth rate λ_d (Table 3); similarly, the proportion of fledglings ranged from 0.315 to 0.429 (mean 0.369) in South NS, whereas a value of 0.453 was expected (Table 3). Given that λ represents the estimated long-term growth rate of a population once it has reached stable age distribution, these differences in age structure may explain the discrepancy between observed (census) population trends and expected growth from λ_d estimates. In particular, short-term projections (visualized in ULM) of annual changes in abundance starting from observed age distributions (i.e., observed HY proportions, with SY and TY+ proportions assumed proportional to stable distribution) suggested a temporary increase in abundance followed by long-term growth rate within ~3 years. Short-term growth before stabilizing at a lower long-term λ is consistent with transient dynamic expectations when the initial reproductive value is higher (i.e., fewer HY birds) than at stable age distribution (Koons et al. 2005).

Recovery Goals and Parameter Perturbations

Perturbation calculations were based upon deterministic matrices and estimates of λ_d, under the assumption that transient growth observed between 1998 and 2003 would soon be replaced by the long-term growth rate (see Discussion). For

Table 4. Variance in deterministic growth rate (λ_d) for Piping Plovers in southern Nova Scotia and the Gulf of St Lawrence 1998–2003, based on variance and sensitivity of each population parameter.

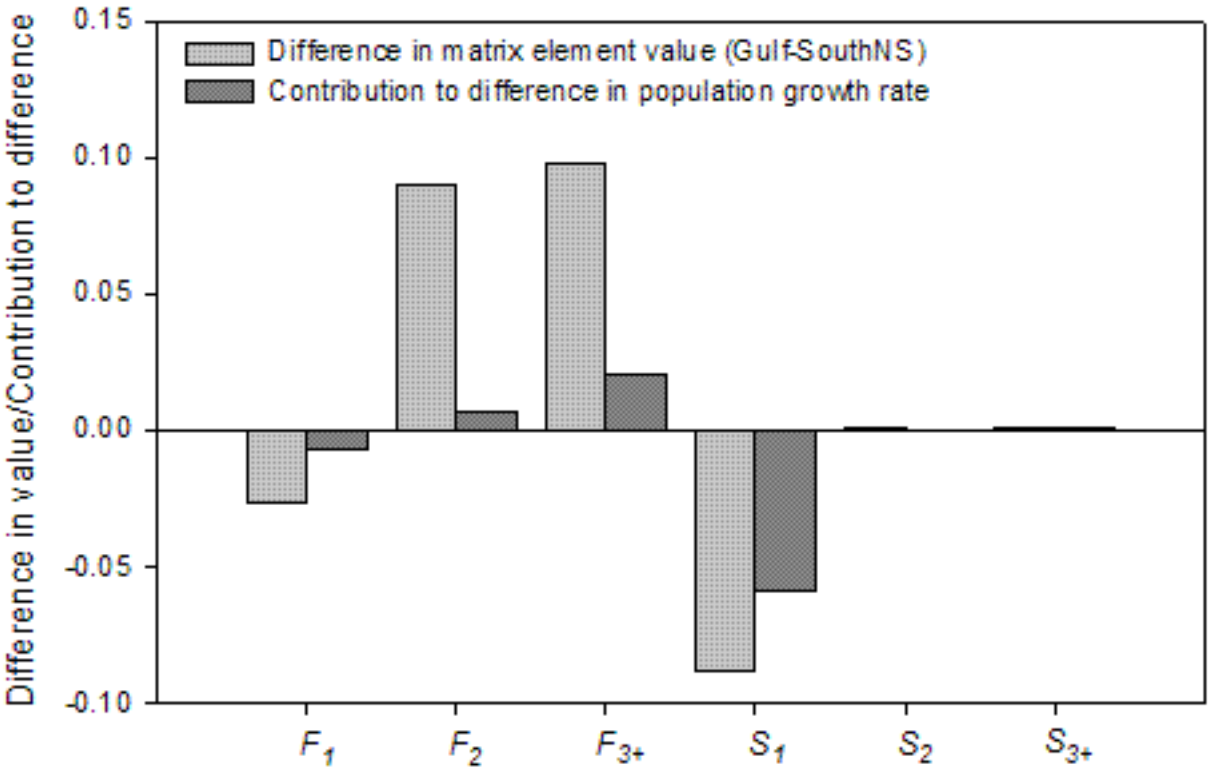
Parameter†	*Value*	*N*	*Variance V(x)*	*Sensitivity* ($\delta\lambda/\delta x$)	*Contribution to variance in* λ: $(\delta\lambda/\delta x)^2 * V(x)$
South NS					
Φ_A	0.7324	57	0.0044	1.0140	0.0045
Φ_J	0.3279	134	0.0039	0.7970	0.0025
y_s	0.8095	28	0.0055	0.0748	<0.0001
y_t	0.9910	28	0.0003	0.0545	<0.0001
E	3.8065	93	0.3317	0.0687	0.0016
h	0.4603	5	0.0229	0.5678	0.0074
				Total $V(\lambda)$	**0.0160**
Gulf					
Φ_A	0.7331	208	0.0015	1.0090	0.0015
Φ_J	0.2395	425	0.0014	0.9404	0.0013
y_s	0.8504	22	0.0058	0.0564	<0.0001
y_t	0.9823	22	0.0008	0.0428	<0.0001
E	3.9389	229	0.0840	0.0572	0.0003
h	0.5120	6	0.0098	0.4400	0.0019
				Total $V(\lambda)$	**0.0049**

† Note that only the annual juvenile survival rate (i.e., the product of fledging success and overwinter survival) is included here, as we have a direct estimate of its variance and the elements of the product *f* and Φ_J^w (i.e., Φ_J) always appear together.

South NS, attaining the stated recovery goal would necessitate a ~126% increase in abundance from 2005 population counts, requiring a value of λ_d = 1.1771 for recovery in 5 years, or λ_d = 1.0850 in 10 years (assuming an immediate change in growth rate). For the Gulf, the recovery goal demands a ~44% increase, requiring a value of λ_d = 1.0757 for recovery in 5 years, or λ_d = 1.0371 in 10 years (again assuming an immediate change in growth rate); vital rates would also have to increase in the Gulf just to attain stability (λ_d = 1). Both population segments, however, demonstrate a high elasticity of Φ_A, where the change in reproductive parameters required to attain long-term growth rates would be approximately threefold the change required in adult apparent survival. All perturbations required for stability or recovery are shown in Table 5.

If conservation efforts continued to target changes in productivity (i.e., fledglings/nest: *E*h*f*), elasticity values suggest that the average South NS productivity observed from 1998–2003 (1.08

Fig. 3. Difference in matrix element values (age-specific fertility F, and survival S) between the two regional eastern Canadian Piping Plover population segments (Gulf–South NS) between 1998 and 2003, and contribution of these differences to the difference in deterministic population growth rate (λ_d = 0.9651 for the Gulf, λ_d = 1.0043 for South NS).



fledglings/nest) should be sufficient for maintenance of that population segment at current levels, whereas 1.41 fledglings/nest (a 30.9% increase; Table 5) would be needed to reach the recovery goal within 10 years (assuming no change in apparent survival rates). In order to maintain the Gulf population segment (where average productivity was 1.41 fledglings/nest from 1998–2003) at its current abundance (i.e., λ_d = 1), productivity would have to increase by 15.5% to 1.63 fledglings/nest; to reach the recovery goal within 10 years, 1.86 fledglings/nest (a 32.0% increase) would be required; (Table 5). Most importantly, if any drop in current efforts to protect nesting beaches entailed a decline in productivity, λ_d would be substantially lower than currently observed and even more drastic parameter perturbations would be needed. For example, a 10% decline in productivity would result in λ_d = 0.978 for South NS plovers and λ_d = 0.943 in the Gulf, far below the growth rates required for recovery.

DISCUSSION

Population Growth and Dynamics of Population Segments

Parameter-specific sensitivities and elasticities provide a tool for identifying the vital rate changes that could bring about population recovery most

Table 5. Individual parameter changes required to attain the recovery targets (Amirault 2006) for two Piping Plover population segments in eastern Canada within 5 or 10 years, based on vital rates and population growth estimated from 1998–2003. Target abundance for recovery is 52 pairs (i.e., a 126% increase from 23 pairs in 2005) for South NS (current growth rate estimated at $\lambda_d = 1.0043$), and 273 pairs (a 44% increase from 190 pairs in 2005) for Gulf Piping Plovers (current growth rate estimated at $\lambda_d = 0.9651$). These parameter changes would be required immediately in order for the population to reach the target abundance within the stated time period, assuming current growth is accurately represented by λ_d. Required values that are not possible (i.e., probability of >1) are indicated as NA.

	Elasticity	*Current value*	*Change required*	*Value required*
South NS				
$\lambda_d = 1.1771$ (recovery within 5 years)				
Adult survival (Φ_A)	0.7398	0.7324	+23.26%	0.9027
Juvenile post-fledge survival (Φ_J^w)	0.2602	0.5314	+66.13%	0.8828
Hatching success (*h*)	0.2602	0.4603	+66.13%	0.7647
Fledging success (*f*)	0.2602	0.6171	+66.13%	*NA* (>1.0)
$\lambda_d = 1.0850$ (recovery within 10 years)				
Adult survival (Φ_A)	0.7398	0.7324	+10.86%	0.8120
Juvenile post-fledge survival (Φ_J^w)	0.2602	0.5314	+30.88%	0.6955
Hatching success (*h*)	0.2602	0.4603	+30.88%	0.6024
Fledging success (*f*)	0.2602	0.6171	+30.88%	0.8077
Gulf				
$\lambda_d = 1$ (stability near current size)				
Adult survival (Φ_A)	0.7666	0.7331	+4.72%	0.7677
Juvenile post-fledge survival (Φ_J^w)	0.2334	0.3415	+15.49%	0.3944
Hatching success (*h*)	0.2334	0.5120	+15.49%	0.5913
Fledging success (*f*)	0.2334	0.7014	+15.49%	0.8100
$\lambda_d = 1.0757$ (recovery within 5 years)				
Adult survival (Φ_A)	0.7666	0.7331	+14.95%	0.8427
Juvenile post-fledge survival (Φ_J^w)	0.2334	0.3415	+49.10%	0.5092
Hatching success (*h*)	0.2334	0.5120	+49.10%	0.7634

(con'd)

Fledging success (*f*)	0.2334	0.7014	+49.10%	*NA* (>1.0)
λ_d = 1.0371 (recovery within 10 years)				
Adult survival (Φ_A)	0.7666	0.7331	+9.73%	0.8044
Juvenile post-fledge survival (Φ_J^w)	0.2334	0.3415	+31.96%	0.4507
Hatching success (*h*)	0.2334	0.5120	+31.96%	0.6757
Fledging success (*f*)	0.2334	0.7014	+31.96%	0.9256

efficiently. For both population segments of Piping Plover in eastern Canada, adult survival had a much higher elasticity than juvenile survival or reproductive parameters, as is common for many migratory birds (Saether and Bakke 2000) and consistent with other Piping Plover populations (Ryan et al. 1993, Plissner and Haig 2000, Wemmer et al. 2001). Despite very similar elasticities, however, the two population segments may be experiencing different dynamics. The census data suggest that transient dynamics between 1998 and 2003 resulted in greater growth in the South NS population segment than in the Gulf (λ = 1.0584 vs. λ = 1.0276, assuming exponential growth), a difference consistent in direction and magnitude with both deterministic and stochastic projection-model long-term λ estimates for the same time period (i.e., more rapid decline in the Gulf than in South NS). However, high inter-annual variability in vital rates resulted in overlapping confidence intervals on λ_d estimates between population segments, and λ_s estimates suggested strong declines in both areas; thus we cannot confidently conclude any differences between the two segments.

Our estimates of annual adult apparent survival probability for both the Gulf (0.7324) and South NS (0.7331) population segments agreed very closely with a rate estimated for Piping Plovers breeding in the Atlantic U.S. (0.738; Plissner and Haig 2000). In contrast, although our South NS estimate of juvenile apparent post-fledging survival (0.5314) was higher than for U.S. Atlantic Piping Plovers (0.484; Plissner and Haig 2000), our much lower Gulf estimate (0.3415) more closely matched Great Plains and Great Lakes populations (0.318 and 0.31, respectively; Larson et al. 2000, Wemmer et al. 2001). Thus, although adult survival had the greatest proportional impact on population growth, the potential difference in regional λ was largely driven by juvenile post-fledging survival estimates.

Juvenile survival in the Gulf could have been underestimated as a result of low resighting effort in the more remote regions (the Acadian peninsula and Newfoundland; D. L. Amirault, personal observation); indeed, we estimated recapture probability to be substantially lower in these areas (26%) than in the rest of the Gulf (55%). However, mark-recapture models account for recapture probability as part of survival and dispersal estimation (White and Burnham 1999) so survival estimates should be unbiased regionally. Natal dispersal away from censused beaches could also result in underestimation of juvenile survival. Long-distance dispersal has been occasionally observed in other Piping Plover populations (e.g., Haig and Oring 1988b, Haig 1992), so natal dispersal observed among regions within the Gulf could also extend to outside areas (Greenwood and Harvey 1982). In particular, deterioration of nesting habitat can decrease philopatry to a natal area (Wiens and Cuthbert 1988, Paton and Edwards 1996, Haig and Oring 1988c), and many eastern Canadian nesting beaches are under threat from human development and disturbance (Amirault 2005). Nevertheless, dispersal of Piping Plovers is often localized (Haig and Oring 1988a,c, Wiens and Cuthbert 1988, Plissner and Haig 2000), and there is only one recorded case of a marked Canadian bird returning to breed in the U.S. (D. L. Amirault, unpublished data). Thus, even some degree of undetected emigration seems unlikely to be great enough alone to cause such low juvenile survival estimates in the Gulf.

The difference in estimates of juvenile apparent survival may, therefore, reflect a real threat posed to juvenile Piping Plovers from the Gulf region during one or more portions of their migratory life cycle. For instance, regular dispersal among breeding sites within the Gulf might itself have lowered juvenile survival if dispersers were at a competitive disadvantage when settling at a new breeding site, or if they failed to nest and, therefore, were not detected as breeders. Alternatively, negative effects of individual leg-bands could have contributed to juvenile mortality (Amirault et al. 2006b), although the same banding protocol was followed in both South NS and the Gulf (Amirault et al. 2006a). Lastly but most critically, we know little about the non-breeding habits of Piping Plovers or any particular dangers faced by Gulf juveniles during migration or overwintering that might reduce their survival (e.g., Goss-Custard et al. 1995, Drake et al. 2001, Haig et al. 2005). Until more is understood about the threats to Piping Plovers during the non-breeding majority of the year, we cannot fully discriminate among these explanations for low apparent juvenile survival in the Gulf.

Uncertainty Surrounding Current Population Trajectory

Incorporation of parameter variance will always give a more realistic representation of population dynamics because virtually all ecological processes are stochastic (Boyce 1992), but stochastic models are most useful if variance terms can be estimated. Given the short time span over which we calculated vital rates, we were unable to separate sampling variance from biologically relevant process variance such as inter-annual fluctuation in vital rates (Link and Nichols 1994, Gould and Nichols 1998). We nonetheless estimated stochastic λ based on this total variance, taking λ_s as the minimal possible growth rate (process variance overestimated), and λ_d as the maximal value (process variance underestimated; Caswell 2001), and the large gap between the two estimates further illustrated our uncertainty in population trajectory. Consequently, differences between observed census trends and model projections may in part reflect unknown process error associated with vital rates for both Piping Plover population segments (as supported by the inclusion of census-derived growth rates within λ_d confidence intervals), and suggest the need for vital rate estimation over longer time periods.

An even more important contributor to the census vs. model discrepancy, however, was the pattern of transient dynamics exhibited by the population over the period of study. Long-term growth rate λ characterizes the expected rate of change for a population at stable age distribution, but until that distribution is reached the rate can greatly differ from λ (Taylor 1995, Caswell 2001, Koons et al. 2005). From 1998–2003, fewer HY plovers were observed during the annual productivity census on breeding grounds than expected at stable distribution. This brought a temporary rate of growth higher than λ because of the greater relative reproductive contribution of AHY birds than HY birds, reflected in the increase in abundance observed on census counts and contrasting decline projected by λ estimates. Transient dynamics not only alter population trajectory in the short term, but also influence vital rate sensitivities (Koons et al. 2005), effectiveness of management strategies (Fefferman and Reed 2006), and overall abundance (Koons et al. 2006). However, despite this short-term transient growth, we felt justified in using long-term λ estimates throughout our analyses, as the short generation times of Piping Plovers and the relatively minor divergence from stable age structure should minimize the overall effects of transient population dynamics (Koons et al. 2006). Indeed, the sharp decline in abundance already observed in 2004–2005 in both regions supports this projection of transitory growth between 1998 and 2003, followed by a decline in the long term in both population segments.

Perturbations and Population Recovery

Historically, improvement of reproductive success has been the focus of most Piping Plover conservation efforts (e.g., Wemmer et al. 2001, Larson et al. 2003), because productivity may vary greatly with environmental conditions (Amirault 2006). Our estimates of mean productivity for both the Gulf (1.41 fledglings/nest) and South NS (1.08) fell within the range suggested by other studies (e. g., Burger 1987, Prindiville-Gaines and Ryan 1988, Plissner and Haig 2000), although South NS was at the lower end, and annual productivity varied in both population segments. Because of low elasticities, relatively major increases in reproductive parameters would be necessary to return eastern Canada Piping Plovers to desired levels, and recovery may be most feasible if several vital rates are improved simultaneously. In particular, the high

elasticity of adult survivorship makes it an important demographic variable to target in conservation efforts. However, adult survival may not actually be a very flexible parameter, as sensitivity is not always related to variability (Morris and Doak 2004) and adult survival for eastern Canadian birds was very similar to that of U.S. Atlantic birds whose population is steadily growing (Haig et al. 2005). Nonetheless, little is known about Piping Plovers during migration or on wintering grounds, and potentially high winter site fidelity further suggests that reduction of adult mortality year round should be a priority for managers (Root et al. 1992, Drake et al. 2001, Haig et al. 2005).

Although eastern Canadian Piping Plovers may be currently experiencing short-term transient growth, we based our projections on deterministic long-term λ values and associated elasticities for use in these perturbation scenarios. Annual population projections suggested that current age distribution could be replaced by the stable age distribution and long-term growth rate within a few years, and census observations indicated that the projected decline may have begun shortly after the time period used for modeling. Moreover, abundance for both population segments remains well below recovery targets, and thus we felt that planning of future conservation efforts should rely upon the more conservative projections of population trajectory (long-term decline suggested by λ estimates) which now appears to have begun (since 2004), instead of the potentially misleading temporary growth demonstrated in census numbers between 1998–2003.

CONCLUSIONS

Identification of the links between habitat and population vital rates is crucial to the protection of critically small populations (Root 1998). For eastern Canadian Piping Plovers, reduced productivity in South NS and extremely low post-fledge survival of juveniles in the Gulf may be a reflection of anthropogenic habitat disturbance at nesting beaches (Patterson et al. 1991, Haig 1992, Melvin and Hecht 1994). However, important habitats throughout the entire annual migratory cycle must be considered comprehensively (Esler 2000, Webster et al. 2002), as even small declines in adult survival could have a much greater impact on λ than equivalent increases in productivity, and non-breeding conditions may affect fitness in subsequent seasons (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004). Thus, although protection of breeding areas may significantly improve reproductive success and site fidelity (Wiens and Cuthbert 1988, Paton and Edwards 1996, Haig and Oring 1988c), this should not be the only focus of conservation efforts (e.g., Crowder et al. 1994, Cuthbert et al. 2001). Indeed, extensive efforts to protect nesting areas for this population (Amirault 2006) were insufficient to prevent sharp declines observed in 2004 and 2005.

Both population segments of eastern Canadian Piping Plover remain well below recovery targets, and much uncertainty exists regarding vital rates and expected population trajectories. Therefore, we suggest three principal directions for their conservation and recovery. First, current protection of nesting beaches should be maintained, given that productivity is low and reproductive parameters may be relatively flexible vital rates. Second, short-term viability requires an understanding of threats to both adult and juvenile survival during non-breeding seasons, and therefore, more research effort must be directed toward this end. Third, long-term sustainability necessitates a quantification of the effectiveness of specific habitat-related conservation actions in increasing population vital rates at nesting, migration and wintering sites. Such measures could be implemented immediately, and continually assessed to monitor their effects. More broadly, our study demonstrates some of the particular challenges of assessing the status and conservation needs of endangered populations, as well as the value of comprehensive monitoring of each phase of the annual cycle of long-distance migrants.

Responses to this article can be read online at:
http://www.ace-eco.org/vol1/iss3/art4/responses/

Acknowledgments:

We wish to thank the Piping Plover Recovery Team and Working Group for supporting this research program. Staff of the Piper Project, Irving Ecocentre - La Dune de Bouctouche, Canadian Parks and Wilderness Society, Island Nature Trust, Attention FragÎles, Nova Scotia Department of Natural Resources, Kejimkujik National Park Seaside

Adjunct, Kouchibouguac National Park, and Prince Edward Island National Park were instrumental in providing field support. We thank the researchers involved in ensuring the success of the regional project, most notably: K. Baker, P. Thomas, P. Laporte, L. MacDonnell, J. Stewart, A. Marsters, A. Boyne, and S. Flemming. Funding for field work was provided by the Canadian Wildlife Service Atlantic and Quebec regions. Funding for modeling work was provided by an Interdepartmental Recovery Fund (Grant 180) to Donald Forbes and the Geological Survey of Canada. Suggestions from S. Walde, M. Leonard, D. Fraser, G. Robertson, R. Rockwell, and an anonymous reviewer greatly improved previous versions of the manuscript.

LITERATURE CITED

Amirault, D. L. (editor). 2005. *The 2001 International Piping Plover census in Canada.* Technical Report Series No. 436. Environment Canada, Canadian Wildlife Service, Atlantic Region, Sackville, New Brunswick, Canada.

Amirault, D. L. 2006. Recovery strategy for Piping Plovers (*Charadrius melodus melodus*) in Canada. [Proposed.] *in Species at Risk Act Recovery Strategy Series.* Environment Canada, Ottawa, Ontario, Canada.

Amirault, D. L., F. Shaffer, and J. Stewart. 2006a. *Eastern Canada Piping Plover banding summary.* Technical Report Series No. 458. Environment Canada, Canadian Wildlife Service, Atlantic Region, Sackville, New Brunswick, Canada.

Amirault, D. L., J. McKnight, F. Shaffer, K. Baker, L. MacDonnell, and P. Thomas. 2006b. Novel anodized aluminium bands cause leg injuries in Piping Plover (*Charadrius melodus melodus*). *Journal of Field Ornithology* **77**:18–20.

Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London Series B* **271**:S215–S218.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**:821–841.

Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* **23**481–506.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics* **49**:1173–1187.

Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. *Condor* **89**:811–818.

Burger, J. 1994. The effect of human disturbance on foraging behavior and habitat use in Piping Plover (*Charadrius melodus*). *Estuaries* **17**:695–701.

Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach.* Springer-Verlag, New York, New York, USA.

Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. *Wilson Bulletin* **94**:531–545.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**:619–627.

Caswell, H. 2001. *Matrix population models: construction, analysis and interpretation.* Second Edition, Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Cooch, E. G., G. Gauthier, and R. F. Rockwell. 2003. Apparent differences in stochastic growth rates based on timing of census: a cautionary note. *Ecological Modelling* **159**:133–143.

Cooch, E. G., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs* **71**:377–400.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**:1412–1423.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and

T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* **4**:437–445.

Cuthbert, R., D. Fletcher, and L. S. Davis. 2001. A sensitivity analysis of Hutton's shearwater: prioritizing conservation research and management. *Biological Conservation* **100**:163–172.

Drake, K. R., J. E. Thompson, K. L. Drake, and C. Zonick. 2001. Movements, habitat use and survival of nonbreeding Piping Plovers. *Condor* **103**:259–267.

Durell, S. E. A. L. V., J. D. Goss-Custard, and R. T. Clarke. 1997. Differential response of migratory subpopulations to winter habitat loss. *Journal of Applied Ecology* **34**:1155–1164.

Efron, B. 1979. Bootstrap methods: another look at the jackknife. *Annals of Statistics* **7**:1–26.

Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. *Conservation Biology* **14**:366–372.

Espie, R. H. M., R. M. Brigham, and P. C. James. 1996. Habitat selection and clutch fate of Piping Plovers (*Charadrius melodus*) breeding at Lake Diefenbaker, Saskatchewan. *Canadian Journal of Zoology* **74**:1069–1075.

Espie, R. H. M., P. C. James, and R. M. Brigham. 1998. The effects of flooding on Piping Plover *Charadrius melodus* reproductive success at Lake Diefenbaker, Saskatchewan, Canada. *Biological Conservation* **86**:215–222.

Fefferman, N. H., and J. M. Reed. 2006. A vital rate sensitivity analysis for nonstable age distributions and short-term planning. *Journal of Wildlife Management* **70**:649–656.

Flemming, S. P., R. D. Chiasson, and P. J. Austin-Smith. 1992. Piping Plover nest site selection in New Brunswick and Nova Scotia. *Journal of Wildlife Management* **56**:578–583.

Goldin, M. R., and J. V. Regosin. 1998. Chick behavior, habitat use, and reproductive success of Piping Plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology* **69**:228–234.

Goossen, J. P., D. L. Amirault, J. Arndt. R. Bjorge, S. Boates, J. Brazil, S. Brechtel, R. Chiasson, G. N. Corgett, R. Curley, M. Elderkin, S. P. Flemming, W. Harris, L. Heyens, D. Hjertaas, M. Huot, B. Johnson, R. Jones, W. Koonz, P. Laporte, D. McAskill, R. I. G. Morrison, S. Richard, F. Shaffer, C. Stewart, L. Swanson, and E. Wiltse. 2002. *National recovery plan for the Piping Plover (*Charadrius melodus*).* National Recovery Plan No. 22. Recovery of Nationally Endangered Wildlife, Ottawa, Ontario, Canada.

Goss-Custard, J. D., R. T. Clarke, K. B. Briggs, B. J. Ens, K. M Exo, C. Smit, A. J. Beintema, R. W. G. Caldow, D. C. Catt, N. A. Clark, S. E. A. L. V. D. Durell, M. P. Harris, J. B. Hulscher, P. L. Meininger, N. Picozzi, R. Prys-Jones, U. N. Safriel, and A. D. West. 1995. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. *Journal of Applied Ecology* **32**:320–326.

Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. *Ecology* **79**:2531–2538.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**:1–21.

Haig, S. M. 1992. Piping Plover. *In* A. Poole, P. Stettenheim, and F. Gill, editors. *The birds of North America*. The Academy of Natural Sciences and The American Ornithologists' Union, Philadelphia PA and Washington DC, USA.

Haig, S. M., and E. Elliott-Smith. 2004. Piping Plover. Number 2 *in* A. Poole, editor. *The Birds of North America Online*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. (online) URL: http://bna.birds.cornell.edu/BNA/account/Piping_Plover/.

Haig, S. M., C. L. Ferland, F. J. Cuthbert, J. Dingledine, J. P. Goossen, A. Hecht, and N. McPhillips. 2005. A complete species census and evidence for regional declines in Piping Plovers. *Journal of Wildlife Management* **69**:160–173.

Haig, S. M., and L. W. Oring. 1988a. Genetic differentiation of Piping Plovers across North America. *Auk* **105**:260–267.

Haig, S. M., and L. W. Oring. 1988b. Mate, site,

and territory fidelity in Piping Plovers. *Auk* **105**:268–277.

Haig, S. M., and L. W. Oring. 1988c. Distribution and dispersal in the Piping Plover. *Auk* **105**:630–638.

Knetter, J. M., S. M. Lutz, J. R. Cary, and R. K. Murphy. 2002. A multi-scale investigation of Piping Plover productivity on Great Plains alkali lakes, 1994–2000. *Wildlife Society Bulletin* **30**:683–694.

Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population size. *Ecological Modelling* **185**:283–297.

Koons, D. N., R. F. Rockwell, and J. B. Grand. 2006. Population momentum: implications for wildlife management. *Journal of Wildlife Management* **70**:19–26.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* **75**:601–607.

Larson, M. A., M. R. Ryan, and B. G. Root. 2000. Piping Plover survival in the Great Plains: an updated analysis. *Journal of Field Ornithology* **71**:721–729.

Larson, M. A., M. R. Ryan, and R. K. Murphy. 2002. Population viability of Piping Plovers: effects of predator exclusion. *Journal of Wildlife Management* **66**:361–371.

Larson, M. A., M. R. Ryan, and R. K. Murphy. 2003. Assessing recovery feasibility for Piping Plovers using optimization and simulation. *Wildlife Society Bulletin* **31**:1105–1116.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**:67–118.

Legendre, S., and J. Clobert. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* **22**:817–824.

Link, W. A., and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos* **69**:539–544.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**:1884–1886.

MathWorks, Inc. 2002. *MATLAB 6.5.* Natick, Massachussetts, USA.

Melvin, S. M., and A. G. C. R. Hecht. 1994. Piping Plover mortalities caused by off-road vehicles on Atlantic coast beaches. *Wildlife Society Bulletin* **22**:409–414.

Morris, W. F., and D. F. Doak. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *American Naturalist* **163**:579–590.

Nicholls, J. L., and G. A. Baldassarre. 1990. Habitat associations of Piping Plovers wintering in the United States. *Wilson Bulletin* **102**:581–590.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London Series B* **271**:59–64.

Paton, P. W. C., and T. C. Edwards. 1996. Factors affecting interannual movements of snowy plovers. *Auk* **113**:534–543.

Patterson, M. E., J. D. Fraser, and J. W. Roggenbuck. 1991. Factors affecting Piping Plover productivity on Assateague Island. *Journal of Wildlife Management* **55**:525–531.

Plissner, J. H., and S. M. Haig. 2000. Viability of Piping Plover *Charadrius melodus* metapopulations. *Biological Conservation* **92**:163–173.

Prindiville-Gaines, E., and M. R. Ryan. 1988. Piping Plover habitat use and reproductive success in North Dakota. *Journal of Wildlife Management* **52**:266–273.

Root, B. G., M. R. Ryan, and P. M. Mayer. 1992. Piping Plover survival in the Great Plains. *Journal of Field Ornithology* **63**:10–15.

Root, K. V. 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications* **8**:854–865.

Ryan, M. R., B. G. Root, and P. M. Mayer. 1993. Status of Piping Plovers in the Great Plains of North America: a demographic simulation model. *Conservation Biology* **7**:581–585.

Saether, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642–653.

Schwarz, C. J., J. F. Schweigart, and A. N. Arnason. 1993. Estimating migration rates using tag recovery data. *Biometrics* **49**:177–193.

Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* **9**:551–558.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* **17**:76–83.

Wemmer, L. C., U. Ozesmi, and F. J. Cuthbert. 2001. A habitat-based population model for the Great Lakes population of the Piping Plover (*Charadrius melodus*). *Biological Conservation* **99**:169–181.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**:S120–S138.

Wiens, T. P., and F. J. Cuthbert. 1988. Nest-site tenacity and mate retention of the Piping Plover. *Wilson Bulletin* **100**:545–553.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer chinook salmon. *Conservation Biology* **17**:782–794.

APPENDIX 1. Equations for calculating required parameter changes for stability (i.e. $\lambda = 1$) or population recovery.

Equation A1: calculating the growth rate required to reach a particular abundance (λ_{target}); this step not required for analyses where the goal is population stability, as λ_{target} is known (=1)

$$\frac{N_{target}}{N_{current}} = \lambda_{target}^{\ t} \quad \rightarrow \quad \lambda_{target} = \sqrt[t]{\frac{N_{target}}{N_{current}}}$$

where N_{target} = abundance objective
$N_{current}$ = current abundance
t = desired time period in which to reach objective

Equation A2: calculating the individual parameter changes required to reach a new growth rate

$$\Delta_i = \frac{\left[\left(\frac{\lambda_{target}}{\lambda_{current}}\right) - 1\right]}{e_i}$$

where λ_{target} = target population growth rate (calculated with Equation A1)
$\lambda_{current}$ = current population growth rate
Δ_i = relative change in parameter i (e.g. Δ=0.05 for +5%, Δ=-0.10 for -10%)
e_i = elasticity value of parameter i