Effects of exploitation on an overabundant species: the lesser snow goose predicament

David N. Koons[1]*, Robert F. Rockwell[2] and Lise M. Aubry[3]

[1]*Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, USA;* [2]*Division of Vertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; and* [3]*Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, USA*

Summary

1. Invasive and overabundant species are an increasing threat to biodiversity and ecosystem functioning world-wide. As such, large amounts of money are spent each year on attempts to control them. These efforts can, however, be thwarted if exploitation is compensated demographically or if populations simply become too numerous for management to elicit an effective and rapid functional response.

2. We examined the influence of these mechanisms on cause-specific mortality in lesser snow geese using multistate capture–reencounter methods. The abundance and destructive foraging behaviours of snow geese have created a trophic cascade that reduces (sub-) Arctic plant, insect and avian biodiversity, bestowing them the status of 'overabundant'.

3. Historically, juvenile snow geese suffered from density-related degradation of their saltmarsh brood-rearing habitat. This allowed harvest mortality to be partially compensated by non-harvest mortality (process correlation between mortality sources: $\rho = -0.47$; 90% BCI: -0.72 to -0.04). Snow goose family groups eventually responded to their own degradation of habitat by dispersing to non-degraded areas. This relaxed the pressure of density dependence on juvenile birds, but without this mechanism for compensation, harvest began to have an additive effect on overall mortality ($\rho = 0.60$; 90% BCI: -0.06 to 0.81). In adults, harvest had an additive effect on overall mortality throughout the 42-year study ($\rho = 0.24$; 90% BCI: -0.59 to 0.67).

4. With the aim of controlling overabundant snow geese, the Conservation Order amendment to the International Migratory Bird Treaty was implemented in February of 1999 to allow for harvest regulations that had not been allowed since the early 1900s (e.g. a spring harvest season, high or unlimited bag limits and use of electronic calls and unplugged shotguns). Although harvest mortality momentarily increased following these actions, the increasing abundance of snow geese has since induced a state of satiation in harvest that has driven harvest rates below the long-term average. More aggressive actions will thus be needed to halt the growth and spread of the devastating trophic cascade that snow geese have triggered.

5. Our approach to investigating the impacts of population control efforts on cause-specific mortality will help guide more effective management of invasive and overabundant species world-wide.

Key-words: additive mortality, capture–mark–recapture, cause-specific mortality, *Chen caerulescens caerulescens*, compensatory mortality, harvest, native invasive species, population control

Introduction

Species invasions are an increasingly common threat to world-wide biodiversity (Vitousek *et al.* 1996; Butchart *et al.* 2010), ecosystem function (O'Connor & Crowe 2005; Peltzer *et al.* 2010) and spread of infectious diseases (Mack *et al.* 2000). In the USA alone, putative damages and costs associated with attempts to control invasive species amount to >$120 billion per year (Pimentel, Zuniga & Morrison 2005). Interestingly, the same problems often apply to overabundant native species (Garrott,

*Correspondence author. E-mail: david.koons@usu.edu

White & White 1993; Valéry *et al.* 2009; Carey *et al.* 2012). Population growth and spread of overabundant and invasive species can thus have widespread biological and economic consequences.

Often times, however, efforts to control such species do not have the anticipated effects because removal efforts are compensated demographically (e.g. density-dependent responses in reproductive success, dispersal or survival), or because the population numerically swamps out the ability of control measures to have any meaningful effect (Simberloff 1997). Most striking is the failure of lethal control measures aimed at reducing survival, a key driver of population dynamics in long-lived species (Sæther & Bakke 2000). Although such efforts have obvious effects on the fates of exploited (e.g. harvested) individuals, the overall survival probability in the targeted population might not be affected because of 'compensatory mortality': a phenomenon that has received a great deal of attention in resource-consumer theory, pest control and harvest management of game species (e.g. Errington 1956; Anderson & Burnham 1976; Hawkins, Thomas & Hochberg 1993).

Several mechanisms can produce compensatory mortality and hinder a manager's ability to control an invasive species. For example, exploitation is commonly thought to lower the seasonal density of a population, thereby freeing up resources for those surviving and potentially improving their survival in the following season (i.e. for every life taken, a life is saved; Boyce, Sinclair & White 1999), but the density-dependent mechanism could occur at various points along the seasonal life cycle (Sedinger & Herzog 2012). Compensatory mortality can also occur when exploitation simply changes the cause of death for 'frail' individuals that would have likely died from other causes (Errington 1956; Lebreton 2005; Péron 2013).

The alternative to compensation is the hypothesis that exploitation has an 'additive' effect on mortality, that is, any exploited individual would have survived in the absence of exploitation. In reality, these hypotheses are just two points on a continuum of possibilities that include partial compensation (e.g. for every two lives taken, one is saved) and overadditivity (Fig. 1), which occurs when natural mortality increases with exploitation-related mortality (e.g. from increased stress or changes in behaviour amongst individuals exposed to the disturbance of exploitation; Pauli & Buskirk 2007; Burke *et al.* 2008). Accurately estimating the effect of exploitation on total mortality along this continuum is essential for measuring the ability to control an overabundant species.

Even if exploitation has an additive effect on mortality, control could still be difficult if efforts are implemented after a species has become overabundant (Mack *et al.* 2000). When a population grows faster than the number exploited, rates of exploitation will become progressively small (Simberloff 1997). In such cases, management efforts will fail unless alternative methods can be found.

These issues are currently top priorities for the management of lesser snow geese (*Chen caerulescens caerulescens*;
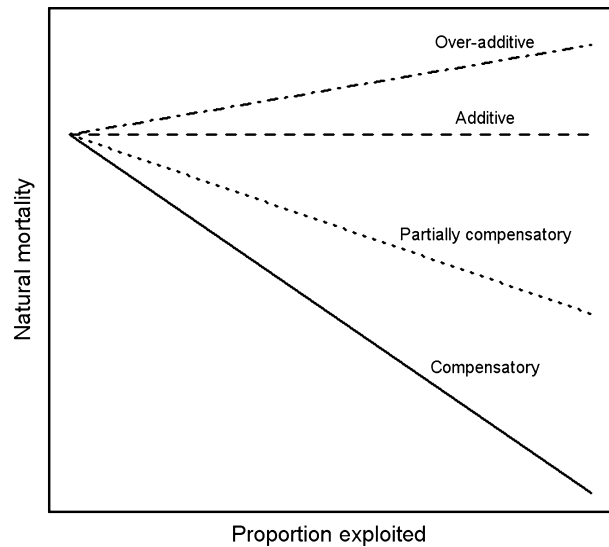

Fig. 1. Variation in natural mortality as a function of variation in the proportion of the population exploited each time step (e.g. the harvest rate). Shown are the complete compensatory (solid line), partially compensatory (dotted line) additive (dashed line) and overadditive (dash-dot line) relationships.

hereafter, snow geese; Leafloor, Moser & Batt 2012). Agricultural changes to the North American landscape have released the mid-continent population of snow geese from food limitation on their migration and wintering grounds (Abraham, Jefferies & Alisauskas 2005). This has led to a demographic explosion (Alisauskas *et al.* 2011), and more snow geese than Arctic and sub-Arctic ecosystems can support during the breeding season. As snow geese flourish, their destructive foraging behaviours have severely degraded coastal breeding habitats in the north; in turn creating a trophic cascade that has reduced the biodiversity of plant, insect and avian species that depend on these habitats (Milakovic & Jefferies 2003; Rockwell *et al.* 2003; Abraham, Jefferies & Alisauskas 2005). Snow geese have avoided classic density-dependent population regulation by invading new habitats on their breeding grounds, eventually propagating the trophic cascade across larger areas of the Arctic and sub-Arctic (Jefferies, Jano & Abraham 2006). These birds have thus been officially listed as 'overabundant' by the Canadian Wildlife Service and the U.S. Fish & Wildlife Service (Leafloor, Moser & Batt 2012).

Studies of additive and compensatory mortality in geese suggest that hunter harvest has an additive effect (Gauthier *et al.* 2001; Alisauskas *et al.* 2006), but could be compensatory when harvest rates are very low (*c.* 1% or lower; Sedinger *et al.* (2007) and Alisauskas *et al.* (2011)). Given this evidence, and the fact that changes in snow goose survival have a much greater impact on snow goose population dynamics than equivalent changes in reproductive success (Rockwell, Cooch & Brault 1997; Aubry, Rockwell & Koons 2010), the Canadian and the USA governments initiated a drastically liberalized harvest management programme in 1999 to reduce the numbers of snow geese in

hope of mitigating ecosystem collapse (i.e. the Conservation Order amendment to the Migratory Bird Treaty). Those attempts have not yet been successful (Alisauskas *et al.* 2011). Here, we revisit the additive and compensatory mortality hypotheses in snow geese using modern statistical approaches that provide direct insight into cause-specific mortality, and the degree to which harvest mortality is compensated by other causes (e.g. Servanty *et al.* 2010).

Given previous research, we had strong reason to think that the amount of compensation in harvest-related mortality among juvenile birds may have changed over time. Until *c.* 1990, juvenile birds suffered from density-related degradation of the saltmarsh habitat near LaPérouse Bay, where families traditionally reared their goslings (Cooch, Rockwell & Brault 2001). After 1990, family groups began dispersing into new habitats (including freshwater marsh habitat). In response to these movements, both gosling body condition and juvenile survival have improved (Aubry *et al.* 2013), indicating that young birds may have been released from bottom-up density regulation. Thus, we hypothesized that the degree of compensation differed between snow goose age classes, and between the time periods when the force of density regulation changed. Moreover, we examined the effect of growing snow goose abundance on harvest mortality to determine whether the population is swamping out hunters and reducing the fraction actually harvested over time. If so, it may simply be too late for current management efforts to have any effect on this overabundant species, thereby providing a scientific basis for consideration of alternative control policies.

Materials and methods

STUDY AREA AND DATA COLLECTION

Data were collected as part of a long-term study of breeding snow geese at La Pérouse Bay and the larger Cape Churchill Peninsula 'CCP' region in northern Manitoba (58°44′ N, 94°28′ W; see Fig. 1 in Rockwell, Gormezano & Koons 2011). Every year in late July when the adults are moulting and before the young can fly, snow geese are rounded up with the aid of a helicopter; then aged, sexed and banded. Birds are marked with uniquely numbered USGS aluminium leg bands. Here, we used data on females captured as goslings, 1-year-olds and adults (2 years old and older '2+') between 1969 and 2010. During this time period, we banded and released 86210 females (not including individuals marked with neck collars or reward bands). Subsequent live recaptures (and resightings) were recorded during the summers of 1970–2011 (4769). We did not include males in the analysis because of their low fidelity to the study area and associated recapture probability that is approximately zero (Cooch, Rockwell & Brault 2001). We also used dead recoveries reported by hunters to the USGS Bird Banding Laboratory between the fall of 1969 and May 2011 (i.e. between September and May of each year; 10126 recoveries). Other types of dead recoveries were rare and not used in analyses. Thorough descriptions of the study site, field methods and data collection protocols are provided by Cooke, Rockwell & Lank (1995).

CAPTURE−REENCOUNTER MODEL FOR CAUSE-SPECIFIC MORTALITY

Rather than using the traditional Burnham (1993) model for joint analysis of live recaptures and dead recoveries, we analysed the data using a multistate model with an alive state (A), a dead state for individuals that were harvested (H; i.e. legally hunted) and an unobservable dead state for individuals that died from non-harvest causes (NH). Under this more flexible modelling framework, we were able to explicitly estimate the probability of individual i dying from cause k between year t and $t+1$ ($\mu_{i,t}^k$) by fixing the survival probabilities for individuals in states A, H and NH to 1, 0 and 0, respectively. In addition, we fixed the probabilities of transitioning 'from' states H and NH to any other state to 0, and the probabilities of 'remaining' in states H and NH to 1 (i.e., the dead states were defined as absorbing states). By fixing these parameters, the remaining transition probabilities from state A to H and from state A to NH become cause-specific mortality probabilities $\mu_{i,t}^k$ (Schaub & Lebreton 2004; Gauthier & Lebreton 2008). The probability of surviving and remaining alive is simply the complement of all cause-specific mortality probabilities (see Fig. 2). This parameterization allowed us to use the logit link to constrain each $\mu_{i,t}^k$ to the interval [0,1] without invoking unnecessary relationships among parameters (which can occur with the generalized logit link).

We estimated the $\mu_{i,t}^k$ conditionally on state-specific probabilities of observing each individual i in state k and year t ($p_{i,t}^k$). We defined $p_{i,t}^A$ as the probability of recapturing a live individual, and $p_{i,t}^H$ as the probability that an individual that was shot and killed by a hunter was actually 'retrieved and reported'. Note that unlike the K and r parameters in the Brownie and Seber models, respectively (Cooch & White 2012), $p_{i,t}^H$ refers only to the probability of a shot bird being 'retrieved and reported' and does not include any component of mortality. Given our data, $p_{i,t}^{NH}$ was not observable and thus fixed to 0. We were nevertheless able to identify estimates of $\mu_{i,t}^{NH}$ by borrowing information from the joint live recaptures and hunting recoveries, and by invoking modelling constraints (see below; Schaub & Lebreton 2004; Schaub & Pradel 2004). In years when there was no banding
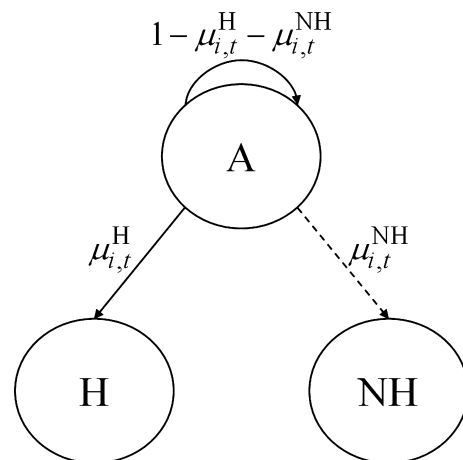

Fig. 2. The observable (solid lines) demographic transitions of remaining alive (A), dying from harvest (H) and the unobservable (dashed line) transition of dying from non-harvest causes (NH), where μ denotes the cause-specific mortality (subscripts are as described in the text).

(1996, 1997, and 2009; the latter of which occurred because of complete nesting failure), or when a given age class was not available for banding (due to extremely late hatch or post-hatch reproductive failure in 2002 and 2004), we fixed the relevant detection probabilities to 0.

DATA ANALYSIS

Cooch, Rockwell & Brault (2001) found that hatch-year (*hy*) survival, fidelity and band recovery probabilities differ from those for after-hatch-year (*ahy*) snow geese in our study population. An analysis of more recent data supported these differences and further found that live recapture probabilities increase with age up to age 3+ (Aubry *et al.* 2013). Given this information, we systematically implemented differences between the *hy* and *ahy* age classes for $\mu_{i,t}^k$ and $p_{i,t}^H$ in our multistate models, and parameterized a 3 age-class effect for $p_{i,t}^A$ (individuals recaptured at age 1, 2 and 3+). In addition, because some females banded as adults may not have been local breeders (e.g. transient moult migrants), heterogeneity in site fidelity exists among this group of banded birds (Cooch, Rockwell & Brault 2001). Rather than discarding the large number of birds banded as adults from the analysis, we parameterized the recapture probability for the year immediately following first capture as an adult separately from subsequent years to isolate and control for a possible effect of transients on $p_{3+,t}^A$ (Pradel *et al.* 1997; given our model, fidelity is subsumed within p^A).

In addition to these effects, we compared alternative forms of temporal variation in the $p_{i,t}^k$ parameters using Akaike Information Criterion (AIC; Akaike 1973). While implementing age-class effects for the $\mu_{i,t}^k$, we compared age class by time bin (temporal change was allowed to occur every 3 years) and age class by cubic time trend models to an age-class model without temporal variation in $p_{i,t}^A$. Exploration of full time variation in $p_{i,t}^A$ indicated that the chance of recapturing a live individual was high in the early years of study when >50% of the birds were banded and solely used La Pérouse Bay, but then dropped as the population grew and expanded. Recapture probabilities have since rebounded in the last decade because we have learned where most of the families now raise their goslings. The cubic time trend in $p_{i,t}^A$ was thus considered to more parsimoniously model this time variation. Rather than expending degrees of freedom on estimating full time variation in $p_{i,t}^H$ (see definition above), we considered it to be a function of previously published band-reporting rates (the probability that a hunter actually reports an in-hand banded bird to the USGS BBL) implemented as a time-varying covariate for each age class. The covariate values were assumed to be equal to those listed in Alisauskas *et al.* (2011). We also considered age class by time invariant and time bin models for $p_{i,t}^H$. We implemented each model in RMark (Laake & Rexstad 2012) and used simulated annealing to maximize model likelihoods. Simulated annealing is effective at finding the global maximum likelihood in multistate data that may have multiple local maxima.

As a step towards examining compensation in the harvest-related mortality probabilities, we implemented the best parameterization for $p_{i,t}^k$ from above alongside full age class by time effects for the $\mu_{i,t}^k$ (Sedinger *et al.* 2010). In addition, we implemented time-varying covariates for the $\mu_{i,t}^k$ that could confound the measurement of compensation if not accounted for. Specifically, we included a covariate for the effect of mean hatch date within a year on $\mu_{hy,t}^{NH}$ because goslings in late hatch years are younger when they are banded relative to early hatch years (and thus, $\mu_{hy,t}^{NH}$ could include varying degrees of non-fledged gosling mortality). This covariate should thus help parse out the effects of gosling mortality on estimates of $\mu_{hy,t}^{NH}$ (Cooch 2002). In addition, snow goose harvest regulations tend to be confounded with population abundance; regulations are more liberal when snow geese are more abundant and *vice versa* (Johnson *et al.* 2012). Unfortunately, this can induce a density-dependent relationship between abundance and harvest-related mortality that biases any assessment of compensation in harvest-related mortality (Sedinger & Herzog 2012). Thus, to account for this source of bias to the best of our ability, we included a covariate for the effect of CCP snow goose abundance (which paralleled the growth of the mid-continent super population; App. S1) on $\mu_{hy,t}^H$ and $\mu_{ahy,t}^H$. We did not include this covariate for non-harvest mortality probabilities because density dependence in natural mortality is hypothesized to be one of the mechanisms that can induce compensation (Lebreton 2005). Extracting this source of variation from a time series of $\mu_{i,t}^{NH}$ estimates would thus be non-sensical when trying to measure the compensatory relationship between cause-specific sources of mortality.

After implementing this model in RMark, we exported the model structure into program MARK (Cooch & White 2012) to implement a Bayesian Markov Chain Monte Carlo (MCMC) approach. This method was used to estimate posterior distributions for the aforementioned model parameters and to estimate the degree of compensation (or lack thereof) in probabilities of harvest mortality (White, Burnham & Barker 2009; Sedinger *et al.* 2010). Given our hypotheses based on previous research (see Introduction), we estimated compensation in $\mu_{hy,t}^H$ before 1990 separately from thereafter.

Following Servanty *et al.* (2010), we added a multivariate normal random effect to the mortality probabilities: $\varepsilon \sim N(\boldsymbol{\beta}, \sum)$, where $\boldsymbol{\beta}$ is a vector of mean mortality probabilities for each age class and cause over time on the logit scale,

$$
\begin{bmatrix}
\beta_{hy,\text{pre}-1990}^H \\
\beta_{hy,\text{post}-1989}^H \\
\beta_{ahy}^H \\
\beta_{hy,\text{pre}-1990}^{NH} \\
\beta_{hy,\text{post}-1989}^{NH} \\
\beta_{ahy}^{NH}
\end{bmatrix}
\qquad \text{eqn 1}
$$

and $\sum$ is a variance–covariance matrix:

$$
\begin{bmatrix}
\sigma_{hy,\text{pre}}^{2H} & 0 & 0 & \rho_{hy,\text{pre}}\sigma_{hy,\text{pre}}^H\sigma_{hy,\text{pre}}^{NH} & 0 & 0 \\
0 & \sigma_{hy,\text{post}}^{2H} & 0 & 0 & \rho_{hy,\text{post}}\sigma_{hy,\text{post}}^H\sigma_{hy,\text{post}}^{NH} & 0 \\
0 & 0 & \sigma_{ahy}^{2H} & 0 & 0 & \rho_{ahy}\sigma_{ahy}^H\sigma_{ahy}^{NH} \\
\rho_{hy,\text{pre}}\sigma_{hy,\text{pre}}^H\sigma_{hy,\text{pre}}^{NH} & 0 & 0 & \sigma_{hy,\text{pre}}^{2NH} & 0 & 0 \\
0 & \rho_{hy,\text{post}}\sigma_{hy,\text{post}}^H\sigma_{hy,\text{post}}^{NH} & 0 & 0 & \sigma_{hy,\text{post}}^{2NH} & 0 \\
0 & 0 & \rho_{ahy}\sigma_{ahy}^H\sigma_{ahy}^{NH} & 0 & 0 & \sigma_{ahy}^{2NH}
\end{bmatrix}
\qquad \text{eqn 2}
$$

Within Σ, the σ^2 parameters measure the temporal variance of each respective mortality probability, and the correlation coefficients (ρ) measure the process correlation between hunting and non-hunting mortality probabilities over time, decoupled from sampling correlation that exists between such estimates in standard maximum likelihood estimation (White, Burnham & Barker 2009). A value of $\rho = -1$ indicates compensation, $-1 < \rho < 0$ indicates partial compensation, $\rho = 0$ indicates an additive effect of harvest and $\rho > 0$ indicates potential overadditive effects (Fig. 1).

We used normal (0, 1·75) prior distributions for the mortality probabilities on the logit scale and inverse γ (0·001, 0·001) prior distributions for the process variance parameters. Prior distributions for the correlation between cause-specific mortality probabilities on the logit scale were uniform [−1, 1] (White, Burnham & Barker 2009). Lastly, we generated three MCMC chains each with 4000 tuning samples, a burn-in period of 2000 samples, and 30 000 subsequent samples were kept to generate posterior parameter distributions for inference. The multiple MCMC chains were used to measure Gelman's (1996) $\hat{R}$ statistic for chain convergence.

Results

While implementing age-class effects for $\mu_{i,t}^k$, we found that models with age class by time bin effects for the detection probabilities did not converge. For models that did converge, however, the model with a 3 age class by cubic time trend effect on $p_{i,t}^A$ and an age class by reporting rate covariate effect on $p_{i,t}^H$ was most supported by the data (the ΔAIC_c for all other converged models was >550); this model structure for detection probabilities was then used in further analyses.

Convergence was attained for all parameters in the Bayesian analysis of age-by-time variation in cause-specific mortality probabilities (all $\hat{R} < 1·2$). However, this analysis indicated a negative relationship between abundance and harvest-related mortality probabilities for both age classes ($\beta_{N,hy} = -1·24$, 90% BCI: −1·51 to −0·97; $\beta_{N,ahy} = -0·68$, 90% BCI: −0·89 to −0·47) and not the positive relationship that can induce bias in the estimation of compensation (Sedinger & Herzog 2012). We thus removed the abundance covariate and conducted the analysis again using a single MCMC chain with 4000, 16 000 and 50 000 respective tuning, burn-in and stored samples.

Using annual estimates of cause-specific mortality probabilities from the final model (with abundance covariates removed and hatch-date covariates retained), we found a compensatory relationship between harvest and non-harvest mortality probabilities for *hy* females before 1990. As harvest mortality increased, non-harvest mortality decreased and *vice versa* (Fig. 3, top panel). After 1989, however, compensation did not appear to occur (Fig. 3, middle panel) nor did it occur for *ahy* females over the duration of the study (Fig. 3, bottom panel). While visually useful, these raw relationships between cause-specific mortality probabilities are nevertheless confounded by sampling co-variation (denoted by error bars in Fig. 3).

Using the hierarchical model, we accounted for this sampling covariance and found strong evidence for partial compensation of harvest mortality probabilities among *hy* females before 1990 ($Mo(\rho) = -0·47$; 90% BCI: −0·72 to −0·04), but positive tracking between the two sources of mortality after 1989 ($Mo(\rho) = 0·60$; 90% BCI: −0·06 to 0·81). There was no clear relationship between harvest and non-harvest sources of mortality in *ahy* females ($Mo(\rho) = 0·24$; 90% BCI: −0·59 to 0·67), indicating that harvest did indeed have an additive effect on the overall mortality probability in adults (see Figs 1 and 3).

Viewed over time, probabilities of non-harvest mortality for *hy* females were variable but generally increased until *c.* 1990. In turn, a lesser fraction died from hunting whenever the probability of non-harvest mortality was high (left of the dashed vertical grey line in the top panel of Fig. 4). After 1989, non-harvest mortality probabilities for *hy* females fluctuated stochastically for about 6 years. The probability of harvest mortality for *hy* females was initially quite high after 1989 (right of the dashed vertical grey line in the top panel of Fig. 4), but by the time the spring Conservation Order was implemented, $\mu_{hy,t}^H$ had slipped to some of the lowest levels ever observed (right of the grey vertical line in the top panel of Fig. 4). At the same time, non-harvest mortality probabilities also dropped below the respective long-term average.

The probability of non-harvest mortality for *ahy* females generally declined since the early years of the study, whereas the harvest mortality probability steadily fluctuated around 10% in most years (Fig. 4, bottom panel). Probabilities of harvest mortality for *ahy* females increased for a few years following implementation of the Conservation Order, but have since declined to average levels for the CCP population (right of the grey vertical line in the bottom panel of Fig. 4). Given little information on the fates of *ahy* females following the final year of the study, 2010 mortality estimates were highly imprecise and thus removed from Fig. 4 for clarity.

Discussion

Understanding the compensatory versus additive nature of exploitation is necessary for evaluating the effectiveness of management programmes aimed at reducing the abundance and spread of invasive and overabundant species. *A priori*, we might expect harvest to have an additive effect on overall mortality in species such as geese because they naturally have low levels of mortality, which offers little room for compensation (Gauthier *et al.* 2001; Péron 2013). The long tradition of testing the additive and compensatory mortality hypotheses in waterfowl and other wild vertebrates has nevertheless been plagued with issues of sampling (co)variation, the assumption in adaptive harvest management programmes that density dependence and compensatory mortality are one and the same, and attempts at relating survival to proxies of harvest rates that are often confounded with other factors (Anderson & Burnham 1976; Nichols *et al.* 1984; Sedinger & Herzog 2012).
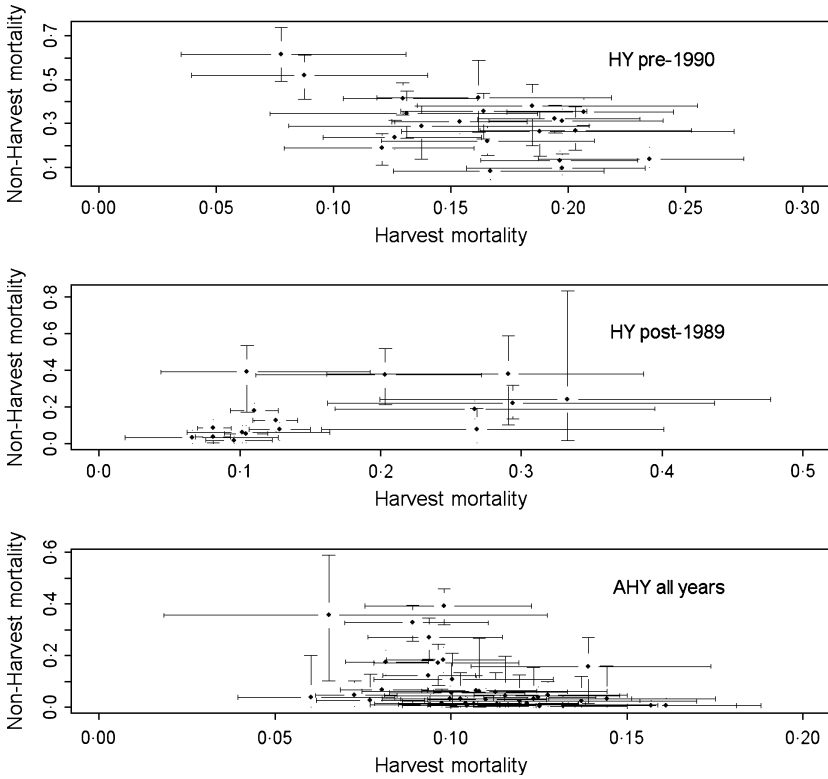
Fig. 3. Relationships between estimated cause-specific mortalities for *hy* female snow geese along the Cape Churchill peninsula before 1990 (top panel), *hy* females after 1989 (middle panel) and *ahy* females across all years of study (bottom panel). The effects of hatch date on non-harvest mortality of *hy* birds were removed from the estimates. Error bars indicate 90% Bayesian credible intervals (i.e. sampling covariance).
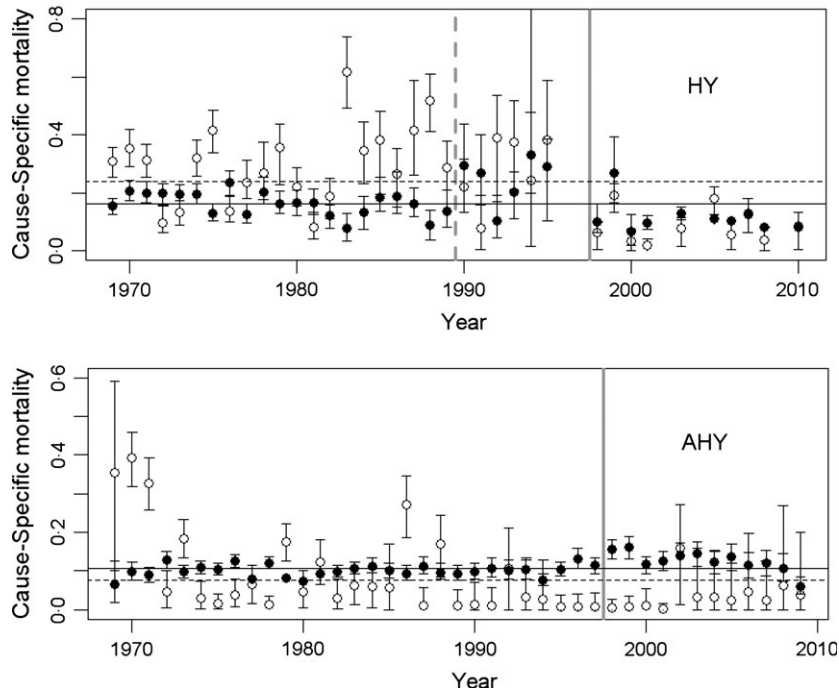

Fig. 4. Trajectories of CCP snow goose harvest (solid circles) and non-harvest (open circles) mortality probabilities over time for *hy* (top panel) and *ahy* (bottom panel) females with 90% Bayesian credible intervals. The effects of hatch date on estimated non-harvest mortality for *hy* birds were removed. The dashed vertical grey line represents when family groups began to move out of degraded habitat around LaPérouse Bay and into new habitats. The solid grey reference lines represent when the Conservation Order harvest was implemented under the international Migratory Bird Treaty. Horizontal solid and dashed reference lines represent long-term averages of harvest and non-harvest mortality, respectively.

Methods for estimating cause-specific mortality from capture–reencounter data have alleviated many of these problems (Schaub & Lebreton 2004), especially when cast in a hierarchical framework that can decouple sampling from process co-variation among mortality causes (Servanty *et al.* 2010). However, a process bias can still affect

estimated relationships between competing risks of mortality in discrete time models, especially when these risks occur primarily in different seasons (Péron 2013). For example, harvest mortality during a seasonal period of hunting can bias the sample of individuals at risk to non-harvest mortality after the hunting season (Heisey & Patterson 2006).

Schaub & Lebreton (2004) developed an equation for approximating this bias with estimates of the mean and variance of natural mortality that occur in the complete absence of exploitation, which are difficult to obtain for any game species. We chose not to implement this correction for two reasons. First, the correction was derived for situations where the mean and variance of mortality in the absence of exploitation are stationary (i.e. fixed or not changing). The mortality dynamics of CCP snow geese, however, seem to be changing in a directed non-stationary fashion (see Fig. 4 and discussion below). Use of the correction could thus be inappropriate in our situation. Secondly, the legal season lengths for hunting snow geese in North America have become so long that substantial amounts of harvest and non-harvest mortality must now be co-occurring throughout much of the year (see Johnson *et al.* 2012). Thus, we have reason to think that process bias should have little effect on estimates of competing mortality risks in snow geese.

Rather than conduct *post hoc* calculations with traditional capture–reencounter methods (*sensu* Péron 2013), we implemented the methodological advances of Servanty *et al.* (2010) without the process-bias correction in the widely used program MARK (Cooch & White 2012) to test the compensatory and additive mortality hypotheses in snow geese. We found that support for each hypothesis depended on age class and prevailing environmental conditions. Juvenile birds suffered from density-related degradation of the traditional saltmarsh rearing habitat up to *c*. 1990, causing an increase in non-harvest mortality (Fig. 4; see also Cooch 2002; Aubry *et al.* 2013). Although the mechanism for density dependence operated during juvenile development (Cooch *et al.* 1991), this opened up an opportunity for compensation of harvest mortality (Fig. 3). The effect of density dependence on juvenile development may have affected heterogeneity among individual *hy* birds entering fall migration and subsequent heterogeneity in risks to being harvested or starving during the winter and spring migration (i.e. frailty: variability in mortality risks across individuals in a population; see Sedinger & Herzog 2012). The density-dependent and individual heterogeneity mechanisms that can compensate for predation or harvest mortality deserve further study. Going forward, we should consider the possibility that these two mechanisms might actually interact with one another in nature.

By *c*. 1990, snow goose family groups reacted to the degradation of their own habitat, and much like anthropogenic suburban sprawl, they cheated density regulation by spreading into new habitats (Cooch, Rockwell & Brault 2001; Jefferies, Rockwell & Abraham 2003).

Non-harvest mortality of *hy* birds did not suddenly decline. Rather, it gradually declined (Fig. 4) because the very action of snow goose grazing was temporarily improving the nutritive quality of their plants (Hik & Jefferies 1990; Zellmer *et al.* 1993). This improved juvenile growth during development (Aubry *et al.* 2013) through a process known as the 'grazing optimization hypothesis' (e.g. van der Graaf, Stahl & Bakker 2005). In addition, we must acknowledge that some of the stochastic variation in non-harvest mortality of *hy* birds during the 1990s (see Fig. 4) could have been attributable to investigators trying to shift banding operations away from the traditional La Pérouse Bay area to cover the spatial expansion of snow geese across the entire CCP region. Geese of all ages were also benefitting from unprecedented subsidies of waste cereal grains during migration and wintering, which relaxed the cross-seasonal limitation of food (Jefferies, Rockwell & Abraham 2004; Abraham, Jefferies & Alisauskas 2005).

In turn, these breeding ground and cross-seasonal processes relaxed the strong density dependence that was occurring in developing juveniles before 1990. As a result, harvest began to have an additive effect on overall *hy* mortality (Figs 1 and 3). Increasing bag limits during regular hunting seasons throughout the 1990s (Johnson *et al.* 2012), thus affected *hy* harvest mortality, which quickly rose to high levels. Since the 1990s, however, *hy* harvest mortality has slipped to some of the lowest levels ever observed (Fig. 4), in part due to the increasing abundance of snow geese (see results section) that seemingly outpaces the ability of the Conservation Order policy to meet management objectives. Although such effects were eluded to by Francis *et al.* (1992), our methodological approach allows for more direct insight into the satiating effects of snow goose abundance on harvest mortality.

Since the early 1970s, non-harvest mortality of adults has dropped precipitously (Fig. 4), which has previously been attributed to increased nutritional subsidies from agricultural waste grain (Abraham, Jefferies & Alisauskas 2005). Since then, adult mortality has never exhibited a response to habitat degradation on the breeding grounds. Similar to large mammalian herbivores (Eberhardt 1977, 2002; Bonenfant *et al.* 2009), prime-aged snow geese seem to be quite robust to environmental change driven by population density. Barring density dependence, individual heterogeneity could still allow for some compensation of harvest (Lebreton 2005). However, we found that, if present, underlying heterogeneity was not substantial enough in adult snow geese to allow for compensation; perhaps because most individual heterogeneity is removed after first exposure to harvest during the *hy* stage of the life cycle (Rexstad & Anderson 1992). Similar to greater snow geese (*Chen caerulescens atlanticus*; Gauthier *et al.* 2001), harvest always had an additive effect on overall adult mortality in our study population (Fig. 3).

Given additive mortality dynamics, managers should have the ability to control snow goose population growth

by reducing adult survival, which, if changed, has a greater effect on population dynamics than juvenile survival and other demographic parameters (Cooch, Rockwell & Brault 2001; Aubry, Rockwell & Koons 2010). It has previously been suggested that implementation of the Conservation Order harvest effectively reduced adult survival in sub-Arctic populations (Alisauskas *et al.* 2011). To decipher the causal effects of management and other factors on survival, however, one must investigate cause-specific sources of mortality (e.g., Murray *et al.* 2010; Sandercock *et al.* 2011). By doing so, we found that harvest mortality of *ahy* females momentarily increased following implementation of the Conservation Order, but similar to *hy* birds, has since declined to average levels for the CCP population (Fig. 4).

As snow goose abundance increases, harvest mortality of all age classes in the CCP population is decreasing, which may be occurring for multiple reasons. First, interest in snow goose hunting may have waned because of the difficulty of hunting snow geese or the labour involved with cleaning large numbers of birds (Johnson *et al.* 2012). Secondly, waterfowl hunters are declining across the continent (Pergams & Zaradic 2008; Vrtiska *et al.* 2013). Thirdly, snow geese have shifted their migration and wintering areas, perhaps to avoid areas of intense hunting pressure (Alisauskas *et al.* 2011). Fourthly, the current number and effectiveness of hunters pursuing snow geese have resulted in a plateau of total annual harvest (Johnson *et al.* 2012), creating what is effectively a 'fixed quota' harvest (e.g. Azar, Lindgren & Holmberg 1996). As a result, the increasing abundance of snow geese is inducing a state of satiation in human hunters and reducing the 'harvest rate' of CCP snow geese (Holling 1959). This is why the mid-continent population of snow geese continues to grow (Alisauskas *et al.* 2011) and propagate a trophic cascade that is continuing to negatively affect other species (Peterson 2012; Iles *et al.* 2013).

The possibility of snow goose population growth outpacing the ability of hunters to control them was noted in the original assessment of population dynamics that ultimately led to the decision of implementing the Conservation Order policy (Rockwell, Cooch & Brault 1997). In fact, it is a general problem in management of all overabundant species (Simberloff 1997). Although it is very difficult to control a species once they have become overabundant, a combination of actions can sometimes produce results (e.g. Courchamp, Chapuis & Pascal 2003). For mid-continent snow geese, however, overall survival is actually improving in both the sub-Arctic (Fig. 4) and Arctic (Alisauskas *et al.* 2011) despite mortality being additive for *ahy* and currently *hy* individuals (Fig. 3). As such, simple continuation of the Conservation Order policy (e.g. spring harvest season, high or unlimited bag limits, and use of electronic calls and unplugged shotguns) has a low potential of achieving the objective of reducing snow goose abundance to a level such that habitat can recover. Management options that increase hunter participation

and take of more snow geese, or even lethal control actions carried out by cooperating agencies, will likely be required to control the mid-continent population of snow geese if total collapse of northern lowland ecosystems is to be avoided. Any such changes in management will nevertheless face challenging legal, economic and ethical issues (see Johnson 1997; Leafloor, Moser & Batt 2012).

In eastern North America, however, a similar spring conservation harvest measure was implemented before targeted greater snow geese became hyper-abundant. Thus far, it seems that the management action has successfully helped curb their growth (Calvert & Gauthier 2005; Calvert *et al.* 2007). More recently, the dilemma of snow goose population growth has propagated to the western Arctic (Kerbes, Meeres & Hines 1999; Burgess *et al.* 2012) where increased abundance is now beginning to cause habitat damage on the breeding grounds and major staging areas (Demarchi 2006; Burgess *et al.* 2012). Before it is too late, we suggest immediate implementation of spring seasons and liberal bag limits in the states and provinces that snow geese breeding in the western Arctic use throughout their annual life cycle.

In summary, management of invasive and overabundant species is too often implemented using a trial and error approach. Demographic models provide a framework for guiding more efficient management through adaptive learning (Walters 1986). Given previous knowledge that changes in survival have a greater impact on our target species than other demographic parameters (Aubry, Rockwell & Koons 2010), we have demonstrated how to use multistate capture-reencounter methods to decompose survival into underlying cause-specific sources of mortality that are relevant to specific management actions (e.g. harvest versus habitat management; Runge *et al.* 2006). This further allows one to assess whether exploitation is directly compensated through decreased mortality from other sources or whether management can even keep up with population growth and induce a meaningful change in the rate of exploitation. Our approach can be used in other systems to help guide the management of overabundant wildlife species. For many invasive species, however, data sets like ours will not be available, and it may be unwise to wait until such data are collected before acting. In such cases, referring to fundamental life-history patterns in mortality and population dynamics may be the best way to make rapid informed decisions (Koons *et al.* 2005; Péron 2013).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Estimating the abundance of CCP breeding snow geese over time.