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RH: Making do with less

Making do with less: must sparse data preclude informed harvest strategies for European waterbirds?

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## Abstract

The demography of many European waterbirds is not well understood because most countries have conducted little monitoring and assessment, and coordination among countries on waterbird management has little precedent. Yet intergovernmental treaties now mandate the use of sustainable, adaptive harvest strategies, whose development is challenged by a paucity of demographic information. In this study, we explore how a combination of allometric relationships, fragmentary monitoring and research information, and expert judgment can be used to estimate the parameters of a theta-logistic population model, which in turn can be used in a Markov decision process to derive optimal harvesting strategies. We show how to account for considerable parametric uncertainty, as well as for different management objectives. We illustrate our methodology with a poorly understood population of taiga bean geese (*Anser fabalis fabalis*), which is a popular game bird in Fennoscandia. Our results for taiga bean geese suggest that they may have demographic rates similar to other, well-studied species of geese, and our model-based predictions of population size are consistent with the limited monitoring information available. Importantly, we found that by using a Markov decision process, a simple scalar population model may be sufficient to guide harvest management of this species, even if its demography is age-structured. Finally, we demonstrated how two different management objectives can lead to very different optimal harvesting strategies, and how conflicting objectives may be traded off with each other. This approach will have broad application for European waterbirds by providing preliminary estimates of key demographic parameters, by providing insights into the monitoring and research activities needed to corroborate those estimates, and by producing harvest management strategies that are optimal with respect to the managers' objectives, options, and available demographic information.

Key-words: adaptive management, demography, geese, harvest, hunting, Markov decision process, stochastic dynamic programming, taiga bean geese, waterbirds

## **Introduction**

Waterbirds have historically been among the most heavily harvested of wildlife species, and by the turn of the 20th century populations in North America (Day 1949) and Europe (Kear 1990) had experienced widespread declines. The subsequent development of international treaties and laws to reduce harvests to more sustainable levels (e.g. Migratory Bird Treaty Act of 1918 in North America, The Directive on the Conservation of Wild Birds in the European Union of 1979; hereafter EU Birds Directive) helped reverse at least some of these declines. The North American system of waterbird management ultimately evolved into perhaps the most sophisticated in the world (Nichols et al. 1995), but much remains to be done in Europe to ensure the sustainability of waterbird harvests. The EU Birds Directive is the European Union's oldest piece of conservation legislation and one of the most important, creating a comprehensive framework for the protection for all wild bird species naturally occurring in the Union. The Directive recognizes hunting as a legitimate activity for many species, as long as it is managed so as to be sustainable. However, a recent update of the conservation status of waterbirds in the EU reports that almost half of the populations of huntable species of the EU Birds Directive (Annex 2) have declining population trends (Madsen et al. 2015a). The European Commission (2008) defined that where a huntable species was "...declining, hunting cannot by definition be sustainable, unless it forms part of a properly running management plan that also involves...other measures that will slow and ultimately reverse the decline." Although not precisely defined, this

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implies that their hunting could only continue under the framework of a plan that achieved coordinated regulation of their hunting that would restore these populations to favorable conservation status, such as would be achieved under an adaptive harvest management plan. Yet most EU countries continue to conduct little monitoring and assessment of the harvest, population size and demographic parameters of migratory waterbird quarry species, and coordination among countries on migratory bird management has little precedent. It has been a decade since Elmberg et al. (2006) and Bregnballe et al. (2007) called for greater coordination of monitoring and management of European waterbird populations, but information remains limited and patchily distributed. Therefore, more collaborative approaches for monitoring and assessment are needed, as well as procedures for establishing sustainable harvest levels when demographic information is limited, as is the case for most Western Palearctic waterbird populations.

Progress towards greater international collaboration has been made with the implementation of the African-Eurasian Migratory Waterbird Agreement (hereafter AEWA, <http://www.unep-aewa.org/>), to which most European countries are signatories. AEWA is an intergovernmental treaty dedicated to the conservation of migratory waterbirds and their habitats across Africa, Europe, the Middle East, Central Asia, Greenland and the Canadian Archipelago, through coordinated actions of contracting parties. In 2016, 11 European countries took the unprecedented step of establishing a European Goose Management Platform (EGMP) under the auspices of AEWA. The purpose of the platform is to coordinate international, flyway-level conservation and management of goose populations, including assessments of sustainability based on population-scale measures of population size and harvest (<http://www.unep->

aewa.org/sites/default/files/document/aewa\_egm\_iwg\_1\_inf\_4\_paris\_declaration.pdf). The development of this coordinated program of goose management followed on the heels of the successful adaptive harvest management program for the Svalbard population of pink-footed geese (*Anser brachyrhynchus*), also under the auspices of the AEWA (Madsen *et al.* 2017). The pink-footed goose was chosen as the first case of coordinated waterbird management because the number of countries within its range is limited (Norway, Denmark, The Netherlands, and Belgium) and because there was a rich base of monitoring data and research from which to develop assessments of sustainable harvest (Trinder and Madsen 2008, Johnson *et al.* 2014).

The EGMP is now in the process of developing flyway-based management plans for other goose species. An International Single Species Action Plan for the taiga bean goose (*Anser fabalis fabalis*) was implemented in 2016 (Marjakangas *et al.* 2015), and planning is underway for three populations of barnacle geese (*Branta leucopsis*) and one population of greylag geese (*Anser anser*). The coordinated management of these species will be much more difficult and complex than that of pink-footed geese, however, due to the existence of multiple populations of varying conservation status, the involvement of many more countries, and because these species lack the well-developed monitoring and assessment schemes operative for pink-footed geese.

The progress in coordinated management activities notwithstanding, European decision makers often lack the most basic demographic information needed to inform waterbird management policies and strategies. Our goal here is to demonstrate how an informed, dynamic, and adaptive harvesting strategy can be developed from a minimum of demographic information by focusing on a species of goose that is an important game bird in Fennoscandia. The abundance of many

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goose species in northern Europe has increased in recent decades, likely as a combination of factors including reductions in hunting pressure, favorable changes in land use, and climate change (Madsen et al. 1999). The taiga bean goose is an exception, however, declining from about 100,000 birds in the mid-1990s to 63,000 in 2009 (Fox et al. 2010). Taiga bean geese breed in Russia, Finland, Sweden, and Norway, and have a highly discontinuous winter distribution, which includes population segments in the United Kingdom and northern Denmark, in southern Sweden and southeastern Denmark, in northeastern Germany and western Poland, and in Central Asia (Madsen et al. 1999). They are hunted principally in Russia, Sweden, southeastern Denmark, and until 2014 in Finland when a temporary moratorium was put into effect. Reliable estimates of harvest are lacking, especially from Russia, but the take may have exceeded 10,000 range-wide prior to hunting restrictions in Fennoscandia. An International Single Species Action Plan (<http://www.unep-aewa.org/en/document/aewa-international-single-species-action-plan-conservation-taiga-bean-geese>) depicts four management units of relatively discrete populations of varying status. We chose to focus on the Central Management Unit of taiga bean geese, which has the largest population and likely the largest harvest (Fig. 1). The other management units encompass imperilled populations of taiga bean geese and their recovery takes precedent over harvest opportunity.

In what follows we suggest that a strategy prescribing annual harvests can be calculated as an optimal solution to a Markov decision problem (MDP). MDPs involve a temporal sequence of decisions, with strategies that identify actions at each decision point depending on the state of the managed system (Possingham 1997). The goal of the manager is to develop a decision rule or strategy that prescribes management actions for each possible system state that maximizes (or

minimizes) a temporal sum of utilities, which in turn are defined by the managers' objectives. A key advantage when optimizing MDPs is the ability to produce a feedback (or closed-loop) strategy specifying optimal decisions for future system states that may occur rather than just for those that are model-based expectations (Walters and Hilborn 1978). This makes optimization of MDPs appropriate for systems that behave stochastically, absent any assumptions about the system remaining in a desired equilibrium or the production of a constant stream of utilities. Moreover, specification of harvest management as a MDP greatly facilitates development of a fully adaptive management program, in which reducing uncertainty about population dynamics is recognized as an explicit goal of management (Johnson and Williams 2015).

Objectives of this article are to demonstrate: (1) how useful models for waterbird harvest assessment can be developed and parameterized with a minimum of demographic information, hence making these methods available for a broader range of species; (2) how a harvest management strategy can be calculated as a solution to a Markov decision process; and (3) the extent to which a harvest strategy can be sensitive to the choice of harvest management objectives. Finally we discuss how derivation of an optimal harvest strategy can explicitly account for uncertainty in population dynamics, and how it can evolve over time in response to what is learned via a monitoring program.

## **Material and methods**

### **Models of population dynamics**

One of the most commonly used models to determine sustainable harvests is the discrete theta-logistic model (Gilpin and Ayala 1973):

$$N_{t+1} = N_t + N_t r \left[ 1 - \left( \frac{N_t}{K} \right)^\theta \right] - h_t N_t,$$

where  $N$  is population size,  $r$  is the intrinsic rate of growth,  $K$  is carrying capacity,  $\theta > 0$  is the form of density dependence,  $h$  is harvest rate, and  $t$  is time (assumed here to be in 1-year increments). We assumed that the anniversary of the annual life cycle is in midwinter following harvest (i.e., a pre-breeding census). In what follows, we will refer to this simple model of population dynamics as the “scalar model.”

The scalar model lacks any age structure (Cooch et al. 2014), however, and may not be a good approximation for geese, which typically do not breed regularly until they are three years old (Cramp and Simmons 1977). Therefore, we also developed an age-structured model for taiga bean geese (Fig. 2). In addition to accounting for age at first breeding, this model allows for age-specific survival rates and for young-of-the-year that may be more vulnerable to harvest than older birds (Baldassarre 2014). The matrix model representation of this life cycle is:

$$\begin{bmatrix} Y_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \gamma s_a (1 - \nu h) \\ s_y (1 - h) & 0 & 0 \\ 0 & s_j (1 - h) & s_a (1 - h) \end{bmatrix} \cdot \begin{bmatrix} Y_t \\ J_t \\ A_t \end{bmatrix}$$

where the three age classes represented are young (Y, birds aged 0.5 years), juvenile (J, birds aged 1.5 years), and adults (A, birds aged  $\geq 2.5$  years),  $t$  represents year, and  $\nu$  represents the differential vulnerability of young to harvest. Vital rates are survival in the absence of harvest,  $s$ , the harvest rate of birds that have survived at least one hunting season,  $h$ , and the reproductive rate,  $\gamma$ . Jensen (1995) provided a density-dependent matrix model with harvest as:



$$\vec{N}_{t+1} = \vec{N}_t + d(\vec{N}_t) \cdot (\underline{M} - \underline{I}) \cdot \vec{N}_t$$

where  $\vec{N}$  is the vector of age-specific abundances,  $\underline{M}$  is the transition matrix with harvest,  $\underline{I}$  is the identity matrix, and  $d(\vec{N}_t)$  is the density-dependent effect:

$$d(\vec{N}_t) = 1 - \left( \frac{\vec{N}_t [1 \ 1 \ 1]'}{K} \right),$$

with carrying capacity,  $K$ . A simple modification allows for non-linear density dependence:

$$d(\vec{N}_t) = 1 - \left( \frac{\vec{N}_t [1 \ 1 \ 1]'}{K} \right)^\theta$$

where  $\vec{N}_t [1 \ 1 \ 1]'$  is total population size (i.e., summation over the vector of age-specific abundances) and  $\theta > 0$ . Because we do not explicitly define a maximum lifespan, however, the density-dependent matrix model with harvest must be reformulated as:

$$\vec{N}_{t+1} = \underline{H}_t (\vec{N}_t + \underline{D}_t (\underline{M} \vec{N}_t - \vec{N}_t)).$$

In this model, the transition matrix without harvest is:

$$\underline{M} = \begin{bmatrix} 0 & 0 & \gamma s_a \\ s_y & 0 & 0 \\ 0 & s_j & s_a \end{bmatrix}.$$

Age-specific density-dependence is:

$$\underline{D}_t = \begin{bmatrix} 1 - \left( \frac{Y_t}{K_y} \right)^\theta & 0 & 0 \\ 0 & 1 - \left( \frac{J_t}{K_j} \right)^\theta & 0 \\ 0 & 0 & 1 - \left( \frac{A_t}{K_a} \right)^\theta \end{bmatrix},$$

where  $K_i = p_i K$ , with  $p_i$  the proportion specified by the stable age distribution of  $\underline{M}$ , for  $i \in \{Y, J, A\}$ . The assumption of age-specific carrying capacities helps to keep the relative sizes of the age classes within biologically realistic bounds (Jensen 1995).

The matrix of age-specific survival from harvest is:

$$\underline{H}_t = \begin{bmatrix} 1 - \nu h_t & 0 & 0 \\ 0 & 1 - h_t & 0 \\ 0 & 0 & 1 - h_t \end{bmatrix},$$

where the harvest rate of birds surviving at least one hunting season is a function of total harvest and autumn population size (i.e., that just prior to harvest):

$$h_t = \frac{\text{harvest}_t}{\nu Y_t^F + J_t^F + A_t^F}.$$

The autumn population size in turn is calculated by assuming that harvest occurs after net population growth:

$$\vec{N}_t^F = \vec{N}_t + \underline{D}_t (\underline{M} \vec{N}_t - \vec{N}_t).$$

## Model parameterization

We parameterized 100,000 independent replicates of both the scalar and matrix population models by drawing samples of demographic parameters from statistical distributions derived as described below.

The concept of sustainable harvesting relies on an assumption of surplus production at population levels below carrying capacity. Development of sustainable harvest strategies thus requires knowledge about potential population growth ( $r$  in the scalar model; using  $s$  and  $\gamma$  in the matrix model) in the absence of density dependence (Runge et al. 2004). In the absence of detailed demographic information, Johnson et al. (2012) relied on detailed mortality records from 1,111 captive individuals of 23 bird species, with body masses ranging from 0.012 to 8.663kg, to predict adult survival in the absence of density dependence as:

$$s_a = p^{1/(\exp(3.22+0.24\log(m)+\varepsilon)-b)}$$

where  $b$  is age at first breeding (assumed to be 3 years in taiga bean geese),  $m$  is body mass in kg,  $\varepsilon$  is model error with  $\varepsilon \sim N(0, \sigma^2 = 0.087)$ , and  $p$  is the proportion of the population

remaining alive at the maximum observed life span ( $\bar{p} = 0.03, sd = 0.017$ ). We allowed for

uncertainty in  $p$  using a beta distribution:  $p \sim \text{Beta}(3.34, 101.24)$ . To apply this approach for taiga bean geese we used the mass of females provided by Dunning (2008)

( $\bar{m} = 2.843, sd = 0.247$ ), and specified a gamma distribution to allow for variation in mass:

$m \sim \Gamma(107.660, 0.026)$ . While it is perhaps biologically realistic to assume that on average birds

of different ages survive natural mortality at a similar rate after surviving their first hunting season, we wanted to account for the fact it is unlikely they will be exactly the same (i.e., we

wanted to be conservative in our recognition of uncertainty). Therefore, we drew independent samples for each age class from the single distribution for  $s_a$  to parameterize the matrices  $\underline{M}_i$ .

We estimated the reproductive rate,  $\gamma$ , using a novel approach by relying on the demographic-invariant method developed by (Niel & Lebreton 2005):

$$r = \left[ \frac{(s_a b - s_a + b + 1) + \sqrt{(s_a - s_a b - b - 1)^2 - 4s_a b^2}}{2b} \right] - 1$$

where  $b$  is age at first breeding, and  $r$  is the intrinsic rate of growth. We first generated 100,000 random samples of adult survival using the methods described above, and then used them to generate 100,000 samples of  $r$  using Niel and Lebreton's (2005) formula and assuming  $b = 3$ .

Next, we used the random samples of  $r$  to specify  $(1 + r)$  (i.e., the intrinsic finite growth rate) as the dominant eigen value of the 100,000 random transition matrices  $\underline{M}_i$  (Caswell 2001). We then calculated  $\gamma$  numerically for each and every  $\underline{M}_i$ , such that the dominant eigen value of  $\underline{M}_i$  was equal to the finite growth rate,  $(1 + r)$ .

The parameter  $\theta$  in the theta-logistic model is often assumed to be equal to one, which specifies linear density dependence. However, density dependence may be non-linear depending on life history (Fowler 1981), and we were unsure whether an assumption of linear density dependence was appropriate for taiga bean geese. Johnson et al. (2012) used point estimates of  $\theta$  provided by Saether and Engen (2002) to fit the following model:

$$\log(\theta) = 1.129 - 1.824r + e ,$$

where  $e \sim \text{Normal}(0, \sigma^2 = 0.942)$ . A negative relationship between  $\theta$  and  $r$  is consistent with both theory and empirical studies (Gilpin and Ayala 1973; Fowler 1981; Sæther et al. 2002; Sæther and Engen 2002; Sibly et al. 2005). We truncated the normal distribution for the error term to the interval  $[-1.5 - 1.5]$  to keep values of  $\theta$  within biologically realistic bounds for birds (Sæther and Engen 2002). We then used this model to estimate  $\theta$  for each and every sample value of  $r$ .

The carrying capacity (i.e., expected population size over the long term in the absence of harvest) is difficult to estimate without a sufficiently long time series of population and harvest estimates. Lacking such data, we elicited expert judgments from several individuals studying taiga bean geese breeding in Fennoscandia. Those scientists suggested that the breeding population in their study area might be 1.3 – 3 times as large in the absence of hunting, with a modal value of about two times as large. We in turn assumed a 90% confidence interval of 1.75 – 2.25 times current population size. Extrapolating the densities of geese in Fennoscandia to the breeding area of the Central Management Unit resulted in a contemporary estimate of population size of about 41,800 individuals at the onset of the breeding season. Using this value and the 90% confidence limits for the relative size of  $K$ , we fit a log-normal distribution to describe the uncertainty about the absolute value of  $K \sim \log N(4.475, 0.042)$ . This distribution describes carrying capacity at the onset of the breeding season; midwinter carrying capacity was calculated as  $K/\sqrt{s_a}$ , which assumes the mid-winter carrying capacity is proportionally higher due to approximately six months of mortality between the winter and breeding periods (assuming an even temporal distribution of mortality outside the hunting season).

## Management objectives

Based on preliminary agreement among stakeholders, the ISSAP calls for restoring and then maintaining the Central Management Unit population of taiga bean geese at a level of 60,000 – 80,000 individuals in winter. We thus considered an objective function that takes into account both the desire to maintain a population near its goal, as well as the desire to provide sustainable hunting opportunities:

$$V^*(\vec{N}_{t+1}, H_t | \vec{N}_t) = \arg \max_{(H_t | \vec{N}_t)} \sum_{t=1}^{\infty} \left\{ w \left( 1 + e^{(|\vec{N}_t[1-1]-\alpha|-\beta)} \right)^{-1} + (1-w) \frac{H_t}{\max H} \right\},$$

where the optimum value  $V^*$  of a harvest strategy  $(H_t | \vec{N}_t)$  maximizes the temporal sum of population and harvest utilities, with  $0 \leq w \leq 1$  being the relative degree of emphasis on maintaining the population near its goal. The first term in the summation uses a generalized logistic function that scales unweighted population utility to the interval 0-1. We used a midwinter population goal of  $\alpha = 70,000$  taiga bean geese, and inflection points of  $[\alpha - \beta, \alpha + \beta]$ , where  $\beta = 15,000$ . The proposed utility function for population size thus expresses near-complete satisfaction with population sizes in the range 60,000-80,000, with satisfaction declining rapidly for population sizes outside this range (Fig. 3). The second term in the summation scales harvest utility by the maximum harvest under consideration, and so harvest utility also falls in the interval 0-1. Using the value  $w = 1$  represents a sole objective related to population size and  $w = 0$  represents a sole objective of maximizing sustainable harvest. Values of  $w$  intermediate between 0 and 1 represent a mix of both objectives. For the sake of simplicity, we assumed additivity of the two objectives; i.e., the utility value of one objective is independent of the utility value of the other (Abbas 2010). The extent to which objectives either compliment or substitute for one another could easily be accommodated with an interaction term,

however (Clemen 1996). For purposes of maximum contrast, we considered two extreme objective functions with  $w = 1$  or  $w = 0$ .

### **Alternative harvest actions**

The ability of countries within the range of taiga bean geese to regulate their harvests is largely unknown. Therefore, we assumed annual, population-level harvest quotas in increments of 1,000 from 0 to 30,000, with the assumption that harvest could be regulated with this degree of precision. These alternative harvest levels could be adjusted as needed when more information about harvest levels and the means to manipulate them become available. Although no data specific to taiga bean geese are available, we assumed that young-of-the-year are twice as vulnerable to harvest as older birds based on studies of other goose species (Frederiksen et al. 2004, Madsen 2010, Alisauskas et al. 2011, Clausen et al. 2017).

### **Optimization and simulation**

A solution algorithm for a Markov decision process is dynamic programming (Puterman 1994), which we used to derive harvest strategies for the Central Management Unit of taiga bean geese. We used the open-source software MDPSolve© (<https://sites.google.com/site/mdpsolve/>) for Matlab (<https://www.mathworks.com/>) to compute optimal solutions based on demographic parameters fixed at their mean values. The optimal harvest strategy based on the matrix model implies that the size of the population, as well as its age structure, must be observed prior to a harvest decision. However, a monitoring program to observe age structure of taiga bean geese in midwinter is almost certainly not practicable due to moulting of young birds during the autumn, making it difficult if not impossible to differentiate them from adults at a distance. A possible,

ad hoc solution is to use the scalar model with no age structure to derive an optimal harvest strategy. Thus, a harvest decision would be based only on observed population size (because the scalar model has no age structure). Although the resulting harvest strategy is sub-optimal (i.e., because it assumes population dynamics are not age structured while they likely are), it can be simulated with the fully age-structured matrix model to determine whether expected performance is acceptable. In other words, “how well might a harvest strategy that does not recognize age structure perform if the population is in fact age structured in its dynamics?”

To predict management performance, we simulated use of both the scalar-model and matrix-model harvest strategies with the fully specified matrix model. We performed 100,000 simulations, each with a different parameterization of the matrix model as derived from random draws of the empirical distributions of demographic rates. Every simulation was run for a period of 20 years. We initialized population sizes as  $\vec{N}_t^i [1 \ 1 \ 1]' = 41,800 / \sqrt{s_a^i}$ , which reflects a contemporary estimate of population size in the Fennoscandia breeding area, inflated to produce a corresponding midwinter estimate. Each initial population vector was parameterized using a random draw from a Dirichlet distribution with parameters equal to the stable age distribution of  $\underline{M}_i$  (in percent). This allowed for uncertain, but plausible, values of the initial age distribution for simulation purposes. Finally, at each time step, we introduced random environmental variation by taking the deterministic outcomes for age-specific population sizes and multiplying each by independent values of  $e^\sigma$ , where  $\sigma \sim \text{Normal}(0, 0.1)$ ; this produces a coefficient of variation of approximately 10% in annual predictions of population size in what otherwise would be deterministic projections. From the simulations, we summarized population sizes, harvests, and the magnitude of year-to-year changes in target harvests. We used empirical, cumulative



probability distributions to depict the range of uncertainty in these performance metrics. All simulations and their analyses were performed using the open-source computing language R (RCoreTeam 2016).

### **Comparison of model predictions with empirical data**

We were interested in having some empirical basis to judge the credibility of our population models, but even basic data on population size and harvest of taiga bean geese are incomplete and highly fragmented. Nonetheless, we used estimates of population size and harvest from the Central Management Unit when available during the period 2007-2015 to develop crude measures of harvest rate, which then could be compared to trends in population size. We stress that this is in no way a proper validation of our population models; rather we are simply asking whether predictions from our models are qualitatively consistent with the sparse demographic data available. We used estimates of population size in spring from southern Sweden (Skjallberg 2015), recognizing that inaccuracies likely exist due to birds actively migrating through the count area (Appendix S1.). We derived estimates of harvest from Sweden and Finland where the bulk of taiga bean geese from the Central Management Unit are taken. Finnish estimates are based on a sample survey of small-game hunters (<http://stat.luke.fi/en/hunting>), while Sweden relies on voluntary reporting of harvests ([http://www.unep-aewa.org/sites/default/files/document/aewa\\_egm\\_iwg\\_2\\_7\\_tbg\\_pop\\_status\\_report\\_0.pdf](http://www.unep-aewa.org/sites/default/files/document/aewa_egm_iwg_2_7_tbg_pop_status_report_0.pdf)). These harvest estimates undoubtedly include some tundra bean geese (*Anser fabalis rossicus*) because differentiation of the subspecies of bean geese is not requested of hunters. However, we believe the relatively small harvests of tundra bean geese in our estimates may be offset by not including the small harvest of taiga bean geese in Denmark. To estimate harvest rate we

required the size of the population in autumn just prior to harvest. We used our scalar model and mean estimates of  $r$ ,  $K$ , and  $\theta$  to project autumn population size. The estimated harvest rate was then simply the total harvest divided by the autumn population size. We then compared estimated harvests, harvest rates, and population size with those expected at equilibrium under maximum sustained yield (MSY) using our scalar model. The MSY harvest rate ( $h_{MSY}$ ), harvest ( $H_{MSY}$ ), and associated population size ( $N_{MSY}$ ) at equilibrium based on the theta-logistic parameters are, respectively (Johnson et al. 2012) :

$$h_{MSY} = r_{\max} \frac{\theta}{(\theta+1)},$$

$$H_{MSY} = r_{\max} K \frac{\theta}{(\theta+1)^{(\theta+1)/\theta}}, \text{ and}$$

$$N_{MSY} = K (\theta+1)^{-1/\theta}.$$

We also compared values of the intrinsic growth rate,  $r$ , and density-dependent parameter,  $\theta$ , from well-studied waterbird species in the published literature with those based on our allometric relationships. We examined these two demographic parameters for nine populations of five species of waterbirds: barnacle goose (*Branta leucopsis*), snow goose (*Anser caerulescens*), pink-footed goose, common pochard (*Aythya ferina*), and mallard (*Anas platyrhynchos*) (Krapu 1979, Larson 1988, Cooch and Cooke 1991, Blums et al. 1993, Gauthier and Brault 1998, Sæther and Engen 2002, Niel and Lebreton 2005, Johnson and Madsen 2016, and U.S. Fish and Wildlife Service 2017). Available estimates of the two demographic parameters in question were provided in the literature for all populations except pink-footed geese and eastern and midcontinent mallards in North America. For these three populations, we used published difference equations of population size (based on survival and reproductive processes) to

estimate  $r$ , assuming no harvest or density dependence, and assuming average environmental conditions. For these three populations, there were several alternative population models provided. We estimated the mean of  $r$  for each population by weighting model-specific values of  $r$  by their respective model weights. For comparison, we calculated  $r$  and  $\theta$  for each species using our allometric methods and female body masses provided by Dunning (2008) (note that masses provided for common pochard were of unknown sex).

## Results

Using the mass-based model of Johnson et al. (2012), the mean survival of adult taiga bean geese expected under ideal conditions was estimated as  $s_a = 0.878$  (90% confidence interval: 0.799 – 0.934). Assuming age at first breeding is 3 years, and using the model of Niel and Lebreton (2005), we estimated the mean intrinsic rate of growth as 0.150 (90% confidence interval: 0.120 – 0.183). We estimated the mean reproductive parameter as  $\gamma = 0.550$  (confidence interval: 0.312 – 0.919). We estimated the mean form of density dependence as  $\theta = 3.049$  (90% confidence interval: 0.697 – 7.926), suggesting the strongest density dependence occurs when the population is near its carrying capacity. Finally, we estimated mean carrying capacity in midwinter as  $K = 93,870$  (90% confidence interval: 86,743 – 101,782), which accounts for mortality between the winter and breeding periods.

A harvest strategy for the matrix model is a very large, 4-dimensional table, in which an optimal harvest level is prescribed for each possible combination of the number of young, juveniles, and adults that may be observed. Thus, it is difficult to depict this strategy graphically. The numbers of juveniles and adults have the most influence on the harvest strategy, so we plotted optimal

harvests for several fixed values of young abundance. For a sole objective to maximize population utility (i.e., maintain the population goal of about 70,000 birds), it is rarely optimal to harvest population sizes below about 60,000, and the maximum harvest (30,000 in our example) is never optimal, even for populations at carrying capacity (Fig. 4). The optimal strategy for an objective to maximize sustainable harvest is considerably more liberal (Fig. 5). For both objectives, the number of young in the population has a strong influence on optimal harvests. The scalar-model policies also suggest a much more liberal harvesting strategy for the objective to maximize harvest than the strategy to maintain the population near goal (Fig. 6).

We were interested in how well an optimal harvest strategy based on the scalar model might perform if in fact population dynamics are governed by age structure. For a sole objective to maximize population utility, the scalar-model and matrix-model harvest policies had remarkably similar simulated performance (Fig. 7A). Simulated population size averaged slightly higher and was slightly more variable using the scalar-model strategy. Annual harvests and the magnitude of the change in annual harvest quotas were largely indistinguishable between the two model-based policies (Fig. 8A and 9A). Both strategies were successful in keeping simulated population sizes near the goal most of the time, albeit with a relatively high frequency of closed hunting seasons (>30%).

For a sole objective to maximize sustainable harvest, simulated population sizes were also similar between the scalar and matrix model strategies (Fig. 7B). However, median population size was somewhat lower than that expected under a sole objective to achieve the population goal. Simulated harvest characteristics were similar between matrix-model and scalar-model

strategies when the objective was to maintain the population near goal (Figs. 8A and 9A).

However, with an objective to maximize harvest, there was a large difference between those strategies based on the scalar and matrix models, with the matrix-model strategy producing much more variability in annual harvests (Fig. 8B). For example, the matrix model strategy suggested that the frequency of closed hunting seasons (i.e., harvest = 0) was >60%; in contrast, the simulated frequency of closed seasons with the scalar-model strategy was only about 20%. Generally, the matrix-model strategy produced more extreme values of harvest, which is reflected in the high variability in year-to-year changes in harvest (Fig. 9B).

Our comparison of spring population sizes and harvest rates suggested a population decline associated with harvest rates >0.15, stabilization at about 45,000 birds associated with harvest rates of approximately 0.12, and an increase associated with harvest rates <0.04 (Fig. 10; Supporting Information). These results are consistent with the MSY analysis of the scalar model based on mean parameter values, in which  $h_{MSY} = 0.105$ ,  $H_{MSY} = 5,856$ , and  $N_{MSY} = 55,994$ . That is, for harvest rates greater than  $h_{MSY}$  and populations greater than  $N_{MSY}$  we would expect population declines. For harvest rates less than  $h_{MSY}$  and populations less than  $N_{MSY}$  we would expect population increases.

Confidence limits of estimates of the intrinsic growth rate,  $r$ , and the density-dependent parameter,  $\theta$ , based on allometric methods did not always encompass published estimates from well-studied species (Table 1). This is perhaps not too surprising given the unquantified precision of the published estimates and the potential for bias in estimates based on population counts, and survival and reproductive rates, which are rarely, if ever, observed in the absence of

harvest and density dependence. However, our allometric-based parameter estimates are in general agreement with empirical evidence of low values of  $r$  and high values of  $\theta$  for geese compared to ducks.

## Discussion

We accounted for considerable uncertainty about population dynamics and a moderate level of environmental variation in deriving and simulating optimal harvest strategies for the Central Management Unit of taiga bean geese. We combined allometric relationships, fragmentary monitoring and research information, and expert judgment to support this analysis. Results suggest that the intrinsic growth rate and form of density dependence in taiga bean geese are similar to those reported for other, well-studied species of geese (Sæther and Engen 2002, Sæther et al. 2002, Hauser et al. 2007, Dillingham and Fletcher 2008, Alisauskas et al. 2011, Johnson et al. 2014). Indeed, our estimate of adult survival under ideal conditions is remarkably similar to the estimate for taiga bean geese banded in the Western Management Unit, where the population is at a low level and is exposed to little or no hunting ( $\bar{s} = 0.879$ ,  $se = 0.032$ ) (A. Fox, personal communication). Accordingly, harvest rates of taiga bean geese in excess of about 10% could be indicative of over-harvest and, even if sustainable, harvest rates of this magnitude could be expected to hold population size below the level of maximum net productivity (i.e.,  $N_{MSY} = 55,994$ ). For either of the two management objectives we examined, the median of the simulated harvests was  $\leq 5,000$ . We emphasize that maintenance of a constant harvest rate is likely to be more sustainable in a varying environment than a constant, absolute harvest (Runge et al. 2004). Using a sole objective to maintain a population size near its goal, along with an optimal, dynamic harvest strategy, resulted in only a 20% (putative) chance that population size

would be <60,000 (i.e. the lower limit of the desired range in population size), as based on 100,000 different parameterizations of the matrix model and assuming a moderate amount of environmental variation over a 20-year period. This is partly explained by closed hunting seasons that occurred in simulations >30% of the time. We stress that prescriptions for harvest must include all sources of hunting mortality, including unretrieved and illegal kill, and lead poisoning from ingestion of lead gunshot in foraging areas.

What we found most remarkable was that harvest strategies predicated on the scalar model performed similarly to the matrix-model strategies, even if population dynamics are in fact age structured. This suggests that a Markov decision process, in which populations fluctuate stochastically and harvest decisions are made annually, may be able to effectively account for the transient dynamics expected of age-structure populations (Koons et al. 2006). It is unclear how general this result may be, but it does hold out hope that managers may be able to use very simple, and easily parameterized, models of population dynamics, along with rudimentary monitoring programs, to effectively manage waterbird population size and harvest. We note, however, that our estimates of intrinsic growth rate (i.e., those in the absence of density dependence and harvest), are what one would expect over evolutionary (rather than ecological) time scales, and we suggest that our estimates of the population's growth potential should be treated as theoretical maximums. For example, even at low densities, taiga bean geese may be unable to attain these theoretical rates of growth because of deleterious environmental conditions that are acting in an additive manner. It is thus somewhat encouraging that optimal harvest strategies based on mean parameter values performed relatively well over the considerable range of uncertainty in demographic parameters. Additionally, the cumulative distribution functions of

simulated population sizes and harvest help express the risk of low objective function values resulting from demographic rates that in reality are lower than the means used in the optimizations. For example, in Fig. 7A, simulated population sizes were below the desired goal of 60,000 – 80,000 birds about 21% of the time. For demographic rates centered on their means, the simulated optimal harvest strategy successfully maintained population sizes in this range about 13% of the time (given our hypothetical amount of environmental variation). The difference in these values helps express the risk associated with actual demographic rates being lower than their theoretical maximums.

In Europe harvest is sometimes viewed as a tool to manage goose population size within acceptable bounds (Madsen et al. 2017). Yet we know that hunters value the hunting opportunity afforded by sustainable populations of waterbirds (Madsen et al. 2015a). Thus, we can specify (at least) two, potentially competing objectives. One is to maintain population size within a range that satisfies conservation, agricultural, and public health and safety concerns. Another is to maximize sustainable hunting opportunity. Both objectives can be accommodated in an optimal harvest strategy by assigning relative weights, reflecting the acceptable tradeoff in meeting the two objectives (Williams and Kendall 2017). The assignment of weights is not the purview of scientists, but of decision makers who must judge how best to balance the desires of different stakeholders. Moreover, we demonstrated that the assignment of weights can have profound effects on harvest strategy and performance. Although the decision about acceptable tradeoffs among objectives is a subjective one, we suggest that the procedures we describe can be used to better inform this decision.



Finally, we note that the management process for the Central Management Unit described in this article does not yet represent a fully adaptive strategy. Adaptation based on what is learned depends on the ability to make predictions about changes in population size that are model-specific, as well as an ability to measure, at a minimum, actual harvest and population size each year. The comparison of monitoring observations and model predictions then permits models to be improved so that better decisions can be made in the future. We suggest that the process we used to estimate key population parameters based on limited data could be used to define the prior distributions of parameters for an integrated population model (Kéry and Schaub 2012). Periodic monitoring data could then be used to compute the joint posterior distribution of model parameters using Bayes theorem (Link and Barker 2009). This joint posterior distribution in turn can be used to derive an updated harvest strategy with stochastic dynamic programming, assuming the joint posterior could be discretized in some acceptable way. Thus, one could derive an optimal strategy based on an expression of model uncertainty (i.e., the joint posterior distribution), and permit the strategy to evolve over time in accordance with what is learned from the management process. This is the essence of adaptive management.

The process we describe is another step forward in the implementation of adaptive management for migratory waterbirds in Europe, following the successful introduction for pink-footed geese (Madsen et al. 2017). Efforts are now underway by AEWA partners to develop adaptive management plans for barnacle and greylag geese. Although data are limited for many goose species, goose demography is generally better understood than that of other waterbirds such as ducks and waders (Elmberg et al. 2006, Bregnballe et al. 2007). While some quarry goose populations are increasing, other huntable goose, duck, and wader populations are declining,

possibly necessitating revision of their formal conservation status (Davidson and Stroud 2006).

This has consequences because some international treaties (e.g., AEWa) invoke adaptive harvest management strategy as a prerequisite to continued hunting. Thus, adaptive harvest management programs may have to be developed in the near future for species that are still relatively common, largely distributed, widely hunted, yet declining (e.g. common pochard *Aythya ferina*). We believe careful application of the approach we describe can provide prior distributions of key demographic parameters, provide insights into the monitoring and research activities needed to corroborate those estimates, and suggest harvest management strategies that are optimal with respect to the managers' objectives, options, and the available demographic information. We stress that international coordination on setting objectives and regulating harvest is essential. We also stress that an adaptive, flyway-based approach to management depends on the ability to develop and implement internationally coordinated monitoring protocols for waterbirds, in which standards for data collection, reporting, and summarization are rigorously applied.

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Table 1. Mean intrinsic growth rates ( $r_d$ ) (and 90% confidence limits) estimated using body mass (in grams, Dunning 2008) and age at first breeding (Age), compared to those from the literature based on demographic data for exponentially increasing populations ( $r_e$ ). Also provided is the estimated form of density-dependence ( $\theta_d$ ) based on the estimate of  $r_d$  and empirical (or assumed\*) estimates from the literature ( $\theta_e$ ).

Species	Mass	Age	$r_d$	$r_e$	$\theta_d$	$\theta_e$	Source
Barnacle goose ( <i>Branta leucopsis</i> )	1586 (122)	3	0.158 (0.127 – 0.192)	0.166	3.710 (0.468 – 11.438)		Larson et al. (1988), Niel and Lebreton (2005)
Snow goose ( <i>Anser caerulescens</i> )	2456 (149)	2	0.194 (0.154 – 0.238)		3.478 (0.439 – 10.727)		
				0.157			Gauthier and Brault (1998), Niel and Lebreton (2005)
				0.09		2.05	Cooch and Cooke (1991), Sæther and Engen (2002)
Pink-footed goose ( <i>Anser brachyrhynchos</i> )	2520 (270)	3	0.152 (0.122 – 0.185)	0.107	3.755 (0.474 – 11.575)		Johnson and Madsen (2016)
Common pochard ( <i>Aythya ferina</i> )	823 (193)	1	0.324 (0.255 – 0.402)	0.82	2.747 (0.335 – 8.483)	0.15	Blums et al. (1993), Sæther and Engen (2002)
Mallard (North America) ( <i>Anas platyrhynchos</i> )	1095 (106)	1	0.315 (0.248 – 0.390)		2.796 (0.351 – 8.633)		
Eastern				0.629			U.S. Fish and Wildlife Service (2018)
Midcontinent				0.235			
Alaska				0.312		1.0*	
Southern Pacific Flyway				0.276		1.0*	

Fig. 1. Management units as currently delineated for taiga bean geese, showing the major divisions by different colors. The numbers refer to estimated population sizes in 2014 (Majakangas et al. 2015) accompanied by indicative trends, and the dashed lines link breeding areas (lighter colours) with respective specific winter areas (darker colours). Note the wintering areas in the Netherlands (defined by dashed red line) are functionally now abandoned. The green dotted line indicates linkages between breeding areas in norther Fennoscandia and known moulting areas in Novaya Zemlya and the Kola Peninsula.

Fig. 2. Life cycle of taiga bean geese based on a mid-winter anniversary date. The three age classes represented are young (Y, birds aged 0.5 years), juvenile (J, birds aged 1.5 years), and adults (A, birds aged  $\geq 2.5$  years). Vital rates are survival in the absence of harvest,  $s$ , the harvest rate of birds that have survived at least one hunting season,  $h$ , the differential vulnerability of young to harvest,  $v$ , and the reproductive rate,  $\gamma$ .

Fig. 3. Possible utility function for midwinter population sizes of taiga bean geese in the Central Management Unit, based on the International Single Species Action Plan's stated goal of maintaining a population around 70,000. A utility of one represents complete satisfaction, while a utility of zero represents complete dissatisfaction. High numbers of taiga bean geese are not desirable because of the agricultural damage they can cause.

Fig. 4. Optimal harvest strategy for the Central Management Unit of taiga bean geese in which the sole objective is to maintain a midwinter population near its goal of 70,000. Each panel represents prescribed harvests (in thousands) for selected fixed numbers of young (in thousands shown above each panel) and varying numbers of juveniles and adults (also in thousands). This

strategy was based on an age-structured, density-dependent, matrix model using the means of 100,000 random samples of demographic rates.

Fig. 5. Optimal harvest strategy for the Central Management Unit of taiga bean geese in which the sole objective is to maximize sustainable harvests. Each panel represents prescribed harvests (in thousands) for selected fixed numbers of young (in thousands shown above each panel) and varying numbers of juveniles and adults (also in thousands). This strategy was based on an age-structured, density-dependent, matrix model using the means of 100,000 random samples of demographic rates.

Fig. 6. Optimal harvest policies for the Central Management Unit of taiga bean geese for two contrasting objectives: maintain a population size around 70,000 and maximize sustainable harvest. This graph represents prescribed harvests for varying sizes of the total population (both in thousands). These policies were based on the scalar model (i.e., no age structure) using the means of 100,000 random samples of demographic rates.

Fig. 7. Cumulative probabilities of population size (in thousands) over 20 years from 100,000 simulated matrix-model parameterizations, using optimal policies for the mean scalar (red) and matrix (black) models of taiga bean geese. The left panel (A) portrays the optimal strategy to meet a sole objective of maintaining population size around 70,000, while the right panel (B) is based on a sole objective to maximize sustainable harvests.

Fig. 8. Cumulative probabilities of annual harvests (in thousands) over 20 years from 100,000 simulated matrix-model parameterizations, using optimal policies for the mean scalar (red) and matrix (black) models of taiga bean geese. The left panel (A) portrays the optimal strategy to

meet a sole objective of maintaining population size around 70,000, while the right panel (A) is based on a sole objective to maximize sustainable harvests.

Fig. 9. Cumulative probabilities of the (absolute) annual change in harvests (in thousands) over 20 years from 100,000 simulated matrix-model parameterizations, using optimal policies for the mean scalar (red) and matrix (black) models of taiga bean geese. The left panel (A) portrays the optimal strategy to meet a sole objective of maintaining population size around 70,000, while the right panel (B) is based on a sole objective to maximize sustainable harvests.

Fig. 10. Numbers (in thousands) of taiga bean geese counted in spring staging areas of southern Sweden as provided by (Skjellberg 2015), compared with overall harvest rates calculated from crude estimates of total harvests in Sweden and Finland and autumn population size as based on the scalar model described in the text. Dotted lines represent missing years of data from 2010 and 2013.



















