Research Article

Effect of Pre-Harvest Mortality on Harvest Rates and Derived Population Estimates

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ABSTRACT Banding waterfowl, in combination with the citizen science provided by hunters that report marks from harvested birds, is a long-standing, institutionalized practice for estimating probabilities of survival and exploitation (i.e., legal harvest from such populations). Range-wide population abundance can also be estimated by combining the number of banded individuals with the number harvested from the population. Waterfowl marking with uniquely identifiable bands done during late summer in North America is often referred to as pre-season banding. For example, mass capture of arctic geese for pre-season banding is normally done in July (nonbreeders) or August (failed breeders and breeders with young) during flightless molt of respective groups. An important assumption for proper inference about harvest probability provided from such samples is that there is no mortality, natural or otherwise, during the interval between when individuals are marked and when hunting seasons begin. We evaluated the effect of variable mortality that could occur between marking and subsequent hunting seasons on estimates of survival, recovery, and harvest probabilities using simulation pertinent to a typical waterfowl species. We fit a Brownie tag-recovery model to the simulated data and calculated the estimator bias that resulted from various pre-harvest mortality scenarios. There was no effect on survival probability during the interval between annual banding in subsequent years, but recovery probability, and thus estimated harvest probability, was directly and inversely related to pre-harvest mortality of juveniles. The magnitude of negative bias in harvest probability of juveniles increased further as the fraction of the population sampled declined. If the probability of pre-harvest mortality differs between marked and unmarked individuals, the negative bias in harvest probability results in overestimates of derived abundance that increases as the proportion of marked individuals in the population declines. We used our observed results to propose an explanation for occasional biologically improbable estimates of abundance of juvenile lesser snow geese (*Anser caerulescens*). © 2021 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS abundance, estimation, harvest rate, Lincoln's estimator, migration mortality, survival.

Crucial metrics for the status and health of populations include range-wide abundance, and change in population size, respectively (Nichols and Hines 2002). Although these apply to any free-ranging populations, they seem particularly important to know for populations exploited through hunting or trapping, with a long-term objective of sustainable harvest. Much of waterfowl decision-making and management in North America, for example, relies on uniquely identifiable

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marks on a sample of the population to provide information about population processes. Institutionalized programs for marking waterfowl exist for this purpose and are used for harvest management of some North American species (Anderson et al. 2018, U.S. Fish and Wildlife Service 2018). The marking and exploitation process associated with waterfowl banding programs serve as samplers of the hunted population, and such a subsample of the population that includes uniquely identifiable individuals can provide information about abundance (Lincoln 1930; Otis 2006; Alisauskas et al. 2009, 2011, 2014), exploitation (i.e., harvest), annual survival (Seber 1970, Brownie et al. 1985), and recruitment (Specht and Arnold 2018).

Many of the estimators of population parameters have several associated assumptions which, if violated, can result in severely biased inference. For example, estimation of annual survival probability (S) using the dead recovery models of Brownie et al. (1985) assumes no mortality

differences between marked and unmarked individuals over the interval between marking and the harvest season (Nichols and Hines 1987). It seems like a reasonable assumption that for many taxa there is little mortality over this interval for adult individuals because of the relatively high survival of adults compared to young; however, for most species, there is likely considerable potential for juvenile mortality during the interval between marking and harvest. Hereafter, we refer to deaths during this interval as pre-harvest mortality, which may differ between marked and unmarked samples. For example, environmental conditions that affect timing of nesting or forage quality during juvenile growth can exacerbate stress associated with the capture and marking process, resulting in a significant number of marked juveniles dying before the harvest sampling (i.e., suffer non-harvest mortality between marking and the harvest season).

The assumption of equivalent mortality between marked and unmarked individuals may be a particularly tenuous assumption for marking schemes involving mass capture, where capture-induced myopathy can contribute to greater pre-harvest mortality among marked compared to un-captured, unmarked birds. Although all individuals, marked and unmarked, may be exposed to common environmental conditions, marked individuals may be particularly susceptible to capture effects leading to increased pre-harvest mortality in years when environmental conditions are poor.

The most obvious implication of potential negative bias in estimates of harvest probability ($\hat{h}$) due to pre-harvest mortality (B) is that management plans that are based on $\hat{h}$ will rely on estimates that are too low. This might lead to management policies that are overly liberal. Any other use of $\hat{h}$ directly will also be influenced by the bias, as long as the subset of the population being used for inference is the subset exposed to pre-harvest mortality sources (e.g., only juveniles or a single sex may be affected). In some cases, harvest probability is not used directly for management purposes and is instead used to derive other parameters of interest, such as abundance. We therefore would expect that bias in harvest probability would propagate to estimates of abundance.

Arctic-nesting geese may represent situations in which pre-season mortality may be greater for young compared to adults. In contrast to prairie-nesting ducks, arctic-nesting geese have a longer migration distance and presumably are subject to more natural hazards before arrival at the first significant harvest areas in southern Canada. Two very common scenarios can lead to increased juvenile mortality associated with poor nutrition during this interval: delayed nesting due to protracted snow melt, leading to reduced time for goslings to fully develop and attain proper nutritional condition before fall migration (Cooch 2002; Ross et al. 2017, 2018); or deteriorating habitat, which can impede proper feeding and nutrition even in early years without temporal constraints on growth but with similar effects on body condition of goslings (Cooch et al. 1993; Williams et al. 1993a; Aubry et al. 2012; Ross et al. 2017, 2018). In both cases, goslings are marked before fledging (i.e., flight capability), but because of poor body condition, many may not develop sufficiently to survive through fledging and fall

migration out of the Arctic to reach the areas of first significant harvest in southern Canada. Both scenarios could act synergistically; in a late year with poor grazing conditions, most goslings may succumb before arrival in southern Canada. For example, Francis et al. (1992) reported most of the increasing mortality of goslings occurred at northern latitudes before autumn migration.

Pre-harvest mortality is typically unobserved (as is most natural mortality) in sampling schemes that rely on dead-recoveries of individually marked animals for inference about certain population processes (but see Hestbeck and Malecki 1989, Krementz et al. 2003 for dead-recoveries studies where pre-harvest mortality was observed). Use of such data to inform harvest management requires understanding the effect of unobserved sources of mortality on estimates of various population parameters derived from dead-recovery data (e.g., survival probability, recovery probability, abundance).

Our objective was to assess the implications of pre-harvest mortality on estimates of survival ($\hat{S}$), recovery ($\hat{f}$), and harvest probability ($\hat{h}$) and derived quantities of abundance ($\hat{N}$). We considered the structure of maximum likelihood estimators for parameter estimation using dead recovery data to assess *a priori* how pre-harvest mortality would potentially influence estimation of key parameters. We predicted that the magnitude of the negative bias in estimated recovery and harvest probabilities would be proportional to the magnitude of pre-harvest mortality. We also predicted that underestimates of harvest probability would lead to overestimates of abundance, especially if pre-harvest mortality was a function of a marker or handling effect. We then used our results to propose an explanation for biologically improbable estimates of juvenile midcontinent lesser snow goose (*Anser caerulescens*) abundance.

STUDY AREA

The data used in the empirical example consisted of midcontinent lesser snow geese that were captured and banded in Canada's eastern and central arctic and subarctic (east of 110°W longitude, and north of 53°N latitude). Recoveries were only of geese reported to the Bird Banding Laboratory as shot by hunting during autumn or spring migration through Prairie Canada (Alberta, Saskatchewan, Manitoba), or during migration and winter in the Central and Mississippi Flyways in the United States (Alisauskas et al. 2011, Calvert et al. 2017).

METHODS

Predicted Effect of Pre-Harvest Mortality on Dead Recovery Parameter Estimation
The expected effect of pre-harvest mortality on parameter estimates from dead recovery analysis can be assessed by considering the structure of the maximum likelihood (ML) estimators introduced by Brownie et al. (1985).

For a single age-class, where survival and reporting probabilities are year-specific but independent of the year of marking, the ML estimator for the probability of dead recovery in year i (f_i) is (adapted from Brownie et al. 1985):

$$\hat{f}_i = \frac{R_i}{M_i} \cdot \frac{C_i}{T_i},$$

where

M_i = the number of individuals marked and released in year i,

R_i = the number of bands recovered from individuals marked in year i,

C_i = the total number of individuals recovered in year i, over all release cohorts, and

T_i = block totals from the recovery table, where $T_1 = R_1$, and $T_i = R_i + T_{i-1} - C_{i-1}$.

This estimator for recovery probability is directly related to the number of newly marked and released individuals (R_i). Yet the number of marked individuals available for harvest is smaller by a fraction (B) than the number originally marked and released (M). Thus, B can be considered as the probability of pre-harvest mortality, which reduces the realized number of marked individuals available for harvest (i.e., will result in a negative bias in estimated recovery probability). The survival probability over interval i is estimated as

$$\hat{S}_i = \frac{R_i}{M_i} \cdot \left(\frac{T_i - C_i}{T_i} \right) \cdot \frac{M_{i+1}}{R_{i+1}}.$$

Because estimated survival is also a function of the number recovered (R), which in turn will be negatively biased in the assumed number of individuals available for harvest, we might expect that estimated survival is also potentially biased by pre-harvest. The estimator for survival is a function of the number released and recovered in successive years, rather than in the year of release alone. If the number of newly marked and released individuals each year i is an independent random variable, and if the magnitude of B is independent of N_i and R_i, then the expectation for $\hat{S}_i$ should be unbiased.

Next, we consider the scenario where juveniles and adults are marked. Because juvenile survival is not estimable from recovery data alone when only juveniles are marked (Anderson et al. 1985), we consider the situation where juveniles and adults are marked, and dead recovery data are analyzed jointly. We focus on estimators for juveniles only because we anticipate pre-harvest mortality effects for this age class only. Assuming that survival and recovery probabilities are different for juveniles in the first year after marking, and the remaining (adult) probabilities are equivalent among both marked groups (i.e., survival and recovery of adults are not a function of age of marking), the ML estimator for year-specific juvenile survival (S_i), adapted from Brownie et al. (1985), is

$$\hat{S}_i = \frac{Q_{i.} - Q_{ii}}{J_i} \cdot \frac{M_{i+1}}{R_{i+1}},$$

where,

M_{i+1} = the number of adults marked and released in year $i+1$,

R_{i+1} = the number of bands recovered from adults marked in year $i+1$,

J_i = the number of juveniles marked and released in year i,

Q_{ii} = the number of bands recovered in year i from juveniles released in year i, and

$Q_{i.}$ = the total number of recoveries from the juveniles banded in year i.

The estimator for juvenile survival (S_i) is an inverse function of the number of juveniles marked and released in year i (J_i). Thus, pre-harvest mortality of juveniles leads to a reduction in the number of marked juveniles available for harvest. This is because the number marked and released (J_i) will not be corrected for unobserved pre-harvest mortality, and this will be biased high, whereas the number recovered through harvest will reflect the number of marked individuals that survive to the harvest season. Thus, number harvested and reported will be negatively biased with respect to the number originally marked and released, leading to an overall reduction in estimated juvenile survival.

We tested whether accounting for pre-harvest mortality leads to a reduction in estimates of juvenile survival, relative to juvenile survival in the absence of pre-harvest mortality. We evaluated our results in terms of percent bias, which is calculated relative to the true survival probability. Given we adopted an annual survival model (Boyce et al. 1999), which assumes temporal separation of mortality hazards, the annual survival probability (S) is the product

$$S = (1 - h)(1 - \theta),$$

where h is harvest probability and θ is the post-harvest natural mortality probability, respectively. Harvest probability is the product of probabilities that a bird is harvested (K) and retrieved by the hunter (c) such that $h = Kc$. This is a sequential seasonal model because mortality events are conditional on separation of these 2 distinct forms of mortality; to be exposed to non-harvest natural mortality, an individual first must survive risk of harvest mortality.

We modified the seasonal model by incorporating B, which precedes both harvest mortality and post-harvest natural mortality, such that

$$S = (1 - B)(1 - h)(1 - \theta). \quad (1)$$

Inclusion of the additional term for pre-harvest mortality changes the meaning of θ because non-harvest mortality is now partitioned over the intervals of pre- and post-harvest (T. W. Arnold, University of Minnesota, personal communication). From equation 1, true annual survival for juveniles will be reduced by the proportion $(1 - B)$, and thus we anticipate that the ML estimator should be reduced by the same proportion, leading to no bias with respect to the true annual survival probability.

The ML estimator for year-specific juvenile recovery probabilities is

$$\hat{f}_i = \frac{Q_{ii}}{J_i}.$$

As was the case for survival, the estimator for juvenile recovery probability is an inverse function of the number of

juveniles marked and released in year i (J_i); thus, we anticipated that pre-harvest mortality reduction of the realized number marked and released birds should lead to a decrease in estimates of juvenile recovery. The true recovery probability, however, is a function of the harvest rate and the reporting probability, neither of which are direct functions of pre-harvest mortality. Because estimated recovery probability should decline with increasing pre-harvest mortality, while true recovery probability stays constant, we anticipated an increasing negative bias in estimated recovery probability with increasing pre-harvest mortality.

Simulation Study: Effect of Pre-Harvest Mortality on Dead Recovery Parameter Estimation

To test our analytical predictions, we conducted a series of simulation experiments based on the seasonal survival model we described in equation 1. For our simulations, we considered both the situation where estimated parameters were independent of age (typically, this implicitly refers to individuals marked as adults only), and the situation where individuals were marked as both juveniles and adults, where estimated parameters varied with age among marked juveniles. Although it is conceivable that adults from some taxa might suffer pre-harvest banding mortality, we think it far more likely that such mortality would affect developing juveniles. This is the case for arctic geese, where pre-harvest mortality is potentially a significant event in some years (Francis et al. 1992, Williams et al. 1993b), which may be exacerbated by capture methods, in which individuals are captured *en masse* while flightless by actively driving them into corral traps using helicopters (Alisauskas et al. 2011). For species captured via passive methods, such as baited swim-in traps for ducks (Ashley and North 2004), capture myopathy may be a less significant source of pre-season mortality.

We simulated data with mortality of marked juveniles between initial capture and harvest varying from $B = 0$ (no pre-harvest mortality) to $B = 0.2$. Juvenile survival is not estimable from recovery data where only juveniles are marked (Anderson et al. 1985), so we also simulated marking, survival, and recovery of adults, and analyzed data from juveniles and adults jointly. For each level of pre-harvest mortality, we simulated dead recovery data using 100 simulated samples, each consisting of 8 marking occasions, with either a fixed number of 5,000 newly marked adults alone (or juveniles and adults) released at each occasion, or a variable number of marked individuals drawn from a random normal distribution with a mean of $5,000 \pm 500$ (SD; to reflect more realistic annual variation in the number of newly marked individuals at each marking occasion).

We analyzed the simulated dead recovery data in Program MARK (White and Burnham 1999) using the Brownie parametrization (Brownie et al. 1985). Under this parameterization, the recovery data reflect the product of the probability of the marked individual is shot and killed by a hunter (K), the probability that the shot marked individual is retrieved (c), and the probability that its band number reported to the Bird Banding Laboratory (λ). Generally,

Table 1. Values of Brownie recovery model parameters used in numerical simulations. Parameter values used in the simulation reflect a typical waterfowl species and do not correspond to a specific species or system.

Parameter	Definition	Age class	
		Juvenile	Adult
$h = K$	Kill probability[a]	0.4	0.2
c	Retrieval probability	1.0	1.0
λ	Reporting probability	0.4	0.4
θ	Natural mortality	0.2	0.1

[a] Because $c = 1$, harvest probability (h) equals kill probability (K).

the product $Kc\lambda$ (often written as $h\lambda$) is the recovery probability (f). The model structure fit to the dead recovery data was based on the generating model used to simulate the data.

For each sample, we computed the percent relative bias (PRB) of an estimated parameter as:

$$\text{PRB}(x) = \frac{100 \times [E(\hat{x}) - x]}{x},$$

where $E(\hat{x})$ is computed as the mean of the estimates calculated over the 100 simulated samples, and x is the true value of the parameter as specified in the simulation, and under the assumption of no pre-harvest mortality.

For all simulations, we used time-invariant parameter values (varying only B among simulations; Table 1). We selected the parameter values to represent a relatively plausible scenario (e.g., probabilities of harvest and post-harvest natural mortality being higher for juveniles), except that, for simplicity, we assumed a retrieval probability of 1.0 for killed birds so that harvest probability equals kill probability, $h = K$. Applying these values to equation 1, true survival probability for adults is calculated as $S_{adt} = (1 - h_{adt})(1 - \theta_{adt}) = 0.72$, whereas for simulations involving a juvenile age class, the true survival probability for juveniles, which are potentially affected by pre-harvest mortality, is calculated as $S_{juv} = (1 - B)(1 - h_{juv})(1 - \theta_{juv}) = 0.48$ for $B = 0$. Thus, true juvenile survival for $B > 0$ is $0.48(1 - B)$. True adult recovery probability in both simulation scenarios (single age class and marked as juveniles and adults) is $f_{adt} = h_{adt}\lambda = 0.08$, whereas juvenile recovery probability is $f_{juv} = h_{juv}c\lambda = 0.16$.

Simulation Study: Harvest Rate Bias, Sampling Fraction, and Lincoln Abundance Estimation

We evaluated the effect of bias in the harvest probability estimator on derived quantities by carrying out a numerical demonstration using Lincoln's estimator for abundance. We used Lincoln's (1930) approach for estimating waterfowl abundance following Alisauskas et al. (2009):

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{h}_i}, \tag{2}$$

where $\hat{H}_i$ is the estimated number of individuals harvested in year i, and $\hat{h}_i$ is the estimated harvest probability in year i. In the presence of pre-harvest mortality, the

denominator in equation 2 will be negatively biased. All other things being equal, if the denominator is too small, then estimated abundance $\hat{N}_i$ will be too high for the segment of the population that experiences pre-harvest mortality.

Alisauskas et al. (2009) proposed that estimates of N should be robust to mortality that occurs between the time of banding and the time of harvest, so long as such mortality is equally represented in both $\hat{H}$ and $\hat{h}$. Following Robson (1969), they suggested that if mortality occurs between the first and second samples in a 2-sample capture-recapture study, and if this mortality applies equally to marked and unmarked animals, then Lincoln's estimator provides an approximately unbiased estimate of abundance at time of marking because the numerator in equation 2 is similarly reduced by $1 - B$.

As described above, we simulated dead recovery data with pre-harvest mortality varying from $B = 0$ (no pre-harvest mortality) to $B = 0.2$. For each level of pre-harvest mortality, we simulated dead recovery data assuming a true population size of 100,000; for simulations that involved adults only, this was the true adult population size, whereas for simulations that involved juveniles and adults, where only juveniles suffered pre-harvest mortality, this was the true juvenile population size. The marked sub-sample of the population (captured alive and individually marked) could suffer pre-harvest mortality, but the remaining un-marked population was not subject to pre-harvest mortality. For each simulation, we generated 100 simulated samples, each consisting of 8 marking occasions. We again assumed time-invariance for the parameter values (varying only B among simulations; Table 1). The model structure fit to the dead recovery data was based on the generating model.

We derived harvest (H) by correcting the number of direct recoveries in each simulation for the reporting probability (which we assume is known; Table 1). Because the parameterization of the generating and fitted model were both time-invariant, we generated the mean estimate of H over the 8 occasions, for each iteration of the simulation. For each sample, we computed the PRB of estimated abundance.

Empirical Example: Analysis of Banding Data for Midcontinent Lesser Snow Geese

We suspect that in practice, violation of the assumption of equivalence in pre-harvest mortality between mass-captured goslings versus uncaptured goslings may explain what intuitively appear to be biologically improbable estimates of gosling abundance. We estimated abundance of midcontinent lesser snow goose goslings and adults alive at the time of marking using Lincoln's (1930) method (Alisauskas et al. 2009, 2011, 2014). Estimates of band reporting (λ_i) were from a metanalysis initially reported by Alisauskas et al. (2014) and recently updated by Arnold et al. (2020). We used the same general approach as Alisauskas et al. (2011) for Lincoln's $\hat{N}$, except that we used the abundance estimator provided in Alisauskas et al. (2014), which addresses bias stemming from low numbers of marked or

recovered animals. As well, we used Taylor's (1961) power law to estimate the standard error of H, where

$$SE(\hat{H}) = 5.0421(H)^{0.6191} \qquad (3)$$

based on estimates of harvest for 42 species of migratory birds harvested in Canada from 1969 to 2017, representing 1,786 pairs of estimates.

RESULTS

Simulation Study: Effect on Dead Recovery Parameter Estimation

As predicted for the general case of a single age class, there was no effect (no generated bias) of pre-harvest mortality of the marked sample on estimated survival (Fig. 1). But the situation was notably different for estimated recovery probability, which showed increasing negative bias with increasing pre-harvest mortality (Fig. 1). As expected, the magnitude of the bias was directly proportional to $1 - B$. Pre-harvest mortality reduces the number of marked individuals that are available for harvest. This negatively biases R_i by a proportion equal to B_i:

$$\hat{f}_i = \frac{(1 - B_i)R_i}{N_i} \cdot \frac{C_i}{T_i}.$$

For example, given true recovery rate $f = 0.08$, then for $B = 0.2$, we expected $\hat{f} = (1 - 0.2)(0.08) = 0.064$, which is negatively biased by -20% with respect to the true recovery rate. This value closely matches what we estimated from the simulated data; mean PRB over 100 simulations for $B = 0.2$ was $-20.01\% \pm 1.24$ (SE; Fig. 1). Results were equivalent for both parameters for simulations where the number released varied over time in our simulations, although the standard error for estimates increased; results are reported for the situation where we held the number marked and released constant over years.

When we analyzed dead recovery data from marked juveniles and adults, where only juveniles experience pre-harvest mortality, there was no effect (no generated bias) of pre-harvest mortality of juveniles on estimates of juvenile survival, with respect to the true annual survival probability when $B > 0$ (Fig. 2A). In addition, pre-harvest mortality of juveniles did not lead to subsequent bias in either adult survival (Fig. 2A) or adult recovery probabilities (Fig. 2B).

As expected, the situation was notably different for estimated juvenile recovery probability, which showed increasing negative bias with increasing pre-harvest mortality (Fig. 2B). The magnitude of the bias was directly proportional to $1 - B$. In other words, estimates of recovery probabilities for juveniles will generally be negatively biased for pre-harvest mortality $B > 0$, with the magnitude of the bias equal to $1 - B$. In practice, this suggests that estimates of harvest rate will also be negatively biased. For example, if $\hat{f} = 0.144$ instead of 0.16, which would result if $B = 0.01$ with $c = 1$ and $\lambda = 0.4$, then $\hat{h} = (0.144/0.4) = 0.36$. So, $B = 0.10$ leads to a 10% negative bias in $\hat{f}$, which in turn creates a 10% negative bias in $\hat{h}$. Thus, any pre-harvest mortality will lead to an underestimate of $\hat{h}$ for juveniles, all other things being equal.
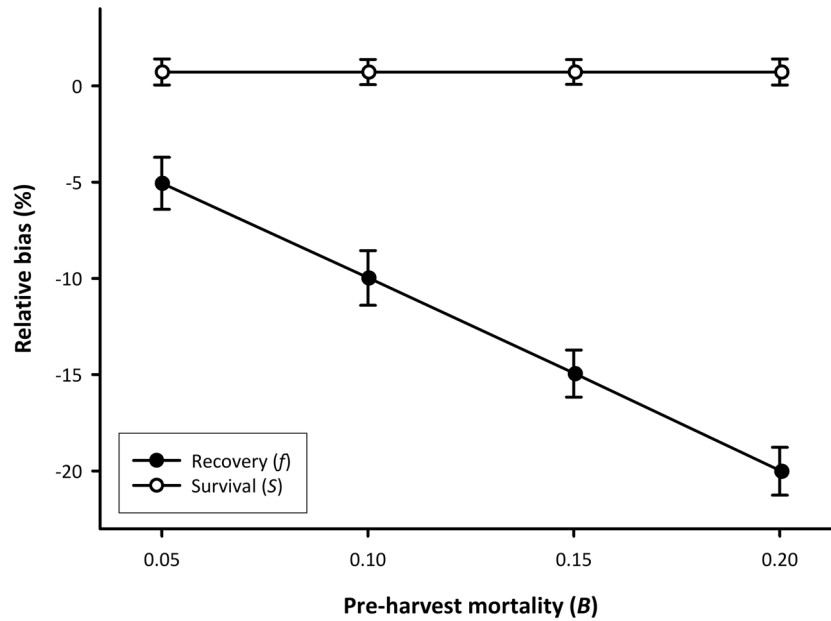
Figure 1. Relationship between probability of pre-harvest mortality (B) and percent relative bias of estimated survival probability ($\hat{S}$) and recovery probability ($\hat{f}$), for a single (adult) age class, where percent relative bias is calculated as the mean difference between the estimated and true value of the parameter, as a percentage of the true parameter value ($S = 0.72$, $f = 0.08$). Plotted points for both parameters represent mean estimates from 100 simulated samples; we derived the estimates by fitting the true estimating model to the simulated recovery data. Error bars are the standard error of the estimated mean values. Parameter values used in the simulation reflect a typical waterfowl species but do not correspond to a particular species or system.

Simulation Study: Harvest Rate Bias, Sampling Fraction, and Lincoln Abundance Estimation

We considered the effect of the negative bias in $\hat{f}$ and $\hat{h}$ on derived estimates of abundance by a simple numerical example. Let true $N = 10,000$. We capture a sample of 1,000, which we mark and release alive. We assume probability of mortality prior to harvest $B = 0.10$, and initially assume it applies equally to both the marked and unmarked sample (assumed by the Brownie dead recovery model). Thus, at the start of annual harvest, the population is expected to consist of 900 marked individuals, and 8,100 unmarked individuals (total population size just before harvest is 9,000). Let true harvest probability $h = 0.4$ (let $c = 1.0$, $\lambda = 0.4$). Also assume harvest probability does not depend on whether the individual is marked or unmarked. So, expected H is $(0.4 \times 9,000) = 3,600$. True $f = (0.4 \times 1.0 \times 0.4) = 0.16$. Given pre-harvest mortality $B = 0.1$, then $\hat{f}$ will be negatively biased as $(1 - B)f = (1 - 0.1)(0.16) = 0.144$. Thus, $\hat{h} = 0.144/(0.4) = 0.36$ (i.e., negatively biased by B relative to true $h = 0.4$).

Thus,

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{h}_i} = \frac{3,600}{0.36} = 10,000.$$

Clearly, estimated abundance perfectly matches the true value for this example. In fact, we can show generally that

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{h}_i} = \frac{[N_i(1 - B_i)h_i]}{(1 - B_i)h_i} = N_i.$$

Therefore, pre-harvest mortality does not bias estimates of abundance based on Lincoln's approach, under the assumption that such mortality affects marked and unmarked individuals equally.

We can explore the implications of possible violations of this assumption of equal pre-harvest mortality between marked and unmarked animals by reconsidering the numerical example just discussed. Again, we let true $N = 10,000$. We capture a sample of 1,000 individuals, all of which we mark and release alive. We assume probability of mortality of marked individuals prior to harvest is $B^M = 0.10$, but rather than assume it applies equally to both the marked and unmarked sample, we assume that it is twice the mortality rate of unmarked (i.e., non-captured) individuals of $B^U = 0.05$. Thus, at the start of harvest, the population consists of $(1,000 \times 0.9) = 900$ marked individuals, and $(9,000 \times 0.95) = 8,550$ unmarked individuals (total population size at the time of harvest is 9,450). Let the true harvest probability $h = 0.4$ (let $c = 1.0$, $\lambda = 0.4$). We assume harvest probability does not depend on whether the individual is marked with a leg band or not. Therefore, H is $(0.4 \times 9,450) = 3,780$ and true recovery rate $f = (0.4 \times 1.0 \times 0.4) = 0.16$. Given pre-harvest mortality for marked individuals of $B^M = 0.1$, then $\hat{f}$ will be negatively biased by $(1 - B^M)f = (1 - 0.1)(0.16) = 0.144$, and $\hat{h} = 0.144/0.4 = 0.36$ will be negatively biased by B^M with regards to true $h = 0.4$. Therefore, our estimate of abundance

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{h}_i} = \frac{3,780}{0.36} = 10,500.$$

is biased high with respect to the true population abundance $N = 10,000$ when marked individuals experience greater pre-harvest mortality than unmarked individuals.
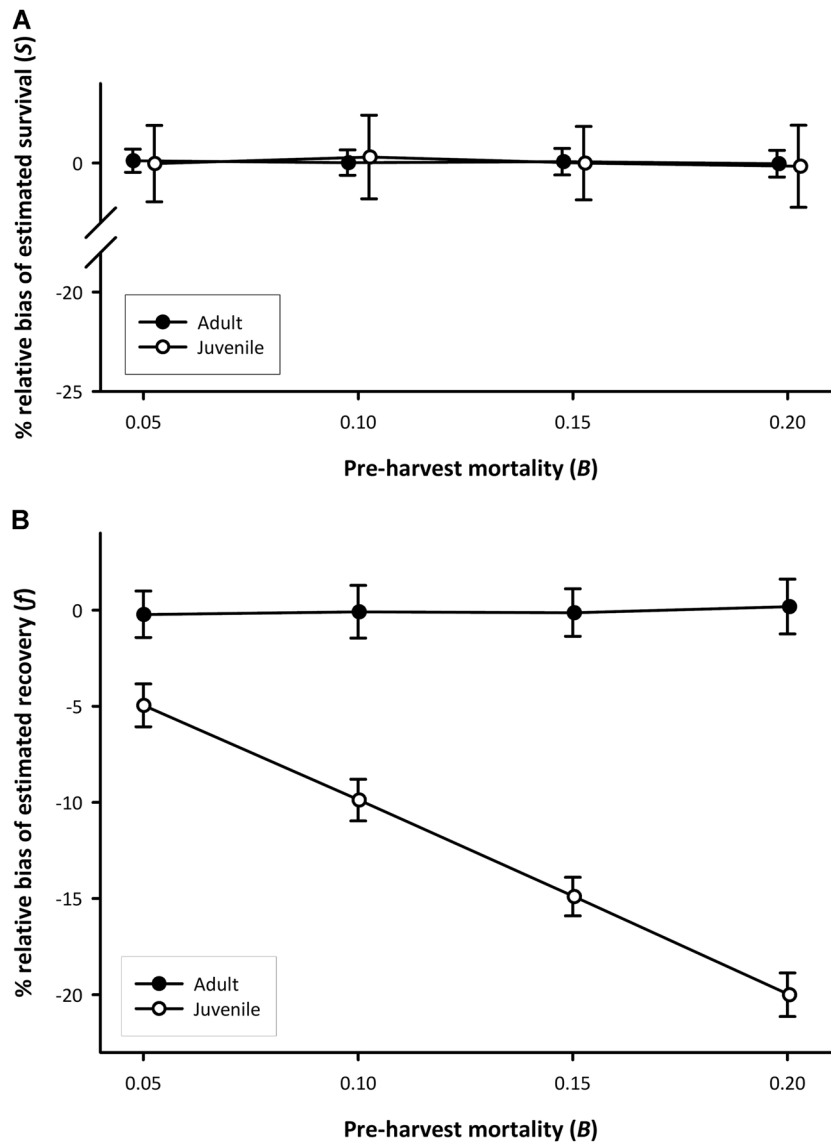
Figure 2. A) Relationship between probability of pre-harvest mortality (B) and percent relative bias of estimated survival probability ($\hat{S}$), for adult and juvenile age classes, where relative bias is calculated as (mean $\hat{S}$ − true S), as percentage of true S ($S_{adt} = 0.72$, $S_{juv} = 0.48$). B) Relationship between probability of pre-harvest mortality and percent relative bias of recovery probability ($\hat{f}$), for adult and juvenile age classes; we calculated relative bias as (mean $\hat{f}$ − true f), given true recovery probability and pre-harvest mortality ($f_{adt} = 0.08$, $f_{juv} = 0.16$). Plotted points for both parameters represent mean estimates from 100 simulated samples; we derived the estimates by fitting the true estimating model to the simulated recovery data. Error bars are the standard error of the estimated mean values. Parameter values used in the simulation reflect a typical waterfowl species but do not correspond to a particular species or system.

Finally, we assume the extreme case where only marked individuals suffer pre-harvest mortality of 0.10 with none suffered by uncaptured goslings. Given $N = 10,000$ from which we capture a sample of 1,000 individuals, all of which we mark and release alive, with $B = 0.10$ for the marked sample only, then at the time of harvest, the population consists of $(1,000 \times 0.9) = 900$ marked individuals, and 9,000 unmarked individuals (total population size at start of harvest is 9,900). Again, we let $h = 0.4$ (let $c = 1.0$, $\lambda = 0.4$) and assume that h is independent of whether the individual is marked or unmarked. So, in this scenario, the expected total kill (i.e., total harvest) is $(0.4 \times 9,900) = 3,960$, and thus abundance is estimated as

$$\hat{N_i} = \frac{\hat{H_i}}{\hat{h_i}} = \frac{3,960}{0.36} = 11,000.$$

Here again we see that the Lincoln's estimated abundance is biased high.

We can show that the magnitude of the bias is a function of the difference in pre-harvest mortality between marked versus unmarked individuals. If B^M is pre-harvest mortality for marked individuals M, and B^U is pre-harvest mortality for unmarked individuals U, then

$$\hat{N_i} = \frac{\hat{H_i}}{\hat{h_i}} = \frac{[M(1 - B_i^M) + U(1 - B_i^U)]h_i}{h_i(1 - B_i^M)},$$

which can be simplified and re-written as

$$\hat{N}_i = M_i + U_i \frac{(1 - B_i^U)}{(1 - B_i^M)}. \qquad (4)$$

If κ is the sampling fraction for the population, then

$$\kappa = \frac{M}{M + U},$$

and therefore

$$U = \frac{M}{\kappa} - M. \qquad (5)$$

If $\hat{N}_i$ is the estimated abundance assuming that pre-harvest mortality is the same for marked and unmarked individuals (where $N_i = M + U$), and $\hat{N}_i^*$ is the estimated abundance assuming pre-harvest mortality differs between marked and unmarked individuals, then after substituting equation 5 into equation 4, the relative bias (expressed as the ratio of $\hat{N}_i^*$ and $\hat{N}_i$) is

$$bias = \frac{\hat{N}_i^*}{\hat{N}_i} = \kappa - \kappa \left(\frac{1 - B_i^U}{1 - B_i^M} \right) + \kappa \left(\frac{1 - B_i^U}{1 - B_i^M} \right). \quad (6)$$

Equation 6 is linear in κ. As the sampling fraction κ approaches 1.0, then the ratio of $\hat{N}_i^*/\hat{N}_i$ approaches 1.0 (i.e., no bias):

$$\frac{\hat{N}_i^*}{N_i} \underset{\kappa \to 1}{\approx} (1) - (1)\left(\frac{1 - B_i^U}{1 - B_i^M} \right) + (1)\left(\frac{1 - B_i^U}{1 - B_i^M} \right) = 1.$$

Alternatively, as the sampling fraction κ declines (i.e., if the number marked is a very small fraction of the total

population exposed to harvest, which is increasingly likely among rapidly growing populations),

$$\frac{\hat{N}_i^*}{N_i} \underset{\kappa \to 0}{\approx} \left(\frac{B_i^U - 1}{B_i^M - 1} \right).$$

For $B_i^U = B_i^M$, an assumption underpinning Lincoln's estimator, then as $\kappa \to 0$, $\hat{N}_i^*/\hat{N}_i$ approaches 1.0 (i.e., no bias). If $B_i^U < B_i^M$, as might be expected if marking increases pre-harvest mortality of mass-captured individuals, then for low sampling fractions, the lower the ratio of B_i^U/B_i^M (i.e., when pre-harvest mortality of marked individuals is proportionately higher than unmarked individual), the higher the bias (i.e., $\hat{N}_i^* > \hat{N}_i$; Fig. 3).

Results for the more general scenario with a single marked age class were equivalent. As predicted, there was no effect on estimates of juvenile abundance, if both the sampled (marked) and unsampled (unmarked) juveniles were subject to the same level of pre-harvest mortality (Fig. 4). As predicted, there was clear positive bias in estimated abundance when pre-harvest mortality affected the marked sample only. The magnitude of bias was entirely consistent with analytic predictions from equation 6 (above; Fig. 3), directly proportional to the magnitude of the pre-harvest mortality, and inversely related to the magnitude of the sampling fraction. In other words, for a given level of pre-harvest mortality, as the sampling fraction declines (as might be expected, say, given a constant sampling effort in a growing population), then positive bias in $\hat{N}$ increases (Fig. 4).

Empirical Example: Analysis of Banding Data for Midcontinent Lesser Snow Geese
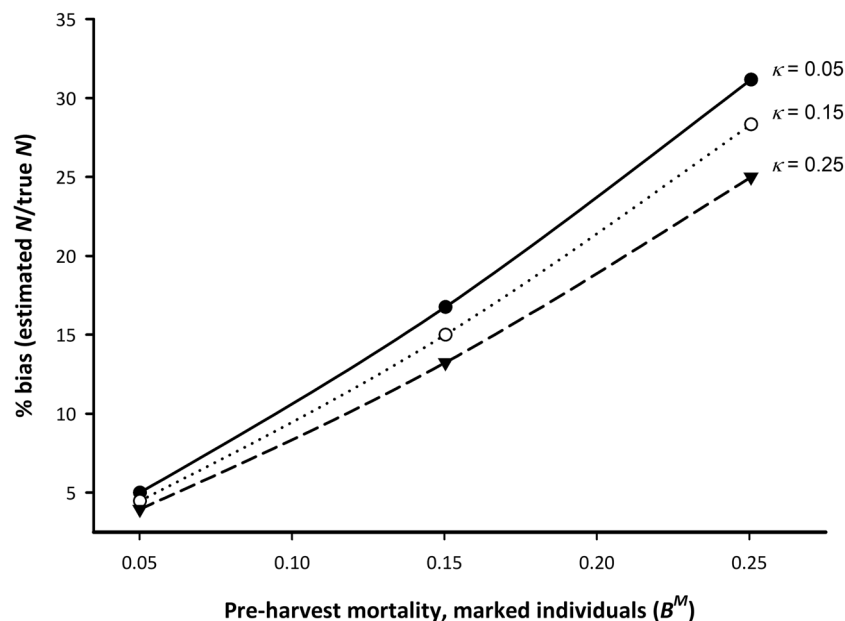We intuitively suggest that abundance of juvenile (hatch year) geese in the years 1989, 1994, 2001, 2008, 2014, and

Figure 3. Predicted bias in estimated population abundance ($\hat{N}$; as a % relative to true N), as a function of probability of pre-harvest mortality of marked individuals (B^M), for different sampling fractions (κ). Lines represent the case where pre-harvest mortality of unmarked individuals (B^U) is assumed to be $B^U = 0.0$, for values of $B^M > 0$. Parameter values used in the simulation reflect a typical waterfowl species but do not correspond to a particular species or system.
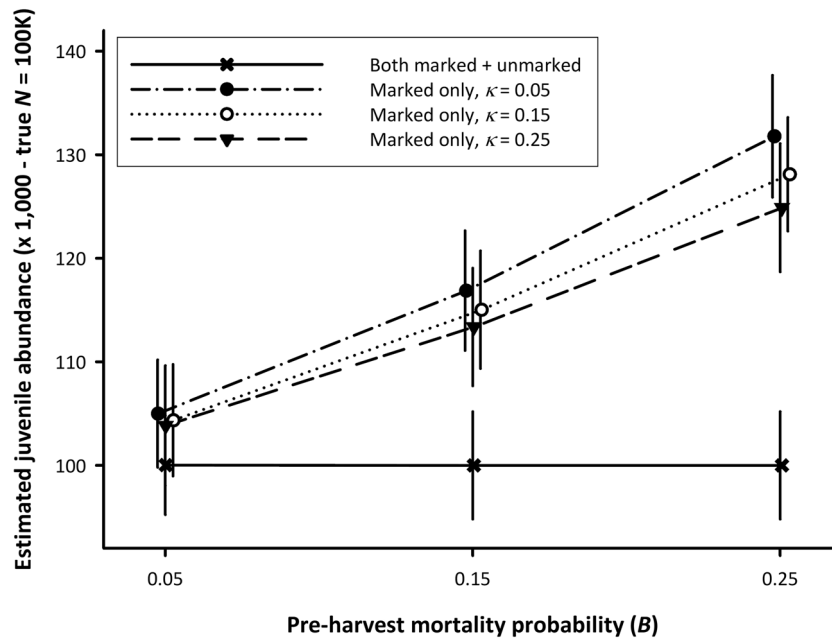
Figure 4. Variation in estimated juvenile abundance ($\hat{N}$; relative to true simulated $N = 100{,}000$ juveniles), as a function of probability of pre-harvest mortality of marked individuals (B^M), for different sampling fractions (κ). Solid line at 100,000 (✖) indicates estimates when pre-harvest mortality was applied equally to both marked and unmarked individuals. Remaining lines represent the situation where $B^M > 0$ for the marked sample, while pre-harvest mortality of unmarked individuals (B^U) is assumed to be $B^U = 0.0$. Error bars are the standard error of the estimated mean values. Parameter values used in the simulation reflect a typical waterfowl species but do not correspond to a particular species or system.

2017 (Fig. 5) was overestimated possibly because the assumption of equal pre-harvest mortality between marked and unmarked goslings was not met, with higher pre-harvest mortality from mass capture in combination with relatively low sampling fraction of the population. In all other years, estimates of juvenile abundance were <6 million for the midcontinent population of lesser snow geese. Estimates of juvenile harvest probability in those years were exceeded by estimates for adult (after hatch year) lesser snow geese (Fig. 6). In all other years,

juvenile harvest probability exceeded those for adult birds, which is a normal expectation because they are more vulnerable to harvest (Alisauskas et al. 2006). We suggest that reduced harvest probability of juveniles in those years was biased and a result of disproportionate pre-harvest mortality of marked goslings.

DISCUSSION

It is often assumed, at least implicitly, that fates of marked individuals do not differ from those of unmarked
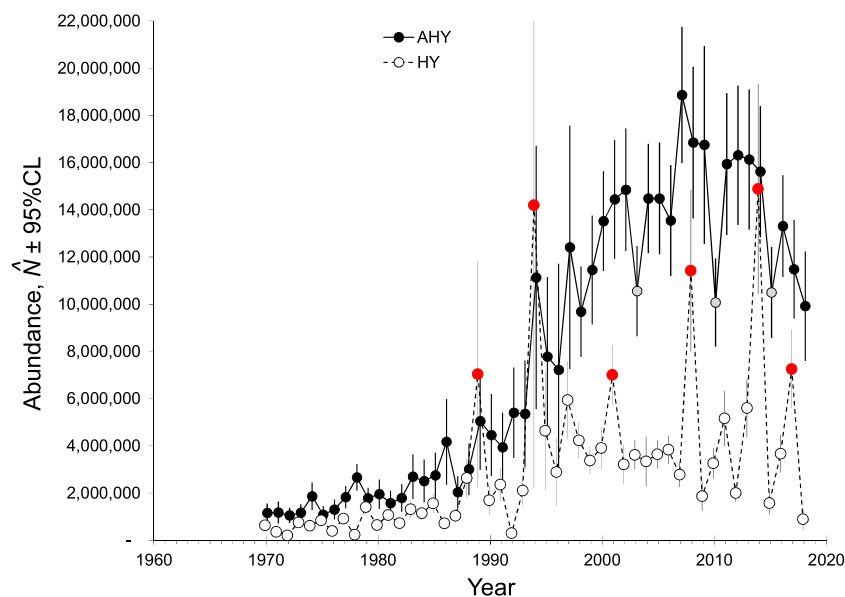

Figure 5. Lincoln (1930) abundance estimates calculated for Midcontinent lesser snow geese alive at the time of marking in August just before fledging in central and eastern arctic and subarctic Canada, 1970–2018. Red symbols represent hatch-year (HY) snow geese in years with unrealistically high estimates of abundance. Grey symbols represent after-hatch-year (AHY) snow geese in years with unrealistically low estimates of abundance.
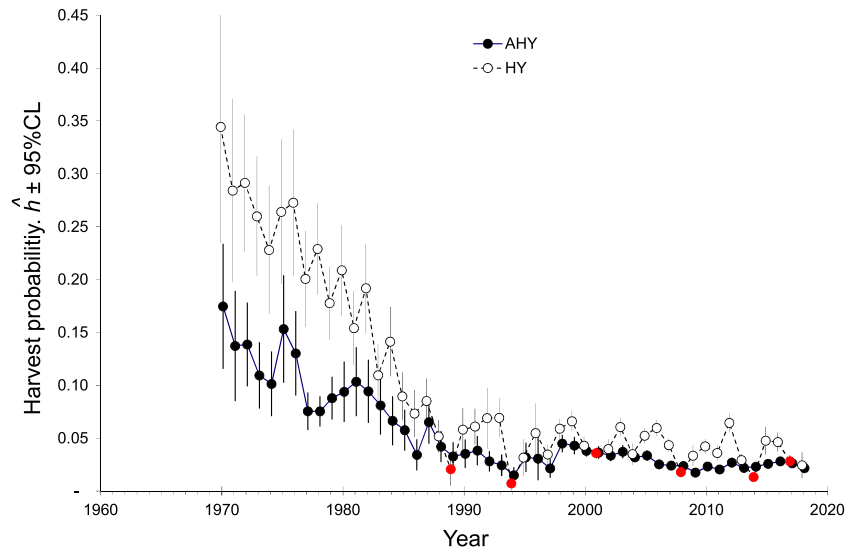
Figure 6. Estimates of harvest probability (*h*) for hatch-year (HY) and after-hatch-year (AHY) Midcontinent lesser snow geese marked in central and eastern arctic and subarctic Canada, 1970–2018. Estimates are based on the direct recovery probability adjusted by band reporting probability. Red symbols represent HY snow geese in years when harvest probability was inferred to be biased low because of pre-harvest mortality either in the arctic, subarctic, or during southward migration to Prairie Canada.

individuals, although violation of this assumption might be likely, depending on the marker type (Kinkel 1989, Calvo and Furness 1992, Lameris and Kleyheeg 2017). Our results demonstrate the potential for bias stemming from pre-harvest mortality in estimating parameters important for management. In addition, our findings are consistent with previous work focused on the effects of tag loss on parameter estimation (McDonald et al. 2003). In some respects, tag loss and pre-harvest mortality are equivalent, in that they both reduce the realized number of tagged individuals subject to sampling by harvest; however, they differ in the sense that pre-harvest mortality involves permanent removal of a marked individual, whereas tag loss is simply permanent loss of the tag. This distinction is important because many of the sampling protocols used to estimate tag loss rate (e.g., double-marking) presume that there is some probability of subsequent encounter with an identifiable individual following loss of one of the tags (Alisauskas and Lindberg 2002, Conn et al. 2004).

One recommendation to reduce pre-harvest mortality among goslings specifically is to focus on captures of smaller numbers of geese per catch when using mass-capture techniques (Menu et al. 2001). In this manner, the time that goslings are retained in captivity is reduced, thereby reducing chances of capture myopathy or injury. Another method for eliminating death or injury of captured goslings is to isolate them from adults during captivity in separate pens and, importantly, to release reunited adults and goslings as a single flock immediately after marking. This should be done after leading them to water so that cohesion of family groups can be re-established, particularly when releases are done in the vicinity of avian predators, which can induce signification predation of goslings separated from parents during mass-capture operations (E. G. Cooch, Cornell University and R. T. Alisauskas, Environment and

Climate Change Canada, personal observations). Although such field protocols to minimize pre-harvest mortality are well-established for most mass-capture marking programs involving arctic-breeding geese, it may not be possible to eliminate such mortality entirely. For example, marked individuals may be in increasingly poor condition because of density-dependent environmental degradation (Cooch et al. 1991, Cooch 2002; Aubry et al. 2012; Williams et al. 1993*b*) or increases to phenological mismatch (Ross et al. 2017, 2018).

An analytical alternative might be to try to estimate the magnitude of pre-harvest mortality and correct for the subsequent bias in estimates of recovery probabilities. Under the Brownie et al. (1985) parameterization, an estimator for natural mortality rate can be derived as:

$$\theta = 1 - \left(\frac{S}{1-h}\right).$$

For example, using parameter values applied to our simulation experiment (Table 1), if true natural mortality probability $\theta = 0.2$, with harvest rate $h = 0.4$, then annual survival (under the Boyce et al. [1999] seasonal model) is calculated as $S = (1 - 0.2)(1 - 0.4) = 0.48$. Substituting,

$$\theta = 1 - \left(\frac{S}{1-h}\right) = 1 - \left(\frac{0.48}{1-0.4}\right) = 0.2,$$

which exactly matches the true value of θ.

Although it is possible to extend this algebra to derive an estimator for pre-harvest mortality separately from post-harvest natural mortality (E. G. Cooch, Cornell University, unpublished data), this fails to solve the problem of estimator bias. Because *h* is estimated as a function of *f* and estimates of *f* are strongly negatively

biased by pre-harvest mortality (Fig. 1, 2), then any algebraic estimator for θ based on estimates of harvest or recovery rate is also biased.

Other approaches toward direct estimation of pre-harvest mortality have included the combination of banding (tagging) with radio-telemetry (Buderman et al. 2014). Additionally, modeling approaches have been considered where the condition of individuals at the time of marking and release is assessed and recorded. If survival or harvest probability scale as functions of individual condition (or time in captivity), the relationship to the covariate can be used to estimate relative pre-harvest (early season) mortality over different condition classes (Latour et al. 2003, Hueter et al. 2006). But an estimate of absolute pre-harvest mortality using this approach would require assuming there is a condition class where pre-harvest mortality is zero and increased handling time necessary to assess individual condition may increase mortality of marked juveniles. In our numerical experiments, we did not evaluate individual heterogeneity in pre-harvest mortality (say, as a function of differences in individual condition at marking). We would anticipate, however, that such heterogeneity would contribute additional negative bias in estimated recovery probability (Nichols et al. 1982).

Estimating pre-harvest mortality directly from dead recovery data alone, based on a single pre-season sampling (which we have assumed), may not be possible. Brownie et al. (1985) developed additional models that made use of multiple sampling events during the year (typically pre- and post-harvest), which could potentially be adapted to estimate pre-season mortality in some situations (Arnold et al. 2016). In addition, joint dead recovery-telemetry data (Buderman et al. 2014) has potential for direct estimation of pre-harvest mortality rates, although application of sufficiently small telemetry devices to juveniles, and potential effects of those devices on pre-harvest and subsequent survival of individuals are likely problematic.

It is generally understood that hatch-year waterfowl, such as juvenile snow or Ross's geese (Chen rossii), normally have higher harvest vulnerabilities than after-hatch-year birds (Alisauskas et al. 2006). Thus, we recommend checking relative vulnerabilities as a diagnosis of pre-harvest mortality in hatch-year birds, which leads to underestimates in band recovery and harvest probabilities, which in turn cause overestimation of abundance when using Lincoln's estimator. For example, in contrast to estimates obtained for lesser snow geese (Fig. 5), harvest rates of hatch-year ducks exceeded after-hatch-year ducks consistently across years for 3 populations of mallards (Anas platyrhynchos) in North America (Alisauskas et al. 2014), as expected. Thus, the apparent irruptions in estimated hatch-year abundance of lesser snow geese (Fig. 4), most likely associated with high pre-harvest mortality of marked goslings in corresponding years, were absent from mallard time series of hatch-year abundances.

MANAGEMENT IMPLICATIONS

Increased pre-harvest mortality of marked individuals due to the capture process violates the explicit assumption of equivalence of fates of marked and unmarked individuals necessary for unbiased estimation of survival and other metrics from the sampled population. Such pre-harvest mortality leads to significant negative bias in estimates of recovery probability for the affected age class (typically juveniles) of some waterfowl species, which in turn can strongly bias estimates of harvest probability and abundance, both of which are functions of estimated recovery probability. Pre-harvest mortality in juvenile arctic-nesting geese seems technically difficult to estimate but may be feasible using telemetry methods. Otherwise, pre-harvest mortality remains an unobservable event. If pre-harvest mortality is potentially significant, then we recommend that estimates of juvenile recovery, and derived estimates based on recovery (e.g., Lincoln estimates of abundance), should be evaluated cautiously, especially in situations where the sampling fraction of individuals from the population is low. Nevertheless, Lincoln estimates of abundance for adult geese generally appear to be unbiased by pre-harvest mortality.

ACKNOWLEDGMENTS

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