Articles

Effects of Liberalizing Harvest Regulations on Canada Goose Demography in Nebraska

Timothy P. Lyons,* Larkin A. Powell, Mark P. Vrtiska

T.P. Lyons
School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska 68503

Present address: Minnesota Department of Natural Resources, Madelia, Minnesota 56062

L.A. Powell
School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska 68503

M.P. Vrtiska
Nebraska Game and Parks Commission, Lincoln, Nebraska 68503

Present address: School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska 68503

Abstract

Harvest regulations are used to manage game species. Across their range, Canada geese Branta canadensis have recovered from near extirpation and are now perceived as overabundant and even a nuisance or a threat to human safety in many regions. Like many states, Nebraska has liberalized harvest regulations to increase recreation opportunities for consumptive users and to control increasing numbers of Canada geese. However, the efficacy of harvest regulations to control goose abundance is unclear. We used a live capture–recapture and dead recovery data set of more than 19,000 Canada geese banded in Nebraska 2006–2017 to determine the effect of liberalized harvest regulations on goose survival and overall growth rate. Our goals were to 1) estimate demographic parameters for Canada geese in five different regions in Nebraska; 2) estimate the effect of increasing daily bag limits during the early September season and regular season on survival of hatch-year, juvenile, and adult Canada geese; and 3) relate the effect of estimated changes in survival to regional growth rates. We found that survival (0.54–0.87), fidelity (0.14–0.99), and productivity (number of young per adult, 0.17–2.08) varied substantially among regions within Nebraska. We found that increasing early-season bag limits, but not regular-season bag limits, reduced survival in Canada geese. However, this effect was greatest when comparing years without an early season to years with the highest daily bag limits used in Nebraska (eight). Survival of juvenile geese (2–3 y posthatch) were unaffected by changes in daily bag limits during any season, though the probability of reporting was greatest for this age class. The observed reductions in survival probability of hatch-year and adult geese due to increased daily bag limits during the early season (< 10%) led to a decrease in regional growth rates of ~5% between years with the most liberal early-season daily bag limits and years without an early season. Our results suggest that increased bag limits during the early season may reduce Canada goose survival, but not enough to affect regional growth rates in Nebraska.

Key words: Burnham model; Canada geese; harvest management; live–dead encounter; Nebraska; population control

Received: December 9, 2019; Accepted: April 21, 2020; Published Online Early: June 2020; Published: December 2020

Citation: Lyons TP, Powell LA, Vrtiska MP. 2020. Effects of liberalizing harvest regulations on Canada goose demography in Nebraska. Journal of Fish and Wildlife Management 11(2):430–442; e1944-687X. https://doi.org/10.3996/122019-JFWM-104

Copyright: All material appearing in the Journal of Fish and Wildlife Management is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: tlyons253@gmail.com
Introduction

State and federal wildlife managers have traditionally used harvest regulations to prevent overexploitation (Leopold 1933) or to prevent take during periods of recovery for game animals. Species such as Canada geese *Branta canadensis*, wild turkeys *Meleagris gallopavo*, wood duck *Aix sponsa*, and white-tailed deer *Odocoileus virginianus* are abundant today but were nearly extirpated in many locations during unregulated hunting before the early 20th century. Reinforcement efforts were central to recovery plans, but state and federal wildlife management agencies also closed hunting seasons or used conservative (limited take) harvest regulations to promote the recovery of these species (Bellrose 1976; Leberg et al. 1994; Schmidt 2004; Dooley et al. 2019).

Efforts to recover these species of game animals have been so successful that agencies have reinstated and even liberalized hunting regulations to allow for greater harvest and recreational opportunities for consumptive users (e.g., Hupp et al. 2015; Dooley et al. 2019). Even with liberal harvest management, subsequent increases in the abundance of some species has led to increasing concerns about overpopulation. For example, Canada and lesser snow geese *Anser caerulescens* now cause substantial environmental degradation and agricultural damage, as well as other human–wildlife conflicts (Ankney 1996; Batt 1997; Collucy et al. 2001; Schmidt 2004). In response, state and federal wildlife agencies have liberalized harvest regulations by increasing season lengths, daily bag limits, and instituting special harvest seasons, all in an attempt to control abundance (U.S. Fish and Wildlife Service 2005; Dooley et al. 2019).

There has been mixed evidence for the ability of liberalized regulations to influence demographics and limit or regulate game species with large numbers. Liberalized harvest regulations appear to reduce survival in some geographic regions (Calvert and Gauthier 2005; Alisauskas et al. 2011; Iverson et al. 2014; Dooley et al. 2019), but not in others (Sheaffer et al. 2005; Groepper et al. 2012; Shirkey et al. 2018). The success of liberalized harvest regulations at reducing survival may depend on the age or breeding status (i.e., successful breeder vs. molt migrant; Calvert and Gauthier 2005; Iverson et al. 2014), or whether harvest occurs during special early seasons (e.g., August and September goose seasons, continental United States) or later in the fall, during the regular hunting season (Calvert and Gauthier 2005; Dooley et al. 2019). Still, it remains uncertain whether the observed reductions in survival are sufficient to control population growth rates or limit abundance (Alisauskas et al. 2011; Iverson 2014).

Understanding the effect of changing harvest regulations on goose demography is vital for their successful management (Roberts et al. 2018), particularly at the state or other spatial scales smaller than the flyway. Though U.S. Fish and Wildlife Service (USFWS) and state wildlife agencies work collaboratively to set appropriate harvest frameworks at the flyway scale, flyway objectives and regulatory frameworks may differ from those at state or local scales. Demographic rates and management goals may differ for geese regionally, even within the same state (e.g., Powell et al. 2003; NGPC 2006). Understanding the spatial and temporal variation in the effects of hunting on goose demography can help managers to set regulatory frameworks that best meet their goals.

In Nebraska, efforts to restore Canada geese have been exceptionally successful, and as their numbers have grown, so have human–wildlife conflicts (Vrtiska and Lyman 2004; NGPC 2006). The NGPC has followed the general trend for state agencies to liberalize harvest regulations to control growth rates and abundance using both special September hunting seasons as well as increasing daily bag limits during the September and regular hunting seasons (Groepper et al. 2012). We used recapture and recovery data to test whether liberalized hunting regulations were able to affect the survival and growth rates of Canada geese banded in Nebraska 2006–2017. Our goals were to examine how the addition of a September hunting season and increasing daily bag limits during the September hunting season and regular season influenced survival and reporting probabilities. We also explored how demographic rates and the effect of increased bag limits on those parameters varied regionally across Nebraska. Finally, we estimated productivity and used a matrix model to relate the estimated changes in survival associated with increased bag limits to regional growth rates.

Methods

Study area

Nebraska was divided into five different harvest units in 2006–2017, with the September hunting season restricted to a small subsection of the East harvest unit (Figure 1). However, demographic rates, hunting pressure, and migratory behavior vary geographically within the state, even within the same harvest unit (Powell et al. 2003). Thus, to better understand the spatial variation in demographic parameters and their interaction with bag limits, we subdivided the state into five regions that differed from harvest units and previous analyses (Figures 1 and 2; Powell et al. 2003). These regions generally correspond to NGPC management districts (NGPC 2006) and ecoregions (Schneider et al. 2011). Both the Northeast and Southeast regions are located primarily in the tallgrass prairie ecoregion (Schneider et al. 2011). Row-crop agriculture, primarily corn *Zea mays* and soybeans *Glycine max*, is the dominant land use in this region, though the Southeast region contains more developed and urban land, including the cities of Lincoln and Omaha and their suburbs. The Platte region falls within the mixed-grass prairie and is also dominated by row-crop agriculture. Precipitation may be lower here, compared with eastern regions, and this region encompasses the central Platte River valley and Rainwater Basin, both important stopover and wintering sites for many species of migratory waterfowl (Vrtiska and Lyman 2004; Schneider et al. 2011). The Sandhills are considered the...
primary breeding habitat for Canada geese in Nebraska and was where initial restoration efforts occurred (NGPC 2006). This region contains limited row-crop agriculture and is still predominantly grassland (Schneider et al. 2011) with more than 4,500 km² of wetland habitats (LaGrange 2005). The Panhandle region is comprised of mostly shortgrass prairie. Almost half of the land is used for crop production, with the remainder in grassland and used for livestock production (Schneider et al. 2011).

Boundaries of the NGPC harvest units have varied over time, but generally remained constant during the 2006–2016 period. During this time frame, units had 105-d hunting seasons, though the exact start and end dates varied (Table S1, Supplemental Material). The hunting season length varied between 89 and 105 d in the Panhandle unit 2006–2012 but increased to 105 d in 2013 (Table S1). All harvest units except the North Central unit used the same season start and end dates beginning in 2013 as well (Table S1). Daily bag limits during the regular season increased from three to five in 2013. Between 2006 and 2010, a special September harvest season was established within the eastern harvest unit (southeastern region; Figures 1 and 2). The daily bag limit during the September season began at five but increased to eight in 2010. The early September season was discontinued after the 2010 hunting season. We performed a spatial overlay analysis to identify the appropriate harvest regulations for each banding location within each region.

**Data collection**

The NGPC banded Canada geese at multiple locations across Nebraska (Figure S1, Supplemental Material). During the study period, the NGPC concentrated banding effort in the Southeast region and did not band geese in the Panhandle or Sandhills regions before 2011 or in the Platte region before 2012. We captured geese during a single visit to each site by driving birds into a corral during their summer molt, when they are incapable of sustained flight (Cooch 1953). We targeted aggregations of geese by the NGPC for banding and included both family groups (adult and young birds) as well as groups of molt migrants (few or no young birds). We used small boats with outboard motors and kayaks to drive geese located over water to the shore. In most cases, we successfully captured all geese when encountered. When escapes did occur, it was almost always adult birds that were capable of flight, by running and dispersing overland, or diving underwater during drives, and primarily when large aggregations of failed or nonbreeding birds were targeted. Upon capture, we aged geese as hatch-year (hatched during the current year) or after hatch-year (hatched sometime before the current season), sexed them, marked them with a standard U.S. Geological Survey (USGS) metal leg band, and immediately released them. The USGS Bird Banding Lab (permit 06515) authorized goose banding.

We obtained banding and recovery records for all Canada geese banded in Nebraska 2006–2017 (including the 2017–2018 hunting season) from the USGS Bird
Band recovery analysis

We used a joint live–dead encounter model to estimate survival ($S$), reporting ($r$; probability a band from dead bird is reported), fidelity ($F$; probability a bird remains in the study area and available to capture), and recapture ($p$) probabilities (Burnham 1993). We used the RMark package (Laake 2013) to build and analyze models in program MARK (White and Burnham 1999) from within R (version 3.5.0; RStudio Team 2018; Data S1, Supplemental Material). We used an information-theoretic approach to compare models among our candidate set (Burnham and Anderson 2002). When developing the candidate set of models, we used a two-step approach (sensu Lebreton et al. 1992; Thomas et al. 2010) to reduce the number of models considered overall. In the first step, we sought to identify covariates that explained variation in parameters due to regional or age-specific differences. In the second step, we focused on determining support for temporal covariates, either annual effects or daily bag limits, in addition to the influential age and region covariates identified in step 1. In both steps, we developed a set of models for each parameter ($S$, $r$, $F$, and $p$) comprised of unique covariates that we had a priori believed to be biologically meaningful and of interest to our research question. For each parameter, we considered models comprised of main, additive, and two-way interactions among covariates. We then considered all possible combinations of parameter models when developing the candidate set within each step. Although the “all combinations” approach is often discouraged in the literature (e.g., Burnham and Anderson 2002; Lukacs et al. 2010), it has been recommended more recently, particularly in cases where model selection is performed on an ensemble of parameters where each parameter is a function of unique covariates (Doherty et al. 2012). Moreover, failure to consider higher-dimension models (additive combinations and interactions) comprised of the aforementioned variables (i.e., age, region) is analogous to a null hypothesis of no differences among groups, which is almost never true (Johnson 1999). We ranked models comprising the candidate set in each step according to Akaike's information criterion corrected for small sample sizes and used the median $\hat{c}$ estimator in Program MARK to correct for overdispersion (quasi-$\text{AIC}_c$; Burnham and Anderson 2002). We used the parameter-specific models contained within the top-ranked model in step 1 as the starting point for the second step of our model development.
During the first step, we considered models for survival and reporting probability that included an intercept-only model (null), regional variation, (i.e., different intercept for each region), and two different age structures. We created a three-age class model, which included a hatch-year age class, a juvenile age class (second- and third-year birds), and an adult age class because failure to account for a juvenile age class may bias survival estimates (Dooley et al. 2019). We developed a four-stage model in a posteriori fashion when we encountered biased reporting estimates (i.e., \( r = 1 \)) using a three-age class model. The four-stage model expanded the aforementioned three-age structure, but allowed for unique survival and reporting estimates for the first period after marking for birds initially encountered as after hatch-year. Thus, birds first encountered as hatch-year transitioned to the juvenile age class before transitioning to the adult class, but birds first encountered as after hatch-year existed in the fourth “unknown” stage class for 1 y before transitioning to the adult class. Lower survival during the first period after capture is often inferred to be evidence of a capture effect on survival or reporting, or some form of heterogeneity in the survival or encounter process (Sandercock 2006). However, we make no such inferences here and treat this as a nuisance parameter in our analysis.

We considered models comprised of an intercept-only, regional variation, and a two-age class structure for fidelity. The two-age classes contrasted fidelity among birds first encountered during their hatch year with all others. We note that fidelity in our models is not fidelity to the region where the bird was initially encountered, but to the state of Nebraska. We lacked sufficient data to parameterize a multistate model that would have permitted movement and fidelity estimates among regions. We did not consider any age effects for recapture probability as geese were captured using targeted drives. We only considered an intercept-only model and one including regional variation in recapture probability. In the second step of our model set construction, we modeled survival and reporting probability as a function of time (different intercept for each year), a linear effect of regular-season bag limits, September-season bag limits, or both, as additive effects. We allowed parameter models to be additive or interactive with covariates contained within the parameter model identified in step 1 but prevented time and bag-limit covariates from appearing in the same model. We did not consider modeling either recapture probability or fidelity as a function of harvest covariates, but did consider models that allowed these parameters to vary through time.

### Regional growth rate modeling

We also examined the effect of increasing bag limits on regional growth rates. We estimated productivity using the widely applied approach of calculating the number of hatch-year birds captured per after-hatch-year bird encountered (initial capture and recaptures combined) for each region and each year (Powell et al. 2003, Specht and Arnold 2018; Zhao et al. 2019). We did not attempt to classify birds encountered as after hatch-year as molt-migrant or breeding individuals (e.g., Iverson et al. 2014) because banding locations comprised of predominantly after-hatch-year birds could include failed breeders from within the region. Failure to include unsuccessful adults would result in positively biased estimates of productivity, though the inclusion of molt migrants from outside the region could negatively bias productivity estimates. We calculated the mean productivity for each region among years to reduce interannual variation attributable to expanded banding efforts, particularly during the latter half of the study period.

We used productivity and survival estimates under the current harvest regulations (regular season only, daily bag limit = 5) to parameterize a postbreeding pulse, stage-structured population projection model (Caswell 2001). We used the popbio package in R (Stubben and Milligan 2007) to estimate the growth rate for each region using the four-stage model, where the juvenile age class was duplicated to allow birds first encountered as hatch-year to persist in the juvenile age class for 2 y before progressing to the adult age class, an absorbing state. Because we directly estimated fidelity in our models, we used apparent survival (S × F) for each region and age class to parameterize the matrix model. Though many geese do not breed before their third year after hatch (Mowbray et al. 2002), we could not age adult geese beyond after-hatch-year in the field. Thus, our estimate of average productivity includes second- and third-year nonbreeders as well as failed breeders. Therefore, we applied the same mean productivity estimate among all age classes within a region when calculating the stage-specific contributions to reproduction. Because our goal was not to conduct a full sensitivity analysis or life table response experiment, we only varied the survival of each age class ± 0.15 to examine how changing survival for any given age class affected regional growth rates. Our estimates of regional growth rates are likely biased because of our inability to classify molt migrants, accurately age successfully breeding adults, and model movement of birds among regions within Nebraska. Therefore, we focused our interpretation on the relative differences in growth rates among regions and variation in growth rates relative to survival for different age classes, rather than the estimate of the growth rate itself.

### Results

We used the banding records of 19,862 geese, including 4,779 recaptures among 3,012 individuals, and 6,486 dead recoveries. We removed models containing year effects from the fidelity parameter and any models containing interactive effects of time and region from the survival, reporting, and recapture parameters because these models resulted in multiple inestimable
Increasing the September daily bag limit was similarly effective at reducing survival in the adult and hatch-year age classes (eight ~ 0.08 decrease; five ~ 0.05 decrease; Figure 3; Table 2). The 85% confidence intervals for adult survival overlapped when comparing September bag limits of five and eight. For hatch-year birds, confidence intervals overlapped when comparing bag limits of zero and five, as well as five and eight, but not for the comparison of bag limits of zero and eight.

Reporting probability estimates were similar among the Panhandle, Platte, and Northeast regions, slightly lower in the Southeast, and lowest in the Sandhills region (Figure 4; Table S3, Supplemental Material). Regardless of the region, reporting probability estimates were greatest among juvenile birds, whereas estimates were similar and lower for hatch-year and adult birds. Reporting probability estimates varied through time but ranged between ~0.35 and ~0.48 in the Panhandle and Northeast for the adult age class and ~0.37 and ~0.5 for the hatch-year age class (Figure 4; Table S3). Reporting probabilities were, on average, greater in the Platte (compared with the Northeast or Panhandle regions), but these differences were small (~0.06; Figure 4; Table S3). Similarly, estimates of reporting probability were lower in the Southeast compared with the Northeast and Panhandle, but not substantially different (~0.03; Figure 4; Table S3). The largest differences existed between the Platte and Sandhills regions, where estimates of reporting probabilities were ~0.15 to ~0.20 greater within the Platte region (Figure 4; Table S3).

Fidelity estimates were greatest among after-hatch-year birds (adult and juvenile age class), regardless of region (Table 3). Adult fidelity estimates were greatest in the Northeast region (0.99), followed by the Platte (0.94), Southeast (0.93), Panhandle (0.85), and lowest in the Sandhills region (0.79, Table 3). Hatch-year estimates of fidelity were greatest in the Panhandle followed by the Platte, Southeast, Sandhills, and Northeast regions. Though the Platte exhibited relatively high fidelity among both age classes, estimates were imprecise (Table 3). Estimates of age ratios (our estimate of fecundity) also varied considerably among regions. The ratio of hatch-year to after-hatch-year birds was greatest in the Northeast (mean = 2.08, SE = 0.28), followed by the Platte (mean = 1.28, SE = 1.08), Southeast (mean = 1.01, 0.02; Figure 4; Table S3).

### Table 1. Model selection results containing the top five models overall for survival (S), recapture (p), reporting (r), and fidelity (F) probabilities of Canada geese Branta canadensis banded in Nebraska 2006–2017. The dot multiplier indicates both main and interactive effects of parameters, whereas a colon indicates interactive effects. Models contain variables representing effects of subpopulation (Pop), age differences among hatch-year, juvenile (second- and third-year posthatch), adult, and unknown (first season postcapture, individuals banded as not hatch-year) birds (4age), daily bag limit during the September hunting season (Sep.Bag), the regular-season daily bag limit (Reg.Bag), and differences between hatch-year and all other birds (HY).

| Model                                                                 | K<sup>a</sup> | ΔQAIC<sup>b</sup> | w<sup>c</sup> |
|-----------------------------------------------------------------------|-----------------|-------------------|--------------|
| S(Pop · 4age + Sep.Bag + 4ageSep.Bag) p(Yr + Pop) r(Pop + 4age + Yr) f(Pop · HY) | 68              | 0                 | 0.98         |
| S(Pop · 4age + Sep.Bag + Reg.Bag) p(Yr + Pop) r(Pop + 4age + Yr) f(Pop · HY) | 66              | 8.28              | 0.01         |
| S(Pop · 4age + Sep.Bag) p(Yr + Pop) r(Pop + 4age + Yr) f(Pop · HY) | 65              | 12.00             | < 0.01       |
| S(Pop · 4age + Sep.Bag + Pop·Sep.Bag) p(Yr + Pop) r(Pop + 4age + Yr) f(Pop · HY) | 65              | 12.00             | < 0.01       |
| S(Pop · 4age + Reg.Bag + 4ageReg.Bag) p(Yr + Pop) r(Pop + 4age + Yr) f(Pop · HY) | 69              | 23.33             | < 0.01       |

<sup>a</sup> Number of parameters.  
<sup>b</sup> Quasi-Akaike’s information criterion adjusted for small sample sizes.  
<sup>c</sup> Model weight.

Parameters, indicating there was insufficient data to support such complex models. After excluding models with insufficient data, there were 799 candidate models in the first step of analysis and 162 in the second step.

The top-ranked model after the second step included four-stage classes for both survival and reporting probabilities (Table 1; Table S2, Supplemental Material). The top-ranked model for survival probability included the main effects of stage class, region, and September-season daily bag limits as well as two-way interactions between the September bag limit and region and the September bag limit and stage class. The best model for reporting probability included the additive effects of region, stage class, and year. The best model for recapture probability included the additive effects of year and region, whereas the best model for fidelity probability included the main effect and the interaction between region and two-age classes (Table 1; Table S2). After correcting for overdispersion (median $\tilde{\chi} = 1.29$) the top model contained ~ 97% of the model weight (Table 1; Table S2). Regular-season daily bag limits were not selected in the top-ranked model for either the survival or reporting parameters (Table 1; Table S2).

Estimates of survival differed among age classes and regions (Figure 3; Table 2). Differences in survival among age classes were larger in the Platte (~15%), Panhandle (~10%), and Sandhills region (~10%) than in the Southeast and Northeast (~6%), though the 85% confidence intervals often overlapped (Figure 3; Table 2). Under current harvest regulations, survival was greatest in the Panhandle, intermediate in the Southeast and Northeast, and lowest in the Sandhills and Platte regions (Figure 3; Table 2). Still, the large amount of uncertainty in the estimates for some regions (e.g., Platte and Sandhills) indicates that observed differences may not be reliable.

Though no other regions were exposed to a September harvest season, increasing the daily bag limit decreased survival for geese in the Southeast region, but only for the hatch-year and adult age classes (Figure 3; Table 2). Juvenile survival within the Southeast increased marginally when September daily bag limits increased, though the differences were small (~0.02; Figure 3; Table 2). Increasing the September daily bag limit was similarly
Juvenile survival was not affected by changing daily bag limits, neither during the September season nor the regular season and was therefore held constant during the growth rate analysis. Regional growth rate estimates varied little with respect to survival parameters (Figure 5). Changing growth rates more than 5% in any region would require a change in survival parameters of approximately 10% (Figure 5). The greatest differences in growth rates among regions appear to be related to estimates of reproduction or hatch-year fidelity. The near-vertical orientation of the growth rate contours among the Northeast, Southeast, and Sandhills regions suggests that, given their relatively low estimates of hatch-year fidelity, changes in survival within the hatch-year age class have little influence on growth rates overall (Figure 5). As fidelity increases, as in the Platte region, growth rate contours appear more horizontal and space between contours along the y-axis decreases, indicating a greater influence of hatch-year survival (Figure 5). By contrast, the Panhandle region had higher fidelity and survival probability estimates compared with other regions, yet the contours remained vertical, indicating minimal influence of hatch-year survival on growth rate. The Panhandle also had the lowest productivity esti-

Table 2. Survival and standard error estimates of Canada geese *Branta canadensis* banded in Nebraska 2006–2016 derived from the top model. Estimates are given for each region, age class, and September-season bag limit.

| September-season bag limit | Age        | Northeast | Sandhills | Southeast | Panhandle | Platte |
|----------------------------|------------|-----------|-----------|-----------|-----------|--------|
| 0 Adult                    | 0.72 ± 0.013 | 0.68 ± 0.030 | 0.77 ± 0.012 | 0.76 ± 0.023 | 0.70 ± 0.062 |
| 5 Adult                    | —          | —         | 0.72 ± 0.013 | —         | —         | —      |
| 8 Adult                    | —          | —         | 0.69 ± 0.022 | —         | —         | —      |
| 0 Juvenile                 | 0.73 ± 0.014 | 0.78 ± 0.023 | 0.75 ± 0.015 | 0.87 ± 0.020 | 0.68 ± 0.057 |
| 5 Juvenile                 | —          | —         | 0.76 ± 0.018 | —         | —         | —      |
| 8 Juvenile                 | —          | —         | 0.76 ± 0.024 | —         | —         | —      |
| 0 Hatch-year               | 0.69 ± 0.025 | 0.71 ± 0.036 | 0.76 ± 0.024 | 0.82 ± 0.033 | 0.54 ± 0.057 |
| 5 Hatch-year               | —          | —         | 0.71 ± 0.026 | —         | —         | —      |
| 8 Hatch-year               | —          | —         | 0.68 ± 0.033 | —         | —         | —      |
mates, suggesting that at extremely low levels, growth rate can be limited by fecundity (Figure 5).

Discussion

Our results demonstrate variable effects of changing harvest regulations on Canada goose demography. Increasing daily bag limits was most effective at reducing survival when they were used during a September harvest season, particularly when the daily bag limit was eight geese. Increasing regular-season bag limits had an undetectable effect on survival and increasing daily bag limits had no effect on survival of juvenile birds, regardless of the season when they were applied. This is consistent with other research on Canada geese, demonstrating at least some ability for special seasons to reduce survival among targeted local aggregations (Shaeffer et al. 2005, Iverson et al. 2014, Dooley et al. 2019). Yet this contrasts with previous research from within Nebraska that did not find any effect of the September harvest on goose survival (Groepper et al. 2012).

This inconsistency may be attributable to two primary differences between our studies. Our current analysis allowed us to account for an additional age class than previous work, which may reduce bias associated with pooling hatch-year and juvenile geese (Dooley et al. 2019). Moreover, only survival of adults and hatch-year birds was influenced by September harvest regulations. Combining juvenile birds with adults may have obscured differences in survival related to changes in harvest regulations (Groepper et al. 2012). Second, the difference in survival was most pronounced when comparing September-season daily bag limits of eight with when the season was closed (Figure 3; Table 2). Thus, by using a more refined approach to classifying seasons, we were able to detect changes in survival that were not apparent in previous research.

Table 3. Fidelity parameter (probability an individual marked in Nebraska returns to Nebraska) estimates for hatch-year (HY) and after-hatch-year (AHY) Canada geese Branta canadensis banded within each region of Nebraska 2006–2017.

| Subpopulation | Age class | F    | Lower  | Upper  |
|---------------|-----------|------|--------|--------|
| Northeast     | AHY       | 0.986| 0.943  | 0.997  |
|               | HY        | 0.135| 0.120  | 0.152  |
| Sandhills     | AHY       | 0.789| 0.727  | 0.840  |
|               | HY        | 0.263| 0.216  | 0.315  |
| Southeast     | AHY       | 0.932| 0.916  | 0.946  |
|               | HY        | 0.285| 0.265  | 0.305  |
| Panhandle     | AHY       | 0.854| 0.810  | 0.890  |
|               | HY        | 0.738| 0.648  | 0.812  |
| Platte        | AHY       | 0.937| 0.396  | 0.997  |
|               | HY        | 0.600| 0.316  | 0.829  |
able to detect the threshold effect of special season harvest regulations on Canada geese.

Regardless of the effect of September-season daily bag limits on survival of hatch-year and adult birds, growth rates were not sensitive to adult and hatch-year survival in four of the five regions. Among the Southeast, Northeast, Panhandle, and Sandhills regions, September-season bag limits would need to be very liberal to achieve only modest decreases in growth rates. For example, the estimated growth rate in the Southeast only declined by 6.7% when comparing seasons without a September season with those when the daily bag limit during the September season was eight. Low fidelity rates among hatch-year birds and the inability to affect juvenile survival rates with a September harvest may partially explain why special early seasons are not more effective at reducing growth rates in Nebraska.

Special seasons are most effective at reducing survival when they effectively target the local breeding aggregations (Sheaffer et al. 2005, Iverson et al. 2014, Dooley et al. 2019). In Nebraska, juvenile geese in the Southeast region, where the September hunting season occurred, showed negligible changes in survival related to increased September daily bag limits. Because many juveniles are nonbreeders, they frequently undertake molt migration (Luukkonen et al. 2008). Consequently, they may be absent from Nebraska during the September season, thereby avoiding the exposure to increased hunting mortality (Dooley et al. 2019). Alternatively, the efficacy of special seasons to control goose abundance may be limited if many of the individuals affected would never be recruited. Though this phenomenon has primarily been associated with the concept of compensatory mortality, it could also include fidelity. The low fidelity rates of hatch-year birds among most regions in Nebraska diluted the effect any decline in hatch-year survival attributable to harvest regulations had on growth rates regardless of the magnitude of decline in survival. Finally, low recruitment may be the result of low productivity, which can also weaken the relationship between hatch-year survival and growth rates. Greater productivity within the Platte region (1.28 young/adult) compared with the Panhandle (0.17 young/adult) led to growth rates being more sensitive to hatch-year survival (Figure 5) despite similarly high rates of hatch-year fidelity between the two regions (Table 3). Moreover, the relatively lower growth rate observed in the Panhandle

Figure 5. Contour plots displaying predicted growth rates of Canada geese *Branta canadensis* banded in Nebraska 2006–2017. Growth rates were estimated by varying hatch year and adult survival while holding juvenile survival probability constant at its mean value under current harvest regulations. Because of our inability to quantify age-specific breeding contributions, absolute estimates of growth rates are biased and we focus on their relationship with survival instead. Dashed lines indicate survival estimates under current harvest regulations. Region names appear above each graph.
Canada Goose Demography in Nebraska

T.P. Lyons et al.

(Figure 5) suggests that limiting productivity may be a more effective way to control goose numbers.

During the regular season, the inability to affect survival and regional growth rates via increased bag limits may be in part due to a dilution effect. Though the overwhelming majority of geese banded in Nebraska are harvested there as well (Powell et al. 2003, Dooley et al. 2019), a harvest derivation analysis, weighted by state-specific banding information, suggested that they only comprise ~45% of the total harvest of Canada geese in Nebraska during the regular hunting season (T. Lyons, unpublished data). By comparison, > 99% of direct recoveries during September seasons originated in Nebraska. Thus, migrant geese from elsewhere in the Central Flyway may reduce the ability of hunters in Nebraska to target resident geese during the regular season.

Other factors may influence the relationship between harvest regulations and demography across both September and regular seasons. Mortality from hunting may be compensatory or partially compensatory among subadults and other molt migrants (Iverson et al. 2014). In Nebraska, reporting rates among juvenile geese were greater than hatch-year or adult birds, indicating a greater risk of mortality related to hunting (the primary source of band reports). Yet survival of juveniles was similar to or greater than other age classes and neither juvenile survival nor reporting probabilities changed in response to increasing bag limits, even during the September season. Whether this pattern results from juvenile goose movement, compensatory shifts between seasons of harvest, compensatory mortality, or multiple factors is unclear. Finally, the ability to control goose abundance via liberal harvest regulations also relies on the assumption of sustained hunter participation, which may not be valid because of hunter satiation or the overall decline in hunters nationwide (Vrtiska et al. 2013; Koons et al. 2014).

More generally, additional research is needed to clarify the ability for liberalized harvest regulations, such as increased bag limits, to affect survival and demography broadly. In many cases, different components of harvest regulations (such as season length or bag limit) are changed simultaneously or for too few hunting seasons to provide a robust framework for testing their effects, which leads to more general categorizations of regulations in banding analyses (Shirkey et al. 2018; Dooley et al. 2019). In our study, the daily bag limit during the September season was eight for a single season and our inferences regarding the magnitude of the effect of increasing bag limits on survival should be considered in light of this. Quantifying the effect of harvest regulations is further complicated because geese migrate and thus may be subjected to varying harvest regulations within and across years. When dividing geese at finer spatial scales, such as we did among regions within Nebraska, movement of geese may mean that harvest regulations from banding locations do not represent the realized mortality risk to birds.

Despite these potential shortcomings, we believe our inferences are still robust. Estimated regional growth rates were relatively insensitive to survival of adult birds. Thus, if our result that an eight-bird daily bag limit reduces survival is an artifact of interannual variation in survival, our ultimate inference that liberalized bag limits have little impact on regional growth is still valid. Additionally, we do not believe that subdividing our banding data among regions adversely affects our results, as more than 80% of geese banded in Nebraska are harvested in Nebraska, within the same region where they were banded (T. Lyons, unpublished data). The Sandhills region is the lone exception to this pattern, with ~47% of all direct recoveries from new bands and recaptures reported from outside of Nebraska (T. Lyons, unpublished data). Still, geese that exhibit movement behavior that enables them to avoid local hunting pressure is yet another mechanism leading to the inability of local harvest regulations to affect goose abundance.

We found substantial variation in multiple demographic parameters among age classes and regions in Nebraska. Survival, fidelity, and productivity all exhibited large differences among regions, which in turn led to differing rates of growth. This confirms earlier research that indicated that Canada geese in Nebraska comprise demographically distinct regions (Powell et al. 2003). Given such variation in survival, productivity, and particularly hatch-year fidelity, we expect the effect of liberalized hunting regulations, particularly September hunting season bag limits, to have variable effects on survival and growth rates among regions. In the eastern regions, the effect of increased bag limits on hatch-year survival was diluted by low hatch-year fidelity. Because fidelity of hatch-year birds is greater in the Panhandle, any reduction in hatch-year survival will more directly affect regional growth rates. Thus, our data could support different harvest units than what currently exists in Nebraska if more liberal harvest regulations (such as the re-establishment of a September season) are adopted. Still additional information, particularly regarding productivity and juvenile movement, are needed to better evaluate the effect of changing harvest regulations on Canada goose demography.

Management implications

The use of harvest regulations to control overabundant species, such as geese, will likely remain a heavily utilized tool in wildlife management. Our research is generally congruent with other studies finding that special harvest seasons, such as the September hunting season in Nebraska, are more effective at reducing survival in geese than liberalizing bag limits during the regular hunting season because of their ability to target locally breeding birds (Dooley et al. 2019). However, we found that the inability to affect juvenile survival and generally low fidelity among hatch-year birds limit the ability of increased bag limits to reduce growth rates at regional scales. Moreover, bag limits would likely need to
equal or exceed previous maximums (eight) to reduce growth rates by more than 5%. Given these complicating factors, reducing the recruitment of young may be a more direct approach to lower growth rates in situations where survival and fidelity are high, though applying it at a scale large enough to affect growth rates will also be challenging. Managers may also need to consider variation in demographic parameters throughout their state when developing harvest regulations, as regional variation in parameters such as productivity or fidelity could lead to inconsistent relationships between bag limits and growth rates. Increased information about other demographic parameters, particularly breeding productivity, juvenile molt-migrant behavior, and hunter behavior are needed to better understand the mechanisms regulating Canada goose population dynamics and identify the most effective methods to control abundance.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Zipped folder containing all files, raw data, and R code to reproduce our joint-encounter analysis of Canada goose Branta canadensis banded in Nebraska 2007–2017. Files are collected as an RStudio Project. The README file provides additional detail about the included folders and files.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S1 (2.95 MB ZIP); also available at https://doi.org/10.32873/unl.dr.20191204

Table S1. Exact season dates and bag limits for Canada goose Branta canadensis harvest units in Nebraska 2006–2017.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S2 (21 KB XLSX).

Table S2. Candidate models from the second step of model selection incorporating effects of bag limits and time on Canada goose Branta canadensis survival, recapture, and recovery. The starting model (top-ranked model from the first step) is highlighted below. The overdispersion parameter is fixed at 1.29. Data were obtained from banding, recapture, and recovery records of Canada goose banded in Nebraska 2006–2017.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S3 (27 KB XLSX).

Table S3. Complete table of reporting probability estimates for each age class, region, year, and early-season bag limit, obtained from the top-ranked model for Canada goose Branta canadensis banded in Nebraska 2006–2017. Values reported include the mean estimate (estimate), standard error (se), and the lower and upper 85% confidence interval (lcl.85, ucl.85).

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S4 (29 KB XLSX).

Figure S1. Map displaying the total number of Canada goose Branta canadensis bands released within each 10’ banding block in Nebraska 2006–2017.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S5 (1.00 MB JPG).

Reference S1. Batt BDJ, editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa, Ontario: Canadian Wildlife Service.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S6 (6.94 KB PDF).

Reference S2. Hupp JW, Ward DH, Whalen ME, Pearce JM. 2015. What is causing the rapid increase of snow goose in northern Alaska? U.S. Geological Survey Factsheet 2015-3062.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S7 (374 KB PDF).

Reference S3. [NGPC] Nebraska Game and Parks Commission. 2006. Management plan for resident Canada geese in Nebraska. Lincoln: Nebraska Game and Parks Commission.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S8 (269 KB PDF).

References S4. Schneider R, Stoner K, Steinauer G, Panella M, Humpert M. 2011. The Nebraska Natural Legacy Project—State Wildlife Action Plan. Lincoln: Nebraska Game and Parks Commission.

Found at DOI: https://doi.org/10.3996/122019-JFWM-104.S9 (7.52 KB PDF).

Acknowledgments

This research was supported by USFWS grant W-128-R. J. Dooley provided helpful suggestions regarding the analysis of banding data. We are grateful for the comments from reviewers, which greatly improved this manuscript. We also thank the many Nebraska Game and Parks employees, especially R. Stutheit, who banded geese, and the hunters who reported bands from harvested birds.

Any use of trade, product, website, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Alisauskas RT, Rockwell RF, Dufour KW, Cooch EG, Zimmerman G, Drake KL, Leafloor JO, Moser TJ, Reed ET. 2011. Harvest, survival, and abundance of mid-continent lesser snow goose relative to population reduction efforts. Wildlife Monographs 179:1–42.
Bellrose FC. 1976. The comeback of the wood duck. Wildlife Society Bulletin 4:107–110.

Burnham KP. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 in Lebreton JD, North PM, editors. Marked individuals in the study of bird populations. Basel, Switzerland: Birkhaeuser Verlag.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. New York: Springer Science + Business Media.

Calvert AM, Gauthier G. 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow goose. Journal of Applied Ecology 42:442–452.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. 2nd edition. Sunderland, Massachusetts: Sinauer Associates.

Collucy JM, Drobney RD, Graber DA, Sheriff SL, Witter DJ. 2001. Attitudes of central Missouri residents toward local giant Canada goose and management alternatives. Wildlife Society Bulletin 29:116–123.

Cooch FG. 1953. Techniques for mass capture of flightless blue and lesser snow goose. Journal of Wildlife Management 17:460–465.

Doherty PF, White GC, Burnham KP. 2012. Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Dooley JL, Szymanski ML, Murano RJ, Vrtiska MP, Bidrowski TF, Richardson JL, White GC. 2019. Age class dynamics of Canada goose in the Central Flyway. Journal of Wildlife Management 83:938–953.

Groeppe SR, Vrtiska MP, Powell LA, Hygnstrom SE. 2012. Evaluation of the effects of September hunting seasons on Canada goose in Nebraska. Wildlife Society Bulletin 36:524–530.

Hupp JW, Ward DH, Whalen ME, Pearce JM. 2015. What is causing the rapid increase of snow goose in northern Alaska? U.S. Geological Survey Factsheet 2015-3062 (see Supplemental Material, Reference S2).

Iverson SA, Reed ET, Hughes RJ, Forbes MR. 2014. Age and breeding stage-related variation in the survival and harvest of temperate-breeding Canada goose in Ontario. Journal of Wildlife Management 78:24–34.

Johnson DH. 1999. The insignificance of statistical significance. Journal of Wildlife Management 63:763–772.

Koons DN, Rockwell RF, Aubry LM. 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. Journal of Animal Ecology 83:365–374.

Laake JL. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Seattle, Washington. https://CRAN.R-project.org/package=RMark (December 2020).

LaGrange T. 2005. Guide to Nebraska’s wetlands and their conservation needs. 2nd edition. Lincoln: Nebraska Game and Parks Commission.

Leberg PL, Stangel PW, Hillestad HO, Marchinton RL, Smith MH. 1994. Genetic structure of reintroduced wild turkey and white-tailed deer populations. Journal of Wildlife Management 58:698.

Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Leopold A. 1933. Game management. Madison: University of Wisconsin Press.

Lukacs PM, Burnham KP, Anderson DR. 2010. Model selection bias and Freedman’s paradox. Annals of the Institute of Statistical Mathematics 62:117–125.

Luukkonen DR, Prince HH, Mykut RC. 2008. Movements and survival of molt migrant Canada goose from southern Michigan. Journal of Wildlife Management 72:449–462.

Mowbray TB, Ely CR, Sedinger JS, Trost RE. 2002. Canada goose (Branta canadensis) version 2.0. Rodewald PG, editor. The birds of North America. Ithaca, New York: Cornell Lab of Ornithology.

[NGPC] Nebraska Game and Parks Commission. 2006. Management plan for resident Canada goose in Nebraska. Lincoln: Nebraska Game and Parks Commission (see Supplemental Material, Reference S3).

Powell LA, Vrtiska, M, Lyman N. 2003. Survival rates and recovery distributions of Canada goose banded in Nebraska. Papers in Natural Resources 433:61–65.

Roberts A, Eadie JM, Howerton DW, Johnson FA, Nichols JD, Runge MC, Vrtiska MP, Williams BK. 2018. Strengthening links between waterfowl research and management. Journal of Wildlife Management 82:260–265.

RStudio Team. 2018. RStudio: Integrated development environment for R. v. 1.1. Boston, MA: RStudio, PBC. Available: https://rstudio.com/products/rstudio/older-versions/ (December 2020).

Sandencock BK. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504–1520.

Schmidt PR. 2004. Canada goose in North America: past success and future challenges. Pages 8–11 in Moser TJ, Lien RD, VerCauteren KC, Abraham KF, Andersen DE, Bruggink JG, Collucy JM, Graber DA, Leafloor JO, Luukkonen DR, Trost RE, editors. Proceedings of the 2003 international Canada goose symposium. Madison, Wisconsin.

Schneider R, Stoner K, Steinauer G, Panella M, Humper M. 2011. The Nebraska Natural Legacy Project—State
Wildlife Action Plan. Lincoln: Nebraska Game and Parks Commission (see Supplemental Material, Reference S4).

Sheaffer SE, Kendall WL, Bowers EF. 2005. Impact of special early harvest seasons on subarctic-nesting and temperate-nesting Canada geese. Journal of Wildlife Management 69:1494–1507.

Shirkey BT, Gates RJ, Ervin MD. 2018. Survival rates and harvest patterns of Ohio-banded Canada geese. Wildlife Society Bulletin 42:1–9.

Specht HM, Arnold TW. 2018. Banding age ratios reveal prairie waterfowl fecundity is affected by climate, density dependence and predator—prey dynamics. Journal of Applied Ecology 55:2854–2864.

Stubben CJ, Milligan BG. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:11.

Thomas L, Buckland ST, Rexstad EA, Løkke JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

[USFWS] U.S. Fish and Wildlife Service. 2005. Final environmental impact statement on resident Canada goose management. Federal Register 70:69985–69986.

Vrtiska M, Lyman N. 2004. Wintering Canada geese along the Platte rivers of Nebraska, 1960–2000. Great Plains Research 14:115–128.

Vrtiska MP, Gammonley JH, Naylor LW, Raedeke AH. 2013. Economic and conservation ramifications from the decline of waterfowl hunters. Wildlife Society Bulletin 37:380–388.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–139.

Zhao Q, Arnold TW, Devries JH, Howerton DW, Clark RG, Weegman MD. 2019. Land-use change increases climatic vulnerability of migratory birds: insights from integrated population modelling. Journal of Applied Ecology 88:1625–1637.