Georgia Journal of Science

Volume 79 *No. 2 Scholarly Contributions from the Membership and Others* Article 1

2021

Estimating the Size of Georgia's Resident Canada Goose Population

Gregory D. Balkcom
Georiga Department of Natrual Resources, greg.balkcom@dnr.ga.gov

Estimating the Size of Georgia's Resident Canada Goose Population

Acknowledgements

I thank the GAWRD staff and the USDA Wildlife Services staff for banding geese, and the USGS Bird Banding Laboratory for providing banding and recovery data. B. Bond provided comments on an earlier draft of this manuscript. The findings and conclusions in this article are those of the author and do not necessarily represent the views of the Georgia Department of Natural Resources.

ESTIMATING THE SIZE OF GEORGIA'S RESIDENT CANADA GOOSE POPULATION

Gregory D. Balkcom
Georgia Department of Natural Resources, Fort Valley, GA 31030
corresponding author: greg.balkcom@dnr.ga.gov

ABSTRACT

Canada geese (*Branta canadensis*) are an important waterfowl species in Georgia, and are hunted across the state. To meet management objectives, managers need to understand the impacts of hunting regulations on the population of interest. Therefore, reliable population estimates are necessary. Population size can be estimated by various methods, including aerial surveys, ground surveys, or population indices such as the Lincoln Estimator. I used annual estimates of resident Canada goose harvest in Georgia from the U.S. Fish and Wildlife Service's Harvest Information Program along with banding and recovery data from the Bird Banding Laboratory in a bias-adjusted version of the Lincoln Estimator. Because of annual variation in the population estimates among years, I compared various trendlines across years, and the top three models generated an average 2018 population estimate of 231,274 resident Canada geese in Georgia.

KEYWORDS

Canada goose, *Branta canadensis*, banding, Georgia, harvest, harvest rate, Lincoln Estimator, population estimate, recovery rate

INTRODUCTION

Canada geese (*Branta canadensis*) are an important waterfowl species throughout North America and are valued for wildlife viewing and recreational opportunities (McCoy 2000, Conover et al. 2015). Although historically migrant to Georgia and other southeastern states, migratory Canada geese are now largely restricted to more northerly portions of the Atlantic Flyway due to changes in available habitat (Crider 1967, Addy and Heyland 1968, Sheaffer and Malecki 1987). Because migrant geese stopped coming to Georgia, the Georgia Department of Natural Resources, Wildlife Resources Division (GAWRD) started a restocking effort, and between 1975 and 1987 relocated 8,000 Canada geese from northern states in the Atlantic Flyway to Georgia. Other states completed restocking efforts as well, and now geese are identified and managed as either migratory or resident, with resident geese being defined as those that nest or reside year-round in the contiguous United States (Rusch et al. 1996, Ankney 1996). The resident goose population in Georgia has increased since the late 1980's, establishing urban and rural subpopulations (Powell et al. 2001, Stephens et al. 2007, Balkcom 2010). Hunting seasons for Georgia's resident goose population began in 1990 as a quota hunt in limited areas and only for selected hunters. By 1995, the 15-day hunting season had opened statewide and was available to all properly licensed hunters. Since 1995, hunting seasons and bag limits have been liberalized over the years, and for 2019, the federal frameworks allowed a hunting season with a maximum length of 107 days (combining a special early season of up to 30 days in September and a regular season of up to 80 days between October 1 and March 10; USFWS 2019a).

To meet management objectives, managers need to understand the impacts of hunting regulations on the population (Williams et al. 2002). Therefore, reliable population estimates are necessary. Population size can be estimated by various methods, including aerial surveys, ground surveys, or population indices such as the Lincoln Estimator (Lincoln 1930). The Lincoln Estimator has been used to estimate the abundance of various species including migratory Mallards (*Anas platyrhynchos*; Alisauskas et al. 2014), Chinese mystery snails (*Bellamya chinensis*) in a Nebraska reservoir (Chaine et al. 2012), Northern bobwhite quail (*Colinus virginianus*: Dimmick et al. 1982), and resident Canada geese in North Carolina (McAlister et al. 2017). Georgia has both banding and recovery data which can be used along with harvest data to estimate population size with the Lincoln Estimator. The objective of this project was to use the Lincoln Estimator to generate annual estimates of the size of Georgia's resident Canada goose population and to find the best fit trendline that describes that population trend across years.

MATERIALS AND METHODS

Study Area

The entire State of Georgia was considered the study area, and banding occurred at 166 different sites across the state between 1995 and 2018 (Figure 1). Goose hunting was allowed statewide, and recoveries of banded geese occurred across the state.

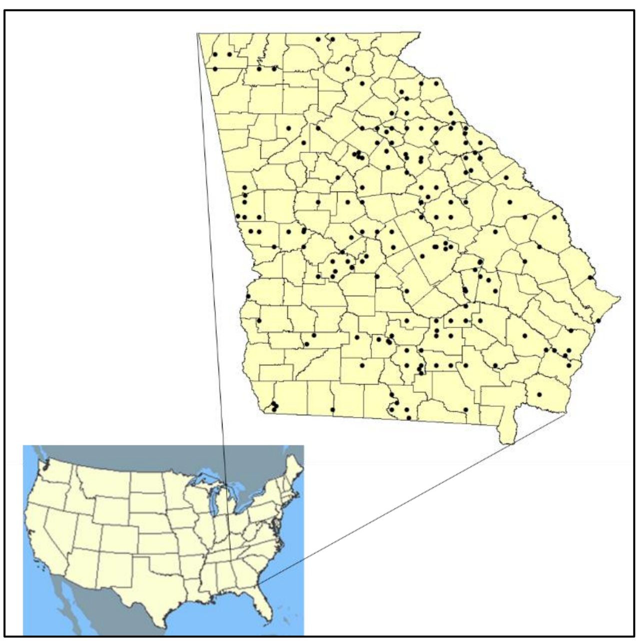

Figure 1. Locations where Canada geese were captured and banded in Georgia, USA, 1995-2018. Note: older locations are depicted as the center of the 10' lat-lon block where banding occurred, and newer locations are depicted as the exact location where banding occurred. Small USA map credit: U.S. Geological Survey. Georgia map credit ESRI and ArcMap, data source TomTom.

Methods

<u>Harvest Estimates</u>

I used annual estimates of resident Canada goose harvest in Georgia from the U.S. Fish and Wildlife Service's (FWS) Mail Questionnaire Survey (MQS; 1995-2001) and the

Harvest Information Program (HIP; 2001-2018; Raftovich et al. 2018). These cooperative State-Federal programs required each state to collect the name and address of each duck or goose hunter who purchased a federal duck stamp for the MQS through 2001, and the name and address of each migratory bird hunter for the HIP survey after 2001. The HIP survey used a different methodology to sample hunters of all migratory game bird species rather than just ducks and geese. The FWS used these data to conduct annual, national, hunter activity and harvest surveys. Hunters selected for the surveys are asked to record the date, location, and number of migratory game birds of various species or species-groups they personally bagged each day they hunted (Raftovich et al. 2018). Sampling error, memory bias, and/or prestige bias can lead to bias and annual variation in harvest estimates (Atwood 1956, Raftovich et al. 2018). Because these surveys have been shown to be biased high, I used a correction factor of 0.67 for harvest estimates generated by the MQS through 2001, and a correction factor of 0.61 for harvest estimates generated by the HIP survey after 2001 (Padding and Royle 2012).

Band Recovery Data and Reporting Rate Estimates

From 1995 through 2018, GAWRD staff and U.S. Department of Agriculture's Wildlife Services (USDA) staff independently captured and banded resident Canada geese from across Georgia annually during the June-July molting period when the geese are flightless. USDA staff captured and translocated geese from urban, developed areas in response to complaints received from the public, and the GAWRD staff caught and banded geese on Wildlife Management Areas and selected private properties where the landowner had an interest in conservation. Flightless geese were herded into corral traps (Cooch 1953) where age (adult, juvenile), sex (male, female), date, and location of banding were recorded. All geese were banded with a standard, numbered FWS aluminum leg band (Dimmick and Pelton 1994).

I collected banding and recovery data from the Bird Banding Laboratory (BBL; U. S. Geological Survey, Patuxent, MD), and summarized the data for geese banded during 1995-2018 and recovered in the subsequent hunting season. Data were accurate as of November 1, 2019. A direct band recovery is defined as the recovery of a banded goose in the hunting season immediately following the pre-season banding period. Only direct recoveries of geese shot or found dead during the hunting season were included in this analysis. However, not all hunters choose to report their band recovery to the BBL. The reporting rate is defined as the probability that a hunter who recovers a banded goose will report the band recovery to the BBL (Henny and Burnham 1976). The reporting rate has increased over time as band inscriptions and reporting methods have changed from mail-in reporting to toll-free telephone reporting to internet-based reporting methods (Zimmerman et al. 2009b).

Lincoln Estimator

The Lincoln Estimator (Lincoln 1930) has three main model assumptions that must be met before use: 1) closed population, 2) equal capture probability between sampling periods, and 3) no tag loss between sampling periods (Williams et al. 2002). Georgia's goose population is a resident population, meaning that essentially no migrant geese come to Georgia during the winter. Banding data shows that 8 of 6802 banded geese recovered in Georgia were migrants, so the probability of a banded goose being a migrant is 0.0012. With no significant number of migrants coming into the state, and no significant immigration or emigration from Georgia into surrounding states, it can be assumed that Georgia's goose population is a closed population. The second assumption typically relates to animals that may become trap shy or trap prone if the same capture methods are used for the first and second sampling periods. Because corral traps were used for the initial capture, and hunter harvest for the second capture period, it can be assumed that there was equal capture probability between capture periods. Finally, I assumed no tag loss between the first and second sampling period because aluminum leg band retention in geese is extremely high (0.9995) and constant for the first 40 months after banding (Zimmerman et al. 2009a).

Because the Lincoln Estimator is biased high when sample size is small, and the magnitude of the bias is inverse to sample size (Williams et al. 2002), I used a bias-adjusted version (Chapman 1951):

$$\hat{N} = \left(\frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} - 1\right) * \hat{p}$$

Where population (N) is calculated by the number of geese banded in a given year (n_1), the number of geese harvested that year (n_2), the number of banded geese in the harvest (m_2), and the reporting rate (p). The variance of the population estimate can be calculated using Seber's (1970) estimate of variance for Chapman's formula:

$$\widehat{var}(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

The 95% confidence interval (CI) is calculated as:

$$CI = \hat{N} \pm 1.96\sqrt{\widehat{var}(\hat{N})}$$

Because of annual variation in the population estimates, I calculated the best fit trendline across years using Program R version 3.6.1 (R Foundation for Statistical Computing, Vienna, Austria) with five different models. I used a linear formula and a variety of non-linear functions suggested by Crawley (2007) to find the best trendline. The candidate functions included: linear regression (y = ax + b), a quadratic equation ($y = x + x^2$), a self-starting Michaelis-Menten asymptotic function (y = ax / (b + x), a four-parameter logistic ($y = a + ((b - a) / (1 + e^{(c - x) / d})$), and a power curve ($y = a * x^b$). I compared performance of the models using Akaike's Information Criteria (AIC; Akaike 1987). Using the best fit trendline yielded a smoother, biologically more acceptable population growth curve across the timeframe of the study.

RESULTS

<u>Harvest Estimates</u>

Bias-adjusted Canada goose harvest estimates ranged from 4288 to 44,722 and averaged 16,602 during the study period (n = 24, SE = 2204; Table 1).

Band Recovery and Reporting Rate Estimates

From 1995 to 2018, 27,625 Canada geese were captured and banded across the state. During the same time period, 2312 direct recoveries were recorded (Table I). Recovery rates ranged from 0.044 to 0.145 and averaged 0.082 during the study period (n = 24, SE = 0.005; Table 1). Reporting rates increased from 0.54 in 1995 to 0.73 in 2002 and have held steady since (Zimmerman et al. 2009b).

Table I. U. S. Fish and Wildlife Service bias-adjusted harvest estimates, Bird Banding Laboratory data on bandings and direct band recoveries, and estimates of band reporting rates for Canada geese in Georgia, 1995-2018.

YEAR	ADJUSTED HARVEST	NEW BANDS	DIRECT RECOVERIES	REPORTING RATE
1995	4288	1027	66	0.54
1996	5628	952	58	0.62
1997	6968	1155	59	0.67
1998	6045	1499	105	0.68
1999	8645	1301	72	0.7
2000	8174	1395	119	0.72
2001	17,487	1969	181	0.72
2002	12,871	1700	129	0.73
2003	15,433	1677	208	0.73
2004	12,932	1395	110	0.73
2005	21,411	496	22	0.73
2006	9089	1675	169	0.73
2007	13,664	1117	97	0.73
2008	19,581	781	71	0.73
2009	44,722	1041	78	0.73
2010	14,457	891	52	0.73
2011	20,984	853	83	0.73
2012	9394	1171	114	0.73
2013	19,642	745	61	0.73
2014	31,598	892	71	0.73
2015	34,492	853	54	0.73
2016	37,702	1000	71	0.73
2017	15,433	715	104	0.73
2018	7809	1325	158	0.73

Lincoln Estimator

Over the entire study period, statewide Canada goose population estimates ranged from 35,535 to 430,621 and averaged 156,152 (n = 24, SE = 24,213, Figure 2). The 2018 population estimate for resident Canada geese using the Lincoln Estimator was 47,543 ± 9371. AIC values indicated the self-starting Michaelis-Menten curve ($y = (a * x) / (b + x)$)

was the best fit trendline (Table II), but the power curve ($y = a * x^b$) and the linear regression ($y = a * x + b$) were also reasonable predictors of population size over time ($\Delta AIC < 1$). The 2018 population estimates using each of the top three models were as follows: Michaelis-Menton: 221,571, power curve: 230,143, and linear regression: 242,076. By using the best fit trendline, I generated annual population estimates that seemed more biologically reasonable than the fluctuating Lincoln Estimates (Figure 3), and the top three models generated an average 2018 population estimate of 231,274 (n = 3, SE = 5944).

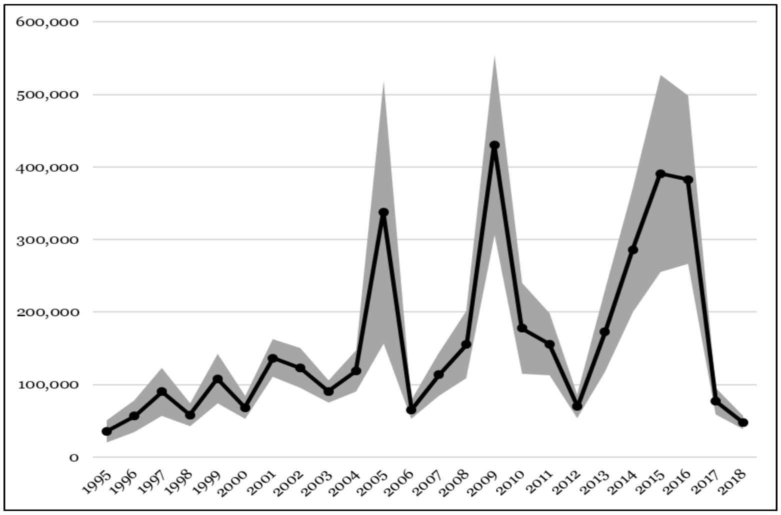

Figure 2. Canada goose population estimates (black line) and 95% confidence intervals (gray shading) based on annual Lincoln Estimates in Georgia, 1995-2018.

Table II. AIC values for the five models used to calculate the best fit trendline through the annual goose population estimates in Georgia, 1995-2018.

MODEL	FORMULA	DF	AIC	Δ AIC
Michaelis-Menton	$y=(323513.62x)/(11.04+x)$	3	627.71	0.00
Power Curve	$y=45510x^{0.510}$	3	627.99	0.28
Linear Regression	$y=7472x+62756$	3	628.59	0.88
Quadratic	$y=22692.2x-608.8x^2-3199.5$	4	629.04	1.33
Four Parameter Logistic	$y=-44410+((211500-44410)/(1+e^{(8.319-x)/2.652}))$	5	631.26	3.55

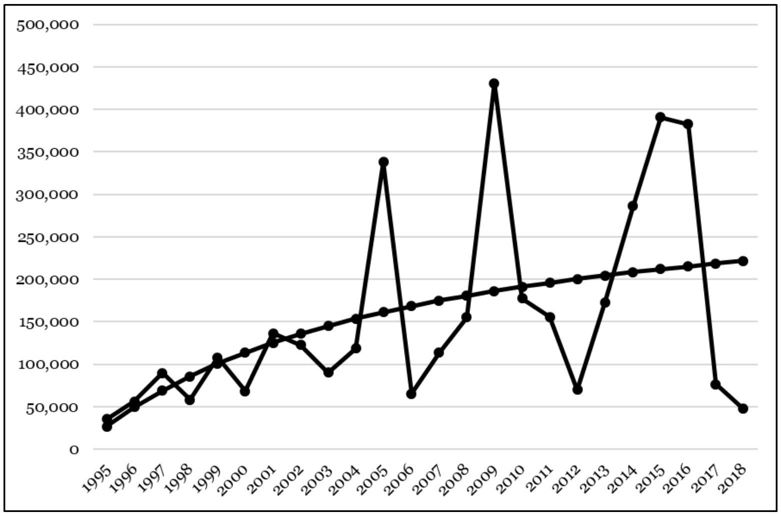

Figure 3. Canada goose population estimates based on annual Lincoln Estimates and the best fit trendline (self-starting Michaelis-Menten curve) in Georgia, 1995-2018.

DISCUSSION

When debating methods of population estimation, researchers generally prefer monitoring activities that generate estimates with confidence intervals rather than population indices. Though often referred to as an estimate, the Lincoln Estimator is still technically considered a population index. While true population estimates may be preferred, Engeman (2003) recommended using the most appropriate method to meet the project objectives whether that be an estimate or an index. Alisauskas et al (2009) believed that abundance estimates from band return methods such as the Lincoln Estimator are acceptable for monitoring long-term trends in the population. McAlister et al. (2017) reported their band return-based method of population estimation was actually more precise than their plot survey-based estimate. McAlister et al. (2017) also indicated that capture and banding was a better monitoring program than plot surveys because of the additional information such as survival rates, harvest rates, and harvest distribution that could be gleaned from the banding data.

The Lincoln-Estimator method of monitoring Georgia's resident goose population did provide annual estimates with confidence intervals, but there was great fluctuation among years. The fluctuation was likely due to two factors: variation in estimates of annual harvest rates and variation in HIP estimates of total harvest. Managers control hunting regulations for geese, but there is inherent uncertainty in the relationship between hunting regulations and band recovery rates (Williams et al. 2002). This uncertainty is termed "partial controllability," and it can lead to annual variation in band recovery rate estimates even when regulations are consistent (Williams et al. 2002). Goose harvest rates can fluctuate because of variation in weather conditions, hunter effort, and other factors (USFWS 2019b). HIP is used to generate estimates of absolute harvest; however, HIP has documented weaknesses and known biases that affect harvest estimates (Sheriff et al. 2002). Using two varying data sets (harvest estimates and band recovery data) to generate a third estimate (population size) seems to lead to compounded errors in some years.

Annual variation in the population estimates led me to explore potential trendlines that may provide a more stable or biologically reasonable population growth curve across time as well as an annual population estimate. From a list of some commonly used non-linear functions provided by Crawley (2007), I tried five different trendlines to approximate the growth of Georgia's resident goose population over time. The functions included a simple linear regression to represent long-term linear growth, a Michaelis-Menten function to represent rapid early growth up to some asymptote (e.g. biological carrying capacity), a four-parameter logistic to represent early growth up to an inflection point with slower growth thereafter, and a power curve and a quadratic equation to represent other potential shapes of population growth across time. The results of the trendline analysis yielded a smoother, biologically more acceptable population growth curve across the timeframe of the study.

GAWRD plans to continue capturing and banding geese for the foreseeable future. Therefore, annual estimates of the goose population can be calculated, and trendline functions can be updated to provide the best possible estimate of Georgia's resident Canada goose population.

ACKNOWLEDGEMENTS

I thank the GAWRD staff and the USDA Wildlife Services staff for banding geese, and the USGS Bird Banding Laboratory for providing banding and recovery data. B. Bond provided comments on an earlier draft of this manuscript. The findings and conclusions in this article are those of the author and do not necessarily represent the views of the Georgia Department of Natural Resources.

REFERENCES

Addy, C. E. and J. D. Heyland. 1968. Canada goose management in eastern Canada and the Atlantic Flyway. Pages 10-23 *in* R. L. Hine and C. Schoenfeld, editors Canada goose management: current continental problems and programs. Dembar Educational Research Service, Madison, Wisconsin, USA.

Akaike, H. 1987. Factor analysis and AIC. Psychometrika, 52, 317-332. http://128.174.199.77/psychometrika_highly_cited_articles/akaike_1987.pdf

Alisauskas R. T., K. L. Drake, and J. D. Nichols. 2009. Filling a void: Abundance estimation of North American populations of arctic geese using hunter recoveries. Pages 463-489 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling Demographic Processes in Marked Populations. Environmental and Ecological Statistics, Vol 3. Springer, Boston, Massachusetts, USA. https://doi.org/10.1007/978-0-387-78151-8_20

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2014. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution, 4(2), 132-143. https://doi.org/10.1002/ece3.906

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management, 60, 217–223. https://www.jstor.org/stable/3802219

Atwood, E. L. 1956. Validity of mail survey data on bagged waterfowl. Journal of Wildlife Management, 20, 1-16. https://www.jstor.org/stable/3797241

Balkcom, G. D. 2010. Demographic parameters of rural and urban adult resident Canada geese in Georgia. Journal of Wildlife Management, 74, 120–123. https://doi.org/10.2193/2009-007

Chaine, N. M., C. R. Allen, K. A. Fricke, D. M. Haak, M. L. Hellman, R. A. Kill, K. T. Nemec, K. L. Pope, N. A. Smeenk, B. J. Stephen, D. R. Uden, K. M. Unstad, A. E. VanderHam. 2012. Population estimates of Chinese mystery snail (*Bellamya chinensis*) in a Nebraska reservoir. Nebraska Cooperative Fish and Wildlife Research Unit – Staff Publications, 104. http://dx.doi.org/10.3391/bir.2012.1.4.07

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics, 1, 131–160.

Conover, M. R., J. B. Dinkins, and R. E. Ruzicka. 2015. Consequences of hunter harvest, winter weather, and increasing population size on survival of non-migratory Canada geese in Connecticut. Journal of Wildlife Management, 79, 1239-1245. https://doi.org/10.1002/jwmg.942

Cooch, G. 1953. Techniques for mass capture of flightless blue and lesser snow geese. Journal of Wildlife Management, 17, 460-465. https://www.jstor.org/stable/3797052

Crawley, M. J. 2007. The R Book. John Wiley and Sons, Ltd. West Sussex, England, UK.

Crider, E. D. 1967. Canada goose interceptions in the southeastern United States with special reference to the Florida flock. Proceedings of the Southeastern Association of Game and Fish Commissioners, 21, 145-155.

Dimmick, R. W. and M. R. Pelton. 1994. Criteria of age and sex. Pages 169-214 *in* T. A. Bookhout, editor. Research and Management Techniques for Wildlife and Habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Dimmick, R. W., F. E. Kellogg, and B. L. Dearden. 1982. Estimating bobwhite quail population size by direct counts and the Lincoln index. National Quail Symposium Proceedings, 2, Article 3. https://trace.tennessee.edu/nqsp/vol2/iss1/3

Engeman, R. M. 2003. More on the need to get the basics right: population indices. Wildlife Society Bulletin, 31, 286-287. https://digitalcommons.unl.edu/icwdm_usdanwrc/213

Henny, C. J. and K. P. Burnham. 1976. A reward band study of mallards to estimate band reporting rates. Journal of Wildlife Management, 40, 1–14. https://www.jstor.org/stable/3800150

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular U.S. Department of Agriculture, 118, 1–4.

McAlister, M. A., C. S. DePerno, J. C. Fuller, D. L. Howell, and C. E. Moorman. 2017. A comparison of field methods to estimate Canada goose abundance. Wildlife Society Bulletin, 41, 685-690. https://doi.org/10.1002/wsb.827

McCoy, N. H. 2000. Economic tools for managing impacts of urban Canada geese. Human Conflicts with Wildlife: Economic Considerations, 12, 117-122. https://digitalcommons.unl.edu/nwrchumanconflicts/12

Padding, P. I. and J. A. Royle. 2012. Assessment of bias in US waterfowl harvest estimates. Wildlife Research, 39, 336–342. https://doi.org/10.1071/WR11105

Powell, L. A., M. J. Conroy, G. D. Balkcom, and J. N.Caudell. 2001. Development of a monitoring program for sustainable harvest and control of resident Canada geese in Georgia. Georgia Department of Natural Resources. Fort Valley, Georgia, USA.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Raftovich, R. V., K. K. Fleming, S. C. Chandler, and C. M. Cain. 2019. Migratory bird hunting activity and harvest during the 2017-18 and 2018-19 hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland, USA. https://www.fws.gov/migratorybirds/pdf/surveys-and-data/HarvestSurveys/MBHActivityHarvest2017-18and2018-19.pdf

Rusch, D. H., J. C. Wood, and G. G. Zenner. 1996. The dilemma of giant Canada goose management. International Waterfowl Symposium, 7, 72-78.

Sheaffer, S. E., and R. A. Malecki. 1987. Distribution and derivation of the 1984-1986 Atlantic Flyway Canada goose harvest. Transactions of the Northeast Section of the Wildlife Society, 44, 48-52.

Sheriff, S. L., J. H. Schulz, B. D. Bales, M. T. Moore, P. I. Padding, and D. A. Shipes. 2002. The current reliability of Harvest Information Program surveys. Pages 51-68 *in* J. M. Ver Steeg and R. C Elden, compilers. Harvest Information Program: Evaluation and Recommendations. International Association of Fish and Wildlife Agencies, Migratory Shore and Upland Game Bird Working Group, Ad Hoc Committee on HIP, Washington, D.C., USA. https://digitalcommons.unl.edu/usfwspubs/340

Stephens, L. R., M. T. Mengak, and D. I. Hall. 2007. Evaluation of resident Canada goose relocation in Georgia. Proceedings of the Wildlife Damage Management Conference, 12, 543-550.

U. S. Fish and Wildlife Service. 2019a. Migratory Bird Hunting; Final Frameworks for Migratory Bird Hunting Regulations. Federal Register, 84, 42996-43032. https://www.federalregister.gov/documents/2019/08/19/2019-17561/migratory-bird-hunting-final-frameworks-for-migratory-bird-hunting-regulations

U. S. Fish and Wildlife Service. 2019b. Adaptive Harvest Management: 2020 Hunting Season. U.S. Department of Interior, Washington, D.C., USA. https://www.fws.gov/migratorybirds/pdf/management/AHM/AHMReport2020.pdf

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California, USA.

Zimmerman, G. S., W. L. Kendall, T. J. Moser, G. C. White, and P. F. Doherty Jr. 2009a. Temporal patterns of apparent leg band retention in North American geese. Journal of Wildlife Management, 73, 82-88. https://doi.org/10.2193/2007-590

Zimmerman, G. S., T. J. Moser, W. L. Kendall, P. F. Doherty Jr., G. C. White, and D. F. Caswell. 2009b. Factors influencing reporting and harvest probabilities in North American geese. Journal of Wildlife Management, 73, 710–719. https://doi.org/10.2193/2008-145