ABSTRACT

Title of Thesis: ESTIMATING POPULATION TRENDS IN AMERICAN WOODCOCK (*SCOLOPAX MINOR)* USING POPULATION RECONSTRUCTION MODELS

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The American woodcock (*Scolopax minor*) population index in North America has declined 0.9% a year since 1968 prompting managers to identify priority information and management needs for the species (Sauer et al 2008). Managers identified a need for a population model that better informs on the status of American woodcock populations (Case et al. 2010). Population reconstruction techniques use long-term age-at-harvest data and harvest effort to estimate abundances with error estimates. Four new models were successfully developed using survey data (1999 to 2013). The optimal model estimates sex specific harvest probability for adult females at 0.148 (SE = 0.017) and all other age-sex cohorts at 0.082 (SE = 0.008) for the most current year 2013. The model estimated a yearly survival rate of 0.528 (SE = 0.008). Total abundance ranged from 5,206,000 woodcock in 2007 to 6,075,800 woodcock in 1999. This study represents the first population estimates of woodcock populations.

ESTIMATING POPULATION TRENDS IN AMERICAN WOODCOCK (*SCOLOPAX MINOR)* USING POPULATION RECONSTRUCTION MODELS

By

Brent Hopkins West

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List of Abbreviations

SGS – Singing Ground Survey

WCS – Wing Collection Survey

HIP – Harvest Information Program

NHS – National Harvest Survey

RPR – Reproductive Potential Ratio

SPR – Spawning Potential Ratio

PBR – Potential Biological Removal

AIC - Akaike's Information Criterion

Chapter 1: Introduction

The American woodcock (*Scolopax minor*) is a woodland migratory bird in the order Charadriiformes and the family Scolopacidae (Howard and Moore 1991). Woodcock are small and well camouflaged, females are larger than males with an average weight of 200 grams and 160 grams respectively (Owen and Krohn 1973). Their plumage differs between age and sex classes (Martin 1964). Woodcock have a long bill that is used for probing into the ground; females have longer bills than males with an average length of 71.0 mm and 64.7 mm respectively (Mendall and Aldous 1943). They are short lived, with an average life expectancy of 1.8 years (Sheldon 1967). The oldest recorded woodcock was 12 years old as reported by a hunter in Wisconsin in 1982 (Lutmerding and Love 2015). The majority of mortalities occur from predators (Keppie and Whiting 1994, McCauley et al. 2005).

The range of the American woodcock is limited in the eastern half of North America. This includes both the eastern half of the United States and southeastern Canada (Keppie and Whiting 1994). The primary breeding range is southeastern Canada and the Midwest and Northeast regions of the United States (Straw et al. 1994). They initiate migration based on photoperiod in the spring and fall in North America (Meunier et al. 2008). Woodcock typically winter along the Gulf Coast or along the southeast Atlantic coast as far north as New Jersey (Straw et al. 1944). Owen et al. 1977 describe 3 major habitat requirements for woodcock: 1) Open areas for displaying and roosting, 2) moist soils that support large populations of earthworms, and 3) early successional habitat that provides cover. Woodcock use early successional habitat and prefer a diverse set of habitat cover types (Nelson and Anderson 2013). Higher densities occur in areas with more forest land cover and they prefer Aspen (*Populus Sp*.) and Birch (*Betula Sp*.) thickets (Thogmartin et al. 2007, Dessecker and McAuley 2001, Nelson and Andersen 2013). Thogmartin et al. (2007) found that woodcock abundance was negatively correlated with human development these habitat traits are important to the breeding ecology of woodcock.

The courtship of woodcock is unique and well documented. Breeding for woodcock occurs in the spring soon after migration is completed (Owen et al. 1977, Keppie and Whiting 1994). Males use a unique courtship display to attract a mate during the breeding season (Straw et al. 1994). This courtship display requires open terrain, called a singing ground, in order for these small birds to be seen by potential mates. The singing ground requires suitable nesting cover nearby consisting of early successional mixed forest which is considered to the main cause of population declines (Dessecker and McAuley 2001). The display consists of calling (peenting) and an aerial display (Owen et al. 1977).

Nesting ecology is important to understanding the life history of woodcock. Successful breeding woodcock nest in close proximity to singing grounds (Owen et al. 1977, Keppie and Whiting 1994, Straw et al. 1994). Females typically lay clutches of four eggs that hatch within 19-22 days (Mendall and Aldous 1943, Straw et al. 1994). The precocial young fledge in 18 days and reach maturity before the second year (Straw et al 1994, Owen et al, 1977).

The American woodcock enjoys a rich hunting tradition and was designated as a game bird to be managed for hunting and birdwatching under the Migratory Bird Treaty Act of 1918 (16 U.S.C. 703). The high demand to hunt, as well as the need to manage for long term sustainability, created the need to study woodcock. Gustav Swanson was the first to study woodcock when he counted displaying males in Maine in 1936 (Owen et al. 1977). His early work led to the start of the present day Singing Ground Survey (SGS) which eventually resulted in a statistically random survey in 1968 (Cooper and Rau 2014). Another survey that was early in woodcock harvest management was the Wing Collection Survey (WCS) that started in 1959 to estimate productivity of woodcock (Owen et al 1977, Martin et al. 1964).

There are three surveys used to monitor woodcock populations the main survey is the SGS. The SGS enables biologists to monitor the breeding population of adult male woodcock; however, it does not provide a population estimate. The survey only provides indices and trends for the population. The SGS, a roadside transect survey, is conducted annually along randomly selected secondary roads across the breeding range (Sauer and Bortner 1991). This index has shown long-term declines in American woodcock populations (Sauer et al. 2008, Sauer and Bortner 1991, Straw et al. 1994). This roadside survey provides only raw counts of adult males and is open to many different biases (Bart and Schoultz 1984). Observers may not hear the bird's peenting, the name of the mating call of the woodcock, because of traffic or other development (Cooper and Kelley 2006). Land along roads may also not be representative of the available breeding habitat as a whole. The migration may change due to weather patterns which has caused concern that the survey may not occur at the appropriate time (Whiting 2006). The SGS has been used to determine relative abundances, which can be used to direct habitat management (Thogmartin et al. 2005). This survey is currently the only tool used to make harvest management decisions (Sauer 2006). The current harvest management thresholds are based on the SGS's lower confidence limit, and if this estimate dips below a certain thresholds it triggers changes in hunting regulations (American Woodcock Harvest Strategy 2010).

The Wing-collection Survey (WCS) was developed to estimate productivity and composition of the harvest. Martin et al. 1964 developed techniques to discern the differences in patterns, size and wear of the wing in order to age and sex sampled individuals (Sepik 1994). The U.S. Fish and Wildlife Service administers the annual survey where a selected number of hunters are asked to send in a wing from every bird they shoot. The wings are identified as adult or juvenile and male or female. This survey provides an index of production for the year and is used as an indication of annual breeding success. These data can also be used to inform models on the age and sex composition of the population since it is designed to collect a random sample of harvested woodcock (Zimmerman et al. 2010).

The last step in responsible management of woodcock is an estimate of how many woodcock are harvested on an annual basis. The Annual Questionnaire Survey (AQS) was designed to estimate hunters and harvest of waterfowl in the US, and was adapted to estimate woodcock harvest and numbers of hunters. This survey asked hunters who purchased the Migratory Bird Hunting and Conservation Stamp (Duck Stamp) to report if they hunted woodcock, how many were harvested and the number of days hunted (Cooper and Rau 2014). A weakness of the AQS was that the sample was restricted to only waterfowl hunters that also hunted woodcock (Straw et al. 1994).

The SGS, the WCS, and the AQS were the primary tools used monitoring Woodcock until the implementation of the Harvest Information Program (HIP) in 1999 (Cooper and Rau 2014). HIP corrected for the biased sample frame with a woodcock specific sample frame. All migratory bird hunters must register for HIP before hunting (Padding et al. 2006). During registration, hunters must provide their name and address as well as information about their previous year's harvest of migratory birds. This information is used for stratifying hunters asked to complete a diary survey form following the Dillman Total Design Method (Dillman 2001). Hunters participating in the survey are asked to provide the date, county of hunt, and number of woodcock bagged for each day hunted. This survey supplies estimates of harvest and days hunted which were inputs for modeling. Canada also conducts a similar survey, the National Harvest Survey (NHS) to monitor their nation's harvest as well, however, all migratory bird hunters not just woodcock hunters are surveyed (Canadian Wildlife Service 2014).

The hunting of woodcock occurs in 34 states and 6 provinces. The hunting is managed in Central and Eastern Regions (Cooper and Rau 2014). These regions were established based on banding data and they conformed to the

Atlantic and Mississippi Flyways (Owen et al. 1977). The season length was 65 days from 1967 to 1985 and allowed a 5 bird daily limit (Straw et al. 1994). The long-term population declines, as measured by the SGS, eventually prompted managers to reduce the season length and bag limit. The current harvest strategy has the season at a 45 day length with a 3 bird daily limit in both management regions (Woodcock Harvest Strategy 2010).

The goals of management are to increase population, as well as hunting and bird watching opportunities (Cooper and Rau 2014). The Association of Fish and Wildlife Agencies Migratory Shore and Upland Game Bird Support Task Force has identified priority needs for American woodcock. The top priority was development of a model for estimating demographic changes in the populations (D.J. Case 2010). Recently, statistical population reconstruction techniques have been adapted to two age class harvest data and utilized all of the surveys discussed (Broms et al. 2010). These methods were originally developed for fisheries management since there is an abundance of catch-at-age data for many fisheries to utilize for monitoring populations. The theory to estimate population size based on age distribution data was developed in the 1980s, which describe methods of solving maximum likelihood functions through use of computer software (Fournier and Archibald 1982).

Although these models can estimate population levels without auxiliary data, studies have shown that adding auxiliary data stabilizes the model and reduces error (Deriso et al. 1985). The auxiliary data sources can include effort data, telemetry or mark-recapture data. The catch-at-age models use the age and sexes of the harvest to estimate an age structure of the population. The age structure combined with effort data can give scale and estimate many parameters including natural survival and harvest probabilities. These maximum likelihood techniques can be used to calculate recruitment for the population (Maunder and Deriso 2003). These models are robust to loss of data including using an average age instead of full age classes and will produce similar trends as full models (Richards and Schnute 1998). The commercial nature of fisheries gave managers large data sources based on catch and resulted in these methods being developed. Wildlife managers have relied primarily on transect-based surveys because of the ease of counting many species of wildlife. These fisheries methods introduced an integrated analysis of many populations where harvest and effort data exist (Dupont 1983).

The use of catch-at-age models in wildlife were adapted to many big game harvest data because large age-at-harvest databases were available (Hanson 1963). Many large mammals can be aged to multiple classes making these data readily available for these maximum likelihood techniques (Skalski et al 2005). The term statistical population reconstruction has been coined for use in wildlife populations but methods are comparable to statistical catch-at-age models that are used in fisheries (Gove et al 2002). Population reconstruction models have been shown to allow for an integrated analysis that produces similar results as transect surveys (Gove et al. 2002, Skalski et al. 2005). These models can incorporate habitat and other additional data that can inform the model on changes in animal abundance (Skalski et al. 2005).

These models have been compared to popular sex-age-kill models and have been shown to outperform these models and may be more appropriate for broad scale population estimates (Millspaugh et al. 2009). Population reconstructions have been completed for elusive species also where transect surveys would be unrealistic (Skalski et al. 2011). Until recently these models needed full age class data to be utilized, many species could be aged to multiple year classes which allows for estimation of the age structure of the population. The techniques have been refined to estimate using reduced age classes (Broms et al. 2010, Richards and Schnute 1998, Skalski et al. 2012). The reduced age data requires addition of banding or telemetry data to inform the model more on the harvest processes and stabilize the models. Although the precision of estimates maybe reduced, the accuracy is not affected (Skalski et al. 2012). These effects may be minimized in short lived species.

These models, although powerful, should be used with caution. The final estimation of abundances must be checked for fit to the data sources, correlation to parameters, and sensitivity analyses should be conducted (Skalski et al. 2012). The estimation of the parameters must be reviewed to determine if they are realistic. They can improve coverage and be more realistic when random effects are incorporated (Gast et al. 2013). Although confidence intervals may have a better coverage this is only appropriate when the individual specific effects are uncorrelated. The addition of auxiliary data is important to stabilize models and improve precision (Clawson et al. 2013).

The use of population reconstruction models in estimating abundance has not been widespread because transect surveys are relatively straight forward, and these model require programming knowledge. They need to be tailored to the question and require knowledge of the process and the species. The estimates produced by a model must be assessed as realistic. When used properly these models utilize many data sources that are readily available and can inform managers about the population in response to changes in hunting or the landscape.

The American woodcock population has seen long term declines in abundance as measured by the Singing Ground Survey (Sauer et al. 2008). These were estimated at -0.9% per year from 1968 to 2006. The American Breeding Bird Survey and Christmas Bird Count Survey both had similar patterns but were not as precise (Sauer et al. 2008). The relative densities of woodcock have been mapped and shown a high correlation to young forest, which suggests that these habitat types should be protected (Thogmartin et al. 2007, Nelson and Andersen 2013). Studies have shown that natural survival does not change between age and sex cohorts (Longcore et al. 1996, Pace 2000, McAuley et al. 2005). One study suggests a lower survival rates for juveniles (Krementz et al. 2003). Hunting has been shown to have no or little additive effect (McAuley et al. 2005, Bruggink et al. 2013).

There has only been one defensible estimate of abundance for American woodcock, however it estimates only the male population based on SGS counts of woodcock per acre of cover type which estimated the abundance at 2.2 million woodcock (Kelley et al. 2008). In an effort to evaluate if hunting is sustainable, Watts et al. 2015 used of a Potential Biological Removal (PBR) model and calculated that a total of ~ 318,000 woodcock could be sustainably harvested. This estimate is biased because the abundance estimate used in this calculation was merely an educated guess by estimating the harvest rate as 10% and dividing that by the estimated harvest as reported from Andres et al. 2006. The survival estimate utilized was based on a composite estimate of different period telemetry studies.

This research project was initiated to determine if population reconstruction methods are effective in estimating American Woodcock populations and are valuable tool for investigating harvest and status of this species. In addition, if determined to be effective, these methods can be used to identify gaps in current woodcock management, data needs, and help direct future methods and directions of management of this nationally significant bird. Trends of harvest, effort, and the SGS were investigated. The suggestion of biological reference points were also estimated.

The objectives of this study were:

1. To estimate American woodcock range-wide population abundances;
2. To estimate natural survival rates for woodcock;
3. To estimate harvest probabilities for woodcock;
4. To investigate trends in harvest, hunting, and woodcock populations;
5. To determine if current harvest levels are sustainable.

Chapter 2: Estimating American Woodcock (*Scolopax minor*) Population Abundances

Introduction

The American woodcock (*Scolopax minor*), a popular game bird in North America, has no formal population estimate. The Singing Ground Survey (SGS) is the main management tool for monitoring the population status of the American Woodcock (Cooper and Rau 2014, Sauer 2008). Managers have conducted the SGS annually since 1968 to monitor populations and have found an average decline of 0.9% per year in adult male abundance. The SGS is also the only management tool managers use to inform changes in harvest regulations. Managers are concerned the SGS may not accurately detect changes in woodcock populations (DJ Case and Associates 2010, Kelley et al 2006). These types of transect road surveys can fail to be representative of the entire landscape and interference from development and traffic can inhibit observations (Anderson 2001).

The SGS, the Christmas Bird Count, and The American Breeding Bird Survey were all analyzed by a hierarchical model and provide trend information for the population. Sauer et al. 2008 suggested using the SGS for management purposed because it has the smallest confidence interval and was specifically designed for woodcock. Using the SGS, the American woodcock Conservation Plan estimated adult male populations by extrapolating the counts of adult males per survey route by estimating the acreage of each survey route and then multiplying by available habitat (Kelley et al. 2008). This method assumes transects are representative and randomly located across the entire landscape. However, the SGS only estimates adult male abundance. Others have integrated banding data and the Wing Collection Survey (WCS) to estimate woodcock productivity, which managers can use as an indicator of annual breeding success (Zimmerman et al. 2010). However, the researchers state there is a lack of appropriate banding data to represent the population. Other research to monitor woodcock populations has centered on tracking period survival using radio-telemetry, but there has only been one such study of survival in the past 10 years (Bruggink et al. 2013). Although multiple data sources exist, managers still do not have accurate population estimates making the development of a population reconstruction model essential to appropriately manage woodcock populations.

Due to the shortcomings of the SGS and other monitoring tools to accurately describe woodcock population dynamics.

,the Association of Fish and Wildlife Agencies' Migratory Shore and Upland Game Bird Support Task Force identified a population model as the top priority for managing the American Woodcock (DJ Cases and Associates 2010). Recently, researchers have established new methods to estimate population abundances from age-at-harvest data with only adult and immature age classes (Broms et al. 2010). Population reconstruction models can estimate abundances, natural survival rates, and harvest probabilities of these abbreviated age class data (Skalski et al. 2012, Broms et al. 2010). Population reconstruction is a similar technique to statistical catch-at-age models that many fisheries managers utilize to analyze fishing pressure (Hilborn and Mangel 1997). These models rely on the age-at-harvest data but need auxiliary inputs such as harvest and hunter effort estimates, radio-telemetry, and index data whenever possible to provide reliable and precise estimates (Skalski et al. 2012, Skalski et al. 2013, Skalski et al. 2007, Deriso et al. 1985). These types of models utilize existing data sources and estimates demographic parameters of American woodcock populations, which can revealing new information about American woodcock (Broms et al 2010, Gast et al. 2013, Richards and Schnute 1998).

The objectives of this study were to integrate age-at-harvest data, harvest estimates, hunter effort estimates, radio-telemetry, and index data to estimate American woodcock population abundances accurately. The models will also provide estimates of annual natural survival and harvest probabilities for American woodcock. This research will show that managers can implement population reconstruction models on large datasets and over large geographic areas. This research will demonstrate the need for a review of the current survey methods to confirm that they meet statistical assumptions of these likelihood methods as these methods can show what effect our confidence in each survey has on our final estimates.

Methods

Data Input Sources

The study models data from the entire range of the American woodcock incorporating data of the WCS, Harvest Information Program (HIP), a radio-telemetry study, and the SGS (Table 1). Population reconstruction is an integrated analysis incorporating multiple data sources. The American woodcock is hunted in 34 eastern states where harvest is estimated annually. There is also woodcock hunting in 6 provinces in Canada (Gendron and Smith 2014). Population reconstruction relies on age-at-harvest data to estimate the population structure by informing the model of the age-sex composition from the harvest. These data are supplied by age-at-harvest data from the Wing Collection Survey (WCS).

Wing Collection Survey

The U.S. Fish and Wildlife Service (USFWS) developed the WCS to track the age and sex composition of harvested migratory birds (Martin 1964). The WCS asks hunters to mail one wing from each woodcock they harvest over the duration of the season to the survey. Over a 15 year period from 1999 through 2013 the Branch of Harvest Surveys, within USFWS, averaged 11,993 wings returned per year. USFWS personnel and volunteers, including state and federal biologists, process the wings once a year after having completed a competency test. This process entails examining feather wear, coloration, shape, and size to determine the age and sex of each wing returned (Martin 1964, Sepik 1994). The USFWS double-enters the data and compares each data set to verify data entry (Padding et al. 2006).

Harvest Information Program and the National Harvest Survey

The Harvest Information Program's diary survey tracks harvest and hunter effort in the US. As part of HIP, hunters are required to register by reporting their name, address, and answer stratification questions on their previous year's harvest success to enable a more efficient sampling scheme (Elden et al. 2002). HIP asks a percentage of hunters to complete a diary survey that documents each hunt with date of hunt, state and county of hunt, and number of birds harvested (Padding et al. 2006). The HIP survey is administered at the state level. HIP provides estimates of annual harvest and hunter effort which is called "days afield".

Canadian managers estimate woodcock harvest in a similar fashion, but the sampling frame includes all migratory game birds (other than waterfowl) hunters resulting in non-species-specific days afield (Gendron and Smith 2014). The harvest estimates from both methods were incorporated into the model, which in 2013 the U.S. was 243,000 woodcock and Canada's was 33,500 woodcock (Table 1). The Canadian harvest is much smaller and exerts a relatively small influence on model estimation. Also, because of a lack of hunter effort data from Canada, the model makes the assumption that Canadian hunting effort has followed a similar pattern as U.S. effort during the study period. This is a reasonable assumption given the U.S. states with the highest harvest levels occur along the Canadian border (Raftovich et al. 2012). The Canadian and U.S. harvest have seen similar declines in harvest during this time (Figure 9 and 10). This is included because all harvest needs to be accounted for, without these estimates, the abundance estimates would be artificially low. The effort is used calculate the harvest probability by scaling it to the harvest. Since there is only a small amount of Canadian harvest and it is only informing trend information which results in difference in Canadian effort having only a marginal effect. The rest of this paper will refer to HIP and NHS synonymously as these data are used for the combine harvest estimates.

Radio-telemetry data

Telemetry data were incorporated to further inform the models on harvest probabilities. Telemetry data have been shown to stabilize models and improve accuracy of estimates (Skalski et al. 2007, Skalski et al. 2012). Due to the limited number of telemetry studies, only one study conducted from 1999 to 2013 was able to be identified for incorporation into our models. Bruggink et al. monitored 1,035 radio-marked American woodcock from 2001 to 2004 during late summer until they migrated from their study areas (in Wisconsin, Minnesota, and Michigan (Table 2). Sixty birds were harvested by hunters during their study. The objective of this study was to determine if there were differences in harvest pressure between hunted and non-hunted areas. All ages and sexes were pooled. This study is a great fit for our use as it was assessing harvest across three of the heaviest harvest states as well as representative of hunted and non-hunted land.

Singing Ground Survey

The SGS was incorporated into models to inform on adult male trend patterns only. The SGS consists of 1500 annual survey routes across the breeding range of American woodcock in the Northern U.S. and Canada (Cooper and Rau

2014). During the survey, observers stop and listen for peenting males right before dusk within a specified time frame. Survey-wide average singing males per route were incorporated to inform the model on adult male population trends. Models were run with and without this index incorporated to compare model estimates to determine the effect the SGS has on demographic parameters.

Model Formulation

Statistical population reconstruction utilizes maximum likelihood estimation processes to determine the best fit of the parameters. Modeling techniques have been developed using joint-likelihood formulations that can derive population abundances with only juvenile and adult age classes (Broms et al. 2010). These models are a combination of age-at-harvest data (WCS), harvest (HIP), hunter effort (HIP), radio-telemetry (Bruggink et al. 2013), and index data (SGS). The models consist of three components for the joint-log-likelihoods (Equation 1). In some instances, a fourth component was included for the SGS index to determine the influence of the SGS index ($\ln(L_{Index})$) on parameter estimates.

$$\ln(L_{Total}) = \ln(L_{Cohort}) + \ln(L_{Harvest}) + \ln(L_{Telemetry}) + \ln(L_{Index})$$

(Equation 1)

These log-likelihoods describe the probability of observing the data given the model and specific values of the parameters. L_{Cohort} is the age-at-harvest likelihood. This multinomial likelihood estimates the proportion of age and sex of harvest by fitting the WCS data with a multinomial likelihood weighted by the number of successful hunters in the WCS. The average number of successful hunters was used instead of the average numbers of wings because the multinomial distribution assumes an independent sample (Hulson et al. 2011). Birds harvested on a single hunting trip may not be independent samples of the population whereas each hunter is assumed independent of other hunters (Skalski et al. 2012, Quinn and Deriso 1999). Four model formulations were examined to estimate American woodcock populations. Model 1 had one harvest probability for all age and sexes without the SGS index incorporated (1HNI). The SGS was incorporated into Model 2 (1HIA). These models were then formulated with the addition of an adult female harvest probability with and without the SGS index model 3 (2HNI) and model 4 (2HIA), which does not change these log-likelihoods other than equation 4 has two harvest probabilities. An adult female specific harvest and a group rate for adult males and juveniles were incorporated to account for higher harvest for adult females.

$$\ln(L_{Cohort}) = \quad SS \sum_{years} \sum_{age} \sum_{sex} P_{y,a,x} \ln(\hat{P}_{y,a,x}) \qquad \text{(Equation 2)}$$

Equation 2 is the multinomial log-likelihood function for the proportion of harvest of each age and sex cohort. SS is the effective sample size; 1200 was used, the average number successful hunters that sent wings from 1999 to 2013. This likelihood describes each age and sex cohort every year of the model estimation process. P_{yax} is the observed proportion of harvest for *y* year, *a* age and x sex cohort. $\hat{P}_{yax}$ is the estimated proportion of harvest for *y* year, *a* age and x sex cohort. This creates a matrix of composition of harvest for each year incorporated.

The log-likelihood for total harvest was modeled using the lognormal likelihood as described in Fournier and Archibald (1982).

$$\ln(L_{Harvest}) = -\frac{1}{2\sigma^2}\sum_{y=1}^{15}(\mathrm{H} - \widehat{H})^2 \qquad \text{(Equation 3)}$$

H is the observed harvest as estimated by the HIP survey. $\widehat{H}$ is the estimated harvest which is a product of the models estimates of survival, harvest probability, and abundance.

$$\widehat{H}_y = \sum(S\ x\ N_{y,a,x}\ \ x\ HP_{y,a,x}) \qquad \text{(Equation 4)}$$

S is the Estimated Survival, N is the abundance in y year, a age and x sex and HP is the harvest probability for each cohort. The harvest probability is derived using the days afield estimate from the HIP and is scaled by a harvest coefficient (Broms et al. 2010). A singular constant survival for every cohort, which the model estimates as a parameter, was used. There is currently not enough data to allow the model to estimate separate survival parameters for each age and sex class. σ is the estimated average standard deviation of the harvest estimates as calculated for the HIP, the log-scale average from 1999 to 2013 was 0.088.

The likelihood for the radio-telemetry data is utilized to inform the model on the harvest rates. This is effective in further informing the model on how the harvest processes take place. $\ln(L_{Telemetry})$ utilizes a binomial likelihood that estimates the harvest probability by fitting it to the radio-telemetry data.

$$\ln(L_{Telemetry}) = \sum_{y=1}^{4} K_y \ln(p) + \left(T_y - \sum_{y=1}^{4} K_y\right)\ln(1-p)$$

(Equation 5)

Where:

T_y is the number of woodcock that were radio marked in year y. K_y is the number of radio marked woodcock that were shot by hunters in year y and p is the estimated harvest probability. There was also the addition of the SGS index data to inform the model on adult male abundance.

The likelihood function utilized is normally distributed

$$\ln(L_{Index}) = -\frac{1}{2\sigma^2}\sum_{y=1}^{15}(S_y - I_y)^2 \qquad (5)$$

The SGS average counts are denoted by S_y where y is the year of the survey. I_y is the estimated index that is assumed to be proportional to adult male abundance and is derived adult male abundance multiplied by a parameter that serves as a scalar.

The parameterized model was input into the open source software ADMB (Fournier et al. 2012). This software uses an algorithm to search numerically for the best fit of these likelihoods. The model estimated 23 parameters where the index was incorporated. The model could not achieve fit to the age-at-harvest data without expressing a separate harvest probability for adult females. This was because females were harvested at larger proportions. The original formulation from Broms et al. (2010) was to estimate juvenile abundances independently for each year and sex. Juvenile abundances were modeled assuming a constant sex ratio over time, this estimated parameter based on WCS. This allowed for the reduction of parameters to stabilize the model. The adult abundances were estimated in the first year and were calculated for subsequent years based on parameter estimates of survival, harvest probabilities and juvenile abundances.

The model selection was a multi-tiered approach of examining the hessian matrix and examining fit visually for each data input. Akaike's Information Criterion (AIC) values were calculated for models with similar data inputs (Hillborn and Mangel 1997, Akaike 1974, Andersen and Burnham 2002).

$$AIC = -\ln(L_{Total}) - 2k \quad (6)$$

Numbers of parameters (k) penalizes the minimized negative log-likelihood for each model. The AIC may only be considered for models with the same data. The model estimates expected data values, which make it suitable for chi-square goodness of fit testing (Hilborn and Mangel 1997). Chi-squared goodness-of-fit values were used to make relative comparisons for each model formulations fit that had different data sources.

$$\chi^2 = \sum[(O_y - E_y)/E_y \quad (7)$$

The chi-square goodness of fit statistic calculated for the age proportion data and the harvest data for each of the four models. The overall likelihood as produced by ADMB can be used to assess models when the same data has been input. In summary, AIC and likelihoods can be compared between 1HNI and 2HNI (No SGS) or 1HIA and 2HIA (with SGS). The use of chi-square can be compared among all models.

Results

The four models used data from the 1999 through 2013 hunting seasons. All four models successfully achieved fit, meaning the Hessian matrix indicated low correlation between parameters. However, the models with a single harvest probability did not fit the age-at-harvest data well and led to inflated abundance estimates. Based on likelihoods, AIC, and chi-square test statistic the best fit model incorporated adult female specific harvest probability (Table 3). This allowed the model to explain the larger proportion of adult females in the harvest as seen in the WCS data. These models were also visually inspected using residual plots and comparing observed data sources to the estimated data. The Chi-Square was calculated for the age-at-harvest proportions. The models with a single harvest probability term had larger likelihoods and Chi-square values than the models with an adult-female-specific harvest probability. When comparing 2HNI and 2HIA, 2HNI had a chi-square for the age-at-harvest lower that 2HIA (χ^2 = 0.023 vs. 0.010 respectively) However, these chi-square values are too similar to solely base a model selection. The AIC and likelihoods should not be compared between models with different data sources (Table 4). The AIC numbers were inconclusive as they were close to the same. The model produced better fit to index when effective sample size of L_{Cohort} was reduced. These two models produced similar results and 2HIA will be used to describe the population. Although the chi-square indicates a slightly better fit to the age-at-harvest data a chi-square of the harvest estimates shows the opposite result, meaning the addition of the SGS data is fitting the harvest data stronger.

The top model estimated natural survival probability for American woodcock at 0.528 ($\widehat{SE} = 0.008$). Total abundance estimates ranged from a low of 5,206,000 ($\widehat{SE} = 602{,}220$) in 2007 to a high of 6,075,800 ($\widehat{SE} = 677{,}460$) in 1999 (Figure 1). The model estimated the juvenile sex ratio at 0.505 ($\widehat{SE} = 0.011$) male. This is estimated from the proportion of wings in the WCS. The harvest rate, as calculated as a proportion of estimated harvest over total abundance, had an average of 0.062 for the period. The harvest probabilities are the probability of harvest given the woodcock has survived to reach the hunting season. The average for adult females was 0.180 and for all other cohorts was 0.101. The average reproductive ratio calculated by dividing juveniles by adults was 1.140 juveniles per adult.

DISCUSSION

There has been minimal information on population levels of American Woodcock. The American Woodcock Conservation Plan estimated there were an average of 2,244,008 adult male American woodcock from 2000 to 2004. To date, this represents the best estimate of American woodcock abundance in North America. However, this method relied on the assumption that the observers covered a certain number of acres per survey route and then extrapolated those survey data across the survey study area. The model estimates the adult male population during the same time as 1,366,825. Andres et al. (2012) also estimated total American woodcock abundance based on a 10% harvest rate given the current harvest estimates, between 2,625,000 and 5,250,000 with the model estimating 5,469,700 ($\widehat{SE}$ = 676,830) in the same year. To date these are the only two population abundance estimates in the published literature. Thus highlighting the importance of the need for statistically defensible population estimates. The model developed in this study will now allow accurate population estimation and enable managers to investigate harvest rates and determine sustainable harvest limits (Watts et al 2015, Runge et al. 2008).

There has never been a population estimate of American woodcock. This is because woodcock cannot be surveyed by traditional transect surveys and there has been little research on population estimations. There has been decreasing banding efforts and this data is spatially and temporally biased to be used as an overall population estimator (Krementz et al. 2003). These data coupled with the recent use of these models to help inform wildlife managers on population responses to management and land changes made this research relevant and useful. The use of statistical population reconstruction warranted a deeper investigation for woodcock populations. The American woodcock has shown declines as indicated in male abundances measured by the SGS. Others have used models to take advantage of pooled age class data to produce accurate estimates (Broms et al. 2010, Skalski et al. 2012, Richards and Schnute 1998). These methods were chosen to estimate American Woodcock abundance because of the large data sets on harvest and effort available in the United States and Canada (Cooper and Rau 2014, Gendron and Smith 2014).

The U.S. and Canada administer similar harvest surveys. The difference is the U.S. has a woodcock specific hunting surveys whereas Canada samples woodcock hunters with all other migratory game bird hunters, which results in no formal estimate of days afield to compliment the harvest estimate for woodcock specifically (Gendron and Smith 2014). Canada estimates hunter activity for all migratory bird hunters together resulting in the inability to estimate woodcock hunting effort independent of other species. Pooled harvest was used in estimations. The lack of reliable effort data from Canada made it necessary to assume the trends in effort in Canada were similar to the US. This is a reasonable assumption as woodcock hunting has been managed using the SGS, WCS, and harvest surveys. The Canadian harvest is much lower than the U.S. which would also minimize any effects. Nova Scotia was used to investigate this assumption. During the study period 86% of Nova Scotia's non-waterfowl migratory bird harvest was woodcock. Days afield for US and Nova Scotia and both showed similar declines, these estimates showing a positive correlation, $R^2 = 0.53$.

Initially, a model was developed to estimate American woodcock abundance utilizing methods similar to Broms et al. 2010. This method produced parameter estimates that were highly correlated, indicating the model does not have enough information to estimate the parameters independently. The Broms et al. (2010) formulation made each year's juvenile abundance by sex an estimable parameter. The new method instead estimates yearly juvenile abundance and then separate the sexes by an estimated deviance based on the proportions observed in the WCS. The use of this method allowed us to decrease the number of estimable parameters which allows the process to run smoother as it reduced the estimation processes. This makes the model more stable and avoids over-parameterization which has been shown to bias models because of over-fitting (Akaike 1973). Broms et al. (2010) also suggests estimating age and sex specific natural survival rates, the new model attempting to estimate these failed to produce reliable results. The results of this model were large standard errors and unrealistic estimates of survival. Some studies have shown no difference in cohort survivals (McAuley et al. 2005), others suggest a slightly lower juvenile survival; population reconstructions are robust to differences (Krementz et al. 2003, Broms et al. 2010). The suggested model also assumes that natural mortality is constant. The lack of additional natural survival data to inform the model is needed and these results are a best-case scenario for available data. The likelihoods were changed to multinomial and lognormal distributions that stabilized the search procedure of ADMB by reducing the looping from the original formulation. The flexibility and robust nature of these models show how they can be extended to American woodcock and other species of migratory game birds at large geographic scales.

Changes in parameterization and likelihoods reduced the correlations observed in the hessian matrix. Although the models now produced abundance estimates, standard errors were large and estimates of model fit suggested the model was not successfully fitting the age-at-harvest data. The model was overestimating juvenile female and adult male abundance while underestimating juvenile male and adult female abundance. The juvenile observed proportions in the harvest as reported by the WCS was close to 50/50 every year. There were a larger proportion of adult females in the harvest than adult males though. The even distribution of juvenile sexes ruled out a difference in proportions of each sex at birth. This indicates that adult females were being harvested at a higher rate. Incorporation of a separate harvest probability for adult females substantially improved model fit (Figure 4, Figure 5). One possible hypothesis for a higher harvest probability of adult females is that their physiological condition due to reproduction makes them more vulnerable (i.e. higher mass as a result of egg production). Straw et al. 1994 supports this hypothesis because they documented heavier female woodcock likely due to the physiological reserves required for egg production and brood rearing. Re-parameterization also resulted in less overestimation of abundance. The initial poor model performance was due to the model attempting to account for the larger proportion of adult females in the WCS data by overestimating the number of juvenile females thus leading to inflation of the total population. Re-parameterization also reduced the model standard errors.

After re-parameterization, the relative fit between the model with and without the SGS index incorporated were evaluated (Figure 2, 3, 4, 5, and 6). The chi-square for the harvest and age-at-harvest proportions for the model with the index incorporated was 35,226 and 0.023, respectively. The chi-square for the model that excluded the SGS for the harvest and age-at-harvest was 35,389 and 0.009, respectively. The difference in scale is due to the fact that the age-at-harvest is a proportion and the harvest is close to 300,000 woodcock per year. The chi-square should only be used in this manner as a relative measure of fit. There is disagreement in the chi-square whether addition of the SGS improves fit.

These models both fit well and produce similar results this is encouraging and allows us to suggest that both are appropriate for use and the model without the SGS may be better if the incorporation of the index does not allow for deeper investigation (Figure 6). The results of the model with the SGS incorporated are reported because of its use of the management tool.

The model is able to estimate yearly natural survival rates, which are similar to what others have found. Estimates of annual survival of woodcock are difficult without extensive banding data and the model estimates annual natural survival at 0.528 ($\widehat{SE} = 0.008$). This is an estimate of natural survival and would be lower if harvest mortality was incorporated. There have been many period telemetry studies on woodcock that informed managers on short periods of survival. The model needs more banding or long term telemetry on individual cohort survival rates. There is some disagreement between survival rates between age and sex cohorts (Dessecker and McAuley 2001). Analysis of banding data from woodcock banded in Michigan from 1978 to 1998 estimated annual survival of adult woodcock at 0.489 ($\widehat{SE} = 0.033$) (Krementz et al. 2003.) Adult male annual survival was estimated for 1987 to 1989 at 0.471 as a composite estimate of period telemetry studies (Longcore et al. 1996). This survival estimate was derived by multiplying survivals for different times of the year. In 1956 banding data reported annual survival of 0.57 for male woodcock banded in Massachusetts (Sheldon 1956). With additional auxiliary information to inform the model it could estimate yearly survivals for all age and sex cohorts. This highlights the need for more banding data and increased telemetry. The radio-telemetry study that was utilized to inform the model on harvest processes was only 4 years of data. A larger sample size of not only birds but larger geographic area would be more appropriate to describe the harvest processes (Bruggink et al. 2015). This model provided reliable estimates of woodcock populations although increased banding and radio-telemetry would provide increased precision.

Management Implications

The use of the statistical population reconstruction is an effective method for estimating population abundance from age-at-harvest data for migratory game birds. The use of maximum likelihood estimation has provided a robust framework to estimate American woodcock abundance and the extension of this method to other harvested migratory species is appropriate. This model has allowed for increased knowledge to be available to managers of woodcock populations. This integrated analysis can combine a variety of data sources to help investigate population dynamics on large scales that would otherwise be difficult or impossible. This has allowed for the first population estimates for American woodcock and harvest probabilities. The model will allow a more in depth analysis on harvest regulations and help set biological reference points. This model could be used to calculate potential biological removal to help determine sustainable harvest levels. The model has wide application with other species that age-at-harvest data is available. Many states already collect this data on non-migratory birds and mammals but rarely incorporate it in statistically robust models to inform management.

Chapter 3: Assessment of American Woodcock (*Scolopax minor*) Management and Population Status

Introduction

The U.S. Fish and Wildlife Service and Canadian Wildlife Service manage American woodcock harvest to increase the population and maximize hunter encounter opportunity (Straw et al. 1994). Woodcock hunting occurs across the eastern half the United States and Canada, which comprises 34 states and 6 provinces. The harvest surveys are conducted in all states in the U.S (Padding et al. 2006). Canada also conducts harvest surveys nationally (Canadian Wildlife Service 2014). Unlike other species of migratory gamebirds, woodcock are not managed using an Adaptive Harvest Management (AHM), which allows for cooperation between scientists and managers (Nichols et al. 2007). The AHM framework allows for dynamic assessment of a population's response to regulation changes and environmental variability. The addition of statistical population models that incorporates surveys data allow for an integrated analysis of the available data to characterize dynamics of changing wildlife populations (Gove et al. 2002). Most wildlife population models have relied on transect surveys to estimate populations based on density observations and available habitat data (Lancia et al. 1994). However, woodcock are difficult to survey in this way because they inhabit forests and are difficult to detect visually (Cooper and Rau 2014).

Currently woodcock managers rely on the Singing Ground Survey (SGS) to set harvest regulations (Cooper and Rau 2014). This survey is an index of adult male population abundance that monitors the number of displaying adult male woodcock in the breeding range. This is the primary survey used for management and more rigorous surveys and analysis of the population are needed (Cooper and Rau 2014). The Association of Fish and Wildlife Agencies' Migratory Shore and Upland Game Bird Support Task Force developed a list of priority needs. The four priorities developed were: 1) creation of a population model to measure changes in populations based on habitat and harvest regulations, 2) strengthen communication and policy, 3) increase knowledge of woodcock land-use and migration, and 4) evaluate the SGS (Case et al. 2010). The success of these priorities will enable managers and scientists to learn how regulations and land-use changes affect population dynamics.

Population reconstruction techniques can be used to effectively estimate population levels utilizing age-at-harvest data and auxiliary survey data (Broms et al. at 2010, Gove et al. 2002. Skalski et al. 2007, and chapter 1). These models enable managers and scientists to investigate population dynamics on species that are difficult to survey due to detection (Gove et al. 2002). In the second chapter, it was shown that these models are successful in not only deriving an abundance estimate but estimating other population parameters like annual survival and harvest probabilities. Having population abundances linked to harvest rates and survival estimates give managers the ability to monitor levels of take.

The HIP, WCS, and SGS should be tested for accuracy by review of their statistical rigor and survey designs (Witmer 2005).

The WCS and SGS are used to monitor changes in the woodcock population. There has been research on the woodcock productivity as measured by the wing collection survey (WCS) and banding data (Zimmerman et al. 2010). Monitoring productivity is a key component in managing woodcock as it is reported in yearly status reports. The recruitment index has shown long term declines which would indicate that the woodcock population is compromised (Cooper and Rau 2014). The SGS is used to trigger regulatory actions which cause changes in harvest regulations. The hierarchal model suggested in Sauer et al. (2008) gives a model that can estimate changes in the SGS and produce reliable confidence intervals. The interim harvest strategy is based on 70% confidence intervals, if the lower interval estimate of singing males based on a three year average dips below the prescribed management threshold regulations will change (American Woodcock Harvest Strategy 2010).

Assessing woodcock populations require an integrated analysis of many data sources. Woodcock abundances were successfully estimated utilizing a statistical population reconstruction. These models integrate available age-at-harvest data to estimate population sizes (Fournier and Archibald 1982, Deriso et al. 1985, Gove et al. 2002). An accurate population estimate is important to many applications of management (Runge et al. 2008, Watts et al. 2015). The methods utilized in this research will provide a holistic view of the woodcock population. The review of existing management tools will highlight the needs of these programs while assessing the population status. This research suggests new management ideas that fisheries management have suggested. The use of existing data in population estimation allows for calculation of biological reference points to steer regulation of woodcock.

The Objectives of this study were to utilize the population model developed to help investigate the status of American woodcock. The review of hunter activity and harvest will be investigated to determine if there has been decreases in hunter activity. Population reconstruction models allow examination of harvest regulation and population viability of woodcock, managers can now assess the effectiveness of current American woodcock management. This study will use population reconstruction models to review current management of American woodcock and suggest possible biological reference points that can allow managers to gauge if management is successful. The use of Potential Biological Removal and Reproductive Potential Ratios will inform whether harvest levels are sustainable.

Methods

Current Surveys

Singing Ground Survey

American woodcock are hunted in the United States and Canada. The United States federal government sets a framework for states as a guideline for hunting regulations. The U.S. currently manages woodcock as two separate units, Eastern and Central (Coon et al. 1977). This is roughly attributed to the Atlantic and Mississippi flyways. The hunting regulations for each of these units are set based on a three year average of the SGS. The SGS is a transect survey that is conducted every spring to listen for displaying male woodcock. This survey relies on observers to conduct a survey at dusk in a specified time period. Each observer is assigned a randomly selected survey route in which 10 listening stops of 5.4 km long are conducted (Cooper and Rau 2014). There are guidelines for acceptable weather and conditions in order to reduce environmental biases. Also, limited budgets require that some routes are not run each year. This survey is analyzed using Bayesian hierarchal modeling to allow for trend analysis. This accounts for random effects of survey variability (Sauer et al. 2008).

Wing Collection Survey

The WCS is a national annual survey of woodcock hunters. This survey asks hunters to send in a wing from every woodcock they harvest. These wings are aged and sexed based on plumage characteristics (Martin et al. 1964). The participants are required to pass a competency test to be able to participate. These data were used as the age-harvest-data for Model 4 from Chapter 2. The data are reported every year as an estimate of productivity (Cooper et al. 2014). The integration of banding data and wing data has been analyzed using Bayesian hierarchal modeling to estimate productivity (Zimmerman et al. 2010).

Harvest Information Program (HIP) and National Harvest Survey (NHS)

The HIP survey started in 1999 as a way to track harvest in the U.S. The HIP program requires all woodcock hunters to register by name and address when buying a license (Padding et al. 2006). This allows the U.S. Fish and Wildlife to conduct allows for a mail survey that asks hunters to record a history of their hunting success over a season. These methods follow the Dillman Total Mail Method (Dillman 2011). The survey estimates harvest by state and nationally. This survey also provides estimates of days afield nationally and by state and determine the number of active hunters by state. The ability to track changes in harvest and effort have been used to inform the model in Chapter 1 to trends of population abundance. The Canadian Wildlife Service also monitors harvest with the National Harvest Survey (NHS) at a sample frame of all migratory game bird hunters.

Statistical Population Reconstruction (SPR)

The population reconstruction model estimates abundance and vital rates from 1999 to 2013. The model is a joint-likelihood that uses the SGS, WCS, HIP, and radio-telemetry data to estimate abundance each woodcock cohort (annual age and sex classes). The use of AD Model Builder utilizes numerical search algorithms to minimize the negative log-likelihood formulation (Fournier and Archibald 1982). This model calculates abundance based on annual cycles of natural mortality, harvest mortality, and recruitment (Fournier and Archibald 1982, Broms et al. 2010, and Deriso et al. 1985). The model also produces estimates of natural survival, which is assumed constant for the period. The model was only able to produce a single estimate of survival for all age and sex cohorts. The accurate estimation of harvest rates and abundances will allow for calculations for investigations of harvest levels and suggest reference points.

Reproductive Potential Ratio (RPR)

The Spawning Potential Ratio (SPR) is a biological reference point used in fisheries management because calculating sustainable harvest rates have proven difficult as they rely on rigid assumptions of population dynamics (Legault and Brooks 2013). SPR is the ratio of a fishes spawning biomass at a set harvest rate over the spawning biomass at an unfished state. An SPR of 40% was suggested for long lived ground fish (Clark 1991). However, this level of SPR has been shown to be a too aggressive for fisheries and an SPR of closer to 50% has been suggested to be more sustainable (Clark 2002). This method is applied to American woodcock populations in order to investigate sustainable harvest levels. This relies on basic life history knowledge, for instance, age at first breeding and natural mortalities by age and sex. This reference point will be referred to as the Reproductive Potential Ratio as it has not been used extensively on wildlife populations. RPR for woodcock will simulate egg production per 100 recruits. In this deterministic case abundance is started at 100 and estimated at each year by the product of previous year abundance, harvest rate and natural survival. The estimates of survival and harvest rates from the population reconstruction model were utilized in the below formulation.

$$E = \sum_{t=1}^{15} \left((N_t \; X \; \hat{S}_t (1 - \widehat{h_t}) \right) X \; e_t \qquad (7)$$

E is the estimated number of eggs that would be expected from one cohort of woodcock simulated until no individuals are left. N is the number of recruits, initialized at 100, which is followed through based on survival and harvest rates. The egg production is then calculated for each year which is a product of abundance, expected number of eggs, and proportion of mature, which is assumed 0 in the first year and 1 in all others. Woodcock have 4 eggs per clutch and are mature after 1 year (Mendall and Aldous 1943). A selectivity factor is usually used in fisheries to account for the proportion of age of fish that are caught in different net sizes. This term is dropped because woodcock cannot be aged other than one mature age class. The simulation also accounts for age at maturity. The egg count per year is calculated as a product of the proportion of mature, assumed at one after the first age class, and the abundance of the year class.

$$RPR_h = \frac{E_h}{E_0} \tag{8}$$

E_h is the sum of the egg count that would be expected under harvest rate h. E_0 is the egg count that would be expected without harvest. Thus, RPR is used to determine if our current woodcock harvest is sustainable

Potential Biological Removal (PBR)

Potential Biological Removal has been used to assess what level of take would be not being detrimental to the sustainability of the populations. This method was described in depth in Watts et al. (2015). This method requires estimates of survival, age at first reproduction, and minimum population size. The PBR is calculated utilizing the same equations and recovery factor as describe in Watts et al. (2015). In Watts et al. the parameter estimates used in the calculation were the best available at the time, including an estimate of populations that was assumed from an assumption that harvest is close to 10 percent of the population (Morrison et al. 2006). This review of woodcock management will update this estimate using the parameters as estimated in chapter one.

$$PBR = \frac{r_{\max} F_R}{2} N_{min} \tag{9}$$

Where r_{max} is the intrinsic rate of change for the population. F_R is the recovery factor as decided by our management objective, with 0 to 1 indicating a desire to increase populations and 1 to 2 a decrease. The analysis will use 0.3, as suggested, which equates to a conservative approach because this decreases the overall number of woodcock that can be taken. N_{min} is the lowest population level estimated which will use the lower 95% confidence interval of the lowest estimated abundance from the model.

$$r_{max} = \lambda_{max} - 1 \tag{10}$$

$$\lambda_{max} \approx \frac{(Sa - S + a + 1) + \sqrt{(S - Sa - a - 1)^2 - 4Sa^2}}{2a} \tag{11}$$

r_{max} is estimated by equation 10. λ_{max} , the maximum annual growth speed, is calculated by equation 11 where S is the survival estimate from the model in chapter 1. a is the age at first reproduction.

Results

The harvest surveys in the US and Canada have shown declines in hunter participation and accounting for hunting effort is imperative to understanding harvest dynamics. This study reviews trends for the study period of 1999 to 2013. The estimates of harvest in the U.S. from 1999 to 2013 years ranged from a low of 238,395 ($\widehat{SE} = 18{,}245$) in 2009 to a high 444,806 ($\widehat{SE} = 45{,}388$) in 1999. The estimates of harvest in the Canada from 1999 to 2013 years ranged from a low of 14,918 ($\widehat{SE} = 5{,}523$) in 2010 to a high 61,702 ($\widehat{SE} = 2{,}452$) in 1999. The harvest for U.S. and Canada from 1999 to 2013 are both declining (t(14) = -2.56, P = 0.024 and t(14) = -5.56, P < 0.001) respectively (Figure 9 and 10). The days afield estimates for the same time period ranged from a low of 414,705 ($\widehat{SE} = 27{,}506$) in 2012 to a high of 726,269 ($\widehat{SE} = 55{,}582$). The days afield also shown a decline for this time period (t(14) = -3.18, P = 0.007) (Figure 8).

The statistical population reconstruction estimated population levels for woodcock from 1999 to 2013. The total abundance estimates ranged from a low of 5,206,000 ± 1,327,822 in 2007 to a high of 6,075,800 ± 1,180,351 in 1999

(Figure 1). The population shows a slight decline over this period (t(14) = -1.99, P = 0.068). Adult male abundances were correlated to the SGS during this time (R^2 = 0.66) (Figure 12). Because the SGS and adult male abundances were correlated, a linear regression was used to extrapolate the SGS index to estimate historic levels of adult male abundance. The historic high of singing males occurred in 1974 with 4.09 per route which corresponds to 1,970,334 males. The low was in 2008 of 2.56 signing males per route which corresponds to 1,278,672. There has been a decrease of 689,934 singing males between these periods (Figure 13).

The RPR was calculated using the most current harvest probability of 0.082 for the first year and used 0.148 which is the estimated adult female harvest rate. Using these estimates the current RPR is 79.51%. The calculated RPR 60% harvest probability would be 0.206 (Figure 11). The harvest probability for RPR 50% and 40% would be 0.301 and 0.434, respectively. The overall harvest rate as calculated as a ratio of harvest to abundance has decline from 1999 to 2013 (t(14) = -3.28, P =0.006) (Figure 7).

The PBR was calculated using the estimated survival of 0.528 and the lower 95% confidence level abundance estimate of 4,025,649 woodcock in 2007, which was the lowest estimated abundance of the time series. This conservative PBR resulted in 415,072 woodcock that could be sustainably harvested per year.

Discussion

The goals of this study were to review the current surveys and evaluate the status of woodcock. The results of this study give an in depth investigation into woodcock population dynamics. The American Woodcock Population Status, published annually by the U.S. Fish and Wildlife Service, reports the status of woodcock based on the surveys conducted on an annual basis. The annual population status report of American woodcock by the U.S. Fish & Wildlife Service reports the status of woodcock based on the SGS, WCS, and HIP survey. The long term trend for woodcock estimated using the SGS as reported from 1968 to 2014 was -1.01% and -0.90% per year for the eastern and central management zones, respectively (Cooper and Rau 2014). The three main surveys, HIP, SGS, and WCS have all shown decreases from 1999 through 2013 (Cooper and Rau 2014). The Canadian Wildlife Service also has reported that there have been declines in the population but report a less severe decline than in the U.S. as measured by the SGS (CWS 2014). Not only have there been declines in singing males but there have also been declines in days afield and harvest. The long-term population declines have been attributed to degradation of habitat and loss of early successional habitat (Dessecker and McAuley 2001). Looking at these surveys by themselves one can only speculate at what is happening to the populations. It is obvious that there has been a decline in populations from historic levels but it was not so clear if hunting was in some way contributing to these declines. The information shown here would indicate that hunting, as previously thought it not the cause for declines. The use of a population reconstruction has produced the ability to look at harvest dynamics and evaluate take in an objective holistic way.

The SGS is the only metric currently used to set harvest regulations for American woodcock (Woodcock Harvest Strategy Working Group 2010). Managers use the same 3 year average thresholds of SGS counts for both the Central and Eastern management zones although they are managed separately. The thresholds are 3.25, 2.00 and 1.00 average singing males per route (Table 5). These numbers correspond with the lower limits for a liberal, moderate, and restrictive season. These regulations include a 3-bird bag limit but only vary in the length of the season, 60, 45, 30 day seasons respectively. This conservative AHM approach triggers a change to regulations if the lower 70% confidence limit estimate of the SGS is below the threshold for three years. The confidence limits are derived by a hierarchal model (Sauer et al 2008). The SGS has long data series and has been shown to correlate to estimated abundances (y = 0.2832x + 13.336, t(14) = 5.05, P = 0.002, R^2 = 0.66) in the model suggested in the population reconstruction for woodcock. The American Woodcock Conservation Plan using an estimate of woodcock per acre multiplied by habitat type for the 1970s and early 2000s estimated a loss of over 839,000 singing males. A loss of 689,934 singing males from 1974, the surveys high, to the low of 2008 was estimated (Figure 13). This result shows consistency that a decline males has occurred and that study links it to habitat loss. The Forest Inventory Analysis National Program, surveys forest in ten year blocks across the U.S., from the 1980s to the 2013 there has been an estimated loss of 2.8 million acres of small diameter forests (Miles et al. 2001). This cover type been shown to be important to woodcock (Kelley et al. 2008).

The priority information needs as outlined in 2010 list evaluating the SGS as a priority. The concern on detection probabilities, sampling design, and observer effects was outlined as factor that could limit the accuracy of this survey (Case et al. 2010). As discussed in other reviews, indexes of abundance should not replace population estimates and should only be relied on if statistically sound (Anderson 2001). The SGS has been relied on too heavily on to manage a species of such historic and national significance. The SGS is a great tool to inform a more integrated analysis such as a population reconstruction, where auxiliary data has been shown to stabilize estimations (Skalski et al. 2007). This survey has been conducted for a long time frame and the importance of that should not be overlooked.

Another survey conducted annually is the WCS. The age and sex data for the population reconstruction as used from the results of the WCS. The accuracy of this data has been questioned as a Wingbee participate only has to pass one test to process wings independently (Krementz and Gbur 2006). The review of this survey is paramount if these methods are continued to manage woodcock. The assumption in utilizing any statistical model is that there is little process error. The sample frame of this survey includes a random sample from successful HIP registrants but also hunters can stay in the survey as it is assumed that the composition of their harvest is random. This could invite bias into the survey. Although informally this has been looked at there has never been a formal review of the WCS and its validity. This is important as Canada and the U.S. both use the WCS to estimate productivity using this method. The WCS was used in conjunction with available banding data to productivity in a Bayesian framework (Zimmerman et al. 2010). Although, these methods are robust the sample frame could be biased. The Wingbee is the event that these wings are processed each year. This event requires each attendant to pass a 25 wing pre-test that only allows one wing misidentified. The process is an attempt to make sure that each classification is correct. A review of this event has shown that many participants take the test multiple times and could be biasing the data (Krementz and Gbur 2006). My suggestion is to conduct the Woodcock Wingbee with greater rigor by using methods similar to the Waterfowl Wingbee. This event has a trained expert that has taken training and is certified through a series of tests of known age-sex wings. This person is referred to as a checker and is responsible to check everyone's work at their table. This process requires at least 2 people to look at each wing. It also has the benefit that a more experienced biologist is there to assist the new comers. The WCS is an important part of woodcock management and should be continued and reviewed.

The HIP Survey supplies annual estimates of harvest and effort for woodcock. These data are important to the population reconstruction as it allows for a description of the harvest processes and can be used to estimate harvest probabilities. The harvest estimates could be biased high but this has only been assessed in waterfowl estimates (Padding and Royle 2012). This bias could artificially inflate the abundance estimates in the population reconstruction.

Although the effects are probably similar year to year so analysis of trend and changes in rates should be consistent year to year. The harvest for woodcock has shown declines since 1999 (Figure 9 and 10). The U.S. days afield estimate has also shown declines since 1999 (Figure 8). This is an indication of that hunting is declining in general for woodcock. The harvest rate as calculated from the model has shown a significant decline (P = 0.006) for the 1999 to 2013 year period. This supports the idea that hunting is declining for woodcock. The U.S. actually increased the season for the eastern zone from a 30 day season to a 45 day season when the new harvest strategy was implemented. Canada has had the same harvest regulations since the 1970s (Straw et al. 1994).

The RPR that is suggested for use in woodcock management an extremely conservative approach with an RPR of 60%. This was suggested as a reference point for long-lived ground fish (Clark 2002) so use for a short-lived species such as woodcock would be very conservative. This method has been used frequently in fisheries management and it provides a proxy for maximum sustainable yields. The conservative reference point suggested provides a level of protection for the use of these methods to allow time for evaluation of their accuracy. The current RPR based on harvest probabilities from 2013 is 79%. In the model, harvest probability is the probability of harvest which is the proportion of the population that is killed by hunting. Harvest probability will be larger than the harvest rate because it is calculated after the natural mortality rate is applied. Harvest probability is treated as a pulse mortality event meaning that it is a percentage taken once during the year. The harvest rate is simply the estimated harvest over the estimated abundance. The RPR utilizes this harvest probability and gives a realistic view of how harvest affects the female portion of the populations. The benefit of utilizing these methods is it protects the breeding adult females. The harvest of adult females is higher than other age-sex cohorts. The RPR of 60% can be interpreted to allow managers to raise hunting bag limits and still have a sustainable woodcock population. The current harvest probability for adult females is 0.15 and if an RPR of 60% is desired, harvest could be almost twice as high and still be just under that threshold (Figure 11).

PBR is the calculation of the number of individuals that can be taken from a population based on the level of risk managers are willing tolerate, the minimum population size, and the rate of change for a population. Watts et al. (2015) calculated this for woodcock at 318,700 woodcock that could be taken from the population sustainably. This formula with model-derived estimates of survival and minimum population size resulted in a PBR of 415,072 woodcock. Their method used a population estimate that was based on an educated guess since no formal population estimate existed until now. The use of the lower 95% confidence interval from the year with the lowest estimated abundance was used, which occurred in 2007, to estimate a more conservative PBR. This PBR was still substantially higher than the combined estimates of U.S. and Canadian harvest of 276,600 in 2013.

This review and analysis of the status of woodcock in North America has shown that use of existing surveys and utilizing newer techniques can give a full picture of woodcock harvest dynamics in the United States. The integration of annual surveys into a population reconstruction have shown to be valuable by allowing the calculation of new information like harvest rates and annual survivals. This method, new to the wildlife field, has seen use for many years in fisheries management. The ideas of RPR and PBR allow for managers to look at harvest in a non-biased way to assess if current regulations are leading to observed declines. The results presented here indicate that the woodcock population declines are not being driven by hunting. Not only is hunting declining but the harvest rates have been declining and below the calculated reference points of sustainability. This study suggests that managers should review current survey methodology and implement stronger habitat policies.

Management Implications

The U.S. Shorebird Conservation Plan Partnership (Andres 2015) labeled woodcock as a species in need of management attention and the results of this study show that the woodcock population is being sustainably harvested. Most managers believe long-term declines are due to the loss of young forest habitat. (Drummond and Loveland 2010, Dessecker and McAuley 2001). The use of RPR and PBR can be extended to other wildlife populations to assess the levels of harvest for other hunted game species. Although this study gives a great start in evaluating this popular game bird there is need to validate these models and investigate how to make them more robust with more data. The model could be modified to assess allowable take as suggested in Runge et al. 2008. The use of statistical population reconstruction and RPR should be extended because these methods have allowed the synthesis of many data sources to inform managers on a much deeper level of population dynamics.

Chapter 4: Conclusions

American woodcock have declined an average 0.9% per year since 1968 as measured by the SGS (Sauer et al. 2008, Cooper and Rau 2014, Sauer and Bortner 1991, Kelley et al. 2009, Cooper and Kelley 2006). The woodcock's habitat consists of early successional forest interspersed with open areas suitable for roosting and breeding (Dessecker and McAuley 2001, Kelley et al. 2006). The breeding ecology of woodcock allowed for the survey of these well concealed birds with the SGS (Mendall and Aldous 1943). Although the SGS has been the main tool for managing woodcock population, it falls short of explaining all of the dynamics of the populations (Anderson 2001, Cooper and Kelley 2006, D.J. Case 2010). The purpose of this study was to utilize new techniques to investigate the status and management of American woodcock. The North American woodcock population was investigated using population reconstruction techniques to help quantify changes in population abundances and harvests.

The SGS is not the only survey conducted to monitor woodcock. The WCS and HIP surveys in the U.S. and the National Harvest survey in Canada monitor hunters and harvest (Padding et al 2006, Raftovich et al 2012, Gendron and Smith 2014). The WCS asks hunters to send in wings from every woodcock they harvest, these wings are aged and sexed based on plumage characteristics (Cooper and Kelley 2006, Martin 1964). The WCS has been used to estimate productivity in the US (Zimmerman et al. 2010) The HIP Survey is a survey which asks hunters to record their hunts and success to be used to estimate harvest, days afield and active hunters at the state level (Padding et al 2006, Cooper and Kelley 2006). The national harvest survey in Canada also estimates harvest in this method but is sampled for all migratory bird hunters so estimates for days afield for woodcock are not available (Gendron and Smith 2014). These surveys have reported long term declines in hunter participation and harvest levels within our study period, 1999 to 2013. Days afield has dropped from 726,300 days hunted to 442,800 and Harvest, combined for the US and Canada has dropped from 444,800 to 243,100 (Table 1). These numbers indicate a drop in participation but can also help to quantify factors that caused changes in population.

Statistical population reconstruction techniques were used to estimate woodcock abundances. These methods that have had a long history as statistical catch at age models in fisheries management (Fournier and Archibald 1982, Hilborn and Mangel 1994, Deriso et al. 1985). These methods were extended to wildlife populations where large data sets of age-at-harvest data was available and also where concealment made other surveys difficult (Broms et al. 2010, Gast et al. 2013, Gove et al. 2002, Skalski et al. 2005, 2007, 2012, 2011). Woodcock abundances were successfully estimated for 4 models from 1999 to 2013. These models incorporated harvest, days afield, age and sex ratios, index counts, and radio-telemetry data to estimate abundance, survival and harvest rates. The radio-telemetry data from Bruggink et al. (2013) helped inform the model of harvest rates (Table 2, Figure 3). There was not enough data to estimate natural survivals for all cohorts and it was assumed constant among the study period.

The 2HIA model was used for analysis and reporting on the population status. The model estimated 5,769,200 ($\widehat{SE} = 676{,}830$) in 2013, the most current year in the analysis. There was a decline in the abundance from 1999 to 2013 averaging 23,037 ($\widehat{SE} = 11{,}583$) a year (P=.068). The overall harvest rate was also declining during the study (P=.006). The annual natural survival was estimated at 0.528 ($\widehat{SE} = 0.008$) for the period. The average harvest probability for adult females was 0.018 and 0.101 for other cohorts. The results show a decrease in hunting effort and success which shows no effect on abundance indicating there is another cause for woodcock declines.

This model was used to investigate the sustainability of hunting of woodcock. The harvest rate decreased from 1999 to 2013. The effort of hunters decreased also. The calculation of PBR and RPR allowed for reference points of sustainability, currently both estimates indicate woodcock are being harvested below the levels that are sustainable. The current PBR was calculated at 415,072 woodcock a year as a sustainable level of harvest. The combined US and Canadian harvest was estimated at 276,628 in 2013. This supports the idea that habitat is the limiting factor for woodcock populations (Kelley et al 2008). The new application of RPR also supports the idea that hunting is not the major factor to woodcock declines. The current RPR was simulated at 79.51% meaning that hunting is only decreasing the lifetime egg production by 20%. The suggested reference point was suggested at an RPR of 60%. This also indicates that woodcock populations are not being over harvested. There has been a conversion of forests and farm land to development in the eastern US that could explain these changes (Drummond and Loveland 2010). The population reconstruction methods utilized in this study could be extended to any species that is harvested and where age class data has been collected. It leads us to suggest that woodcock managers should review current surveys for statistical soundness, increase annual banding and telemetry studies, and increase the awareness for the importance of early successional habitat. It is also of concern that participation in woodcock hunting is declining, since these people have been a great support base for conservation efforts. Making more opportunities for hunters could help raise awareness and support for habitat efforts.

Tables

Table 1. American woodcock (*Scolopax minor*) population reconstruction data sources from 1999 to 2013 from US Fish and Wildlife Service and Canadian Wildlife Service. The data sources were Wing Collection Survey (WCS), Harvest Information Program (HIP), National Harvest Survey (NHS), and the Singing Ground Survey (SGS). The radio-telemetry data was taken from Bruggink et al. 2013.

Data Source	Estimates Provided	Geographic Coverage	Years Used
WCS	Age and sex composition of harvest	All woodcock hunting states in US	1999-2013
HIP	Harvest and days afield	All woodcock hunting states in US	1999-2013
NHS	Harvest	All woodcock hunting states in Canada	1999-2013
SGS	Counts of breeding males	Northern breeding range	1999-2013
Radio-Telemetry	Harvest rates	Michigan, Wisconsin, and Minnesota	2001-2004

Table 2. American woodcock (*Scolopax minor*) population reconstruction input data from 1999 to 2013 from US Fish and Wildlife Service and Canadian Wildlife Service.

Year	Number of Wings	Harvest	Days Afield	Singing Males
1999	9,605	506,508	726,300	2.92
2000	9,655	442,169	648,500	2.96
2001	9,758	387,800	586,000	2.83
2002	9,049	314,696	591,300	2.73
2003	11,250	337,263	522,200	2.79
2004	10,402	329,808	501,500	2.89
2005	12,379	391,163	520,300	2.92
2006	14,312	347,784	420,600	2.79
2007	12,803	316,020	503,500	2.73
2008	12,186	305,879	538,800	2.56
2009	10,549	255,344	500,300	2.57
2010	14,027	393,238	539,100	2.70
2011	14,165	328,863	506,500	2.73
2012	14,739	299,798	414,700	2.76
2013	12,797	276,628	442,800	2.74

Table 3. American woodcock (*Scolopax minor*) population reconstruction input data from 1999 to 2013. Radio-telemetry data from Bruggink et al. 2013, a study to assess harvest mortality in Minnesota, Wisconsin, and Michigan. Number harvested indicate shot by a hunter in that year.

Year	**2001**	**2002**	**2003**	**2004**
Radio-Marked	68	336	292	339
Harvested	1	15	32	28
Harvest Probability	0.015	0.045	0.110	0.083

Table 4. American woodcock (Scolopax minor) population reconstruction fit statistics from 1999 to 2013. Model names indicate either a single harvest probability (1H) or 2 harvest probabilities (2H) were utilized. Also, if the SGS index was incorporated (IA) into the model or not (NI). AIC and log-likelihood should not be compared between models with different data inputs.

Model	Negative Log-Likelihood	K	AIC	Wing Chi-Square	Harvest Chi-Square
1HNI	-24983	21	-25025	0.233	34,533
2HNI	-24848	22	-24892	0.010	35,389
1HIA	-24989	22	-25033	0.237	36,393
2HIA	-24861	23	-24907	0.023	35,227

Table 5. American woodcock (Scolopax minor) population reconstruction log-likelihoods for each data component from 1999 to 2013. Model names indicate either a single harvest probability (1H) or 2 harvest probabilities (2H) were utilized. Also, if the SGS index was incorporated (IA) into the model or not (NI).

Negative Log-Likelihood	**1HNI**	**IHIA**	**2HNI**	**2HIA**
Telemetry	-273.64	-273.65	-273.66	-273.78
Harvest	-7.26	-7.56	-7.39	-7.35
Cohort	-24701	-24703	-24567	-24575
Index	NA	-3.53	NA	-5.07
Overall	-24982.6	-24988.6	-24848.1	-24861.2
Parameters	21	22	22	23

Table 6. American woodcock (Scolopax minor) population reconstruction abundance and harvest probability estimates 1999 to 2013. Model 2HIA (2 harvest probabilities and Singing Ground Survey incorporated).

Year	**1999**	**2000**	**2001**	**2002**	**2003**
$\widehat{N}_{Total}$	6,075,800	5,701,700	5,514,600	5,633,900	5,646,700
$\widehat{SE}$	677,460	647,980	634,220	646,900	654,020
$\widehat{HP}_{y,A,F}$	0.231	0.209	0.191	0.193	0.172
$\widehat{SE}$	0.025	0.023	0.021	0.022	0.020
$\widehat{HP}_{y,Others}$	0.131	0.118	0.107	0.108	0.096
$\widehat{SE}$	0.013	0.011	0.010	0.011	0.009

Year	**2004**	**2005**	**2006**	**2007**	**2008**
$\widehat{N}_{Total}$	5,710,500	5,628,400	5,472,400	5,206,000	5,398,000
$\widehat{SE}$	659,480	644,990	636,670	602,220	621,340
$\widehat{HP}_{y,A,F}$	0.166	0.195	0.163	0.166	0.177
$\widehat{SE}$	0.019	0.022	0.019	0.019	0.020
$\widehat{HP}_{y,Others}$	0.092	0.109	0.090	0.093	0.099
$\widehat{SE}$	0.009	0.011	0.009	0.009	0.010

Year	**2009**	**2010**	**2011**	**2012**	**2013**
$\widehat{N}_{Total}$	5,264,500	5,504,100	5,474,800	5,469,700	5,769,200
$\widehat{SE}$	605,580	625,810	639,150	639,690	676,830
$\widehat{HP}_{y,A,F}$	0.166	0.215	0.167	0.139	0.148
$\widehat{SE}$	0.019	0.024	0.019	0.016	0.017
$\widehat{HP}_{y,Others}$	0.092	0.121	0.093	0.077	0.082
$\widehat{SE}$	0.009	0.012	0.009	0.008	0.008

Table 7. American woodcock (Scolopax minor) population reconstruction estimated adult male abundances at each regulatory level from 1999 to 2013. These numbers were estimated using the linear relationship between observed Singing-Ground Survey counts and estimated male abundances from 1999 to 2013. These levels are the regulatory thresholds that cause change in hunting season length.

Regulatory Levels	Average Singing Males	Estimated Male Abundances
Liberal	3.25	1,553,752
Moderate	2.00	1,090,543
Restrictive	1.00	821,583

Table 8. American woodcock (Scolopax minor) parameters used in reproductive potential ratio simulations from 1999 to 2013. Reproductive potential ratio of 60% is shown with estimates of harvest probability and survival estimate used from 2013 estimate of the woodcock population reconstruction.

Age	Proportion Mature	Average Egg Production per Woodcock	Natural Survival	Harvest Mortality	Abundance (N)	Egg Production per Year
1	0	0	0.528	0.186	100.000	0.000
2	1	4	0.528	0.320	42.953	171.814
3	1	4	0.528	0.320	15.419	61.676
4	1	4	0.528	0.320	5.535	22.140
5	1	4	0.528	0.320	1.987	7.947
6	1	4	0.528	0.320	0.713	2.853
7	1	4	0.528	0.320	0.256	1.024
8	1	4	0.528	0.320	0.092	0.368
9	1	4	0.528	0.320	0.033	0.132
10	1	4	0.528	0.320	0.012	0.047
11	1	4	0.528	0.320	0.004	0.017
12	1	4	0.528	0.320	0.002	0.006
13	1	4	0.528	0.320	0.001	0.002
14	1	4	0.528	0.320	0.000	0.001
15	1	4	0.528	0.320	0.000	0.000

Figures

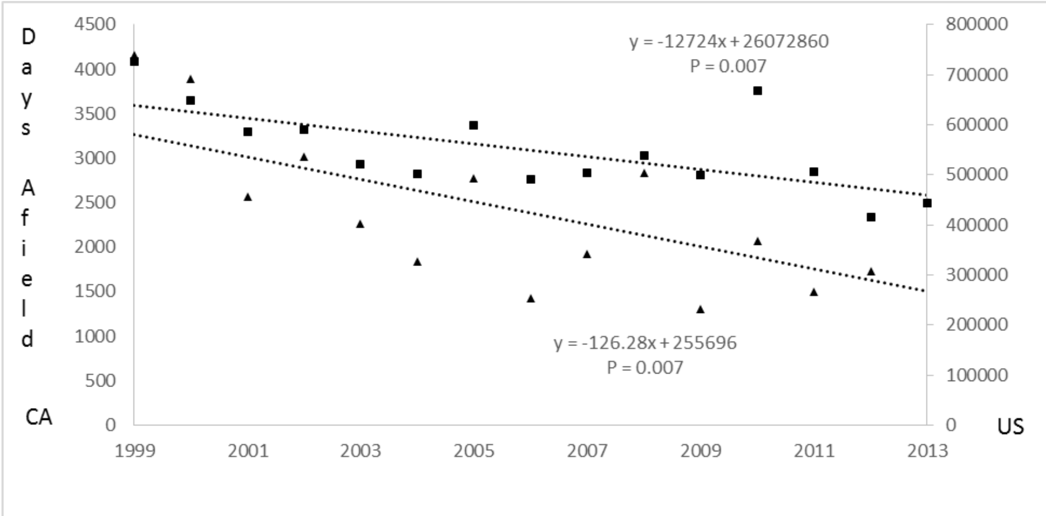

Figure 1. (1999 to 2013) Comparison of US Days afield estimates with Nova Scotia for same period. Average of 86% of harvest in Nova Scotia was woodcock during this period. Suggests US and Canadas effort trends were similar for study period. Changes in Nova Scotia's days afield estimate have positive correlation with US days afield estimates, R^2= 0.53.

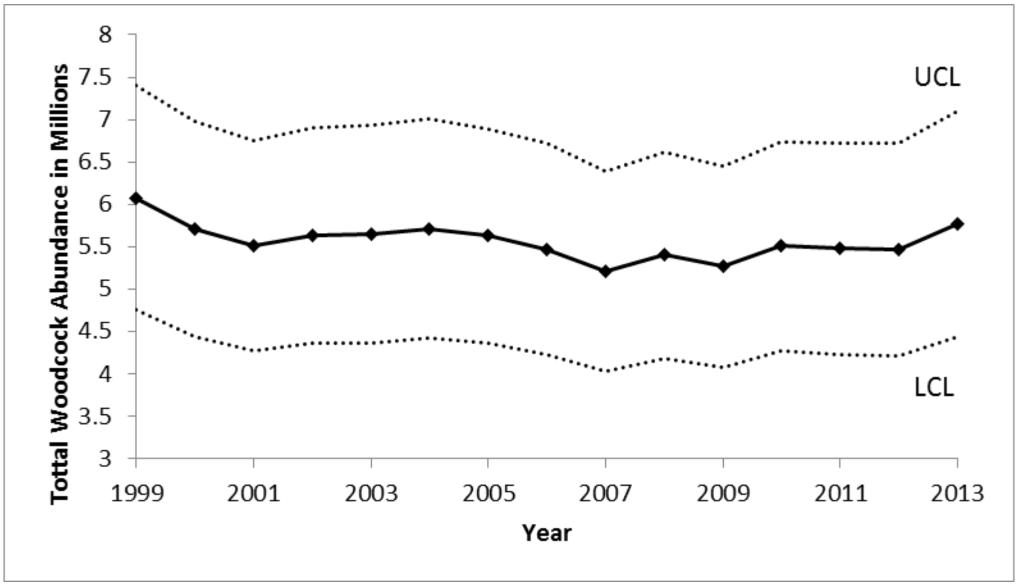

Figure 2. Total abundance of American woodcock from 1999 to 2013 in millions derived from a population reconstruction model with 95% confidence intervals (UCL and LCL).

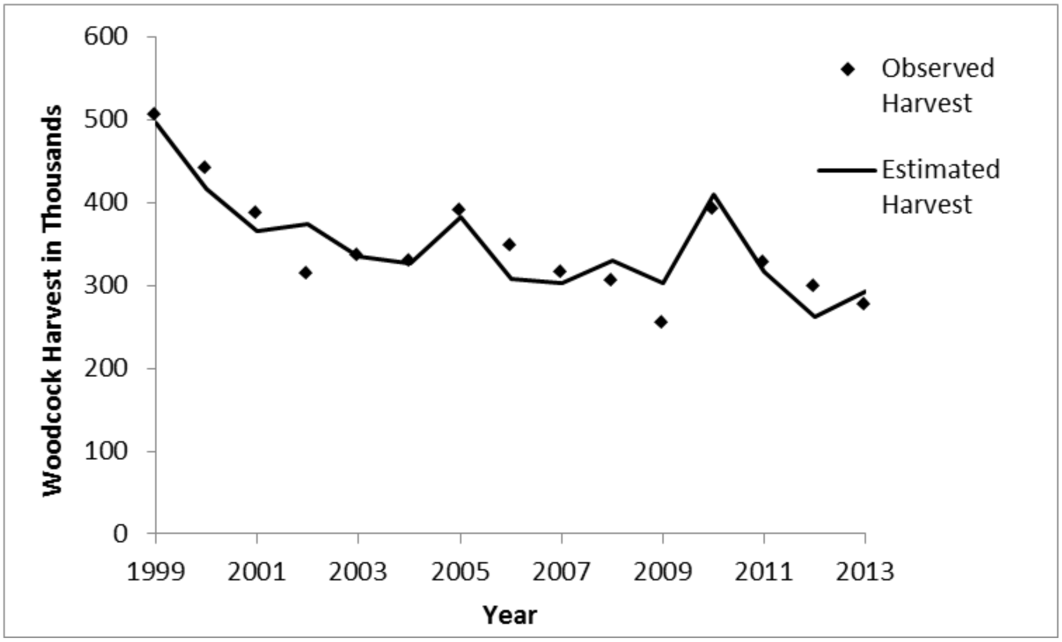

Figure 3. Population reconstruction derived and Harvest Information Program estimates (♦) of harvested American woodcock (in thousands) from 1999 to 2013.

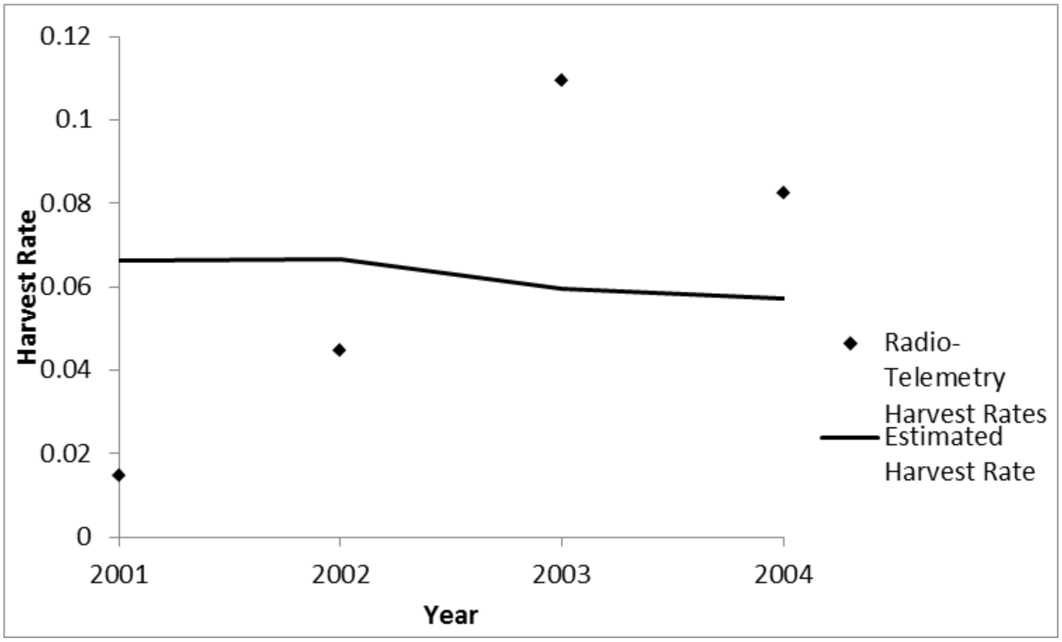

Figure 4. Radio-telemetry (Bruggink et al. 2013) (♦) and population reconstruction derived harvest rates of American woodcock from 2001 to 2004. Highlights importance of need for increased telemetry data.

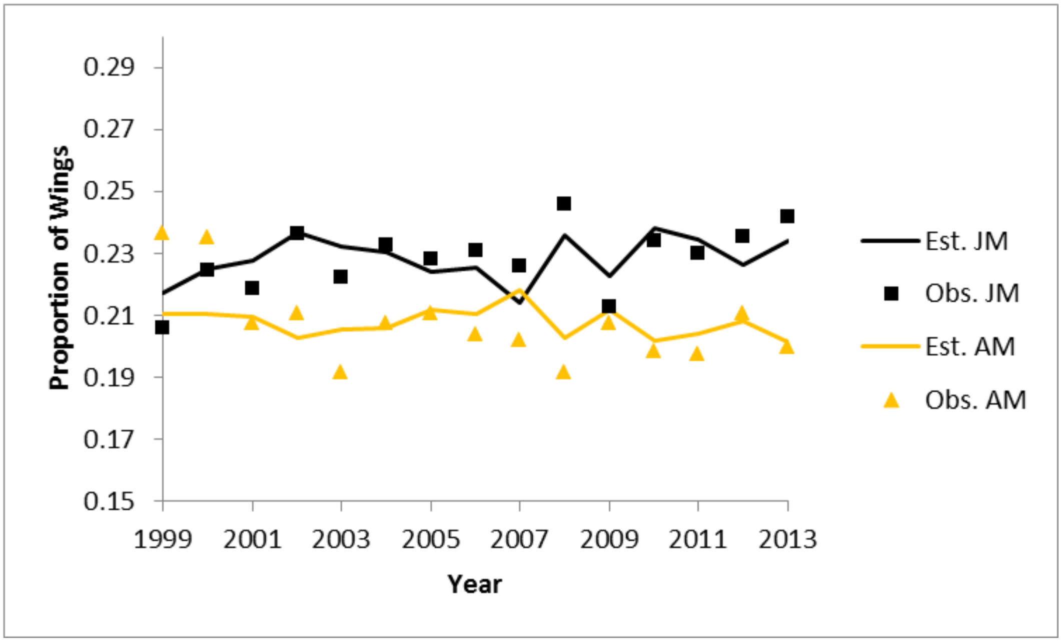

Figure 5. Population reconstruction derived and Wing Collection Survey estimates of proportion of juvenile and adult male (JM and AM) harvested American woodcock from 1999 to 2013.

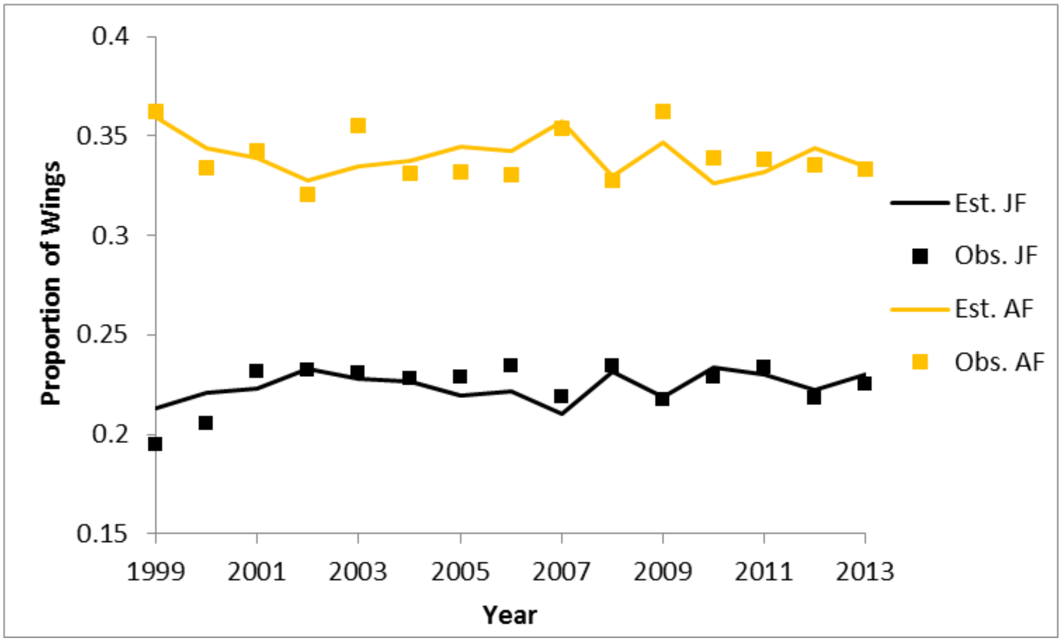

Figure 6. Proportion of juvenile female (JF) and adult female (AF) comparing models with observed proportions from Wing Collection Survey from 1999 to 2013. Model used incorporated adult female specific harvest rate and Signing Ground Survey data.

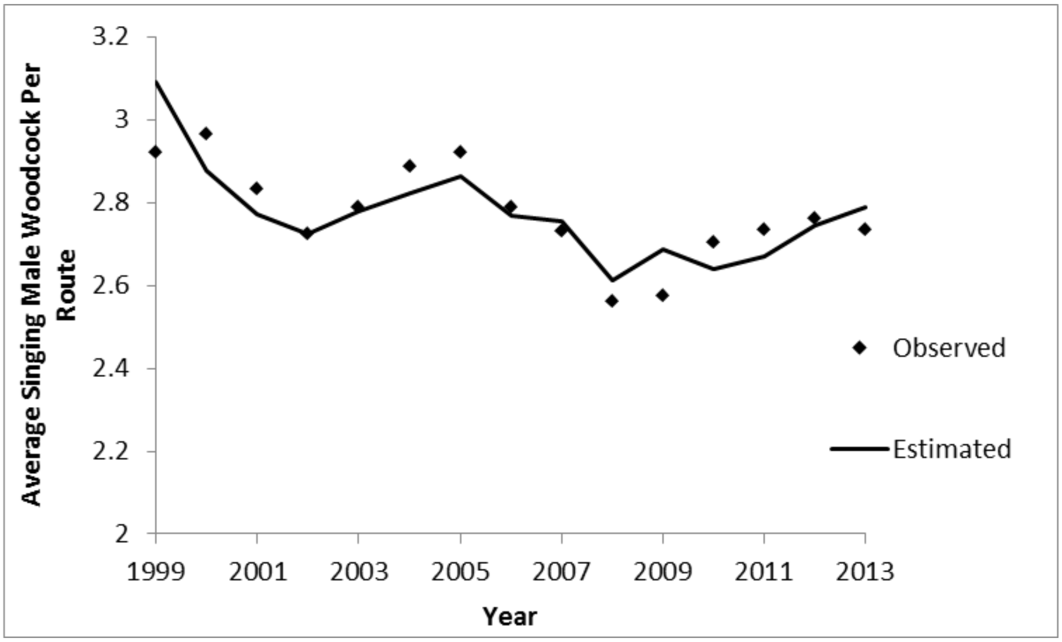

Figure 7. Population reconstruction derived and Singing Ground Survey estimates (♦) of singing American woodcock from 1999 to 2013.

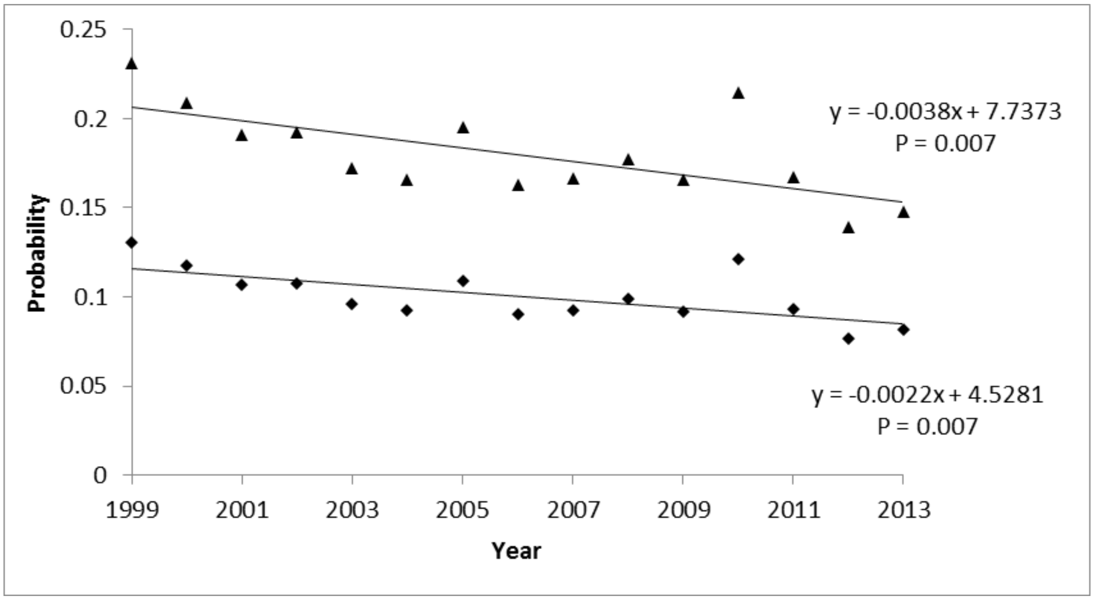

Figure 8. Graph of adult female harvest probability (▲) and harvest probability for all other cohorts (♦) from top to bottom respectively. Estimated for American Woodcock from 1999 to 2013 from statistical population reconstruction that included Singing Ground Survey ($R^2 = 0.44, on\ both$).

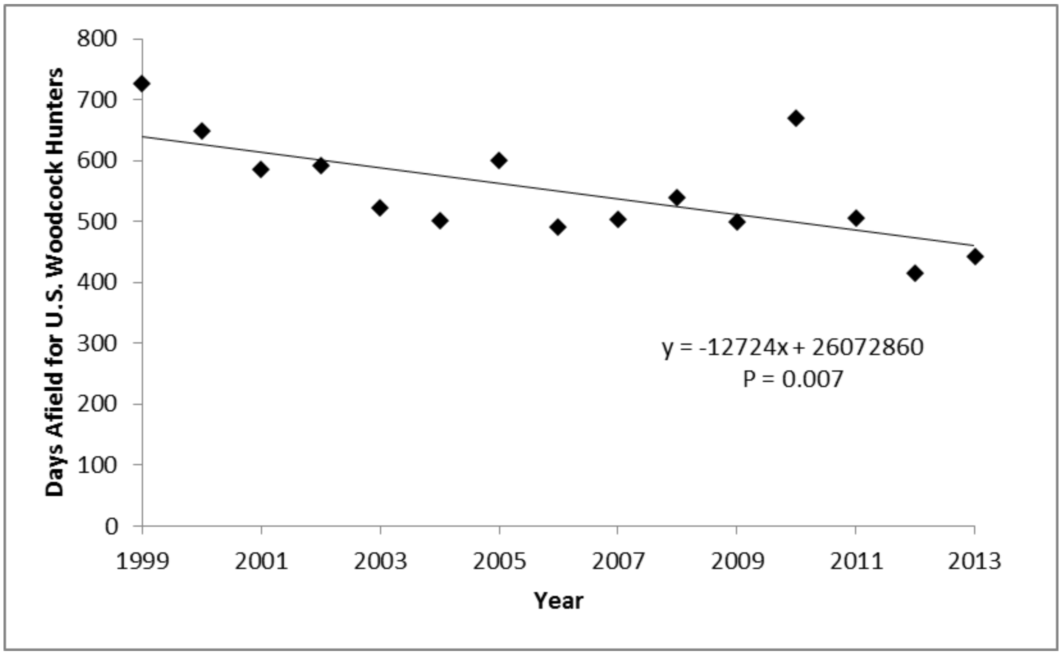

Figure 9. Days afield estimate as reported by Harvest Information Program from 1999 to 2013. Linear correlation superimposed. ($R^2 = 0.44$)

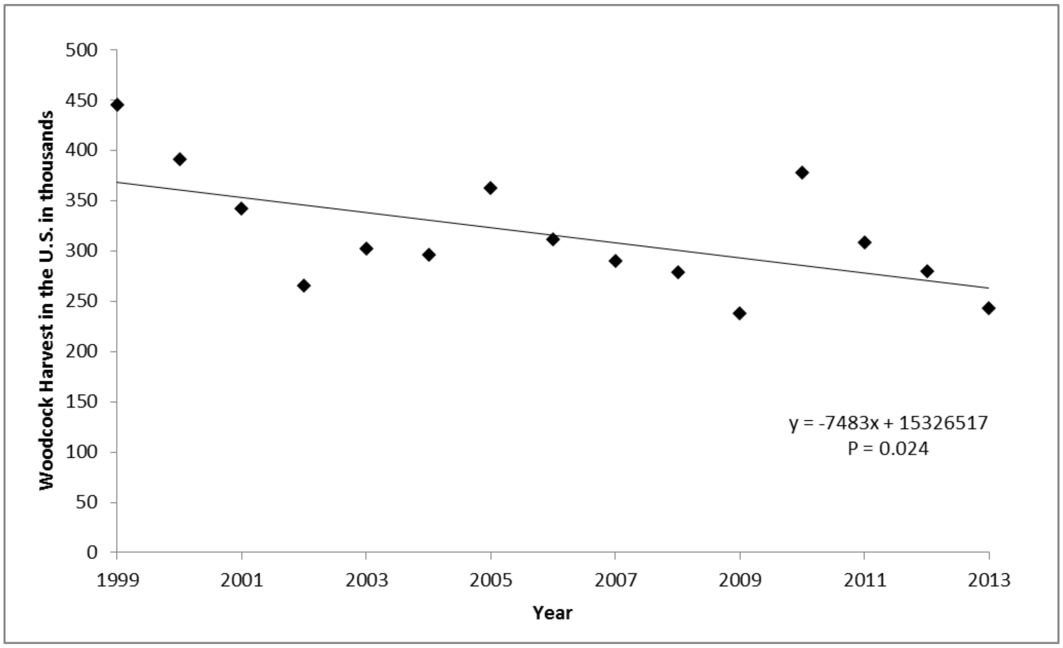

Figure 10. Annual harvest estimate for U.S. as reported by Harvest Information Program from 1999 to 2013. Linear correlation superimposed. ($R^2 = 0.33$)

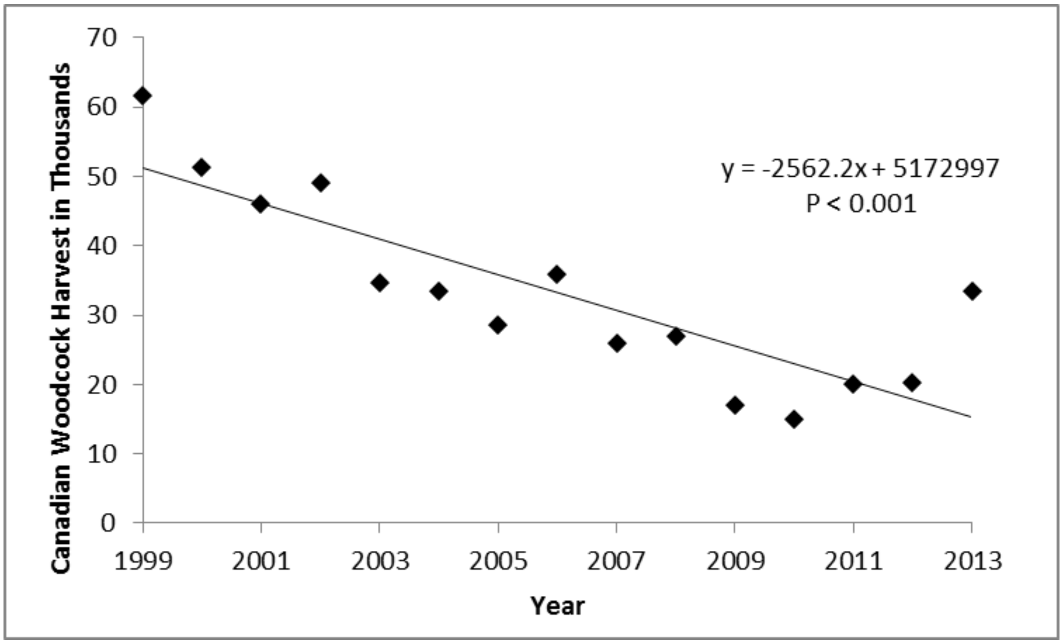

Figure 11. Annual harvest estimate for Canada as reported by the Canadian National Harvest Survey from 1999 to 2013. Linear correlation superimposed. ($R^2 = 0.70$)

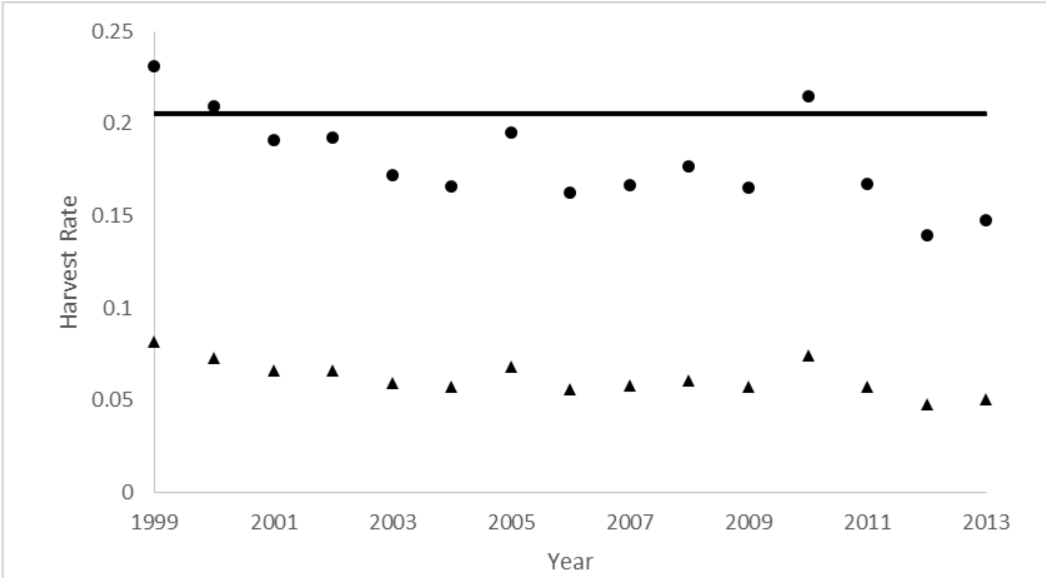

Figure 12. Graph of Reproductive Potential Ratio (RPR) 60% (Solid Black Line) plotted against adult female harvest probability (•) and yearly total harvest rate (▲). The population reconstruction estimated from 1999 to 2013. The harvest probability is the portion of woodcock harvested after model assumes natural mortality. Total harvest rate is annual harvest over annual abundance.

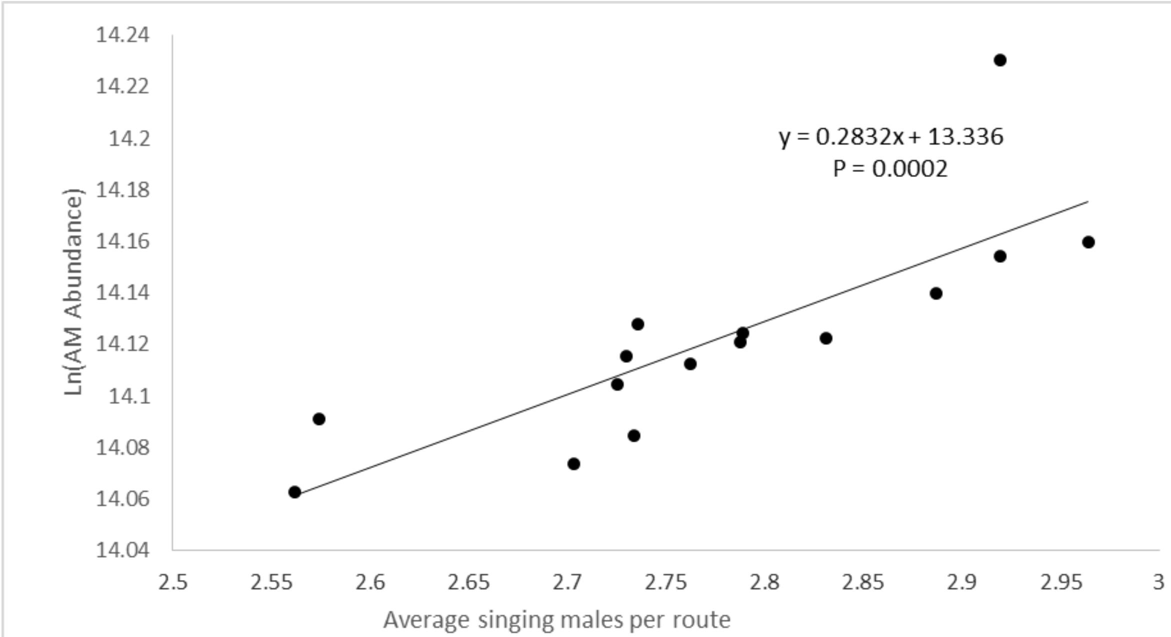

Figure 13. Linear correlation of SGS males per route and natural log of adult male abundance as estimated by population reconstruction for 1999 to 2013. ($R^2 = 0.66$)

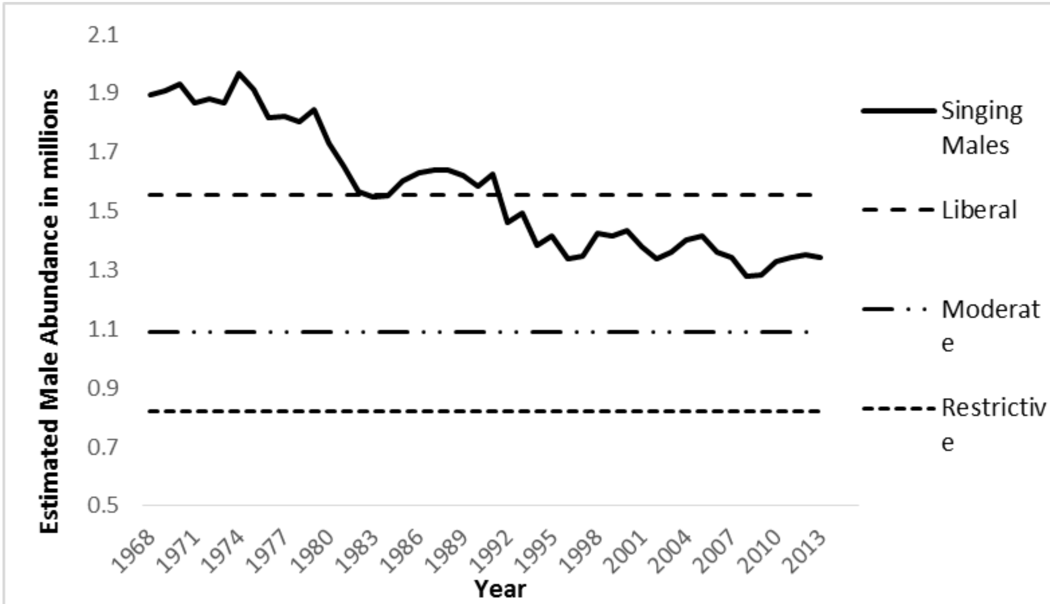

Figure 14. Extrapolation of linear correlation using counts from SGS to estimate historic levels of adult male abundance from 1968 to 2013. The colored lines are the regulatory thresholds for management action as set by the 2010 woodcock harvest strategy.

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