5-2009

Population Reconstruction Model to Analyze Harvest and Banding Data For Mourning Doves in South Carolina

Christopher Chumbley
Clemson University, cchumbl@clemson.edu

POPULATION RECONSTRUCTION MODEL TO ANALYZE HARVEST AND BANDING DATA FOR MOURNING DOVES IN SOUTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

---

by
Christopher Alan Chumbley
May 2009

Accepted by:
Dr. Greg Yarrow, Committee Chair
Dr. Patrick Jodice
Dr. William C. Bridges, Jr.
Billy Dukes, Small Game Project Supervisor, SCDNR

ABSTRACT

Mourning dove (*Zenaida macroura*) call count indices for South Carolina indicate a negative trend over the past 42 years (1.2% decline per year, $p < 0.05$). Total harvest estimates in the state increased from 2003-2007. Banding data from doves banded in South Carolina and data from annual examinations of harvested mourning dove wings during 2003–2007 were collected and analyzed. Data sets used contained 6,600 banded doves and 21,240 harvested dove wings. Survival estimates from band recovery analyses for adult and juvenile doves were 0.44 (± 0.04 SE) and 0.35 (± 0.06 SE), respectively. Survival rates were constant from year to year while recovery rates differed annually for adults and juveniles. The average natural mortality estimates for adults and juveniles in the presence of hunting were 0.45 ± 0.122 and 0.47 ± 0.189, respectively, during the study period. The average harvest and kill rates for adults and juveniles were also estimated. Age-at-harvest ratios adapted from annual wing examinations during the harvest were used with recovery rates to derive estimates of annual productivity in the population. Linear regression analysis of productivity estimates found a significant decline in productivity during 2003-2007 (-0.21, $p < 0.10$). The average productivity estimate was 1.43 (± 0.33 SE) juveniles per adult and the estimated productivity required to maintain a stable population was 1.60 (± 0.30 SE). The effects of constant survival rates, varying hunting mortality estimates and declining productivity estimates were discussed in relation to breeding populations in rural areas of South Carolina.

DEDICATION

This thesis is dedicated to my parents, Jim and Deedra Chumbley. Mom's endless optimism and dad's adventurous spirit in searching for the truth have provided the basis of my motivation to pursue success through knowledge.

ACKNOWLEDGMENTS

Dr. Greg Yarrow and Billy Dukes have my utmost gratitude for granting me the opportunity to earn my graduate degree from Clemson University. Their support and guidance have been paramount in allowing me to complete my studies. Dr. William C. Bridges, Jr. also deserves recognition for the countless hours spent with me going over statistics. I would also like to thank the South Carolina Department of Natural Resources personnel whom made this thesis possible through countless man hours of banding and checking doves during the five years of this study. There are many people I would like to thank for their support, but I would especially like to thank the following people: Arnold "Papa" Chumbley, Mr. and Mrs. Gil and Marie Dudsic, Lisa Chumbley, Todd Chumbley, and Emily Chumbley. Above all I thank my wife, Céline, whose love, devotion, support and sacrifice throughout my academic career have been never ending. She is my best friend, my biggest fan; truly one of a kind. Thank you Céline, I love you.

TABLE OF CONTENTS

LIST OF TABLES

List of Tables (Continued)

LIST OF FIGURES

INTRODUCTION

Historical Perspective

The mourning dove (*Zenaida macroura*) is one of the most widely distributed and abundant birds in North America (Sauer et al. 2007). This member of the Columbidae family has persisted in North America for approximately 1.8 million years (Reeves and McCabe 1993). Remains of fossilized mourning doves have been unearthed at locations in the United States from California to Florida, and in Mexico and the Caribbean. Human fossils, dated from before 7000 B.C., suggest that the mourning dove was consumed by the native peoples of North America (Williams-Dean 1978; Reeves and McCabe 1993). Scientific descriptions and illustrations of this bird date back to the exploration and settlement of North America (Reeves and McCabe 1993).

The mourning dove is similar in physical characteristics and, as recent as the early 1900's, was often confused with the now extinct passenger pigeon (*Ectopistes migratorius)*. The abundance of passenger pigeons at the time that North America was being settled has been estimated to be as high as 5 billion birds (Reeves and McCabe 1993). The last known passenger pigeon died while in captivity in the Cincinnati Zoological Garden in 1914 (Reeves and McCabe 1993). The extinction of the passenger pigeon was due in part to its perpetual gregariousness and concentrated distribution which made it more susceptible to disease, parasitism, habitat destruction, natural disasters and human exploitation (Reeves and McCabe 1993). The primary causes of the passenger pigeon's demise are believed to be habitat destruction and unregulated, unsustainable harvesting (Reeves and McCabe 1993). The less gregarious mourning dove endured while its fellow Columbid did not primarily because it is a highly adaptable species, a habitat generalist, and was not a highly preferred game bird in the early game markets of the late 19th and early 20th centuries (Reeves and McCabe 1993).

Throughout the 18th and 19th centuries the mourning dove was not intensively sought after for commercial harvest. The mourning dove was not considered a game species in northern states where its population was sparse. In other parts of the country, especially in the Southeast, hunting of mourning doves was a popular recreational activity (Reeves 1993). The inconspicuous size and lackluster plumage made the mourning dove less desirable in game markets than the larger, more colorful birds like the passenger pigeon and various waterfowl species. The popularity of the mourning dove as a game species is a fairly recent development, despite being considered a game bird since 1900 in some states. Many wildlife and game publications as late as the 1960's do not even include the mourning dove as a species of interest (Reeves and McCabe 1993).

The task of regulating the harvest of mourning doves and other migratory species in the United States was designated to the federal government with the passage of the Migratory Bird Treaty Act of 1918. The U.S. Fish and Wildlife Service (USFWS) is the bureau within the Department of the Interior that is charged with the management and enforcement of federal wildlife laws, including those governing mourning doves. Annually the USFWS publishes hunting regulations that stipulate when, where, and by which methods dove hunting may occur and how many birds may be taken daily. The hunting regulatory agency within each state has the option of adopting these regulations and may modify them as long as the state guidelines are within the guidelines of the USFWS regulations.

As a result of analyses of mourning dove banding studies conducted from 1954 to 1957, the USFWS delineated three distinct zones within the continental United States (Kiel 1959; Tomlinson 1993). Each zone contains mourning dove populations that are considered to be independent of the mourning dove populations in the other zones (Kiel 1959; Tomlinson 1993). These zones are the Eastern (EMU), Central (CMU), and Western (WMU) management units (Figure 1). Management decisions and harvest regulations concerning mourning dove populations have been constructed separately for each management unit (Reeves 1993).

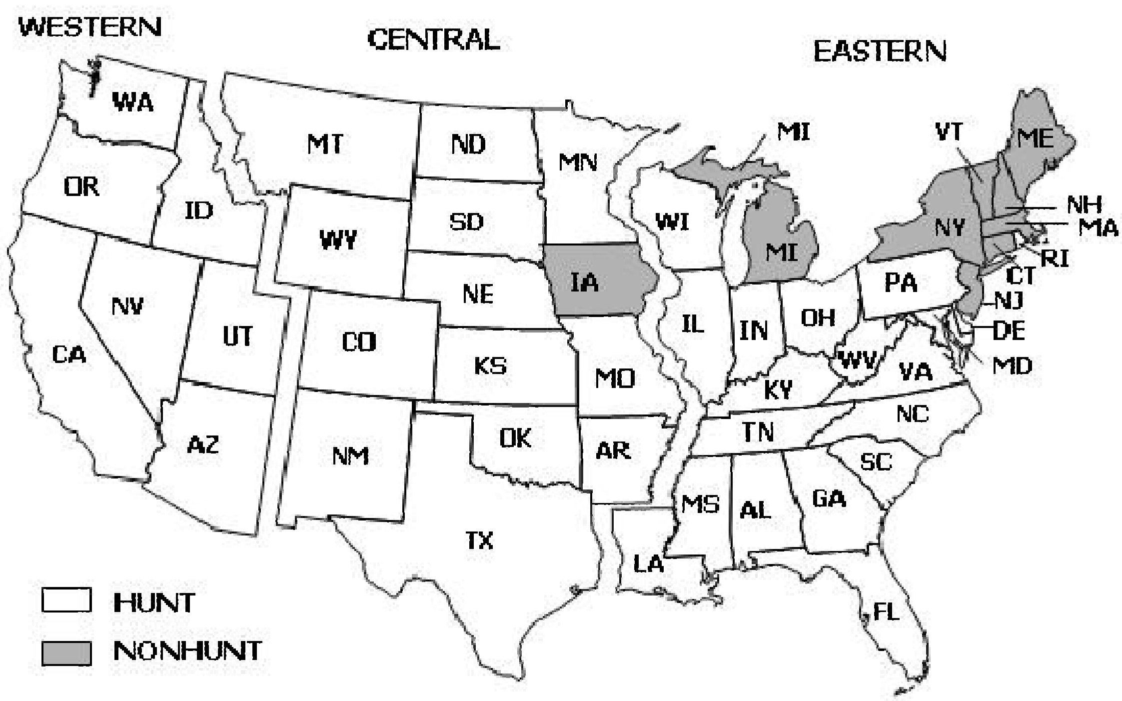

Figure 1. Mourning dove management units in the United States for 2006 with hunting and non-hunting states (*from* Dolton et al. 2007).

When managing wildlife populations, the objectives may be to reduce population size, increase population size, or maintain population size. Dinsmore and Johnson (2005) suggest that the goal of managers of wild game is to maintain populations of game species at levels that afford surpluses for harvest. In order to accomplish this objective, management officials require estimates of current population size as well as historical population trends to facilitate the formulation of effective harvest regulations. In 1966 the USFWS instituted the Mourning Dove Call Count Survey (CCS) in an effort to produce an annual index to population size of mourning doves throughout the United States. The survey, conducted annually within the 48 contiguous states, is comprised of approximately 1000 driving routes stratified by physiographic region (Fenneman 1931, Dolton 1993). Routes are 32 kilometers (20 miles) in length and usually located on lightly traveled secondary roads. Twenty listening stations are located on each route at 1.6 km (1.0 mile) intervals where observers stop for 3 minutes and record the number of mourning doves seen, the number heard calling and the intensity of interference which impairs their ability to hear doves (Dolton 1993). Counts are conducted from mid-May to early June and begin one-half hour before sunrise and continue for about two hours (Dolton et al. 2008). The surveys are not performed when wind speeds surpass 19.3 km (12 miles) per hour or when it is raining. Calculation of population trends and annual indices of population size during the breeding season from doves heard on each route have been described by Dolton et al. (2008). During the 2006 – 2007 hunting season, harvest of mourning doves was permitted in 39 of the 48 contiguous United States (Figure 1), including South Carolina (Dolton et al. 2008). In that same season, preliminary estimates of harvest data indicated approximately 1 million hunters spent a cumulative total of 3.4 million person days hunting and harvested approximately 19.2 million mourning doves nationwide (Dolton et al. 2008). During the 2006 - 2007 mourning dove hunting season in South Carolina, an estimated 36,200 (± 13%) hunters spent 118,500 (± 15%) days hunting and harvested approximately 696,200 (± 13%) mourning doves statewide (Dolton et al. 2008). Current trends suggest that the annual mourning dove harvest nationwide is declining. Despite these trends, the mourning dove continues to be a valuable game bird, as indicated by the fact that nationwide more doves are harvested annually than all other migratory game birds combined (Dolton et al. 2008).

From 2003 – 2005 the South Carolina Department of Natural Resources (SCDNR) participated in a national mourning dove banding program (Otis et al. 2008b) with the intent of generating data that would deliver estimates of descriptive population parameters. These parameters estimate survival and recovery rates of mourning doves in South Carolina from which other parameters can be derived for analyses of the population. Population analysis, according to Eberhardt (1971:457), is defined as the "process of attempting to determine the structure of a population and the forces controlling past and future composition of that population." Population reconstruction uses demographic data to reproduce the historical trends in animal abundance (Eberhardt 1971).

Mourning Dove Life History and Biology

The breeding range of the mourning dove is widespread from southern Canada, throughout the continental United States into Baja California and Mexico south to Puebla, possibly into northern portions of Middle America, and includes most of the Caribbean islands (Aldrich 1993, Otis et al. 2008a). Mourning doves winter throughout the majority of their breeding range with the exception of central Canada and the north central United States (Otis et al. 2008a).

The precise timing of the spring and fall migrations of mourning doves to and from their wintering sites is difficult to determine because of the presence of overwintering populations in many areas. However, temporal changes in sequential roadside counts, call count surveys, and band recovery patterns have led to the conclusion that the spring migration of wintering birds to more northern nesting areas is believed to begin in March, peak in April, and end in May (Otis et al. 2008a, Tomlinson 1993). The fall migration usually initiates before September, peaks in October, and ends in November (Tomlinson 1993, Otis et al. 2008a). Not all mourning dove populations are migratory. Recoveries of doves banded in North and South Carolina provide evidence to suggest that these populations are relatively sedentary and do not migrate to other areas (Tomlinson 1993). Tomlinson (1993) used data from direct recoveries of mourning doves banded in the Carolinas during 1966 – 1971 to estimate that 96% of the birds banded in the Carolinas were recovered in the Carolinas. Furthermore, results of a national banding study conducted from 2003-2005 show that 83% of the mourning dove bands recovered in South Carolina during that time period were originally banded in South Carolina (Otis et al. 2008b). This suggests that the mourning dove population in South Carolina is mostly a resident population. The significance to wildlife managers is the suggestion that annual production of mourning doves recruited into the statewide population will primarily come from within South Carolina.

The nesting season for mourning doves begins in February and lasts until October, peaking during spring-early summer (Otis et al. 2008a). Two mourning dove nesting studies conducted in North Carolina reported peak nesting activity occurred in May (Taylor 1941, Quay 1951). Mourning doves are monogamous. The bond formed by a mated pair will persist throughout the nesting season and possibly throughout the year and subsequent nesting seasons (Sayre and Silvy 1993). Mourning doves are determinant layers with a typical clutch size limited to two eggs per nesting cycle. Clutch sizes of 3 and 4 have been reported (Weeks 1980); however, in a study conducted in central Iowa, Westmoreland and Best (1987) suggest that clutch size is typically limited to two eggs because of limited parental ability to feed three offspring and an increased risk of predation. Both the male and female participate in incubation of the eggs and crop milk production for the feeding of the nestlings. The incubation period is usually 14 to 15 days, followed by 11 to 15 days of the nestling stage (posthatching) (Mirarchi 1993a; Sayre and Silvy 1993). During the nestling stage the young mourning doves, called squabs, undergo rapid development as a result of receiving nutrient rich crop milk from both parents. Crop milk consists of epidermal cells sloughed off of the crop and is rich in lipids, proteins and growth promoting factors (Blockstein 1989). After the nestling stage, the squabs fledge and leave the nest. On average, mated pairs require a 32 day interval between the initiation of the first successful clutch and the following clutch (Mirarchi 1993a). Adult females may nest five or six times in a single nesting season, while literature sources suggest an estimate of 3.6 young are fledged annually per mated pair nationwide (Mirarchi 1993a). This information is of interest to mourning dove harvest managers as annual production is a key element in the estimation of population abundance and trends.

Fledglings that leave the nest after each nesting cycle have a full complement of feathers but are distinguishable from adults by the presence of light-tipped (buff to white) coverts (Swank 1955). Juvenile mourning doves (i.e., hatch year (HY) stage), begin to molt soon after leaving the nest and will establish a full adult, or after hatching year (AHY), plumage at approximately 160 days posthatching (Mirarchi 1993a). The method of examining plumage in order to age a mourning dove becomes unreliable when the wing molt proceeds to primary eight, typically in late summer to early autumn, because at this stage the molt of the light-tipped primary coverts is complete (Mirarchi 1993b). During this phase of the molt the HY doves may be indistinguishable from AHY. Age determination between HY and AHY can be accomplished after the molt of primary eight by examining primaries nine and ten. These two primaries will be worn along the fringes of AHY doves from use since the previous molt; whereas, primaries nine and ten of HY doves will not. However, this technique is not as useful in environments where conditions accelerate normal wear of the feather fringes, such as with the harsh vegetation and soil conditions of the Southwest U.S. (Mirarchi 1993b). Additionally, when investigators lack the proper knowledge or experience in using the fringe wear method of aging, the method may prove less reliable.

Adult mourning doves have a higher annual survival rate than juveniles although overall annual survival rate for the species is relatively low. Juvenile life spans in the United States average 1.0 year and adults' average about 1.5 years (Baskett and Sayre 1993). Despite being the most sought after and harvested game bird in the United States, there is evidence that indicates that the majority of mourning dove mortality is due to factors other than hunter harvest (Sadler 1993). Nonhunting factors affecting mortality of mourning doves include predation (other than human), unfavorable weather conditions, disease, accidents, and environmental contaminants.

In the Eastern Management Unit, the characteristics and management of mourning dove populations has been examined at great length (Martin and Sauer 1993). A population dynamics study was conducted in South Carolina from 1992 to 1996 (McGowan and Otis 1998). Another study conducted in Illinois in 1993 describes the effects of hunting and extension of hunting hours on mourning dove foraging and physiology (Roy and Woolf 2001).

Current Status and Research Objectives

Analysis of the South Carolina call-count index (CCI) during the 42 year period from 1966-2007 indicates a significant negative trend (-1.2% per year) in the number of mourning doves heard along call count routes ($p<0.05$; Dolton et al. 2007). During the ten year period from 1998-2007 a negative trend (-3.1% per year) was also reported ($p<0.10$; Dolton et al. 2007). Dolton et al. (2007) do not consider the 10 year trend significant because they defined statistical significance for their report as $p<0.05$. In recent years, CCI analyses for South Carolina have returned similar results that show a significant decline in the number of mourning doves heard along call count routes since 1966; but, insignificant trend results for the previous ten year periods (Dolton and Rau 2003-2006; Dolton et al. 2007). The significant decline in the South Carolina CCI since 1966 has raised concerns within the SCDNR about the mourning dove population in the state.

Data published by the USFWS in recent years indicate an increase in the estimated number of harvested mourning doves in South Carolina from 526,000 (±15% [95%CI]) in the 2003-2004 season to a preliminary estimate of 865,900 (±18%) in the 2007-2008 season (Dolton and Rau 2004, Dolton et al. 2008). Furthermore, evidence presented by McGowan and Otis (1998) indicates that, at least on intensively managed shooting fields, hunting mortality rates may be significantly higher than has been previously published in the literature. The relationship of the increased harvest numbers and higher hunting mortality rates to the decline in South Carolina's CCI is unknown.

The South Carolina Department of Natural Resources, Wildlife Section, suggested a study to analyze dove banding and harvest data (B. Dukes, Small Game Project Supervisor, SCDNR, per. comm.). Based upon the management needs of the SCDNR, the objectives of this study were to: (1) develop a population reconstruction model of annual mourning dove populations in South Carolina, incorporating survival and recovery rates from 2003-2007, data from the statewide banding study, and age ratio data collected in South Carolina during that period; (2) identify priority information needs to improve the precision and accuracy of the annual mourning dove population reconstruction models; and (3) calculate productivity required to maintain a stable mourning dove population based on estimated survival rates.

METHODS AND MATERIALS

Trapping and Banding

The trapping and banding of mourning doves, conducted by the South Carolina Department of Natural Resources (SCDNR), began on July 1 and concluded on August 20 during 2003-2007. During 2003-2005 South Carolina participated in a national mourning dove banding study (Otis et al. 2008b). In Otis et al. (2008b) South Carolina was placed in the South Atlantic subregion of the Eastern Management Unit (EMU) with North Carolina and Virginia. Banding quotas for this study were established in an effort to accomplish the objective of a standard error of 5% for the reporting rate in each subregion (Otis et al. 2008b). The quotas for the 2003 through 2005 banding periods in South Carolina were 300 hatching year (HY) and 300 after-hatching year (AHY) mourning doves (Billy Dukes, pers. comm.). Following the completion of the national banding study in 2005, SCDNR continued to band mourning doves in 2006 and 2007. Mourning dove banding quotas were not established by SCDNR for 2006 and 2007, rather the effort was made to band as many mourning doves as possible in order to improve the precision of statewide harvest rate estimates (Billy Dukes, pers. comm.). Modified Kniffin funnel traps (Reeves et al. 1968) were used by the SCDNR to trap mourning doves on Wildlife Management Area (WMA) lands and on private lands. Trap sites were largely selected based on convenience and availability of staff while still trying to band a geographically representative sample (Billy Dukes, pers. comm.). Figures 2-6 illustrate the approximate locations of banding sites used during 2003-2007. Table A-I in

Appendix A lists descriptions and the approximate latitude and longitude coordinates (degrees and minutes) obtained from SCDNR for each of the banding sites used during the 2003-2007 banding periods. Each dove was fitted with a U.S. Fish and Wildlife Service (USFWS) size 3A butt-end leg band. All doves captured were aged by examining plumage characteristics, given a molt score (Mirarchi 1993a), banded and released. Banding data from 2003-2007 was obtained from the SCDNR and used in this study. Doves which were banded but were missing data essential to at least one of the population analyses were removed from the data set (Appendix B).

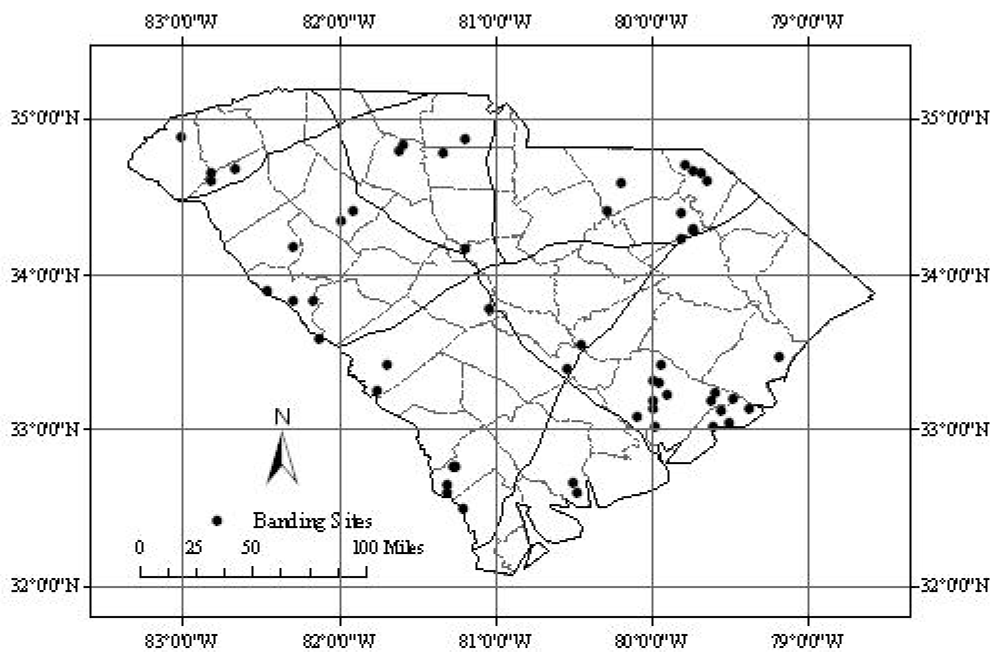

Figure 2. Locations of banding sites during the 2003 banding season in South Carolina.

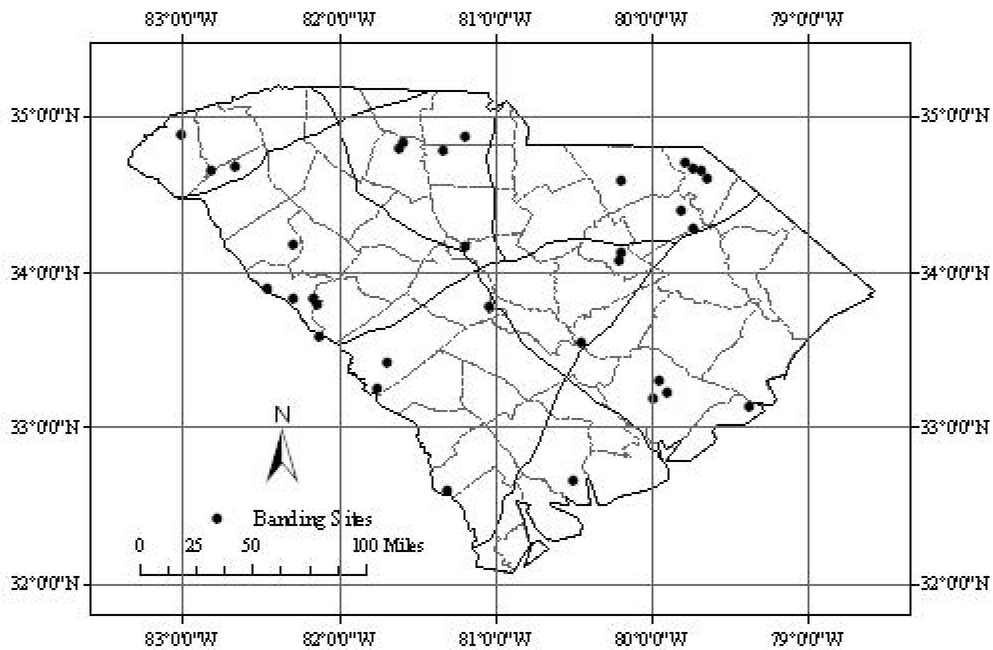

Figure 3. Locations of banding sites during the 2004 banding season in South Carolina.

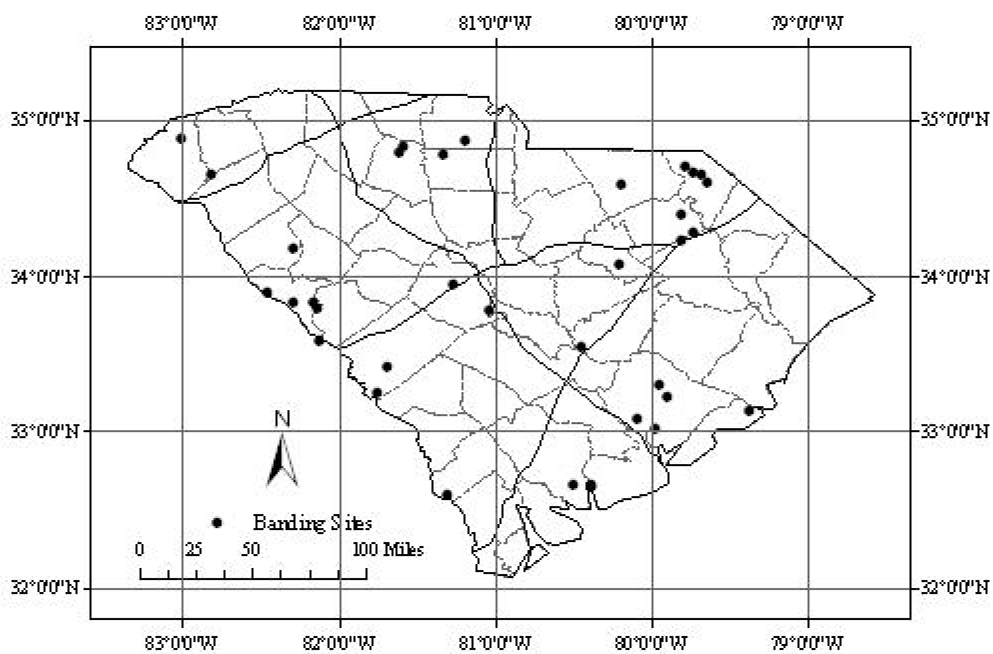

Figure 4. Locations of banding sites during the 2005 banding season in South Carolina.

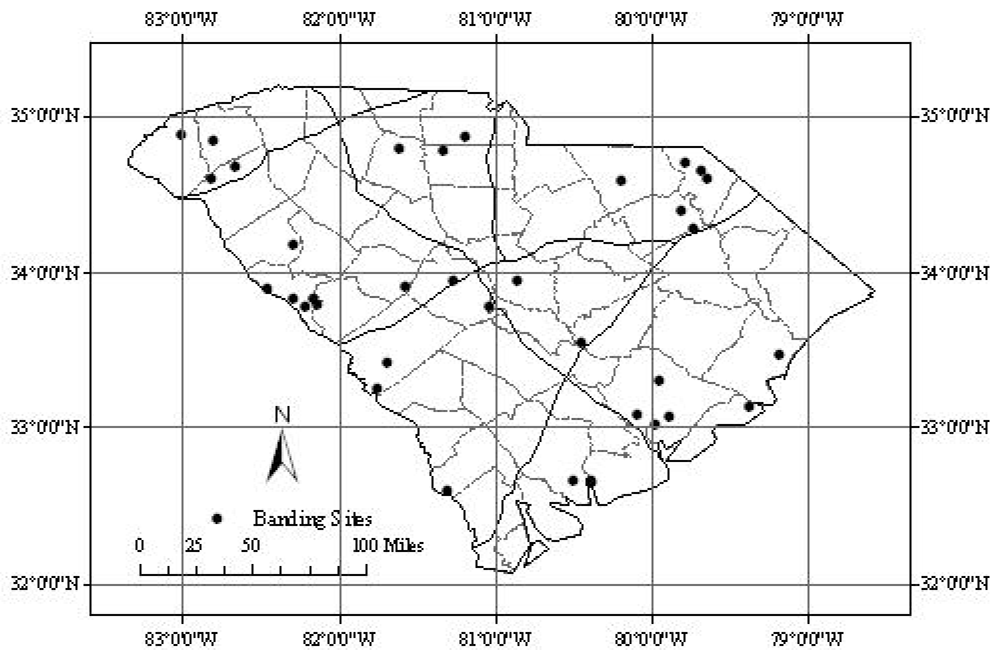

Figure 5. Locations of banding sites during the 2006 banding season in South Carolina.

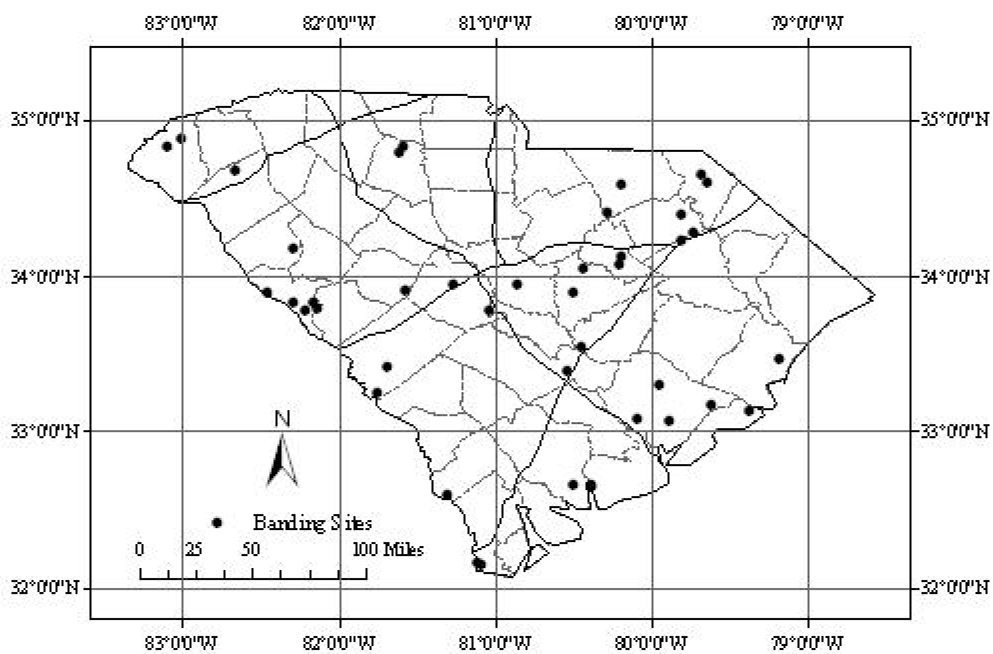

Figure 6. Locations of banding sites during the 2007 banding season in South Carolina.

Harvest Information

During each year of the study, harvested dove wings from public and private dove fields were aged and given a molt score by biologists and technicians from the SCDNR. Sites for mourning dove wing examinations were selected annually based upon the availability of staff at each location and wings were collected, at least once during each season, from approximately 60% of the public fields in South Carolina (Billy Dukes, pers. comm.). Records of harvested mourning dove wings which were missing data essential to at least one of the population analyses (e.g., unknown molt score) were removed from the data set (see Appendix B). In 2003 and 2004, harvest data were collected at least once during each week of September. However, in the later part of the month the frequency of unknown age harvested doves, in molts 8-10, increased from earlier in the month. An increase in unknown age harvested doves decreases the precision of the age-at-harvest ratio calculation. For this reason, the SCDNR decided to limit harvested dove wing examinations to the first week of the September hunting season in the subsequent years in order to minimize the number of unknown age doves in the sample (Billy Dukes, pers. comm.). This study uses harvest data collected between September 1 and September 8 during the 2003 – 2007 harvests in order to maintain a consistent data sampling period for each year.

Parameter Estimation and Analyses Derived from Band Recovery Data

Band recovery data were used to estimate survival and recovery rates for after-hatching year (AHY) and hatching year (HY) doves by using the techniques of Brownie et al. (1985) and the software program MARK (White and Burnham 1999). The methods developed by Brownie et al. (1985) allow for estimation of survival and recovery rates for two age classes based on a series of band recovery models. Each model integrates different age and time specific assumptions while goodness of fit tests aid the researcher in selecting the model with the best fit for the given data. The band recovery models from Brownie et al. (1985) are abbreviated with the model numbers H_1, H_{01}, H_{02}, H_2 and H_3. Model H_2 was not used to analyze the band recovery data for this study because the model assumes that the reporting rate for newly released birds is different from the reporting rate for survivors of previously released cohorts (Brownie et al. 1985). This study uses the reporting rate for South Carolina estimated by Otis et al. (2008b). In estimating this reporting rate, Otis et al. (2008b) assumed that the reporting rate was constant across years and age classes. Furthermore, model H_3 was not used to analyze the band recovery data for this study because the model assumes that annual survival and recovery rates are age dependent for the first two years of life (Brownie et al. 1985). Brownie et al. (1985) explains that this assumption accounts for a sub-adult age class that may be mixed with the adult age class at the time of banding and release. After-hatching year (AHY) and hatching year (HY) are the only two age classifications used for mourning doves, hence model H_3 is not used. The remaining three models (H_1,

H_{01}, H_{02}) were examined in the analysis of the band recovery data. Model H_1 assumes that 1) survival and recovery rates are age specific and 2) survival and recovery rates are different from year to year (Brownie et al. 1985). Model H_{01} assumes that 1) survival and recovery rates are age specific, and 2) survival and recovery rates are constant from year to year (Brownie et al. 1985). Model H_{02} assumes that 1) survival and recovery rates are age specific, 2) recovery rates are year specific, and 3) survival rates are constant from year to year (Brownie et al. 1985). The structure of models H_1, H_{01}, and H_{02} are found in Appendix C.

Program MARK (White and Burnham 1999) provides for modeling of band recovery data sets of various complexities by which the user can define assumptions associated with the model being investigated. In this study the assumptions associated with age and time specific survival and recovery were defined as recommended by Brownie et al. (1985) for the three aforementioned recovery models. The band recovery matrices for this study were input into program MARK (White and Burnham 1999). One result of the analyses of recovery models in program MARK (White and Burnham 1999) is an Akaike Information Criterion (AIC) for each model. The Akaike Information Criterion (Akaike, H. 1985; White and Burnham 1999) statistic is an adjustment of the likelihood ratio that accounts for the number of parameters estimated in each model. In general, the AIC attempts to "penalize" the likelihood ratio for an increase in parameters estimated within each model. Lebreton et al. (1992) recommended selecting the model with the smallest AIC. Furthermore, Burnham and Anderson (2002) suggest that the absolute AIC value is "only comparative, relative to other AIC values in the model set"

(p. 71). They recommend using the AIC differences, $\Delta AIC = AIC_i - AIC_{min}$, where AIC_i is the AIC value of the model and AIC_{min} is the lowest AIC value of all the models, to evaluate the models that best fit the given data. Burnham and Anderson (2002) recommend, as a "rule of thumb"(p.70), if ΔAIC is between 0-2, there is substantial empirical support of model *i*; if ΔAIC is between 4-7, there is considerably less support of model *i*; and model *i* is essentially not supported if ΔAIC > 10. The Burnham and Anderson (2002) "rule of thumb" was used in this study to select the model with the most support based upon the ΔAIC values for the three Brownie et al. (1985) models (H_1, H_{01}, H_{02}).

Harvest and kill rate estimates were derived from recovery rate estimates using the methods described by Atkinson et al. (1982), which require estimates of reporting rate and crippling loss. The reporting rate used in this study to derive harvest rate estimates is a result of data analyses conducted by Otis et al. (2008b) from a national reward banding study carried out from 2003-2005 in which South Carolina participated. The estimated reporting rate (λ) for South Carolina from 2003-2005 was 0.635 (SE = 0.178) (Otis et al. 2008b). The crippling loss (c) for South Carolina (37% ± 5%) as reported by McGowan (1995) was used in this study to derive kill rate estimates (see Table I). Natural mortality rates in the presence of hunting were calculated for each year of the study using the methods described by Pollock et al. (1994) which incorporate survival and kill rate estimates (see Table I).

Table I. Definitions and techniques used for estimation and derivation of mourning dove population parameters.

Parameter	Definition	Estimation technique
S_t	probability that a dove alive at the time of banding in year *t* survives until the time of banding in year *t* + 1.	Brownie et al. (1985) in program MARK
f_t	probability that a banded dove alive at the time of banding in year *t* is shot or found dead during the hunting season of year *t* and is reported.	Brownie et al. (1985) in program MARK
λ	probability that a banded dove found dead, or shot and retrieved by a hunter is reported.	Otis et al. 2008b
c	the proportion of hunter-downed (killed, or wounded and lost) doves not retrieved.	McGowan 1995
H_t	estimated statewide harvest total in year *t*	Dolton and Rau 2003 - 2006 and Dolton et al. 2007
h_t	probability that a dove alive at the time of banding in year *t* is shot and retrieved by hunter during the year *t* hunting season.	$h_t = \frac{f_t}{\lambda_t}$
N_t	estimated mourning dove population size in year *t* prior to the breeding season	$N_t = \frac{H_{AHY,t}}{h_{AHY,t}}$
K_t	probability that a dove alive at the time of banding in year *t* dies as a result of hunting (including crippling loss) during the year *t* hunting season.	$K_t = \frac{h_t}{1 - c_t}$
v	probability of natural mortality that occurs in the presence of hunting (expected natural death)	$v = 1 – S - K$
p	the differential vulnerability to hunting between hatching year (HY) and after-hatching year (AHY) doves.	$p = \frac{f_{HY}}{f_{AHY}}$

Table I. (continued)

r	the ratio of HY doves to AHY doves in the harvest.	annual harvested dove wing examinations
P	preseason age ratio (estimated productivity)	$P = \frac{r}{p}$

Estimation of Age Distribution for Doves of Unknown Age at Harvest

Estimation of the age-at-harvest ratio (r) is fundamental to the estimation of productivity in the population (see Table I). The precision of this annual ratio (r) is reduced because of the unknown age doves in the harvest sample each year. Hatching year (HY) mourning doves in North and South Carolina during 1968-1974 molted at an average rate of one feather every 10.6 days (Haas and Amend 1976) and adults molted one feather every 14.0 days (Haas and Amend 1979). In an attempt to improve the estimate of the age-at-harvest ratio (r), the data from the banding samples in each year of this study were used with the results of Haas and Amend (1976 and 1979). The expected molt-at-harvest (m_h) for individual banded doves was calculated by using the equation:

$$m_h = m_b + (\Delta d \div \text{days per molt}),$$

where m_b is the observed molt-at-banding, Δd is the number of days between banding and the end of the first harvest week (September 8), and days per molt is dependent upon the observed age-at-banding, 10.6 for HY and 14.0 for AHY (Haas and Amend 1976 and 1979). The molt-at-harvest estimations (m_h) were calculated using SAS® Software (SAS

Institute 2008). The FLOORZ function in SAS (SAS Institute 2008) was used to truncate the expected molt-at-harvest (m_h) estimates to the largest integer less than or equal to the estimate (e.g. $m_h = 8.6$ is recorded as molt 8 not molt 9). Truncating in this manner prevents m_h estimates from being rounded up, which would prematurely group a dove into a higher molt category.

Frequency distribution tables of expected molt scores from banding data and observed molt scores in the harvest data were produced for AHY and HY doves in each year of the study using the PROC FREQ command in SAS (SAS Institute 2008). Chi-square goodness-of-fit tests were conducted to test if the expected molt frequency distributions fit the observed molt frequency distributions in molts 4-7 for AHY and HY mourning doves. The expected molt frequencies of AHY and HY mourning doves in molts 8-10 were then used to distribute the unknown-age doves in the harvest data to an age class (AHY or HY). The unknown age doves in molts 8-10 were distributed by applying the expected molt frequencies by age to each molt class rather than to the set of unknowns within each molt class. This method allowed mourning doves from the harvest data in molts 8-10 with a known age (AHY or HY) to be included in the frequency distributions of each molt.

Annual Mourning Dove Productivity and Trend Estimates

Following the distribution of unknown age doves from the harvest records into age classes (AHY and HY); the age-at-harvest ratio (r) was calculated. The age-at-harvest ratio (r) for each year of the study was then divided by the differential vulnerability to hunting (p) to produce estimates of pre-season age ratios, or annual productivity (P) (see Table I). This method of estimating pre-season age ratios has been described by Nichols and Tomlinson (1993) and used in previous mourning dove studies (Berdeen 2004, McGowan and Otis 1998). A one-tailed t-test was conducted using the PROC REG command in SAS (SAS Institute 2008), in which the null hypothesis was that the trend in annual productivity was not different from zero and the alternative hypothesis was that the trend in annual production was less than zero. Significance for the productivity trend was set at $p < 0.10$ to ensure avoidance of a Type II error. The estimate of productivity required to maintain a stable population, in terms of HY per AHY, was calculated by dividing total AHY mortality rate by HY survival rate (Atkinson et al. 1982). Productivity (P) for this study is defined as the number of juveniles recruited into the fall population per adult. This definition has been used in previous studies of mourning doves (Miller et al. 2001, Meyers et al. 2006).

Estimates of Mourning Dove Breeding Population Size

The formula recommended by the U.S. Fish and Wildlife Service (USFWS) (Anonymous 2005) for estimating annual change in population size of mourning doves,

$$N_{t+1} = N_t \, [S_{AHY} + S_{HY} \text{ x } P],$$

was used to estimate population size (N_t) for each year of the study with the exception of 2006. In this formula, population size (N_t) is the number of AHY mourning doves in the breeding population in year *t*. The total number of AHY mourning doves in the 2006 harvest ($H_{AHY, 2006}$) was estimated using the formula

$$H_{AHY,\,2006} = \frac{H_{2006}}{r_{2006} + 1},$$

where H_{2006} is the estimated total harvest in South Carolina during 2006 and r_{2006} is the age-at-harvest ratio (HY:AHY) in 2006, estimated from harvest record and distribution of unknown age doves into age classes (HY and AHY). The estimated total statewide harvest in South Carolina during 2006 (H_{2006} = 696,200 ±46,177 SE) was obtained from the annual USFWS publication *Mourning Dove Population Status, 2006* (Dolton and Rau 2006). The estimated breeding population size in 2006 (N_{2006}) was calculated using the formula

$$N_{2006} = \frac{H_{AHY,2006}}{h_{AHY,\,2006}},$$

where $h_{AHY,2006}$ is the harvest rate estimate for AHY doves in South Carolina during 2006. This method of estimating population size has been previously described (Nichols and Tomlinson 1993, Otis 2006). The 2006 breeding population size estimate was used in the USFWS formula listed above along with annual survival and productivity estimates to derive the breeding population size estimates for the other years of this study (2003-2005 and 2007). The total harvest estimate during 2006 in South Carolina was used in this study because it had the smallest standard error of all of the total harvest estimates during 2003-2007 (Dolton and Rau 2003-2006, Dolton et al. 2007).

RESULTS

Banding and Recovery Totals

During 2003-2007, 7,534 doves were banded. A total of 934 banded doves were excluded from the banding data set (see Appendix B). The number of banded doves included in the banding data set for this study was thus 6,600 (3,466 were HYand 3,134 were AHY).

Bands were recovered from 459 (≈ 7.0%) of the doves in the banding data set. None of the bands recovered were from doves excluded from the banding data set. Tables II and III show banding and recovery results by year for AHY and HY doves during 2003-2007 in South Carolina.

Table II. Number of AHY doves banded and recovered during 2003-2007 in South Carolina.

		Recovery Year				
Banding Year	No. Banded	2003	2004	2005	2006	2007
				Recoveries		
2003	637	36	14	5	3	1
2004	368		14	4	1	1
2005	838			19	15	5
2006	747				39	13
2007	876					35
Totals	3,466	36	28	28	58	55

Table III. Number of HY doves banded and recovered during 2003-2007 in South Carolina.

		Recovery Year				
Banding Year	No. Banded	2003	2004	2005	2006	2007
				Recoveries		
2003	404	39	8	2	2	1
2004	495		41	6	5	1
2005	643			37	7	2
2006	710				46	8
2007	882					49
Totals	3,134	39	49	45	60	61

Mourning Dove Wings Checked at Harvest

Examination of mourning dove wings from dove hunt fields during the five years of this study returned data on 23,278 harvested mourning doves. There were 2,038 harvested mourning doves that were removed from the harvest data set (see Appendix B). The number of harvested doves included in the harvest data set is 21,240; 13,786 are HY, 3,593 are AHY and 3,861 are unknown age doves. In each year, the number of HY doves recorded during the harvest wing examinations was greater than the number of after-hatching year doves and unknown age doves combined. Table IV displays the results from the harvested mourning dove wing examinations that took place in the first week of September in each year of the study.

Table IV. Numbers of hatching year (HY), after-hatching year (AHY), and unknown age (UNK) doves recorded during the first week of September in South Carolina from 2003-2007.

Year	HY	AHY	UNK	Totals
2003	1249	191	171	1611
2004	1871	272	498	2641
2005	3266	857	809	4932
2006	4298	1075	1321	6694
2007	3102	1198	1062	5362

Survival, Recovery, Harvest, Kill, and Natural Mortality Rates

Program MARK (White and Burnham 1999) analysis of the three models reported that model H_{02} had the lowest AIC value, 3870.51. Furthermore, the ΔAIC for models H_1 and H_{01} were 4.12 and 7.85, respectively (Table V**)**. By following the "rule of thumb" recommended by Burnham and Anderson (2002), survival and recovery rate estimates from model H_{02} were selected for use in this study. Model H_{02} assumes that survival is constant across years but varies between age classes and recovery rates vary across years and between age classes. The estimated annual survival rate for adult mourning doves (S_{AHY} = 0.4442 ± 0.0802) appeared to be greater than for juveniles (S_{HY} = 0.3481 ± 0.1166). In each year of the study, the estimated recovery rates for AHY mourning dove were less than the estimated recovery rates for HY mourning doves (Tables VI and VII).

The average harvest rate for AHY mourning doves (h_{AHY} = 0.066 ± 0.016) appeared to be less than for HY mourning doves (h_{HY} = 0.113 ± 0.026). Furthermore, HY mourning doves had greater annual harvest rates than AHY mourning doves in each year of the study (Table VIII). Correspondingly, the average kill rate estimate for AHY doves was less than for HY doves, as was the case for each year of the study (Table VIII). The annual natural mortality estimates for AHY and HY mourning doves were comparable during each year of the study (Table VIII), as were the average natural mortality estimates (v_{AHY} = 0.450 ± 0.025, v_{HY} = 0.473 ± 0.039).

Table V. Model selection statistics for three band recovery models (Brownie et al. 1985) used to estimate mourning dove survival and recovery rates in South Carolina during 2003-2007.

Model from Brownie et al. (1985)	k[a]	AIC	ΔAIC	AIC Weight
H_{02}	12	3870.51	0	0.87
H_1	18	3874.63	4.12	0.11
H_{01}	4	3878.36	7.85	0.02

[a] Number of parameters in the model

Table VI. Recovery (f_{AHY}) and survival (S_{AHY}) rates for AHY doves in South Carolina during 2003-2007.

Year	Estimate	Std. Err.	95% CI
Recovery Rates (f_{AHY})			
2003	0.0568	0.0092	0.0389 - 0.0748
2004	0.0453	0.0077	0.0301 - 0.0605
2005	0.0263	0.0045	0.0175 - 0.0351
2006	0.0457	0.0060	0.0340 - 0.0575
2007	0.0368	0.0051	0.0269 - 0.0467
Survival Rate (S_{AHY})			
Constant	0.4442	0.0409	0.3641 - 0.5243

Table VII. Recovery (f_{HY}) and survival (S_{HY}) rates for HY doves in South Carolina during 2003-2007.

Year	Estimate	Std. Err.	95% CI
Recovery Rates (f_{HY})			
2003	0.0973	0.0147	0.0685 - 0.1262
2004	0.0833	0.0124	0.0590 – 0.1076
2005	0.0571	0.0091	0.0392 – 0.0750
2006	0.0647	0.0092	0.0466 – 0.0828
2007	0.0556	0.0077	0.0404 – 0.0707
Survival Rate (S_{HY})			
Constant	0.3481	0.0595	0.2315 – 0.4647

Table VIII. Estimates of harvest rate (h), kill rate (K) and natural mortality (v) for AHY and HY mourning doves in South Carolina from 2003- 2007.

Year Age	h	95% CI	K	95% CI	v	95% CI
2003						
AHY	0.089	(0.032, 0.146)	0.142	(0.050, 0.234)	0.414	(0.291, 0.537)
HY	0.153	(0.057, 0.249)	0.243	(0.086, 0.400)	0.409	(0.213, 0.605)
2004						
AHY	0.071	(0.026, 0.116)	0.113	(0.039, 0.187)	0.443	(0.333, 0.553)
HY	0.131	(0.049, 0.213)	0.208	(0.075, 0.341)	0.444	(0.268, 0.620)
2005						
AHY	0.041	(0.014, 0.068)	0.066	(0.023, 0.109)	0.490	(0.398, 0.582)
HY	0.090	(0.033, 0.147)	0.143	(0.051, 0.235)	0.509	(0.360, 0.658)
2006						
AHY	0.072	(0.029, 0.115)	0.114	(0.041, 0.187)	0.442	(0.334, 0.550)
HY	0.102	(0.039, 0.165)	0.162	(0.060, 0.264)	0.490	(0.335, 0.645)
2007						
AHY	0.058	(0.023, 0.093)	0.092	(0.033, 0.151)	0.464	(0.364, 0.564)
HY	0.088	(0.035, 0.141)	0.139	(0.051, 0.227)	0.513	(0.366, 0.660)
Pooled Averages						
AHY	0.066	(-0.030, 0.162)	0.106	(-0.051, 0.263)	0.450	(0.211, 0.689)
HY	0.113	(-0.048, 0.274)	0.180	(-0.083, 0.443)	0.473	(0.103, 0.843)

AHY and HY Expected Frequency of Molt Distributions

The chi-square goodness of fit tests conducted for 2003-2007 supported the fit of the expected molt frequency distributions from banding data to the observed frequencies in molts 4-7 of the harvest data for at least one of the two age classes (Table IX). Since expected molt frequencies of at least one of the age classes fit the observed data, the expected molt frequencies in molts 8-10 were used to distribute the unknown age doves into age classes. The expected molt frequency distributions for 2003-2007 indicated that the majority of unknown age doves in molts 8 and 9 were AHY mourning doves in each of the years (Table X).

Table IX. Chi-square and p-value results testing the fit of the expected molt frequency distributions to the observed molt frequencies during 2003-2007 for AHY and HY mourning doves in South Carolina.

	df	χ^2	p-value
2003			
HY	3	0.209	0.976
AHY	3	8.500	0.037
2004			
HY	3	17.762	0.001
AHY	3	3.028	0.387
2005			
HY	3	14.176	0.003
AHY	3	5.119	0.163
2006			
HY	3	12.308	0.006
AHY	3	1.929	0.587
2007			
HY	3	9.572	0.023
AHY	3	3.155	0.368

Table X. Expected frequency distribution of AHY and HY mourning doves in molts 8-10 at harvest from South Carolina banding data during 2003-2007.

Year Molt	AHY Expected frequency	AHY 95%CI	HY Expected frequency	HY 95%CI
2003				
8	0.7739	(0.700, 0.848)	0.2261	(0.152, 0.300)
9	0.5820	(0.425, 0.739)	0.4180	(0.261, 0.575)
10	0.3800	(0.063, 0.697)	0.6200	(0.303, 0.937)
2004				
8	0.6831	(0.625, 0.741)	0.3169	(0.259, 0.375)
9	0.6053	(0.540, 0.670)	0.3947	(0.330, 0.460)
10	0.3000	(0.133, 0.467)	0.7000	(0.533, 0.867)
2005				
8	0.7569	(0.719, 0.795)	0.2431	(0.205, 0.281)
9	0.6182	(0.561, 0.675)	0.3818	(0.325, 0.439)
10	0.3333	(0.179, 0.487)	0.6667	(0.513, 0.821)
2006				
8	0.7596	(0.729, 0.791)	0.2404	(0.209, 0.271)
9	0.6093	(0.567, 0.651)	0.3907	(0.349, 0.433)
10	0.3885	(0.272, 0.506)	0.6115	(0.495, 0.729)
2007				
8	0.6541	(0.618, 0.690)	0.3459	(0.272, 0.420)
9	0.5914	(0.538, 0.644)	0.4086	(0.252, 0.566)
10	0.4350	(0.292, 0.578)	0.5650	(0.248, 0.882)

Distribution of Unknown Age Doves In Molts 8-10

During the 2003-2007 harvests, the total numbers of doves recorded in molts 8 and 9 during the first week of September were greater than in molt 10 (Table XI). Furthermore, there were greater numbers of doves recorded in molt 8 than in molt 9 during each year. The number of mourning doves recorded in the unknown age class also followed this gradient in molts 8-10 in each year of the study (Table XI). The distributions of the unknown age doves recorded in the harvest of each year, based upon the expected molt frequency distributions (Table XII), show that the number of AHY mourning doves expected in the unknown age class is much greater than HY doves. The total number of AHY and HY mourning doves in molts 8-10 from the 2003 -2007 harvest records after distribution of the unknown age doves is shown in Table XII.

Table XI. Number of mourning doves by age in molts 8-10 recorded in the first week of September in South Carolina during 2003-2007.

		Molt			
Year	Age	8	9	10	Total by age
2003					
	AHY	0	0	0	0
	HY	102	5	10	117
	UNK	124	38	9	171
	Total by molt:	226	43	19	288
2004					
	AHY	0	0	0	0
	HY	337	52	2	391
	UNK	251	218	29	498
	Total by molt:	588	270	31	889
2005					
	AHY	0	0	0	
	HY	413	19	1	433
	UNK	489	284	36	809
	Total by molt:	902	303	37	1242
2006					
	AHY	0	0	0	
	HY	577	53	10	640
	UNK	746	508	67	1321
	Total by molt:	1323	561	77	1961
2007					
	AHY	16	3	1	20
	HY	250	12	0	262
	UNK	687	329	46	1062
	Total by molt:	953	344	47	1344

Table XII. The total number of AHY and HY mourning doves in molts 8-10 from the 2003-2007 harvest records after distribution of the unknown age doves.

		Molt			
Year	Age	8	9	10	Total by age
2003					
	AHY	124	25	7	156
	HY	102	18	12	132
	Total by molt:	226	43	19	288
2004					
	AHY	251	163	9	423
	HY	337	107	22	466
	Total by molt:	588	270	31	889
2005					
	AHY	489	187	12	688
	HY	413	116	25	554
	Total by molt:	902	303	37	1242
2006					
	AHY	746	342	30	1118
	HY	577	219	47	843
	Total by molt:	1323	561	77	1961
2007					
	AHY	629	205	21	855
	HY	324	139	26	489
	Total by molt:	953	344	47	1344

Annual Mourning Dove Productivity and Trend Estimates

The annual productivity required to maintain a stable population in terms of HY per AHY was estimated to be 1.60 (± 0.30SE). The estimated productivity in 2003 was greater than this required rate. However, annual productivity estimates from 2004 -2007 were less than the rate required to maintain a stable population (Table XIII). The average estimated productivity during the five years (1.43 ± 0.33 SE) was also less than the productivity required for a stable population. Figure 7 illustrates the trend in annual productivity and displays a significant decline of -0.212 ($p < 0.10$) HY per AHY doves per year during the study years. Annual productivity estimates are compared with productivity required to maintain a stable population in Figure 8. Table XIII shows the estimates of the age-at-harvest ratio, differential vulnerability to hunting, and productivity.

Table XIII. Mourning dove age-at-harvest ratios (r), differential vulnerability (p), and productivity (P) estimates in South Carolina during 2003-2007.

Year	r	p	P
2003	3.64	1.71	2.12
2004	2.77	1.84	1.51
2005	2.19	2.17	1.01
2006	2.05	1.42	1.45
2007	1.64	1.51	1.09

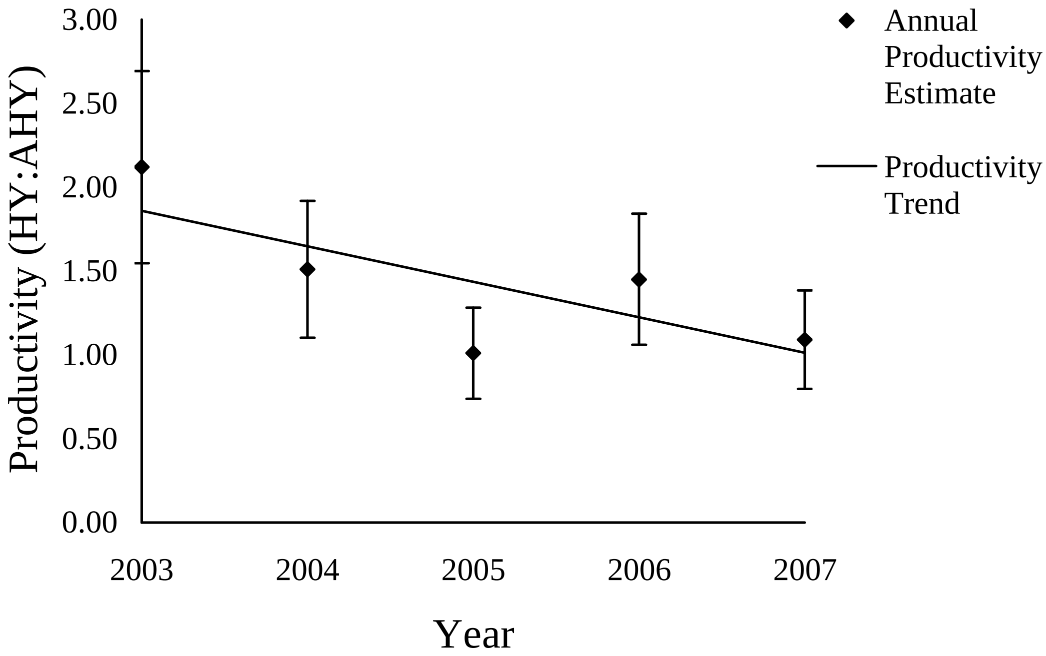

Figure 7. Annual mourning dove productivity estimates and trend in South Carolina during 2003-2007 with error bars showing ± 1 SE. Slope= -0.212, 95% Confidence Interval = (-0.416, -0.008), $p < 0.10$.

.

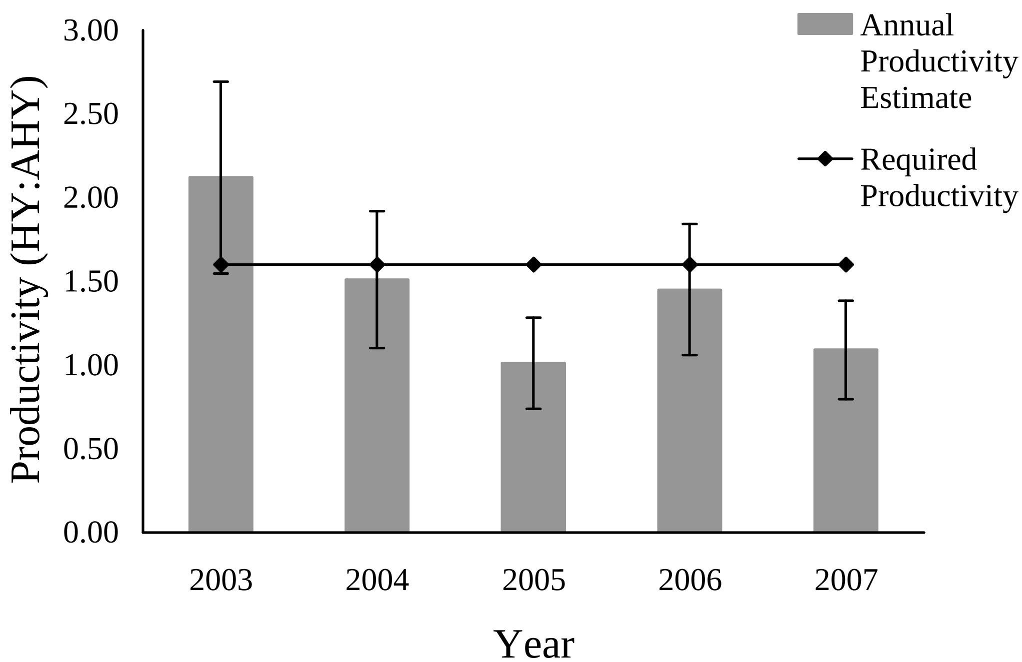

Figure 8. Annual mourning dove productivity estimates, with error bars showing ± one SE, versus productivity required to maintain a stable mourning dove population in South Carolina from 2003-2007.

Estimates of Mourning Dove Breeding Population Size

Estimates of mourning dove breeding population size in South Carolina during 2003-2007, as estimated from USFWS formula, ranged from about 3 million to 4 million. The 95% confidence intervals for these estimates were between 64% and 70%, relative to the breeding population size estimates (Table XIV**)**.

Table XIV. Estimates of total mourning dove breeding population size (N_t) in South Carolina during 2003-2007.

Year *t*	N_t	95% CI
2003	3,474,813	(1,028,186, 5,921,439)
2004	4,107,826	(1,360,108, 6,855,545)
2005	3,983,897	(1,440,362, 6,527,433)
2006	3,170,310	(1,227,430, 5,113,189)
2007	3,008,449	(1,071,657, 4,945,242)

DISCUSSION

Age Ratio of Banded Mourning Doves

The annual banding ratio of HY doves to AHY doves during 2003 – 2007 was different for each banding period. It may be tempting to infer that these age ratios are indicative of the overall mourning dove population for each year. However, given that a total of 934 banded birds were removed from the data set, these ratios may have been different if those data were able to be included. Furthermore, the age ratios of mourning doves banded may vary based upon the daily, as well as seasonal, time of trapping. Lewis and Morrison (1973) reported that during a study to examine the efficiency of traps and baits in Oklahoma, 80% of the AHY mourning doves caught in traps were captured during the evening hours. They also indicated that the probability of catching adults during June was significantly greater ($p < 0.005$) than in July or August. Location of trapping may also influence the age ratios of doves trapped for banding as suggested by Henry et al. (1976), whom found that adults comprised 81% of doves caught in roadside traps compared to 34% captured in field traps. Any one, or a combination of these situations, may have resulted in the annual variation in the age ratio of banded mourning doves during this study. Annual variation in age ratios of banded mourning doves has also been reported in previous multi-year banding studies (Atkinson et al. 1982, McGowan and Otis 1998) and should not be considered an indicator of the annual population age ratio.

Survival and Recovery Rates

The survival rate for AHY found in this study (44.4%) is similar to the mean adult survival rates reported by Atkinson et al. (1982) in Missouri (42.4%) and Martin and Sauer (1993) for South Carolina (42.8%). The HY survival rate found in this study (34.8% ± 6.0% SE) was slightly greater than the HY survival rates reported by Atkinson (1982) in Missouri, and Martin and Sauer (1993) in South Carolina (25.1% and 24.2% respectively). However, these estimates of HY survival rate were not significantly different from the HY survival rate found in this study. It should be noted that Atkinson et al. (1982) and Martin and Sauer (1993) also used the Brownie models to estimate survival and recovery rates in each of their studies.

Average recovery rates for AHY and HY found in this study (4.22% ± 0.65% and 7.2% ± 0.96%, respectively) are only slightly greater than the recovery rates reported by Martin and Sauer (1993) for South Carolina (3.4% for AHY and 5.2% for HY) and Atkinson et al. (1982) in Missouri (2.47% for AHY and 3.30% for HY). A likely reason for the higher recovery rates found here is that the true reporting rate was higher during this study. The reporting rate used in this study (0.635) was taken from the results of a national reward banding study conducted from 2003 – 2005 (Otis et al. 2008b). Reporting rate estimates found by Otis et al. (2008b) were considerably greater than reporting rate estimates found in previous reward banding studies (Tomlinson 1968, Reeves 1979), and greater than the reporting than the reporting rate used by Atkinson et al. (1982) and Martin and Sauer (1993). Otis et al. (2008b) suggests that the higher reporting rates from the more recent reward banding study may be attributed to the inscription of a telephone number on the dove bands for reporting rather than a mailing address used in previous studies.

Derived Population Parameter Estimates

Harvest rate estimates for AHY and HY mourning doves in the South Carolina during 1966-1971 derived from Martin and Sauer (1993), 11% and 16%, respectively were greater than the estimates found in this study. The difference between the harvest rates reported in this study and those derived from Martin and Sauer (1993) may be a result of different reporting rates used to calculate these estimates. Martin and Sauer (1993) used a reporting rate of 32% found by Tomlinson (1968) as the average reporting rate from a reward banding study conducted in 10 states ranging from California to South Carolina. Tomlinson's (1968) reporting rate may not have been accurate for South Carolina during 1966-1971 and therefore could have resulted in imprecise harvest rate estimates for the state. Harvest rate estimates in South Carolina during 2003-2007 would compare more favorably to those during 1966-1971 if the true reporting rate in South Carolina during 1966-1971 was greater than the estimate used by Martin and Sauer (1993). Atkinson et al. (1982) reported mourning dove harvest rates in Missouri that compare favorably to those reported in this study. Furthermore, harvest rates derived from Haas (1978) were 6.5% for AHY and 11.6% for HY mourning doves in north-central South Carolina from 1968-1974, which are nearly the exact values found in this study. Atkinson et al. (1982) used the reporting rate found by Tomlinson (1968) and Haas (1978) used the reporting rate of 31% found by Reeves (1979) for the Eastern Management Unit.

Estimates of mortality attributable to hunting, or kill rate, from this study are comparable to previous studies. Average kill rates for AHY and HY doves found in this study (10.6% and 18.0%, respectively) are slightly less than those reported by Martin and Sauer (1993) and McGowan (1995). Furthermore, the AHY kill rate estimate found in this study is slightly less than reported by Atkinson et al. (1982), while the HY kill rate estimates are the same.

Hunting mortality varied annually for AHY and HY doves from 2003-2007 while survival rates appear to be constant from year to year, according to analyses of the Brownie et al. (1985) models. This may suggest that mourning doves in South Carolina during 2003-2007 were operating under the compensatory mortality hypothesis. This hypothesis suggests that overall survival is not affected by an increase in hunting mortality, below a certain threshold (c), because non-hunting mortality compensates for the increase (Rexstad 1992). There may be a threshold (c) at which hunting mortality in South Carolina would be sufficient to have a negative effect on survival, but that threshold is unknown.

The crippling rate used in this study (37.5%) to estimate kill rates was assumed to be the same for AHY and HY mourning doves. There is no evidence to suggest that AHY and HY may have different crippling rates since crippled doves are not retrieved. The crippling rate used here was taken from McGowan (1995), who calculated this estimate based upon 44 hunter interviews on a study site in Bennettsville, South Carolina. The precision of this estimate is unknown. However, Haas (1977) estimated crippling rate to be between 27 and 41 percent in north-central South Carolina. Haas (1977) recommends that crippling rates should be reported as upper and lower limits after he discovered trapped AHY doves that contained shot, presumably from the previous hunting season, which contradicts the assumption that 100% of all doves shot die.

McGowan (1995) reported greater natural mortality rates for AHY and HY doves than those reported here. These higher natural mortality rates likely stem from low survival rates reported by McGowan (1995) on two hunting sites in the Coastal Plain of South Carolina. Using the method recommended by Pollock et al. (1994), natural mortality rates derived from Atkinson et al. (1982) were slightly greater for HY doves and slightly less for AHY doves than those reported in this study. The average natural mortality rates found in this study for AHY and HY doves were nearly equal to one another (45% and 47%, respectively). Furthermore, the annual natural mortality rate estimates for AHY and HY mourning doves were not significantly different in any year of this study. One may interpret these results to propose that AHY and HY natural mortality rates are the same, thus suggesting a natural mortality rate applicable to the entire population during 2003-2007. An interpretation such as this should be avoided given the large standard errors associated with the natural mortality estimates. Furthermore, previous studies have reported natural mortality rate estimates for AHY and HY mourning doves that are not similar to one another.

Distribution of Unknown Age Doves in Molts 8-10

The method used in this study to estimate the annual age distribution of unknown age mourning doves in molts 8-10 during the harvest has not been found in previous studies and therefore deserves discussion. This method operates upon the assumption that age distributions among molt scores in year *t* of the banding data set will be realized in the harvest data set for year *t* given the age-specific molt rates found by Haas and Amend (1976, 1979). If this is assumed to be true, then one would have to assume that the probability of trapping a mourning dove of age *a* in year *t* is the same as the probability of harvesting and reporting a dove of age *a* in year *t* (recovery rate). Previous studies suggest that trapping rates for mourning doves vary by age and sex based upon type of bait used, location, time of day, and month of trapping. The annual trapping rates for mourning doves in this study are unknown. This method was used to estimate the annual age distribution of unknown age doves in molts 8-10 during the harvest because in each year of this study, the observed age distribution in the harvest among molts 4-7 fit well to the expected estimates.

In the 2003-2006 distributions, all of the unknown age doves in molt 8 were categorized as AHY doves. In the 2007 distribution, 89% of the unknown age doves in molt 8 were categorized as AHY doves. These distributions resulted from applying the expected age ratios for molt 8 to the entire molt. It is not unlikely that the majority of unknown age doves in the harvest data set are truly AHY doves. However, it is unlikely, but not impossible, that 100% of the unknown age doves in any molt are truly AHY doves. All unknown age doves in molts 8-10 could truly be AHY doves if all HY doves in molts 8-10 were properly aged at the time of the wing examinations. Age distribution results would differ if the expected age ratios for molts 8-10 were applied to the unknown age dove data set rather than to the molt. Distributing the unknown age doves in such a manner would result in greater age-at-harvest ratios (HY:AHY) and greater productivity estimates than reported in this study. However, the greater productivity estimates would still suggest a significant decline in productivity during 2003-2007 ($p < 0.10$). The expected age ratios were applied to the entire molt in this study rather than to the unknowns because chi square tests supported this method for at least one of the age classes in each year.

<u>Breeding Population Size Estimates and Annual Productivity</u>

The large confidence interval for the 2006 mourning dove harvest estimate produced large confidence intervals for the derived breeding population size estimates (N_t) found in this study for 2003-2007 in South Carolina. Nichols and Tomlinson (1993) state that the method used in this study to estimate the breeding population size in 2006 often provides the only means of estimating population size of mourning doves. However, they discourage relying on these estimates because, “those estimates invariably are quite imprecise and may be biased,” (Nichols and Tomlinson 1993, p.279). The breeding population size estimates reported in this study should be interpreted as largely imprecise estimates, given their large confidence intervals. Furthermore, these estimates should not be interpreted as an estimate of the statewide mourning dove breeding population. Considering that the data used to calculate these estimates originated in rural areas of South Carolina where mourning dove hunting takes place, N_t should be interpreted as estimates of the mourning dove breeding population in rural areas of South Carolina during year *t*. Inferring that these estimates are indicative of the statewide mourning dove breeding population would be erroneous since no mourning dove data from urban areas in South Carolina were used in this study.

The U.S. Fish and Wildlife Service (USFWS) recommends multiplying population size in year *t* (N_t) by a growth factor,[$S_{AHY} + S_{HY}$ x P], hereafter abbreviated (*g*), to estimate population size in year t + 1. Population size from year *t* to $t + 1$ will increase when $g > 1$, decrease when $g < 1$, and remain the same when $g = 0$. During 2003-2007, mourning dove productivity was the only variable of *g* that changed, since AHY and HY survival were assumed to be constant. This suggests that productivity was responsible for the changes in the mourning dove breeding population size estimates from year to year during this study.

The significant decline in productivity reported in this study during 2003-2007 may lead to the conclusion that the true breeding population declined during these years, based upon the USFWS formula. Productivity necessary to maintain a stable population was only achieved in 2003. In 2004-2007, productivity estimates were not sufficient to make $g \geq 1$. This may suggest that from 2003-2007 there was an overall decline in the breeding population of mourning doves in rural areas of South Carolina and an underlying cause was a decrease in productivity in these areas. However, this may not be the case. Many areas where mourning dove hunting occurs are intensively managed to attract doves and may act as “sink” habitats (Pulliam 1988). Pulliam states that “sink habitats may support very large populations despite the obvious fact that the sink population would eventually disappear without continued immigration.” Even though mourning doves in South Carolina are typically considered a resident population, localized immigration from non-hunting areas may help maintain local breeding population sizes on hunting sites. If this is the case and these immigrants represent a true surplus from non-hunting areas, this suggests that the total breeding population in South Carolina may be either stable or increasing. The degree to which these local migrations occur, and what, if any, influence they have on the breeding population in hunting areas is not known. One hypothesis from this possibility is that annual immigration of mourning doves into these hunting areas is sufficient to compensate for annual hunting mortality. Another hypothesis is that productivity in these areas is density dependent and the decline is a result of an increase in mourning dove density. Long term data does not exist concerning the density dependent or independence of productivity in mourning doves. It is not likely that competition for breeding sites is a factor, but fecundity may be influenced by the availability of food resources (Otis et al. 2008a).

Another possibility is that these “sink” habitats are contributing to a decline in the breeding population. Berdeen (2004) reported evidence to suggest that under demographic conditions typical of the Carolinas Subunit in the Eastern Management Unit, if 11-30% of the landscape were sink habitats, a population decrease would occur. The percentage of sink and source patches in South Carolina in unknown.

Annual nesting success within the harvestable mourning dove population has a direct effect on annual productivity. The annual productivity necessary to maintain a stable population size during 2003-2007 can also be expressed as 3.20 HY per breeding pair. Since mourning doves typically lay two eggs per clutch, the annual breeding population would have to average 1.60 successful nesting attempts per breeding pair. Furthermore, this estimation relies on the assumptions that the male to female ratio among breeding adults is 1:1 and that 100% of adults eligible for breeding will find a mate and attempt to breed. Should the male to female ratio among breeding adults be different than 1:1, or less than 100% of adults attempt to breed, the annual productivity per breeding pair required to maintain a stable population would increase. Numerous studies reviewed by Mirarchi (1993a) report adult sex ratios that varied widely. All of the studies which reported skewed adult sex ratios were skewed by a predominance of adult males. In cases where the adult sex ratio is skewed greatly towards either sex, it is unlikely that 100% of the adult population of mourning doves would breed, given this species' monogamous breeding behavior. Therefore, while the productivity necessary to maintain a stable population reported in this study as HY per AHY in the population would remain the same, but would increase in terms of HY per breeding pair. Furthermore, if the true sex ratios during this study were skewed or less than 100% of adults paired for breeding, then productivity estimate reported in this study for 2003-2007, in terms of HY per breeding pair, may be less than the true productivity during those years. In the formula recommended by the USFWS for estimating population size, the USFWS define productivity as the ratio of female recruits into the population per breeding female. The absence of sex ratio data currently prevents the calculation of this estimate in South Carolina.

The standard error of the estimate of required productivity to maintain a stable population produces a 95% confidence interval that includes the productivity estimates for 2003-2007. This suggests that if the true required productivity was on the lower end of the confidence interval, then the population may have been stable in all years. Furthermore, if the true breeding population size decreases from year t to t +1, then the annual productivity in year t + 1 will have to be greater than the required productivity for a stable population in order for the breeding population size in year t +2 to return to the size of year t. Achieving population growth sufficient enough to replenish the losses from previous years is difficult when the productivity trend is significantly declining.

Recommendations for Further Research

Further research is needed to understand the effects of productivity change on mourning dove populations in hunted areas of South Carolina. The recommended USFWS formula is a very basic model for use in analyzing population changes. The parameters (i.e. productivity, survival) used in this model may have associated extrinsic factors responsible for changes in the parameter estimates (Anonymous 2005). These factors, once understood, can be added to the model to create a more comprehensive model. A nesting study would be one investigative method to use to examine extrinsic factors that may be affecting changes in productivity. Parameters such as nest success, nest density, and breeding population sex ratio should be estimated from such a study and their effects on productivity should be investigated.

Another investigation should attempt to discover to what degree local migrations from non-hunting areas into hunting areas occur. Scott et al. (2004) reported that the harvest rate of mourning doves banded in urban sites of Ohio was negligible and less than that experienced by doves banded in rural sites. However, they suggest that more research is needed to understand the ecology of mourning doves in urban landscapes and the effect that those landscapes may have on large scale estimated population trends. A multi-year study in which doves in urban areas are banded and their recaptures and/or recoveries from hunting areas are measured is one method that could be used to investigate local migrations. Findings from such a study may provide a better understanding of factors (e.g. population density and immigration to replace hunting loss) possibly affecting mourning dove populations in hunted areas of South Carolina.

CONCLUSION

The parameter estimates in this study must be recognized for the context in which the data were gathered. The sampling design of this study suggests that parameter estimates determined here are descriptive of the mourning dove population in rural areas of South Carolina and probably do not describe the overall statewide population. The stability of the mourning dove population in South Carolina cannot conclusively be determined based on the given data and analyses in this study. Productivity during 2003-2007 declined; however, the effect of this decline on the mourning dove population in South Carolina cannot be ascertained from the data. The significant decline in productivity detected in this study should be investigated further by examining the relationships of breeding population sex ratio, nest success and nest density on productivity. Trap sites and hunting fields, by design, are meant to attract mourning doves and may be sink habitats that attract non-local doves to these areas. If so, non-hunted areas may be source habitats that replace dove losses in hunted areas. This hypothesis should be investigated further by banding doves in more urban areas and analyzing the urban bands recovered from rural, hunted areas.

Banding and harvest wing examinations should continue in order to monitor survival and recovery as well as production. Including gender identification in the banding records will provide male and female survival and recovery estimates that will be useful in understanding productivity. The production estimates and required productivity reported herein would double if one were interested in productivity per breeding pair.

APPENDICES

APPENDIX A

The following table describes the location of banding sites in South Carolina during the 2003 – 2007 banding periods.

Table A-I. Banding site names, locations, latitudes and longitudes of mourning dove banding sites during the 2003-2007 banding periods in South Carolina obtained from SCDNR.

Site Name	Location	Latitude	Longitude
Savannah NWR[5]	≈ 9 miles S of Hardeeville, SC	32° 09' 00" N	81° 05' 00" W
Savannah NWR[5]	≈ 9 miles S of Hardeeville, SC	32° 10' 00" N	81° 07' 00" W
Tillman Sand Ridge[1]	≈ 10 miles W of Ridgeland, SC	32° 30' 00" N	81° 12' 00" W
Bear Island WMA[1]	≈ 10 miles SE of Green Pond, SC	32° 36' 00" N	80° 28' 00" W
Webb Center[1,2,3,4,5]	James W. Webb WMA, Hampton County, SC	32° 36' 00" N	81° 18' 00" W
ACE Basin NWR I[3,4,5]	Hollywood, SC	32° 39' 00" N	80° 23' 00" W
McKenzie Property[1]	≈ 1 mile N of James W. Webb WMA, Hampton Co., SC	32° 39' 00" N	81° 18' 00" W
ACE Basin NWR II[3,4,5]	Hollywood, SC	32° 40' 00" N	80° 23' 00" W
Donnelly WMA[1,2,3,4,5]	≈ 2 miles South of Green Pond, SC	32° 40' 00" N	80° 30' 00" W
Barnes Property[1]	≈ 2 miles NW of Estill, SC	32° 46' 00" N	81° 15' 00" W
Bowers' Farm[1]	≈ 2 miles NW of Estill, SC	32° 46' 00" N	81° 15' 00" W
Jarrell Farms[1]	≈ 1 mile NW of Estill, SC	32° 46' 00" N	81° 16' 00" W
Walnut Grove[1]	≈ 9 miles SW of McClellanville, SC	33° 01' 00" N	79° 36' 00" W
Medway Plantation[1,3,4]	≈ 5 miles NE of Goose Creek, SC	33° 01' 00" N	79° 58' 00" W
North Tibwin[1]	≈ 2 miles SW of McClellanville, SC	33° 03' 00" N	79° 30' 00" W
Bonneau Ferry WMA[4,5]	≈ 5 miles S of Cordesville, SC	33° 04' 00" N	79° 53' 00" W
Chappelear Residence[1,3,4,5]	≈ 7 miles SW of Moncks Corner, SC	33° 05' 00" N	80° 05' 00" W
Wambaw Unit - FMNF[1]	≈ 5 miles NW of McClellanville, SC	33° 07' 00" N	79° 33' 00" W
Santee Coastal Reserve[1,2,3,4,5]	≈ 8 mile NE of McClellanville, SC	33° 08' 00" N	79° 22' 00" W
Mulberry Plantation[1]	≈ 5 miles S of Moncks Corner, SC	33° 08' 00" N	79° 59' 00" W
E. Vaughn Residence[5]	≈ 9 miles SE of Jamestown, SC	33° 10' 00" N	79° 37' 00" W
Vaughn Residence[1]	≈ 11 miles NW of McClellanville, SC	33° 11' 00" N	79° 37' 00" W
Mahan Residence[1,2]	≈ 1 mile E of Moncks Corner, SC	33° 11' 00" N	79° 59' 00" W

Table A-I. (continued)

Gutpile near Elmwood[1]	≈ 7 miles N of McClellanville, SC	33° 12' 00" N	79° 28' 00" W
Tom Harkins Residence[1,2,3]	≈ 7 miles SE of Bonneau, SC	33° 13' 00" N	79° 54' 00" W
Northhampton Unit (FMNF)[1]	≈ 7 miles SE of Jamestown, SC	33° 14' 00" N	79° 35' 00" W
Crackerneck WMA[1,2,3,4,5]	≈ 5 miles S of Jackson, SC	33° 15' 00" N	81° 45' 00" W
Dennis Wildlife Center[1,2,3,4,5]	Near Bonneau, SC	33° 18' 00" N	79° 57' 00" W
Ryan Bowles' Residence[1]	≈ 2 miles W of Bonneau, SC	33° 19' 00" N	79° 59' 00" W
Shuler Residence[1,5]	≈ 8 miles SW of Santee, SC	33° 23' 00" N	80° 32' 00" W
Canal WMA[1,3]	≈ 1 mile NW of Saint Stephen, SC	33° 25' 00" N	79° 56' 00" W
Caudell Residence[1,2,3,4,5]	Near New Ellenton, SC	33° 25' 00" N	81° 41' 00" W
Samworth WMA[4,5]	≈ 10 miles NE of Georgetown, SC	33° 28' 00" N	79° 11' 00" W
Bluff Unit Santee NWR[1,2,3,4,5]	Near Summerton, SC	33° 33' 00" N	80° 27' 00" W
Mason Tract[1,2,3]	≈ 5 miles S of Clarks Hill, SC	33° 36' 00" N	82° 07' 00" W
San Fratello Property[1,2,3,4,5]	≈ 4 miles W of Sandy Run, SC	33° 47' 00" N	81° 02' 00" W
Parksville Dove Field[4,5]	≈ 0.25 mile N of Parksville, SC	33° 47' 00" N	82° 13' 00" W
Key Bridge Work Center[2,3,4,5]	≈ 5 miles E of Parksville, SC	33° 48' 00" N	82° 08' 00" W
Cunningham Field[1,2,3,4,5]	≈ 5 miles E of Plum Branch, SC	33° 50' 00" N	82° 10' 00" W
Plum Branch [1,2,3,4,5]	≈ 1 mile E of Plum Branch, SC	33° 50' 00" N	82° 17' 00" W
Bland Tract WMA [5]	≈ 2 miles NE of Wedgefield, SC	33° 54' 00" N	80° 30' 00" W
Bordeaux Waterfowl Area[1,2,3,4,5]	≈ 2 mi. SW of Bordeaux, SC	33° 54' 00" N	82° 27' 00" W
Alveshire Residence[4,5]	≈ 2 miles N of Batesburg, SC	33° 55' 00" N	81° 34' 00" W
Hawkinhurst[4,5]	≈ 0.5 mile E of Horrell Hill, SC	33° 57' 00" N	80° 51' 00" W
Hook Residence[3,4,5]	≈ 3.5 mi SW of Lexington, SC	33° 57' 00" N	81° 16' 00" W
E. Laney Residence[5]	≈ 6 miles SE of Rembert, SC	34° 03' 00" N	80° 26' 00" W
Dog Island Rd. PDF[2,3,5]	≈ 3 miles SW of Wisacky, SC	34° 05' 00" N	80° 12' 00" W
Wisacky - Region 2[2,5]	≈ 0.5 mile West of Wisacky, SC	34° 08' 00" N	80° 11' 00" W
Ruth Residence[1,2]	≈ 8 miles N of Irmo, SC	34° 10' 00" N	81° 11' 00" W
Greenwood DNR Office[1,2,3,4,5]	≈ 5 miles E of Abbeville, SC	34° 11' 00" N	82° 17' 00" W
Florence Wildlife Office[1,3,5]	≈ 2 miles N of Florence, SC	34° 14' 00" N	79° 48' 00" W
Pee Dee Research and Education Center[1,2,3,4,5]	≈ 7 miles N of Florence, SC	34° 17' 00" N	79° 44' 00" W
Dargan's Pond[1]	≈ 7 miles N of Florence, SC	34° 18' 00" N	79° 44' 00" W
Crisp Farm[1]	Near Mountville, SC	34° 21' 00" N	81° 59' 00" W

Table A-I. (continued)

Damon Gun Club [1,2,3,4,5]	≈ 5 miles E of Dovesville, SC	34° 24' 00" N	79° 48' 00" W
McBee WMA [1,5]	≈ 4 miles E of Bethune, SC	34° 25' 00" N	80° 17' 00" W
McKinney Residence [1]	≈ 3 miles SW of Clinton, SC	34° 25' 00" N	81° 54' 00" W
Carolina Sandhills NWR[1,2,3,4,5]	Chesterfield Co., SC	34° 35' 00" N	80° 11' 00" W
David Lynch Farm [1,2,3,4,5]	≈ 3 miles E of Bennettsville, SC	34° 36' 00" N	79° 38' 00" W
Private Field in Anderson County[1,4]	≈ 8 miles S of Clemson, SC	34° 36' 00" N	82° 49' 00" W
Lake Wallace PDF[1,2,3,4,5]	≈ 1 mile N of Bennettsville, SC	34° 39' 00" N	79° 41' 00" W
Clemson DNR Office[1,2,3]	≈ 2 miles S of Clemson, SC	34° 39' 00" N	82° 49' 00" W
Jeff Quick Farm[1,2,3]	≈ 10 miles E of Cheraw, SC	34° 40' 00" N	79° 44' 00" W
Fleming Residence[1,2,4,5]	≈ 10 miles E of Pendleton, SC	34° 41' 00" N	82° 40' 00" W
Erik Martin Residence[1,2,3]	≈ 7 miles NW of Bennettsville, SC	34° 42' 00" N	79° 47' 00" W
Plemmons Residence[1,2,3,4]	≈ 7 miles W of Lowry's, SC	34° 47' 00" N	81° 20' 00" W
Scales Farm[1,2,3,4,5]	≈ 7 miles N of Union, SC	34° 48' 00" N	81° 37' 00" W
Heatherly Farm[1,2,3,5]	≈ 0.5 mile SW of Kelton, SC	34° 50' 00" N	81° 35' 00" W
Ross Mountain[5]	≈ 6 miles SW of Tamassee, SC	34° 50' 00" N	83° 06' 00" W
Porter PDF[4]	≈ 5 miles SW of Pickens, SC	34° 51' 00" N	82° 48' 00" W
Draper WMA[1,2,3,4]	≈ 2 miles E of McConnells, SC	34° 52' 00" N	81° 11' 00" W
Piedmont Tree Nursery[1,2,3,4,5]	≈ 2 miles NW of Salem, SC	34° 53' 00" N	83° 00' 00" W

[1,2,3,4,5] Superscripts 1-5 correspond to banding years 2003-2007 respectively (e.g. 1 = 2003, 2 =2004, etc.)

APPENDIX B

The following tables list the numbers of exclusions and reasons for the exclusion of mourning doves from the 2003 – 2007 banding and harvest data sets.

Table B-I. Number and reasoning for excluding data from the banding data set.

Year	Data entries excluded	Reason
2003	282	No age data [a]
2004	128	No age data
2005	194	No age data
2006	155	No age data
	3	Unknown molt [b]
2007	170	No age data
	2	Unknown molt

[a] Necessary for survival and recovery rate estimates and frequency of molt progression estimates.
[b] Necessary for expected age distribution estimates.

Table B-II. Number and reasoning for excluding data from the harvest data set.

Year	Data entries excluded	Reason
2003	271	Unknown molt [a]
2004	362	Unknown molt
	3	Unknown age, molt < 8 [b]
2005	239	Unknown molt
	5	Unknown age, molt < 8
2006	619	Unknown molt
	28	Unknown age, molt < 8
2007	506	Unknown molt
	5	Unknown age, molt < 8

[a] Necessary for chi square goodness-of-fit test of expected age distribution estimates.

[b] Dove ages are identifiable with molts less than 8

APPENDIX C

The following tables show the structure of the expected numbers of band recoveries for models H_1, H_{01}, and H_{02} from Brownie et al. (1985). The notations used in the tables are also from Brownie et al. (1985) and are as follows: k = the number of years of banding

ℓ = the number of year of recovery

s = the number of years when no release is made but recoveries are recorded

f_i' = recovery rate in year i for doves banded and released as young in year i, $i = 1,\ldots, k$

S_i' = survival rate for year i for doves banded and released as young in year i, $i = 1,\ldots, k - 1$ if $\ell = k$, and $1,\ldots, k$ if $\ell > k$

f_i = recovery rate for adults in year i, $i = 1,\ldots, \ell$

S_i = survival rate for adults in year i, $i = 1,\ldots, \ell - 1$

Table C-I. Expected numbers of band recoveries under model H_1 for a banding study with $k = 3$, $\ell = 5$, $s = 2$.

Year banded	Number banded	Year of Recovery				
		1	2	3	4	5
		Birds banded and released as adults				
1	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2S_3f_4$	$N_1S_1S_2S_3S_4f_5$
2	N_2		N_2f_2	$N_2S_2f_3$	$N_2S_2S_3f_4$	$N_2S_2S_3S_4f_5$
3	N_3			N_3f_3	$N_3S_3f_4$	$N_3S_3S_4f_5$
		Birds banded and released as young				
1	M_1	M_1f_1'	$M_1S_1'f_2$	$M_1S_1'S_2f_3$	$M_1S_1'S_2S_3f_4$	$M_1S_1'S_2S_3S_4f_5$
2	M_2		M_2f_2'	$M_2S_2'f_3$	$M_2S_2'S_3f_4$	$M_2S_2'S_3S_4f_5$
3	M_3			M_3f_3'	$M_3S_3'f_4$	$M_3S_3'S_4f_5$

Table C-II. Expected numbers of band recoveries under model H_{01} for a banding study with $k = 3$, $\ell = 5$, $s = 2$.

Year banded	Number banded	Year of Recovery				
		1	2	3	4	5
		Birds banded and released as adults				
1	N_1	N_1f	N_1Sf	N_1SSf	N_1SSSf	N_1SSSSf
2	N_2		N_2f	N_2Sf	N_2SSf	N_2SSSf
3	N_3			N_3f	N_3Sf	N_3SSf
		Birds banded and released as young				
1	M_1	M_1f_1'	$M_1S'f$	$M_1S'Sf$	$M_1S'SSf$	$M_1S'SSSf$
2	M_2		M_2f'	$M_2S'f$	$M_2S'Sf$	$M_2S'SSf$
3	M_3			M_3f'	$M_3S'f$	$M_3S'Sf$

Table C-III. Expected numbers of band recoveries under model H_{02} for a banding study with $k = 3$, $\ell = 5$, $s = 2$.

Year banded	Number banded	Year of Recovery				
		1	2	3	4	5
		Birds banded and released as adults				
1	N_1	N_1f_1	N_1Sf_2	N_1SSf_3	N_1SSSf_4	N_1SSSSf_5
2	N_2		N_2f_2	N_2Sf_3	N_2SSf_4	N_2SSSf_5
3	N_3			N_3f_3	N_3Sf_4	N_3SSf_5
		Birds banded and released as young				
1	M_1	M_1f_1'	$M_1S'f_2$	$M_1S'Sf_3$	$M_1S'SSf_4$	$M_1S'SSSf_5$
2	M_2		M_2f_2'	$M_2S'f_3$	$M_2S'Sf_4$	$M_2S'SSf_5$
3	M_3			M_3f_3'	$M_3S'f_4$	$M_3S'Sf_5$

The computer program BROWNIE and the source publication (Brownie et al. 1985) can be accessed on the internet at the USGS Patuxent Wildlife Research Center's software archive webpage, http://www.mbr-pwrc.usgs.gov/software.html#a (Hines 2002).

LITERATURE CITED

Akaike, H. 1985. Prediction and entropy. Pages 1-24 *in* Atkinson, A.C. and S.E. Fienberg, eds., A Celebration of Statistics, the ISI Centenary Volume. Springer-Verlag, New York.

Aldrich, J. W. 1993. Classification and distribution. Pages 47-54 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Anonymous. 2005. Mourning dove national strategic harvest management plan. U.S. Fish and Wildlife Service, Laurel, MD.

Atkinson, R.D., T.S. Baskett, and K.C. Sadler. 1982. Population dynamics of mourning doves banded in Missouri. Spec. Sci. Rept. – Wild. 250. U.S. Fish and Wildlife Service. Washington, D.C. 20 pp.

Ault, J.W., III, V.J. Heller, J.C. Lewis, and J.A. Morrison. 1976. Delayed molt of primary feathers of mourning doves during winter. The Journal of Wildlife Management. 40: 184-187.

Baskett, T.S. and M.W. Sayre. 1993. Characteristics and Importance. Pages 1-6 *in* Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Berdeen, J.B. 2004. Harvest dynamics of mourning doves in the coastal plain of South Carolina. Ph.D. Dissertation. Clemson Univ., Clemson, South Carolina. 195pp.

Blockstein, D.E. 1989. Crop milk and clutch size in mourning doves. Wilson Bulletin. 101: 11-25.

Brownie, C., D.R. Anderson, K.P. Burnham, and D.S. Robson. 1985. Statistical inference from band recovery data – a handbook. Second edition. Resource Pub. 156. U.S. Fish and Wildlife Service. Washington, D.C. 305 pp.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA. 488 pp.

Dinsmore, S.J. and D.H. Johnson. 2005. Population analysis in wildlife biology. Pages 154-184 *in* C.E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Dolton, D.D. 1993. The call-count survey: historic development and current procedures. Pages 233-252 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Dolton, D.D. and R.D. Rau. 2003. Mourning dove population status, 2003. U.S. Fish and Wildlife Service, Laurel, Maryland. 27 pp.

Dolton, D.D. and R.D. Rau. 2004. Mourning dove population status, 2004. U.S. Fish and Wildlife Service, Laurel, Maryland. 19 pp.

Dolton, D.D. and R.D. Rau. 2005. Mourning dove population status, 2005. U.S. Fish and Wildlife Service, Laurel, Maryland. 19 pp.

Dolton, D.D. and R.D. Rau. 2006. Mourning dove population status, 2006. U.S. Fish and Wildlife Service, Laurel, Maryland. 19 pp.

Dolton, D.D., R.D. Rau, and K. Parker. 2007. Mourning dove population status, 2007. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Dolton, D.D., K. Parker, and R.D. Rau. 2008. Mourning dove population status, 2008. Pages 1-21 *in* Mourning dove, white-winged dove, and band-tailed pigeon population status, 2008. U.S. Fish and Wildlife Service, Laurel Maryland, USA.

Eberhardt, L.L. 1971. Population analysis. Pages 457-495 *in* R.H. Giles, Jr., editor. Wildlife management techniques. The Wildlife Society, Washington, D.C.

Fenneman, N.M. 1931. Physiography of western United States. McGraw Hill Book Co., New York. 534 pp.

Haas, G.H. 1977. Unretrieved shooting loss of mourning doves in north-central South Carolina. Wildlife Society Bulletin. 5: 123-125.

Haas, G.H., and S.R. Amend. 1976. Aging immature mourning doves by primary feather molt. The Journal of Wildlife Management. 40: 575-578.

Haas, G.H. 1978. Mourning dove harvest characteristics, survival, and population trend in North and South Carolina. Proc. Ann. Conf. S.E. Assoc. Fish & Wildl. Agencies 32: 280-290.

Haas, G.H., and S.R. Amend. 1979. Primary feather molt of adult mourning doves in North and South Carolina. The Journal of Wildlife Management. 43: 202-207.

Henry, D.L., T.S. Baskett, K.C. Sadler, and W.R. Goforth. 1976. Age and sex selectivity of trapping procedures for mourning doves. The Journal of Wildlife Management. 40: 122-125.

Hickey, J.J. 1955. Some American population research on gallinaceous birds. Pages 326-396 *in* A. Wolfson, ed., Recent studies in avian biology. Univ. Illinois Press, Urbana.

Hines, J. "Patuxent Software Archive." Patuxent Wildlife Research Center. 09 July 2002. U.S. Geological Survey. 01 April 2008.

Kiel, W.H., Jr. 1959. Mourning dove management units – a progress report. Spec. Sci. Rept. – Widl. No. 42. U.S. Fish and Wildlife Service. Washington, D.C. 24 pp.

Lebreton, J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs. 62: 67-118.

Lewis, J.C. and J.A. Morrison. 1973. Efficiency of traps and baits for capturing mourning doves. Wildlife Society Bulletin. 1: 131-138.

Martin, F.W. and J.R. Sauer. 1993. Population characteristics and trends in the Eastern Management Unit. Pages 281-304 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

McGowan, D.P., Jr. 1995. Population dynamics of two local breeding populations of mourning doves in the coastal plain of South Carolina. M.S. Thesis. Clemson Univ., Clemson, South Carolina. 72 pp.

McGowan D.P., Jr., and D.L. Otis. 1998. Population demographics of two local South Carolina mourning dove populations. The Journal of Wildlife Management. 62: 1443-1451.

Meyers, P.M., W.D. Ostrand, M.R. Conover, and J.A. Bissonette. 2006. Assessing differences in mourning dove *Zenaida macroura marginella* nesting activity after 40 years. Wildlife Biology. 12: 171-178.

Miller, M.R., C.L. Stemler, and D.S. Blankenship. 2001. Mourning dove productivity in California during 1992-95: Was it sufficient to balance mortality?. The Journal of Wildlife Management. 65: 300-311.

Mirarchi, R.E. 1993a. Growth, Maturation and Molt. Pages 129-142 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Mirarchi, R.E. 1993b. Aging, sexing and miscellaneous research techniques. Pages 399-408 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Nichols, J.D. and R.E. Tomlinson. 1993. Analyses of banding data. Pages 269-280 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Otis, D.L. 2006. Mourning dove hunting regulation strategy based on annual harvest statistics and banding data. The Journal of Wildlife Management. 70: 1302-1307.

Otis, D.L., J.H. Schulz, D. Miller, R. E. Mirarchi and T. S. Baskett. 2008a. Mourning Dove (*Zenaida macroura*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/117

Otis, D.L., J.H. Schulz, and D.P. Scott. 2008b. Mourning dove (*Zenaida macroura*) harvest and population parameters derived from a national banding study. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R3010-2008, Washington, D.C.

Pollock, K.H., K. Tsai, and J.M. Hoenig. 1994. Band return models: use of solicited bands and separation of hunting and natural mortality. The Journal of Wildlife Management. 58: 193-198.

Pulliam, H.R. 1988. Sources, sinks and population regulation. The American Naturalist. 132: 652-661.

Quay, T.L. 1951. Mourning dove studies in North Carolina. North Carolina Wildlife Resources Commission, Raleigh. 90pp.

Reeves, H.M. 1979. Estimates of reporting rates for mourning dove bands. The Journal of Wildlife Management. 43: 36-42.

Reeves, H.M. 1993. Mourning dove hunting regulations. Pages 429-448 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Reeves, H.M., A.D. Geis, and F.C. Kniffin. 1968. Mourning dove capture and banding. Spec. Sci. Rept. 117. U.S. Fish and Wildlife Service. Washington, D.C. 63pp.

Reeves, H.M. and R.E. McCabe. 1993. Historical perspective. Pages 7-46 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Rexstad, E.A. 1992. Effect of hunting on annual survival of Canada geese in Utah. The Journal of Wildlife Management. 56:297-305.

Roy, C. and A. Woolf. 2001. Effects of hunting and hunting-hour extension on mourning dove foraging and physiology. The Journal of Wildlife Management. 65: 808-815.

SAS Institute, Inc. 2008. SAS user's guide: statistics. Version 9.1.3. SAS Institute, Inc., Cary, North Carolina.

Sauer, J.R., D.D. Dolton, and S. Droege. 1994. Mourning dove population trend estimates from call-count and North American breeding bird surveys. The Journal of Wildlife Management. 58: 506-515.

Sauer, J.R., J. E. Hines, and J. Fallon. 2007. The North American Breeding Bird Survey, Results and Analysis 1966 - 2006. Version 10.13.2007. USGS Patuxent Wildlife Research Center, Laurel, MD.

Sadler, K.C. 1993. Other Natural Mortality. Pages 225-230 *in* T.S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Sayre, M.W. and N.J. Silvy. 1993. Nesting and Production. Pages 81-104 *in* T. S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Scott, D.P, J.B. Berdeen, D.L. Otis, R.L. Fendrick. 2004. Harvest parameters of urban and rural mourning doves in Ohio. The Journal of Wildlife Management. 68: 694-700.

Swank, W.G. 1955. Feather molt as an aging technique for mourning doves. The Journal of Wildlife Management. 19: 412-414.

Taylor, M.H. 1941. Breeding and nesting activities of the eastern mourning dove in North Carolina. M.S. thesis, North Carolina St. Coll., Raleigh. 81pp.

Tomlinson, R.E. 1968. Reward banding to determine reporting rate of recovered mourning dove bands. The Journal of Wildlife Management. 32: 6-11.

Tomlinson, R.E. 1993. Migration. Pages 57-80 *in* T. S. Baskett, M.W. Sayre, R.E. Tomlinson, and R.E. Mirarchi, eds., Ecology and management of the mourning dove. Stackpole Books, Harrisburg, PA.

Weeks, H.P., Jr. 1980. Unusual egg deposition in Mourning Doves. Wilson Bulletin. 92: 258-260.

Westmoreland, D. and L.B. Best. 1987. What limits mourning doves to a clutch of two eggs? The Condor. 89: 486-493.

White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study. 46 (Supplement):S120-S138.

Williams-Dean, G.J. 1978. Ethnobotany and cultural ecology of prehistoric man in southwest Texas. Unpubl. Ph.D. dissertation. Texas A&M Univ., College Station. 302 pp.