ABSTRACT

Title of Thesis: BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*)
POPULATION PRODUCTIVITY AND DENSITY DEPENDENT
EFFECTS IN MICHGAN, 1961-2010

Kendall Lyn Simon, Master of Science, 2013

Thesis directed by: Professor William W. Bowerman
Department of Environmental Science and Technology

The bald eagle (*Haliaeetus leucocephalus*) population in Michigan has undergone a significant recovery following the ban of the pesticide dichlorodiphenyltrichloroethane (DDT), and its subsequent derivatives, mainly dichlorodiphenyl-dichloroethylene (*p,p'*-DDE). This recovery however, has not been uniform throughout the state. Michigan is a heterogeneous habitat, causing the best-fit, experienced breeding pairs to settle in high quality breeding areas first. This high quality habitat mainly occurs in the inland regions of Michigan. These areas experienced the greatest productivity until the 1990's, quickly recovering from the detrimental effects of DDT. Great Lakes breeding areas, particularly Lake Michigan and Lake Huron, are now more productive than inland breeding areas. These Great Lakes breeding pairs however, are the least efficient breeders with greater amounts of changeover between nesting pairs within one breeding area in comparison to inland pairs. A constant turnover of breeding pairs may overshadow any underlying effects causing decreased reproductive fitness in Great Lakes adults.

BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*) POPULATION PRODUCTIVITY AND DENSITY DEPENDENT EFFECTS IN MICHGAN, 1961-2010

by

Kendall Lyn Simon

Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Master of Science
2013

Advisory Committee:

Professor William W. Bowerman
Dr. Jennifer L. Murrow
Professor Mary Ann Ottinger

ACKNOWLEDGEMENTS

For my family who has always been my greatest source of strength and support. I also thank Jessy Beurkens, Michelle Weber, Pete Datema, and Josh Peters for their neverending encouragement and humor. My committee, Dr. William Bowerman, Dr. Jennifer Murrow, and Dr. Mary Ann Ottinger has patiently taught me more than I could imagine throughout these past two years. I am forever grateful to Dr. Bowerman for providing me with continual guidance, confidence, and opportunities throughout my graduate career. Lastly, I thank Teryl Grubb for always offering an optimistic or reassuring thought, especially when I was in need of it the most.

TABLE OF CONTENTS

Page

Chapter One: A REVIEW OF BALD EAGLE (HALIAEETUS LEUCOCEPHALUS) POPULATION PRODUCTIVITY AND RECOVERY IN MICHIGAN, 1961-2010

Chapter Two: BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*) PRODUCTIVITY AND REPRODUCTIVE FITNESS IN MICHGAN, 1961-2010

Table of Contents (continued) Page

Chapter Three: SETTLEMENT PATTERNS AND DENSITY-DEPENDENT EFFECTS IN A RECOVERING BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*) POPULATION IN MICHGAN, 1961-2010

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

FIGURE PAGE

CHAPTER ONE

A REVIEW OF BALD EAGLE (HALIAEETUS LEUCOCEPHALUS) POPULATION PRODUCTIVITY AND RECOVERY IN MICHGAN, 1961-2010

INTRODUCTION: BALD EAGLES AS BIOMONITORS

The bald eagle (*Haliaeetus leucocephalus*) is one of eight sea eagle species found worldwide. A significant portion of the Great Lakes bald eagle population is a non-migratory, year around resident. The bald eagle population in Michigan has undergone a significant recovery following the ban of the pesticide dichlorodiphenyltrichloroethane (DDT), and its subsequent derivatives, mainly dichlorodiphenyl-dichloroethylene (*p,p'*-DDE), by the Environmental Protection Agency in the 1970's (Postupalsky 1978; Grier 1982; Bowerman et al. 1998). Population productivity and recovery however, has been uneven throughout the state of Michigan because of the difference in exposure to environmental contaminants in specific regions (Best et al. 1994; Bowerman et al. 1995; Bowerman et al. 1998).

Bald eagles are tertiary predators with a mainly piscivorous diet, making them an ideal sentinel species to assess contaminant levels in the Great Lakes Basin. Because of the tendency of organochlorine chemicals to bioaccumulate in the adipose tissue of fishes, bald eagles have been proposed as a key wildlife sentinel by the International Joint Commission (IJC 1991; Bowerman et al. 2003). Average core home ranges for adult nesting bald eagles during the breeding period are approximately 4.9 km^2; meaning contaminants accrued from forage ranges are limited to local watersheds (Watson 2002). Nestlings accumulate significant levels of polychlorinated biphenyls (PCBs), *p,p'*-DDE, 2,3,7,8-tetrachlordibenzo-p-dioxin equivalents

(TCDD-EQ) in their tissues and are indicative of aquatic contaminants occurring in the proximate environment (Bowerman et al. 1995; Giesy et al. 1995; Bowerman et al. 1998).

Bald eagles are well-studied and much is known regarding their life history and habitat preferences. Michigan bald eagle reproductive output data has been continuously monitored for 52 breeding seasons in Michigan from 1960-2012. These data provide insight for any population level effects caused by environmental contaminants (Bowerman 2003). This population has been 'measured' through the use of aerial surveys since 1961.). A preliminary survey was conducted by Michigan Department of Natural Resource (MDNR) pilots and contracted observers during egg-laying and incubation periods to document occupancy of breeding areas. A breeding area was considered occupied if one or both adults were attending in close proximity to a nest, if one bird was in incubating posture, a nest had visible repairs/ enlargements or relining with new sticks and bedding material not from the previous breeding season, or if eggs or young were observed (Fraser et al. 1983). A second survey determined nest success or failure. A nest was considered successful if at least one young reached minimum acceptable age for assessing success (Steenhof and Newton 2007). When a breeding area was successful, age and number of nestlings or eggs produced were documented by aerial observers. Coordinates (latitude and longitude) of successful nests were recorded using Global Positioning System (GPS) units. A third survey was conducted when field teams use GPS coordinates to locate and climb a subset of successful nest trees to band nestlings and collect tissue samples for contaminant analysis. The result of the second survey was then corrected based on results of the nest visits (Fraser et al. 1983; Bowerman et al. 1998; Bowerman et al. 2003; Best et al. 2010).

Bald eagle productivity is dependent on three main factors: habitat availability, degree of human disturbance to nesting eagles and, contaminant concentrations in the prey of nesting eagles (Stalmaster 1987). Habitat availability includes any territory unoccupied by another breeding pair. Nesting, perching, and roosting trees, along with foraging territories and a sufficient amount of prey are essential habitat elements for a successful nesting pair. A nesting pair may build several nests in their territory but will only use one per year (Elliott and Harris 2001). Habitat availability has not been a limiting factor for bald eagle populations in Michigan. The Chippewa National Forest in Minnesota however, has experienced decreased productivity, possibly correlated to density dependent factors. This may result in overall lower regional productivity (Bowerman 1993; Mathisen et al. 1993; Bowerman et al. 1995)

Human disturbance leading to nest abandonment is dependent on the type, degree, amount and timing of each disturbance (Bowerman et al. 1995). Aquatic and aircraft activities elicit the most frequent responses caused by human disturbance in breeding bald eagles. Pedestrian, vehicular and ground-related activities caused the most severe disturbances and may pose the most threat to breeding bald eagles. These intense and frequent disturbances near breeding bald eagles or their habitat can modify adult behavior and often result in lower productivity (Grubb et al. 1992).

Lastly, concentrations of environmental contaminants, namely *p,p'*-DDE and PCBs, must be below the no observable adverse effect concentration (NOAEC). Concentrations above the NOAEC threshold are associated with decreased productivity, addled eggs or egg lethality, and congenital malformations. Currently, persistent chlorinated hydrocarbons in the environment are the main factor limiting the Michigan bald eagle population (Best et al. 1994; Bowerman et al. 1994; Bowerman et al. 1995; Bowerman et al. 2002; Best et al. 2010).

Eagles nesting within 8.0 km of the Great Lakes shorelines have greater PCB and *p,p'*-DDE concentrations, and decreased productivity rates than those nesting in more interior regions (Bowerman.1993; Wierda 2009). Hazard assessments conducted on anadromous-accessible rivers below barrier dams indicate that concentrations of PCBs and TCDD-EQ in fishes downstream of dams pose a risk to bald eagles foraging on those waterways (Best et al. 1994; Giesy et al. 1994; Bowerman et al. 1995; Datema 2012). Because poor productivity in these areas is inversely correlated with high contaminant concentrations, these breeding areas act as a “population sink” despite the historic abundance of unoccupied nesting habitat in these areas. Interior breeding areas, where contaminant concentrations are below the NOAEC act as a “population source” (Bowerman et al. 2003). Density dependent factors in highly productive interior breeding areas such as the Chippewa National Forest provide uncontaminated breeding eagles to “population sink” areas along the Great Lakes shorelines and anadromous-accessible rivers. Modeling population dynamics in these areas is difficult because of increased adult mortality and depressed productivity while significant immigration of young, inexperienced replacement adults is occurring (Kozie and Anderson 1991; Best et al. 1994; Bowerman 1995; Bowerman et al. 1998; Best et al. 2010)

STUDY AREA

My study area consisted of all bald eagle breeding areas within the state of Michigan. Breeding areas served as the sampling unit for all analyses. Breeding areas were divided and compared on multiple spatial and temporal scales. An overall productivity analysis was first performed on all breeding areas throughout the state. I then divided the state into three geographic scales that further compared productivity among subregions within the state.

Category

The first geographic scale classification was Category which compared Great Lakes (GL) to Inland (IN) breeding areas. All areas within 8.0 km Great Lakes shorelines, as well as tributaries open to passage of Great Lakes fishes were considered GL breeding areas. All areas greater than 8.0 km from Great Lakes shorelines and tributaries open to the passage of Great Lakes fishes were considered IN breeding areas (Bowerman et al. 1994; Bowerman et al. 2003; Wierda 2009).

Subpopulation

The Subpopulation geographic scale subdivided the Category spatial scale into four GL and two IN groups. Historically, IN subpopulations have been shown to recover quicker than GL Subpopulations. This geographic scale was used to determine specifically which GL Subpopulations recovered following IN Subpopulations. The GL Subpopulations consisted of Lake Superior (LS), Lake Michigan (LM), and Lake Huron (LH). The IN Subpopulations consisted of Upper Peninsula (UP), and Lower Peninsula (LP). (Best et al. 1994; Bowerman et al. 2003). Lake Erie was removed from all analyses due to small sample sizes.

Watersheds

The Michigan Watershed spatial scale divided breeding areas based on Great Lakes Watersheds. Lake Huron Inland (LH IN), Lake Michigan Inland Lower Peninsula (LM IN LP), Lake Michigan Inland Upper Peninsula (LM IN UP), and Lake Superior Inland (LS IN) represent all IN breeding areas. LM IN was divided into UP and LP because of the large spatial distance and difference in historic recovery between both substantial breeding area watersheds. The LM IN Watershed was divided into Upper and Lower Peninsulas for productivity analysis only. Lake Huron Great Lake (LH GL), Lake Michigan Great Lake (LM GL), and Lake Superior Great Lake (LS GL) breeding areas represented GL breeding areas. (Wierda 2009).

OBJECTIVES

The overall objective of this study was to determine recovery and productivity patterns accross various geographic scales within the state of Michigan for 1961-2010 breeding areas. These patterns will give insight into the spatial and temporal trends of the bald eagle population throughout Michigan. Chapter Two has four objectives for assessing Great Lakes productivity patterns by determining: (1) spatial and temporal productivity patterns, (2) evidence of recent “population sink” or “source” breeding areas , (3) the effects of the length of site occupancy on productivity and success, and (4) reproductive fitness of breeding adults by comparing length of site occupancy and decadal success rate between bald eagle Subpopulations. Chapter Three has three objectives for identifying the existence of density dependent factors in inland breeding areas by determining whether: (1) Michigan bald eagles are following settlement patterns according to the Habitat Heterogeneity Hypothesis or the Individual Adjustment Hypothesis (2) if an increase in breeding area intersect is negatively correlated to productivity, and (3) if breeding area distance to refugia, or remnant populations, impacted population recovery.

CHAPTER TWO

BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*) PRODUCTIVITY AND REPRODUCTIVE FITNESS IN MICHGAN, 1961-2010

INTRODUCTION

The bald eagle (*Haliaeetus leucocephalus*) is one of eight sea eagle species found worldwide. A significant portion of the Great Lakes bald eagle population is non-migratory, year-round residents. The bald eagle population in Michigan has undergone a significant recovery following the ban of the pesticide dichloro-diphenyl-trichloroethane (DDT), and its subsequent derivatives, mainly dichlorodiphenyl-dichloroethylene (*p,p'*-DDE), by the Environmental Protection Agency in the 1970's (Postupalsky 1978; Grier 1982; Bowerman et al. 1998). Population productivity and recovery however, have been uneven throughout the state of Michigan because of the higher load and persistence of contaminants in specific regions (Best et al. 1994; Bowerman et al. 1995; Bowerman et al. 1998).

Bald eagles are tertiary predators with a mainly piscivorous diet, making them an ideal sentinel species to assess contaminant levels in the Great Lakes Basin. Because of the tendency of organochlorine chemicals to bioaccumulate in the adipose tissue of fishes, bald eagles have been regarded as a key wildlife biomonitor in within the Great Lakes by the International Joint Commission (IJC 1991; Bowerman et al. 2003). Average core home ranges for adult nesting bald eagles are approximately 4.9 km^2, meaning foraging ranges are limited to local watersheds (Watson 2002). Nestlings accumulate significant levels of polychlorinated biphenyls (PCBs), *p,p'*-DDE, 2,3,7,8-tetrachlordibenzo-p-dioxin equivalents (TCDD-EQ) in their tissues, indicative of aquatic contaminants occurring in the proximate environment (Bowerman et al. 1995; Giesy et al. 1995; Bowerman et al. 1998).

Bald eagle productivity monitoring in Michigan has been continuous for 52 breeding seasons. These data provide insight for any population level effects caused by environmental contaminants (Bowerman 2003). Eagles nesting within 8.0 km of the Great Lakes shorelines have greater PCB and *p,p'*-DDE concentrations, and decreased productivity rates than those nesting in more interior regions (Best et al. 1994; Giesy et al. 1994; Bowerman et al. 1995; Datema 2012). Contaminated adults that originated from these areas may contribute to a decreased rate of recovery because of their inability to reproduce at sufficient levels to support a healthy population (Wierda 2009).

Because poor productivity along regions of the Great Lakes shorelines has been inversely correlated with high contaminant concentrations, these breeding areas act as a “population sink” (Bowerman et al. 2003). Population sinks are considered habitat in which some reproduction occurs but is not sufficient to match mortality; productivity is greater than zero but less than 0.70 (Sprunt et al. 1973). Interior breeding areas act as a “population source”. Population sources are considered habitat in which reproduction exceeds mortality; productivity is greater than one (Danielson 1992). Density dependent factors in highly productive interior breeding areas such as the Chippewa National Forest, Minnesota, may provide uncontaminated breeding eagles to population sinks areas along the Great Lakes shorelines and anadromous-accessible rivers (Bowerman 1993).

Many studies have established that adult survivorship and subadult survivorship have the most profound influence on population sensitivity models, whereas nest success and reproductive rates are comparatively insignificant within the same analyses.

Population dynamics therefore, are more dependent on survival rather than reproduction (Newton 1979; Grier 1980; Stalmaster 1987). Historically decreased recovery rates in highly contaminated areas such as near the Great Lakes shorelines or anadromous-accessible rivers below barrier dams may be because of an increased adult mortality, chronic inability to reproduce, decreased attempts to reproduce or abnormalities in parental behavior by adults in these regions (Grasman et al. 1998; Elliott and Harris 2001). Modeling population productivity in these areas is difficult when significant immigration of young, inexperienced replacement adults is occurring (Kozie and Anderson 1991; Best et al. 1994; Bowerman 1995; Bowerman et al. 1998; Best et al. 2010). In this study, I compared the reproductive fitness of breeding pairs through the length of time one breeding pair occupies one breeding area, and the decadal success rate, or the percentage of productive years per breeding attempt. Breeding areas with a decreased length of site occupancy or decadal success rate may be experiencing chronic inabilities to reproduce (Grasman et al. 1998; Elliott and Harris 2001).

Chapter Two has four objectives for assessing Great Lakes productivity patterns by determining: (1) spatial and temporal productivity patterns, (2) evidence of “population sink” or “source” breeding areas, (3) the effects of the length of site occupancy on productivity and success, and (4) reproductive fitness of breeding adults by comparing length of site occupancy and decadal success rate between bald eagle Subpopulations.

STUDY AREA

My study area consisted of all bald eagle breeding areas within the state of Michigan. Michigan is surrounded by four of the five Laurentian Great Lakes: Lake Michigan, Lake Superior, Lake Huron and Lake Erie (Figure 3.1). Michigan's geomorphology is classified as Central Lowland plains. Elevations range from 175 to 396 m and 176 to 256 m in the Lower and Upper Peninsulas of Michigan, respectively. Low gradient streams drain into Lakes Superior, Michigan, and Huron in the Upper Peninsula, and into Lakes Michigan, Huron and Erie in the Lower Peninsula. Streams within the southernmost portion of both peninsulas drain into the Ohio-Mississippi drainages. Small to medium lakes are present but not abundant in the Lower Peninsula, while numerous lakes and wetlands are found in low lying areas in the Upper Peninsula. Wetlands may seasonally flood in low-lying glacial lakebeds (McNab and Avers 1994; Wierda 2009).

Vegetation along the southern shore of Lake Superior is dominated by aspen (*Populus grandidentata, P. tremuloides),* spruce (*Picea mariana, P. glauca*), and balsam fir (*Abies balsamea*). The shores of Lakes Michigan and Huron are dominated by maple (*Acer rubrum, A. saccharum*), oak (*Quercus rubra, Q. alba*), and pine (*Pinus strobus, P. banksiana, P. resinosa*). Southern shores of Lakes Michigan, Huron and Erie are mainly dominated by mixed-cover and oak forests (Bowerman 1993).

METHODS

Surveys

Occupancy and reproductive success for the bald eagle population of Michigan has been measured annually with aerial surveys since 1961. A breeding area (or nesting territory) was defined as an area that contains, or historically contained, one or more nests within the home range of a mated pair: a confined locality where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time (Steenhof and Newton 2007). A preliminary survey was conducted by Michigan Department of Natural Resource (MDNR) pilots and contracted observers during egg-laying and incubation periods to document occupancy of breeding areas. A breeding area was considered occupied if one or both adults were attending in close proximity to a nest, if one bird was in incubating posture, a nest had visible repairs/ enlargements or relining with new sticks and bedding material not from the previous breeding season, or if eggs or young were observed (Fraser et al. 1983). A second survey determined nest success or failure. A nest was considered successful if at least one young reached minimum acceptable age for assessing success (Steenhof and Newton 2007). When a breeding area was successful, age and number of nestlings or eggs produced were documented by aerial observers. Coordinates (latitude and longitude) of successful nests were recorded using Global Positioning System (GPS) units. A third survey was conducted when field teams use GPS coordinates to locate and climb a subset of successful nest trees to band nestlings and collect tissue samples for contaminant analysis. The result of the second survey was then corrected based on results of the nest visits (Fraser et al. 1983; Bowerman et al. 1998; Bowerman et al. 2003; Best et al. 2010).

Breeding areas served as the sampling unit for all analyses. Breeding areas were divided and compared on multiple spatial and temporal scales. An overall productivity analysis was first performed on all breeding areas throughout the state. I then divided the state into three geographic scales that further compared productivity among subregions within the state.

Category

The first geographic scale classification was Category which compared Great Lakes (GL) to Inland (IN) breeding areas. All areas within 8.0 km Great Lakes shorelines, as well as tributaries open to passage of Great Lakes fishes are considered GL breeding areas. All areas greater than 8.0 km from Great Lakes shorelines and tributaries open to the passage of Great Lakes fishes are considered IN breeding areas (Bowerman et al. 1994; Bowerman et al. 2003; Wierda 2009; Figure 2.1).

Subpopulation

The Subpopulation geographic scale subdivided the Category spatial scale into four GL and two IN groups. Historically, IN subpopulations have been shown to recover quicker than GL Subpopulations (Best et al. 1994; Bowerman et al. 2003). This geographic scale was used to determine specifically which GL Subpopulations recovered following IN Subpopulations. The GL Subpopulations consisted of Lake Superior (LS), Lake Michigan (LM), and Lake Huron (LH). The IN Subpopulations consisted of Upper Peninsula (UP), and Lower Peninsula (LP) (Figure 2.2). Lake Erie was removed from all analyses due to small sample sizes.

Watersheds

The Watershed spatial scale divided breeding areas based on Great Lakes Watersheds. Lake Huron Inland (LH IN), Lake Michigan Inland Lower Peninsula (LM IN LP), Lake

Michigan Inland Upper Peninsula (LM IN UP), and Lake Superior Inland (LS IN) represent all IN breeding areas. LM IN was divided into UP and LP because of the large spatial distance and difference in historic recovery between both substantial breeding area watersheds. The LM IN Watershed was divided into Upper and Lower Peninsulas for productivity analysis only. Lake Huron Great Lake (LH GL), Lake Michigan Great Lake (LM GL), and Lake Superior Great Lake (LS GL) breeding areas represented GL breeding areas. (Wierda 2009; Figure 2.3).

Productivity Data

Bald eagle population definitions and calculations followed the methodology of Postupalsky (1974) and Steenhof and Newton (2007). Productivity was defined as the number of young that reach the minimum acceptable age for assessing success; usually reported as the number of young produced per territorial pair or per occupied territory in a particular year (Steenhof and Newton 2007). Productivity rate was calculated as the total number of fledged young per occupied breeding territory divided by the total number of years occupied within each five year increment. Nests had to be active for at least 3 of the five possible years to be considered an active breeding area. A productivity rate of 1.0 or greater was indicative of a growing population. A productivity rate of 0.70 was representative of a stable population. A productivity rate of below 0.70 was indicative of a declining population (Sprunt et al. 1973).

Productivity was calculated for Category, Subpopulation, and Watershed. Data from 1961-2010 were divided into ten periods by five-year increments; Period One: 1961-1965, Period Two: 1966-1970.....Period Ten: 2006-2010. Bald eagle reproductive rates were averaged between five-year periods to accommodate the effects of yearly variations in weather (Wiemeyer et al. 1993).

Length of Site Occupancy

Length of site occupancy was defined as the mean number of years one breeding pair occupied one breeding area between breeding pair changeovers. Active years was the number of years one breeding pair attempted to reproduce in a breeding area. A minimum of three consecutive years occupancy was considered the same breeding pair. Three or more consecutive inactive years was considered to be a change in breeding pairs.

Decadal Success Rate

The number of years a breeding pair occupied a breeding area was determined from 1981 to 2010, when the bald eagle population had recovered from acute lethal effects. The Decadal Success Rate was used during this time period to determine evidence of chronic reproductive ability between breeding pairs. Three or more inactive years constituted a change in breeding pairs. Mean number of years between changeovers, referred to as the length of site occupancy, was determined between GL and IN breeding areas. The Decadal Success Rate for breeding areas from 1981-2010 was determined for GL and IN breeding areas. To analyze trends, 1981-2010 was divided into decades: 1981-1990, 1991-2000, 2001-2010, and the Decadal Success Rate was calculated with the following equation:

$$\text{Decadal Success Rate} = \#\text{ Years Productive} / \#\text{ Years Active}$$

Assumptions/ Biases

We are not able to locate and track the yearly movements of individual fledglings or breeding adults/ pairs. Because of this, we cannot make certain predictions as to the degree of philopatry, immigration/ emigration, home ranges, and yearly return/ turnover rates within the Michigan bald eagle population, biasing productivity data. The arbitrary boundaries differentiating Category, Subpopulation, and Watershed subregions may also bias productivity results. Furthermore, the assumption that three consecutive occupied years constitutes the same breeding pair or three consecutive inactive years constitutes a change in breeding pairs within one breeding area may biase length of site occupancy and decadal success rate results.

Statistical Analysis

Statistical Analysis was performed using SAS® 9.2 statistical package (SAS Institute Inc., 2009). Productivity was initially compared for Category, Subpopulation, Watershed and Period using analysis of variance (ANOVA) to determine significant differences. When significant differences were detected, a post-hoc analysis using generalized linear mixed model (GLIMMIX) was conducted to determine spatial and temporal significant differences between Category, Subpopulation, Watershed and Period. A generalized linear mixed model was also used to determine significant differences within decades for reproductive fitness analyses.

RESULTS

Productivity was significantly different between Periods (F = 15.46, df = 9, $p < 0.0001$). Productivity increased sequentially for all Periods except Period Nine, where it dropped to levels prior to Period Five (Figure 2.4).

Category

IN and GL breeding areas experienced a significantly different cumulative productivity when compared over the entire 50 year period (F = 13.55, df = 1, 2451, p = 0.0002). The number of productive IN and GL breeding areas increased from 100 to 634, and 86 to 629, respectively. Productivity for IN and GL breeding pairs increased from 0.61 to 1.04 and 0.22 to 1.06, respectively.

Productivity between GL and IN breeding areas within each 5 year Period was uneven. IN breeding areas were significantly more productive than GL breeding areas during Periods 1-7. Productivity between GL and IN becomes non-significant for Periods Eight, Nine, and Ten (Table. 2.1). The highest producing were IN Period Seven (1.07), GL Period Ten (1.06), IN Period Eight (1.03), and IN Period Ten (1.01; Figure 2.5).

When the rate of change between IN and GL productivity was compared, GL indicated a greater overall positive rate of change between all Periods. The greatest GL rate of change productivity increase occurred between Periods Two and Three. The greatest IN rate of change productivity increase occurred between Periods Three and Four. IN breeding areas experienced a greater negative rate of change than GL breeding areas between Periods Eight and Nine (Table 2.2)

Subpopulation

Productivity was uneven throughout the 50 year period with UP and LP Subpopulations recovering before GL Subpopulations. There were significant differences among Subpopulation productivity within the 50 year period (F = 7.25, df = 2, 2448, P < 0.0001). LP had the greatest collective productivity of .99 from 752 breeding areas. UP had most breeding areas (n = 875) with a productivity of 0.92. LS was the least successful with a productivity of 0.79.

Productivity among Subpopulations was also uneven within each 5 year Period. Significant differences among Subpopulations were found within Periods One (F = 3.08, df = 4, 94, p = 0.0197),Two (F = 5.50, df = 4, 99, p = 0.0005), Four (F = 3.34, df = 4, 93, p = 0.0134), Five (F = 5.07, df = 4, 124, p = 0.0008), Six (F = 3.88, df = 4, 184, p = 0.0048), and Seven (F = 4.83, df = 5, 265, p = 0.0009, and Eight (F = 2.46, df = 4, 353, p = 0.0449; Table 2.3).

Parallelisms

IN Subpopulations were the first to recover, particularity UP with a productivity greater than 0.70 in Period Three and 1.00 in Period Five (Figure 2.6). LP was then the most successful of all Subpopulation and Periods with a productivity of 1.11, 1.20, and 1.13 during Periods Six, Seven, and Eight, respectively. LS was the first GL Subpopulation to recover, reaching a productivity greater than 7.0 during Period Five. LM and LH are now the most productive Subpopulations with a productivity of 1.10 and 1.08, respectively, during Period Ten. Productivity decreased to less than 1.0 for all Subpopulations during Period Nine.

Watershed

Productivity was uneven throughout the 50 year period with IN Watersheds experiencing higher productivity until Period Ten, when GL Watersheds became more productive. There were significant differences among cumulative productivity of Watersheds within the 50 year period (F = 4.72, df = 6, 2446, P = <0.0001).

Productivity among Watersheds was also uneven within each 5 year Period. Significant differences among Watersheds were found within Periods Two (F = 4.33, df = 6, 97, p = 0.0006), Four (F = 2.96, df = 6, 91, p = 0.0110), Five (F = 3.33, df = 6, 122, p = 0.0045), Six (F = 2.90, df = 6, 182, p = 0.0100), and Seven (F = 3.22, df = 6, 263, p = 0.0046; Table 2.4).

Parallelisms

IN and GL Watersheds varied in productivity throughout the 50 year period. LH IN experienced the greatest IN productivity during Periods Six, Seven, Eight and Ten (Figure 2.7). LH GL increased in productivity from Period Three until Period Six despite only marginally greater numbers of active breeding areas (Figure 2.8). LM IN, particularly LM IN UP, contained the greatest number of productive breeding areas throughout all Periods. LM IN LP was the least productive IN Watershed prior to Period Five and then became the most productive IN Watershed following Period Five. LM GL was the most productive GL Watershed from Period Seven through Ten (Figure 2.8). LS IN became the least productive, though not statistically significant, of all Watersheds during Periods Nine and Ten. LS GL was the greatest producing Watershed from Period

One until Period Six. It then became the least productive Watershed from Period Seven until Period Ten (Figure 2.9).

Length of Site Occupancy

IN breeding areas had a significantly longer length of site occupancy than GL breeding areas during Decade One ($F = 5.96$, df = 1, 613, $p = 0.0150$), Decade Two ($F = 3.91$, df = 1, 345, $p = 0.0488$), and Decade Three ($F = 11.81$, df = 1, 174, $p = 0.0007$). Length of site occupancy was also significantly different among Watersheds within Decade One ($F = 2.85$, df = 5, 609, $P = 0.0149$), and Decade Three ($F = 3.35$, df = 5, 170, $P = 0.0065$; Table 2.5).

Length of site occupancy is decreasing over time in GL Watershed in comparison to IN Watersheds. Among all Watersheds and Decades, GL breeding areas had shorter site occupancy during Decade Three than during Decade One, IN ($t = 6.22$, df = 483, $p < .0001$), GL ($t = 5.41$, df = 483, $p < .0001$), Decade Two IN ($t = -6.61$, df = 483, $p < .0001$), GL ($t = -4.03$, df = 483, $p < .0001$), and Decade Three IN ($t = -5.36$, df = 483, $p < .0001$; Figure 2.10). During Decade Three, LH GL had a significantly short length of site occupancy than LH IN ($t = -3.00$, df = 170, $p = 0.0031$), LM IN ($t = -3.25$, df = 170, $p = 0.0014$), LS IN ($t = -3.21$, df = 170, $p = 0.0016$), and LS GL ($t = -2.13$, df = 170, $p = 0.0348$). LM GL also had a significantly shorter length of site occupancy than LH IN ($t = -2.06$, df = 170, $p = 0.0411$), LM IN ($t = -2.28$, df = 170, $p = 0.0241$), and LS IN ($t = -2.30$, df = 170, $p = 0.0229$).

Decadal Success Rate

IN breeding pairs were more productive per breeding attempt than GL breeding pairs. IN breeding areas had a greater Decadal Success Rate than GL breeding areas during Decade Two (F = 12.28, df = 1, 345, p = 0.0005) and Decade Three (F = 30.13, df = 1, 174, p < .0001).

Decadal Success Rates varied among Watersheds. All Watersheds achieved a similar decadal success rate during Decade One. The rate divergence between Watersheds increased to a level of significance during Decade Two (F = 3.22, df =6, 344, P = 0.0043; Figure 2.11) and Decade Three (F = 6.15, df = 6, 170, p < 0.0001; Figure 2.12; Table 2.6). LH GL and LM GL first experienced the highest decadal success during Decade One. By Decade Three however, these Watersheds experienced the least decadal success rates meaning that they are least reproductively successful per breeding attempt, or the least efficient breeders.

DISCUSSION

Category

Multiple factors can be attributed to the uneven recovery of the Michigan bald eagle population including food supply, weather, age, predation, persecution, and habitat destruction (Best et al. 2010). Varying chlorinated hydrocarbon concentrations however, have been the leading factor affecting spatial and temporal trends in population recovery (Bowerman 2003). The GL bald eagle breeding areas along the shorelines of Lakes Superior, Michigan, Huron, and Erie have historically experienced less productivity than IN breeding areas because of higher concentrations of contaminants (Bowerman et al.

1995). The most recent data from 2003 continue to demonstrate this trend, indicating that GL breeding areas continue to act as a population sink, with a decreased productivity caused by the effects of PCBs and *p,p'*-DDE (Bowerman et al. 2003).

A recovering population of peregrine falcon (*Falco peregrinus*) in California showed a similar source-sink dichotomy between interior and coastal Subpopulations. The peregrine coastal Subpopulation was a sink until the early 1990's when vigorous management and introductions occurred. The interior population had recovered quickly, followed by a declining growth rate upon saturation. This decline was attributed to an increasing proportion of nonbreeders (territorial pairs that do not produce eggs; Steenhof and Newton 2007) and limited territory availability. Population projections indicate that the recovery of the coastal Subpopulation would have failed without management intervention, and dispersal from the interior Subpopulation. This study also noted that interior birds exhibited little propensity for dispersal to coastal habitat, preferring to wait years to acquire a breeding site in their natal habitat despite the abundance of high quality coastal habitat (Kauffman et al. 2004).

Much like this peregrine population, IN bald eagles exhibiting similar affinity to natal habitat could be reluctant to nest in GL breeding areas. This would, in part, explain the delayed recovery in GL breeding areas. Variation of age at first reproduction in IN juveniles may also contribute to the population persistence at carrying capacity, circumventing density dependent effects that would normally force breeding pairs to settle in GL habitat (Ferrer et al. 2004).

The discrepancy in productivity between GL and IN breeding areas lessened between Period Seven (1991-1995) and Period Ten (2006-2010). Bald eagle productivity in IN breeding areas peaked at 1.07 during Period Seven (Figure 2.5). IN populations began to stabilize or decline following Period Seven, whereas GL breeding populations continued to increase. IN breeding areas may have reached saturation during these periods. Saturated bald eagle populations in Southeast Alaska have increased competition for resources between breeders and nonbreeders, thereby decreasing overall productivity (Hansen 1987). A stable population of bald eagles can have 45-51% of nonbreeders (Kenward et al. 2000). The prevalence of nonbreeders within IN breeding areas may have simultaneously furthered the stabilization of IN productivity by forcing breeding pairs to nest in unoccupied GL breeding areas, thereby increasing GL productivity.

Productivity in IN and GL breeding areas decreased during Period Nine (2001-2005). The cause of this decline is difficult to explain. Variable weather events such as wind and snow storms during sensitive breeding and brooding periods may have caused widespread nest failure. Drought during these years could have decreased prey abundance, impacting parental energetics and ability to support multiple nestlings. IN and GL both recovered in Period Ten. IN breeding areas continued to outnumber GL areas by Period Ten. GL breeding areas however, achieved a greater productivity in comparison to IN breeding areas by Period Ten, indicating a substantial recovery from previous impaired reproduction.

Subpopulation

Inland subpopulations, particularly UP, were the first to recover until Period Five. UP seemed to be least affected by the deleterious effects caused by environmental contaminants. Lake Superior was also the first GL Subpopulation to recover. The remoteness of UP and LS within the Upper Peninsula of Michigan could have resulted in minimal direct exposure to DDT within these areas. These results are in agreement with previous studies establishing the delayed recovery of GL breeding areas due higher contaminant concentrations (Bowerman et at. 1998; Bowerman et al. 2003). Higher contaminant concentrations in GL breeding areas may have negatively affected parental abilities to forage. Bald eagles nesting on the shores of Lake Superior have been shown to have significantly lower prey delivery rates than Inland nesting birds, resulting in a lower productivity (Dykstra et al. 1998). Analogous to Category results, Subpopulations indicated a significant decrease in productivity during Period Nine. Because all Subpopulations were equally affected, westerly weather or lake-effect snow storms were not likely to be the cause of nest failures during Period Nine. Additionally, the greater negative rate of change for IN breeding areas indicates that GL breeding areas were less affected than IN breeding areas by the weather events occurring between Periods Eight and Nine.

Watershed

Steep gradients in habitat quality have been widely recognized to mediate population dynamics and settlement patterns (Kauffman et al. 2004). Recovering bald eagle population generally followed the Ideal Pre-emptive Distribution in which the most fit breeding pairs select the highest quality habitat first (Pulliam and Danielson 1991; Krüger and Lindström 2001), resulting in high quality source and low quality sink populaitons (Kauffman et al. 2004). Habitat variation may further enhance interactions between stochastic environments, density-dependent factors, and disturbance (Thomas et al. 1996), causing spatial and temporal transitions in source-sink dynamics (Watkinson and Sutherland 1995; Kauffman et al. 2004).

The highest quality source territories were IN breeding areas, particularly LS, until Period Six. Following Period Six, LH and LM UP became source populations as the most productive IN Watersheds. LM IN Watersheds provided high quality nesting habitat, supporting the largest number of breeding areas throughout all Periods. Being the greatest producing watersheds during Period Ten, LM GL and LH GL appear to have recovered from the deleterious reproductive effects caused by DDT and its subsequent derivatives. All Watersheds, with the exception of LS IN, experienced a productivity of greater than 1.0 during Period Ten. This indicates that these Watersheds continue to support an increasing breeding bald eagle population (Sprunt et al 1973).

Length of Site Occupancy

GL breeding pairs experienced a decreased length of site occupancy by Decade Three, indicating the length of time GL breeding pairs are reproductively capable has shortened. This also indicated that turnover rates between adult breeding pairs within one breeding area must increase to sustain productivity levels. Site occupancy has been used as a measure of territory quality in black kite (*Milvus migrans*) populations. Infrequently occupied breeding territories with low food availability and high predation rates resulted in decreased breeding success, adult survival, and long-term nest viability, leading to nest abandonment. Because these territories were of unvaryingly lower quality, they were more frequently occupied by younger individuals arriving later in the season (Francis and Cooke 1986; Sergio and Newton 2003). Spanish Imperial Eagles (*Aquila adalberti*) abandon a territory after a breeding failure and subsequently move to a higher quality area, contributing to a higher variation in local population productivity (Ferrer and Donazar 1996, Forero et al. 1999). The shortened length of site occupancy in GL breeding areas indicates poor quality habitat or accumulating contaminant burdens in adult breeding pairs, leading to chronic effects of shortened reproductive ability. An increase in young, inexperienced eagles attempting to breed in GL territories, especially LH GL and LM GL, may also exaggerate nest failures, leading to a shortened length of site occupancy and increase in breeding pair turnover rates during Decade Three.

Decadal Success Rate

Survival and lifespan are usually limiting factors determining the variance in lifetime reproductive success of long-lived, slow-reproducing birds, such as bald eagles, with delayed breeding (McIntyre et al. 2006). Bald eagles originating from GL breeding areas, specifically LM and LH between 2001-2010 however, may experience 'residual' reproductive effects, not necessarily indicative of their current body burden, limiting lifetime breeding success. *In ovo* or early developmental exposure, leading to 'second generation' effects, have been suggested as a cause for depressed productivity in Northern California bald eagle populations despite declines in body contaminant burdens (Risebrough 1988; Elliot and Harris 2001). Delayed or shortened reproductive capability may be a residual effect causing shortened site occupancy and a reduced decadal success rate in GL breeding areas. Spanish Imperial Eagles are highly philopatric, with 84% of breeders return to their natal population within Doñana National Park (Ferrer and Donazar 1996). These decreased reproductive effects will be particularly evident if LH and LM GL fledglings with *in ovo* contaminant exposure, leading to decreased reproductive abilities, exhibit a comparable degree of natal philopatry as the Spanish Imperial Eagles in Doñana National Park when returning to breed.

Another residual, chronic reproductive effect in GL breeding areas leading to nest failures may be contaminant-induced abnormalities in parental behavior (Grasman et al. 1998). Contaminated breeding adults in a herring gull (*Larus smithsonianus*) colony on Lake Ontario left their nests unattended three times longer than uncontaminated adults, resulting in a 1^{0}C lower average egg temperature and greater vulnerability to predation. Altered parental behavior in GL breeding areas could cause more nest failures per breeding attempt, decreasing Decadal Success.

IN Watersheds, specifically LH IN, are not experiencing chronic reproductive effects. IN Watersheds may also be more efficient, with longer lengths of site occupancy caused by a greater percentage of experienced or best-fit adults in high quality territory.

Despite low reproductive fitness, LM and LH GL were the most productive Watersheds from 2006-2010. GL Watersheds also increased from 185 breeding areas in Period Nine to 265 breeding areas in Period Ten. The demographic contribution of floaters (birds capable of breeding but not able to secure the habitat and forage base to do so; Evans et al. 2009) and nonbreeders may compensate for residual reproductive inability or adult mortality because of contaminants in GL breeding areas, buffering productivity (Penteriani et al. 2005). The low reproductive fitness, yet high productivity of GL breeding areas is suggestive of a high turnover rate within the GL breeding population. A high population turnover rate, along with the substantial increase in breeding areas, could be masking chronic reproductive effects or loss of breeding adults.

Increased productivity within bald eagle populations on the southern shore of LS were attributed to a younger breeding population, with low contaminant levels, dispersing from the IN population (Kozie and Anderson 1991).

CONCLUSION

GL breeding areas are now more productive than IN breeding areas. Decreased length of site occupancy and decadal success rates however, may be causing GL breeding areas to still be experiencing chronic reproductive effects, making them dependent on immigration of adults from IN source populations. High turnover rates of adults in GL breeding areas, resulting in greater productivity, may overshadow any underlying effects causing decreased reproductive fitness in GL breeding adults. Survival rate comparisons should be made between GL and IN breeding adults to further determine the health and status of the Michigan bald eagle population.

CHAPTER THREE

SETTLEMENT PATTERNS AND DENSITY-DEPENDENT EFFECTS IN A RECOVERING BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*) POPULATION IN MICHGAN, 1961-2010

INTRODUCTION

The bald eagle (*Haliaeetus leucocephalus*) population in Michigan has undergone a significant recovery following the ban of the pesticide dichloro-diphenyl-trichloroethane (DDT) and its derivatives, mainly dichlorodiphenyl-dichloroethylene (*p,p'*-DDE), by the Environmental Protection Agency in the 1970's (Postupalsky 1978; Grier 1982; Bowerman et al. 1998). Bald eagle populations in the U.S. have increased an average of 8% annually since an estimated low of 417 total pairs in 1963 (Sprunt 1963; Watts et al. 2005). As a result of this substantial increase in breeding populations, the bald eagle was reclassified from endangered to threatened in 1995 (Millar 1995) and then removed from the federal list of threatened and endangered species by the U.S. Fish and Wildlife Service (USFWS) in 2007 (USFWS 2010).

Recovering raptor populations follow definitive settlement patterns according to the Ideal Pre-emptive Distribution Hypothesis (IPD). IPD assumes that the superior breeding pairs (experienced or dominant) select the highest quality habitat first, rendering it unavailable (Pulliam and Danielson 1991; Krüger and Lindström 2001). High population densities could lead to breeding pairs nesting in poor quality habitats in a heterogeneous environment. The Habitat Heterogeneity Hypothesis (HHH) suggests that mean fecundity will be reduced in a density dependent population in which inferior breeding pairs (inexperienced or subordinate) select suboptimal habitat, lowering breeding success. Opposed to this theory, the Individual Adjustment Hypothesis (IAH) or interference competition hypothesis states that as a response to increasing population densities, all habitat and resources are affected equally (Ferrer et al. 2006). This forces individuals to adjust their behavior, causing more agonistic encounters and an overall decrease in fecundity. (Fernandez et al. 1998; Krüger and Lindström 2001; Sergio and Newton 2003; Ferrer et al. 2006). Mean productivity in populations consistent with the HHH is typically negatively correlated with its coefficient of variation. This infers that high quality breeding areas will result in little year-to-year variation in productivity; as density increases, variation in productivity will increase with the addition of progressively poorer breeding areas (Sergio and Newton 2003).

Historically, lower quality habitat in Michigan is considered to be coastal regions within 8 km of Great Lakes shorelines mainly because of the higher loads or persistence of contaminants (Best et al. 1994; Bowerman et al. 1995; Bowerman et al. 1998). Concentrations of environmental contaminants, namely *p,p'*-DDE and polychlorinated biphenyl (PCBs), must be below the no observable adverse effect concentration (NOAEC). Unhatched eggs with concentrations above the NOAEC threshold are associated with decreased productivity, egg lethality, and congenital malformations. Persistent chlorinated hydrocarbons in the environment have been the main factor limiting the bald eagle population in coastal regions of Michigan (Best et al. 1994; Bowerman et al. 1994; Bowerman et al. 1995; Bowerman et al. 2002; Best et al. 2010).

Density dependent factors in highly productive interior breeding areas of Michigan may contribute to population persistence or recovery by providing relatively uncontaminated adults to highly contaminated Great Lakes areas. Nonbreeders (floater birds that are capable of breeding but cannot secure the resources to do so, and territorial pairs that do not produce eggs) (Steenhof and Newton 2007; Evans et al. 2009) from refugia, or remnant source populations from the

1970's whose habitat was least affected by environmental contaminants, may act as a buffer affecting productivity in coastal populations (Kauffman et al. 2004). Density dependent factors could also cause decreased recovery in highly productive regions caused by the lack of unoccupied nesting habitat, decreased forage territory and increased occurrence of competitive behaviors between breeding pairs and nonbreeders (Kozie and Anderson 1991; Best et al. 1994; Bowerman 1995; Bowerman et al. 1998; Anthony 2001; Penteriani et al. 2005; Best et al. 2010). Many raptor studies have found increasing density results in reduced breeding success (Carrete et al. 2006; Ferrer et al. 2006). This is usually a result of regulation by either (1) intraspecific competition for food or (2) social intolerance and territorial behavior (Bretagnolle et al. 2008). In this study, we determine density dependent effects on productivity by comparing the amount of shared territory or breeding area intersect between each breeding area in highly occupied areas.

Rapid recovery of bald eagles in northwestern Ontario following the ban of DDT was attributed to a high turnover among breeding adults (Grier 1982). Refugia, or remnant bald eagle populations that were most resilient to the population-level effects of DDT, mainly occur upriver of dams that halt the passage of Great Lakes fish runs. These refugia areas, occupying primarily high quality inland territory and acting as a population source, may provide uncontaminated breeding adults to areas depressed reproductively by high contaminant concentrations (Bowerman 1993; Figure 3.1). The distance to refugia therefore, could be a factor affecting recovery through the dispersal of uncontaminated adults from refugia to proximate areas. Increasing productivity in these neighboring areas may then aid in the recovery and expansion of the population. Thus, it is necessary to determine if breeding area distance to refugia has influenced the productivity and recovery of the Michigan bald eagle population.

Chapter Three has three objectives for identifying the existence of density dependent factors in inland breeding areas by determining whether: (1) Michigan bald eagles are following settlement patterns according to the Habitat Heterogeneity Hypothesis or the Individual Adjustment Hypothesis (2) if an increase in breeding area intersect is negatively correlated to productivity, and (3) if breeding area distance to refugia, or remnant populations, impacted population recovery.

STUDY AREA

My study area consisted of all bald eagle breeding areas within the state of Michigan. Michigan is surrounded by four of the five Laurentian Great Lakes: Lake Michigan, Lake Superior, Lake Huron and Lake Erie (Figure 3.1; 3.2). Michigan's geomorphology is classified as Central Lowland plains. Elevations range from 175 to 396 m and 176 to 256 m in the Lower and Upper Peninsulas of Michigan, respectively. Low gradient streams drain into Lakes Superior, Michigan, and Huron in the Upper Peninsula, and into Lakes Michigan, Huron and Erie in the Lower Peninsula. Streams within the southernmost portion of both Peninsulas drain into the Ohio-Mississippi drainages. Small to medium lakes are present but not abundant in the Lower Peninsula, while numerous lakes and wetlands are found in low lying areas in the Upper Peninsula. Wetlands may seasonally flood in low-lying glacial lakebeds (McNab and Avers 1994; Wierda 2009).

Vegetation along the southern shore of Lake Superior is dominated by aspen (*Populus grandidentata, P. tremuloides),* spruce (*Picea mariana, P. glauca*), and balsam fir (*Abies balsamea*). The shores Lakes Michigan and Huron are dominated by maple (*Acer rubrum, A. saccharum*), oak (*Quercus rubra, Q. alba*), and pine (*Pinus strobus, P. banksiana, P. resinosa*).

Southern shores of Lakes Michigan, Huron and Erie are mainly dominated by mixed-cover and oak forests (Bowerman 1993).

METHODS

Surveys

Occupancy and reproductive success for the bald eagle population of Michigan has been measured annually with aerial surveys since 1961. A breeding area (or nesting territory) was defined as an area that contains, or historically contained, one or more nests within the home range of a mated pair: a confined locality where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time (Steenhof and Newton 2007). A preliminary survey was conducted by Michigan Department of Natural Resource (MDNR) pilots and contracted observers during egg-laying and incubation periods to document occupancy of breeding areas. A breeding area was considered occupied if one or both adults were attending in close proximity to a nest, if one bird was in incubating posture, a nest had visible repairs/ enlargements or relining with new sticks and bedding material not from the previous breeding season, or if eggs or young were observed (Fraser et al. 1983). A second survey determined nest success or failure. A nest was considered successful if at least one young reached minimum acceptable age for assessing success (Steenhof and Newton 2007). When a breeding area was successful, age and number of nestlings or eggs produced were documented by aerial observers. Coordinates (latitude and longitude) of successful nests were recorded using Global Positioning System (GPS) units. A third survey was conducted when field teams use GPS coordinates to locate and climb a subset of successful nest trees to band nestlings and collect tissue samples for contaminant analysis. The result of the second survey was then corrected based on results of the nest visits (Fraser et al. 1983; Bowerman et al. 1998; Bowerman et al. 2003; Best et al. 2010).

Productivity Data

Bald eagle population definitions and calculations followed the methodology of Postupalsky (1974) and Steenhof and Newton (2007). Productivity was defined as the number of young that reach the minimum acceptable age for assessing success; usually reported as the number of young produced per territorial pair or per occupied territory in a particular year (Steenhof and Newton 2007). Productivity rate was calculated as the total number of fledged young per occupied breeding territory divided by the total number of years occupied within each five year increment. Nests had to be active for at least 3 of the five possible years to be considered an active breeding area. A productivity rate of 1.0 or greater was indicative of a growing population. A productivity rate of 0.70 was representative of a stable population. A productivity rate of below 0.70 was indicative of a declining population (Sprunt et al. 1973).

Productivity was calculated for Category, Subpopulation, and Watershed. Data from 1961-2010 were divided into ten periods by five-year increments; Period One: 1961-1965, Period Two: 1966-1970.....Period Ten: 2006-2010. Bald eagle reproductive rates were averaged between five-year periods to accommodate the effects of yearly variations in weather (Wiemeyer et al. 1993).

Statistical Analysis

Settlement Patterns

HHH and IAH settlement patterns were determined using the coefficient of variation and skewness of productivity to avoid biases associated with increasing sample size from 1961-2010 for both IN and GL breeding areas. Coefficient of variation and skewness were determined by modeling the variation in productivity among years. A greater coefficient of variation and skewness of productivity indicated a more heterogeneous habitat. This suggested that the best-fit, highly productive individuals settled in high-quality habitat first, forcing the least-fit, least productive individuals to settle in lower-quality habitat (Ferrer and Donazar 1996). All statistical analysis were performed using SAS® 9.2 statistical package (SAS Institute Inc., 2008). Generalized linear model (GLM) regression analysis was used to determine significant linear relationships. The F ratio statistic was used to test if the slope of the data was significantly different from 0 (Ferrer and Donazar 1996). Statistical significance was set at $P < 0.05$.

Breeding Area Intersect

Breeding area intersect was defined as the total amount of overlap or territory that a breeding pair was forced to share with one or more conspecific breeding pairs within the 5 km radius of their nesting territory. Breeding area intersect was calculated using ArcGIS® software (ESRI 2011). The midpoint between all active nests was found for each active IN nesting territory. Midpoints for each breeding area were buffered by 5 km. This value was derived from a similar density dependence study in osprey (*Pandion* *haliaetus*) (Bretagnolle et al. 2008). This value was also approximated from the average core home range area of 4.9 km^2 for adult nesting bald eagles in western Washington (Watson 2002). The amount of overlap or intersect from one or more neighboring nesting territories was calculated for each breeding area. All IN breeding areas for Periods 6-10 were used to determine the association between breeding area intersect and productivity. Only Periods 6-10 were used as IN bald eagle populations were hypothesized to not have recovered enough to reach carrying capacity thresholds until Period Six (1986-1990). This analysis was performed on 1) breeding areas within the five densest populated IN counties (Dickenson, Gogebic, Iron, Menominee, and Roscommon) and 2) all remaining IN breeding areas. Generalized linear model (GLM) regression analysis was used to determine linear relationships between IN breeding areas and productivity. The F ratio statistic was used to test if the slope of the data was significantly different from 0 (Ferrer and Donazar 1996). Statistical significance was set at $P < 0.05$.

Distance to Refugia

All active breeding areas from 1971-1975 were considered refugia, or remnant populations that were least affected by DDT during the height of the Michigan bald eagle decline. Refugia areas mainly occurred upriver of dams that halt the passage of Great Lakes fish runs (Figure 3.1). Distance to refugia was defined as the mean distance from each active breeding area to refugia. Distance to refugia was also calculated using ArcGIS® software. The distance from refugia was calculated for every active nest and then averaged in each breeding area for Periods 6-10. Distances were also divided into 5 classes based on the Geometrical Interval Classification Method to determine correlations between refugia and productivity. This method was used to reduce variance within our data which was largely skewed because of the large of number nests proximate to refugia. The Geometric Interval Classification Method evenly distributed the number of breeding areas into 5 classes with Class One being the least distance as more breeding areas are proximate to refugia and Class Five being the greatest distance as less breeding areas further from refugia. The distance classes were quintiled as Class One: 0.0 – 1.94 km, Class Two: 1.95 – 7.94 km, Class Three: 7.95 – 26.41 km, Class Four: 26.42 – 83. 24 km, Class Five: 83. 25 – 258.19 km (Figure 3.2). Statistical analysis was performed using an ANOVA to test for overall significant differences between periods. A Generalized linear mixed model (GLIMMIX) was used to test for significant differences between periods within each class. SAS® 9.2 was used to determine significant differences.

Assumptions/ Biases

We are not able to locate and track the yearly movements of individual fledglings or breeding adults/ pairs. Because of this, we cannot make certain predictions as to the degree of philopatry, immigration/ emigration, home ranges, and yearly return/ turnover rates within the Michigan bald eagle population, biasing breeding area intersect data. Furthermore, the arbitrary boundaries differentiating GL and IN breeding areas, as well as IN counties, also biases settlement pattern and breeding areas intersect results.

RESULTS

Settlement Patterns

Productivity was inversely related to its coefficient of variation (r = -1.087, df = 1, 48, p <0 .0001) and skewness (r = -1.771, df = 1, 48, p < 0.0001), suggestive of settlement patterns according to the HHH (Ferrer and Donazar 1996; Table 3.1). The correlation between IN breeding area productivity and its coefficient of variation (r = -0.853, df = 1, 49, p < .0001) and skewness (r = -1.516, df = 1, 49, p < .0001) was less severe than GL breeding areas (Figure 3.3), indicating a greater proportion of high quality, best-fit individuals (Ferrer et al. 2006). GL breeding areas showed a greater negative association for coefficient of variation (r = -2.137, df = 1, 47, p < .0001) and skewness (r = -2.798, df = 1, 47, p < .0001; Figure 3.4) indicating a greater proportion of poor quality habitat and least-fit individuals (Ferrer et al. 2006).

Breeding Area Intersect

Breeding area intersect was only associated with productivity for the five densest counties (r = 0.002, df = 1, 390, p = 0.0128). Period Nine was the only period with a correlation (r = 0.006, df = 1,98, p = 0.0006). This positive correlation suggests that densely populated IN counties experienced a greater productivity as the amount of shared territory between breeding areas increased during Period Nine. Analysis of the remaining less-densely populated IN breeding areas did not result in a correlation (r = 0.0015, df = 1, 365, p = 0.1714). A positive correlation in these breeding areas during Period Six (r = 0.008, df = 1, 20, P = 0.111) stabilized, and then became negative by Period Ten (r = -0.001, df = 1, 173, p = .989; Table 3.2). An increase in breeding area intersect is representative of a rise in population density, possibly resulting in a stronger negative correlation as productivity decreases within these IN breeding areas in the next five to ten years.

Distance to Refugia

The mean nest distance to refugia increased from 13.83 km in Period Six (1986-1990) to 33.345 km in Period Ten (2006-2010). The number of active nests also increased from 177 in period six to 554 in Period Ten. Overall ANOVA results indicated that distance to refugia was different between Periods (f = 13.10, df = 4, p < .0001). Generalized linear mixed models performed within each of the geometric interval classes were only different for Class Four (f = 4.02, df = 4, 462, p = 0.0032). Breeding pairs nesting in Class Four nested farther from refugia during Period Ten than from breeding pairs nesting during Period Six (t = -2.01, df = 462, p = 0.0447), Seven (t = -2.38, df = 462, p = 0.0178), and Eight (t = -3.45, df = 462, p = 0.0006). Class Four also contained the highest number of breeding areas which occurred during Periods Nine and Ten (n = 128,193, respectively; Table 3.3, Figure 3.5).

Generalized linear model results indicated that distance to refugia was not correlated to productivity (r = 0.001, df = 1, 1703, p = 0.4908). Further, no correlations were found for Period and Class using a generalized linear mixed model. Although breeding area location is influenced by distance to refugia, this did not translate into increased productivity.

DISCUSSION

Settlement Patterns

The bald eagle population has not made a uniform recovery throughout the state of Michigan (Bowerman et al. 1998), increasing from 14 to 273 GL active breeding areas and 38 to 354 IN breeding areas from 1961 to 2010. IN breeding areas were the first-occupied. Because these areas provide higher quality habitat and are inhabited by the best-fit individuals, IN breeding areas experience less year-to-year variation in productivity. As these breeding areas become saturated, new pairs must nest in lesser-quality habitat in accordance with the HHH (Carrete et al. 2006; Ferrer et al. 2006). The negative correlation between productivity and its coefficient of variation and skewness in IN breeding areas confirms this hypothesis (Ferrer and Donazar 1996; Ferrer et al. 2006).

Settlement patterns in GL breeding areas also follow the HHH. GL breeding areas however, experienced a stronger negative correlation between productivity and its coefficient of variation and skewness than IN breeding areas. This increased variation in year-to-year productivity indicates that GL breeding areas are in a highly heterogeneous habitat, with greater proportion of poor-quality habitat (Ferrer and Donazar 1996; Ferrer et al. 2006).

Breeding success is determined by a combination of territory quality and individual quality which affect reproductive performance and survival of the individual bird, along with the spatial distribution of competitors (Penteriani et al. 2003; Carrete et al. 2006; Ferrer et al. 2006). Therefore, GL breeding areas could have higher variation in productivity caused by multiple factors, such as:

1. *Residual Contaminants in the Great Lakes*

Blood plasma sampled from nine subpopulations of GL nestlings exhibited concentrations of DDE and total PCBs that were inversely correlated to the productivity and success rate within those breeding areas (Bowerman 2003). Concentrations of PCBs, dieldrin, DDE, DDT, nonachlor, oxychlordane, heptachlor epoxide, and mirex were also higher in GL breeding pairs compared to nests at IN sites (Best et al. 2010). Exposure to these residual contaminants *in ovo* or in adults following settlement in GL areas may affect reproductive ability, causing variations in productivity. Patchy distribution of "PCB hotspots" around the Great Lakes may be another potential reason for variation in productivity (Best et al. 2010). The mobilization of these lipophilic contaminants from fat stores, resulting in adverse reproductive effects, during cold weather in GL breeding areas may also contribute to variations in productivity (Bowerman 1993).

2. *Forage Base*

GL breeding areas may experience a variation in productivity because of the minimal availability of shallow foraging area on shorelines. Various raptor studies have reported the importance of food availability on reproduction (Korpimäki 1992; Potapov 1997). Prey abundance can substantially limit golden eagle (*Aquila chrysaetos*) reproduction (Steenhof et al. 1997). Bald eagle food delivery rates to nestlings on the Lake Superior shoreline were 56% lower than inland. Lake Superior nests also experienced increase nestling mortality caused by predation. Thus, increased foraging time and parental absence resulted in a greater nestling mortality. Dykstra et al. (1998) also suggested that late ice-out could make foraging difficult for eagles until mid-April for Lake Superior eagles, resulting in productivity fluctuations by as much as 50% with varying yearly ice conditions. Warm spring weather also increases temperatures in IN ponds and rivers, causing fish to become more active and vulnerable to predation earlier in the breeding season for IN breeding pairs (Bowerman 1993).

Surface plunging for fish within the top 1 m of water is the main technique of aerial predation used by bald eagles. Shallow foraging areas are of great importance (Bowerman 1993). Great Lakes ospreys foraging on linear coastal marine habitat reach population carrying capacity sooner because of a decreased forage base in deeper sea waters out to ~1 km outshore, and more suitable foraging habitat, in comparison to continental osprey populations occupying lakes and river systems (Bretagnolle et al. 2008). GL breeding areas foraging solely along shorelines may also experience difficulties caused by water depth, making fish less vulnerable to predation.

Greater diversity in food habits has been associated with relatively stable annual raptor populations. The ability to prey on numerous species throughout the year decreases the probability that all will be scarce at the same time (Mindell et al. 1987). When comparing two bald eagle populations in British Columbia, a decreased productivity was recorded in nesting territories with prey deliveries consisting of more small fish and fewer birds and mammals. Prey delivery rates however, were similar between the two populations (Elliott et al. 1998). The greater annual prey diversity of bird, fish, and mammal is available to IN breeding pairs (Bowerman 1993), contributing to the stability of the breeding population and productivity in these breeding areas.

3. *Weather*

Weather heavily influences reproduction in several bird of prey species (Krüger and Lindström 2001). Kestrel (*Falco tinnunculus*) density and breeding success was highly dependent on winter temperature and amount of snow cover, specifically during the breeding season (Kostrzewa and Kostrzewa 1991). The percentage of laying golden eagle pairs was also inversely related to winter weather severity (Steenhof et al. 1997). Weather is a stochastic modifier, causing site-dependent population regulation in goshawk (*Accipiter gentilis*) populations (Rodenhouse et al. 1997; Krüger and Lindström 2001) GL breeding areas are located within 8-km from Great Lakes shorelines, consequently these nests experience greater exposure to often more severe lake-effect weather conditions during the egg-laying period. This, in turn, can lead to lower or a higher variability in overall productivity in GL breeding areas. Lower temperatures during the egg-laying period often result in smaller clutch sizes and eggs caused by energy limitations in many avian species (Pendlebury and and Bryant 2005). This can effect population-level reproductive output as clutch size limits the potential offspring that can be produced in a breeding attempt, and larger egg sizes can improve hatchability and early survival of the offspring, particularly during poor conditions (Williams 1994, Christians 2002).

4. *Inexperienced Breeding Pairs*

Raptor breeding competence increases with age and experience for long-lived species (Forslund and Pärt 1995; Bretagnolle et al. 2008). Therefore, if a greater proportion of GL breeding pairs are comprised of young and inexperienced eagles, a higher variation in productivity is expected. Kestrels (*Falco tinnunculus*) arriving later in the spring are invariably younger than those arriving earlier to claim the highest-quality habitat (Village 1985; Sergio and Newton 2003). Newly settled pairs of Spanish Imperial eagles (*Aquila adalberti*) also establish later than experienced pairs, nesting where fewer prey are available. High variation in reproductive success occurred as the number of inexperienced pairs in low-quality sites increased, especially in years of a low overall productivity (Ferrer and Donazar 1996). Age differences have also been proposed as an alternative hypothesis explaining productivity variation in bearded vultures (*Gypaetus barbatus*) (Bretagnolle et al. 2008) and Bonelli's and golden eagles (Carrete et al. 2006).

5. *Agnostic Encounters with Nonbreeder Populations*

High concentrations of nonbreeding birds around breeding territories may increase the time spent in agnostic encounters, reducing breeding success through intraspecific interactions (Carrete et al. 2006). GL breeding areas may be experiencing a higher amount of agnostic encounters with nonbreeders emigrating from IN breeding areas or Minnesota and Wisconsin. As inexperienced breeding pairs, GL eagles will be less effective when defending territory and securing prey resources. Though a minor factor affecting breeding success, agnostic encounters could contribute to variation in GL productivity.

Breeding Area Intersect

For many raptors, proximity to neighboring breeding areas (measured as nearest-neighbor distance, and number of occupied nests within a 5-km radius) is negatively correlated with productivity, lay date, growth rate and fledging success (Carrete 2006; Bretagnolle et al. 2008). Contrary to these findings, the five greatest counties with the greatest concentrations of occupied breeding areas in Michigan (Dickenson, Gogebic, Iron, Roscommon and Menominee) showed a positive correlation between breeding area intersect, or density, and productivity. These counties provide high quality nesting territory through a large forage base with relatively uncontaminated prey in many lakes with close proximity, and a low amount of human disturbance (Bowerman 1993). These counties are capable of sustaining high bald eagle populations, thus alleviating any density dependent effects caused by high amounts of shared territory. This may also indicate that these IN breeding areas have not yet reached the threshold for the population carrying capacity.

The remaining IN breeding areas proved to be more sensitive to increases in breeding area intersect throughout the 50 year period. Though not significant, the negative correlation between breeding area intersect and productivity experienced from 2006-2010 indicates that these counties may provide lesser quality habitat. Breeding areas within these counties may become seriously vulnerable to density dependent effects within five to ten years. In a study with Golden eagles (*Aquila chrysaetos*) and Bonelli's eagles (*Hieraaetus fasciatus*), subadults experienced a decrease in competitive ability when interacting with neighbors from a lack of experience defending breeding sites and food resources, reducing breeding performance (Carrete et al. 2006). IN breeding pairs may be competing with other Michigan breeding pairs and breeding pairs immigrating from Wisconsin or Minnesota. This may also suggest, in part, the susceptibility of the remaining IN counties to interference competition as the least-quality heterogeneous habitat, being settled by less experienced adults.

Spanish Imperial Eagles (*Aquila adalberti*) increased the mean time of population persistence at carrying capacity by density-dependent variation in age at first breeding. The longer the life expectancy and immaturity period of young eagles, the longer the population was buffered at the upper limit of saturation (Ferrer et al. 2004). Age variation in IN juveniles may contribute to the population persistence at carrying capacity, circumventing density dependent negative effects within these breeding areas.

IN counties, specifically Dickenson, Gogebic, Iron, Roscommon and Menominee, may also have density dependent effects mitigated through the emigration of young and subadults to GL breeding areas, Wisconsin, and Minnesota. The movement of uncontaminated eagles from IN “source” populations to GL breeding areas may buffer GL “sink” breeding populations (Pulliam 1998; Danielson 1992; Ferrer and Donazar 1996).

Distance to Refugia

It is difficult to determine whether distance to refugia impacted rates of recovery for the Michigan bald eagle population. The optimum distance to refugia varied for each period as the population has recovered and dispersed from refugia. Proximate distance to refugia may have been of greater importance for breeding adult replacement during earlier recovery periods. Our results however, indicate that nest sites located approximately 47-51 km may be the optimum distance to buffer bald eagle populations as of Period Ten (Table 3.2). Greater flamingos (*Phoenicopterus roseus*) in the Galápagos Islands disperse to refugia areas during periods of drought, maintaining populations through annual disturbances (Vargas et al. 2008; Sergio et al. 2011). As IN breeding areas have fully recovered by Period Ten, bald eagles may now benefit by nesting within 47-51 km from refugia to resist disturbances such as drought and years of low prey abundance. These disturbances may not necessarily occur during the breeding season. Migrating to high quality refugia for a stable food source during non-breeding periods may maintain adult breeding populations. This may also suggest why distance to refugia did not indicate an effect on productivity.

CONCLUSION

Less variation in productivity for IN breeding areas compared to GL breeding areas is indicative of high-quality habitat and a marginally increasing or stabilizing population (Ferrer and Donazar 1996). The settlement patterns and reproductive success of the Michigan bald eagle population have not been uniform because of residual contaminants in the Great Lakes, an uneven forage base, varied weather conditions and exposure, inexperienced breeding pairs, and agnostic encounters. Breeding area intersect analyses indicated IN breeding areas are not experiencing density dependent effects because of the high quality habitat capable of sustaining large numbers of breeding pairs in close proximity. The emigration of young to lower quality GL breeding areas may also mitigate some of these effects. Breeding area distance to refugia may also be an important factor determining nest site location as adults have the option to migrate to high quality refugia habitat during periods of disturbance.

The Michigan bald eagle population provides insight into the complex dynamics of a large-scale population recovery in a heterogeneous habitat. Determining specific correlations between subpopulations and environmental stressors is imperative for defining carrying capacity thresholds, leading to population-level management strategies.

CHAPTER FOUR

Summary

The bald eagle population in Michigan has undergone a significant recovery following the ban of the pesticide dichloro-diphenyl-trichloroethane (DDT), and its subsequent derivatives, mainly dichlorodiphenyl-dichloroethylene (*p,p'*-DDE), by the Environmental Protection Agency in the 1970's (Postupalsky 1978; Grier 1982; Bowerman et al. 1998). Population productivity and recovery however, have not been even throughout the state of Michigan. Great Lakes breeding areas along the shorelines of Lakes Superior, Michigan, Huron, and Erie have historically experienced less productivity than inland breeding areas because of higher concentrations of contaminants (Best et al. 1994; Bowerman et al. 1995; Bowerman et al. 1998). This decreased productivity may also be due, in part, to an uneven forage base, varied weather conditions and exposure, inexperienced breeding pairs, and agnostic encounters between Great Lakes breeding pairs and non-breeders.

Michigan is a heterogeneous habitat, causing the best-fit, experienced breeding pairs to settle in high quality breeding areas first. This high quality habitat mainly occurs in the inland regions of Michigan, specifically Dickenson, Gogebic, Menominee, Iron, and Roscommon counties. These areas experienced the greatest productivity until the 1990's, quickly recovering from the detrimental effects of DDT. These inland breeding areas are not experiencing reduced productivity caused by density dependent effects. The remaining inland breeding areas that do not provide as high of quality habitat may experience a negative correlation between productivity and population growth within the next five to ten years. All inland breeding areas may temporarily alleviate density dependent effects through the emigration of nonbreeding eagles to Great Lakes breeding areas.

All Great Lakes Watersheds, with the exception of inland Lake Superior, experienced a productivity greater than 1.0 during Period Ten. This indicates that these watersheds continue to support an increasing breeding bald eagle population (Sprunt et al 1973). Great Lakes breeding areas, particularly Lake Michigan and Lake Huron, are now more productive than IN breeding areas. These Great Lakes breeding pairs however, are the least efficient breeders with greater amounts of changeover between nesting pairs within one breeding area. This indicates that Great Lakes breeding pairs are less reproductively fit than inland breeding pairs. This reproductive insufficiency could be caused by chronic residual reproductive effects from *in ovo* contaminant exposure.

The demographic contribution of floaters (birds capable of breeding but not able to secure the habitat and forage base to do so; Evans et al. 2009) and nonbreeders may compensate for residual reproductive inability or adult mortality caused by contaminants in Great Lakes breeding areas, buffering productivity (Penteriani et al. 2005). The low reproductive fitness, yet high productivity of Great Lakes breeding areas is suggestive of a high turnover rate within the Great Lakes breeding population. A constant turnover of breeding pairs may overshadow any underlying effects causing decreased reproductive fitness in Great Lakes adults. Survival rate comparisons should be made between Great Lakes and inland breeding adults to further determine the health and status of the Michigan bald eagle population.

The Michigan bald eagle population is an ideal example of a recovering raptor population involving distinct yet connected subpopulations that are unequally affected by various environmental stressors. Defining these stressors and the magnitude of their effect on specific subpopulations within the Michigan bald eagle population, rather than evaluate the population as a whole, is essential to effective management decisions.

CHAPTER TWO TABLES

Table 2.1. ANOVA results denoting significance between Inland (IN) and Great Lake (GL) Category between productivity for bald eagles nesting in Michigan, 1961-2010.

Period	**Productivity**		**F value**	**df**	**P>F**
	IN	**GL**			
One 1961-1965	0.61	0.23	9.06	1, 97	0.0033
Two 1966-1970	0.74	0.19	17.25	1, 102	<0.0001
Three 1971-1975	0.76	0.35	7.61	1, 92	0.0070
Four 1976-1980	0.97	0.46	9.28	1, 96	0.003
Five 1981-1985	1.00	0.56	15.32	1, 127	<0.0001
Six 1986-1990	1.01	0.71	12.02	1, 187	0.0007
Seven 1991-1995	1.06	0.81	12.17	1, 268	0.0006
Eight 1996-2000	1.03	0.92	2.95	1, 356	0.0868
Nine 2001-2005	0.90	0.90	0.01	1, 477	0.9707
Ten 2006-2010	1.01	1.07	1.64	1, 631	0.2013

Table 2.2. Rate of change between Inland (IN) and Great Lake (GL) bald eagle productivity within Michigan, 1961-2010.

Periods (Years)	**Rate of Change**	
	Inland (IN)	**Great Lake (GL)**
One (1961-1965) – Two (1966-1970)	2.692	-1.072
Two (1966-1970) – Three (1971-1975)	1.398	3.896
Three (1971-1975) – Four (1976-1980)	3.228	2.196
Four (1976-1980) – Five (1981-1985)	0.238	2.144
Five (1981-1985) – Six (1986-1990)	0.334	2.84
Six (1986-1990) – Seven (1991-1995)	1.242	2.072
Seven (1991-1995) – Eight (1996-2000)	-0.78	2.538
Eight (1996-2000) – Nine (2001-2005)	-2.584	-0.862
Nine (2001-2005) – Ten (2006-2010)	2.222	3.072

Table 2.3. Mean productivity, and generalized linear mixed model results for 5 year periods with significant variation in bald eagle productivity among Inland Subpopulations: Lower Peninsula (LP), and Upper Peninsula (UP), and Great Lakes Subpopulations: Lake Huron (LH), Lake Michigan (LM), Lake Superior (LS) within Michigan, 1961-1970, 1976-2000. Letters signify significant differences among productivity.

Period (Years)	**Subpopulation**	**Productivity**	**t value**	**df**	**P> ǀ t ǀ**
One (1961-1965)	UP	0.68 A	8.01	94	<0.0001
	LP	0.50 A	4.73	94	<0.0001
	LS	0.32 A B	1.97	94	0.0522
	LM	0.29 A B	1.47	94	0.1460
	LH	0.00 B	-0.00	94	1.0000
Two (1966-1970)	UP	0.83 A	10.80	99	<0.0001
	LP	0.56 B	5.18	99	<0.0001
	LS	0.23 B	1.58	99	0.1183
	LM	0.19 B	0.78	99	0.4385
	LH	0.06 B	0.22	99	0.8255
Four (1976-1980)	UP	1.04 A	12.31	93	<0.0001
	LP	0.84 A	6.96	93	<0.0001
	LS	0.61 A B	3.25	93	0.0016
	LH	0.33 B	0.93	93	0.3570
	LM	0.07 B	0.19	93	0.8535
Five (1981-1985)	UP	1.01 A	16.09	124	<0.0001
	LP	1.01 A	11.99	124	<0.0001
	LS	0.74 A	5.44	124	<0.0001
	LH	0.55 A B	2.44	124	0.0162
	LM	0.23 B	1.18	124	0.2408
Six (1986-1990)	LP	1.11 A	15.23	184	<0.0001
	UP	0.96 A B	16.75	184	<0.0001
	LS	0.77 B	7.55	184	<0.0001
	LM	0.70 B	5.17	184	<0.0001
	LH	0.61 B	3.66	184	0.0003

Seven (1991-1995)	LP	1.19 A	18.51	265	<0.0001
	UP	0.98 B	17.98	265	<0.0001
	LH	0.85 B	8.13	265	<0.0001
	LM	0.85 B	7.94	265	<0.0001
	LS	0.77 B	8.44	265	<0.0001
Eight (1996-2000)	LP	1.12 A	21.04	353	<0.0001
	LM	1.03 B	11.15	353	<0.0001
	UP	0.95 B	19.36	353	<0.0001
	LH	0.90 B	10.26	353	<0.0001
	LS	0.87 B	10.69	353	<0.0001

Table 2.4. Mean productivity, and generalized linear mixed model results for 5 year periods with significant variation in bald eagle productivity among Inland Watersheds: Lake Huron (LH IN), Lake Michigan Lower Peninsula (LM IN LP), Lake Michigan Upper Peninsula (LM IN UP), Lake Huron (LH IN), and Great Lakes Watersheds: Lake Huron (LH GL), Lake Michigan (LM GL), and Lake Superior (LS GL) within Michigan, 1996-1970, 1976-2000. Letters signify significant differences among productivity.

Period (Years)	**Watershed**	**Productivity**	**t value**	**df**	**P> ǀ t ǀ**
Two (1966-1970)	LM IN UP	0.93 A	8.57	97	<0.0001
	LS IN	0.77 A B	6.94	97	<0.0001
	LH IN	0.62 A B C	4.97	97	<0.0001
	LM IN LP	0.34 B C	1.73	97	0.0861
	LS GL	0.23 C	1.59	97	0.1154
	LM GL	0.19 C	0.78	97	0.4348
	LH GL	0.06 C	0.22	97	0.8241
Four (1976-1980)	LS IN	1.21 A	9.84	91	<0.0001
	LM IN UP	0.89 A B	7.85	91	<0.0001
	LH IN	0.89 A B	6.34	91	<0.0001
	LM IN LP	0.68 B C	3.16	91	0.0021
	LS GL	0.61 B C	3.28	91	0.0015
	LH GL	0.33 B C	0.94	91	0.3517
	LM GL	0.07 C	0.19	91	0.8519
Five (1981-1985)	LM IN LP	1.01 A	6.60	122	<0.0001
	LM IN UP	1.00 A	12.16	122	<0.0001
	LS IN	1.00 A	10.35	122	<0.0001
	LH IN	0.99 A	9.89	122	<0.0001
	LS GL	0.73 A	5.40	122	<0.0001
	LH GL	0.55 A B	2.42	122	0.0171
	LM GL	0.23 B	1.17	122	0.2446
Six (1986-1990)	LM IN LP	1.22 A	8.94	182	<0.0001
	LH IN	1.07 A B	12.35	182	<0.0001
	LS IN	1.03 A B C	11.10	182	<0.0001
	LM IN UP	0.91 B C D	12.58	182	<0.0001
	LS GL	0.77 C D	7.55	182	<0.0001

	LM GL	0.70 D	5.17	182	<0.0001
	LH GL	0.61 D	3.66	182	0.0003
Seven (1991-1995)	LM IN LP	1.19 A	10.75	263	<0.0001
	LH IN	1.19 A	14.99	263	<0.0001
	LM IN UP	0.99 A B	14.26	263	<0.0001
	LS IN	0.96 AB	10.85	263	<0.0001
	LH GL	0.85 B	8.10	263	<0.0001
	LM GL	0.85 B	7.91	263	<0.0001
	LS GL	0.77 B	8.41	263	<0.0001

Table 2.5. Mean length of site occupancy and generalized linear mixed model results for decades with significant variation in bald eagle site occupancy among Inland Watersheds: Lake Huron (LH IN), Lake Michigan (LM IN), Lake Huron (LH IN), and Great Lakes Watersheds: Lake Huron (LH GL), Lake Michigan (LM GL), and Lake Superior (LS GL) within Michigan from 1981-1990, 2001-2010. Letters signify significant differences among productivity.

Decade (Years)	**Watershed**	**Length of Site Occupancy**	**t value**	**df**	**P > ǀ t ǀ**
One (1981-1990)	LH IN	7.82 A	37.98	609	<0.0001
	LM IN	7.17 B	39.61	609	<0.0001
	LH GL	7.04 B	28.84	609	<0.0001
	LS IN	6.95 B	22.47	609	<0.0001
	LM GL	6.84 B	28.78	609	<0.0001
	LS GL	6.79 B	23.41	609	<0.0001
Three (2001-2010)	LS IN	7.44 A	17.44	170	<0.0001
	LM IN	7.29 A	23.79	170	<0.0001
	LH IN	7.23 A	17.73	170	<0.0001
	LS GL	6.60 A B	13.14	170	<0.0001
	LM GL	5.62 B C	8.39	170	<0.0001
	LH GL	4.73 C	6.50	170	<0.0001

Table 2.6. Mean Decadal Success Rate and generalized linear mixed model results for decades with significant variation in bald eagle decadal success rates among Inland Watersheds: Lake Huron (LH IN), Lake Michigan (LM IN), Lake Huron (LH IN), and Great Lakes Watersheds: Lake Huron (LH GL), Lake Michigan (LM GL), and Lake Superior (LS GL) within Michigan from 1991-2010.

Decade (Years)	**Watershed**	**Decadal Success Rate**	**t value**	**Df**	**P > ǀ t ǀ**
Two (1991-2000)	LH IN	0.72 A	23.29	341	<0.0001
	LM IN	0.64 B	26.69	341	<0.0001
	LS IN	0.61 B C	16.34	341	<0.0001
	LH GL	0.58 B C	13.63	341	<0.0001
	LM GL	0.57 B C	13.51	341	<0.0001
	LS GL	0.55 C	14.36	341	<0.0001
Three (2001-2010)	LH IN	0.68 A	17.17	170	<0.0001
	LM IN	0.62 A	20.91	170	<0.0001
	LS IN	0.62 A	14.97	170	<0.0001
	LS GL	0.46 B	9.54	170	<0.0001
	LH GL	0.44 B	6.27	170	<0.0001
	LM GL	0.31 B	4.77	170	<0.0001

CHAPTER THREE TABLES

Table 3.1. Inland (IN) and Great Lake (GL) productivity (number of fledged young per occupied breeding area), coefficient of variation, and skewness, for bald eagles nesting in Michigan, 1961-2010.

Breeding Area	Year	Productivity	CV	Skewness
IN	2010	1.0508475	0.7896812	0.1439459
	2009	1.0327381	0.8799233	0.2713872
	2008	1.0136986	0.8094909	0.1624844
	2007	1.0095847	0.8221861	0.185101
	2006	1.0212014	0.8407422	0.2978121
	2005	0.9236364	0.9509823	0.4098659
	2004	0.9280303	0.9101523	0.3281345
	2003	0.8672199	0.9348701	0.3895092
	2002	0.8385827	1.0124759	0.5492838
	2001	0.9433198	0.9587259	0.311689
	2000	1.0862069	0.817798	0.0916466
	1999	1.0681818	0.8673321	0.3156969
	1998	1.2139303	0.8109036	0.0987544
	1997	0.89	0.9610242	0.310759
	1996	0.9536082	0.9201002	0.3231818
	1995	1.1581921	0.7577848	-0.008834
	1994	1.0617978	0.8265169	0.0311536
	1993	0.9813665	0.8859335	0.267338
	1992	1.1748252	0.7974304	0.1117989
	1991	0.9710145	0.9223194	0.304776
	1990	0.9375	0.9346073	0.2653277
	1989	1.023622	0.8389789	0.1834845
	1988	1.0661157	0.8278348	0.017568
	1987	1.1176471	0.856668	0.3124556
	1986	0.9157895	0.9644292	0.4508129
	1985	1.04	0.8526101	0.187057
	1984	1	0.9067647	0.1828548
	1983	0.9673913	0.9502687	0.4124796

	1982	1	0.8834522	0.326214
	1981	1.1204819	0.874859	0.2304978
	1980	1.0447761	0.8566268	0.1719469
	1979	1.0142857	0.9268921	0.2942034
	1978	0.890411	1.0515697	0.5366444
	1977	1.2666667	0.782329	0.2060878
	1976	1.04	0.8576986	0.155115
	1975	1	0.9669876	0.3537846
	1974	0.6811594	1.1672337	0.6434371
	1973	0.8194444	1.0101948	0.5050928
	1972	0.7464789	1.1921525	0.778403
	1971	0.8571429	0.9584777	0.434874
	1970	0.7323944	1.105823	0.5318957
	1969	0.7272727	1.066311	0.7253395
	1968	0.7887324	1.0480354	0.5721623
	1967	0.71875	1.1750499	0.9067943
	1966	0.8507463	1.0682083	0.6789761
	1965	0.530303	1.3321575	0.9697086
	1964	0.7666667	1.1100711	0.644996
	1963	0.5	1.4770979	1.4041548
	1962	0.8095238	1.0994133	0.6120457
	1961	0.8947368	1.0325299	0.4347783
GL	2010	1.21245	0.77098	0.05393
	2009	1.09796	0.82386	0.10662
	2008	1.0362	0.8171	0.20301
	2007	0.95215	0.89046	0.3304
	2006	1.03349	0.83464	0.25292
	2005	1.08743	0.79084	0.14475
	2004	0.92683	0.94531	0.42046
	2003	0.82517	0.96815	0.32633
	2002	0.83673	1.11061	0.6437
	2001	0.9375	1.01723	0.5136
	2000	1.112	0.82528	0.15625
	1999	0.82906	1.02996	0.50655
	1998	1.10784	0.80242	-0.0424
	1997	0.87629	1.07074	0.63801
	1996	0.88172	0.98716	0.335

1995	0.89247	0.92666	0.44017
1994	0.82759	1.04575	0.3445
1993	0.77528	1.19478	0.90557
1992	0.77333	1.11629	0.59075
1991	0.8	1.04962	0.39802
1990	0.71154	1.08992	0.55928
1989	0.66667	1.22474	0.70049
1988	0.61905	1.33267	1.10437
1987	0.94872	0.90314	0.1013
1986	0.58065	1.39022	0.94021
1985	0.53571	1.38967	1.02907
1984	0.61905	1.29998	0.84445
1983	0.52381	1.43106	1.09187
1982	0.4375	1.66272	1.43345
1981	0.76471	1.08718	0.49649
1980	0.73333	0.95963	0.43303
1979	0.53846	1.22613	0.86261
1978	0.21429	2.70169	2.80334
1977	0.35714	1.77331	1.68712
1976	0.23077	1.90029	1.45113
1975	0.33333	2.3355	2.05524
1974	0	N/A	N/A
1973	0.4	2.10819	1.77878
1972	0.6	1.40546	1.00056
1971	0.5	1.7097	1.29293
1970	0.28571	2.13937	2.16528
1969	0.33333	1.85164	1.79155
1968	0.27778	1.6592	1.08486
1967	0.14286	3.67171	3.51963
1966	0.17391	2.8234	2.99044
1965	0.36364	1.80937	1.6597
1964	0.17391	2.22843	1.84306
1963	0.13636	3.42879	3.62105
1962	0.13333	3.87298	3.87298
1961	0	N/A	N/A

Table 3.2. Generalized linear model results for effect of breeding area intersect on bald eagle productivity in the five densest Inland (IN) counties of Michigan and the remaining breeding areas during five post-DDT Periods: Period Six (1986-1990), Period Seven (1991-1995), Period Eight (1996-2000), Period Nine (2001-2005), and Period Ten (2006-2010).

Period	**Five Densest IN Counties**			**Remaining IN breeding areas**		
	r	df	P>F	r	df	P>F
1986-1990	-0.0010	1, 50	0.7316	0.0085	1, 20	0.1119
1991-1995	0.0001	1, 54	0.9530	0.0047	1, 29	0.2562
1996-2000	0.0031	1, 82	0.2276	0.0010	1, 51	0.6926
2001-2005	0.0068	1, 97	0.0006	0.0023	1, 84	0.3239
2006-2010	0.0013	1, 98	0.4305	-0.000	1, 173	0.9888

Table 3.3. Mean distance to refugia, standard deviation, and number of active breeding areas by Class for Periods Six (1986-1990), Seven (1991-1995), Eight (1996-2000), Nine (2001-2005), and Ten (2006-2010).

Class (Distance km)	**Period (Year)**	**Mean Distance to Refugia (km)**	**Std Dev**	**Number of Breeding Areas**
One	Six (1986-1990)	0.10	0.34	84
(0.0–1.94 km)	Seven (1991-1995)	0.11	0.35	89
	Eight (1996-2000)	0.18	0.47	95
	Nine (2001-2005)	0.16	0.40	95
	Ten (2006-2010)	0.19	0.44	111
Two	Six (1986-1990)	5.14	2.02	20
(1.95–7.94 km)	Seven (1991-1995)	4.94	1.93	27
	Eight (1996-2000)	5.28	1.83	38
	Nine (2001-2005)	4.94	1.89	49
	Ten (2006-2010)	4.75	1.76	60
Three	Six (1986-1990)	16.17	5.15	46
(7.95 – 26.41 km)	Seven (1991-1995)	16.85	5.41	58
	Eight (1996-2000)	16.24	5.33	80
	Nine (2001-2005)	16.32	5.52	117
	Ten (2006-2010)	16.30	5.62	148
Four	Six (1986-1990)	43.92	12.02	22
(26.42 – 83. 24 km)	Seven (1991-1995)	45.01	13.81	49
	Eight (1996-2000)	43.69	13.51	76

	Nine (2001-2005)	47.92	14.92	128
	Ten (2006-2010)	50.86	16.41	193
Five (83. 25 – 258.19 km)	Six (1986-1990)	125.51	70.63	5
	Seven (1991-1995)	134.57	74.84	15
	Eight (1996-2000)	92.18	6.90	19
	Nine (2001-2005)	123.09	60.34	39
	Ten (2006-2010)	141.31	66.28	42

CHAPTER TWO FIGURES

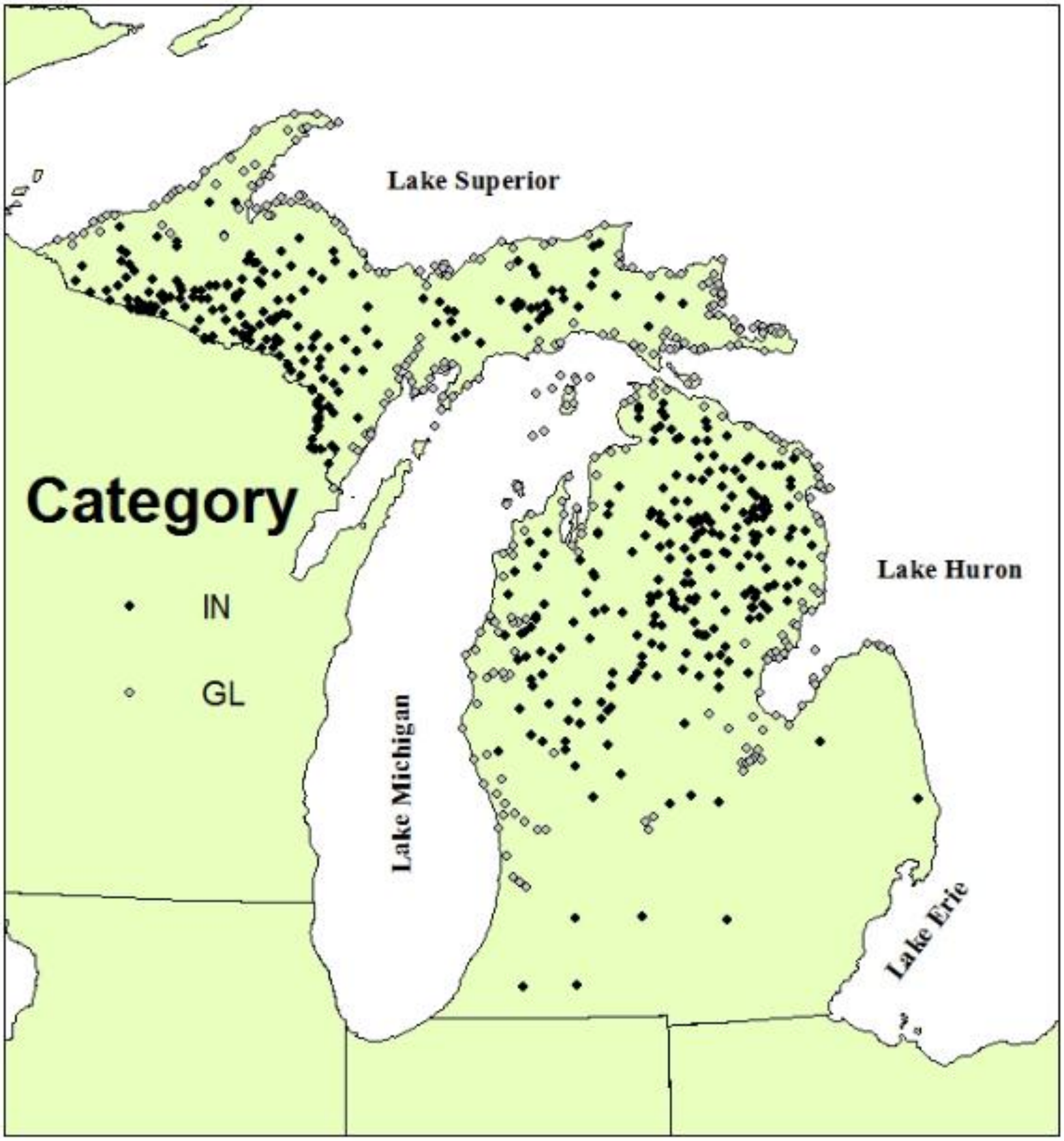

Figure 2.1. Breeding areas by Category in Michigan, 1961-2010. Categories: Inland (IN) and Great Lake (GL).

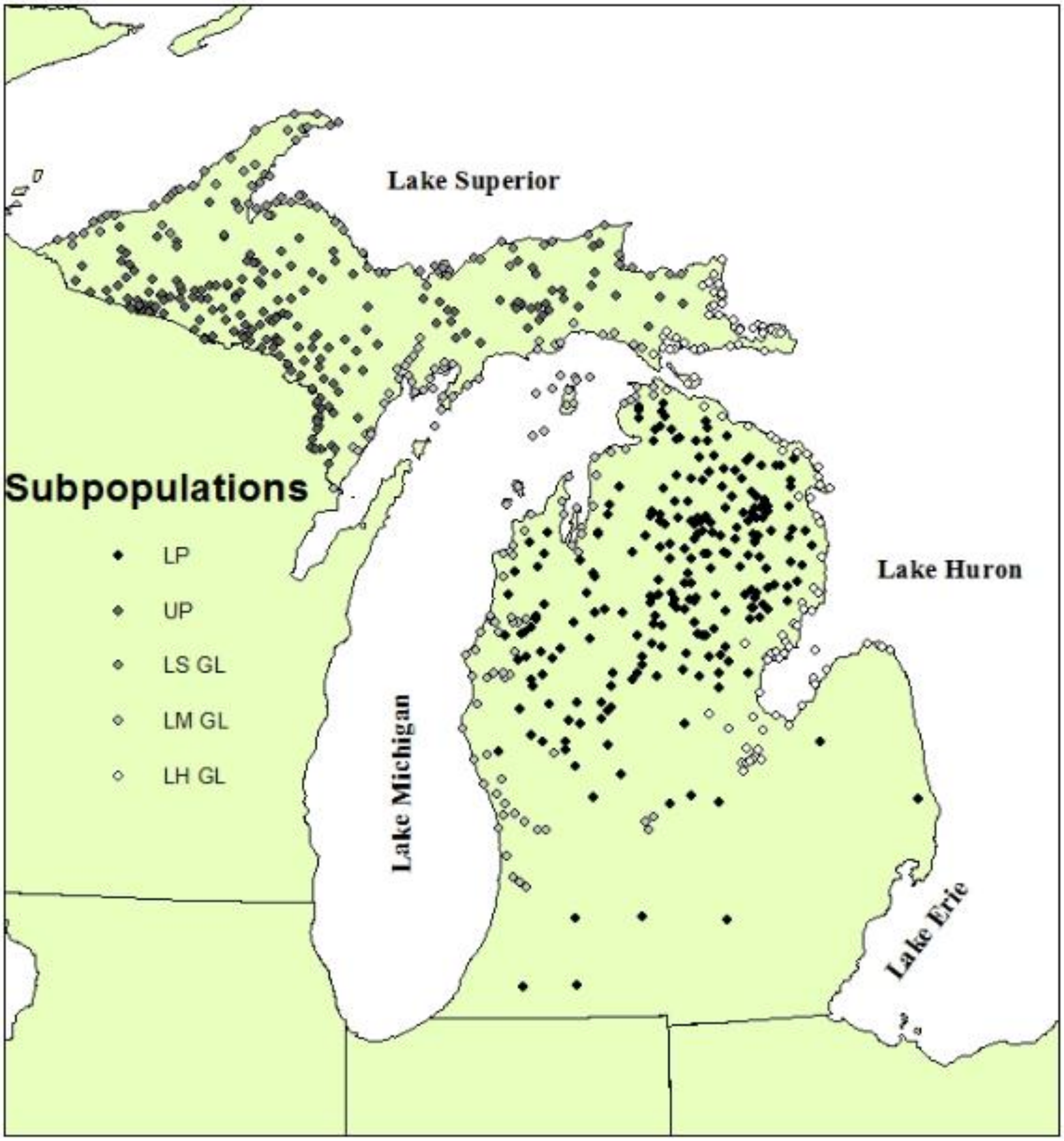

Figure 2.2. Breeding areas by Subpopulation in Michigan, 1961-2010. Subpopulation: Lower Peninsula (LP), Upper Peninsula (UP), Lake Superior Great Lake (LS GL), Lake Michigan Great Lake (LM GL), and Lake Huron Great Lake (LH GL).

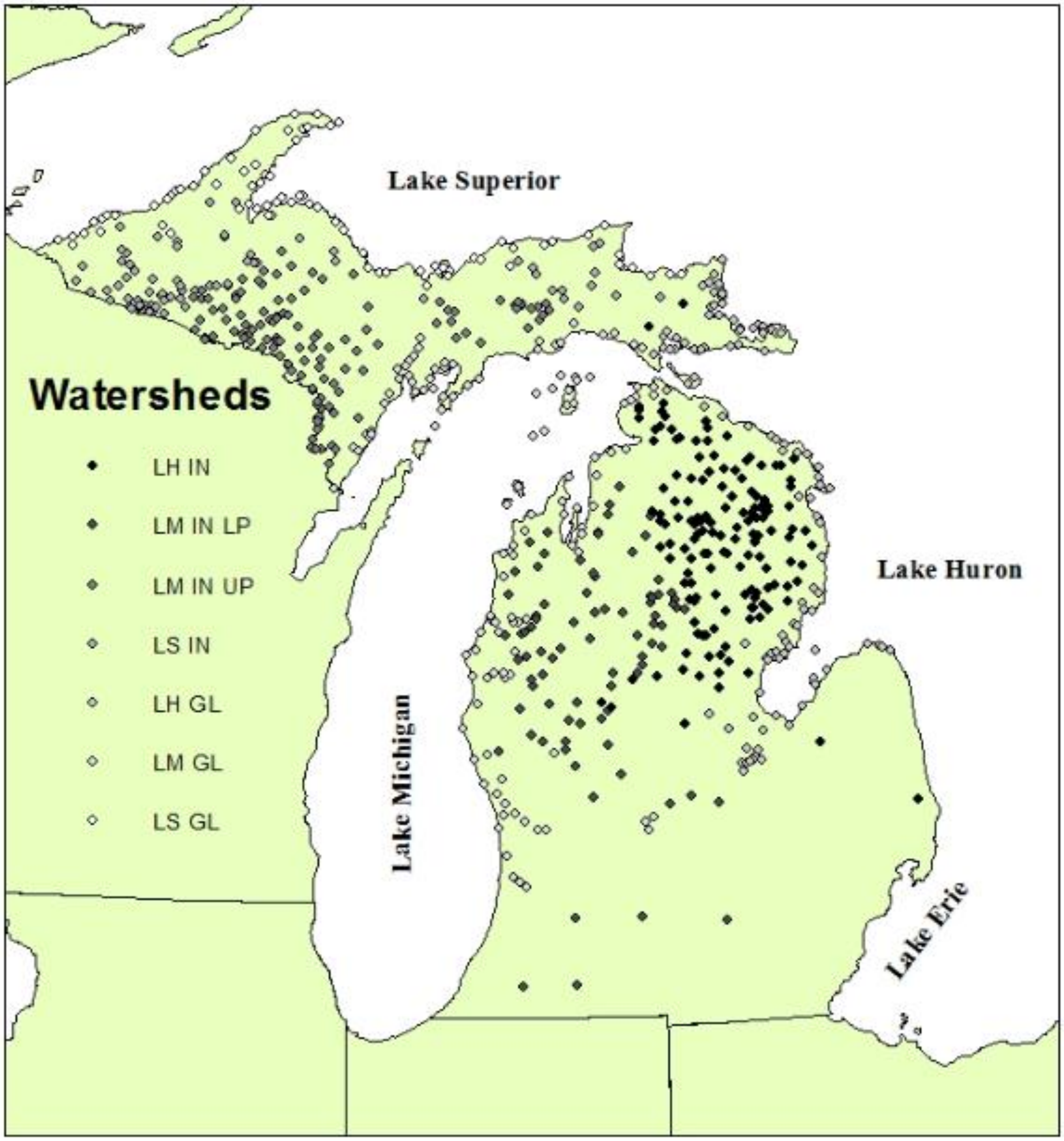

Figure 2.3. Breeding areas by Watershed in Michigan, 1961-2010. Watersheds: Lake Huron Inland (LH IN), Lake Michigan Inland Lower Peninsula (LM IN LP), Lake Michigan Inland Upper Peninsula (LM IN UP), Lake Superior Inland (LS IN), Lake Huron Great Lake (LH GL), Lake Michigan Great Lake (LM GL), and Lake Superior Great Lake (LS GL).

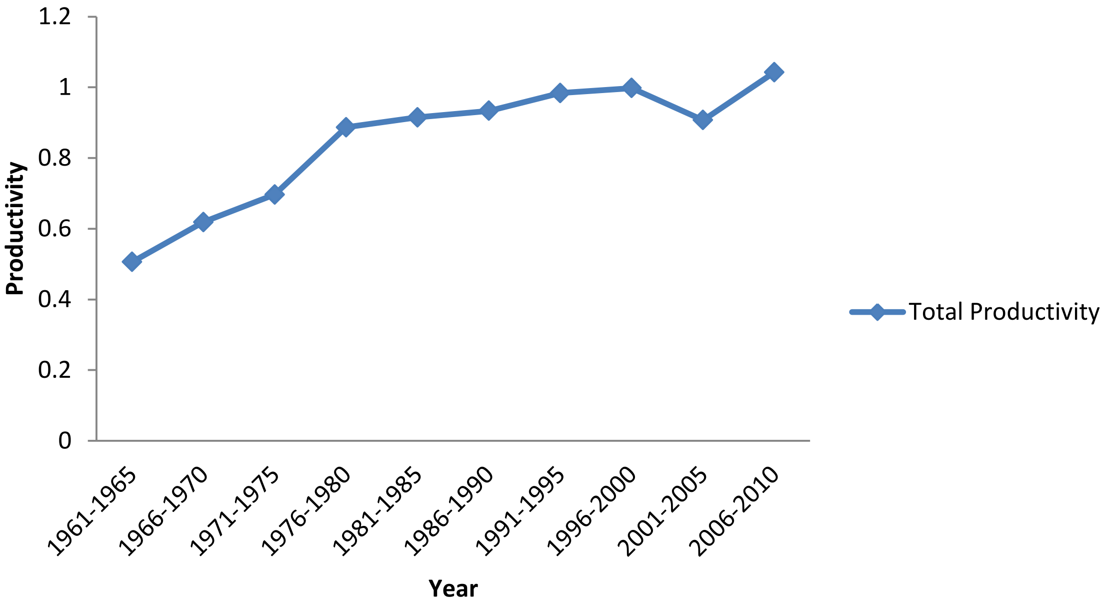

Figure 2.4. Total bald eagle productivity (fledged young/ occupied breeding area) for each breeding area in Michigan by five year periods, 1961-2010.

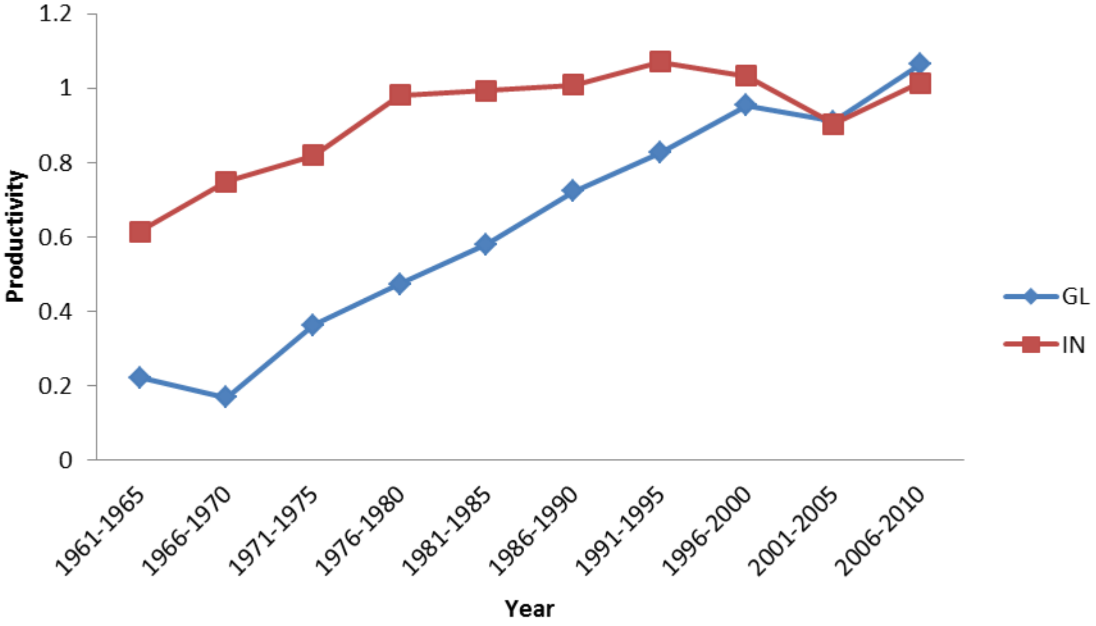

Figure 2.5. Bald eagle productivity (fledged young/ occupied breeding area) between Category (Great Lakes (GL) and Inland (IN)) breeding areas in Michigan by five year periods, 1961-2010.

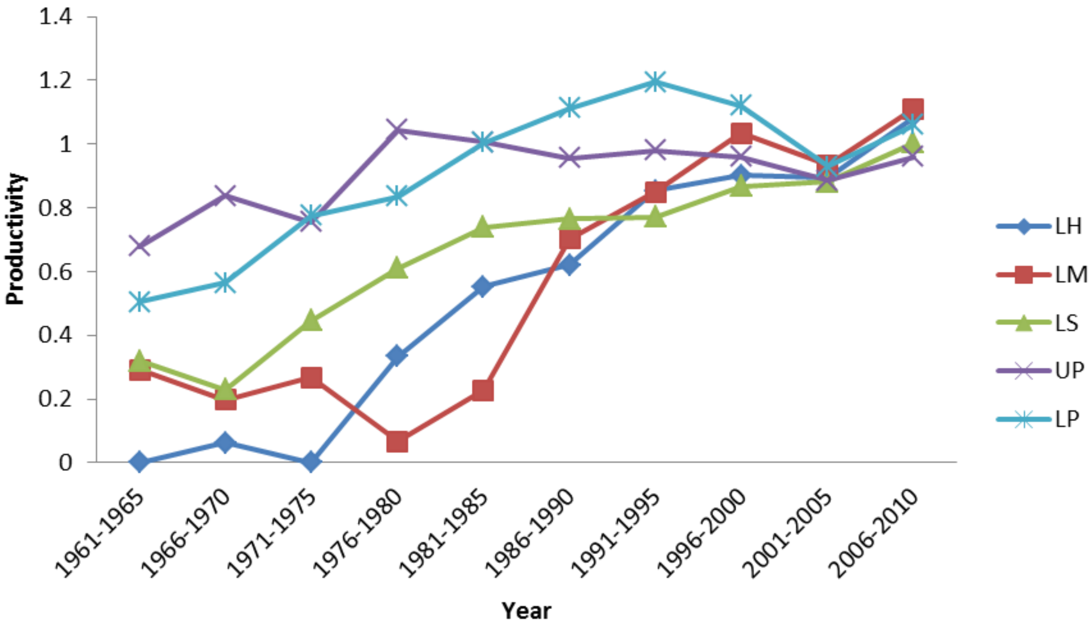

Figure 2.6. Bale eagle productivity (fledged young/ occupied breeding area) among Subpopulations (Lake Huron (LH), Lake Michigan (LM), Lake Superior (LS), Upper Peninsula (UP) and Lower Peninsula (LP)) breeding areas in Michigan by five year periods, 1961-2010.

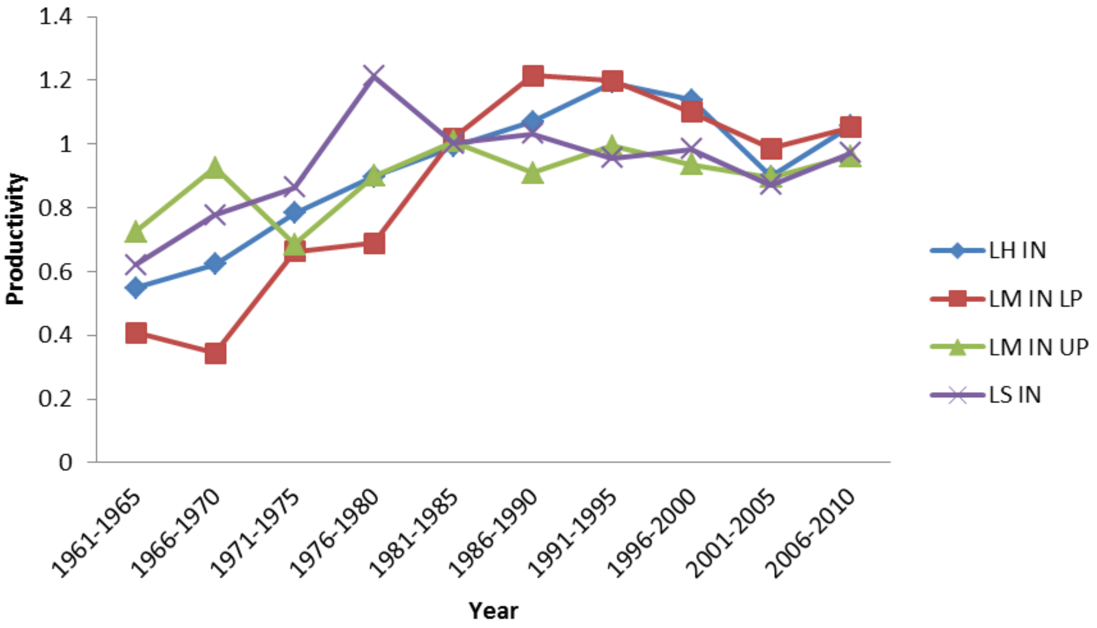

Figure 2.7. Bald eagle productivity (fledged young/ occupied breeding area) among Inland Watersheds (Lake Huron Inland (LH IN), Lake Michigan Inland Lower Peninsula (LM IN LP), Lake Michigan Inland Upper Peninsula (LM IN UP), and Lake Superior Inland (LS IN)) breeding areas in Michigan by five year periods, 1961-2010.

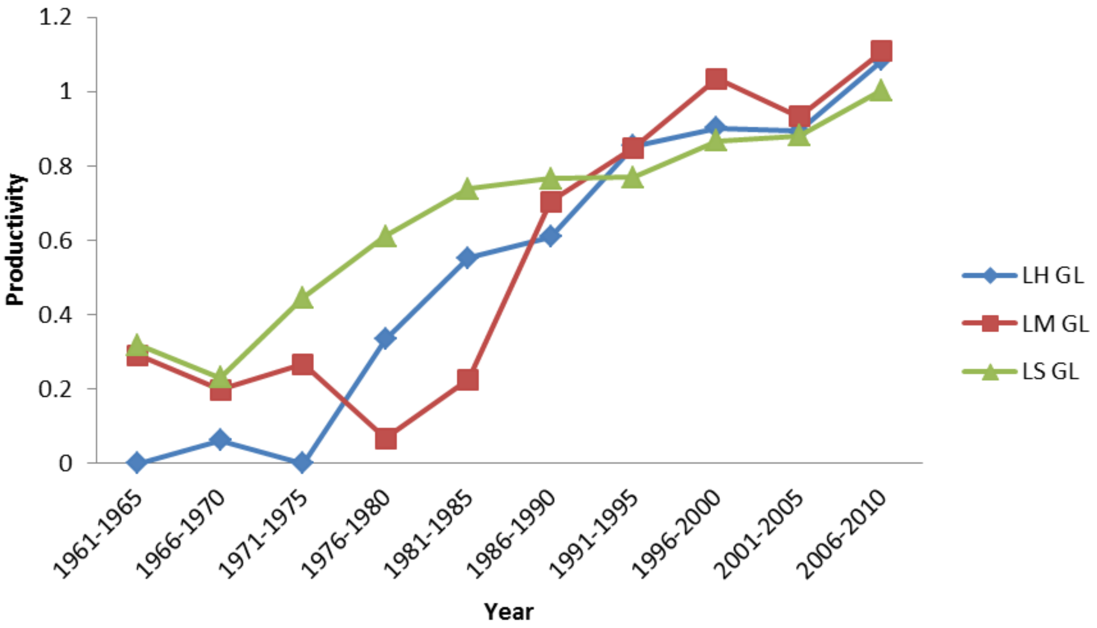

Figure 2.8. Bald eagle productivity (fledged young/ occupied breeding area) among Great Lake Watersheds (Lake Huron Great Lakes (LH GL), Lake Michigan Great Lakes (LM GL), and Lake Superior Great Lakes (LS GL)) breeding areas in Michigan by five year periods, 1961-2010.

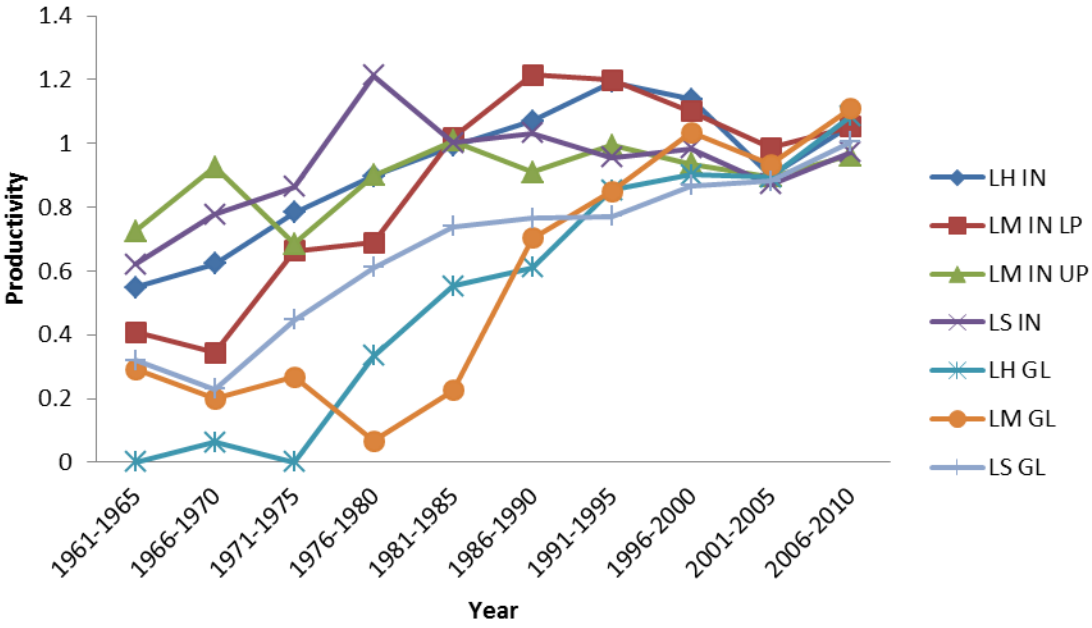

Figure 2.9. Bald eagle productivity (fledged young/ occupied breeding area) among all Watersheds (Lake Huron Inland (LH IN), Lake Michigan Inland Lower Peninsula (LM IN LP), Lake Michigan Inland Upper Peninsula (LM IN UP), Lake Superior Inland (LS IN), Lake Huron Great Lake (LH GL), Lake Michigan Great Lakes (LM GL) and Lake Superior Great Lake (LS GL)) breeding areas in Michigan by five year periods, 1961-2010.

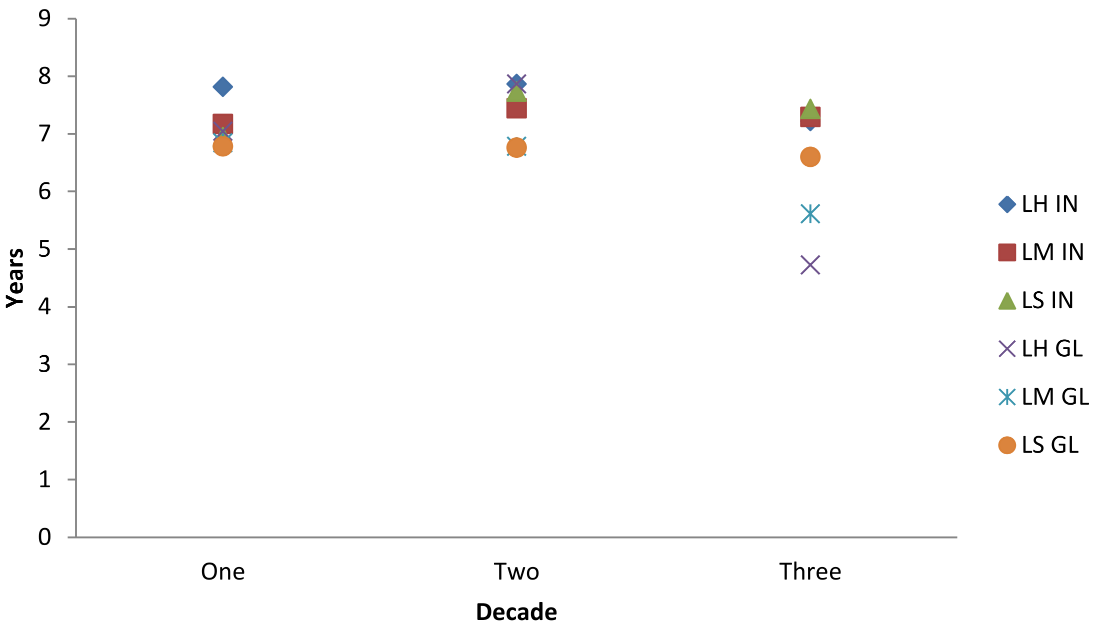

Figure 2.10. Bale eagle Length of Site Occupancy (mean number of years one breeding pair occupies one breeding area) between Lake Huron Inland (LH IN), Lake Michigan Inland (LM IN), Lake Superior Inland (LS IN), Lake Huron Great Lake (LH GL), Lake Michigan Great Lake (LM GL), and Lake Superior Great Lake (LS GL) breeding areas in Michaing by decades, 1981-2010 .

.

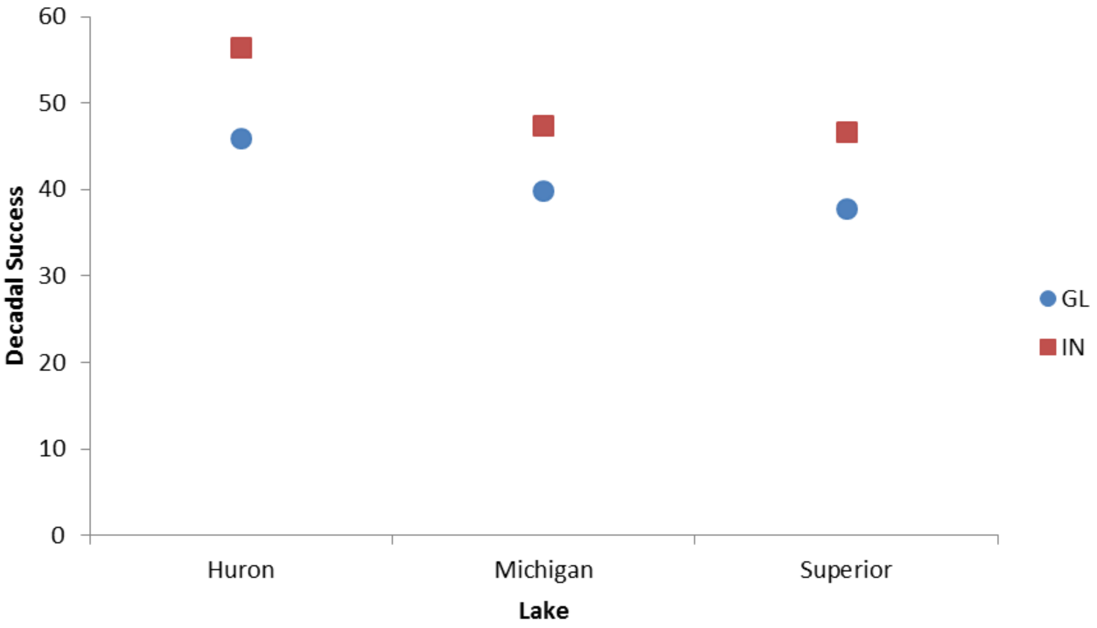

Figure 2.11. Great Lakes (GL) and Inland (IN) bald eagle Decadal Success Rates (productive years/ active years) for Lake Huron, Lake Michigan, and Lake Superior bald eagle breeding areas in Michigan from 1991-2000.

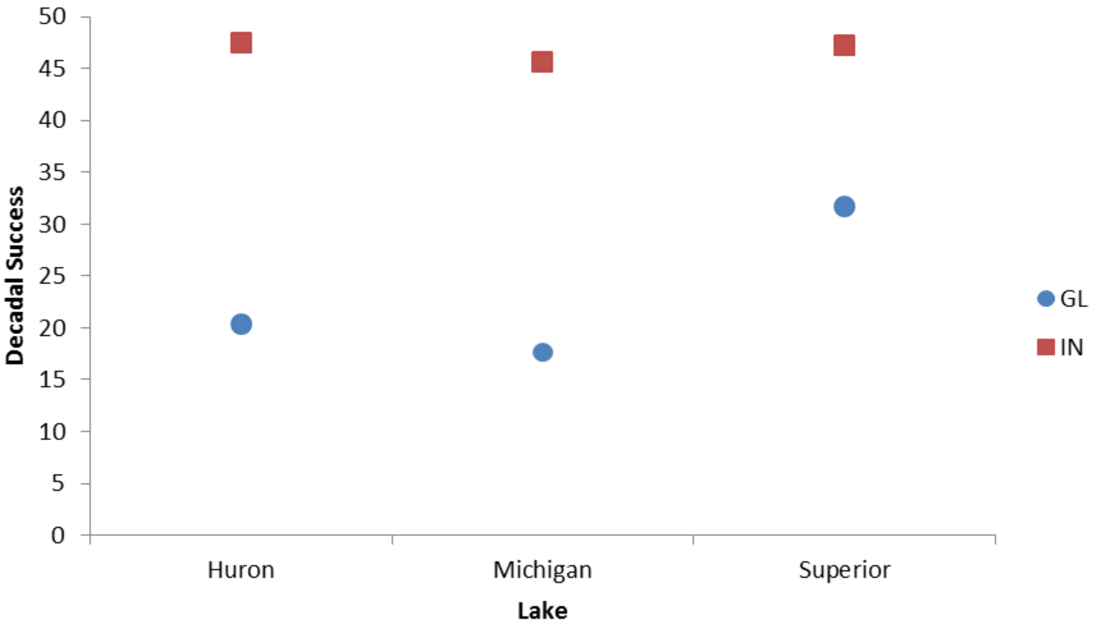

Figure 2.12. Great Lake (GL) and Inland (IN) bald eagle Decadal Success Rates (productive years/ active years) for Lake Huron, Lake Michigan, and Lake Superior bald eagle breeding areas in Michigan from 2001-2010.

CHAPTER THREE FIGURES

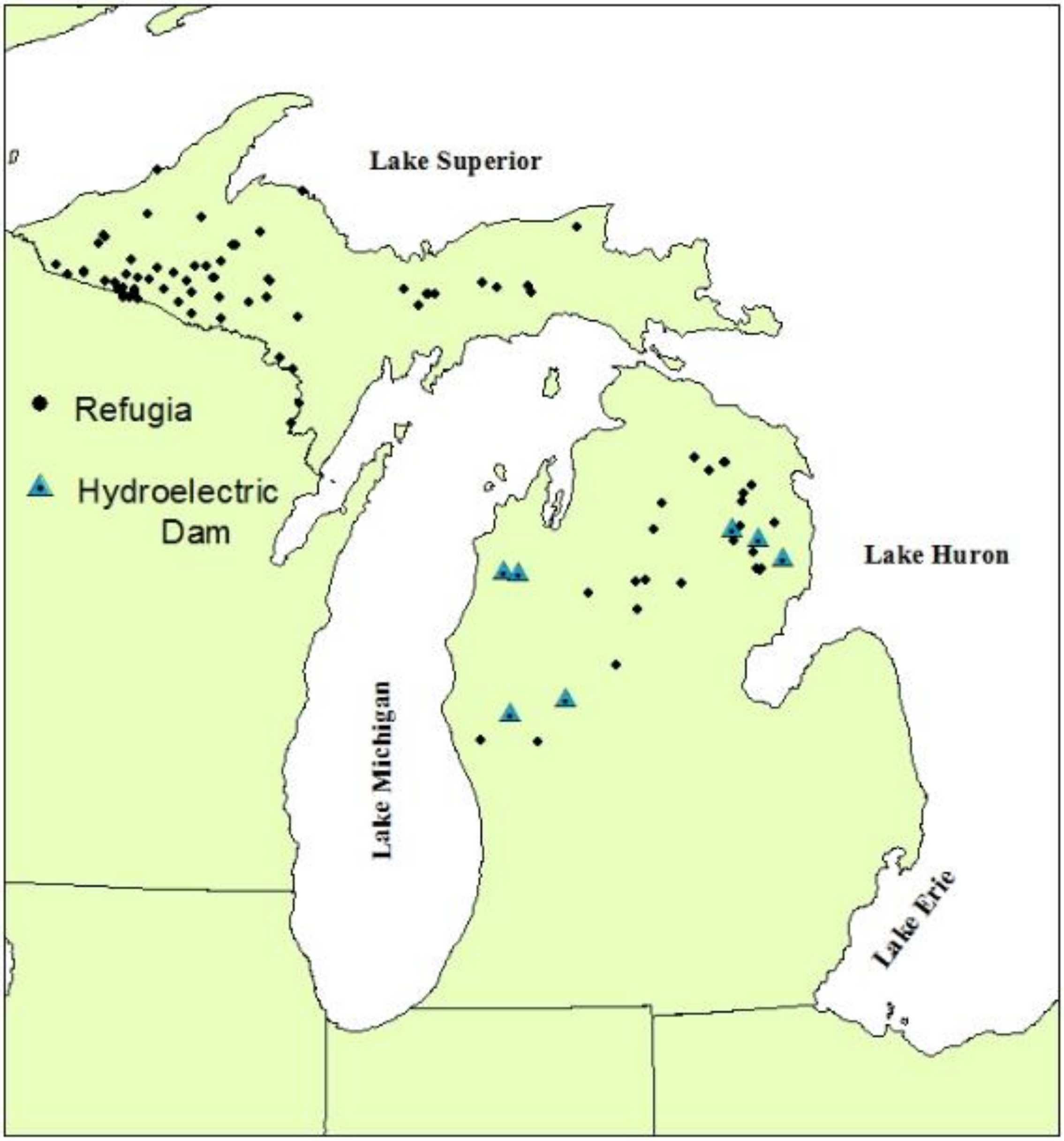

Figure 3.1. Refugia, or remnant bald eagle populations from 1971-1975 that were most resilient to the population-level effects of DDT, mainly occurring upstream of hydroelectric dams halting the passage of Great Lakes fish runs.

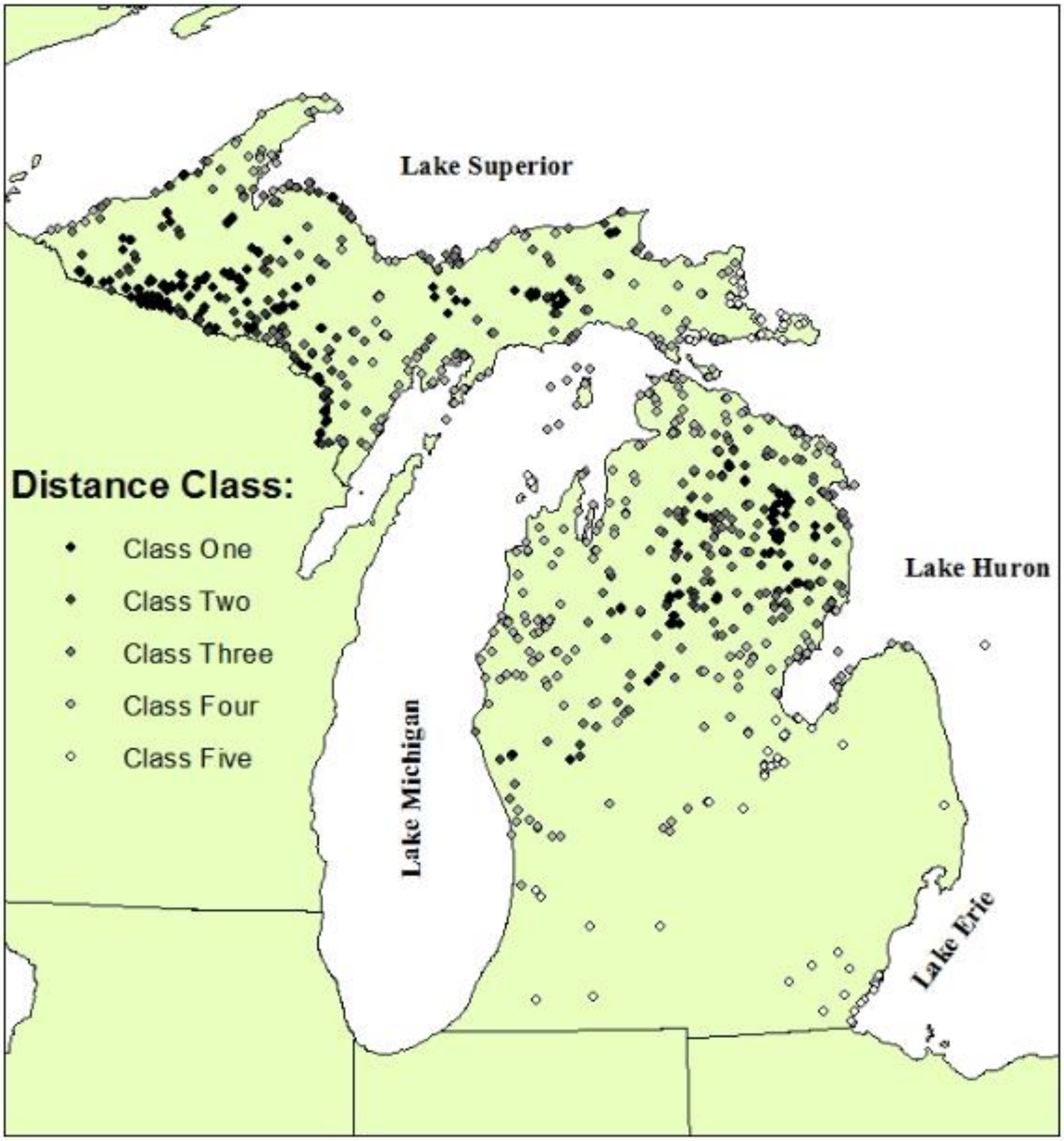

Figure 3.2. Breeding area distance to refugia (all active breeding areas, or remnant populations from 1971-1975 that were least affected by DDT during the height of the Michigan bald eagle decline) in Michigan, 1961-2010 by Class: Class One: 0.00 – 1.94 km, Class Two: 1.95 – 7.94 km, Class Three: 7.95 – 26.41 km, Class Four: 26.42 – 83. 24 km, Class Five: 83.25 – 258.19 km.

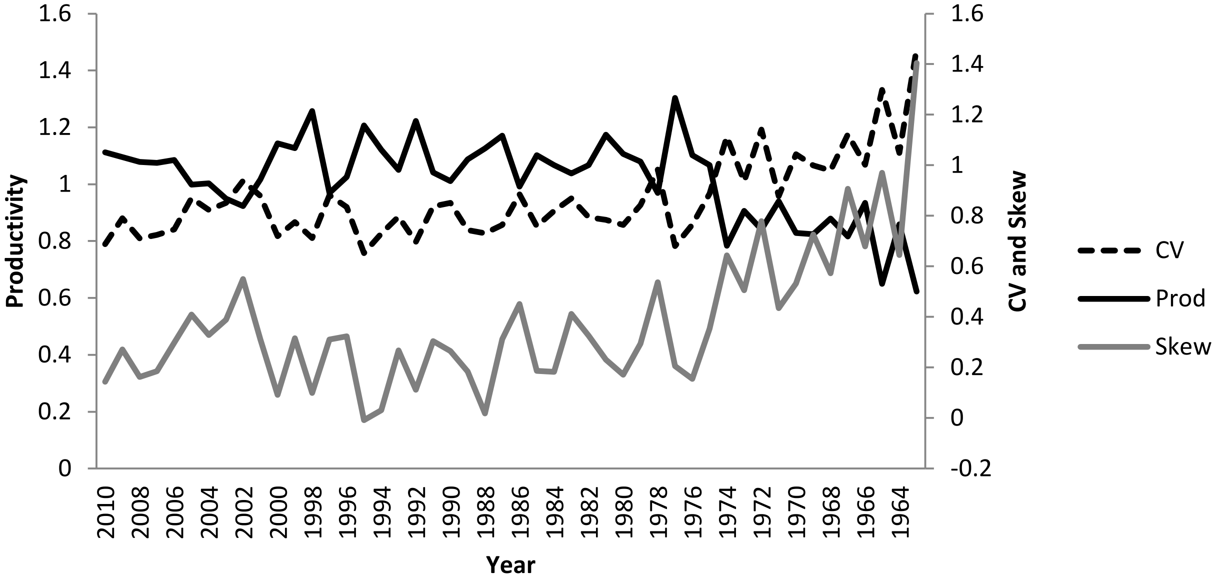

Figure 3.3. Inland (IN) productivity (number of fledged young per occupied breeding area) mean, coefficient of variation (CV), and skewness, for bald eagles nesting in Michigan, 1961-2010.

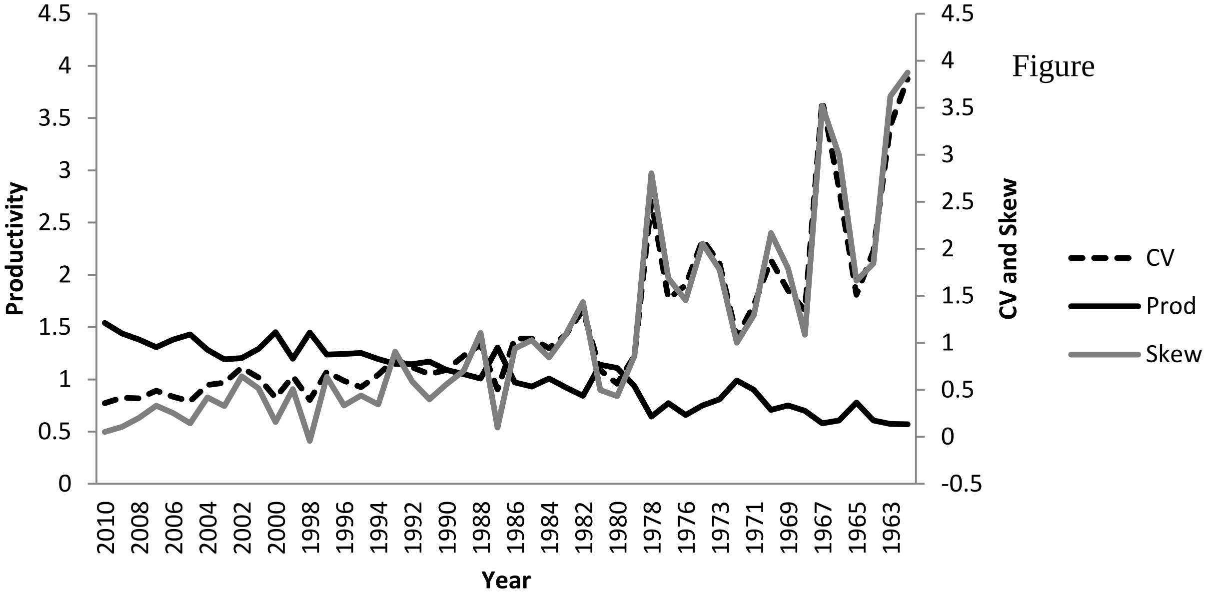

Figure 3.4. Great Lake (GL) productivity (number of fledged young per occupied breeding area) mean, coefficient of variation (CV), and skewness, for bald eagles nesting in Michigan, 1961-2010.

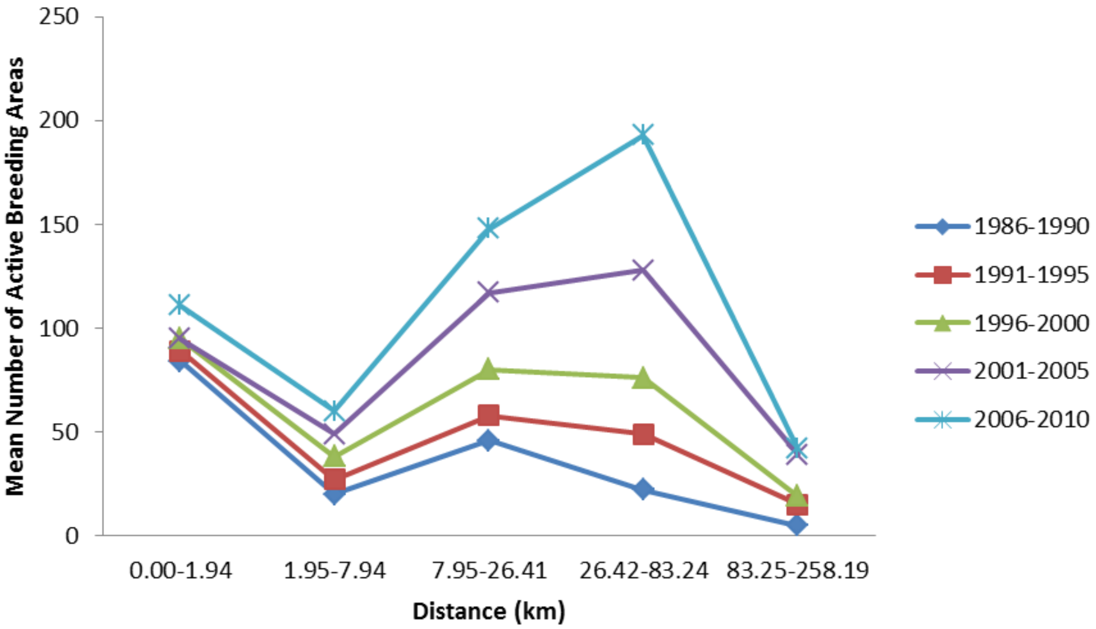

Figure 3.5. Mean number of active bald eagle breeding areas within the five geometric interval distances to refugia (all active breeding areas, or remnant populations from 1971-1975 that were least affected by DDT during the height of the Michigan bald eagle decline) classes in Michigan from 1986-2010.

LITERATURE CITED

Anthony, R.G. 2001. Low productivity of bald eagles on Prince Whales Island, Southeast Alaska. Journal or Raptor Research. 35:1-8.

Best D.A., W.W. Bowerman, T.J. Kubiak, S.R. Winterstein, S. Postupalsky, M. Shieldcastle. 1994. Reproductive impairment of bald eagles along the Great Lakes shorelines of Michigan and Ohio. In: Raptor Conservation Today. East Sussex, U.K.:World Working Group on Birds of Prey and The Pica Press 697-702.

Best, D.A., K.H. Elliott, W.W. Bowerman, M.Shieldcastle, S. Postupalsky, T.J. Kubiak, D.E. Tillitt, J.E. Elliott. 2010. Productivity, embryo and eggshell characteristics, and contaminants in bald eagles from the Great Lakes, USA, 1986 to 2000. Environmental Toxicology and Chemistry 29(7):1581-1592.

Bowerman, W.W. 1993. Regulation of bald eagle *(Haliaeetus leucocephalus)* productivity in the Great Lakes Basin: An ecological and toxicological approach. PhD dissertation, Michigan State University, East Lansing, MI.

Bowerman, W. W., E. D. Evans, J. P. Giesy and S. Postupalsky. 1994. Using feathers to assess risk of mercury and selenium to bald eagle reproduction in the Great-Lakes region. Archives of Environmental Contamination and Toxicology 27(3):294-298.

Bowerman, W.W., J. P. Giesy, D. Best and V.J. Kramer. 1995. A review of factors affecting productivity of bald eagles in the Great Lakes region: Implications for recovery. Environmental Health Perspectives 103: 51-59.

Bowerman, W.W., D. A. Best, T.G. Grubb, G. M. Zimmerman and J. P. Giesy 1998. Trends of Contaminants and Effects in Bald Eagles of the Great Lakes Basin. Environmental Monitoring and Assessment 53(1): 197-212.

Bowerman, W.W., A.S. Roe, M.J. Gilbertons, D.A. Best, J.G. Sikarskie, R.S. Mitchell and C.L. 2002. Using bald eagles to indicate the health of the Great Lakes' environment. Lakes & Reservoirs: Research and Management 7: 183-187.

Bowerman, W.W., D.A. Best, J.P. Giesy, M.C. Shieldcastle, M. Meyer, S. Postupalsky and J.G. Sikarskie. 2003. Associations between regional differences in PCBs and DDE in blood of nestling bald eagles and reproductive productivity. Environmental Toxicology and Chemistry 22(371-376).

Carrete, M., J.A. Sánchez-Zapata, J.L. Tella, J.M. Sánchez, and M. Moleón. 2006. Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. Oikos 112:680-690.

Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews 77:1–26.

Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evolutionary Ecology 6:399-411.

Datema, P.P., 2012. Using bald eagles to monitor hydroelectric projects liscense requirements along the Au Sable, Manistee and Muskegon River, Michigan. Masters Thesis. Clemson University, Clemson, SC.

Dykstra, C.R, M.W. Meyer, D.K. Warnke, W.H. Karasov. 1998. Low reproductive rates of Lake Superior blad eagles: low food delivery rates or environmental contaminants? Journal of Great Lakes Res. 24(1):32-44.

Elliott, J.E., I.E. Moul, K.M. Cheng. 1998. Variable reproductive success of bald eagles on the British Columbia coast. The Journal of Wildlife Management. 62(2):518-529.

Elliott, J.E, M.L. Harris. 2001. An ecotoxicological assessment of chlorinated hydrocarbon effects on bald eagle populations. Reviews in Toxicology 4:1-60.

ESRI (Environmental Systems Resource Institute). 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Evans, R.J, J.D. Wilson, A. Amar, A. Douse, A. Maclennan, N. Ratcliffe, D.P. Whitfield. 2009. Growth and demography of a re-introduced population of White-tailed Eagles *Haliaeetus albicilla*. Ibis 151:244-254.

Fernandez, C., P. Azkona, and J.A. Donazar. 1998. Density-dependent effects on productivity in the Griffon Vulture Gyps fulvus: the role of interference and habitat heterogeneity. Ibis 140: 64-69.

Ferrer, M., J.A. Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. Ecology 77 1:69-74.

Ferrer, M., F. Otalora, J.M. Garcia-Ruiz. 2004. Density-Dependent age of first reproduction as a buffer affecting persistence of small populations. Ecological Applications 14(2):616-624.

Ferrer, M., I. Newton, E. Casado. 2006. How to test different density-dependent fecundity hypotheses in an increasing or stable population. Animal Ecology 75: 11-117.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypotheses and tests. Trends in Ecology and Evolution 10:374-378.

Francis, C.M, and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548-556.

Fraser, J.D., L.D. Frenzel, J.E. Mathisen, F. Martin, M.E. Shough. 1983. Scheduling bald eagle reproduction surveys. Wildlife Society Bull. 11:13-16.

Forero, M.G., Donázar, J.A., Blas, J., F. Hiŕaldo, F. 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. Ecology 80:1298-1310.

Giesy, J.P., D.A. Verbrugge, R. Othout,, W.W. Bowerman, M.A. Mora, P.D. Jones, J.L. Newsted, C. Vandervoort, S.N. Heaton, R.J. Aulerich, S.J. Bursian, D.S. Tillitt, J. Johnson, J.P. Ludwig, M. Ludwig, G. Dawson, T.J. Kubiak, D.A. Best, R. Welsh. 1994. Contaminants in fishes from Great Lakes-influenced sections and above dams of three Michigan rivers: I. Concentrations of organochlorine insecticides,PCBs, dioxin equivalents, and mercury. Archives of Environmental Contamination and Toxicology. 27:202-212.

Giesy, J. P., W.W. Bowerman, M.A. Mora, D.A. Verbrugge, R.A. Othoudt, J.L. Newsed. 1995. Contaminants in fishes from Great Lakes-influenced sections and above dams of three

Michigan rivers: III. Implications for health of bald eagles. Archives of Environmental Contamination and Toxicology 29(1): 309–321.

Grier, J.W. 1980. Modeling approaches to bald eagle population dynamics. Wildlife Society Bulletin 8(4):316-322.

Grier JW. 1982. Ban of DDT and subsequent recovery of reproduction in bald eagles. Science 218:1232-1235. The Journal of Wildlife Management 32(1): 1-6.

Grubb, T.G. and R.M. King. 1992 Assessing Human Disturbance of Breeding Bald Eagles with Classification Tree Models. The Journal of Wildlife Management 55(3):500-511.

Grasman, K.A., P.F. Scanlon, G.A. Fox. 1998. Reproductive and physiological effects of environmental contaminants in fish-eating birds of the Great Lakes: A review of historical trends. Environmental Monitoring and Assessment. 53(1):117-145.

Hansen, A.J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. Ecology 68(5):1387-1392.

International Joint Commission. 1991. Proceedings of the Expert Consultation Meeting on Bald Eagles in the Great Lakes Basin (ed. M. Gilbertson). International Joint Commission, Windsor, Ontario, Canada.

Kauffman, M.J., J.F. Pollock, B. Walton. 2004. Spatial structure, dispersal, and management of a recovering raptor population. American Naturalist 164(5):582-597.

Kenward, R.E., S.S. Walls, K.H. Hodder, M. Pahkala, S.N. Freeman, V.R. Simpson. 2000. The prevalence of non-breeders in raptor populations; evidence from rings, radio-tags and transect surveys. Oikos 91:271-279.

Krüger, O. and L. Lindström. 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. Journal of Animal Ecology 70:173-181.

Korpimäki, E. 1992. Diet composition, prey choice, and breeding success of long-eared owls; effects of multiannual fluctuations in food abundance. Canadian Journal of Zoology 70:2373-2381.

Kostrzewa, A. and R. Kostrzewa. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian kestrels, common buzzards, and northern goshawks. Auk 108: 342-347.

Kozie, K.D., R.K. Anderson. 1991. Productivity, diet, and environmental contaminants in bald eagles nesting near the Wisconsin shoreline of Lake Superior. Archives of Environmental Contamination and Toxicology 20:41-48.

Krüger, O. and L. Lindström. 2001. Habitat heterogeneity affects population growth in goshawk Accipiter gentilis. Journal of Animal Ecology 70:173-181.

Mathisen, J.E. 1993. Annual bald eagle productivity report. unpubl. rep., Chippewa National Forest, Cass Lake, Minnesota.

McIntyre, C.L., M.W. Collopy, M.S. Lindberg. 2006. Survival probability and mortality of migratory juvenile golden eagles from interior Alaska. Journal of Wildlife Management 70(3):717-722.

McNab, W. H. and P. H. Avers (1994). Ecological subregions of the United States: Section Descriptions. U. S. F. Service. Washigton DC.

Millar, J.G. 1995. Endangered and threatened wildlife and plants; final rule to reclassify the bald eagle from endangered to threatened in all of the lower 48 states. Federal Register 60:36000-36010.

Mindell, D.P., J.L.B. Albuquerque, C.M. White. 1987. Breeding population fluctuations in some raptors. Oecologia 72:382:388.

Newton, I. (1979). Population Ecology of Raptors. Vermillion, SD, Buteo Books.

Pendlebury, C.J., and D.M. Bryant. 2005. Effects of temperature variability on egg mass and clutch size in great tits. The Condor 107:710–714.

Penteriani, V., J. Balbontín, M. Ferrer, 2003. Simultaneous effects of age and territory quality on fecundity in Bonelli’s eagle Hieraaetus fasciatus. Ibis 145:E77-E82.

Penteriani, V., F. Otalora, M. Ferrer. 2005. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. Oikos 108:523-534.

Postupalsky S. 1974. Raptor reproductive success: Some problems with methods,criteria and terminology. In: Hamerstorm FN, Harrell BE, Ohlendorff RR (eds)

Management of Raptors, Proc. Conf. Raptor Cinserv. Techniques, Raptor Reearch. Report No. 2, 21-31.

Postupalsky, S. 1978. The Bald Eagles return. Natural History 87(7):62-63.

Potapov, E.R. 1997. What determines the population density and reproductive success of rough-legged buzzards, Buteo lagopus, in the Siberian tundra? Oikos 78:362-378.

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

Pulliam, H.R. and B.J. Danielson. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:50-66.

Risebrough, R.W. 1988. A DDE:PCB correlation with productivity of bald eagles in northern California, Unpubl. Report, University of California, Santa Cruz, CA.

Rodenhouse, N.L., T.W. Sherry, R.T Holmes. 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78:2025-2042.

SAS Institute Inc., SAS® 9.2 Enhanced Logging Facilities, Cary, NC: SAS Institute Inc., 2008.

Sergio, F., I. Newton. 2003. Occupancy as a measure of territory quality. Animal Ecology 72:857-865.

Sergio, F., J. Blas, L. López, A. Tanferna, R. Díaz-Delgado, J.A. Donázar, F. Hiraldo. 2011. Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. Oecologia 166:79-90.

Sprunt A., W.B. Robertson, S. Postupalsky, R.J. Hensel, C.E. Knoder, F.J Ligas. 1973. Comparative productivity of six bald eagle populations. Trans. N. Am. Wildlife Natural Resources Conference 38:96-106.

Stalmaster M. V. 1987. The Bald Eagle. New York, New York. Universe Books.

Steenhof, K., Kochert, M.N., McDonald, T.R. 1997. Interactive effects of prey and weather on golden eagle reproduction. Animal Ecology 66:350-362.

Steenhof, K. and I. Newton. 2007. Assessing nesting success and productivity. Pages 181-192 *in* D. M. Bird and K. L. Bildstein, editors, Raptor Research and Management Techniques. Hancock House, Blaine, WA.

Thomas, C.D., M.C. Singer, D.A. Boughton. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. American Naturalist 148:957-975.

U.S. Fish and Wildlife Service. 2010. Post-delisting Monitoring Plan for the Bald Eagle (Haliaeetus leucocephalus) in the Contiguous 48 States. U.S. Fish and Wildlife Service, Divisions of Endangered Species and Migratory Birds and State Programs, Midwest Regional Office, Twin Cities, Minnesota. 75 pp.

Vargas, F.H. S. Barlow, G. Jimenez-Uzcátegui, J. Chavez, S. Naranjo, D.W. Macdonald. 2008. Effects of climate variation on the abundance and distribution of flamingos in the Galápagos Islands. Zoology 276:252-265.

Village, A. 1985. Spring arrival time and assortative mating of kestrels in south Scotland. Animal Ecology 54:857-868.

Watkinson, A.R., W.J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Animal Ecology 64:126-130.

Watson, J.W. 2002. Comparative home ranges and food habits of bald eagles nesting in four aquatic habitats in western Washington. Northwestern Naturalist 101-108.

Watts, B.D., G.D. Therres, M.A. Byrd. 2005. Recovery of the Chesapeake bay bald eagle nesting population. Journal of Wildlife Management 72(1): 152-158.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biological Reviews 69:35-60.

Wiemeyer S. N., Bunck, C. M., Stafford, C. J. 1993. Environmental contaminants in bald eagle eggs-1980-84-and further interpetations of relationships to productivity and shell thickness. Arch Environmental Contaminant Toxicology 24:213-227.

Wierda, M.R. 2009. Using nestling bald eagles to track spatial and temporal trends of contaminants in Michigan’s aquatic ecosystem. PhD dissertation. Clemson University. Clemson, SC.