MODELING LONG-TERM CHANGES, 1958-2011, IN THE REPRODUCTION AND

TERRITORY DYNAMICS OF BALD EAGLES OF FLORIDA BAY, SOUTHERN

COASTAL EVERGLADES

by

Jason W. Bosley

A Dissertation Submitted to the Faculty of

Charles E. Schmidt College of Science

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy
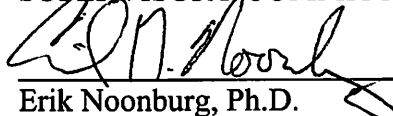
Florida Atlantic University

Boca Raton, FL

May 2017

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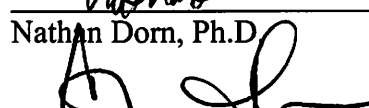COASTAL EVERGLADES

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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. Erik Noonburg, Department of Biological Sciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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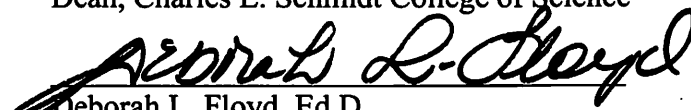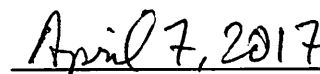Dissertation Advisor

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ACKNOWLEDGEMENTS

# ABSTRACT

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Title:             Modeling Long-Term Changes, 1958-2011, In The Reproduction
                   And Territory Dynamics Of Bald Eagles Of Florida Bay, Southern
                   Coastal Everglades

Institution:       Florida Atlantic University

Dissertation Advisor: Dr. Erik Noonburg

Degree:            Doctor of Philosophy

Year:              2017

As top-level piscivores, Bald Eagles are a compelling subject for the study of
territory dynamics and are highly representative of the distinctive suite of avian species
that occupy Florida Bay. Despite successful recovery of Bald Eagles (*Haliaeetus
leuocephalus*) throughout the species range, the population breeding within Florida Bay
has not mirrored this trend. Beginning in the late 1980s, Florida Bay has suffered in its
capacity to support species diversity and abundance as a result of extreme changes in
hydrology related to altered flows of incoming freshwater. In fact, Bald Eagle territory
use in Florida Bay has declined by as much as 43% as year to year variation and
sensitivity to transitions between territory states have increased. Florida Bay's
populations of other large, conspicuous fish-eating birds, including Ospreys, Great White
Herons, Roseate Spoonbills, and Reddish Egrets each exhibit a similar pattern of decline.

The effects of environmental degradation throughout Florida Bay are magnified at higher trophic levels. The negative trend in territory occupancy is most pronounced in southeast Florida Bay whereas effects on territory occupancy in the northwest are minimal. The presence of spatial patterns in territory occupancy, despite regionally available breeding birds, suggests that individuals are evaluating differences in habitat quality for which certain territories are no longer considered viable. Building on our current understanding of the health of this population of Bald Eagles, we have successfully implemented modeling approaches that identify key territory breeding decisions. Loss of early breeding season activity (occupied and active territories) despite maintaining high breeding success indicates that changes in territory dynamics are the result of a failure to breed and not a reproductive failure. As such, future conservation actions should promote early breeding season activity (decisions by breeding pairs to initiate nesting) in areas of Florida Bay that were historically occupied but are now abandoned.

MODELING LONG-TERM CHANGES, 1958-2011, IN THE REPRODUCTION AND

TERRITORY DYNAMICS OF BALD EAGLES OF FLORIDA BAY, SOUTHERN

COASTAL EVERGLADES

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LONG-TERM CHANGES, 1958-2010, IN THE REPRODUCTION OF BALD EAGLES

OF FLORIDA BAY, SOUTHERN COASTAL EVERGLADES

ABSTRACT

The population of Bald Eagles (*Haliaeetus leucocephalus*) breeding in Florida

Bay, located within Everglades National Park, has been the subject of one of the longest

running monitoring programs for any large raptor species world-wide, with reproductive

data collected for 49 breeding seasons since 1958. The overall reproductive trends in this

nesting population indicated that the population has transitioned from one at or near

carrying capacity to one in decline, with territory occupancy decreasing as much as 43%.

This contrasted with observed trends for the state of Florida, where populations increased

>300% over the past 25 yr. The rate of nesting attempts in Florida Bay remained high

$(0.83 \pm 0.11$ [SD]; number of active territories/number of occupied territories) over the

period. Mean annualized brood size was $1.48 \pm 0.16$ young/successful territory and mean

productivity was $0.81 \pm 0.21$ young/occupied territory, which are comparable to those of

other Bald Eagle populations. There were significant increases in ratios of active

territories/occupied territories, successful territories/occupied territories, and young/occupied territory, despite decreased occupancy. Increases in these rates have allowed overall production of the Florida Bay population to remain stable, however, given the current decreasing trend in territory occupancy, this population should be considered at risk. Changes in Bald Eagle reproductive parameters corresponded with significant ecological changes documented in Florida Bay and southern coastal Everglades and may serve as possible long-term indicators for the health and recovery of the southern Everglades as restoration efforts progress.

INTRODUCTION

The Bald Eagle (*Haliaeetus leucocephalus*) is an iconic species whose populations have exhibited dramatic declines and recoveries, and is one of the most well studied raptor species (Buehler 2000). In the late 1940s, Charles Broley (1947, 1950, 1958) linked dichloro-diphenyl-trichloroethane (DDT) and habitat destruction to declines in the number of successfully breeding Bald Eagle pairs. Surveys in 1963 found a total of only 417 pairs in the lower 48 states of the U.S.; occupied nests produced on average only 0.59 young (Sprunt 1963). Following the ban of DDT in 1972, along with other conservation and recovery efforts, Bald Eagle populations rebounded across much of their range with recovery and growth typifying most regional Bald Eagle populations in the lower-48 states. For example, in the Chesapeake Bay, the population grew from 73 pairs in 1977 to 601 pairs in 2001, with a doubling time of 8.2 yr (Watts et al. 2008). As a result of range-wide recovery, the Bald Eagle was officially removed from the Endangered Species Act (ESA) in August of 2007 (U.S. Fish and Wildlife Service [USFWS] 2007).

In Florida, the southeastern most part of their range, the population has recovered from a low of only 88 pairs in 1973, when state-wide monitoring began, to more than 1300 estimated in 2008 (Florida Fish and Wildlife Conservation Commission, FWC, 2008). The USFWS Southeastern States Bald Eagle Recovery Plan1989 concluded that although state Bald Eagle populations in the southeast U.S. had declined 25% to 100% from historic levels, Florida retained a significant nesting population of about 350 pairs (USFWS 1995, USFWS 1999). Robertson (1978) had estimated that the original population in Florida exceeded 1000 nesting pairs. The state of Florida currently supports about 70% of the nesting population in the southeastern U.S. and 11% in the lower 48 states (FWC 2008).

Bald Eagles form breeding pairs that defend exclusive territories and exhibit mate and site fidelity (e.g., Stalmaster 1987, Jenkins and Jackman 1993, Buehler 2000). In Florida, Bald Eagles exhibit a high degree of philopatry with relatively short natal dispersal distances (Wood 2009). A highly mobile species, the Bald Eagle has demonstrated ecologically flexibility with the ability to utilize a diversity of habitats of varying quality throughout its range (Buehler 2000). Florida eagle habitats vary from inland lake or river, to coastal mangroves and shallow estuaries. Although the Bald Eagle population trend for the state of Florida continues to be one of strong recovery and growth, a historically important regional population of the southern coastal region of the Everglades in Florida Bay shows a contrasting population trend.

STUDY AREA

At the southern edge of the greater Everglades ecosystem is the 2200-km$^2$ area known as Florida Bay (Fig. 1). Located between the southern tip of the Florida mainland

and the Florida Keys, this shallow mangrove estuary lies primarily within Everglades

National Park (EVER, established in 1947), and much of the rest in the Florida Keys

National Marine Sanctuary (FKNMS, established in 1990).  There are approximately 237

mangrove islets (keys), ranging from 0.1 to 144 ha (Enos 1989) in Florida Bay that are

home to an historic nesting population of Bald Eagles, and represent the extreme

southeastern range of the species.  During the study period (1958-2010), 30 breeding

territories were identified in Florida Bay; these generally consist of an
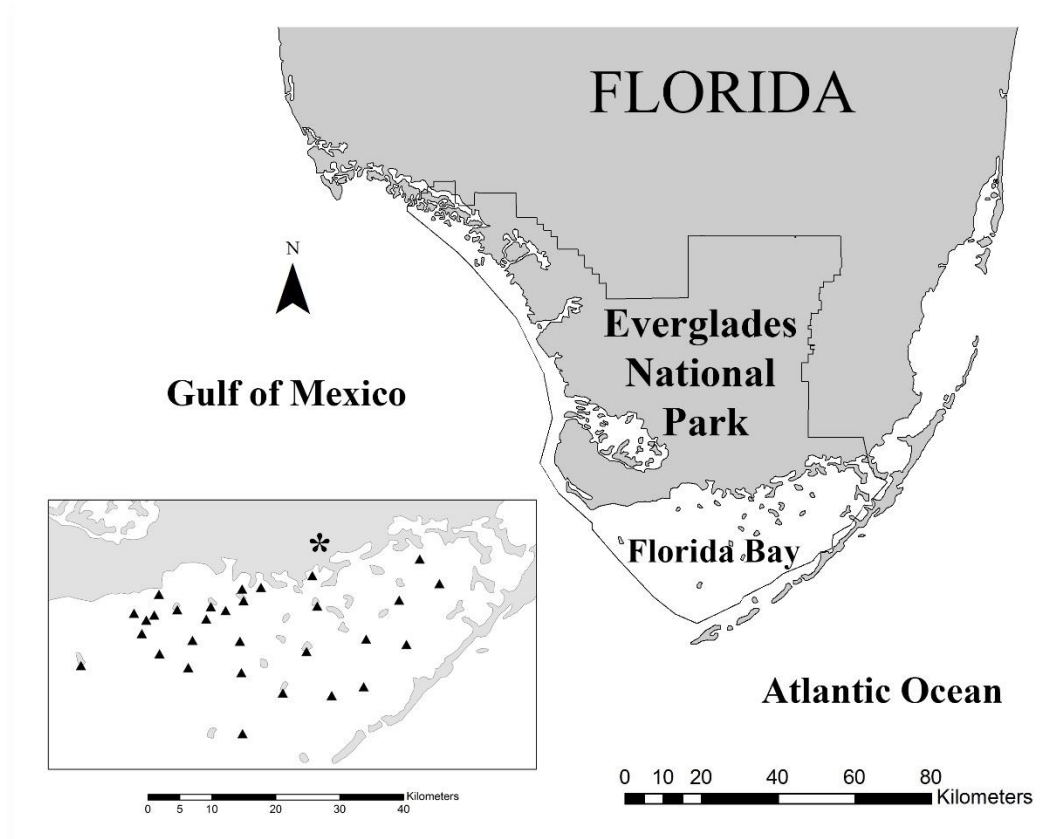


**Figure 1.1** The Bald Eagle study area in Florida Bay, in the southern coastal system of
Everglades National Park, Florida, U.S.A. and location of 30 breeding territories identified
during the study period (1958-2010).

individual key or a small group of keys.  Despite the habitat protection provided within

EVER and FKNMS, Florida Bay is directly impacted by the natural upstream hydrology

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of the greater Everglades and the anthropogenic changes to that hydrology that have occurred (McIvor et al. 1994, Hall et al. 1999, Fourqurean and Robblee 1999, Rudnick et al. 2005). During the 1960-70s the population seemed, to local experts, to be in a wild, undisturbed state that was relatively free from the effects of pesticides (Robertson 1978, Curnutt 1991, 1996) and may have been at carrying capacity (Ogden 1975).

Recently, changes in reproductive parameters from historical benchmarks have been observed. These changes, coupled with regional ecosystem degradation, have led us to examine trends in Bald Eagle occupancy, nesting activity, nesting success, and productivity in Florida Bay during the breeding seasons 1958-2010. A common difficulty inherent in most species' recovery efforts is determining historical population levels, as most population survey efforts occur after populations have already diminished. Here, we provide a synthesis of the long-term reproductive trends in a regional Bald Eagle population that is apparently declining and whose historical population is known.

SURVEYS

Surveys of the Bald Eagle breeding population in Florida Bay were initiated by EVER personnel in 1958 in response to growing concern over declining eagle populations in the state of Florida and nationwide. Systematic and intensive aerial surveys were conducted by fixed wing aircraft (Cessna 182, J3 Cub, or Lake Buccaneer, flying at about 244 m) to detect eagle presence on known breeding territories and other potential nest sites (keys which had not been used previously). Monthly surveys were conducted each year from October through May or June (e.g. 1972 season is Oct. 1972 – Jun. 1973). The 1980, 1981, 1984, and 1985 breeding seasons were surveyed less frequently and were excluded from analyses. During the study period from 1958-2010,

49 of the 53 breeding seasons, 30 individual territories were documented. The most recent territory was added in 1973.

Ground surveys and photo documentation were conducted during the survey period when necessary and feasible, to supplement and confirm aerial surveys. Aerial surveys, when limited to early and late breeding season flights, can underestimate occupancy and reproductive success (Grier et al. 1981, Fraser et al. 1984, Nesbitt et al. 1998). Sampling error was minimized by conducting multiple surveys (mean 5-7 surveys per nest site) over the breeding season, and surveying all potential nesting habitat with multiple flights in combination with ground surveys. Over 53 years the EVER nest surveys have been conducted by a succession of different personnel using the same basic protocol with direct observations of individual birds and nests. These raw data were transferred and formatted in a custom Access database from field notebooks, EVER archives, and reports.

REPRODUCTIVE PARAMETERS AND ANALYSES

Based on previous work (Postupalsky 1974, Steenhof and Newton 2007), we define nesting activity and reproductive success during each nesting season as follows. Breeding territories were considered "*occupied"* if a pair of adults was observed in the territory on at least one visit during the breeding season, or if at least one adult was seen in the territory and there was evidence of recent nest maintenance *(e.g.,* fresh lining, structural maintenance). Territories were defined as "*unoccupied*" if they did not meet the criteria of occupied. An occupied territory was considered "*active"* if there was observation of an adult in an incubating posture on the nest, or if eggs or young were present. A territory was defined as "*successful"* if one or more young of fledgling size

were present.

We defined occupancy rate, activity rate, and success rate as the percentage of occupied, active, and successful territories surveyed per breeding season. We defined nesting success as the percentage of occupied nests that contained ≥1 young and productivity as the number of young per occupied nest. Brood size was defined as the number of young per successful nest.

STATISTICAL ANALYSES

The annual variation in the number of occupied territories was calculated as the log ratio of occupied territories between years $\ln(Oc_{t+1}/Oc_t)$. A univariate, nonparametric, Mann-Kendall test was used to determine statistical significance of monotone temporal trends (Kendall and Gibbons 1990). To identify differences among decades, the ratio of productivity and occupancy was tested using a one-way analysis of variance (ANOVA); comparisons among years were made using the Tukey-Kramer method (Sokal and Rohlf 1995). Residual inspection of the data showed that assumptions for normality and heteroscedascity were met. Results were deemed significant if $P \le$ 0.05.

OVERALL REPRODUCTIVE RATES

From 1958-2010, 1389 territory-years were monitored during 49 of 53 Bald Eagle breeding seasons. We analyzed the reproductive outcome for a total of 1059 occupied territories. The annual number of occupied territories ranged from a high of 28 (1974 and 1983) to a low of 12 (2001), with a mean of 21.6 ± 4.56 (SD). Annual territory occupancy rates ranged from a low of 0.40 in 2001, to 1.00 in 1959 and 1969, with a mean of 0.77 ± 0.16. For the occupied territories, we documented 866 breeding attempts

(active territories) representing an annual mean of $0.83 \pm 0.11$ (active territories/occupied territories), which ranged from 0.56-1.0 over the study period. Overall annual rate of breeding success, defined as the proportion of active territories that were successful in fledging $\geq 1$ young, was $0.67 \pm 0.15$. Nesting success, occupied territories that were successful in fledging $\geq 1$ young, had an overall annual rate of $0.55 \pm 0.14$. A total of 828 young were fledged during the 49 breeding seasons with a mean of $16.9 \pm 4.1$ young per season. The overall productivity per season was $0.81 \pm 0.21$ young/occupied territory and the mean brood size per season was $1.48 \pm 0.16$ young/successful nest.

CHANGES IN TERRITORY OCCUPANCY, BREEDING, AND SUCCESS

During the period from the early 1960s until to the mid-1980s, the population was characterized by high occupancy rates and was thought to be at or near carrying capacity for Florida Bay (Sprunt et al. 1973, Ogden 1975, Curnutt 1991). This period of population stability was characterized by small annual variation in occupancy ($\leq \pm 0.10$; Fig. 2). Since the mid-1980s, however, there has been a dramatic increase in variation of annual occupancy (Levene's test for equality of variance; $tau = 2.449$, d.f.$= 46$, p<0.01). Initial variability in annual occupancy variance in the data set (pre-1960) was due to the discovery of new territories in the first few years of surveys.
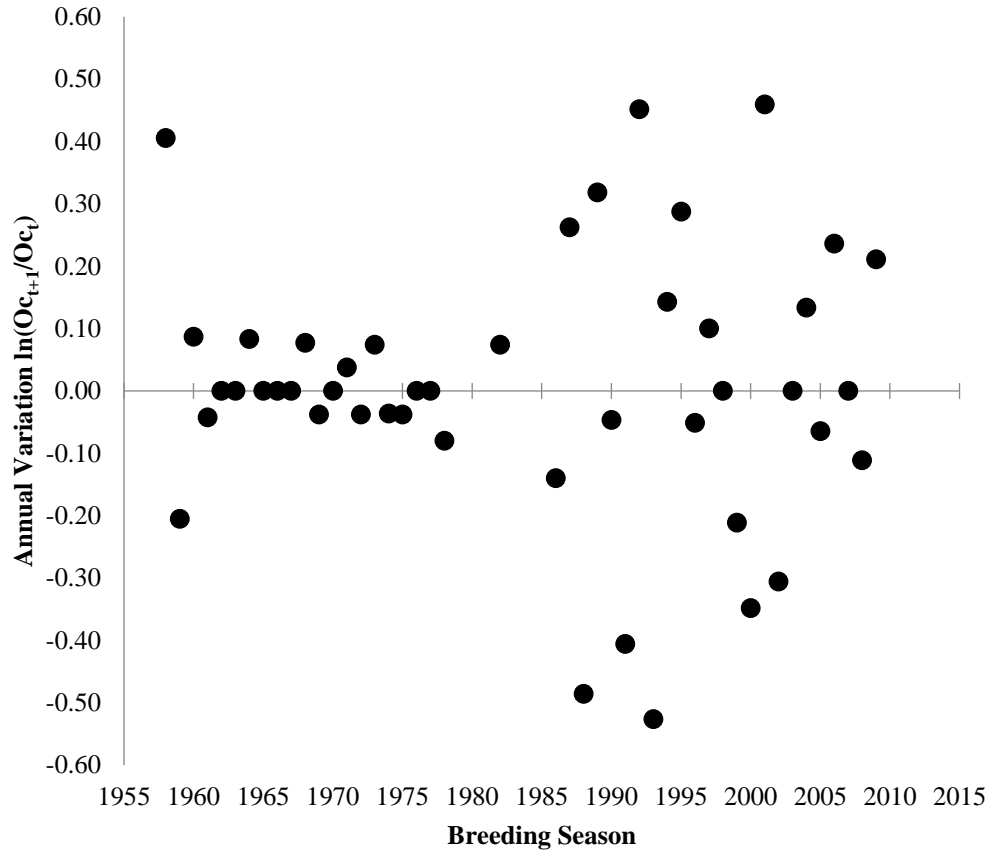
**Figure 1-2.** Annual variation in the number of occupied territories (Oc) calculated as $\ln(Oc_{t+1}/Oc_t)$.

Within the study period, the annual occupancy remained > 80% until 2001, when a decline to 40% was observed (Fig. 3). The highest five-year occupancy period of the study (1972-1976, 26.8 ± 0.83 occupied territories) had an occupancy rate of 0.925 ± 0.036. By comparison, the final five-year period of the study (2006-2010, 17.5 ± 1.9 territories) had an occupancy rate of 0.601 ± 0.08, a 32% decrease from historical highs. The period immediately preceding the final five years (2001-2005, 15.0 ± 2.65) territories) had the lowest five-year occupancy rate in the study, 0.5 ± 0.08, a 43% decrease from the historical high. A Mann-Kendall test revealed that this overall decrease in occupancy rates was significant ($tau$ = -0.397, $P \leq 0.001$, $n = 49$).

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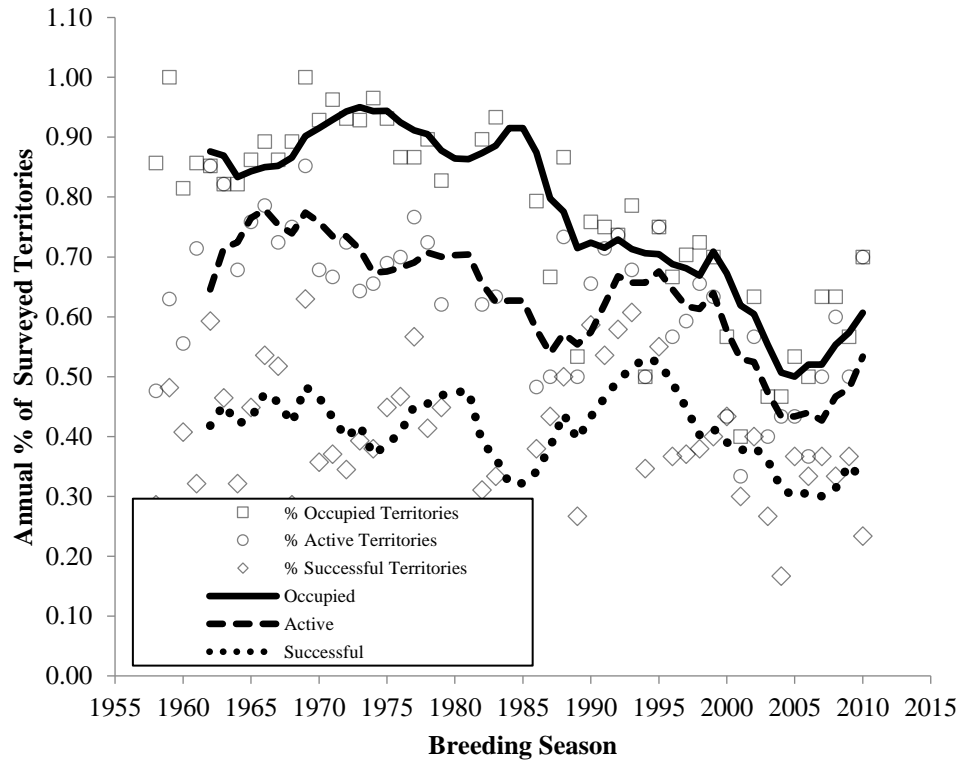
**Figure 1-3.** Percentage of surveyed territories occupied (Mann-Kendall test, *tau* = -0.397, *P* ≤ 0.001, *n* = 49), percentage of surveyed territories active (Mann-Kendall test, *tau* = -0.385, *P* ≤ 0.001, *n* = 49), and percentage of surveyed territories successfully producing at least one young (Mann-Kendall test, *tau* = -0.177, *P* ≤ 0.077, *n* = 49) shown as 5-yr moving averages for the period 1958-2010.

The annual activity rate also showed a significant decrease over the study period (Mann-Kendall test, *tau* = -0.385, *P* ≤ 0.001, *n* = 49; Fig. 3), however, we documented a high mean rate of breeding attempts 0.83 ± 0.11 (active/occupied) over all years. The progression from an occupied territory to an active territory (breeding attempt) represents an important step in the breeding process. The 1958-2010 rate of breeding attempts (active/occupied) showed a significant increase (Mann-Kendall test, *tau* = 0.236, *P* ≤

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0.018, $n = 49$). This was due to the decreasing number of occupied territories without a concomitant decrease in the number of active territories, which resulted in an increased rate of breeding attempts (i.e., a greater percentage of occupied territories became active in recent years).

Although the rate of occupancy declined in the mid-1980s, the annual success rate did not change significantly 1958-2010 (Mann-Kendall test, $tau = -0.177$, $P \leq 0.077$, $n = 49$; Fig. 3). As a result, the ratio of successful/occupied nests significantly increased during the study period (Mann-Kendall test, $tau = 0.248$, $P \leq 0.012$, $n = 49$). This increase was due to a loss in the number of occupied nests without a loss in the number of successful nests. The mean nesting success (successful territories/occupied territories) from 1960-1975 was $0.48 \pm 0.11$ and for the last 15 yr (1995-2010) has been $0.59 \pm 0.13$. The transition from an active territory to a successful territory (breeding success), which reflects the ability to successfully raise young to fledgling size, has not changed significantly during the 53-yr period ($0.67 \pm 0.21$ successful territories /active territories, Mann-Kendall test, $tau = 0.175$, $P \leq 0.079$, $n = 49$). For the period 1960-1975, the breeding success was $0.60 \pm 0.10$, and for 1995-2010 was $0.69 \pm 0.18$.

PRODUCTION OF YOUNG

The number of young produced each year in Florida Bay had a mean of $16.9 \pm 4.1$, with a high of 28 in 1969 and a low of 8 in 2004. Overall, Florida Bay territories yielded a mean brood size of $1.48 \pm 0.16$, which showed no significant trend (Mann-Kendall test, $tau = 0.166$, $P \leq 0.099$, $n = 49$) and a mean productivity of $0.81 \pm 0.21$ young/occupied territory, which increased significantly (Mann-Kendall test, $tau = 0.315$, $P \leq 0.002$, $n = 49$) over the study period (Fig.4). Productivity increased beginning in the

mid-1980s (Fig. 4).  This increase in productivity coincided with a decrease in the

number of occupied territories during the same period. The number of young produced

per active territory also increased (Mann-Kendall test, *tau* = 0.24, *P* ≤ 0.016, *n* = 49; Fig.

4).
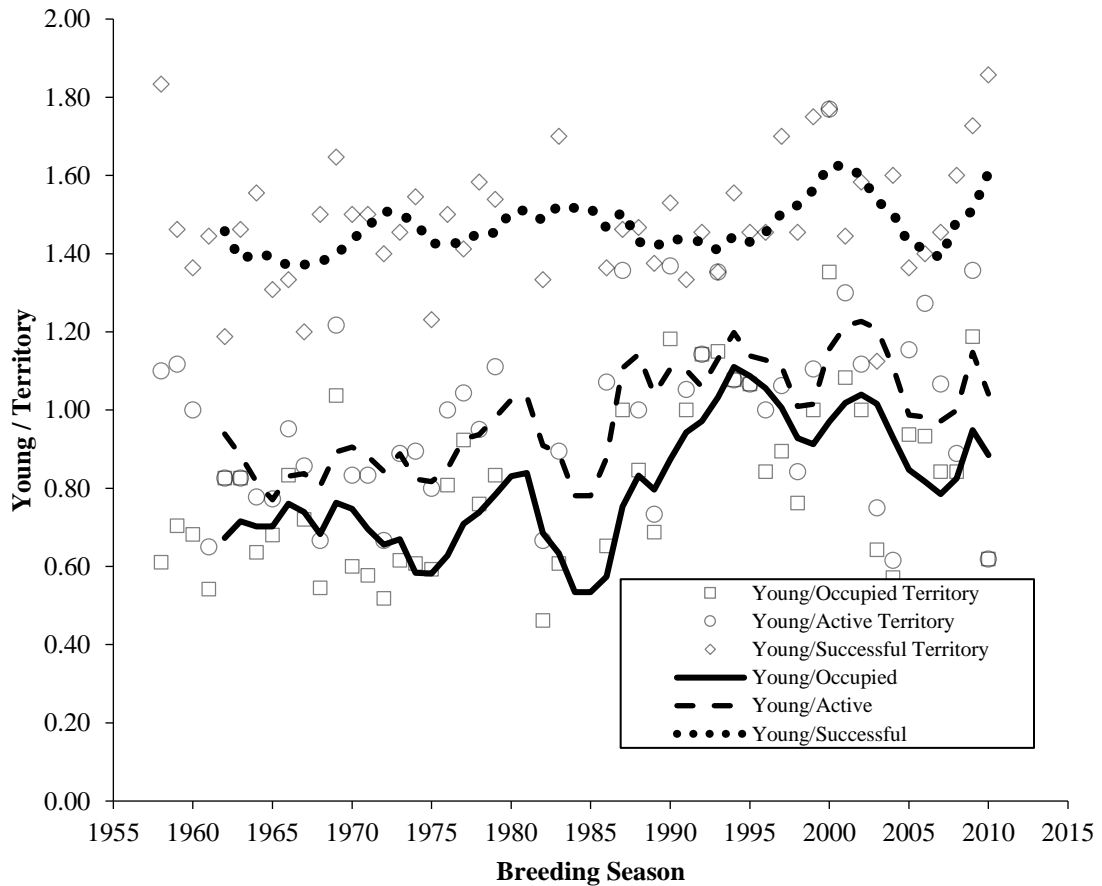


**Figure 1-4.** The production ratios of young/successful territory (Mann-Kendall test, *tau* = 0.166, *P* ≤ 0.099, *n* = 49), young/active (Mann-Kendall test, *tau* = 0.24, *P* ≤ 0.016, n =

49), and young/occupied territory (Mann-Kendall test, *tau* = 0.315, $P \leq 0.002$, n = 49) shown as 5-yr moving averages for the period 1958-2010.

To investigate temporal changes, we examined the relationship between the mean annual occupancy (number of pairs present on territory) and annual productivity (young/occupied territory) by decade (Fig. 5). There was a significant difference in the number of occupied territories and productivity from 1958 to 2010 ($P \leq 0.0001$). The years 1958-1989 and 1990-2010 made up two statistically distinct groups. The period from 1958-89 (*n* = 28 yr) had a mean productivity of $0.70 \pm 0.15$ young/occupied territory and a mean annual occupancy of $24.3 \pm 2.9$. The period from 1990-2010 (*n* = 21) had a mean productivity of $0.96 \pm 0.20$ and a mean annual occupancy of $17.4 \pm 3.04$ pairs.
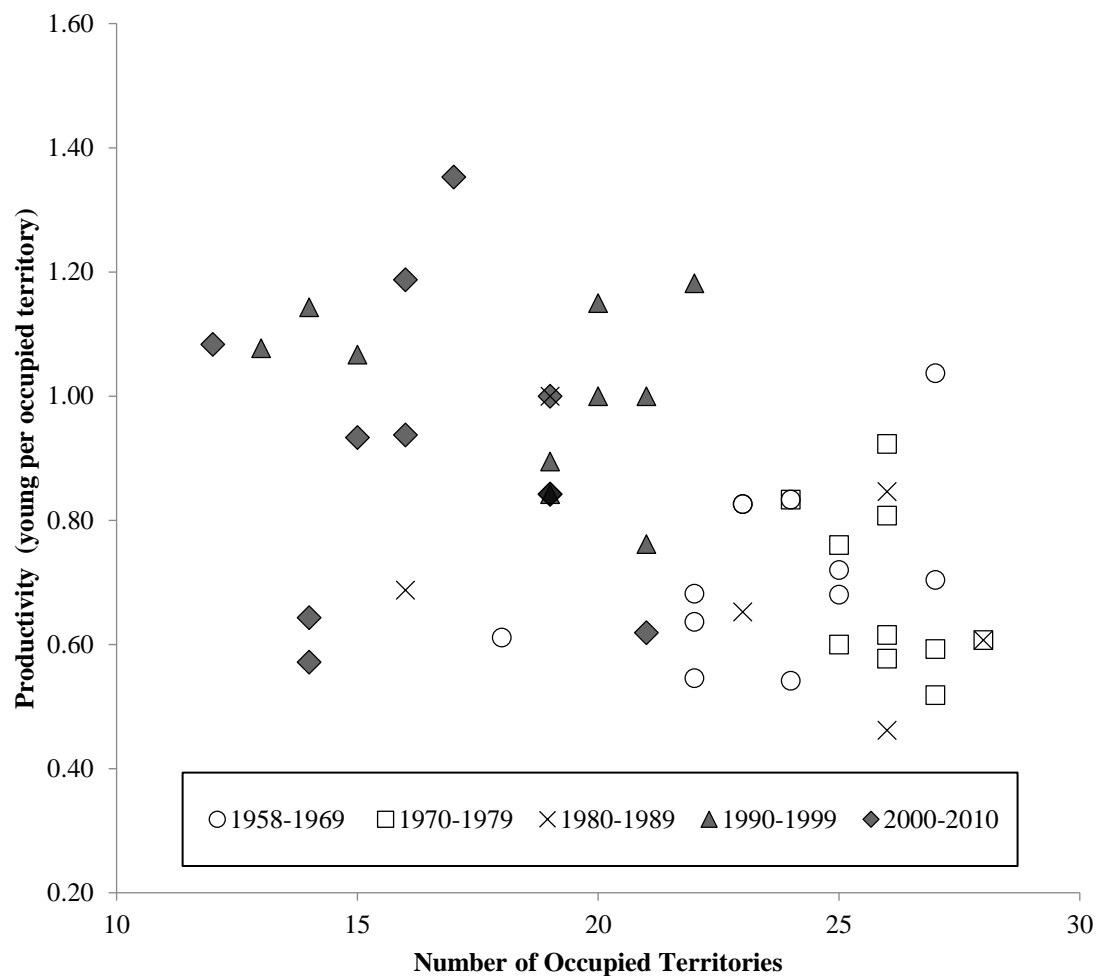
**Figure 1-5.** Productivity as a function of occupancy from 1958-2010. Markers with shading and those without signify statistically similar groupings ($P \leq 0.05$).

DISCUSSION

The Bald Eagle population in Florida Bay shifted from a period of reproductive

stability pre-1980s to a period of declining nesting population and increased variability

since then.  During the time period when most Bald Eagle populations in the contiguous

United States were in severe decline, the Florida Bay population remained robust and was

considered at or near the carrying capacity for the Florida Bay system.  DDT appears to

have had little, if any, effect on the Florida Bay population, which remained stable during

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the 1960s, 70s, and into the 1980s.  Changes in annual occupancy variation showed a transitional downward shift from a population with high stability to a population in flux with increased annual occupancy variation.  The failure of adults to occupy territories is believed to be the main factor driving the breeding dynamics in Florida Bay.

The parameters often used to describe reproductive rates of Bald Eagle populations, are nesting success (successful/occupied), productivity (young/occupied territory), and brood size (young/successful territory).  In Florida Bay, overall nesting success ($0.55 \pm 0.14$) was greater than the 0.5 level suggested as the minimum for population maintenance for Bald Eagles (Sprunt et al. 1973: used "active" in sense of occupied) and was greater than 0.5 for the last 15 yr of the study period (1996-2010, 0.58 $\pm 0.12$).  Data from EVER (1961-72) were included as one of six populations used by Sprunt et al. (1973) to generate their widely accepted benchmarks for Bald Eagle population maintenance.  Florida Bay data indicated that occupied territories became active and successful at rates suitable for population maintenance, and were comparable to those of other regions.  Nesting success in North America has ranged from 0.45 in Minnesota and Arizona (Grim and Kallemeyn, 1995; Driscoll et al., 1999), 0.44-0.77 in Alaska (Steidl et al. 1997, Zwiefelhofer 2007.), 0.63 in Colorado and Wyoming (Kralovec et al. 1992), 0.65 Washington state (Watson et al. 2002), and 0.71 in the Chesapeake Bay (Watts et al. 2008).  In Florida, nesting success averages 0.74 (Nesbitt 2001) and the state's management goal is 0.68 nesting success (Brush and Nesbitt 2009).

Productivity greater than 0.7 young per occupied territory is often cited in the literature as necessary for population maintenance (Sprunt et al. 1973) and >1.0 for achieving population restoration and management goals (Buehler et al. 1991).  We

documented an average productivity of $0.81 \pm 0.21$ young/occupied territory, which has

increased for the period 1995-2010 to $0.91 \pm 0.21$. These rates were comparable to

productivity in other regions, *e.g.* 0.68 in Minnesota (Grim and Kallemeyn 1995), 0.69 in

Arizona (Driscoll et al. 1999), 0.77 in Alaska (Steidle et al. 1997), 0.95 Washington

(Watson et al. 2002), 1.21 in Colorado and Wyoming (Kralovec et al. 1992), and 1.3 in

the Chesapeake Bay (Watts et al. 2008). Productivity of Florida's Bald Eagle population

has averaged 1.17 for 1999-2008 (Brush and Nesbitt 2009).

Similarly, a benchmark of 1.5 young/successful territory is generally cited as

typical of a healthy population of eagles (Buehler 2000). We documented an average

brood size of $1.48 \pm 0.16$ young per successful territory, which was very stable across

time periods in Florida Bay and which was similar to values for other populations such as

Alaska (1.47; Steidle et al. 1997), Washington (1.49; Watson et al. 2002), Arizona (1.5

Driscoll et al. 1999), Florida (1.55; Brush and Nesbitt 2009), and Chesapeake Bay (1.7;

Watts et al. 2008).

Although nesting success, productivity, and brood size of the Florida Bay

population, were similar to those in other populations, caution must be taken when

comparing these parameters often cited as benchmarks for population health and stability.

The reproductive performance of a population is ultimately gauged by its reproductive

output, which is determined by the relationship between nesting success and brood size.

Of the three frequently cited benchmarks (nesting success, productivity, and brood size),

productivity (>0.7 young/occupied territory) is the most appropriate. Because brood size

in Bald Eagles remains fairly constant, we interpret increases in nesting success leading

to increases in productivity as indicative of healthy populations. There are two possible

ways that population productivity (young/occupied territory) may increase.  The first is by increasing the total number of young produced, which is a result of increased nest success.  The second is by maintaining a steady production level (young) while decreasing the number of occupied nests contributing to the parameter (decreasing occupancy).  Although a steady production of young is considered good, the loss of contributing territories contributing is considered unfavorable, and our study indicated that it is the latter that has occurred in the Florida Bay population.  If the number of contributing territories continues to decrease, total production will eventually suffer.

One possible factor contributing to these changes might be the loss of territories that had historically low reproductive performance, or were occupied only for a few years.  These territories may be suboptimal, and as a result may be occupied by young adults making their first nesting attempts, which may not be successful.  Another possible factor is increased territoriality by pairs occupying "active territories" in response to a reduced carrying capacity for Florida Bay.  A reduction in availability of resources (food) may lead to an increase in territory size and may limit recruitment of young birds or pairs to the population.  Both these factors would lead to a breeding population consisting of mostly older pairs, which typically have higher breeding success and occupy higher-quality territories, and thus would maintain high productivity.  Further analysis of individual territories, including the age and identity of the breeding birds and their reproductive rates, would be required to examine this hypothesis.

For species, such as eagles, which exhibit late maturation, long lifespan, and low fecundity, changes in breeding patterns often precede changes in population size.  Decrease in the age at first breeding has been proposed as an indicator of changes in

breeding populations of Bonelli's Eagle (*Hieraaetus fasciatus*), and was correlated with

decreased productivity (Balbontín et al. 2003). Recent unpublished reports of some

mixed-age Bald Eagle pairs (immature/mature) in Florida Bay need further investigation;

they may be an indication that the number of potential mature mates has decreased. A

second line of evidence that would suggest a loss in the number of mature eagles

maintaining territories in Florida Bay is the abandonment of the year-round communal

roost of Bald Eagles; this roost was located near Mahogany Hammock, on the mainland

of EVER (Curnutt 1992). Approximately 40 nonbreeding eagles roosted there during the

1990 breeding season (77% subadults). Curnutt (1992) and Robertson (unpubl. data)

hypothesized at the time that the aggregation of subadults/nonbreeders may be

characteristic of all pristine populations of large raptors, which mature slowly and live a

long time, as occurrence of breeding vacancies in such populations was rare. In

southeastern Alaska during the 1970s, Hansen and Hodges (1985) found high rates of

nonbreeding adult Bald Eagles with stable population densities and suggest that the

surplus of nonbreeders may be an indication of food limitations that produce more

individuals than available breeding sites. No eagles roosted at Mahogany Hammock

during the 2009 or 2010 breeding seasons and the roost may not have been used since

2001. In 2001, a nesting pair established a nesting territory at the site, and it is possible

they discouraged the subadults/nonbreeders from roosting there. Alternatively, the roost

may have been abandoned after a reduction in local food availability, as nonbreeding

eagles congregate and often form roosts close to reliable food resources (Issacs and

Anthony 1987, Keister et al. 1987, Wilson and Gessaman 2003).

     During the period 1987-1991, dramatic and rapid ecological changes occurred in

Florida Bay (Hall et al. 1999, Fourqurean and Robblee 1999), which coincide with the decline in occupancy found in the Bald Eagle data.  The first was the massive sea-grass, *Thalassia testudinum,* die-offs in 1987 across much of Florida Bay (Robblee et al. 1991), which have been triggered by multiple environmental stressors including hyper-salinity and high summer temperatures among others (Zieman et al. 1999, Madden et al. 2009).  The sea-grass die-off was followed by a cascade of other ecological events, which transformed Florida Bay in 1991 from a primarily clear water system to one with extensive and persistent turbidity and phytoplankton blooms (Fourqurean and Robblee 1999).  The release of nutrients and sediments from the loss of sea-grass is a likely contributor to the increased number of algal blooms (Madden et al. 2009).  Phytoplankton blooms were more intense and covered larger areas of Florida Bay during the winter months (Butler et al. 1995) which is the breeding season for Florida Bay Bald Eagles.  The associated increase in turbidity could also have had a negative effect on Bald Eagle foraging by reducing their ability to visually detect fish prey.  In more recent years, blooms in the northeastern region of Florida Bay have also occurred, while conditions in western Florida Bay have improved, as indicated by chlorophyll *a* biomass (Boyer et al. 2009).

Changes in freshwater inputs have caused changes in the salinity patterns in Florida Bay (Kelble et al. 2007), which in turn influences and shapes a variety of ecological processes (Zieman et al. 1999).  Because the effects of these changes often affect multiple trophic levels, fish-eating birds in Florida Bay, such as the Bald Eagle, are particularly sensitive to fluctuations in salinity level and freshwater flow (Matheson et al. 1999, Crozier and Gawlik 2003, Davis et al. 2005, Frederick et al. 2009, Lorenz et al.

2009).  For example, distributions and productivity of the spotted seatrout (*Cynoscion nebulosus*) a contributing prey item within Florida Bay, vary with salinity (Thayer et al. 1999, Powell 2003).  Distributions of other important fish prey species such as hardhead catfish (*Arius*) and mullet (*Mugil*), are also affected by salinity levels (Sogard et al. 1989, Armstrong et al. 1996).  Populations of wading birds, another important prey item for eagles, have also undergone decreasing fluctuations in size and reproduction in Florida Bay and the southern Everglades (Powell and Powell 1986, Powell et al. 1989, Ogden 1994).  For example, Florida Bay populations of the Roseate Spoonbill (*Ajaia ajaja*) have exhibited a decline in the number of nests over the same time period as the present Bald Eagle study period (Lorenz et al. 2009, J. Lorenz pers. comm.).  Roseate Spoonbill reproductive rates also correlated with species composition, abundance, and availability of prey fish, each of which is a function of hydrological conditions and salinity (Powell et al. 1989, Lorenz 2000, Lorenz and Serafy 2006, Lorenz et al. 2009).  In the Chesapeake Bay, salinity levels were correlated with breeding densities of Bald Eagles (Watts et al. 2006), with provisioning rates and instantaneous growth rates of first-hatched nestlings (Markham and Watts 2008b), with biomass of prey items delivered to Bald Eagle nests, but not with prey composition (Markham and Watts 2008a).  Salinity was also correlated with differences in regional population growth of Bald Eagles and other piscivorous birds within the Chesapeake Bay ecosystem (Viverette et al. 2007).  Although there are a small number of foraging studies on freshwater lakes from central and north Florida (McEwan and Hirth 1980, Nesbitt et al. 2004, FWC 2008), there is very limited information on foraging by Bald Eagles in Florida's mangrove estuaries, such as Florida Bay.

A key stage in reproduction for Bald Eagle pairs is the occupation of a territory. Due to the declining number of occupied territories in Florida Bay and because of the negative effects these declines may have on the population's reproductive output, continued long-term monitoring of Bald Eagle territories, reproductive success, and nest locations in Florida Bay and Everglades National Park is important. The similarity in timing of changes occurring both in the Florida Bay ecosystem and its Bald Eagle population warrants further investigation as the Bald Eagle may serve as a bioindicator of ecosystem change. Future research should emphasize understanding the environmental factors that influence the decisions by adults to occupy particular territories. In the case of mangrove estuaries such as Florida Bay, this requires a better understanding of the Bald Eagle's foraging ecology in the southern coastal Everglades/Florida Bay and the relationship between the upstream freshwater ecosystem and the estuary-breeding eagles.

# A MULTISTATE MARKOV CHAIN APPROACH TO MODELING LONG-TERM BALD EAGLE TERRITORY DYNAMICS: THE IMPORTANCE OF RETAINING ECOLOGICAL DATA IN OCCUPANCY MODELS

ABSTRACT

Occupancy models provide a useful framework for exploring species distributions and habitat selection. We present a case for modeling species occurrence using a multistate Markovian approach to describe territory dynamics when sufficient data is available. Changes in the territory dynamics for a population of Bald Eagles breeding within Florida Bay, Everglades National Park are based on observed frequencies of territory use collected over a 49 year period. In contrast to the successful recovery throughout much of the Bald Eagle's range this regionally important population exhibits declining territory use. Comparison of two 15 year periods, before and after an ecosystem wide crash of Florida Bay, shows that the number of successful territories is more sensitive to changes in transition probabilities following a reduction in territory use. The increased sensitivities of transition elements is likely attributable to a loss in territory utilization, characterized by an increased rate of abandonment and reduced colonization in recent years. Observed changes in territory use coincide with changes in hydrology and prey availability for Florida Bay. Restoring annual transition matrices to more closely resemble 1960-1975 conditions would likely dampen year to year variability and increase territory use in addition to acting as a measure of ecosystem restoration for the

southern terminus of the Greater Everglades and Florida Bay. Meanwhile, Markov chain models help direct management actions for this species by focusing conservation efforts on territory states with the greatest impact on actionable recovery objectives.

INTRODUCTION

The proportion of territories occupied by a species relative to changes in species-habitat relationships is an important dynamic in ecology. Applications related to source-sink dynamics, metapopulation studies, and the evolutionary component of site quality on reproductive fitness can each be modeled using transitions between various states of territory use (Putinam 1988, Runge et al 2006, Fretwell 1972, Franklin et al 2000). Efforts to develop methods for estimating and modeling occupancy dynamics are based on repeated visits to territories where species presence or absence are recorded, and it is recognized that detection may be imperfect (Mackenzie et al 2006). Acquiring sufficient data to conduct territory monitoring studies can be costly (Mackenzie et al 2006), consequently, long-term monitoring programs are inherently rare despite their importance to our understanding of species.

Multistate occupancy models are a useful tool for management and conservation programs seeking to address questions related to transitional dynamics and animal behavior at individual territories. Often important ecological processes, including demographic changes, occur over decade long periods (Clutton-Brock and Sheldon 2010). The efficacy of predicting species occurrence in occupancy models is improved by increased sampling frequency both within a single season and over multiple seasons (Mackenzie et al 2006). Markov chain analysis provides a framework to investigate state

specific occupancies, retaining information on multiple categories of territory use not captured when modeling presence/absence alone.

Territory occupancy for raptor populations are highly dynamic with frequent transitions between states (Jimenez-Franco et al 2010). Territory selection and frequency of use are closely related and are often used as indicators of habitat quality (Sergio and Newton 2003). Territory use may provide insight into how Bald Eagles evaluate territory quality following ecological change. Eagles are particularly well suited for evaluating landscape level responses as they are long-lived, territorial, and have a high degree of site fidelity (Stalmaster 1987, Jenkins Jackman 1993, Buehler 2000, Wood 2009).

In order to quantify the changes in territory use, we created a multistate occupancy model using demographic data, 1958-2010 for all known territories, from the Everglades National Park (EVER)'s Bald Eagle , (*Haliaeetus leucocephalus*) monitoring program. Using a long-term state specific occupancy dataset for a territorially breeding population we identify territory states with the greatest relative contribution to breeding activity and productivity. This provides a unique opportunity to investigate longitudinal changes in territory dynamics. Territory use data captured before and after changes to Florida Bay offer insight into how changes in occupancy contribute to the present pattern of decline. Despite the historical stability of breeding activity within Everglades National Park (EVER) and the subsequent recovery nationwide there is an opposing pattern of declining territory use following changes in hydrologic conditions of Florida Bay (Baldwin et al 2012). Beginning in the early 1990's breeding activity measured by the abundance of occupied territories had fallen by 43% (Baldwin et al 2012).

Here we extend the basic occupancy models to characterize additional categories of territory use in a multistate Markov chain model. Transitions from one state to another between years can be represented as a Markov chain, as Bald Eagles establish persistent territory sites and are not restricted in their transition between states in subsequent years. A similar Markov chain approach was used previously to describe occupancy dynamics in a multispecies raptor community (Jimenez et al 2011, Lopez-Lopez et al 2009, Sara et al 2016). To examine how transition probabilities have changed, we apply this methodology, but for a single species with multiple states of territory use as measured by breeding effort. Using a well-documented ecological shift in the Bald Eagle's breeding habitat, we compare territory dynamics characterized by before and after change.

DATA COLLECTION

Surveys of the Bald Eagle breeding population in Florida Bay were initiated by EVER personnel in 1958, prior to documented large scale changes to hydrology, in response to declining eagle populations in the state of Florida and nationwide. A combination of monthly aerial surveys and ground inspections conducted during the breeding months of October-May/June to ensure fates of all territories were known. Four breeding seasons (1980, 1981, 1984, and 1985) were surveyed less rigorously and are excluded from analysis. For the study period, 1958-2010, a total of 49 years of breeding including 30 unique territories were recorded.

TERRITORY STATES

Repeated within season monitoring of all territories allowed us to categorize territories beyond presence/absence. The additional surveys greatly improve detection of early territory activity that would otherwise go undetected. Each territory was

categorized into one of four states based on end of season progress following criteria established by Postupalksy 1974. Breeding territories were considered Occupied (O) if a pair of adults was observed in the territory on at least one visit during the breeding season, or if at least one adult was seen in the territory and there was evidence of recent nest maintenance (e.g. fresh lining, structural maintenance). Territories were categorized as Unoccupied (U) if they did not meet the criteria for occupied. An occupied territory was considered Active (A) if there was an adult observed in an incubating posture on the nest, or if eggs or young were present. A territory was defined as Successful (S) if one or more young of fledgling size were observed.

STUDY AREA

Florida Bay lies at the southern edge of the greater Everglades ecosystem. Positioned between Florida mainland and the Florida Keys; Florida Bay is a shallow mangrove estuary covering 2,220 $km^2$. There are approximately 237 mangrove islets (keys) that range in size from 0.1 to 144 Ha. Territories exist predominantly on these small mangrove keys within the boundaries of Everglades National Park and to a lesser extent Florida Keys National Marine Sanctuary (FKNMS). For the study period (1958-2010) a total of 30 territories were identified within Florida Bay (Figure 1-1). Territories are typically are represented by an individual key or group of smaller keys. Florida Bay is a highly variable and heterogeneous landscape consisting of several semi-connected shallow basins with variable benthic bottom types. The hydrological effects of tides and incoming freshwater from the Everglades are non-uniform across the basins (Kelble et al. 2007). Although protected within EVER and FKNMS, Florida Bay is positioned less than 100km south of Florida's most densely populated cities, and is subject to extensive

anthropogenic impacts on the upstream hydrology of the greater Everglades ecosystem (Kotun and Renshaw 2014).

Freshwater input from Taylor Slough feeds into Northeast Florida Bay (NEFB) (Fourqurean and Robblee 1999). However, following the implementation of the South Dade Conveyance System (SDCS) in 1984 and the construction of the C-31N/C-111 canals, freshwater flow was redirected into a series of smaller sounds at the eastern extreme of Florida Bay and Manatee Bay (Kotun and Renshaw 2014, Baratta and Fennema 1994). Effects on hydrology are exacerbated during the dry winter, concurrent with the Bald Eagle breeding months, where portions of Florida Bay frequently become hypersaline. Hypersaline conditions are most severe in basins with reduced tidal mixing and limited freshwater inflow. It is not uncommon to find salinities in excess of 50ppt in NEFB during winter months (Lorenz 2014). Using paleoecological techniques, reconstructed salinity patterns support evidence that Florida Bay had historically lower salinities attributable to freshwater inflows from Taylor Slough (Halley et al. 1994, McIvor et al. 1994, Brewster-Wingman and Ishman 1999, Haley Roulier 1999, and Swart et al 1999). Freshwater input from Taylor Slough was four times greater prior to construction of the C-111 canal, further supporting a link between saltwater intrusion and community composition (Meeder et al. 1996, Marshall et al 2008). For the purposes of this study we characterize Bald Eagle territory utilization in Florida Bay relative to two distinct hydrologic periods separated by the completion of the C-111 canal from 1960-1975 and 1995-2010.

TRANSITION MATRICES AND PARAMETER ESTIMATION

An average annual transition matrix was created using all territories (n=30). Transition matrices were populated according to the probability of a given territory at time $t$ transitioning to another state or remaining in the same state in the following year $t+1$:

$$P = \;\; t\begin{array}{c} \phantom{t}\;\;\;\;\; t+1 \\ \begin{bmatrix} UU & UO & UA & US \\ OU & OO & OA & OS \\ AU & AO & AA & AS \\ SU & SO & SA & SS \end{bmatrix} \end{array}$$

A total of 43 annual transition matrices were created using the maximum number of consecutive two year periods from the monitoring data collected between 1958 and 2011. Consequently, the first, last, and years surrounding where survey data has been omitted (1980, 1981, 1984, 1985) did not contribute to the transition probabilities.  Parameters used by Jimenez-Franco et al (2010) for describing transition matrices were adapted to fit a single species multiple state model.

*Persistence*  The probability of a territory of a given state at time $t$ remaining in the same state at $t+1$:  P($UU,OO,AA,SS$)

*Colonization*  The probability of an unoccupied territory at time $t$ becoming occupied, active, or successful at $t+1$:  P($UO,UA,US$)

*Abandonment*  The probability of an occupied, active, or successful territory at time $t$ becoming unoccupied at t+1:  P($OU,AU,SU$)

*Advancing*  The probability of a territory at time $t$ achieving a higher state at $t+1$: P(*OA, OS, AS; includes Colonization*)

*Receding*  The probability of a territory at time *t* falling to a lower state at *t+1*: P(*SA, SO, AO; includes Abandonment*)

*Turnover time*  Average number of years for a territory at time *t* to transition to a different state at *t+1*:  $T_i = 1/(1 - p_{ii})$

*Convergence*  An estimation based on the damping ratio, $\rho$, of the rate at which the population returns to the stable state distribution: $\rho = \lambda_1 / |\lambda_2|$ where $\lambda$ is the first and second eigenvalues of transition matrix P

*Stable State Distribution*  The dominant right eigenvector $\mathbf{w_1}$ of transition matrix P describes the equilibrium distribution of territories

SENSITIVITY ANALYSIS

Each territory is capable of transitioning to any of the four territory states in the subsequent year.  Consequently, the distribution of states is a combination of direct and indirect transitions over successive years.  Some transitions contribute directly to the number of successful territories (*US, OS, AS, SS*) while others may contribute indirectly over several years.  For example, receding to a lower state may affect the number of successful territories if the new lower state contributes to an advancing state (*AO* followed by *OS* in a following year).  The number of permutations that describe the effects of small changes to individual transition elements necessitates an analytical approach.  Use of sensitivity analysis establishes the relative effect of each transition element on a given territory state, in our case we use the proportion of successful territories given by the stable state distribution (SSD) as a measure of productivity.

With respect to Markov models, sensitivity analyses can quantify the relative contribution each transition has in determining territory use at equilibrium (Spencer 2006). We describe sensitivity as the change in stable state distribution (dominant eigenvector $\mathbf{w_1}$) relative to small changes (0.0001%) to individual transition elements. Given that in a Markov Chain columns of matrix P must sum to 1, remaining elements are adjusted proportionally to their initial values when evaluating sensitivity with respect to single transition elements (Hill et al. 2004). Sensitivities were calculated numerically and follow methodology outlined by Caswell (2001), Hill et al. (2004), and Spencer (2006). Transition elements with sensitivities of greater magnitude have a greater potential effect on the composition of the SSD. Sensitivities >1 represent an effect size greater than the corresponding change to a particular transition element. Sensitivities <1 represent an effect size less than the corresponding change to a particular transition element. Sensitivities =1 represent a proportional effect. As such, we report sensitivities with the greatest effect on the number of successful territories as a means to maximize productivity. All statistical analysis and simulations were performed with R version 3.2.2 (R development Core Team 2016).

RESULTS

We observed a total of 1,245 territorial transitions across 43 annual transition matrices from 1958-2010. The mean SSD of territory use in 1960-1975 is characterized by high territory utilization (Table 2-1). Changes in territory use in 1995-2010 indicate a replacement of intermediate breeding activity (occupied and active states) by the unoccupied state. Between periods, productivity (young/successful territory) remained the same (Baldwin et al 2012). Despite a 36% decline in overall territory utilization, the

average number of successful territories between periods changed the least of the four

states.

**Table 2-1**. Mean stable state distribution for all territories (n=30) between periods, 1960-1975 and 1995-2010.

| Period | Unoccupied | Occupied | Active | Successful |
|---|---|---|---|---|
| **1960-1975** | 2.5 | 5.2 | 9.2 | 13.1 |
| **1995-2010** | 10.9 | 2.4 | 5.6 | 11.1 |
| **% Change** | 336.00% | -53.85% | -39.13% | -15.27% |

For the historical period, 1960-1975, the stable state distribution (SSD)

characterizes a distribution of territory states consistent with high use (92%) and

infrequent abandonment (Figures 2-1g,b).  In contrast, the most recent period of 1995-

2010 had much lower territory use (65%), and a fourfold increase in the proportion of

unoccupied territories.  Despite an increase in the proportion of unoccupied territories the

number of successful territories remained relatively unaffected (Figure 2-1g).  Instead we

see a shift away from intermediate territory states (occupied and active) to a pattern of

territory use dominated by unoccupied and successful states.

The probability of colonization remained low for both periods (Figure 2-1a).  However,

the frequency of territory abandonment between 1995-2010 exceeded the 1960-1975

values for all territory states.  Low probability of colonization combined with frequent

territory abandonment resulted in a 27% decrease in territory use between periods.  The

frequency of territory abandonment has increased for all territory states for 1995-2010,

most noticeably in the transition away from an occupied state (Figure 2-1b).  Average

turnover time for all territories was between 2-3 years with unoccupied and successful

territories having slightly longer turnover times and higher probability of

BLACK= 1960-75 WHITE= 1995-2010
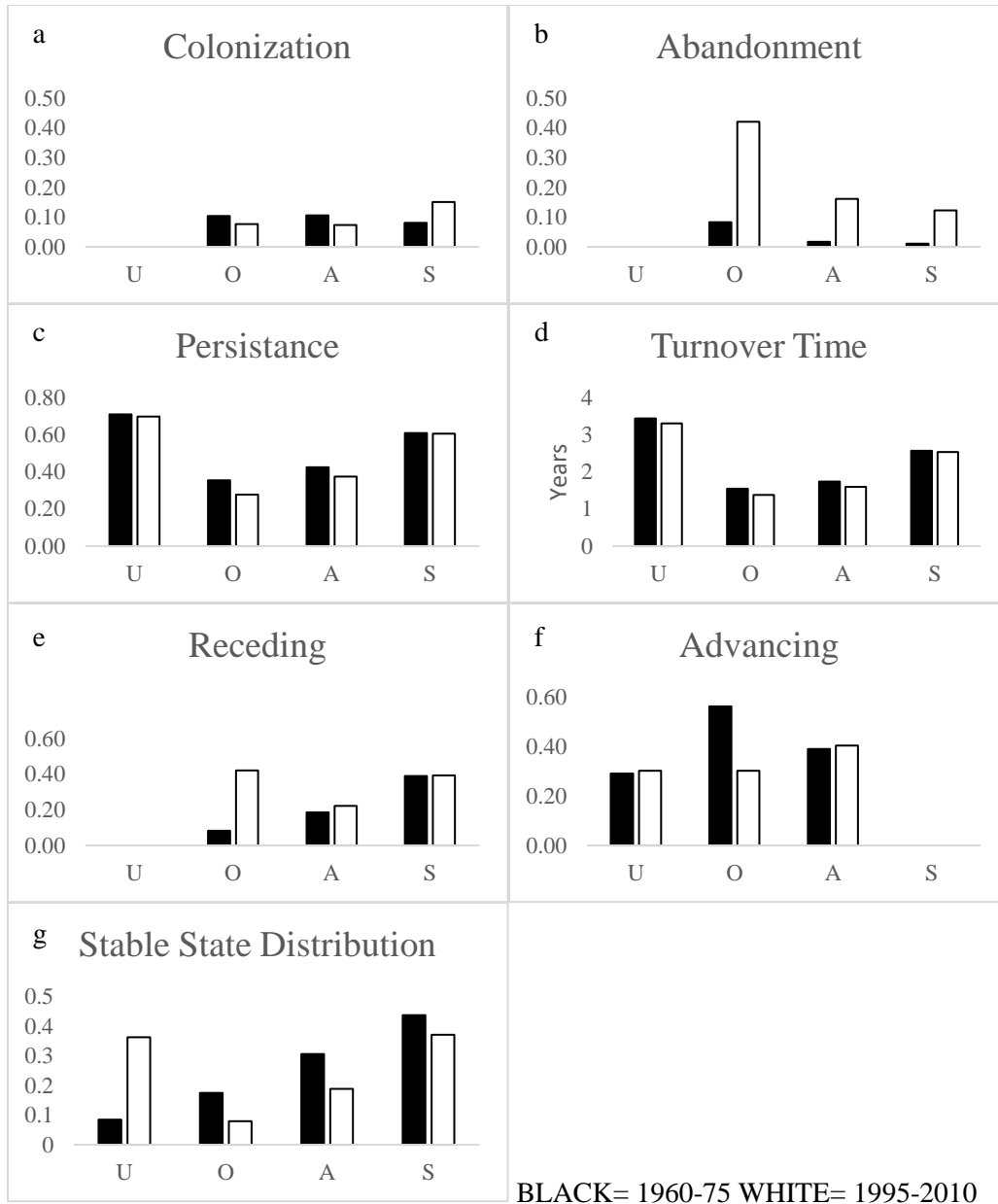
**Figure 2-1.** Comparison between average transition matrices 1960-1975 (**black**) and 1995-2010 (**white**) for the territory states: unoccupied (**U**), occupied (**O**), active (**A**), and successful (**S**).  **a** Probability of colonization of a previously unoccupied territory, **b** probability of territory abandonment, **c** probability that a territory remains in the same state the following year, **d** number of years for a territory to transition to a different state, **e** probability that a state is replaced by a lower state, **f** probability that a state is replaced by a higher state, **g** stable state distribution of territories at equilibrium.

Persistence for both periods (Figure 2-1c,d). The probability of persistence, remaining in the same state, has not changed. For both periods the transition probabilities of remaining unoccupied (UU) or successful (SS) were greater than the persistence in the two intermediate states (OO and AA). The likelihood of a territory advancing to a higher state or receding to a lower states gives some indication that territory use is contracting or expanding (Figure 2-1e,f). Between periods the transition probability for advancing and receding of active (A) and successful (S) territories were similar, however, there was a shift in the transition of occupied territories. Before change (1960-1975) an occupied territory was more likely to advance in the following year but after change (1995-2010) is more likely to recede.

The SSD for each period shows the relative number of territories expected in each state. The effect of a transition element on the SSD can be categorized as advancing, receding, or persisting in the following year. The net balance of individual transition elements has shifted away from advancing to a higher state to an increased likelihood of receding to a lower state while persistence has not changed. The result is an overall reduction in territory use.

All transition elements for 1960-1975 had sensitivities <1 (Figure 2-2a). The largest sensitivities for 1960-1975 are mostly direct, transitioning to a successful territory (_S) or away from a successful territory (S_). Between 1960-1975, the transition element with the greatest effect on the number of successful territories was the persistence of a successful territory (SS). In contrast, transition elements for 1995-2010 have greater sensitivities (Figure 2-2b). Two transition elements had effect sizes that exceed their input size (SU = 1.248 and US = -1.144). Transitions between unoccupied and successful

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states had the greatest effect on the number of successful territories. Reduced frequency of intermediate territory states, occupied and active, for this period contributes to the increased sensitivity for the remaining transitions on successful territories as fewer transitions weighs each more heavily.

a. Sensitivities 1960-1975
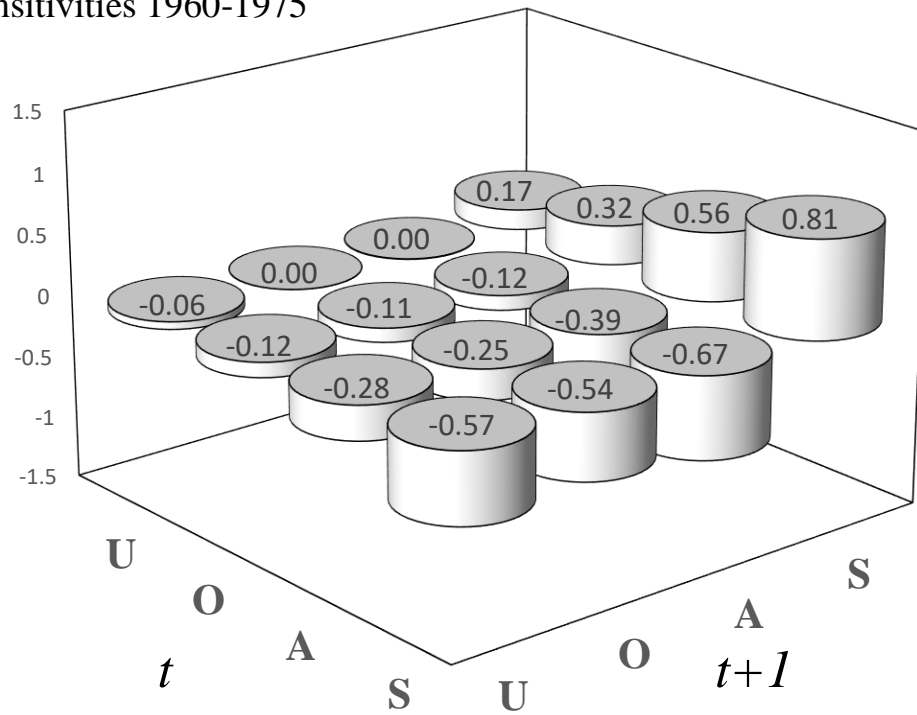


b. Sensitivities 1995-2010
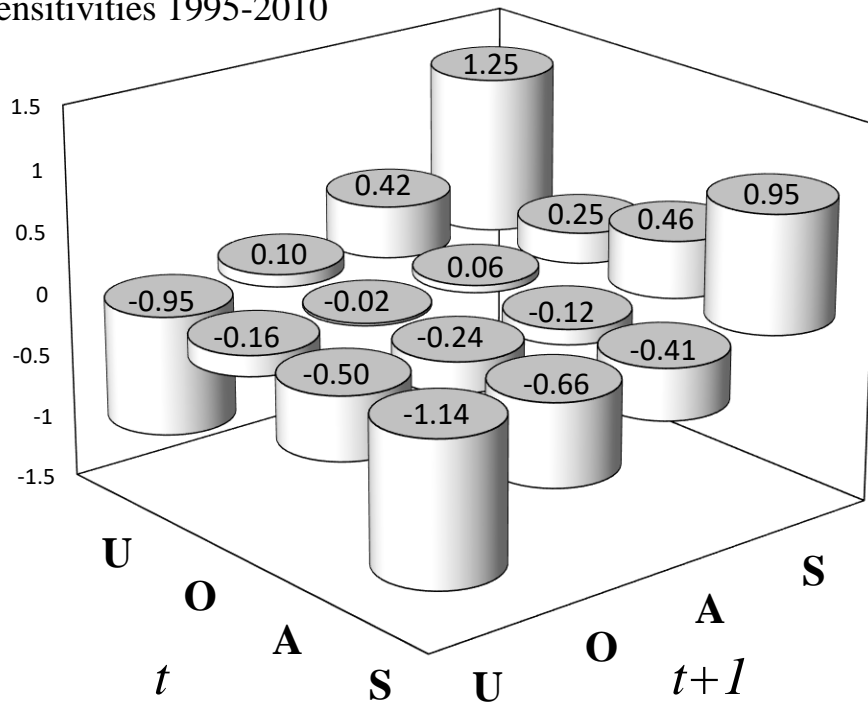


**Figure 2-2.** Sensitivity of the successful territories to changes in the transition probabilities between each of the possible states of territory use. a 1960-1975 b 1995-2010

Stable state distributions and the proportion of successful territories, varied in their sensitivity to changes in transition elements between periods. The sign of sensitivities mostly correspond with the respective transition, positive for elements resulting in higher states, negative for lower states. However, there are a few sensitivities that do not follow intuition and are likely the result of numerically indirect relationship. These sensitivities are small and as such are negligible or unlikely to have actionable management implications relative to other transition elements. For the time period of 1960-1975 the proportion of successful territories was most sensitive to changes in transitions that characterized failed breeding effort and persistence of successful territories. In contrast the 1995-2010 proportion of successful territories at equilibrium had greater sensitivity to changes in transition elements characterized by decisions to initiate breeding. The current territory dynamic is dominated by transitions between unoccupied and successful states (*US, SU*), with reduced relative contribution by transitions of intermediate states (occupied and active).

The relative contribution of transitions from an unoccupied state (*UU, UO, UA, US*) on the proportion of successful territories increased (from -0.06, 0.001, 0, 0.167 to -0.95, 0.099, 0.419, 1.248). Increased volatility in the 1995-2010 transition matrix is supported by the increased sensitivity to transition elements, particularly by the number of elements with sensitivities greater than 1.

DISCUSSION

By successfully incorporating intermediate territory states into a Markov chain style occupancy model and conducting subsequent sensitivity analyses, this approach identified transitions with the greatest effect on the stable state distribution. Using changes in the proportion of successful territories as a substitute for productivity, the number of successful territories is more sensitive to changes in transition elements moving between unoccupied and successful states. Increased sensitivity to these transitions are likely the result of reduced intermediate territories, particularly in the number of occupied territories. Loss of occupied territories suggests territory dynamics have shifted from high utilization/high competition to one characterized by frequent territory abandonment. Reproductive success remains unchanged despite a decrease in reproductive effort (Baldwin et al 2012). Bald Eagles are showing less initiation of breeding effort (i.e., occupancy) but initiated nests tend to be more successful. The extent of territory loss in Florida Bay is not limited to reproductive effort. The loss of juvenile and sub-adult roosts once found in a nearby inland mahogany hammock coincides with the shifts in territory dynamics observed within the most recent period of record (pers. comm. O.L. Bass).

The relatively unchanged number of successful territories from 1960-1975 to 1995-2010 suggests a consolidation of the higher quality territories despite reduction in overall territory use in 1995-2010. Low colonization rates coupled with high probability of persistence for unoccupied territories is concerning. We see increasing evidence that territories fluctuate from year to year, but are being absorbed by the unoccupied state. Eagle territories that are unoccupied have a very low probability of being used in the

following years, and even lower chance of successfully producing young (Sergio and Newton 2003). The persistence of successful territories becomes increasingly important as overall territory use decreases. Maintaining individual territory histories allows us to identify territories with the greatest contribution to productivity, as well as ones with the highest capacity to recover from a disturbance (storm event, loss of breeding partner, anthropogenic interaction). In order to manage for greatest territory use and productivity we investigated the sensitivity of SSD relative to changes in transition probabilities. The number of successful territories has become more sensitive to changes in the persistence of successful territories remaining successful between years.

Longitudinal studies are inherently rare, but especially useful for studying long-lived, philopatric species like the bald eagle (Clutton-Brock and Sheldon 2010). Occasionally, these studies allow us to investigate ecosystem, level changes when data collection begin before and continued after changes occurred. Where typically data only exists for recovery or post collapse conditions. The effects of hypersalinity on Florida Bay began in the 1990's, however, monitoring data for Bald Eagles pre-dates ecological changes and helps corroborate paleoecological evidence of changing hydrologic conditions. Within season monitoring provides meaningful insight into territory dynamics beyond presence/absence data typical of other eagle studies. Categorizing individual territory states across decade long periods provides information on how eagles prioritize reproductive effort as well as respond to ecosystem changes.

The high proportion of territory use in 1960-75 suggests a population at or near carrying capacity. Reproductive failures during this period were likely stochastic, re-colonization rates were high, with infrequent abandonment. Territory use and success

was distributed geographically throughout Florida Bay. Territories were likely to remain used in subsequent years.

Florida Bay underwent a series of ecological changes that may have affected Bald Eagle territory use, namely changes in hydrologic conditions, the resultant sea-grass die-offs, algal blooms, and changes in prey abundance and assemblages. Decreased territory use between periods (Baldwin et al. 2012) can be characterized by an absorption of occupied and active territories into unoccupied states. Loss of marginally performing territories appears to coincide with areas of Florida Bay most affected. A similar decline in breeding activity was observed for Ospreys (*Pandion haliaetus*) utilizing the same habitat, the number of Osprey nests fell from 200 in 1970-80 to 70 in 1993 (Poole 1989, Ogden 1993). Increased year-to-year variation in territory utilization and the disappearance of a sub-adult/nonbreeding population of Bald Eagles further support the impact changes to Florida Bay has had on this population.

Despite total productivity remaining largely unaffected (Baldwin et al. 2012), the perceived availability of viable territories by Bald Eagles appears to have decreased. For territories that remain in use, the probability of territory success is high, suggesting that eagles are reasonably capable of assessing territory quality at the time of arrival, prior to committing to reproductive effort. We see that territory use and ultimately success may be influenced by the decision to initiate reproduction. Consequently, territory loss for this population of Bald Eagles constitutes are failure to breed (decision to initiate reproduction) and not a breeding failure (attempted but not successful reproduction).

Productivity, as measured by proportion of successful territories responds differently between the two periods. When territory use is high, success is most sensitive

to the persistence of successful territories. The remaining sensitivities are somewhat evenly distributed with a slight bias towards transitions that directly contribute to success. Additionally, transition elements that advance territories to a higher state exceed values of elements that result in receding to a lower state, and net colonization is greater than abandonment territories have a path, directly and indirectly, to becoming successful in following years.

In contrast, when territory use was low, as seen in 1995-2010 transition matrix the increased proportion and persistence of unoccupied territories characterizes a boom or bust dynamic. The proportion of successful territories becomes increasingly sensitive to changes in the transition between unoccupied and successful states. The relative importance of each territory increases as fewer territories contribute to overall territory dynamics. Not all transitions can be managed (Soutullo 2008) nor is it always biologically feasible (Mills 1999, Lubben 2008). Specifically, managing for increased territory use but at the cost of successful territories would be counter-productive. Accordingly, transition elements SU and US have the greatest magnitude effect on the proportion of successful territories (-1.144 and 1.248 respectively). Potential management actions should emphasize protecting successful territories and improving habitat quality in unoccupied territories. Additionally, increasing the number of intermediate territory states might mitigate the "boom or bust" dynamic present in the current transition matrix, reducing the contribution of unoccupied territories on the SSD. Polarization in territory use (high unoccupied, high successful) for 1995-2010 suggests a loss of marginal territories, anchored by a few highly successful territories.

We acknowledge that without data on individual breeding pairs it is difficult to attribute causation to the reduction in the number of occupied and active territories. Particularly when breeding success, number of young per successful territory, has not changed (Baldwin et al. 2012). It is possible that non-breeding habitats occupied during nonbreeding months (North/Central Florida) have improved to the point juveniles are no longer recruiting into the small population in Florida Bay. Alternatively, as the Bald Eagle population has rebounded throughout the state of Florida and the Southeast competitive exclusion may be impacting juvenile survival negatively, effecting recruitment back into Florida Bay. Our capacity to evaluate these hypotheses at this time are limited and although they may have some effect on the population of Bald Eagles we breeding in Florida Bay, the timing and extent of breeding changes in the Bay are also correlated with changes to other species using the Bay. Changes in hydrologic conditions and subsequent prey communities strongly suggest that changes observed in Bald Eagle territory use are related to detrimental impacts on the Florida Bay ecosystem (Lorenz 2014, Hanson and Baldwin 2016, Hanson and Baldwin 2017).

Territory use throughout Florida Bay has declined significantly (Baldwin et al. 2012). Current territory dynamics have shifted away from high-occupancy high-utilization of available territories. Loss of marginally performing territories along the eastern extent of Florida Bay coincides with areas most affected by environmental changes experienced over the last several decades. Significant work has been done in attempt to restore hydrologic conditions across the southern and coastal everglades as a part of the Comprehensive Everglades Restoration Plan (CERP). Changes in Bald Eagle provisioning rates and prey community composition may contribute to reduced territory

utilization (Hanson and Baldwin 2016, Hanson and Baldwin 2017).  Reduction in overall

territory use and the subsequent increases in sensitivity to particular transition elements

mirrors observed changes throughout the Florida Bay ecosystem.

Markov Chain models are well suited for describing territory dynamics (Martin et

al. 2009, Mackenzie et al. 2009).  In our case, transition probabilities and their respective

sensitivities help optimize limited research resources when working to restore occupancy

dynamics.  Moving forward, management decisions that target historically utilized

territories but are currently unoccupied have the greatest potential to increase the number

of successful territories.  Ensuring successful territories remain successful is equally

important, however, the location of successful territories has remained largely unchanged.

Management actions that promote early breeding season decisions (increasing the number

of occupied territories) may also benefit similarly affected species in Florida Bay.  With

the implementation of this model we present a novel approach to quantifying species'

response to ecosystem changes in Florida Bay, be it incidental or via a conservation plan.

With limited resources, this model allows us to focus on which states are of greatest

return on investment from a management perspective.

ASSESSING THE EFFECTS OF SPATIAL AND TEMPORAL VARIATION ON

BALD EAGLE TERRITORY DYNAMICS IN FLORIDA BAY, EVERGLADES

NATIONAL PARK

ABSTRACT

Effective management strategies for territorial species distinguish areas of
frequent use (high-quality) from areas of low-quality in order to determine to population
trends.  Using spatially explicit models and a long-term (1958-2011) dataset of breeding
Bald Eagles (*Haliaaetus leucocephalus*) in Florida Bay, Everglades National Park we
quantify the effects of the previous year's occupancy, location, and site-specific
neighborhood on territory dynamics for a declining population.  The probability of a
territory being occupied decreased along a southeast axis, number of occupied neighbors,
and year.  While colonization probability is also negatively associated along a west-east
gradient, the effects of year are positive.  Our results indicate a strong effect of location
and year on territory dynamics.  Given that territory occupancy confers habitat quality
and the heterogeneous availability of breeding habitat in Florida Bay, we expect Bald
Eagles to exhibit exogenous spatial dependence preferentially selecting higher quality
habitat.  Over 49 years of observations the location of high-use/high-quality territories
remains unchanged but their overall quality has declined, as measured by territory
occupancy.  Similarly, the loss of low-quality territories has increased as otherwise
marginal territories are no longer being occupied (perceived fitness too low).  Effects of

time and space are corroborated by observed changes seen in other avian communities occupying Florida Bay. Changes in hydrologic conditions have been linked to seagrass die-offs and subsequent prey food limitations. Despite a reduction in overall occupancy we have yet to see a loss in productivity for Bald Eagles breeding in Florida Bay.

INTRODUCTION

Many species occupy heterogeneous, or patchy, environments where habitat and resource availability vary over some spatial and temporal scale (Torres et al. 2008, Torres 2009). The explanation of occupancy patterns has been under investigation for over 45 years and significant theoretical and empirical progress has been made towards improving our understanding of species occupancy with respect to changes in habitat quality (Levin 1976, Mackenzie et al 2006). Evolutionary ecology provides the primary conceptual framework for how individual decisions and habitat features influence habitat selection (Fretwell and Lucas 1970). Variation in breeding habitat characteristics and the associated effect of habitat selection on breeding success and fitness is a fundamental premise of natural selection (Fairbain and Reeve 2001, Oro 2008). In this context, are assumed to select available habitat and occupy a territory based on the expected fitness of the territory. Individuals with breeding experience are presented with two options once deciding to breed: remain at a territory previously occupied or colonize a new territory. Individuals are predicted to leave a territory that was previously occupied if there is another territory with a greater perceived fitness. This hypothesis is dependent on three prerequisites. First, that habitat quality is heterogeneous; without variation in habitat quality habitat selection would be irrelevant. Second, that breeding success is repeatable in a given location (temporal autocorrelation, Boulinier and Lemel 1996). Third, that

individuals are capable of determining habitat quality before initiating breeding activity (Danchin et al 1991, Petit and Petit 1996).  Accordingly, territory quality can be described by the frequency of territory occupancy, where high probability of occupancy corresponds to high territory quality, and the effect of bird quality (breeding experience) is additive (Burger 1982, Newton 1991, Sergio and Newton 2003).

Large raptors, including Bald Eagles (*Haliaaetus leucocephalus*) are good candidates for evaluating landscape level responses given they are long-lived, territorial, and exhibit a high degree of site fidelity (Stalmaster 1987, Jenkins Jackman 1993, Buehler 2000, Wood 2009).  Territory continuity in raptor populations across multiple years, in some instances decades, presents a natural opportunity to contrast the occurrence of individuals with environmental changes that may have occured along similar time intervals.  The frequency of territory selection is closely related to territory quality, such that changes in territory occupancy also reflect changes in habitat quality (Sergio and Newton 2003).  The territories that Bald Eagles choose to occupy or choose not to occupy describes how Bald Eagles are evaluating territory quality in the face of a changing environment.

The habitat selection of Bald Eagles, specifically breeding territory site selection, has not been described for a population within a subtropical mangrove estuary.  We assume that mobile species select the best available habitat, unless limited by competition (Kokko et al 2004).  In this study we address territory occupancy dynamics for a population of Bald Eagles at the southern extent of their range.  Bald Eagles form breeding pairs that defend exclusive territories and exhibit mate and site fidelity (e.g., Stalmaster 1987, Jenkins and Jackman 1993, Buehler 2000).  Bald Eagles exhibit a high

degree of philopatry with relatively short natal dispersal distances (Wood 2009). A highly mobile species, the Bald Eagle has demonstrated ecologically flexibility with the ability to utilize a diversity of habitats of varying quality throughout its range (Buehler 2000). Bald Eagle habitats vary from inland lake or river, to coastal mangroves and shallow estuaries. Although the Bald Eagle population trend for the state of Florida continues to be one of strong recovery and growth, a historically important regional population of the southern coastal region of the Everglades in Florida Bay shows a contrasting population trend.

The relationship between changes in territory dynamics, defined as patterns of presence and absence on a territory, and changes in Florida Bay are poorly understood. Territory occupancy for raptor populations are highly dynamic with frequent transitions between states (Jimenez-Franco et al. 2010). In order to quantify changes in territory dynamics, we use demographic data collected from a long-term eagle monitoring program initiated in 1958 by Everglades National Park (EVER) to identify territory states with greatest relative contribution to breeding activity and productivity. This Bald Eagle monitoring program established by EVER provides a unique opportunity to investigate territory dynamics of Bald Eagles in response to a shifting ecosystem where data captured before and after changes to Florida Bay offer insight into how changes in occupancy contribute to the present pattern of decline (Baldwin et al 2012).

To understand how Bald Eagles respond to changing environments, we evaluate three territory dynamics models based on approaches established by Mackenzie et al (2006), Royle Kery (2007), and Bled (2011) that describe changes in territory presence and absence. Each model estimates the effects of time and space on territory occupancy,

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persistence, and colonization. Territory occupancy describes the presence of a breeding pair on a territory for a single breeding season. While territory persistence, the probability of a territory being occupied and remaining occupied in the following year, reflects the probability of a breeding pair returning to a territory or being immediately replaced if one or both members of the breeding pair died or emigrated. Colonization, the probability of a territory not occupied in the previous year being occupied, reflects the probability of a breeding pair selecting a vacant territory or opting to breed after skipping a year. We expect persistence and colonization probabilities to be positively associated with territory occupancy. That is to say persistence and colonization, are functions of whether or not a territory is occupied given that it was present or absent in the previous year.

A reduction in the number of occupied territories and changes in number of young per occupied territory (Baldwin et al. 2012), in combination with regional ecosystem degradation of Florida Bay, have led us to examine trends in Bald Eagle territory dynamics for the breeding seasons from 1958-2010. A common difficulty inherent in most species' recovery efforts is determining historical population levels, as most population survey efforts occur after populations have already diminished. Here, we provide a synthesis of the long-term reproductive trends in a regional Bald Eagle population that is experiencing declining territory occupancy where historical territory occupancy is known.

DATA COLLECTION AND STUDY AREA

We used data collected from a long-term bald eagle monitoring program initiated by Bill Robertson in 1958 and continued by Everglades National Park staff to present day. The population of Bald Eagles breeding in Florida Bay establish territories on small mangrove islands. "Individuals come and go and nest sites change, but eagle nesting territories are virtually forever." (B. Robertson, personal communication, 1981). Over the study period nest site location may change within the context of a single territory, however, the distribution and relation of territories in space to one another remains unchanged in part due to the limited availability of landmass for nesting. The monitoring program identifies territory occupancy and territory-specific productivity. Monthly aerial surveys were conducted to determine the fate of each territory. Occasionally, confirmation by small boat and personnel was necessary for territories obscured by foliage.

At the southern edge of the greater Everglades ecosystem is the 2200-km$^2$ area known as Florida Bay (Figure 1-1). Located between the southern tip of the Florida mainland and the Florida Keys, this shallow mangrove estuary lies primarily within Everglades National Park (EVER, established in 1947), and much of the rest in the Florida Keys National Marine Sanctuary (FKNMS, established in 1990). There are approximately 237 mangrove islets (keys), ranging from 0.1 to 144 ha (Enos 1989) in Florida Bay that are home to an historic nesting population of Bald Eagles, and represent the extreme southeastern range of the species. During the study period (1958-2010), a total of 30 territories were identified in Florida Bay; these generally consist of an individual key or a small group of keys. Despite the habitat protection provided within

EVER and FKNMS, Florida Bay is directly impacted by the natural upstream hydrology of the greater Everglades and the anthropogenic changes to that hydrology that have occurred (McIvor et al. 1994, Hall et al. 1999, Fourqurean and Robblee 1999, Rudnick et al. 2005). During the 1960-70s the population appeared to be in a wild, undisturbed state that was relatively free from the effects of pesticides (Robertson 1978, Curnutt 1991, 1996) and may have been at carrying capacity (Ogden 1975).

SPATIAL NETWORK

In order to investigate any relationship between neighboring territory use (occupied, not occupied) and site specific dynamics it is necessary to establish the spatial structure of the territory population. The spatial structure is defined by the proximity of each territory to one another which we used to create a connection network based on the local density and proportion of occupied neighboring sites. We assume a threshold distance between territories beyond which neighboring occupancy no longer influences local territory use. Without a priori knowledge of territory size and dispersal distances for Bald Eagles in Florida Bay we used the mean distance between all territories, 17.3 km, as the threshold distance to approximate territory size. Using mean distance between territories is comparable to mean territory size for a population of Bald Eagles breeding along the Columbia River (21.7km) (Garrett et al 1993). It is perhaps noteworthy nonetheless, that territories established along a river are situated along a linear ecosystem feature with two neighbors and whereas territories in Florida Bay are distributed along a plane with territories located on all sides. Territories are considered connected, $w_{ij}=1$, if neighboring territory is within a threshold distance of 17.3 km, and not connected, $w_{ij}=0$, if the distances between $i$ and $j$ exceed the threshold distance.

OCCUPANCY STATE MODEL

The collected occupancy data consists of $i = 1, 2, \ldots,$ M spatial units (i.e.

territories), over $t = 1, 2, \ldots,$ T years. Occupancy dynamics are accounted for by two

parameters, persistence probability $\varphi$ (and its compliment site specific extinction $1-\varphi$),

and colonization probability $\gamma$. Let $Z_{i,t}$ be the occupancy of territory $i$ in year $t$ such that if

territory $i$ is occupied in year $t$ $z_{i,t} = 1$, otherwise let $z_{i,t} = 0$. We are interested in the

probability $\mu_{i,t} = \Pr(Z_{i,t} = 1 | z_{i,t-1})$, or the probability that a territory is occupied conditional

on its state in the previous year. We may also define an annual persistence probability $\varphi_t$

as the probability of remaining occupied from time $t$ to $t+1$, $\varphi_t = \Pr(Z_{i,t+1} = 1 | z_{i,t} = 1)$.

Now let $\gamma_t$ represent colonization probability from time $t$ to $t+1$, $\gamma_t = \Pr(Z_{i,t+1} | z_{i,t} = 0)$.

Given site specific persistence and colonization parameters we can expressed the

probability of territory occupancy $Z_{i,t}$ as the outcome of a Bernoulli random variable with

expected value $\mu_{i,t}$:

$$Z_{i,t} | z_{i,t-1} \sim \text{Bern}(\mu_{i,t})$$

where

$$\mu_{i,t} = \Pr(Z_{i,t} = 1 | Z_{i,t-1} = z_{i,t-1})$$

$$= z_{i,t-1} * \varphi_{t-1} + (1 - z_{i,t-1}) * \gamma_{t-1}$$

such that the expected value of occupancy at time $t$ depends on the previous state. For a

hypothetical state history h=01100 colonization occurs in the second year, followed by a

persistence event, then an extinction event, and finally failure to colonize. Written as a

series of probabilities this history would be expressed as $\Pr(Z=h) = \gamma \times \varphi \times (1-\varphi) \times (1-\gamma)$.

SPATIAL STRUCTURE

Florida Bay is a highly heterogeneous landscape made up of small mangrove islands separated into a series of basins characterized by anastomosing mudbanks in the west and hardbottom calcium carbonate substrate in the east (Sogard et al 1989, Butler et al 1992). Movement of water and thus resources (nutrients and prey) varies from basin to basin with more frequent tidal exchange to the west and seasonally variable freshwater inflows from the everglades via Taylor and Shark River Sloughs in the east.

In order to capture some of the spatial structure of territories relative to each other we consider the effects of neighboring occupancy on individual territories. Autocorrelation in space-time can arise from two assumptions: 1. Site characteristics are autocorrelated ("exogenous spatial dependence"); or 2. Sites are connected through dispersal or behavioral cues that lead to patterning such as aggregation or regular spacing ("endogenous spatial dependence") (Bled 2011). Without the ability to retroactively measure environmental characteristics unique to each territory we rely on the assumption that habitat quality varies in space such that territories that are closer together are more similar than territories that are farther apart ("exogenous spatial dependence"). We investigate the potential role spatial structure may have on the dynamics parameters occupancy, persistence, and colonization using the latitude, longitude, and a connectivity matrix $D_{i,t}$.

Let $D_{i,t}$ be defined as the sum of occupied neighbors that lie within the connection network of territory $i$ for all territories $N$:

$$D_{i,t} = \sum_j^N \ (z_{j,t} \times w_{i,j})$$

where $w_{i,j}$ is used to specify a spatial relationship, within a given distance, between a neighbor $j$ and territory $i$. We define a threshold distance beyond which the occurrence at site $j$ no longer influences territory $i$ as the mean a distance between all territories (~ 17 km). Neighboring territories within the threshold influence distance are considered connected, $w_{i,j}=1$ otherwise $w_{i,j}=0$.

MODEL FITTING AND PARAMETERS

We used logistic regression to estimate the effects of location, time, and territory specific neighborhood connectivity on three dynamics parameters; territory occupancy, persistence, and colonization. Location, latitude and longitude of territory coordinates, was included in all models while year and connectivity terms were included sequentially. Location was considered a potentially important variable because the geography of Florida Bay dictates that the estuary opens into the Gulf of Mexico to the west and is surrounded by mainland Florida and the Florida keys to the north, east, and south; an east-west gradient describes changes we believe to be related to tidal exchange and water depth (Torres 2009, Kelble et al. 2007). In addition, a north-south gradient may capture changes in water conditions related to freshwater inflow from Taylor and Shark River Sloughs. We believed there was a long-term trend in the data so we included year as a continuous variable. Connectivity, previously defined as $D_{ij}$, and the interaction between connectivity and year were used in order to determine the influence of neighboring territory occupancy on territory dynamics. Lastly, the interaction between latitude and year was included to describe any effects of being closer to the mainland in recent years. Each model was then selected according Akaike's Information Criteria (AIC) (Table 3-

1).  All models were implemented using the free software package R 3.32 (R

Development Core Team 2016).

RESULTS

    We report a total of 1470 observations distributed across 30 territories for 49

years (1958-2010).  Over this period there were 1079 occupancies, 946 persistence

events, and 108 colonizations of vacant territories.  The model with the strongest support

for both occupancy (weight = 0.999) and persistence (0.992) included each term while

the next nearest models showed little support (weights ≤ 0.006, Table 3-1).  Among

colonization models we observed strongest support for the model that included only

effects of latitude, longitude, year, and connectivity (weight = 0.457) but modest support

was also given to the location + year model and location + year + connectivity +

connectivity x year model (Table 3-1).  Significant model coefficients from the selected

models presented in Table 3-2 indicate a negative effect of year, longitude, and

connectivity on territory occupancy.  Despite the negative effect of year on occupancy the

interaction with latitude suggests that territories closer to the mainland now have a

greater chance of being occupied.  Territory occupancy is negatively affected along an

east-west gradient, with occupancy lowest in eastern portions of Florida Bay.  A similar

pattern exists in a north-south orientation but to a lesser extent, with occupancy lowest

along the southern region of Florida Bay.  Lastly, the effects of connectivity are negative

while the interaction between connectivity and year is positive.

    The fitted persistence model has similar main effects as the occupancy model.

Consequently, the probability of persistence follows a similar pattern of decline.

Significant model coefficients indicate a negative effect of east-west location, time, and

connectivity for occupancy and persistence estimates but a positive effect of latitude and interactions.

Total occurrence of colonization events are a function of vacant territories. Consequently, the observed frequency of colonization was lower (n = 108 events) relative to the frequency of persistence events (n = 946). The probability of a previously vacant territory being occupied in the following year is dependent on longitude and year. Territories are more likely to be colonized in the west and in more recent years because there are more vacant territories. The effects of year on colonization are smaller and positive compared to occupancy and persistence. We see an increasing probability of colonization as the

**Table 3-1.** Territory occupancy, persistence, and colonization of Bald Eagles in Florida Bay, EVER. Selection results (based on Akaike's information criterion) are shown for models including territory specific latitude (lat), longitude (long), year, and connectivity (D) as covariates. The AIC in boldface is the selected model.

| Model | Occupancy | | | Persistence | | | Colonization | | |
|---|---|---|---|---|---|---|---|---|---|
| | AICc | delta | weight | AICc | delta | weight | AICc | delta | weight |
| *lat + long* | 1601.4 | 122.1 | 0 | 1832.2 | 212.15 | 0 | 776.4 | 21.33 | 0 |
| *lat + long + year* | 1502.3 | 22.99 | 0 | 1644.4 | 24.39 | 0 | 756.8 | 1.78 | 0.188 |
| *lat + long + year + D* | 1497.5 | 18.18 | 0 | 1632.1 | 12.08 | 0.002 | **755** | **0** | **0.457** |
| *lat + long + year + D + year x D* | 1488.5 | 9.16 | 0.01 | 1630.4 | 10.36 | 0.006 | 756.2 | 1.13 | 0.259 |
| *lat + long + year + D + year x D + lat x year* | **1479.3** | **0** | **0.99** | **1620.1** | **0** | **0.992** | 758.1 | 3.11 | 0.097 |

**Table 3-2.** Coefficient estimates (and 95% CIs) from the best-approximating models using AIC selection from the analysis examining factors related to territory dynamics of Bald Eagles in Florida Bay, EVER. Estimates in bold indicate strong support (p<0.05).

| Parameter Covariate | Occupancy probability | Persistence probability | Colonization probability |
|---|---|---|---|
| intercept | **-427.46 (-598.24,-258.34)** | **405.62 (-565.40,-246.76)** | -165.71 (-351.29,19.38) |
| latitude | 2.343 (-2.83, 7.47) | 2.066 (-2.875, 6.957) | 0.421 (-3.178, 4.119) |
| longitude | **-4.615 (-5.97, -3.32)** | **-4.427 (-5.667, -3.223)** | **-1.887 (-3.611, -0.109)** |
| year | **-7.285 (-11.63, -3.04)** | **-7.591 (-11.917, -3.377)** | **0.0277 (0.012, 0.044)** |
| connectivity, $D_{it}$ | **-0.139 (-0.207, -0.071)** | **-0.116 (-0.181, -0.051)** | -0.055 (-0.111, 0.000) |
| $D_{it}$ X year | **0.003 (0.001, 0.005)** | 0.002 (-0.000, 0.004) | - |
| latitude X year | **0.287 (0.118, 0.460)** | **0.299 (0.131, 0.471)** | - |

proportion of vacant territories increased. It may be worth noting that the effect of connectivity is also negative, but the parameter was marginally insignificant (p > 0.0517).

As a means of comparing changes between two characteristically distinct periods, separated by the completion of the SDCS C-111 canal in 1984 and statistically significant changes in productivity (Baldwin et al. 2012), we investigate territory occupancy, persistence, and colonization means before (1960-1975) and after (1995-2010) (Figure 3-1). The average probability of occupancy was 0.853 ($\sigma^2$=0.125) pre-canal and 0.590 ($\sigma^2$=0.242) post-canal. The average probability of persistence was 0.823 ($\sigma^2$=0.146) pre-canal and 0.482 ($\sigma^2$=0.250) post-canal. The average probability of colonization was 0.032 ($\sigma^2$=0.031) pre-canal and post- 0.116 ($\sigma^2$=0.103) post-canal.
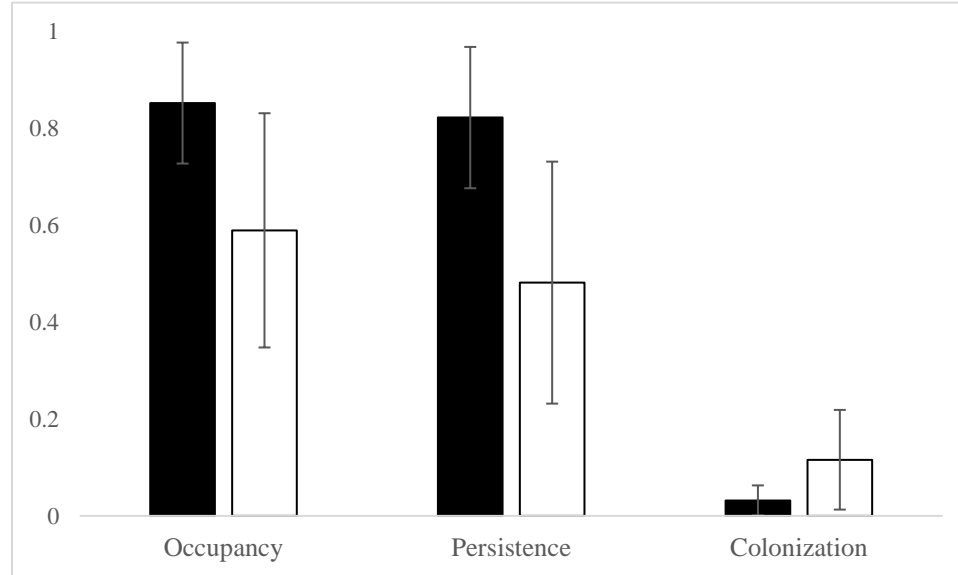
**Figure 3-1.** Comparison of territory dynamics parameters before, 1958-1984 (black), and after, 1984-2011 (white) implementation of the South Dade Conveyance System (SDCS) and the construction of the C-31N/C-111 canals.

The probability of occupancy and persistence trends downward becoming more variable with time. A similar shift occurred in the probability of colonization characterized by a period of low colonization trending upward with increased variability. A visual representation of the territories in Figure 3-2def shows the spatial effects for each of the dynamics parameters. Each territory is denoted by a circle corresponding to its location within Florida Bay. The size of the circle represents the total connectivity for that territory with larger circles having more connected neighbors. The shading of each circle represents the likelihood of the corresponding dynamic parameter occurring where black indicates a 100% probability of occurrence. All three parameters support a similar pattern of territory use concentrated in the northwest portion of Florida Bay. Additionally, territory connectedness is highest for territories located on the interior while

peripheral territories or territories along the margins, particularly along the southern end had fewer connections.  Since the connection network is a function of distance and occupancy between neighbors territories along the margins have inherently fewer neighbors and may be more sensitive to changes in their connectivity.  Distances between territories has not changed, however, the relative occupancies for a territory and the surrounding neighborhood has changed and follows a downward trend.
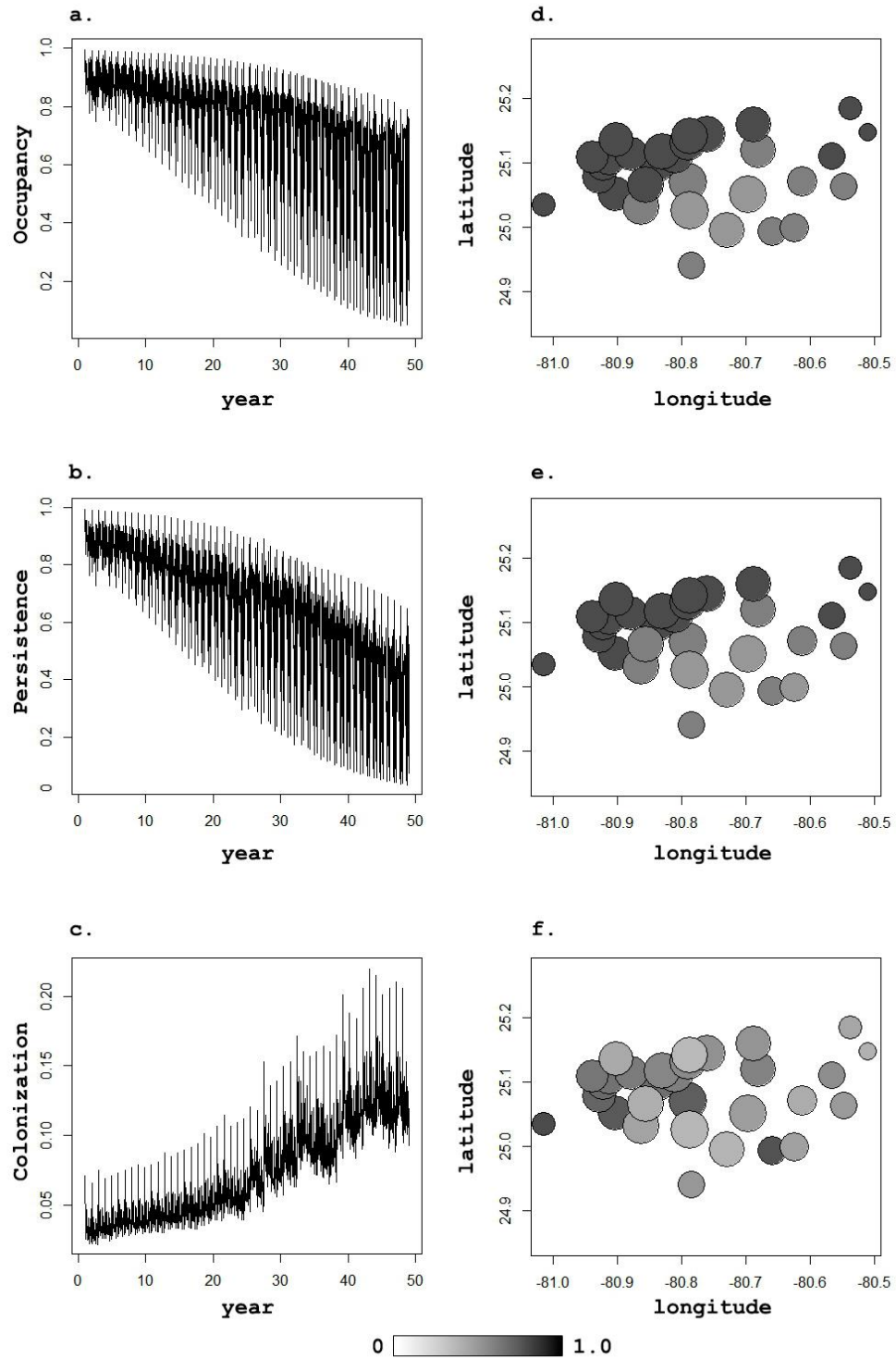
**Figure 3-2.** Estimates of dynamics parameters as a function of time (a,b,c) and location and connectivity (d,e,f). Circle size indicates territory connectivity, shading indicates probability of occurrence.

DISCUSSION

Changes in our dynamics parameters indicate declining territory utilization is linked in space and time. Territories on northwest Florida Bay consistently outperform other territories. Similarly, there are good years and bad years. There is strong support in our models that occupancy and persistence have decreased. The effects of these changes are strongest towards the southeast portion of Florida Bay in the most recent years. The probability of colonization, dependent on vacant territories, has increased in response to fewer occupied territories but not enough to supplant the overall increase in abandoned territories.

Despite a loss in number of occupied territories the mean number of successful territories and mean probability of a successful territory remaining successful in the following year has not changed (Baldwin et al 2012, Bosley chapter 2). Productivity (young/successful territory) and breeding success (success/breeding attempt) are in agreement with established measures for population maintenance (Baldwin et al 2012). However, it is important that to recognize that productivity stays the same or increases despite declining territory occupancy. Following the loss of low quality territories only the high quality territories remain and as a result productivity increases. The pre-1980s population of Bald Eagles was considered to be at or near carrying capacity for Florida Bay where territory occupancy exceeded 90% of the available habitat. The habitat heterogeneity hypothesis (HHH) suggests that mean fecundity may be reduced for density dependent populations where inexperienced or subordinate breeding pairs select suboptimal habitat (Ferrer and Donazar 1996). We see evidence for HHH in breeding attempts along marginal territories, as defined by breeding success. A combination of

suboptimal habitat and inexperienced breeders may explain territory occupancy while this population experienced density dependence pre-1980s.  As population size decreases, post-1980s, suboptimal territories would be first to become unoccupied.  Location and timing of territory vacancies help identify which areas of Florida Bay have undergone a change in habitat quality.  We suggest that high quality territories remain high quality in the short term (t to t+1) but low quality territories are susceptible to changes in habitat quality and are more likely to be abandoned for suitable breeding habitat (perceived fitness too low).

Formally stating the effects of space and time on bald eagle territory dynamics provides a stable framework to evaluate site specific conditions that determine territory success.  A concentration of occupied territories consistently within proximity of shallow mudflats suggests important characteristics for territory use.  The explanatory power of our model could be improved by establishing foraging behavior, distances to foraging areas, and movement patterns of breeding adults.  Unfortunately, we need a means of tracking individuals either by banding and observation or telemetry/satellite tracking in order to incorporate these relationships into our model.

The timing in the shift of territory dynamics is documented across many communities in Florida Bay.  Changing hydrologic conditions and repeated hypersaline events resulted in ecosystem wide seagrass die-offs (Robblee 1991).  *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* covered roughly 80% of Florida Bay prior to a 1987 die-off (Zieman et al 1989, Robblee 1991).  Seagrass die-offs exacerbate problems for aquatic communities that depend on seagrass as a food resource and are susceptible to changes in water quality.  The release of nutrients and sediments

from the loss of sea-grass is a likely contributor to the increased number of algal blooms (Madden et al. 2009). Because the effects of these changes often affect multiple trophic levels, fish-eating birds in Florida Bay, such as the Bald Eagle, are particularly sensitive to fluctuations in salinity level and freshwater flow (Matheson et al. 1999, Crozier and Gawlik 2003, Davis et al. 2005, Frederick et al. 2009, Lorenz et al. 2009). For example, distributions and productivity of the spotted seatrout (*Cynoscion nebulosus*) a contributing prey item within Florida Bay, vary with salinity (Thayer et al. 1999, Powell 2003). Distributions of other important fish prey species such as hardhead catfish (*Arius*) and mullet (*Mugil*), are also affected by salinity levels (Sogard et al. 1989, Armstrong et al. 1996). Populations of wading birds, another important prey item for eagles, have also undergone decreasing fluctuations in size and reproduction in Florida Bay and the southern Everglades (Powell and Powell 1986, Powell et al. 1989, Ogden 1994). For example, Florida Bay populations of the Roseate Spoonbill (*Ajaia ajaja*) have exhibited a decline in the number of nests over the same time period as the present Bald Eagle study period (Lorenz et al. 2009, J. Lorenz pers. comm.). Roseate Spoonbill reproductive rates also correlated with species composition, abundance, and availability of prey fish, each of which is a function of hydrological conditions and salinity (Powell et al. 1989, Lorenz 2000, Lorenz and Serafy 2006, Lorenz et al. 2009).

The loss of occupied territories is concentrated along the southeast periphery of Florida Bay, these territories historically exhibited marginal performance but for 1995-2010 are more likely to be vacant. Considerable effort and financial resources have been allocated towards the restoration of Florida Bay and the Greater Everglades. This population of Bald Eagles is uniquely positioned at the southern terminus of a highly

interconnected ecosystem where their occurrence acts as sentinel for ecosystem health and recovery.  Ongoing efforts focus on directing freshwater flow through the Everglades and into Florida Bay via Taylor Slough, however, those effects on Bald Eagle territory use are not yet apparent.  The concentration of relatively high quality territories as described by probability of territory occupancy in northwest Florida indicates a geographic area of importance that is likely important to a wide range of species. Ensuring the protection of these areas, in addition to identifying areas that are no longer occupied have changed are critical to the long-term conservation and restoration efforts of Florida Bay and the Greater Everglades.

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