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BREEDING PRODUCTIVITY, NEST DISTRIBUTION, AND POPULATION ECOLOGY OF WOOD DUCKS IN FLOODPLAIN AND UPLAND FORESTS OF SOUTHERN ILLINOIS

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by

Robert Gray Anderson

B.S., Tennessee Technological University, 1990
M.S., Tennessee Technological University, 1996

A Dissertation
Submitted in Partial Fulfillment of the Requirements
for the Doctor of Philosophy Degree

Department of Zoology
in the Graduate School
Southern Illinois University Carbondale
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DISSERTATION APPROVAL

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in the field of Zoology

Approved by:

Richard Halbrook, Chair

Robert Gates

George Feldhamer

Eric Schauber

Graduate School
Southern Illinois University Carbondale
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AN ABSTRACT OF THE DISSERTATION OF

ROBERT GRAY ANDERSON, for the Doctor of Philosophy degree in Zoology, presented on 27 October 2003, at Southern Illinois University Carbondale.

TITLE: BREEDING PRODUCTIVITY, NEST DISTRIBUTION, AND POPULATION ECOLOGY OF WOOD DUCKS IN FLOODPLAIN AND UPLAND FORESTS OF SOUTHERN ILLINOIS

MAJOR PROFESSOR: Dr. Richard Halbrook/Dr. Robert Gates

Wood ducks are thought to depend on mature hardwood forests juxtaposed with palustrine wetlands but these habitats have been continuously degraded or destroyed since European settlement. Wood ducks are adaptable and the use of marginal habitats and nest boxes has extended their range and probably was important to the recovery of wood duck populations. Until now no study has analyzed the contribution of upland nesting to local population growth and maintenance. I investigated predation effects on nest site selection using wood duck nests and simulated nests placed in natural cavities. Using demographic data collected on wood ducks in southern Illinois, I created a population model to compare growth rates of population segments that nested in upland and floodplain habitats. During 1993-1998, 179 of 244 radiomarked hens remained on the study area as resident hens. One hundred-four nests were located by following radiomarked hens and 66% of nests were found in upland forests. Nests in the floodplain were initiated earlier than nests in the upland. Thirty-six percent of known nest cavities were used in subsequent years but <10% were used by the same hen. Nest success was greater in upland habitats (0.78 ± 0.10) than in floodplain habitats (0.54 ± 0.18). Hen survival through the nesting season was 0.80 ± 0.03 and did not differ between habitats or age classes. Sixty-five percent ($n = 43$) of simulated floodplain nests were destroyed compared to 33% ($n = 45$) in the upland. Logistic regression models of simulated nest data indicated cavity security could be important in the fragmented floodplain forests of Union County Conservation Area (UCCA). No physical characteristics of wood duck nest cavities differentiated successful and unsuccessful nesting attempts. The growth rate of the local population was positive and estimated to be about 3%. Lambda was most sensitive to upland nesting parameters and floodplain parameters appeared to have little impact on lambda. Hens nesting in the area appear to have adapted to predation pressure by nesting in more secure floodplain cavities at UCCA or by nesting in the upland habitats. Floodplain and upland habitats are ecologically intertwined and the local wood duck population would not survive if either habitat were destroyed or severely degraded.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The wood duck (*Aix sponsa*) is endemic to North America and seldom occurs outside of the lower 48 United States or southern Canada. Early explorers reported that wood ducks were possibly the most abundant duck in the eastern portion of the continent, rivaled only by mallards (*Anas platyrhynchos*), but European settlement of North America caused wood duck populations to decline. Wood duck populations in several areas were nearly extirpated during the late 1800's but, contrary to popular belief, the wood duck was not near extinction at any time in recorded history (Bellrose and Holm 1994).

Wood ducks are commonly associated with mature hardwood forests juxtaposed with palustrine wetlands dominated by shrub-scrub or herbaceous vegetation. Wood duck nesting habitats have been continuously degraded or destroyed since European settlement as nesting habitats near human communities were lost, followed by habitat degradation that spread from human population centers (Bellrose 1990).

Just over 50% of all wetlands in the conterminous U.S. have been destroyed in the last 200 years. Ten states, including Illinois, have lost >70% of their original wetlands (Dahl 1990). Forested wetlands are some of the most degraded wetlands (Mitsch and Gosselink 1993), but amounts of bottomland hardwoods lost since settlement are difficult to estimate precisely (Abernethy and Turner 1987). Recent studies have shown that forested wetlands have declined annually for the last 5 decades (Abernethy and Turner 1987, Dahl and Johnson 1991), although annual loss has slowed recently (Dahl 2000) and approximately 25% of the Mississippi Alluvial plain is now forested (Twedt and Loesch 1999).

About 23% of presettlement Illinois was wetland but 85-90% of these wetlands were converted or drained to increase row-crop acreage (Suloway and Hubbel 1994), which exceeded the continental average over the same period (Dahl 1990). Ecologically and economically valuable bottomland hardwood forests were nearly eradicated in Illinois, with over 90% of bottomland hardwoods eliminated by clearing or draining (Robertson et al. 1984).

The southern distribution of wood ducks made the species susceptible to humans throughout their annual life cycle, as unregulated hunting allowed year-round sport and commercial harvest of wood ducks. Habitat destruction and overharvest lowered wood duck populations to a level that was first noticed by conservationists in the late 1800s (Bellrose 1990, Bellrose and Holm 1994). The first effective protection of wood ducks came when hunting seasons were temporarily closed after the Migratory Bird Treaty was ratified in 1918.

Closing the wood duck season and eliminating market hunting after years of overharvest allowed populations to grow after 1918 with increases being largely attributed to reduced harvest pressure and habitat management (Bellrose and Holm 1994). The use of nest boxes as surrogate nesting cavities was suggested as early as 1912 and was implemented across the U.S. where lack of cavities may limit production (Bellrose and Holm 1994). Nest box programs have often been considered the cornerstone of wood duck management since the 1930's and are often cited as important contributors to the recovery of wood duck populations (Bellrose and Holm 1994). Despite their popularity as a management tool, nest boxes contribute little to continental population levels but can enhance local populations (Soulliere 1986). Bellrose (1990) calculated that only 4-5% of autumn populations are produced from nest boxes and noted that contributions to the autumn population were negligible before the 1980's because of low numbers of nest boxes.

Approximately 95% of North American wood ducks are produced from natural cavities regardless that the amount of forests suitable to support nesting populations has declined in recent decades. Total U.S. forest cover increased during the period of wood duck recovery (1940-1980) but forested wetlands showed a net loss during the same period (Abernethy and Turner 1987).

Although wood ducks are secretive, they are remarkably tolerant of human encroachment (Reeves 1990). Wood duck populations have expanded their historic breeding range to include areas where they were previously extirpated (Bellrose 1990). Ladd (1990) noted that Central Flyway wood ducks were becoming more abundant in the Great Plains as river bottoms became forested with stands of cottonwoods (*Populus* spp.). Wood ducks have readily adapted to urban environments where there were suitable nest trees (Bellrose 1990). Use of presumably “marginal” habitats (e.g., upland forests) also could be important to population growth (Bellrose 1990) and may have contributed to the recovery of wood duck populations.

Most research has been conducted on wood ducks that nested in floodplain habitats (see Bellrose and Holm 1994). However, Hawkins and Bellrose (1940) noted that wood ducks readily used nest boxes in upland habitats. They proposed that upland habitats might be preferred to floodplain habitats for nesting. Subsequent researchers reported wood ducks nesting in upland habitats (Bellrose 1953, Robb and Bookhout 1995) but none have documented the potential importance of the use of upland habitats to local wood duck population growth and stability.

Ryan et al. (1998) estimated that 82% of radiomarked hens nested in upland habitats up to 3.2 km from adjacent floodplain forests. Ryan et al. (1998) suggested that loss and fragmentation of floodplain forests might have caused wood ducks to nest in upland forests but provided no direct comparisons of nesting productivity between upland and floodplain habitats. Ryan et al. (1998) hypothesized that predation pressure was higher in the floodplain and local nesting wood ducks responded by either nesting in safer habitats (e.g., the upland forest) or nesting in safer cavities (e.g., higher with smaller entrances).

Many studies of nesting wood ducks focused on floodplain areas because wood ducks were assumed to require floodplain forests for nesting. Consequently, only floodplain areas were searched for nests (e.g., Grice and Rogers 1965, Prince 1965, Teels 1975, Lowney and Hill 1989). Studies that assumed wood ducks nest only in forested wetlands would be unaware of nesting in nearby upland habitats. Each of several studies that included upland habitats reported hens nesting in upland habitats (Bellrose et al. 1964, Soulliere 1988, Robb and Bookhout 1995, Ryan et al. 1998). Some studies (Robb and Bookhout 1995, Ryan et al. 1998) compared upland and floodplain habitats but none have estimated the contribution of nesting hens in each habitat to local population growth and stability.

This study followed previous work on wood ducks nesting in upland and floodplain habitats of southern Illinois (Kawula 1998, Ryan et al. 1998). In conjunction with concurrent research by Zwicker (1999) and Selle (1998), I investigated effects of predation pressure on nest cavity selection using actual wood duck nests and simulated nests placed in natural cavities. I used demographic data estimated from the southern Illinois wood duck population and other data to create models that compared annual growth rates between upland and floodplain habitats. Using sensitivity analysis, I compared the influence of vital rates (e.g., clutch size and nest survival) on population growth between each habitat. These data could provide better understanding of wood duck nesting ecology as well as the contribution of upland nesting to the local population. Recent work published after this data was collected (Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006) has developed and defined ecological traps which, if a trap occurred, could have major ramifications for species using habitats that have been abruptly altered like the floodplain forests. I interpret the findings from my work and others working on this study area within the framework of an ecological trap as defined by Robertson and Hutto (2006) to determine if a trap could be influencing wood duck nesting in southern Illinois.

I investigated the use of upland forests by nesting wood ducks and compared wood duck nesting productivity between upland and floodplain forests in southern Illinois. Chapter 2 presents data on wood duck nest distribution between upland and floodplain habitats during the study and investigates the possibility that upland nesting hens are displaced from floodplain habitats. Chapter 3 includes comparisons of breeding productivity between upland and floodplain habitats. The influence of predators on nest site selection is examined by comparing physical characteristics of cavities between successful and unsuccessful wood duck nests. These comparisons were done with both simulated and actual wood duck nests in natural cavities. Chapter 4 presents comparisons of nesting hen survival rates in upland and floodplain habitats to help elucidate differences that could influence wood duck nesting distribution. Annual survival was estimated for the local population for potential use in population models (Chapter 5). Population models are used in Chapter 5 to estimate population growth rate and the contribution of nests located in upland and floodplain habitats to population growth rate. Chapter 6 discusses floodplain and upland forests in the context of nesting habitat quality and the potential for ecological traps to offer management suggestions to maintain local wood duck breeding populations.

STUDY AREA

This study was conducted on the extreme northern end of the Mississippi Alluvial Valley in southwestern Illinois. Study sites included Union County Conservation Area (CA), LaRue Swamp-Pine Hills Research Natural Area (RNA), and Oakwood Bottoms Green-tree Reservoir (GTR) in Jackson and Union Counties, Illinois (Figure 1). Each study site included forests located within the Mississippi River floodplain and upland forests immediately adjacent to the floodplain. This juxtaposition of habitats provided a relatively continuous forest of mature trees suitable for nesting wood ducks.

All 3 study areas contained portions of 2 physiographic regions: the Mississippi River Bottomlands Division or the Ozark and Shawnee Hills Division (Schwegman 1973). Elevation of the Mississippi River Bottomlands Division ranges from 104 - 116 m and elevation of the adjacent upland forests of the Ozark and Shawnee Hills Division ranges from 110 - 273 m. I will refer to these divisions as upland and floodplain forests or habitats.

Study area boundaries were determined by known distributions of wood duck nest sites (Zwicker 1999). The LaRue Swamp - Pine Hills RNA contains 4,449 ha of contiguous floodplain and upland habitats. The floodplain and upland habitats are managed by the U.S. Forest Service (USFS) as a

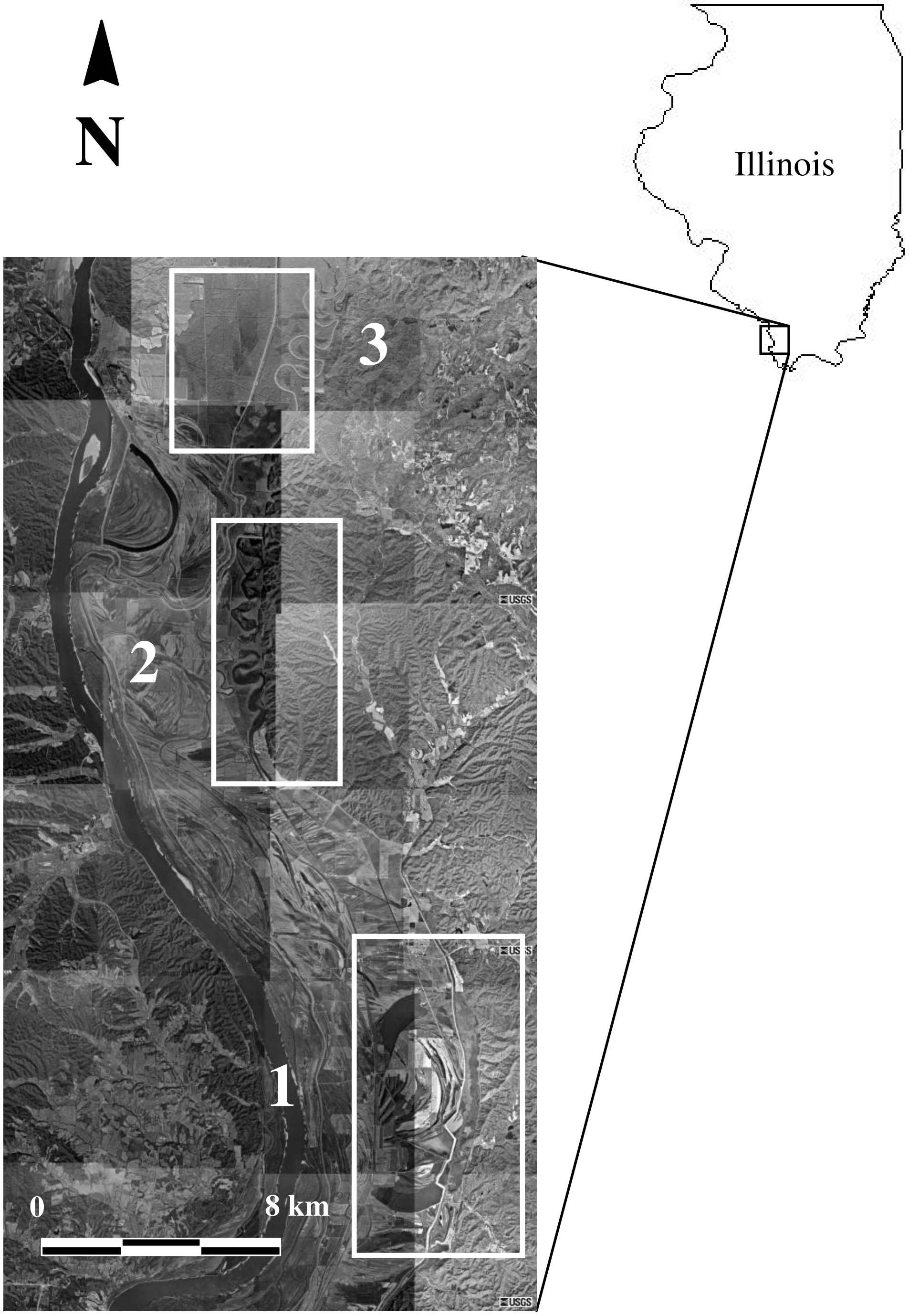


Figure 1. Locations of Oakwood Bottoms Greentree Reservoir (3), LaRue Swamp - Pine Hills Research Natural Area (2), and Union County Conservation Area (1) in Illinois.

natural area. Oakwood Bottoms GTR consists of 4,158 ha of predominantly seasonally flooded forested wetlands. This area is managed by controlled flooding and de-watering of shallow impoundments by the USFS. I refer to Union County CA as the 5,413 ha (Zwicker 1999) of upland forest managed by the USFS and floodplain habitats consisting of agricultural crops highly interspersed with floodplain forests, seasonal wetlands, and permanent lakes that are managed by the Illinois Department of Natural Resources.

Floodplain forests were dominated by 4 forest types: 1) American elm (*Ulmus americana*), red maple (*Acer rubrum*), 2) cottonwood (*Populus deltoides*), 3) sycamore (*Platanus occidentalis*), pecan (*Carya illinoensis*), American elm (*Ulmus americana*), and 4) mixed lowland hardwoods (Zwicker 1999). Upland forests were dominated by 2 forest types: 1) mixed *Quercus* species and 2) tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), and red oak (*Quercus rubra*). Kawula (1998) described the Union County CA floodplain habitats as cropland (49%), temporarily flooded forests (18%), seasonally flooded forests (11%), open water (7%), scrub-shrub (6%), and uncultivated cropland or grassland (3%). LaRue Swamp - Pine Hills RNA floodplain habitats were dominated by pin oak (*Quercus palustris*) forests, swamp, and open water with no agricultural activities. Additional information and more detailed analysis of upland and floodplain forest structure and wetland habitats can be found in Zwicker (1999) and Kawula (1998).

CHAPTER 2

NEST DISTRIBUTION

Nesting wood ducks have been studied since the early 1900s, yet little is known about how nests are distributed across the landscape. Wood ducks are known to use upland habitats (Bellrose et al. 1964, Gilmer et al. 1978, Soulliere 1988, Robb 1986, Ryan et al. 1998) but very little is known about upland nesting ecology or the contribution of upland nests to local populations. Most studies of wood duck breeding biology focused on nest boxes placed in wetland habitats so the contribution of upland forests to nesting productivity has likely been under-appreciated.

Wood ducks will nest in upland forests but all other elements of the life cycle require wetland habitats (Bellrose and Holm 1994). The proximity to feeding, loafing, and brood rearing areas likely influence the suitability of nest sites as "the value of a nest tree increases as its distance from water decreases" (Bellrose and Holm 1994:41).

A majority of wood duck hens nested in upland habitats in southern Illinois (Ryan et al. 1998) but there was little evidence to suggest why hens would nest in upland areas. I hypothesized that nesting wood ducks were being displaced from the floodplain habitats into nearby upland habitats.

As wood duck nesting populations increased and apparent competition for limited nest-boxes increased, the proportion of juvenile wood ducks nesting in boxes decreased (Bellrose and Holm 1994). Although exact displacement mechanisms are unknown, Bellrose and Holm (1994) surmised that the yearling age-class was “nesting farther afield” and had been displaced from prime nesting locations. If southern Illinois upland forests primarily supported displaced hens, then proportionally more yearlings should have nested in the upland than the floodplain.

Female wood ducks are believed to be primarily responsible for nest searching and inspection with males rarely involved in nest-site selection (see review in Bellrose and Holm 1994). A male wood duck does not establish territories near the nest or defend a specific territory but rather defends a “moving territory” surrounding his mate while she is off the nest (Bellrose and Holm 1994). The lack of participation in nest searching and territory defense by males provides reasonable expectation that comparing age ratios of nesting females between upland and floodplain habitats should be a test of whether young females are displaced from the floodplain nesting area.

Hepp and Kennamer (1992) found 79% of box-nesting hens returned to the same wetland complex and 42% reoccupied the same box. They suggested that habitat quality could influence habitat use and nest-site fidelity. If floodplain cavities are preferred, they should be occupied at a higher frequency than upland cavities.

Female-based philopatry decreases time and energetic costs invested during the breeding season by hens returning to familiar breeding areas. The potential benefits of philopatry are improved feeding efficiency, increased nest success, and knowledge of brood rearing areas (Rohwer and Anderson 1988, Baldassarre and Bolen 1994). Juvenile female wood ducks tend to home to natal breeding grounds (Grice and Rogers 1965, Hepp et al. 1989) and areas that consistently produce successful nests should have higher nest densities in subsequent years (Bellrose 1953). Conversely, areas will have fewer homing juvenile hens where factors such as predation limit production.

Ryan et al. (1998) found hens nesting in upland and floodplain forests but it was unclear whether hens were selecting the upland habitats or if hens were displaced from the floodplain. I hypothesized that upland nesting hens were displaced from floodplain nesting habitat in my study areas. Therefore, objectives of this chapter were to: 1) determine the proportions of wood ducks nesting in upland

and floodplain forests, 2) compare nesting hen age ratios between habitats, and 3) compare cavity reoccupancy rates between habitats.

METHODS

Capture and Marking

Wood ducks were captured during February - May with permanent and portable swim-in traps (Major and Hager 1996), floating bait traps, and rocket-propelled nets at Union County CA, LaRue Swamp-Pine Hills RNA, and Oakwood Bottoms GTR during 1993-1998. Data collected during 1993 - 1995 were reported by Ryan (1995) and Kawula (1998). Selle (1998) reported nesting effort data from 1993 - 1997 and Zwicker (1999) compared nest cavity availability and use. Trapping was conducted during pre-nesting and nesting periods in all years. Captured hens were fitted with 7.5 - 9.0 g necklace-type radio-transmitters mounted on Herculite (Herculite Products, Inc.) fabric bibs and No. 5 U.S. Fish and Wildlife Service aluminum leg bands.

Radiomarked hens were monitored until broods fledged or transmitters expired. Hens were located 2-3 times per week by homing to strongest signal (Mech 1983) to determine nesting status. Hens suspected of nesting were tracked to nest trees, flushed, or had their radios recovered. Aerial searches were conducted when radiomarked hens could not be located on study areas. Hens not located after repeated (>4) aerial or ground searches were assumed to have emigrated. Nesting effort was estimated as the proportion of resident radiomarked hens that were alive on the study areas and determined to have initiated a nest (Selle 1998).

Age was determined by shape and color intensity of greater and middle secondary coverts (Harvey et al. 1989, Carney 1992) and by measuring the eye patch posterior to the eye (Bellrose and Holm 1994). Selle (1998) found this method to be 100% correct when aging adults but was less accurate (~80%) when aging first-year hens. Comparisons of nest initiation dates between age classes were made using *t*-tests. Age ratios of nesting hens in upland and floodplain forests were compared with *G*-tests (Sokal and Rohlf 1995).

Most nest trees were found by following radiomarked hens but nests also were found incidentally during other study activities. Hen identification number, capture site, nest site, and nest initiation date were noted when nest trees were located. Nest initiation was determined by back-dating from estimated incubation start date based on nests of radiomarked hens. I assumed the laying period (i.e., time from nest initiation to start of incubation) to be 12 days which is about 1 egg laid per day for an average clutch of 12 eggs (Bellrose and Holm 1994). If there were multiple days between radio checks of a hen and the hen began incubation between observations, then midpoint between the observations was used as the start of incubation. Nest trees were marked with metal tags or paint. Distribution of nests between upland and floodplain forests was compared with *a G*-test. I compared nest initiation dates between habitats with *t*-tests.

Reoccupancy

Nest trees were revisited in most years after they were discovered to determine if trees were reoccupied. Nest checks were concurrent with the nesting season and all cavities in the tree were inspected for evidence (e.g., eggs, feathers) of nesting hens. During 1993 - 1995, cavity checks for reoccupancy were not a priority and only 13 total inspections of 39 known nest trees were conducted. All known nest trees were inspected annually during 1996 - 1998. As a result, some nest trees located in 1993 could have been checked 5 times for reoccupancy. Multiple cavities in the same tree were individually identifiable by entrance height above ground. In 1997, 20 randomly selected trees (10 in each habitat) found to be unoccupied during reoccupancy checks were reclimbed a second time before the breeding season ended to determine if nesting attempts were missed (e.g., initiated after reoccupancy checks were conducted). Tree reoccupancy rate was estimated as the number of cavities reoccupied divided by the number of cavities revisited during the 6-year study. Cavity reoccupancy was compared using data from consecutive years only. *G*-tests were used to compare tree and cavity reoccupancy rates.

Potential capture site bias was investigated by comparing nesting locations for hens captured near and far from upland habitats at Union County CA (Figure 2). The dividing line between near and far capture sites was determined primarily by landscape features (i.e., agricultural fields). Although a qualitative measure of distance, the categorization of capture sites as near or distant was done prior to analysis. Comparison of capture site location and ultimate nesting location (i.e., upland or floodplain) was made with a *G*-tests.

RESULTS

Nesting Effort and Distribution

Two hundred forty-four hens were radiomarked at Union County CA (203), LaRue Swamp-Pine Hills RNA (19), and Oakwood Bottoms GTR (22) during 1993-1998. No radiomarked hens nested in Oakwood Bottoms GTR during 1993-1996 so the area was not sampled in 1997 or 1998.

One hundred seventy-nine of 244 (73%) radiomarked hens remained within the study area during the 1993 - 1998 breeding seasons (hereafter resident hens) and were included

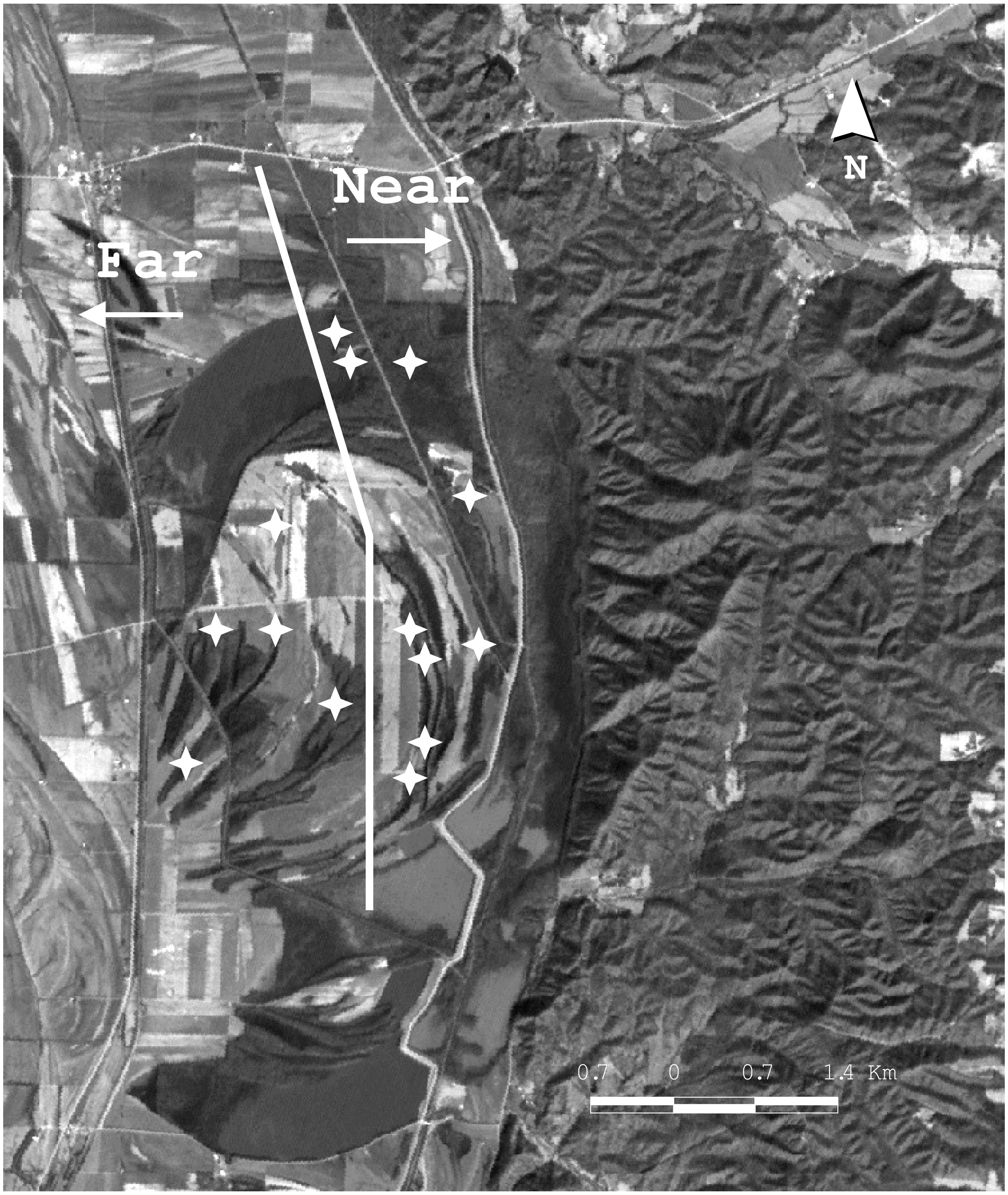


Figure 2. Location of wood duck capture sites defined as near and far from upland forests at Union County Conservation Area in southern Illinois during 1993 - 1998.

in analyses of nesting effort. Fifty-eight percent of resident hens nested during the 6 year study and no difference in nesting effort ($G = 5.01$, df = 4, $P = 0.286$) was detected among years (58 - 80%). More radiomarked hens nested in upland forests (66%) than in the floodplain forests (34%). Average date of nest initiation was earlier in floodplain forests (March 27 vs. April 9) than in upland forests ($t = -4.28$, df = 86, $P < 0.001$).

The capture site analysis indicated nest distribution between habitats was not independent of capture location ($G = 16.72$, df = 1, $P < 0.001$). Forty-nine of 64 (77%) hens captured near upland forests nested in upland forests and 17 of 24 (71%) hens captured far from upland forests nested in floodplain forests.

Seventy-three juveniles (30%) and 171 adults (70%) were captured during 1993-1998. Age ratios of captured hens was similar ($G = 0.56$, df = 1, $P = 0.453$) to nesting hens. Seventy-seven of 104 (74%) nests of radiomarked hens were initiated by adults and 27 (26%) were initiated by juveniles. Proportions of adults and juveniles that initiated nests were similar among years ($G = 6.34$, df = 4, $P = 0.175$). Pooling all years, there appeared to be proportionally more juvenile hens nesting in the upland forest when compared to the floodplain forest (30% vs. 19%) but there was no statistical difference ($G = 1.53$, df = 1, *P* = 0.216) in age ratios between upland and floodplain habitats (Table 1). There was no difference (*t* = -0.53, df = 1, *P* = 0.596) in mean nest initiation dates between juvenile (April 2) and adult (April 3) hens.

Reoccupancy

A total of 146 checks of 63 previously occupied nest trees was conducted during 1994-1998. None of the 20 trees revisited a second time in 1997 were found to have nests. There was no difference (*G* = 1.54, df = 1, *P* = 0.22) in tree reoccupancy between upland (29%, 26 of 91) and floodplain (39%, 18 of 46) habitats. Occupation of floodplain cavities in the prior year increased the likelihood of subsequent occupation (*G* = 8.80, df = 1, *P* = 0.003) with 17 of 33 (52%) occupied cavities but only 1 of 13 (8%) unoccupied cavities used in the subsequent nesting season. This trend was not apparent (*G* = 0.74, df = 1, *P* = 0.39) in upland forests where 13 of 52 (25%) occupied cavities were used the following year, compared to 13 of 39 (33%) unoccupied cavities in the previous year being occupied. There also was evidence of potential bias from assuming cavities were reoccupied by the same hen in multiple years because 3 of 12 (25%) cavities occupied by hens known to have perished were reoccupied the following breeding season.

Table 1. Nest habitat location for radiomarked wood ducks in southern Illinois during 1993-1998.

Year	Age[1]	Upland	Floodplain	Total
1993	Adult	5	3	8
	Juvenile	0	0	0
	Year Total	5	3	8
1994	Adult	4	2	6
	Juvenile	6	0	6
	Year Total	10	2	12
1995	Adult	16	4	20
	Juvenile	4	0	4
	Year Total	20	4	24
1996	Adult	6	6	12
	Juvenile	1	1	2
	Year Total	7	7	14
1997	Adult	7	8	15
	Juvenile	3	5	8
	Year Total	10	13	23
1998	Adult	9	7	16
	Juvenile	6	1	7
	Year Total	15	8	23
All Years	Adult	47	30	77
	Juvenile	20	7	27
	Grand Total	67	37	104

[1] Adults were hens in at least their second breeding season whereas juvenile hens were in their first breeding season.

I could not determine if the hen reoccupying the cavity had previously used the cavity in most cases but I observed 2 radiomarked hens that returned to the exact nest cavity in consecutive years. However, information gathered from leg-banded or radiomarked hens showed that 5 hens nested in multiple years but had switched nest sites between years. These hens nested in the vicinity (<100 m) of previously used cavities but did not reoccupy the same cavity. Only 1 hen switched nesting habitats between years. She initially nested in the floodplain within 50 m of the upland/floodplain interface and in the second year she nested in the uplands but still within 50 m of the upland/floodplain interface.

There was no association between nest fate and the likelihood of cavity reoccupancy during the following nesting season in floodplain ($G = 0.80$, df = 1, $P = 0.37$) or upland ($G = 0.76$, df = 1, $P = 0.38$) habitats. Sixty percent (9 of 15) of successful and 44% (8 of 18) of unsuccessful floodplain nests were reoccupied the following year, whereas 29% (10 of 35) of successful upland nests and 18% (3 of 17) of unsuccessful upland nests were reoccupied.

DISCUSSION

I have argued that the importance of upland nesting habitat for wood ducks has been underestimated because previous investigators searched for nests where they presumably occurred — within or near wetland or floodplain habitats. Many researchers have found hens nesting in upland habitats but there has been little effort to assess the potential explanations for hens to nest at often great distances from permanent water. I suggest that hens may prefer the floodplain forest for nesting but some hens are successfully exploiting the adjacent upland forests as a nesting habitat.

All hens were captured over bait within the floodplain and Kawula (1998) demonstrated that both floodplain and upland nesting hens spent all of their time in floodplain habitats when they were not at their nests. Consequently, by following radiomarked hens that were captured away from nest sites, I should have obtained a sample of hens that represented the distribution of nests in my study population. Nevertheless, post hoc analysis of capture location in relation to nest location suggested that hens captured closer to upland forest tended to nest in upland forest, while hens captured farther from the upland-floodplain boundary nested more predominantly in the floodplain. Although upland forest nests were an indisputably important source of nesting productivity in my study population, the importance of upland forest may have been overestimated if upland nesting hens were over-sampled by placing a disproportionate amount of capture effort in areas closest to the floodplain-interface. Trapping effort and success was not recorded, and a variety of methods that differed in their inherent effectiveness were employed at different trap sites. Wood ducks were trapped wherever they were known to congregate, and by whatever methods proven to be effective in a particular setting. Although the association between trap location and eventual nest-site location suggests a sampling bias, it does not necessarily prove that the sample of radio-marked hens was not representative of the population as a whole. We placed traps (most were mobile) wherever we found birds using an area so our capture locations broadly reflect the local distribution of wood ducks on the site.

The unintentional capture bias disallowed the simple comparison of nesting density between the 2 habitats as I had initially intended. The use of other collected data (e.g., habitat availability, age ratios) did provide valuable information on potential mechanisms to explain the apparent regular use of the upland habitats by nesting hens.

Nesting effort was lower during most years of the study than many researchers may consider normal. McPherson et al. (2003) generated some interesting conclusions about the potential to underestimate nesting effort in mallards. While I cannot assert that no nesting attempts were missed, I believe the potential bias' identified by McPherson et al. (2003) should be minimized in my work. The behaviors of radiomarked wood ducks were used as a cue that hens were initiating nests and most nests were located within 1-2 days of incubation. Additionally, no hen was known to renest during my study while the mallard study indicated multiple renesting attempts were an important component of the mallard reproductive ecology. There is little reason to believe that any potential bias would not be equal in both habitats and should not influence the proportion of nests located in upland of floodplain habitats.

Several lines of evidence suggest that wood duck hens preferred to nest in floodplain forest. Although density of suitable tree cavities were nearly equal between habitats, a greater proportion of hens nested in the floodplain than would be predicted from the proportional availability of floodplain vs. upland forest nesting habitat (Zwicker 1999). Furthermore, floodplain nests were initiated earlier and were re-occupied at a higher rate in subsequent years compared to upland nests. There was weak evidence that more juvenile hens nesting in the upland forest but I did not find strong evidence for the idea that sub-adult hens were displaced from floodplain to upland habitats as might be expected if earlier-nesting adults out-competed younger hens for the most suitable nest sites. As many as 20% of juvenile hens may have been misclassified as adults because of the difficulty in aging juvenile hens in Spring (Selle 1998). Consequently, the proportion of juvenile hens nesting in both habitats is likely conservative.

Any preference for floodplain nest sites was not sufficiently strong to fill even a modest proportion of available nest sites, as < 5% of apparently suitable tree cavities in the floodplain were used by nesting wood ducks (Zwicker 1999). A plausible explanation for the observed distribution of nests is that the breeding population, limited by some factor other than the availability of suitable nest sites, spreads it's nests over a wide area to avoid detection by nest predators. This lowering of density is suggested as a common strategy (Picman 1988, Ackerman et al. 2004, Caro 2005) for birds that experience high rates of predation when nests are concentrated in small fragments of suitable habitat.

Regardless of when or how wood ducks began using upland habitats for nesting, research has shown that hens often use the same areas during each breeding season (Hester 1962, Grice and Rogers 1965, Hepp et al. 1987, Hepp et al. 1989). I found hens may return to their previous nesting habitat but returned to natural cavities they had previously occupied at a lower rate than reported in nest box studies Bellrose et al. 1964, Fredrickson 1980, Bellrose and Holm

1994). Only 2 radiomarked hens were known to reoccupy the same cavity in successive years during this 6-year study. I interpret the literature and my data to suggest that wood duck hens likely return to occupy habitats near previously used nest locations regardless of where the nest location fell on the continuum of forested habitats from floodplain to upland.

Fidelity to a nesting habitat has been shown to enhance local productivity (Baldassarre and Bolen 1994) if nest success is sufficiently high and other essential factors (e.g., brood habitat) were available. Even birds using a suboptimal habitat displayed site fidelity when nearby optimal habitats became available (Krebs 1971). The upland nesting hens likely return to upland habitats annually and if nesting productivity is sufficiently high, the upland forest could be an important component of local nesting.

Although I observed little fidelity to specific nest trees or cavities by hens whose nests were found in successive years, there was strong fidelity to a general nest location, and therefore also to upland or floodplain nesting areas. Individual hens may have nested in different trees in successive years so that individual nest predators did not “learn” the precise location of nest sites. Alternatively, wood duck hens may also have moved their nest sites in successive years to avoid the build-up of nest ectoparasites (Merino and Potti 1995, Johnson 1996, Rendell and Verbeek 1996, Utsey and Hepp 1997, Weddle 2000).

My study was not designed to determine the historic mechanism that allowed wood duck hens to exploit upland habitats for nesting. The examination of age ratios did not provide insight into potential displacement mechanisms from the floodplain and I could not possibly determine (or assume) if the upland forest is a part of the wood ducks fundamental nesting niche or if use of upland habitats was a result of niche expansion. Regardless of how or when wood ducks began using the upland forests there appears to be regular use of the habitat. The floodplain habitat may actually be the preferred habitat but there appears to be an established tradition of nesting in the upland habitat. The use of the upland habitats could be an important component to local nesting effort and ultimately local population dynamics.

CHAPTER 3

BREEDING ECOLOGY

Successful reproduction is a key factor in maintaining viable populations and low vital rates (e.g., clutch size, nest success) can diminish breeding productivity and cause local breeding populations to decline (Dow and Fredga 1983, Cowardin et al. 1988, Gavin and Bollinger 1988, Gauthier 1990, Hepp and Kennamer 1992). Ryan et al. (1998) hypothesized that nest predation influenced nest site selection and distribution in southern Illinois but their study was not designed to investigate these hypotheses. This chapter investigates factors that could cause wood duck nesting populations to increase or decrease over time by focusing on nesting productivity and potential influences on nesting productivity.

PRODUCTIVITY

Wood duck breeding biology has been studied over several decades (see reviews *in* Fredrickson et al. 1990 and Bellrose and Holm 1994). This chapter presents nesting ecology data collected from 1993 to 1998 including some data previously reported by Ryan et al. (1998). My objective was to compare breeding productivity between upland and floodplain habitats to determine if the high proportion of hens that Ryan et al. (1998) found nesting in upland forests of southern Illinois were associated with by differences in vital rates between upland and floodplain forests.

NEST SITE CHARACTERISTICS

Cavity entrance height above ground is thought to enhance nest success in wood ducks (Haramis 1990, Robb and Bookhout 1995) and other cavity-nesting birds (Nilsson 1984, Rendell and Robertson 1989, Albano 1992). Nilsson (1984) concluded that cavity-nesting species may select higher cavities to escape predation.

Stuewer (1943) noted that small cavity entrance size also increased wood duck nest success. Bellrose (1953) found that nest boxes with elliptical entrances just large enough for the hen to enter were readily used by hens and excluded raccoons. Nest boxes and natural cavities with smaller entrances were used more frequently and had lower predation rates than those with larger entrances (Bellrose et al. 1964, Robb 1986, Robb and Bookhout 1995).

Haramis’ (1990) review supported the hypothesis that nests located higher in trees with smaller entrances are less likely to be depredated than other nests. Robb and Bookhout (1995) also suggested this was true but were unable to substantiate the hypothesis. Ryan et al. (1998) thought floodplain nesting hens selected higher cavities with smaller entrances to escape predation in floodplain forests. Zwicker (1999) confirmed that physical characteristics of tree cavities used by nesting wood ducks in southern Illinois differed between upland and floodplain habitats and that floodplain nesting hens selected more physically secure tree cavities. Zwicker (1999) hypothesized that predation may be the mechanism influencing these differences. Using the potentially suitable cavities identified by Zwicker (1999) and actual wood duck nests located from 1993 to 1998, I compared the physical characteristics of tree cavities between successful and unsuccessful nests to determine whether nest success may be affected by the physical characteristics of wood duck nest sites.

SIMULATED NESTS

Predation is often the most important factor reducing nesting success in ducks (Bellrose and Holm 1994). Previous studies have not demonstrated that nest site selection by wood ducks is affected by predation (Haramis 1990, Robb and Bookhout 1995) but these studies of natural cavities attributed the inability to detect effects of predation to low sample sizes. Because of the logistical constraints of working with wood duck nests in natural cavities, simulated nests should help quantify differences in predation pressure between upland and floodplain habitats and test the possible influence of predation pressure on nest site selection.

Many researchers have used simulated nests to study predation, including one study on wood ducks (Nagel 1969). Studies have used simulated nests to infer actual rates of nest predation but results have been contradictory if simulated nests survive at similar (e.g., Götmark et al. 1990) or different (Storaas 1988, Willebrand and Marcström 1988, Guyn and Clark 1997, King et al. 1999) rates than actual nests. I chose not to use simulated nests to infer actual nest survival rates but rather to compare predation pressure and examine patterns of predation on nests which simulated nests are often considered best suited (Burger et al. 1994).

Hens nested in upland and floodplain habitats but little information was known about the productivity of hens in upland forests (Ryan et al. 1998). Additionally, predation may have been higher in the floodplain and influenced nest site selection. Objectives of this chapter were to: 1) compare demographic parameters of wood ducks that nested in upland and floodplain habitats, 2) determine if physical characteristics of nest cavities influenced nest success, and 3) use simulated nests to compare predation pressure between upland and floodplain habitats.

METHODS

Nest cavities of radiomarked hens (hereafter radio nests) were located using methods described in Chapter 2. Nests of radiomarked hens were monitored by locating the hen 2-3 times per week by homing to the strongest signal (Mech 1983) to determine nest status. Nests of unmarked hens were checked opportunistically through the incubation period to check hen status. A final check of the nest was conducted after the expected hatch date. Cavities were reached by ascending ropes or using climbing spikes after nest trees were discovered. Additional nests were located annually (see Chapter 2) by climbing trees used by radiomarked hens during previous years (hereafter reclimb nests) or found incidentally during other phases of the study (hereafter incidental nests). Cavities were visually inspected with a mirror and flashlight if necessary. Nest trees located during laying were climbed again during incubation. Eggs were counted to determine clutch sizes. All accessible eggs were candled (Hanson 1954) to estimate expected hatching dates. Nest fate, number of eggs hatched, and number of ducklings that left the nest cavity were determined after nest attempts were terminated (as determined by movements of radiomarked hens or cavity inspection after the expected hatching date).

Data collected from nests were used to determine mean clutch size, nest parasitism rates, egg hatchability, and nest success. Nests were considered parasitized if they contained > 14 eggs (Semel and Sherman 1992, Bellrose and Holm 1994). Average clutch size was estimated from incubated, non-parasitized clutches only but clutch size analyses to test the effect of parasitism on nesting efficiency (i.e., egg hatchability) were conducted with all nests. Nests were considered successful if at least one duckling hatched and left the nest cavity. Egg hatchability was estimated by comparing the number of hatched and unhatched eggs in successful nests. Unclimbable trees (i.e., hazardous snags) and inaccessible nests (i.e., cavities too deep) were excluded from calculations of clutch size, nest parasitism rates, egg hatchability, and nest success. Nests in unclimbable trees or inaccessible cavities were considered successful if the radiomarked hen was later observed with a brood. Kruskall-Wallis tests (*H*) were used to compare clutch size, egg hatchability, number ducklings leaving the nest and egg success between upland and floodplain habitats.

Nest success was estimated using the staggered-entry Kaplan-Meier design (Pollock et al. 1989) using daily survival intervals. Only data from radiomarked hens were used and data were combined over all years. Because I was primarily interested in comparing nest success between habitats, data were standardized to a 42-day breeding cycle (i.e., 12 days laying and 30 days of incubation) and left-truncated. If the exact date of nest termination was unknown, I used the midpoint between the last and previous nest check as the terminal date. Nest survival was compared between upland and floodplain habitats with log-rank tests (Pollock et al. 1989) and estimates are presented with 95% confidence intervals.

Cavity Characteristics and Simulated Nests

Physical characteristics of nest trees and nest cavities were measured when nesting attempts terminated. Measurements included: habitat (floodplain or upland forest), slope, aspect, tree slope position (i.e., bottom, middle, top) of upland nest trees, tree species, tree diameter at breast height, alive or dead, number of suitable nest cavities in tree, cavity height above ground, cavity type (side entrance, bucket or combination), source of cavity formation (e.g., woodpecker or limb break), bole diameter at cavity entrance, number of entrances to cavity, opening height, opening width, cavity depth (measured from bottom of entrance), and entrance orientation. Entrance opening area was estimated from entrance opening height and width using the equation for the area of an ellipse.

I placed simulated nests in cavities located by Zwicker (1999). Physical characteristics of simulated nest cavities were recorded identically to actual nest cavities. Union County CA was used in 1997 and 1998 but LaRue Swamp - Pine Hills RNA was used only during 1998. In each trial, 2 nests were placed in 1 habitat and 1 nest was placed in the other habitat. This sampling distribution was alternated between the 10 trials in each study area so that annual sample sizes were equal between upland and floodplain forests. Nests were separated by >200 m so that simulated nests would be independent of each other.

Each simulated nest consisted of 4 domestic call duck (small domestic mallard) eggs or domestic Bantam hen eggs placed in suitable cavities. I made no attempt to add nest material or create nest bowls in cavities. Eggs were minimally handled to reduce contamination with human scent. Nests were checked 14 days after deployment and signs of disturbance or predation recorded. Destruction or removal of at least 1 egg was considered predation. Simulated nest trials began concurrent with wood duck nest initiation and continued through the breeding season (circa 1 April - 1 June; Selle 1998).

Physical cavity characteristics included the same parameters measured on actual wood duck nests. I compared simulated and actual nests separately but used the same set of candidate models for both data sets.

I developed 3 groups of candidate models, each of which represented general hypotheses about factors that affect nesting success of wood ducks. These candidate model sets represented stages of understanding of factors that affect nest success in wood ducks. The candidate model sets included variables thought to represent 1) factors that affect nest predation in nest boxes, 2) nest placement and cavity selection from Ryan et al. (1998), and 3) local differences in forest landscapes observed by Zwicker (1999). The first model set included the independent variables distance to habitat edge, date of nest initiation, and type of nest cavity chosen (bucket, limb, or bole). The second model set contained variables related to differences between upland and floodplain habitats and the effect of predation pressure on selection of more secure cavities. Variables for this model set included nesting habitat (upland or floodplain), cavity entrance area, and cavity height above ground. The third model set included the variables previously described and a new variable that compared the fragmented floodplain forest at Union County CA with the other more continuous upland forests at Union County CA uplands and the upland and floodplain forests at LaRue Swamp – Pine Hills RNA). This group of variables contained distance to habitat edge, date of nest initiation, type of nest cavity selected, UCCA floodplain (1) or not (−1) and the interaction between UCCA floodplain and cavity entrance area and the interaction between UCCA floodplain and cavity entrance height.

Models were created by selecting all possible model combinations of independent variables within each candidate model set. Burnham and Anderson (2002) cautioned against using all possible models but I considered my work to be exploratory since only a few studies have investigated the influence of predation on nest selection in natural cavity nesting wood ducks.

Forty candidate logistic regression models (redundant models were considered only once) were created and considered to have potential explanatory value in determining the physical characteristics of a tree cavity that could influence nest success. I followed Burnham and Anderson's (2002) information-theoretic approach to model selection. The adequacy of the global model to fit the collected data was tested with the deviance test as suggested by Burnham and Anderson (2002:17) and reported as the log likelihood chi-square (LRX^2, Long 1997:94, Driscoll et al. 2005). If the global model had poor explanatory value, I did not proceed with the model selection process. Candidate models were compared using Akaike's Information

Criterion corrected for small sample sizes (AIC_c) and ranked based on weight of evidence (w_i).

Sample sizes throughout this chapter varied widely because complete data for each hen and nest cavity were practically impossible to obtain given the variety of methods (e.g., radiomarked hens, reclimb hens, and incidental hens) used during this study. Every data point collected was used even if complete data for that hen or nest was not available.

RESULTS

Nesting Productivity

One hundred sixty-three wood duck nesting attempts were documented during 1993-1998. Nesting attempts were located by following radiomarked hens to nest sites (64%), reclimbing previously used trees (29%), and incidentally during other study activities (7%).

Nest fate was determined for 152 of 163 nests located. The fates of 10 upland (4 successful, 6 unsuccessful) and 6 floodplain (3 successful, 3 unsuccessful) nests were determined at LaRue Swamp - Pine Hills RNA. Nest fate was determined for 132 nests at Union County CA where 83 upland (57 successful, 26 unsuccessful) and 49 floodplain (24 successful, 25 unsuccessful) nests were located. Four upland nests (all unsuccessful) were never assigned to a study area because the nest was located off the study site (n = 1) or the nests sites were not located before the nest failed (n = 3).

Apparent nest success in the floodplain nest success was lower (0.54 ± 0.18 vs. 0.78 ± 0.10) than in upland forest (X^2 = 5.14, df = 1, P = 0.023). Mean (SE) incubated clutch size was 10.9 eggs (0.3, n = 55) with no differences in incubated clutch sizes (X^2 = 0.033, df = 1, P = 0.857) between upland (11.0 ± 0.3, n = 36) and floodplain (10.7 ± 0.6, n = 19) forests. Successful nests had similar egg hatching rates (G = 2.16, df = 1, P = 0.14) in floodplain (93%, n = 13) and upland (88%, n = 35) habitats. Parasitized nests in the floodplain had higher (G = 6.67, df = 1, P = 0.010) egg hatching rates (93%, n = 3) than parasitized nests in the upland (78%, n = 6). Mean (SE) number of ducklings leaving the nest cavity was 11.2 (0.5, n = 50) and there was no difference (X^2 = 2.080, df = 1, P = 0.149) between upland (10.6 ± 0.5, n = 36) and floodplain (12.5 ± 1.2, n = 14) habitats.

Cavity Characteristics

Sixty-five nest trees were used in logistic regression models used to analyze the relationship of nest cavity characteristics to success versus failure of actual wood duck nests. Forty candidate models were evaluated (Table

2). The highest ranking candidate model had a w_i of 0.116 and differed from the null model by 1.862 AIC_C points. The global model fit also was not significant ($LRX^2 = 9.47$, df = 9, $P = 0.395$). Since the models had little explanatory value given the data, no further interpretation was made from this data set.

Ninety simulated nests were placed but 2 floodplain nests were removed early and subsequently censored from the data set. Forty-three (49%) of 88 simulated nests were depredated during the 2 year study (Table 3). More floodplain nests (65% vs 35%, $n = 88$) were depredated than upland nests ($G = 8.9$, df = 1, $P = 0.003$) but this difference only occurred at Union County CA.

The same 40 candidate models used for actual wood duck nests were tested with simulated wood duck nests (Table 4). The global model fit was significant ($LRX^2 = 36.33$, df = 9, P < 0.001). A 6-variable model was selected as the best model given the data but the w_i was only 0.34 and the ΔAIC_C of the next highest ranked model was less than 2, indicating considerable model selection uncertainty (Burnham and Anderson 2002). I used model averaging to determine relative importance of all variables used in the candidate models based on the w_i estimates for the models (Burnham and Anderson 2002). The sum of $w_{i,}$ for all models that included each variable, indicated that location (Union County CA

Table 2. Candidate logistic regression models for predicting actual wood duck nest fate in southern Illinois during 1993-1998. Model rankings based on differences (Δ) in Akaike's Information Criteria corrected for small sample sizes (AIC_c) and Akaike's weights (w_i).

Models[a] (K[b])	AIC_c	Δ AIC_c	w_i
Date (3)	79.035	0.000	0.175
Hab (3)	79.467	0.432	0.141
Dist + Date (4)	80.016	0.981	0.107
Null (2)	80.897	1.862	0.069
Dist (3)	81.056	2.022	0.064
Hab + Ent (4)	81.122	2.087	0.062
Date + Type (4)	81.293	2.259	0.057
Hab + Hgt (4)	81.392	2.357	0.054
UCFP (3)	81.468	2.434	0.052
Dist + Date + Type (5)	82.347	3.313	0.033
Ent (3)	83.009	3.974	0.024
Type (3)	83.090	4.055	0.023
Hgt (3)	83.093	4.058	0.023
Dist + Type (4)	83.318	4.283	0.021
Hab + Ent + Hgt (5)	83.339	4.305	0.020
UCFP*Hgt[c] + Date (6)	84.309	5.275	0.013
UCFP*Ent + Date (6)	84.550	5.515	0.011
Ent + Hgt (4)	85.280	6.245	0.008
UCFP*Ent (5)	85.580	6.545	0.007
UCFP*Hgt (5)	85.895	6.860	0.006
Dist + UCFP*Hgt + Date (7)	86.456	7.421	0.004
Dist + UCFP*Ent + Date (7)	86.621	7.586	0.004
UCFP*Hgt + Date + Type (7)	86.817	7.782	0.004
UCFP*Ent + Date + Type (7)	86.950	7.915	0.003
Dist + UCFP*Ent (6)	87.233	8.198	0.003
Dist + UCFP*Hgt (6)	87.487	8.452	0.003
UCFP*Ent + Type (6)	87.877	8.842	0.002
UCFP*Hgt + Type (6)	88.298	9.263	0.002
Dist + UCFP*Hgt + Date + Type (8)	89.058	10.023	0.001
UCFP*Hgt + UCFP*Ent + Date (8)	89.087	10.052	0.001
Dist + UCFP*Ent + Date + Type (8)	89.152	10.118	0.001
Dist + UCFP*Ent + Type (7)	89.676	10.641	0.001
Dist + UCFP*Hgt + Type (7)	89.989	10.954	0.001
UCFP*Hgt + UCFP*Ent (7)	90.413	11.378	0.001
Dist + UCFP*Hgt + UCFP*Ent + Date (9)	91.457	12.422	0.000
UCFP*Hgt + UCFP*Ent + Date + Type (9)	91.683	12.648	0.000
Dist + UCFP*Hgt + UCFP*Ent (8)	92.235	13.200	0.000
UCFP*Hgt + UCFP*Ent + Type (8)	92.882	13.848	0.000
Dist + UCFP*Hgt + UCFP*Ent + Date + Type (10)	94.184	15.150	0.000
Dist + UCFP*Hgt + UCFP*Ent + Type (9)	94.854	15.819	0.000

Table 2. Continued.

[a] Hab = nesting habitat (upland or floodplain)
Hgt = cavity height above ground
Dist = distance from cavity to habitat edge
Date = date of nest initiation
Ent = cavity entrance area
Type = cavity type (bucket, side entrance, or combination)
UCFP = nest location in Union County Conservation Area floodplain versus not
UCFPHgt = cavity height above ground for nests in Union County Conservation Area floodplain habitat compared to all other nests
UCFPEnt = cavity entrance area for nests in Union County Conservation Area floodplain habitat compared to all other nests
Null = model with no explanatory variables

[b] Number of estimable parameters

[c] Models with interaction variables also include all main effects

Table 3. Fate of simulated wood duck nests placed in natural cavities in southern Illinois during 1997 and 1998.

Study site	Habitat	Survived	Depredated	Total
UCCA[1]	Upland	22	8	30
	Floodplain	7	21	28
LS-PH RNA[2]	Upland	8	7	15
	Floodplain	8	7	15
Total		45	43	88

[1] Union County Conservation Area

[2] LaRue Swamp-Pine Hills Research Natural Area

Table 4. Candidate logistic regression models for predicting simulated wood duck nest fate in southern Illinois during 1997 and 1998. Model rankings based on differences (Δ) in Akaike's Information Criteria corrected for small sample sizes (AICc) and Akaike's weights (wi).

Models[a] (K[b])	AIC_c	Δ AIC_c	w_i
Dist + UCFP*Ent[c] + Date + Type (8)	107.345	0.000	0.342
Dist + UCFP*Hgt + UCFP*Ent + Date + Type (10)	108.505	1.160	0.192
Dist + UCFP*Hgt + Type (7)	110.593	3.248	0.068
Dist + Date + Type (5)	110.693	3.349	0.064
Dist + UCFP*Ent + Type (7)	111.414	4.069	0.045
UCFP*Hgt + Date + Type (7)	111.905	4.560	0.035
UCFP*Ent + Date + Type (7)	112.032	4.687	0.033
Dist + UCFP*Hgt + UCFP*Ent + Type (9)	112.113	4.769	0.032
UCFP*Hgt + UCFP*Ent + Date + Type (9)	112.382	5.037	0.028
Dist + UCFP*Ent + Date (7)	112.725	5.380	0.023
Dist + UCFP*Hgt + Date (7)	112.839	5.494	0.022
Dist + UCFP*Hgt + UCFP*Ent + Date (9)	113.975	6.630	0.012
UCFP*Hgt + Type (6)	114.084	6.740	0.012
UCFP*Hgt + Date (6)	114.167	6.823	0.011
Dist + Type (4)	114.184	6.839	0.011
Dist + UCFP*Hgt (6)	114.409	7.065	0.010
UCFP*Ent + Date (6)	114.571	7.226	0.009
Dist + Date (4)	115.178	7.833	0.007
UCFP*Hgt + UCFP*Ent + Date (8)	115.250	7.906	0.007
UCFP*Hgt + UCFP*Ent + Type (8)	115.810	8.465	0.005
UCFP*Hgt (5)	115.896	8.551	0.005
Dist + UCFP*Ent (6)	115.914	8.569	0.005
UCFP*Ent + Type (6)	116.007	8.663	0.005
Dist + UCFP*Hgt + UCFP*Ent (8)	116.225	8.880	0.004
UCFP (3)	116.635	9.291	0.003
Dist + UCFP*Hgt + Date + Type (8)	117.141	9.796	0.003
Dist (3)	117.770	10.425	0.002
UCFP*Hgt + UCFP*Ent (7)	117.857	10.512	0.002
UCFP*Ent (5)	118.131	10.786	0.002
Hab (3)	119.190	11.845	0.001
Hab + Hgt (4)	119.491	12.146	0.001
Hab + Ent + Hgt (5)	119.550	12.206	0.001
Hab + Ent (4)	119.830	12.486	0.001
Date + Type (4)	122.538	15.193	0.000
Date (3)	123.434	16.090	0.000
Ent + Hgt (4)	125.360	18.015	0.000
Type (3)	125.498	18.154	0.000
Hgt (3)	125.840	18.495	0.000
Null (2)	126.090	18.745	0.000
Ent (3)	126.350	19.006	0.000

Table 4. Continued.

[a] Hab = nesting habitat (upland or floodplain)
Hgt = cavity height above ground
Dist = distance from cavity to habitat edge
Date = date of nest initiation
Ent = cavity entrance area
Type = cavity type (bucket, side entrance, or combination)
UCFP = nest location in Union County Conservation Area floodplain versus not
UCFPHgt = cavity height above ground for nests in Union County Conservation Area floodplain habitat compared to all other nests
UCFPEnt = cavity entrance area for nests in Union County Conservation Area floodplain habitat compared to all other nests
Null = model with no explanatory variables

[b] Number of parameters which include intercept, regression coefficients, and residual variance

[c] Models with interaction variables also include all main effects

floodplain vs. other, 0.9123), cavity type (0.8730), and distance to habitat edge (0.8411) were of similar importance, followed by date of nest placement (0.7883), cavity entrance area (0.7456), cavity entrance area in the Union County CA floodplain (0.7441), cavity entrance height above ground (0.4472) and the interaction of cavity entrance height above ground with location (0.4456).

DISCUSSION

Upland and floodplain forest habitats were similar with respect to most (e.g., clutch size, unparasitized nest egg hatchability) but not all (i.e., nest success, parasitized nest egg hatchability) nesting productivity parameters in southern Illinois. Hens nested successfully in upland forests and nesting productivity was similar to that reported by other investigators (see review *in* Bellrose and Holm 1994). The primary difference between upland and floodplain habitats was that nest success was higher in the upland than in the floodplain forests. This finding was corroborated by the lower survival probabilities of simulated nests placed in floodplain compared to the upland forests.

Actual and simulated nest survival rates were not directly comparable because simulated nests were exposed for 14 days, compared to the 28-30 full incubation period of wood duck nests. Nevertheless, nest survival rates were lower in floodplain than in upland forests nests both actual (-24%) and simulated nests (-30%). I believe that these differences were directly related to higher predation pressure on nests located in the floodplain.

I intended to use Union County CA and LaRue - Pine Hills RNA as replicate samples for my study. However, comparison of data collected on the 2 areas indicated the study sites were not good replicates. I did not measure differences in habitat structure between the study areas but of the floodplain at LaRue - Pine Hills RNA was a single large patch of contiguous floodplain forest compared to the fragmented floodplain forest interspersed with crop land that characterized Union County CA. Edge types at LaRue - Pine Hills RNA were mostly feathered edges leading from mature forest to open water, whereas, the Union County CA floodplain had mostly hard edges between strips of mature forest and row-cropped agricultural fields. Furthermore, the floodplain forest was completely contiguous with upland forest at Larue-Pine Hills whereas many of the floodplain forest patches were separated from upland forest by crop fields, a grass-covered levee, and large floodplain lakes at Union County CA. I believe the highly fragmented nature of the floodplain forest at Union County CA provided greater access by predators to wood duck nests in the floodplain.

Furthermore, Wilson and Nielsen (2007) documented high population densities of raccoons at union County CA where the interspersion of crop, wetland, and forest habitats provided abundant food resources to nest predators such as raccoons.

Ryan et al. (1998) noted differences in cavity characteristics between upland and floodplain forests and thought predation in the floodplain may have caused hens to nest in more secure tree cavities. Nest success has been shown to increase with nest security in several cavity- (Nilsson 1984, Rendell and Robertson 1989, Albano 1992) and open-nesting (Wilson and Cooper 1998) species, and similar results were suggested for wood ducks (Haramis 1990, Robb and Bookhout 1995). Predation may have influenced nest site selection on my study sites as Zwicker (1999) found that floodplain nesting hens used a more physically secure subset (i.e., higher cavities with smaller entrances) of available cavities.

The simulated nest study was designed to examine patterns of predation on nests placed in natural cavities. The best supported model indicated that cavity security (i.e., smaller entrances) was important in the floodplain habitats of Union County CA. Additional factors found to influence simulated nest success were ‘distance from habitat edge’ (a possible response to avoid edges where predators may have concentrated their searches for food), ‘date of nest placement’ (later nest initiation may have facilitated concealment of nests as leaf out progressed), and ‘cavity type’ (exposed bucket cavities in snags were most heavily preyed upon). This model provided evidence that secure nest sites were important for successful nesting in high predation areas.

No model for success of actual wood duck nests was well supported by the data, indicating that successful and unsuccessful wood duck nests could not be differentiated. This may be a result of small sample sizes but could be explained by the finding that wood ducks selected more secure nest cavities in the Union County CA floodplain, thereby sustaining comparable nest success rates to other forest types. Simulated nests were placed in a thoroughly random sample of suitable tree cavities that spanned the full range of physical characteristics and locations where wood ducks nested on my study areas. Predation events on simulated nests tended to occur in less secure (e.g., larger entrances) cavities located closer to habitat edges, regardless of forest type and location. Zwicker (1999) showed that wood ducks in the Union County CA floodplain appeared to avoided these less secure cavity types. Regardless, some predation events occurred in more secure nest cavity types so physical cavity characteristics did not differentiate successful and depredated nests. I suggest that wood ducks sustained similar rates of nest success in floodplain and upland forests by selecting more physically secure tree cavities in the floodplain. Floodplain nesting hens used some of the highest cavities and smallest entrances available (Zwicker 1999); consequently, predation pressure could not be compared between upland and floodplain forests without the random sample of suitable nest cavities in both habitats types similar to that provided by simulated nests.

Selective behavior reduced the realized nesting niche space to a subset of the fundamental niche space in floodplain but not upland forests. Although selective use of tree cavities enhanced the probability of nest success in the Union County CA floodplain, there may have been a cost incurred through higher competition for nest sites in floodplain compared to upland forest (especially in light of higher nest densities in the floodplain, see Chapter 2). Roy Nielsen et al. (2006) used genetic analyses to determine parentage of wood duck eggs on my study area and found that floodplain nests contained more parasitized eggs than upland nests.

My results supported the hypothesis that predation influenced nest success and nest site selection in the Union County CA floodplain forest. Floodplain nesting hens at Union County CA adopted a strategy of using secure cavities in response to higher predation pressure in the Union County CA floodplain. Use of secure cavities in the floodplain forest probably enhanced nesting success but hens were overall more successful when they nested in upland forest. Consistent annual use and predominance of nesting in upland forest, combined with high rates of nest success provide strong evidence that upland habitats can provide productive nesting habitat for wood ducks.

CHAPTER 4

HEN AND BROOD SURVIVAL

BREEDING SEASON HEN SURVIVAL

The importance of survival during the breeding season is considered critical compared to other seasons (i.e., hunting season, overwinter) of the year for waterfowl (Ringleman and Longcore 1983, Kirby and Cowardin 1986). Survival of hens and broods during the breeding season is a primary component of current and future breeding productivity but except for Robb and Bookhout (1990) breeding season survival of wood duck hens is largely understudied in wood ducks.

Loss of a nest eliminates only production of juveniles but depredation of hen and nest also diminishes future production (Ball et al. 1975, Ringelman and Longcore 1983, Kirby and Cowardin 1986). Although nests in the floodplain forest had lower success rates, hens appeared to return annually to the habitats they previously occupied (Chapter 3). If hen survival is higher in one habitat, then the nesting population should increase in that habitat because successful hens and their offspring would return to the same general area to nest in subsequent years. Under this scenario, upland and floodplain nesting populations could grow at different rates and the eventual impacts of predation on hens, nests, and broods from each nesting habitat would be reflected in nest distribution. If predation rates on hens and broods from floodplain nests are higher than upland nests, then the predominance of upland nests on my study area might be explained by differential hen and brood survival rates.

ANNUAL HEN SURVIVAL

Few studies have estimated annual survival rates of wood ducks. Most studies estimated survival from mark/recapture studies of box-nesting populations (Hepp et al. 1987, Dugger et al. 1999) or band recovery analysis on a regional scale (Kelley 1997). Survival estimates obtained from mark/recapture studies of box-nesting populations differ from natural cavity studies and could be biased because breeding season survival is enhanced by predator-proof nest boxes (Hepp et al. 1987, Bellrose and Holm 1994, Purcell et al. 1997, Dugger et al. 1999, Evans et al. 2002).

Band recovery analysis works well for some waterfowl species but wood duck banding programs often do not band enough birds to provide useful survival estimates. Suitably large sample sizes are often not attained until banding programs are grouped into regions for analysis (e.g., Trost 1990, Kelly 1997) but this introduces heterogeneity into estimates (Pollock and Raveling 1982, Nichols et al. 1982, Johnson et al. 1986, Trost 1990). I compared the geographic distribution of band recoveries to determine if banded hens used in my analyses were representative of the region.

The most recent and comprehensive wood duck band recovery analyses were conducted by Kelly (1997). Using multi-response permutation procedures (MRPP) to delineate wood duck subpopulations, Kelly (1997) determined that survival was best assessed at the subpopulation level (i.e., 6 geographic divisions within the Atlantic and Mississippi Flyways). This analysis included southern Illinois in the northern end of the southern subpopulation. However, Kelly (1997) recognized that boundaries based strictly on recovery locations would pose problems for state-based management programs. Therefore, states that were split into several MRPP subpopulations (e.g., Illinois, Missouri, Kentucky, Ohio) were grouped based on state boundaries to simplify management and interpretation.

The subpopulation divisions proposed by Kelly (1997) are likely the best means of estimating wood duck survival on a large scale. Applying Kelly's (1997) survival estimates on a smaller scale could prove inappropriate, as Dugger et al. (1999) reported that wood ducks in southeast Missouri survived at a rate more similar to Kelly's (1997) southern subpopulation than the north-central subpopulation. This indicates that areas such as southern Illinois and southeast Missouri, which border two subpopulations, may not be well represented by Kelly's (1997) subpopulation system to delineate the population.

BROOD SURVIVAL

Floodplain habitats are positioned closer to brood habitats than upland habitats in southern Illinois (Kawula 1998). Several authors (Leopold 1951, Bellrose 1953, Ball et al. 1975) have suggested that extensive wood duck brood movements may reduce brood survival. Similarly, studies of other duck species (Keith 1961, Dzubin and Gollop 1972, Rotella and Ratti 1992, Leonard et al. 1996) found that long overland movement of broods were associated with lower average brood size, but other studies did not corroborate these findings (Evans and Black 1956, Talent et al. 1983, Dzus and Clark 1997, Guyn and Clark 1999, Yerkes 2000, Simpson et al. 2007). The distances that upland-hatched broods must travel from nest tree to wetland may result in decreased survival compared to floodplain-hatched broods.

In this chapter, I focus on comparing hen and brood survival between upland and floodplain habitats. Specific objectives of this chapter were to: 1) estimate breeding season hen survival, 2) estimate annual hen survival, 3) compare geographic distribution of band recoveries for hens used in banding analyses, and 4) estimate brood survival.

METHODS

Breeding Season Hen Survival

Survival (with 95% confidence intervals) during the breeding season was estimated from radiomarked hens using staggered entry Kaplan-Meier procedures (Pollock et al. 1989). Survival estimations were based on weekly intervals between the Julian dates corresponding to 23 February (day of first hen capture) and 26 July (last brood observation). No attempt was made to compare survival between years because annual sample sizes were relatively small. Only radiomarked hens were used and comparisons were made with log rank tests (Pollock et al. 1989).

Annual Hen Survival

Annual survival was estimated using wood duck banding and recovery data obtained from the U.S. Fish and Wildlife Service Bird Banding Laboratory (BBL). Band returns from 1980-1997 were used for the analysis. Returns from southeast Missouri, western Kentucky, and southern Illinois were used for annual survival analysis to increase sample sizes.

Banding data were analyzed using the recoveries only program within Program MARK (White and Burnham 1999). Global model goodness-of-fit (GOF) was estimated using parametric bootstrap techniques in Program MARK by ranking estimated model deviations for each of the 1000 iterations. The global model deviance was then compared to the ranking and model fit was determined by the probability of a bootstrap model having a higher deviance. Bootstrap techniques also were used to estimate the over-dispersion quasi-likelihood parameter ($\hat{c}$). Using $\hat{c}$, the corrected Akaike Information Criterion (AICc) was adjusted and recalculated as the quasi AICc (QAICc) to improve measurement of model support. The most parsimonious model was then selected using the information-theoretic approach suggested by Burnham and Anderson (2002). Model averaging was employed when there were competing models.

Comparisons of geographic recovery distributions between hens banded as adults and hens banded as juveniles and direct (i.e., first hunting season after banding) and indirect (i.e., after first hunting season) recoveries were made with the multiresponse permutation procedure (MRPP) in BLOSSOM (Slauson et al. 1991, Mielke and Berry 2001, Cade and Richards 2005). Geographic distributions of recoveries were delineated with adaptive kernel estimates using the home range extension (Rodgers and Carr 1998) in ArcView (Environmental Systems Research Institute, Incorporated, Redlands, California). The 95% and 50% probability distributions were estimated for each group and compared using the MRPP methods to determine if recovery distributions differed between ages or recovery time (i.e., direct vs indirect). The MRPP generates the test statistic δ and a *P*-value to test if the distributions of band recoveries were similar among age and recovery type categories (Cade and Richards 2005).

Brood Observations

Broods were observed during repeated surveys on designated routes and opportunistically on areas where surface water was present on Union County CA, LaRue Swamp-Pine Hills RNA, and Oakwood Bottoms GTR. Observations were made with binoculars or 20 - 60 x spotting scopes on window or tripod mounts. All brood ages were estimated to class (Gollop and Marshall 1954) and total brood size was estimated. Kruskall-Wallis tests (*H*) were used to compare brood sizes between years.

Brood survival to fledging was estimated by including whole-brood loss and brood size attrition as suggested by Ball et al. (1975). Attrition was estimated from brood observations and included only broods up to Class IIb as brood mortality after Class IIb (about 5 weeks) was considered negligible (McGilvrey 1968, Ball et al. 1975). Brood attrition was estimated as the mean class IIb brood size divided by mean brood size at hatching. Whole-brood survival was the number of broods with radiomarked hens surviving to class IIb divided by total number broods with radiomarked hens. Whole brood loss was assumed to have occurred when a radiomarked hen was found dead, emigrated from the study area, or exhibited long erratic movements that were not characteristic of brooding hens before the brood reached class IIb.

I attempted to sight radiomarked hens with broods to more directly calculate brood attrition and whole-brood loss but such observations proved impractical. Without direct estimation of broods of radiomarked hens I could not account for differential brood attrition between upland and floodplain habitats. Brood survival was calculated by multiplying observed brood attrition rates (pooled among habitats) by whole-brood survival of upland- and floodplain-hatched broods. Any habitat-specific estimates of brood should be considered conservative since attrition rates were identical.

RESULTS

Annual Hen Survival

There were 22,704 female wood ducks (7,355 adults and 15,349 juveniles) banded in the southern Illinois region during 1980 - 1997, and 1,240 of these bands (380 adults and 860 juveniles) were returned from harvested birds and suitable for this analysis. The global model for southern

Illinois wood duck survival included age dependent survival (S_a) with age- and time-dependent recoveries (r_{a*t}). I initially included time dependence in the survival estimates but the data were too sparse and robust estimates could not be generated with the additional parameter. Consequently I removed time dependent survival from consideration. Comparing global model deviance to bootstrap derived deviances ($P = 0.457$) indicated that the global model was a good fit to the data. The $\hat{c}$ estimate (1.597) was used to adjust the AICc for overdispersion.

Two models ($S_a r_t$ and $S\ r_t$) had QAICc values that differed by 0.26 and had nearly identical QAICc weights (0.476 vs. 0.417) were considered competing models with nearly equal support that could not be separated based on weight of evidence in support of them (Table 5). Therefore most parsimonious model ($S\ r_t$) was used to estimate survival and recovery rates, and parameters incorporated model averaging to account for model selection uncertainty. This model assumed constant survival (0.545 SE = 0.015) and time-dependent recovery rates for wood ducks (Table 6).

Breeding Season Hen Survival

Thirty-two (15%) of 208 resident radiomarked hens used for the survival analyses died during 6 seasons of study. Seven (12%) of 60 juveniles and 25 (17%) of 148 adults died

Table 5. Models estimating annual survival (S) and recovery (r) of female wood ducks banded in southern Illinois, western Kentucky, and eastern Missouri. Models may have age- (a) or time- (t) dependent variables. All models were ranked by models weights (w_i) estimated from Akaike Information Criterion corrected for overdispersion and small sample sizes (QAICc).

Model	QAICc	Δ QAICc	w_i	No. Parameters
S(a)r(t)	8046.9	0.00	0.476	20
S(.)r(t)	8047.1	0.26	0.417	19
S(a)r(.)	8052.2	5.32	0.033	3
S(.)r(a*t)	8052.8	5.93	0.025	37
S(.)r(.)	8052.8	5.94	0.024	2
S(a)r(a)	8053.7	6.86	0.015	4
S(a)r(a*t)	8054.8	7.92	0.001	38

Table 6. Model averaged recovery rates (r_t, corrected for $\hat{c} = 1.597$) for wood ducks banded in southern Illinois, southeast Missouri, and western Kentucky during 1980–1997.

Recovery Year	Band Recovery Rate (SE)
1980	0.0784 (0.0155)
1981	0.0673 (0.0126)
1982	0.0863 (0.0142)
1983	0.0965 (0.0121)
1984	0.0640 (0.0104)
1985	0.0620 (0.0102)
1986	0.0585 (0.0109)
1987	0.0602 (0.0091)
1988	0.0391 (0.0074)
1989	0.0520 (0.0080)
1990	0.0450 (0.0068)
1991	0.0515 (0.0070)
1992	0.0498 (0.0076)
1993	0.0553 (0.0091)
1994	0.0495 (0.0076)
1995	0.0631 (0.0082)
1996	0.0751 (0.0090)
1997	0.0653 (0.0084)

during the study. Kaplan-Meier survival estimates were similar (X^2 = 0.739, df = 1, P = 0.39) between adult and juvenile hens. No differences (X^2 = 0.483, df = 1, P = 0.49) were found between survival rates of nesting (0.77 ± 0.14, n = 98) and non-nesting (0.82 ± 0.13, n = 110) hens or between upland (0.77 ± 0.13, n = 64) and floodplain (0.87 ± 0.20, n = 34) nesting hens (X^2 = 0.632, df = 1, P = 0.43). The final breeding season survival estimate (0.80 ± 0.10) pooled adults and juveniles in both habitats.

Geographic distribution of recoveries

There were no differences (δ = 0.0814, P = 0.374) in geographic distributions of direct band recoveries between wood ducks banded as adults and versus juveniles (Figure 3). Distributions of indirect band recoveries of hens banded as adults versus juveniles (Figure 4) also were not different (δ = 0.1868, P = 0.445). There also were no differences in geographic distributions of direct and indirect recoveries for adult wood duck hens (Figure 5, δ = −0.5337, P = 0.208) but there were differences (δ = −8.9948, P < 0.001) between direct and indirect recovery distributions for juvenile hens (Figure 6). Geographic distributions of band recoveries revealed that wood ducks banded in southern Illinois winter in Louisiana and seldom stray outside the Mississippi

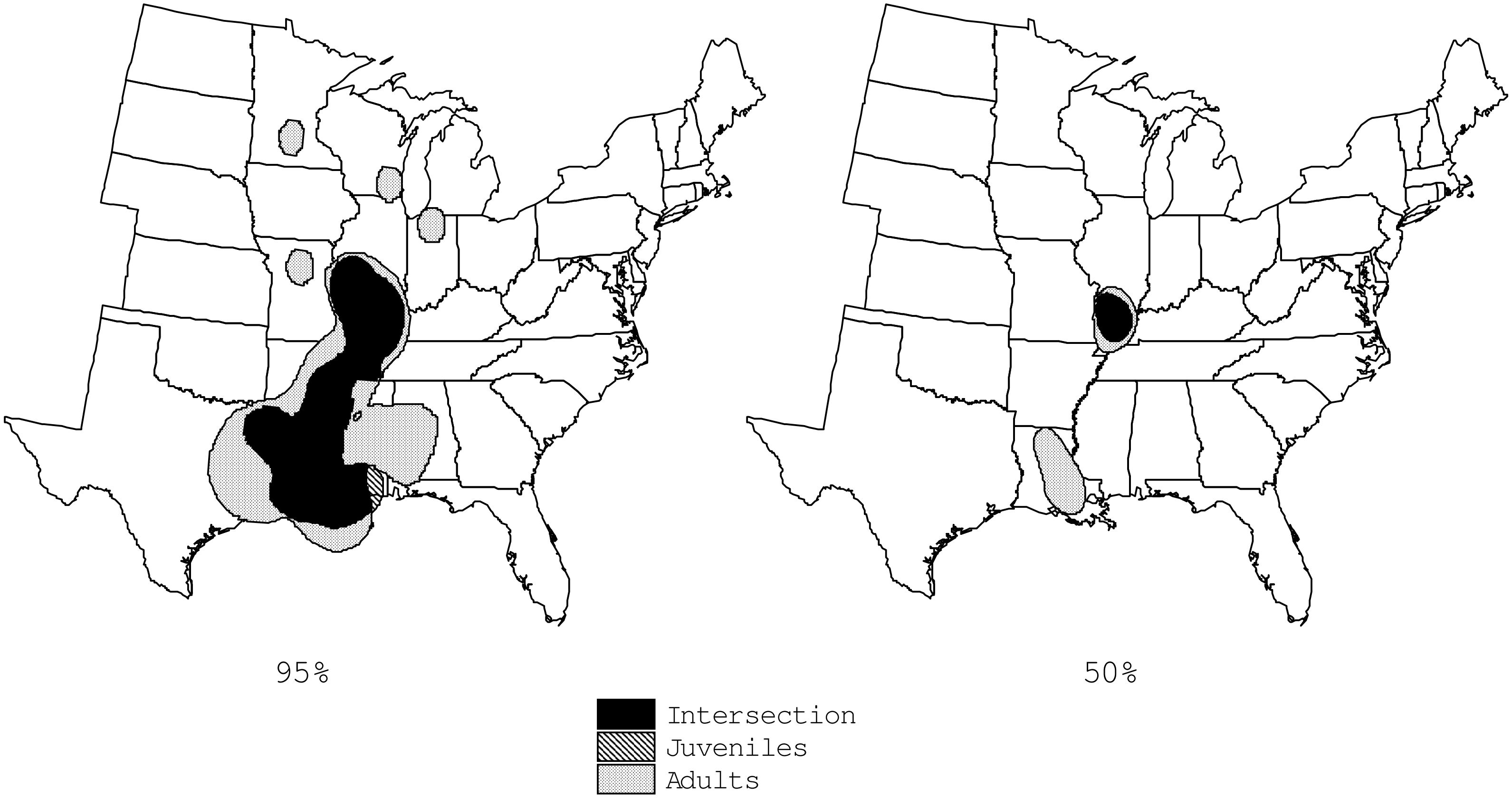


Figure 3. Geographic distributions of direct wood duck recoveries for adult and juvenile hens banded in southern Illinois during 1980-1997. Distributions are represented as hypervolumes (95% and 50%) estimated using adaptive kernel home range estimation.

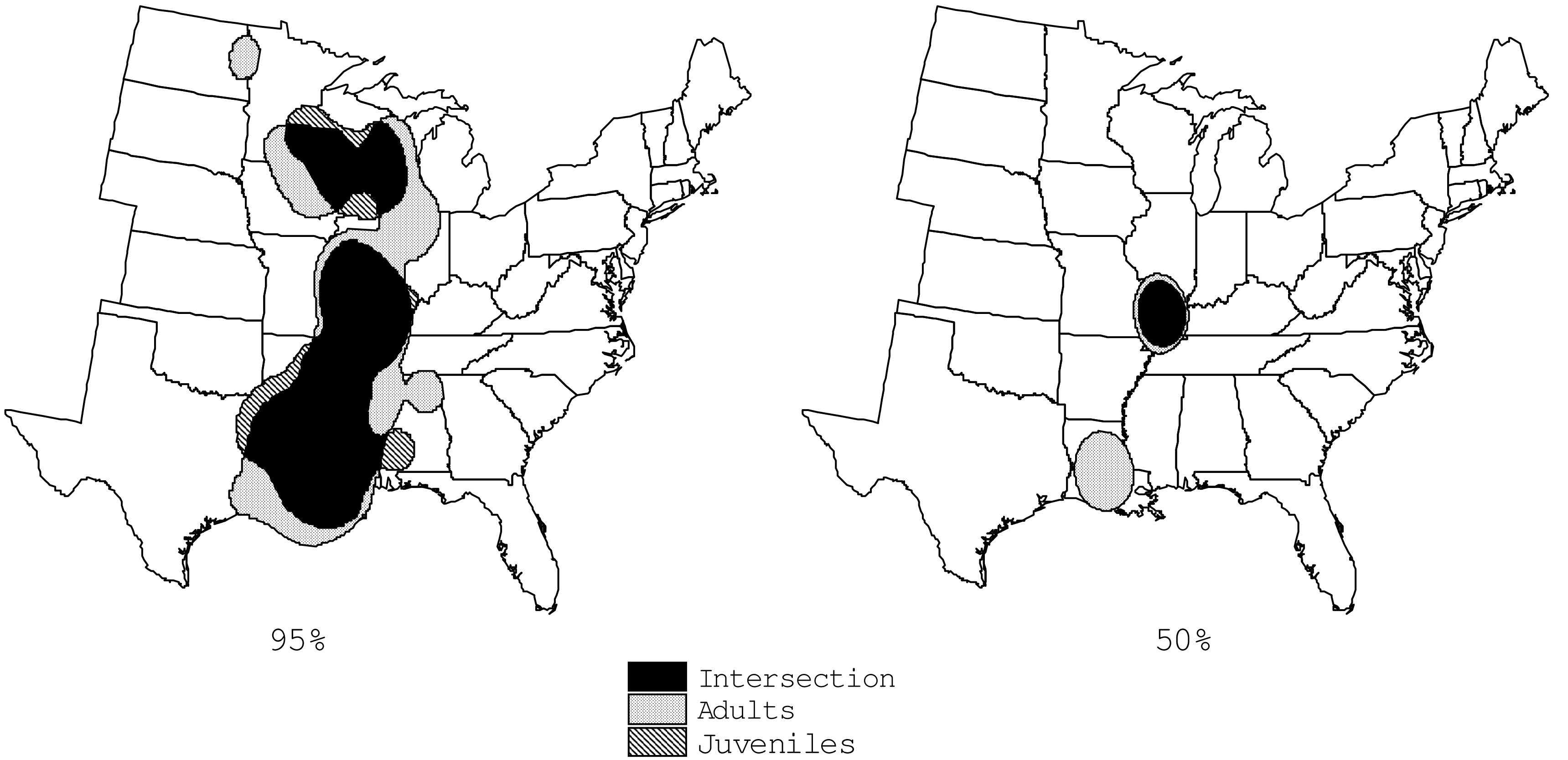


Figure 4. Geographic distributions of indirect wood duck recoveries for adult and juvenile hens banded in southern Illinois during 1980-1997. Distributions are represented as hypervolumes (95% and 50%) estimated using adaptive kernel home range estimation.

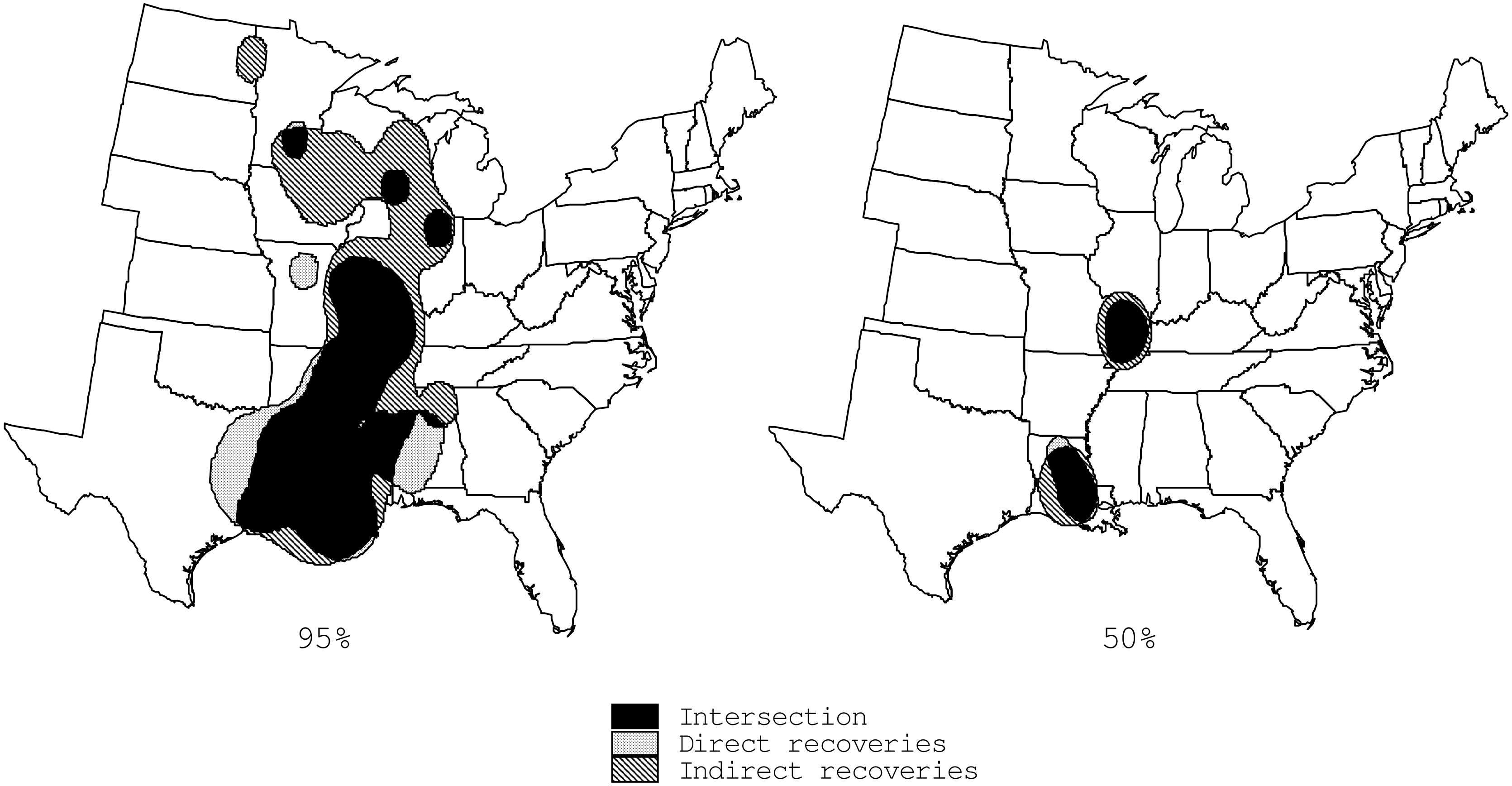
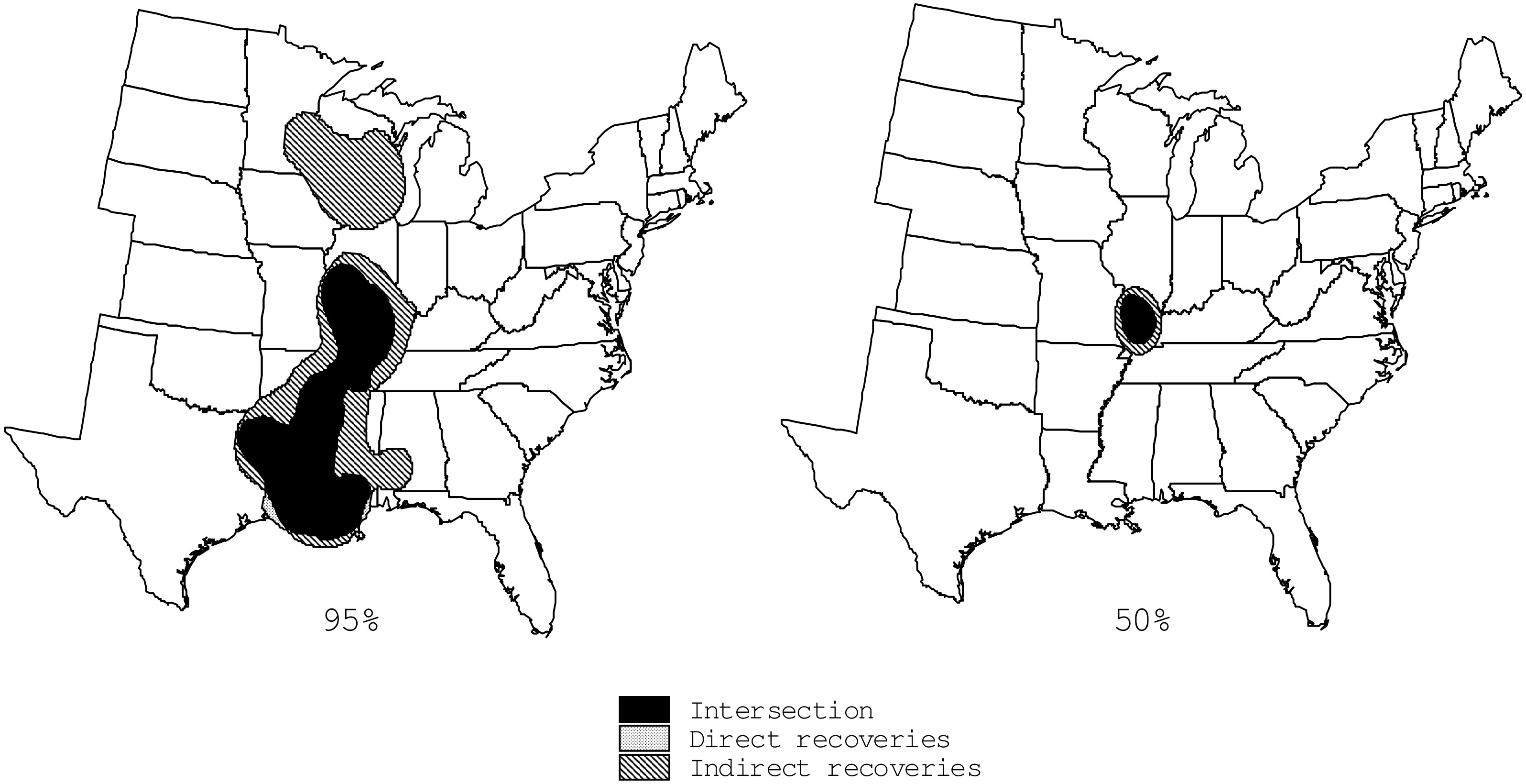


Figure 5. Geographic distributions of direct and indirect recoveries from adult female wood ducks banded in southern Illinois during 1980-1997. Distributions are represented as hypervolumes (95% and 50%) estimated using adaptive kernel home range estimation.



95%

50%

Figure 6. Geographic distributions of direct and indirect recoveries from juvenile female wood ducks banded in southern Illinois during 1980-1997. Distributions are represented as hypervolumes (95% and 50%) estimated using adaptive kernel home range estimation.

Flyway. Direct and indirect band recoveries north of the following radiomarked hens were lost to unknown sources of mortality during the brood region suggest post-breeding dispersal or molt migration to the northern great lakes region, particularly Wisconsin. Most of the annual harvest occurs either in Illinois or Louisiana.

Brood Survival

Four hundred seventy-two brood observations were recorded at Union County CA (n = 266), LaRue Swamp RNA (n = 193), and Oakwood Bottoms GTR (n = 13) during 1993-1998. Brood sizes did not vary ($H < 10.76$, $P > 0.056$) among years (Table 7). Six of 55 (11%) broods monitored by rearing period. Six of 37 (16%) monitored broods that hatched from upland nests were lost, while 0 of 18 monitored broods that hatched from floodplain nests were lost. Five of the 6 broods were considered lost because the hen was depredated, and the sixth brood was considered lost when the hen emigrated from the study area before the expected fledging date. Observed brood survival was estimated to be 57% (i.e., 6.3 class IIb/11.2 that left the nest). Multiplying the converse of whole-brood loss (11%) and observed duckling survival I estimate 50% of ducklings leaving the nest survived to fledging.

Table 7. Mean (SE, *n*) sizes of wood duck broods by age class observed in southern Illinois during 1993–1998.

	Age Class						
Year	IA	IB	IC	IIA	IIB	IIC	III
1993	8.6 (0.6, 14)	9.9 (1.0, 11)	8.0 (1.0, 3)	7.8 (1.7, 6)	7.5 (0.5, 2)	11.0 (2.0, 3)	N/A
1994	6.8 (0.9, 20)	5.5 (0.9, 11)	6.9 (1.0, 10)	5.3 (1.0, 7)	7.3 (1.9, 4)	7.0 (0.9, 7)	N/A
1995	6.6 (1.0, 13)	6.7 (0.7, 24)	8.5 (1.1, 10)	6.0 (0.9, 7)	6.3 (0.8, 6)	5.7 (2.9, 3)	5.6 (0.5, 7)
1996	6.5 (0.3, 8)	5.6 (1.1, 13)	5.6 (0.6, 14)	6.4 (0.7, 15)	7.5 (0.6, 19)	5.7 (1.1, 13)	7.9 (1.0, 10)
1997	8.0 (1.3, 8)	7.0 (0.5, 24)	6.2 (0.6, 17)	4.5 (0.6, 17)	5.1 (0.6, 18)	6.0 (0.9, 10)	3.7 (0.5, 9)
1998	9.3 (1.2, 12)	7.1 (0.5, 24)	6.0 (0.5, 22)	5.3 (0.6, 17)	5.6 (0.9, 15)	5.5 (1.2, 11)	N/A
Total	7.6 (0.4, 75)	6.9 (0.3, 114)	6.5 (0.3, 76)	5.6 (0.3, 69)	6.3 (0.4, 64)	6.2 (0.5, 47)	5.8 (0.5, 26)

DISCUSSION

Survival analyses assume that banded birds represent the population of interest to the investigator. Hens used in my survival analyses that did not breed in southern Illinois could bias survival estimates but I had no way to know whether birds banded during summer in southern Illinois also were breeding there. Since portions of 50% probability distributions were centered on southern Illinois, I believe most females marked in southern Illinois probably bred in southern Illinois. Direct recoveries of juvenile hens were either from southern Illinois or the Mississippi Alluvial Valley (MAV). Direct recoveries of adult hens tended to be south of southern Illinois but there was a small proportion of bands recovered farther north that could have been northward movements by postbreeding wood ducks (Bellrose and Holm 1994).

This northward movement is not well understood but could be in response to decreasing habitat quality through the summer or to molt migration. Juveniles are thought to participate in northward movements after they fledge (Stewart 1979, Bellrose and Holm 1994). However, 95% recovery probability distributions of juvenile hens did not include areas north of southern Illinois, as did recovery distributions of adult hens. Indirect recoveries of females marked as juveniles were similar to recoveries of females marked as adults. Although I did not conduct intra-year and annual temporal analyses of band recoveries, some hens that seemed to be making northward postbreeding movements were likely members of more northern breeding populations.

Annual survival estimates for female wood ducks banded in southern Illinois were lower than annual estimates (0.63 SE = 0.02) made by Dugger et al. (1999), but higher (adult 0.52 SE = 0.01, juvenile 0.43 SE = 0.02) than reported by Kelly (1997). This was expected because Dugger et al. (1999) used mark-recapture techniques on a box-nesting population that should have higher survival because of added predator protection often afforded by nesting in boxes. Annual survival estimates from southern Illinois should be greater than Kelly's (1997) estimates because wood ducks breeding at lower latitudes tend to have higher survival rates (Nichols and Johnson 1990).

Only 1 other study (Robb and Bookhout 1990) estimated survival of wood duck hens during the breeding season. Robb and Bookhout (1990) found that hen survival decreased during the breeding season and they concluded, similar to Kirby and Cowardin (1986), that this resulted from vulnerability to predation during nesting. Unlike other studies, this study had a large non-incubating resident portion (Selle 1998) that provided an opportunity to estimate the cost of breeding in terms of increased survival. Assuming that non-nesting hens were correctly identified and no disease or other detrimental factors that caused hens not to nest, I found that survival of nesting hens was similar between habitats and survival was unexpectedly similar between nesting and non-nesting hens. Savard and Eadie (1989) also found no apparent survival cost of reproduction in cavity-nesting Goldeneyes (*Bucephala spp.*) by comparing annual survival rates from homing rates of females.

I detected no difference in breeding season survival between hens that nested in upland and floodplain habitats. Therefore there is no reason to suspect that hen survival influenced nesting effort or distribution in my study.

Brood survival estimates in my study were similar to other studies (Bellrose and Holm 1994). There were differences in brood survival between habitats because all known cases of whole-brood loss were from upland hatched broods. I was unable to monitor broods closely enough to estimate habitat-specific brood attrition rates so my estimates of differences in juvenile survival between floodplain- and upland-hatched broods were conservative. It is conceivable that brood attrition was higher among upland hatched broods since whole brood loss was only observed in upland-hatched broods. As previously mentioned, studies of brood survival have historically been split on whether or not the distance of overland movements reduces duckling survival. A confounding issue is that most duckling survival research includes the initial move from nest to wetland as well as multiple secondary movements in subsequent weeks of the brood rearing period. Duncan (1987) is the only research I found that estimates the potential impacts of the initial movement of ducklings from nest to brood habitat and he found that a 3 km walk did not significantly reduce energetic reserves or have long-term impacts on growth. Additionally, Duncan (1987) and several other studies (Talent et al. 1983, Leonard et al. 1996, Gendron and Clark 2002) suggest that the overland movement is not the cause of the reported loss of ducklings but rather other factors that occur on the wetland. Leonard et al. (1996) report that predation disturbance on a wetland may have caused the broods to move as several broods were known to have lost ducklings prior to the overland movement. Most recent research appears to note little (Gendron and Clark 2002) or no influence (Granfors and Flake 1999, Simpson et al. 2007) of overland movements on brood survival and Davis et al. (2005) reports a positive relationship between increased wood duck brood movements and survival.

The key issue for my study was the potential impact of the move from the nest to the wetland. Duncan (1987) reported that there was no effect and energy reserves in day-old ducklings were sufficient to complete a 3 km journey with no effects. The other confounding issue is to assume that only the upland nesting hens make extensive movements to brood rearing habitats. Granfors and Flake (1999) reported that hens nesting in wetland habitats often made extensive initial brood movements to other wetlands. Overall, brood survival research does not elucidate factors influencing brood survival in my opinion and my study was not designed to delve into the differences in brood survival between the upland and floodplain habitats. The modeling exercise in Chapter 5 may provide a means to assess if large differences in duckling survival between the habitats can have impacts on the population as a whole.

CHAPTER 5

POPULATION MODELING

Female wood ducks at Union County CA and LaRue Swamp – Pine Hills RNA in southern Illinois have been studied extensively with regard to their use of upland and floodplain forests for nesting (Kawula 1998, Ryan et al. 1998, Selle 1998, Zwicker 1999). Apparent differences in nesting biology (Ryan et al. 1998), nest density (Zwicker 1999), and nest success (Chapter 3) were observed between upland and floodplain habitats. Lower nest success and higher predation pressure could impact local nesting populations and decrease overall fitness. No information regarding the contribution of these habitats to sustaining the local population is available. Comparing population growth rates between forests types provides insight into the relative habitat quality of upland and floodplain forests.

The relative habitat quality of upland and floodplain forests for nesting wood ducks in southern Illinois is difficult to compare quantitatively. Fretwell and Lucas' (1970) ideal-free distribution model provides a basis for comparing habitat quality between upland and floodplain forests. The ideal free distribution model predicts that the habitat with highest inherent quality with the highest would be the habitat that supports the highest population density. However, wood duck population densities are difficult to measure and wood duck nest site philopatry may obscure the nest density measure of habitat quality. Morrison et al. (1998) suggested that studies assessing habitat quality should investigate annual productivity (i.e., fitness) of a species using a habitat. Such methods follow Van Horne’s (1983) argument that population density can be a misleading indicator of habitat quality.

Local population growth rates should be a useful measure of mean individual fitness of hens that nested in upland and floodplain habitats. The highest quality nesting habitats should support the highest population growth rates. Matrix-based population models are used to estimate intrinsic population growth rates in ecological studies (Leslie 1945, Leslie 1948). Matrix model sensitivity and elasticity analyses provide valuable tools to identify life history parameters that most affect population growth (Crouse et al. 1987, Noon and Biles 1990, Wisdom and Mills 1997). Sensitivity analysis, an analytical procedure that measures changes in population growth rate in relation to changes in model parameters, is easily accomplished using matrix methods to measure the response of population growth to changes in demographic parameters (Caswell 1978). Refinements were introduced to ecological studies when elasticity analysis (i.e., proportional sensitivity) was introduced (de Kroon et al. 1986). Similarly, matrix methods can be a valuable tool for population management (Nelson and Peek 1982), understanding effects of environmental change on populations (North 1985), understanding a species' life history (McGraw and Antonovics 1983, Brault and Caswell 1993), or comparing life history traits (Werner and Caswell 1977, Caswell and Werner 1978).

Rogers (1968), working with interregional human demographics, noted that

> "perhaps the most important contribution of matrix formulation of the population growth rate and distribution is the separation of the process from the population that is undergoing this process. Use of a projection operator to 'grow' an interregional population forward through time allows one to focus on the projection process itself, it's (sic) application to another population, and it's (sic) long-term implication."

Rogers (1985) further discussed that the matrix analysis is

> "independent of the starting population distribution and depend(s) only on the growth regime defined by the projection matrix."

The ability to remove initial population levels from the modeling process allowed demographic analyses of wood ducks for which population estimates are difficult to obtain. Therefore, I considered fitness as a surrogate measure of habitat quality (Van Horne 1983, Morrison et al. 1998) without using estimates of population density.

Modeling is often conducted using point estimates of mean vital rates (Wisdom and Mills 1997). Such studies assumed that vital rates were measured accurately under all conditions and did not incorporate variation in vital rates. Using single parameter values for model construction can produce misleading results because of model assumptions (Nelson and Peek 1982), unknown or inaccurate parameter estimates (Wisdom and Mills 1997), and unknown or inaccurate initial conditions (Caswell 2001).

Applying matrix population models to the southern Illinois wood duck population allowed me to estimate population growth rates in upland and floodplain habitats. Elasticity analyses can provide insight into life history traits or vital rates that influence population growth rate. The estimates of fitness (i.e., per capita population growth) within each habitat could then be interpreted as measures of habitat quality (Van Horne 1983, Morrison et al. 1998) with which to compare upland and floodplain habitats. Therefore, specific objectives of this chapter were to: 1) compare population growth rates between upland and floodplain habitats, and 2) determine life history traits and vital rates that most influenced population growth.

METHODS

I used a stage-based matrix model to compare wood duck nesting populations in upland and floodplain forests (Caswell 2001). This model assumed a 1-year projection interval with an annual time-step beginning with the initiation of incubation. Hens were divided into juvenile and adult breeding categories. Although it is a misnomer, the juvenile breeding category results from the fact that most hens were aged before nesting when they were still less than 1 year old. Therefore, hens were considered juveniles until fledging following their first reproductive cycle (~14 months after their hatch).

Model Parameters

Demographic data were collected on female wood ducks during the breeding season at Union County CA and LaRue-Pine Hills RNA (see Chapters 2-4). When possible, demographic parameters were estimated for each habitat. Parameters and sampling bounds (i.e., $\bar{x} \pm 1.96*SE$) used for modeling are presented in Table 8. Model parameters and sampling bounds, except annual survival and floodplain whole brood loss, were estimated as the mean of annual estimates (1993-1998). As reported in Chapter 4, I estimated annual wood duck survival but the best age-specific model did not add additional information compared to the competing model given the data.

Table 8. Mean ($\bar{x}$) and sampling bounds (± 1.96 * standard error) for vital rates used for southern Illinois wood duck population models.

Vital Rate	$\bar{x}$	Lower	Upper
Clutch size			
Upland	12.27	11.27	13.27
Floodplain	11.96	10.38	13.53
Egg hatchability			
Upland	0.88	0.80	0.97
Floodplain	0.90	0.83	0.98
Nesting effort			
Upland	0.56	0.46	0.65
Floodplain	0.56	0.46	0.65
Nest success			
Upland	0.78	0.68	0.88
Floodplain	0.54	0.36	0.73
Brood attrition			
Upland	0.50	0.40	0.60
Floodplain	0.50	0.40	0.60
Whole brood survival*			
Upland	0.84	0.72	0.96
Floodplain	1.00**	0.89	1.00
Annual adult survival			
Upland	0.52	0.50	0.55
Floodplain	0.52	0.50	0.55

Table 8. Continued.

Vital Rate	$\bar{x}$	Lower	Upper
Annual juvenile survival			
Upland	0.43	0.39	0.46
Floodplain	0.43	0.39	0.46
Breeding season survival			
Upland	0.80	0.70	0.89
Floodplain	0.80	0.70	0.89

[*] Proportion of broods with at least 1 duckling surviving to fledging.

[**] No floodplain hatched broods were known to have lost all ducklings. This vital rate ranged from the mean of all broods observed (0.89) to the observed value (1.00).

I believe this may have been an artifact of the sampling and not biologically realistic as adult and juvenile survival are known to differ (Bellrose and Holm 1994). Therefore, annual adult and juvenile survival estimates were taken from the north-central subpopulation delineated by Kelly (1997). Whole brood loss was not observed among broods that hatched from floodplain nests. I used a range of estimates for the model based on empirical data collected and information collected from the literature. I assumed that floodplain-hatched broods should survive at a higher than average rate compared to the entire population because I observed that no radio-marked hens that nested in the floodplain lost entire broods before fledging. To allow for the likely possibility that whole brood loss does indeed occur among floodplain-nesting hens, I allowed the model parameter of whole brood survival to range from the habitat-combined mean (0.89) to my observed value (1.00).

Brood survival estimates were derived from field data collected on whole brood loss and brood attrition. Although whole brood loss was estimated using radiomarked hens known to have nested in each forest type, I was not able to accurately determine the number of young birds that were attended by radio-marked brood hens. I estimated brood attrition rates by observing brood sizes of various age-classes, but there was no way to determine which of these broods were hatched from floodplain versus upland nests. Consequently, brood attrition was assumed to be the same for upland- and floodplain-hatched broods. This was a conservative assumption in my modeling of differences in population growth between floodplain and upland habitats because I would expected floodplain-hatched broods to have lower brood size attrition rates, given the empirical evidence of higher rate of whole-brood loss among upland hatched broods. I conducted a sensitivity on the final model iterations to investigate the potential impact of differences in brood attrition on brood survival between habitats. My aim was to estimate how much upland brood attrition would need to be raised to eliminate any apparent difference in the local lambdas. I reproduced the model iterations exactly but incrementally increased upland-hatched brood attrition by 5% while holding all other variables constant. Average lambda for each proportionally increased model was then compared to estimate the level at which upland-hatched brood survival offset interhabitat differences in lambda.

Clutch size and egg hatchability estimates included normal and parasitized nests and therefore do not match estimates presented in Chapter 3. Subpopulation interchange between years was documented in only 1 hen and a statistically defensible range estimate for the models was not possible. Believing that some subpopulation exchange likely occurred, I created a range of values based largely on qualitative assumptions and I allowed the parameter to range from 1% to 8% (observed). I capped the range at my observed estimate because all hens observed to nest in multiple years used the same general area and the 1 hen that switched habitats between years crossed my boundary line between upland and floodplain habitats but, like other hens, remained in the same area as used previously. Models were created with S-Plus 4.0 software (MathSoft 1997).

Model Design

The goal of this analysis was a wood duck population model that incorporated the demographics of hens in upland and floodplain habitats. The 2-habitat model was composed of smaller models that depicted dynamics within each habitat and the movements between the habitats.

The structure for the modified Leslie matrix for a 2-stage model (Cooke and Leon 1976, North 1985) was,

$$\boldsymbol{A_h} = \begin{pmatrix} F_{jh} & F_{ah} \\ P_{jh} & P_{ah} \end{pmatrix} ,$$

where $\mathbf{A_h}$ was the projection matrix for the southern Illinois wood duck population in habitat type h. The elements of $\mathbf{A}$ consist of habitat specific juvenile (F_{jh}) and adult (F_{ah})

fecundity and habitat specific juvenile (P_{jh}) and adult (P_{sh}) survival and transition probabilities. Each element, except P_{ah}, was subsequently comprised of multiple vital rates. Estimates of fecundity for age ‘g’ hens in habitat ‘h’ were calculated as

$$F_{gh} = ½(CS_h)(EH_h)(NE_h)(P_{gh}) \ ,$$

where fecundity equals one-half (to remove males from the model) the product of clutch size (CS_h), egg hatchability (EH_h), nesting effort (NE_h), and adult or juvenile survival rates with transition probabilities (P_{gh}). Juvenile annual survival rates were the product of nest success, brood survival, and overwinter survival. Overwinter survival was estimated as the quotient of age-specific annual survival divided by age-specific breeding season survival (Cowardin and Johnson 1979). Annual adult survival rates do not incorporate lower-level vital rates in my models.

The 2-habitat model was constructed to incorporate the upland and floodplain populations. The matrix, $\mathbf{A}_T$, was 4 2x2 submatrices that describe the dynamics within and interaction between habitats. The model structure was

$$\boldsymbol{A}_T = \begin{pmatrix} \boldsymbol{A}_u & \boldsymbol{M}_{f \to u} \\ \boldsymbol{M}_{u \to f} & \boldsymbol{A}_f \end{pmatrix} = \begin{pmatrix} F_{ju} & F_{au} & 0 & 0 \\ P_{ju} & P_{au} & M_{jfu} & M_{afu} \\ 0 & 0 & F_{jf} & F_{aj} \\ M_{juf} & M_{auf} & P_{jf} & P_{af} \end{pmatrix} .$$

The submatrices A_u and A_f were the 2x2 matrices describing the dynamics of upland and floodplain populations. The submatrices $M_{u \to f}$ and $M_{f \to u}$ describe the exchange rates between habitats where the elements $M_{gh_1h_2}$ were the exchange rates of age "g" hens from habitat "1" to habitat "2". The age-specific fecundity estimates for each habitat were calculated similarly to the 2x2 model. Age- and habitat-specific survival rates (P_{gh}) were adjusted to include population exchange and were estimated as the product of annual survival (S_{gh}) and the complement of age-specific population exchange rates ($m_{gh_1h_2}$). The age-specific population exchange rate between habitats ($M_{gh_1h_2}$) was adjusted for annual mortality by multiplying $m_{gh_1h_2}$ by S_{gh}. Parameters for annual survival (S_{gh}) were estimated similarly to annual survival included in the 2x2 models.

The population model was run 1000 times with variables selected from a uniform distribution within their 95% confidence intervals to incorporate uncertainty of model parameter estimates (Table 7). Mean values over the 1000 iterations were calculated for model parameters and matrix elements. Mean values for overall population growth rate (λ) and growth rates within each habitats were estimated along with 95% prediction intervals (Hahn and Meeker 1991). While elasticity analysis may be preferred over sensitivity analysis in some cases, I found that elasticity equations for elements a_{12} and a_{21} in a 2x2 matrix were identical and may not produce independent results. Therefore, I chose to use sensitivity analysis rather than elasticity analysis when comparing matrix elements and lower-level parameters.

The eigenanalysis was an asymptotic analysis and spatially structured models were therefore driven by the subpopulation with the dominant eigenvalue (Caswell 2001). I determined which subpopulation segment was dominant given the randomly selected population model parameters by comparing habitat-specific growth rates (i.e., λ_h).

RESULTS

The average estimated finite rate of increase for the 1000 model iterations was 1.03 (95% PI 0.82 - 1.24) indicating a potentially increasing local population. The average growth rate in the floodplain habitat was 0.88 (95% PI 0.67 - 1.12) and 1.01 (95% PI 0.78 - 1.24) for the upland habitat. The inclusion of 1 in the 95% prediction intervals of all λ estimates provides evidence that subpopulation may not grow (or decline) in all years.

Sensitivity analysis of matrix elements indicated that population growth was most sensitive to upland juvenile survival and likely had almost 3 times (1.11 vs. 0.38) the effect as other important elements (Table 9). Upland juvenile fecundity, upland adult survival, and floodplain

Table 9. Mean matrix element sensitivity estimated from 1000 iterations of the southern Illinois wood duck population model.

Matrix element	Mean (SE)	Rank
Upland juvenile fecundity	0.38 (0.006)	2
Upland adult fecundity	0.13 (0.002)	8
Upland juvenile survival	1.11 (0.017)	1
Upland adult survival	0.37 (0.006)	4
Juvenile migration from floodplain to upland	0.32 (0.008)	5
Adult migration from floodplain to upland	0.12 (0.003)	9
Floodplain juvenile fecundity	0.11 (0.006)	10
Floodplain adult fecundity	0.04 (0.002)	12
Floodplain juvenile survival	0.38 (0.017)	3
Floodplain adult survival	0.13 (0.006)	7
Juvenile migration from upland to floodplain	0.31 (0.007)	6
Adult migration from upland to floodplain	0.11 (0.003)	11

juvenile survival had similar sensitivity values (i.e., 0.36 – 0.38). Juvenile migration from floodplain to upland (0.32) and juvenile migration from upland to floodplain (0.30) followed in importance.

Comparing vital rates (Table 10), the model was most sensitive to factors associated with the upland nesting subpopulation. Upland annual adult survival (0.73) and upland nesting effort (0.72) had almost identical sensitivity estimates. Post-hatch events (e.g., upland brood survival and upland juvenile overwinter survival) were ranked next followed by movement of hens from upland to floodplain. The remaining important upland nesting factors (e.g., upland egg hatchability and upland nesting success) were ranked next. The first floodplain parameters (i.e., floodplain annual adult survival and floodplain nesting effort) were ranked next but their estimates were about 3 times less sensitive (0.22 - 0.24 vs. 0.72 - 0.73) than top sensitivity estimates.

Sensitivity analyses using incremental increases in upland-hatched brood attrition indicated that, similar to matrix sensitivity analysis, lambda was relatively sensitive to changes in upland hatched brood attrition. When upland hatched brood attrition was modeled as 80-100% of the estimated value, lambda dropped by about 2% for each 5% drop in upland hatched brood survival (Table 11). Lambda became

Table 10. Mean lower-level sensitivities estimated from 1000 iterations of the southern Illinois wood duck population model.

Variable	Mean (SE)	Rank
Upland clutch size	0.03 (0.001)	17
Upland egg hatchability	0.45 (0.008)	7
Upland nesting effort	0.72 (0.012)	2
Upland nesting success	0.33 (0.005)	8
Upland brood survival	0.61 (0.010)	3
Upland juvenile overwinter survival	0.48 (0.008)	4
Upland annual adult survival	0.73 (0.011)	1
Juvenile movement from upland to floodplain	0.47 (0.007)	5
Adult movement from upland to floodplain	0.46 (0.005)	6
Floodplain clutch size	0.01 (0.001)	18
Floodplain egg hatchability	0.13 (0.006)	15
Floodplain nesting effort	0.22 (0.011)	10
Floodplain nesting success	0.13 (0.006)	16
Floodplain brood survival	0.16 (0.008)	13
Floodplain juvenile overwinter survival	0.15 (0.007)	14
Floodplain annual adult survival	0.24 (0.011)	9
Juvenile movement from floodplain to upland	0.17 (0.007)	12
Adult movement from floodplain to upland	0.20 (0.007)	11

Table 11. Estimates of lambda with 5% increases in upland-hatched brood attrition.

Variable Efficiency (%)	Upland Hatched Brood Attrition	Overall Lambda
100	0.50	1.03
95	0.47	1.01
90	0.45	1.00
85	0.42	0.98
80	0.40	0.96
75	0.37	0.95
70	0.35	0.94
65	0.32	0.93
60	0.30	0.92
55	0.27	0.91
50	0.25	0.91
45	0.22	0.91
40	0.20	0.90
35	0.17	0.90
30	0.15	0.90

increasing less sensitive to the changes as upland-hatched brood attrition in the model was reduced below 80% of the estimated value. An overall lambda similar to the floodplain lambda (0.88) would not be reached until upland brood attrition had been increased so the parameter was about 50% of the modeled value.

DISCUSSION

The demographic parameters that I modeled for my study population were sufficient for apparent positive population growth ($\lambda = 1.03$) but floodplain and upland nesting populations ($\lambda = 0.88$ and $\lambda = 1.01$, respectively) may not to contribute equally to this population. Since the prediction intervals of lambda contained 1 for both habitats, I could not conclude that either habitat was a source or sink.

The model was most sensitive to upland demographic parameters estimates for adult survival and nesting effort. This is contrary to studies (Cowardin and Johnson 1979, Cowardin et al. 1985, Cowardin et al. 1988, Baldassare and Bolen 1994, Hoekman et. al 2002) that concluded that nest success is likely the most important vital rate affecting population growth for waterfowl. The estimated importance of a vital rate in a waterfowl population modeling, in my opinion, likely depends on species life history. Ground nesting populations often suffer high nest depredation rates but this may be partially offset by high nesting effort and renesting intensity (Hoekman et. al 2002). Wood ducks nesting on my study areas differed in that there was competition for suitable cavities, although many apparently suitable sites are unused (Zwicker 1999). Additionally, nesting effort was relatively low (Selle 1998) and renesting was not observed. These factors were apparently offset by high nest success rates afforded by nesting in protective tree cavities.

Several waterfowl population models also considered brood survival an important vital rate in the waterfowl life cycle (Cowardin et al. 1985, Johnson et al. 1987, Hoekman et. al 2002). I had incomplete information on differences in brood survival between upland and floodplain hatched broods, but overland movements of upland hatched broods may have increased mortality, based on observations of whole brood loss as 5 of 6 whole-brood loss events were attributable to loss of hen. Additional unmeasured effects (e.g., energy resources expended, disease susceptibility) of long range brood movements on survival are unknown and ultimately may be proven to be factors that reduce upland nesting productivity. Sensitivity analysis indicated that modeling brood attrition as similar between habitats was not unrealistic because upland hatched brood attrition would need to be increased so the modeled values were about 50% of measured values to eliminate differences in habitat-specific lambdas. Ball et al. (1975) reported about a 20% decline in brood size (8.53 vs. 6.77) that was associated with overland brood movements. My models assume about a 10% difference in brood survival between habitats while sensitivity analysis indicated a 50% decrease in brood attrition would be required to equalize habitat specific lambdas. I found no study that has reported such extremes in brood survival to eliminate difference between upland and floodplain lambdas based on my models. This gives me some level of confidence that, although I likely underestimated upland-hatched brood attrition, there is little chance that this would have biologically significant impacts on growth rates.

Overwinter survival was an important vital rate for upland hatched juvenile hens but I did not attempt to estimate the impact of harvest on the population because my primary interest concerned factors occurring during breeding season. This vital rate should be consistent for upland and floodplain hatched hens but the model was not very sensitive for floodplain-hatched hens.

Factors that are ultimately tied to overwinter survival of hens that nested in each habitat include interchange between upland and floodplain habitats of hens that return to nest. Wood ducks are philopatric but I found little evidence that hens returned to the exact tree at a rate similar to box-nesting hens. Hens apparently returned to the same vicinity of previously used nest sites. If any interchange of hens occurs between nesting habitats by individual hens in successive years, it would be mostly by hens that nest near the upland-floodplain boundary. The only hen that changed nesting habitats between years remained near the upland-floodplain boundary. The range of values that I used to model nesting habitat interchange (1 – 8%) was conservative and based primarily on my finding that hens radiomarked in multiple years generally did not move far from previous nest sites. However, estimated values for adult and juvenile hens moving from the upland to the floodplain habitats between years were relatively important vital rates influencing population growth. Annual supplementation of the floodplain breeding subpopulation by hens that nested or were hatched from the upland forests returning to the area but nesting in a different habitat appear to be important determinants of habitat-specific population growth rates.

The local breeding population was not especially sensitive to floodplain vital rates. The most important floodplain vital rate, annual adult survival, had about 1/3 the sensitivity as the leading upland vital rate (0.24 vs. 0.73). Floodplain vital rates appeared to have little influence on population growth.

One might question whether the local population could sustain a positive growth rate without the upland nesting component. The floodplain subpopulation growth rate was low but sufficient to support positive growth rate when modeled with the upland habitat. The estimated 95% prediction intervals for the local λ estimates for upland and floodplain habitats broadly overlapped and both contained 1. This local variability is not an unexpected result for population dynamics in a patchy environment (Begon et al. 1996) and may indicate that both local subpopulations could be a source or sink (Pulliam 1988) in any given year. Pulliam (1988) used deterministic models to frame his source and sink dynamics arguments and subsequent determination of a source or sink by his definition would be unchangeable. Growth based on an assumed inherent habitat quality may be relatively constant but will have some annual, unpredictable variation. If such annual variability occurs in a habitat, I would argue that subpopulations do not need to grow or shrink in every year in order to be a long term source or sink. Similarly, a stable population will not have $\lambda = 1$ in all years. The long term trajectory should define a source or sink, not small annual perturbations that will not likely impact the eventual long term growth of the population. Ultimate determination of a source or sink would depend on the ability of a habitat to support a population that has a growth rate above or below 1.

If the inherent quality (e.g., no predation) of the upland and floodplain habitats could be measured, I believe the floodplain would have a higher inherent quality for nesting wood ducks. However, the realized quality of these habitats differs (based on model sensitivities) due to differential predation pressure (Chapter 3). Such external pressures can create transient dynamics that lead a metapopulation away from equilibrium (Thomas and Jones 1993, Begon et al. 1996) and I would argue that transience on a local scale could have the similar but smaller local effect. Although the floodplain lambda appeared dramatically lower the upland lambda the prediction intervals overlapped and both contained 1. If the difference in the two lambdas was biologically significant, the difference could be great enough to cause transience. However, given the non-significant statistical tests there is no strong evidence the within habitat growth rates differ.

Adding the external pressure of predation to a habitat will reduce the habitat quality (as defined by fitness measures) to some degree by negatively influencing several vital rates with subsequent impacts on the magnitude of annual variation. If external pressures increase and become persistent (e.g., predation pressure likely increases as forest fragmentation increases), then local population transience may occur and the long-term population growth rate in a habitat would decline. Ultimately, the long-term growth rate may average below $\lambda = 1$ even though there may be sufficient annual variation for the growth rate to exceed $\lambda = 1$ in some years.

The model prediction intervals indicated the floodplain and upland habitats could be a source or a sink given the range of model inputs although there was apparent growth. The average of the 1000 iterations generated an average growth rate of about 3%. To get this relatively low growth rate, it would not be unreasonable for the subpopulations to fluctuate above and below 1 in any given year. However, based on average model outputs the long term trajectory of the population appears to be positive and exceeds 1.

My modeling was based primarily on data collected in southern Illinois but I had no means to validate the models. While the models were designed primarily to investigate demographic differences between upland and floodplain habitats, the opportunity to address source-sink dynamics is compelling. I cannot say with certainty that nesting populations in either habitat are growing or shrinking. However, I do have reasonable evidence that the upland habitat consistently had higher λ values and had the dominant influence on local population dynamics. From this

I conclude that the realized quality of the upland forest was at least equal, if not higher than that of the floodplain forest. This basic comparison of wood duck individual fitness within each habitat was the primary aim of my population modeling exercise and gives reasonable evidence but not irrefutable evidence that the upland habitat quality was at least equal to or higher than the floodplain habitat for nesting wood ducks.

The ability of a local population that is distributed across 2 seemingly different breeding habitat types to maintain sufficient productivity for population growth is important to understand for wood ducks and other species that may use multiple habitats. Wood duck research and management have generally ignored upland habitats as major contributors to productivity of the nesting population but my study demonstrates that the upland breeding was an important component for this local population. I cannot speculate on how or when wood ducks began using the upland forests adjacent to the floodplain habitat in southern Illinois. Data presented in earlier chapters provided credible evidence that there is consistent nesting in the upland habitat. We do know that wood ducks nest consistently in upland habitats in southern Illinois and other areas (Bellrose et al. 1964, Gilmer et al. 1978, Soulliere 1988, Robb 1986, Ryan et al. 1998). The use of upland forests for nesting habitat with fitness measures that are similar to or greater than floodplain habitats suggests that the use of upland forests is an established tradition and not an ephemeral event. This could be especially true and important in highly disturbed landscapes, like the Mississippi River floodplain of southern Illinois, where all the components required for wood duck breeding are present but their juxtaposition and interspersion may be drastically different than what may have been present historically.

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Wood ducks depend on wetland habitats as a source of food and cover throughout most of their life cycle (Bellrose and Holm 1994, Kawula 1998) but have long been known to nest in upland habitats, often at great distances from water (Hawkins and Bellrose 1940, Bellrose et al. 1964, Soulliere 1988, Robb and Bookhout 1995, Ryan et al. 1998). Wood ducks may perceive upland and floodplain habitats as one continuous nesting habitat and being precocial birds with nidifugous young that are capable of moving long distances after hatching (Leopold 1951, Bellrose 1953, Ball et al. 1975, Bellrose and Holm 1994), wood ducks are not necessarily limited to nesting near wetlands. Nevertheless, brood mortality that occurs during overland travel from nest sites to brood rearing habitat should favor nesting near wetlands. If so, preference for nesting near wetlands should have favored hens that nested in or near floodplain forests before European settlement.

Wood ducks were abundant across portions of what is now the eastern United States at the time Europeans settled North America. Illinois, like many other midwestern states, lost most of its upland and floodplain old-growth forests to logging after European settlement, eliminating vast areas of nesting habitat. Habitat loss probably limited wood duck populations for many years (Bellrose and Holm 1994). Forest cover has regenerated in recent decades (Abernethy and Turner 1987) and wood duck populations appear to be increasing (Bellrose and Holm 1994). Although much of the historic floodplain forest was converted to cropland, upland forests were regenerating and have matured to provide a source of nest cavities once again (Roy Nielsen et al. 2007). Remnant floodplain forests are declining or at best stable, while upland forest acreage is increasing (Abernethy and Turner 1987, Dahl and Johnson 1991, Twedt and Loesch 1999).

Wood ducks are largely constrained to nesting in cavities and mature trees are the obvious source of natural cavities for nesting wood ducks. All animals are evolutionarily constrained to a range of suitable life-history strategies and life-history strategies are often relatively fixed (Begon et al. 1996). Animals that have some behavioral or evolutionary plasticity that allow tactical modifications of life-history strategies are more capable of adaptation to existing resources (Hansen and Urban 1992, Martin 1993, Begon et al. 1996). Decline of floodplain forests would constrain wood duck population growth by removing optimal nesting habitats and potentially extirpating local populations if floodplain forests are an ecological trap and the population is unable to adapt to altered conditions (Dwernychuk and Boag 1972, Gates and Gysel 1978, Reese and Ratti 1988, Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006). Ecological traps result from habitat alterations that cause individual animals to settle in habitat types where their fitness is lower than in other suitable habitats. This occurs when habitat alteration does not affect or possibly even enhances settling cues despite that suitability of that habitat is lower than for alternative habitats.

I suggest that all things being equal, wood ducks would select nest sites near wetlands where they can easily forage during the nesting season and later rear their young. Thus, proximity to water should be an important settling cue for nesting wood ducks, albeit of secondary importance to abundance of physically suitable tree cavities. Having evolved in the largely closed canopy and continuous forests that historically characterized the eastern U.S., wood ducks do not seem deterred by forest edges juxtaposed with anthropogenic habitats (e.g., crop land) that support high densities of nest predators. Data indicate that this population nested earliest (see Chapter 2) and in the highest densities (Zwicker 1999) in floodplain forests, where they were exposed to higher predation pressure (see Chapter 3) compared to upland forest habitat. Nests were widely distributed across both habitat types despite great abundance of unoccupied tree cavities that were suitable for nesting wood ducks (Zwicker 1999). This pattern of nest initiation and distribution was consistent with some form of behavioral spacing, perhaps to avoid dense concentrations of nests that would be more readily exploited by nest predators. The pattern of nest initiation, density, and distribution among habitat types suggest an “ideal free distribution” (Fretwell and Lucas 1970) of nests between upland and floodplain habitats. I can only speculate that wood duck nesting was distributed between upland and floodplain habitats in the “ideal free” manner proposed by Fretwell and Lucas (1970), now and before European settlement. Ecological density of nests and inherent habitat suitability should have been higher in the Union County CA floodplain than in upland habitats but the Union County CA floodplain habitats are a potential ecological trap for nesting wood ducks because they have been fragmented or destroyed as a consequence of human activity.

Ryan et al. (1998) speculated that nest site selection and nest distribution may be a response to severe predation in floodplain forests. Hens appeared to avoid nest depredation by using more secure nest sites in floodplain forests, or by simply by nesting in upland forests. Ryan et al. (1998) posed these questions years before Robertson and

Hutto (2006) provided a framework to define an ecological trap. Their observations suggested that my study area fit Robertson and Hutto's (2006) criteria for an ecological trap. I initiated this study to investigate the contribution of upland nesting hens to local productivity but I further applied Robertson and Hutto's (2006) ecological trap framework with additional data and analyses.

Many examples of ecological traps have been described in the literature. Robertson and Hutto (2006) recently proposed three criteria that must be demonstrated to provide empirical evidence of an ecological trap: (1) individuals must exhibit behavioral preference for one or more alternative habitat types; (2) some measure (actual or surrogate) of fitness must exist among habitats; and (3) individuals that settle in preferred habitat(s) must have lower fitness than would be attained in alternative habitats. I consider each of these criteria in turn to evaluate whether floodplain forest was an ecological trap for my study population.

Criterion 1. Individuals exhibit a behavioral preference for a habitat. The data were not uniformly consistent, but I believe that individual wood ducks in my study population exhibited behavioral preference in their selection of nesting habitat. The strongest evidence to support this conclusion is that nest initiation averaged nearly 2 weeks earlier in floodplain than in upland forest (see Chapter 2). Nest success declined with nest initiation date (see Chapter 3), so early nesting should have been advantageous to members of this population. Floodplain nest cavities also were reoccupied during successive years at higher rates than upland nest cavities (Chapter 2). Individual radio-marked hens also showed annual fidelity to nest locations within habitat types, although they did not show fidelity to individual nest trees or tree cavities (Chapter 2). Settlement patterns (i.e. nest initiation date) and site fidelity (e.g., to nest locations within habitats) are two of five multiple lines of evidence that Robertson and Hutto (2006) postulated as indicative of individual preference. A third, distribution of dominant individuals, was supported by my observation that age ratios (adult vs. yearling) did not differ between females that nested in upland versus floodplain forest but this finding may be best considered inconclusive because of relatively weak support provided in the statistical test. A fourth line of evidence, temporal variation in population size, was weakly supported in that annual proportions of radio-marked hens located in floodplain versus forest nests varied among years, with higher proportions of floodplain-nesting hens observed when nesting effort (proportions of hens tracked to nests) was lower (Gates et al. unpublished, Geboy 2006). The fifth line of evidence, results from individual choice experiments, is impossible to evaluate for a wild wood duck population.

Although not considered a line of evidence supporting individual preference by Robertson and Hutto (2006), nesting wood ducks did not use suitable tree cavities randomly with respect to availability in floodplain as they did in upland forests. That wood ducks selected different types of tree cavities in the floodplain than in upland forests in response to differences in predation pressure among forest types is an additional line of evidence that individual behavioral preferences were responsible for the observed distribution of nests among habitat types.

The determination of whether wood duck hens observed equal preference, or higher preference for floodplain over upland habitat types is less clear. Settlement patterns (i.e., nest initiation date) and site fidelity (annual re-occupancy of nests) were the strongest lines of evidence supporting unequal preference. However, higher ecological densities (nests/forested area, Zwicker 1999) of nests in the floodplain seems also to weakly support higher preference for floodplain forest if nest distribution was indeed ideal free (Fretwell and Lucas 1970).

Criterion 2. Individual fitness differs between habitats. My simulated nest experiment demonstrated that, independent of nest placement, the probability of clutch failure (e.g., predation pressure) was greater for floodplain than for upland nests (see Chapter 3). However, wood ducks used more secure tree cavities in the floodplain allowing them to compensate for higher predation pressure in the floodplain. Nevertheless, nest success was still lower for wood duck hens that nested in floodplain versus upland forests (see Chapter 3). This difference in nest success could be compensated by higher survival rates of broods hatched from floodplain versus upland nests, but I found that potential difference in brood loss between habitats are likely not sufficient to crate a realistic impact on the local population (Chapter 5).

Criterion 3. Individual fitness is lower in preferred or equally preferred habitat. Survival of nesting hens was similar between upland and floodplain habitats (Chapter 4) but their reproductive capabilities were limited in the floodplain. Upland nest survival was 20% higher than floodplain nest survival, giving strong indication that hens nesting in floodplain habitats, had lower fitness.

I created a population model to compare population growth rates (λ) for wood ducks nesting in floodplain versus upland habitats. Although the local population had a slightly increasing growth rate, the within habitat estimates of λ were potentially biologically different as the upland-nesting subpopulation had a positive λ and the floodplain-nesting population had a negative λ that was well below 1. Although prediction intervals overlapped and both contained 1. Individual fitness parameters (e.g., nest success) differed between habitats but the translation of these differences to into divergent population trajectories between the habitats was not statistically demonstrated. The model is nevertheless suggestive that fitness may be lower in the floodplain habitats.

The implications of not statistically differentiating habitat-specific λ values may be that wood ducks use the local area as a single habitat resource with no regard to anthropocentrically defined differences in habitat type (Kawula 1998), tree species composition (Zwicker 1999), and physiography (Schwegman 1973). However, I would argue that potential biological differences in local λ estimates (i.e., 0.88 vs. 1.01) along with habitat-based philopatry and differences in nest selection, nest initiation, reoccupancy rates, nesting density (Zwicker 1999), and nest success provide evidence that habitats are best defined and managed by anthropocentric definitions. Union County CA supports one of the highest densities of raccoons ever recorded

(Wilson and Nielsen 2007) and predator pressure likely dictated differences in behavior and nesting ecology. In my opinion, the upland and floodplain habitats should be considered as separate habitats for nesting wood ducks rather a single continuous habitat.

The Union County CA floodplain appears to be on the verge of becoming an ecological trap meeting Robertson and Hutto's (2006) criteria and interpretation of my data. I am hesitant to declare that the floodplain was clearly demonstrated to be an ecological trap in the absence of statically significant differences on modeled growth rates of floodplain and upland nesting subpopulations. Nevertheless, based on Robertson and Hutto's (2007) implementation of their previously defined framework regarded differences in nest success between habitats to offer sufficient evidence of fitness differences and indicative of an ecological trap. I will simply state that upland and floodplain habitats are used annually by wood ducks but there are reasonable indications that floodplain forests are the preferred nesting habitat for wood ducks on my study area. Floodplain forests obviously provide the proper ques to illicit settling in a preferred habitat but fitness, as measured by nest success (Robertson and Hutto 2007) was lower in floodplain than in upland forest. However, I was not able to definitively demonstrate that the difference in nest success was sufficiently large to declare the floodplain to be a population sink.

If the Union County CA floodplain is on the verge of meeting the criteria of an ecological trap then the importance nest site selection by nesting hens becomes an increasingly important issue. Had the Union County CA floodplain hens used cavities across the full range of available cavities then nest success would have been reduced to what the simulated nest study showed. Such a large reduction (>20%) in nest success could be sufficient to impact fitness and lower the Union County CA floodplain growth rate to below one and create an ecological trap.

My study showed that upland habitats made important contributions to local nesting populations but this still leaves unanswered the question of whether upland nesting is a recent and geographically widespread phenomenon associated with loss of bottomland forest habitat. Alternately, this may be an on-going, under-recognized phenomenon with origins that historically predate contemporary losses of bottomland forest within the wood duck range. Lacking data and the means to test these ideas, one can only speculate on their veracity, but my study provides some insights. Wood ducks quite likely have always nested in upland forests near wetlands but may have become more reliant on upland forest in response to loss and fragmentation of floodplain forests and subsequent increase in nest depredation (Wilcove 1985, Robinson et al. 1995, Lloyd et al. 2005). There also has been a concurrent aging of upland forests that should provide an increasing supply of suitable nest cavities (Roy Nielsen et al. 2007). Indeed wood ducks have shown their ability to pioneer new habitats in response to population growth and habitat changes. This is particularly evident as their range expanded into the Great Plains, where woody growth along riparian areas and near glacial wetlands has increased the availability of suitable nest sites (Ladd 1990).

Bland and Temple (1990) found Himalayan snowcocks (*Tetraogallus himalayensis*) used suboptimal foraging habitat in response to greater predation-risk in higher quality foraging habitats. Southern Illinois wood ducks may be responding similarly in that the floodplain habitat was fragmented to a level that compromised nest security. The initial increase in importance of upland nest sites to wood ducks may have occurred in response to predation-risk but upland nesting is now likely sustained by annual philopatry of females to a habitat type where individual fitness is enhanced (Baldassare and Bolen 1994). Ultimately, the reliance on upland habitats where nest success is high demonstrates that plasticity in use of a novel or underutilized habitat may be more important for population stability than use of a traditional habitat (Martin 1993).

Upland and floodplain forests appear to provide suitable nesting habitat for wood ducks, but losses, fragmentation, and natural succession that occurs in both forest types affects their relative suitabilities, and so the distribution of nesting wood ducks. I contend that wood ducks have always used both types of habitats for nesting, and that the relative importance of these habitats in terms of nesting productivity does and has varied spatially and temporally with both human and non-human sources of disturbance. Furthermore, I contend that the relative importance of forest types to this population of wood duck may have shifted from floodplain to upland forests in response to loss and fragmentation of forested wetlands. The re-growth and maturation of upland forests that occurred during the latter half of the 20th century (Dahl and Johnson 1991, Suloway and Hubbel 1994, Abernethy and Turner 1997, Dahl 2000) may now be the most important source of nesting habitat for wood ducks in this area.

Floodplain forests are changing with human induced influences (e.g., altered flooding regimes and higher water levels) and historic habitats are not regenerating with the same spatial distribution or species composition (Knutson and Klaas 1997, 1998). Some species may respond positively to fragmentation of floodplain forests (Knutson et al. 1999), but others generally will not (Donovan et al. 1995, Robinson et al. 1995, Lloyd et al. 2005).

If a habitat is altered too abruptly and there is insufficient time for a species to adapt to changing conditions, the species could be caught in an ecological trap (Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006). The ability for a species to escape the trap will depend on it's level of life-history plasticity (Battin 2004). Begon et al. (1996) notes that life-history variation allows for modifications and some species show wider variation within their genotype than other species. The species with a wider range of variability will likely adapt to a changing environmental stressor better than a species with a narrow range of variability (Rothstein 1973). The speed with which a species can overcome the stressor will depend on the species' adaptability (Rothstein 1975). If stressors reduce the population faster than the species can adapt then an "evolutionary lag" may cause the population to become extirpated or extinct (Rothstein 1975, Robinson and Morse 2000, Battin 2004). The California condor (*Gymnogyps californianus*) or the ivory-billed woodpecker (*Campephilus principalis*) may be examples of aplastic species that lacked the ability to adapt to shrinking or degraded habitats. Many other species have been shown capable of very rapid changes or microevolution when confronted with negative stressors (Ashley et al. 2003).

The comparative speed at which species are capable of adapting to a stressor (Rothstein 1975, Battin 2004) is often considered a theoretical construct and is difficult realistically measure and compare. This does not make the “speed” at which a species may adapt an invalid consideration for discussion. Speed of wood duck adaptation on my study areas appears to have been swift enough so the increased reliance on upland nesting habitats “overtook” the negative impacts of the fragmented floodplain forest. This may not have been the case for all floodplain dependent populations in the southern Illinois region that were present before the decline of floodplain forests.

Floodplain and upland habitats are ecologically intertwined and the local wood duck population would not survive if either habitat were destroyed or severely degraded. Without productivity from upland forests the southern Illinois wood duck population would not likely offset annual mortality, but the floodplain forests and associated wetland habitats are essential for food resources and brood rearing. Species with the ability to survive the loss of the floodplain forest by using novel habitats or some other behavioral mechanism likely still depend on the floodplain area for some major life cycle needs. The plasticity in resource use may allow additional freedom to better exploit novel resources. However, the magnitude of the change probably cannot be so dramatic as to completely eliminate floodplain habitats from the life cycle of a species that is traditionally floodplain dependent.

MANAGEMENT IMPLICATIONS

My study area is managed by the U.S. Forest Service and the Illinois Department of Natural Resources. These 2 agencies should attempt to cooperatively manage the upland and floodplain forests or the long-term effect on wood ducks and other species could be detrimental. The population depends on the upland forest for suitable secure nest sites and on the floodplain for all other foraging and loafing resources during the breeding season. If either were disturbed or degraded to a large degree, the result could be detrimental to nesting wood ducks. The problem could be mitigated by retiring portions of agricultural fields to increase the floodplain forest and reduce fragmentation.

Management on a regional or national scale that will establish suitable, functional floodplain forest blocks for neotropical migrants (Twedt and Loesch 1999) will dictate that restoration efforts come from cooperation among a variety of agencies, non-governmental organizations and private landowners. Planning efforts should be stepped down from the national or at least regional scale to ensure maximum cooperation to incorporate multiple programs from large-scale acquisition efforts (e.g., North American Wetland Conservation Act) to small scale buffer establishment programs (e.g., Wildlife Habitat Incentives Program). Effort should be focused on areas that provide the greatest opportunity for linking existing forest patches to increase connectivity and patch size (Twedt and Loesch 1999). Additionally, I suggest that consideration be given to connectivity of upland and floodplain forests and not just focus on single habitat restoration (i.e., floodplain forests only). This study has shown that 2 apparently different habitat types form a continuum and can function synergistically to sustain bird populations. Acquisition of smaller floodplain habitats that would be contiguous with existing large upland forest tracts (or vice versa) could likely provide functional habitats to meet the expected needs of wildlife.

Nest box programs are popular and provide a perception of impact on the local population. However, a very small proportion of the continental wood duck population is produced from boxes (Soulliere 1986, Bellrose and Holm 1994). Production in boxes may offset some losses from natural cavity nesting hens in the floodplain but I doubt the additional production from the boxes is worth the time and money since an established natural cavity nesting population is already thriving. This may be true in many other areas where nest box programs are being implemented.

I suggest small-scale management tools like establishing shrub or native-grass buffers between agricultural and forested habitats on Union County CA. Not all edges are the same and buffered edges may have some effect to alleviate predation (Saracco and Collazo 1999). Union County CA has many hard edges compared to LaRue-Pine Hills RNA. Buffers may help with wood duck nest predation but they may also help provide habitat for escape, foraging, or nesting cover for many other associated floodplain or forest edge species as well.

Long-term solutions based on forest regeneration would not provide benefits for 5-6 decades. The best probable short-term solution is cooperative management of the upland/floodplain interface by State and Federal agencies with the understanding that these 2 very different habitats provide a continuum for nesting wood ducks and probably many more species. The upland and floodplain habitats of LaRue-Pine Hills RNA are managed as a single unit. The area generally has soft edges and reasonably intact forest linkages between the 2 habitats which have contributed to the low nest predation during this study. Most of the upland forests used by wood ducks are on steep highly erodible slopes unsuitable for forest harvest practices without negative environmental consequences. Allowing the upland forests near the floodplain, as well as floodplain forests, to mature will provide suitable cavities and stable environments to allow this population to persist for future generations.

LITERATURE CITED

Abernethy, Y., and R. E. Turner. 1987. U.S. forested wetlands: 1940-1980. BioScience 37:721-727.

Ackerman, J. T., A. L. Blackmer, and J. M. Eadie. 2004. Is predation on waterfowl nests density dependent? - Tests at three spatial scales. Oikos 107:128-140.

Albano, D. J. 1992. Nesting mortality of Carolina chickadees breeding in natural cavities. Condor 94:371-382.

Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M Gende, and J. S. Brown. 2003. Evolutionarily enlightened management. Biological Conservation 111:115-123.

Baldassare, G. A. and E. G. Bolen. 1994. Waterfowl ecology and management. John Wiley and Sons, New York, New York, USA.

Ball, I. J., D. S. Gilmer, L. M. Cowardin, and J. H. Riechmann. 1975. Survival of wood duck and mallard broods in north-central Minnesota. Journal of Wildlife Management 39:776-780.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482-1491.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations and communities, Third edition. Blackwell Science, Ltd., Oxford, United Kingdom.

Bellrose, F. C. 1953. Housing for wood ducks. Illinois Natural History Survey Circular 45. Urbana, Illinois, USA.

Bellrose, F. C. 1990. The history of wood duck management. Pages 13-20 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Bellrose, F. C., and D. J. Holm. 1994. Ecology and management of the wood duck. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Bellrose, F. C., K. L. Johnson, and T. U. Meyers. 1964. Relative value of natural cavities and nesting houses for wood ducks. Journal of Wildlife Management 28:661-676.

Bland, J. D., and S. A. Temple. 1990. Effects of predation risk on habitat use by Himalayan snowcocks. Oecologia 82:187-191.

Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales. Ecology 74:1444-1445

Burger, L. D., L. W. Burger, Jr., and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. Journal of Wildlife Management 58:249-354.

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

Cade, B. S., and J. D. Richards. 2005. User manual for Blossom statistical software: U.S. Geological Survey, Fort Collins Science Center Open-File Report 2005-1353. Colorado, USA.

Carney, S. M. 1992. Species, age, and sex identification of ducks using wing plumage. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois, USA.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology 14: 215-230.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H., and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipascus sylestris* Huds.). Ecology 59:53-66.

Cooke, D., and J. A. Leon. 1976. Stability of population growth determined by 2x2 Leslie matrix with density-dependent elements. Biometrics 32:435-442.

Cowardin, L. M., and D. H. Johnson. 1979. Mathematics and mallard management. Journal of Wildlife Management 43:18-35.

Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92.

Cowardin, L. M., D. H. Johnson, T. L. Shaffer, and D. W. Sparling. 1988. Applications of a simulation model to decisions in mallard management. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 17.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Dahl, T. E. 1990. Wetland Losses in the United States 1780's to 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous United States 1986 to 1997. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Dahl, T. E., and C. E. Johnson. 1991. Status and trends of wetlands in the conterminous United States, mid-1970's to mid-1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Davis, J. B., R. R. Cox, Jr., R. M. Kaminski, and B. D. Leopold. 2005. Survival of wood duck ducklings and broods in Mississippi and Alabama. Journal of Wildlife Management 71:507-517.

de Kroon H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Dow, H., and S. Fredga. 1983. Breeding and natal dispersal of the goldeneye. Journal of Animal Ecology 52:681-695.

Driscoll, M. J. L., T. Donovan, R. Mikey, A. Howard, and K. K. Fleming. 2005. Determinants of wood thrush nest success: a multi-scale, model selection approach. Journal of Wildlife Management 69:699–709.

Dugger, K. M., B. D. Dugger, and L. H. Fredrickson. 1999. Annual survival rates of female hooded mergansers and wood ducks in southeastern Missouri. Wilson Bulletin 111:1–6.

Duncan, D. C. 1987. Nest-site distribution and overland brood movements of northern pintails in Alberta. Journal of Wildlife Management 51:716–723.

Dwernychuk, L. W., and D. A. Boag. 1972. Ducks nesting in association with gulls — an ecological trap? Canadian Journal of Zoology 50:559–563.

Dzubin, A., and J. B. Gollop. 1972. Aspects of mallard breeding ecology in Canadian parkland and grassland. Pages 113–152 *in* Population ecology of migratory birds: a symposium. U.S. Bureau Sport Fisheries Wildlife Research Report 2. Washington, D.C., USA.

Dzus, E. H., and R. G. Clark. 1997. Overland travel, food abundance, and wetland use by mallards: relationships with offspring survival. Wilson Bulletin 109:504–515.

Evans, C. D., and K. E. Black. 1956. Duck production studies on the prairie potholes of South Dakota. U.S. Fish and Wildlife Service, Special Science Report Wildlife 32. Washington, D.C., USA.

Evans, M. R., D. B. Lank, W. S. Boyd, and F. Cooke. 2002. A comparison of the characteristics and fate of Barrow's goldeneye and bufflehead nests in nest boxes and natural cavities. Condor 610–619.

Fredrickson, L. H. 1980. Management of lowland hardwood wetlands for wildlife: problems and potential. Transactions North American Wildlife and Natural Resources Conference 45:376-386.

Fredrickson, L. H., G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. 1990. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gates, E. J., and L. W. Gysel. 1978. Avian nest dispersion and fledging nest success in field-forest ecotones. Ecology 59:871-883.

Gauthier, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in buffleheads. Auk 107:126-132.

Gavin, T. A., and E. K. Bollinger. 1988. Reproductive correlates of breeding site fidelity in Bobolinks. Ecology 69:96-113.

Geboy, R. A. 2006. Influence of habitat conditions on nesting activity of wood ducks (*Aix Sponsa*) in tree cavities. Thesis, Ohio State University, Columbus, USA.

Gendron, M., and R. G. Clark. 2002. Survival of gadwall and mallard ducklings in southcentral Saskatchewan. Journal of Wildlife Management 66:170-180.

Gilmer, D. S., I. J. Ball, L. M. Cowardin, J. E. Mathisen, and J. H. Reichman. 1978. Natural cavities used by wood ducks in north-central Minnesota. Journal of Wildlife Management 42:288-298.

Gollop, J. B., and W. H. Marshall. 1954. A guide for aging duck broods in the field. Mississippi Flyway Council Technical Section, Minneapolis, Minnesota, USA.

Götmark, F., R. Neergaard, and M. Alhund. 1990. Predation of artificial and real arctic loon nests in Sweden. Journal of Wildlife Management 54:429-432.

Granfors, D. A., and L. D. Flake. 1999. Wood duck brood movements and habitat use on prairie rivers in South Dakota. Journal of Wildlife Management 63:639-649.

Grice, D., and J. P. Rogers. 1965. The wood duck in Massachusetts. Federal Aid Project W-19-R. Final Report. Massachusetts Division Fish Game, Boston, USA.

Guyn, K. L., and R. G. Clark. 1997. Cover characteristics and success of natural and artificial duck nests. Journal of Field Ornithology 68:33-41.

Guyn, K. L., and R. G. Clark. 1999. Factors affecting survival of northern pintail ducklings in Alberta. Condor 101:369-377.

Hahn, G. J., and W. Q. Meeker. 1991. Statistical intervals: a guide for practitioners. John Wiley & Sons, New York, New York, USA.

Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: the role of species' life histories. Landscape Ecology 7:163-180.

Hanson, H. C. 1954. Criteria of age of incubated mallard, wood duck, and bob-white quail eggs. Auk 71:267-272.

Haramis, G. M. 1990. The breeding ecology of the wood duck: a review. Pages 45-60 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Harvey, W. F., IV, G. R. Hepp, and R. A. Kennamer. 1989. Age determination of female wood ducks during the breeding season. Wildlife Society Bulletin 17:254-258.

Hawkins, A. S., and F. C. Bellrose, Jr. 1940. Wood duck habitat management in Illinois. Transactions of the North American Wildlife Conference 5:392-395.

Hepp, G. R., R. T. Hoppe, and R. A. Kennamer. 1987. Population parameters and philopatry of breeding female wood ducks. Journal of Wildlife Management 51:401-404.

Hepp, G. R., R. A. Kennamer, and W. F. Harvey, IV. 1989. Recruitment and natal philopatry of wood ducks. Ecology 70:897-903.

Hepp, G. R., and R. F. Kennamer. 1992. Characteristics and consequences of nest site fidelity in wood ducks. Auk 109:812–818.

Hester, F. E. 1962. Survival, renesting, and return of adult wood ducks to previously used nest boxes. Proceedings of the Annual Southeastern Association of Game and Fish Commissioners 16:67–70.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analysis of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883–900.

Johnson, D. A., D. W. Sparling, and L. M. Cowardin. 1987. A model of productivity of the mallard duck. Ecological Modelling 38:257–275.

Johnson, F. A., J. E. Hines, F. Montalbano III, and J. D. Nichols. 1986. Effects of liberalized harvest regulations on wood ducks in the Atlantic Flyway. Wildlife Society Bulletin 14:383–388.

Johnson, L. S. 1996. Removal of old nest material from the nesting sites of house wrens: effects on nest site attractiveness and ectoparasite loads. Journal of Field Ornithology 67:212–221.

Kawula, R. J. 1998. Breeding season movements and resource selection of female wood ducks in southern Illinois. Dissertation, Southern Illinois University, Carbondale, USA.

Keith, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs 6.

Kelley, J. R., Jr. 1997. Wood duck population monitoring initiative: final report. Atlantic Flyway Council, Mississippi Flyway Council, U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

King, D. I., R. M. DeGraaf, C. R. Griffen, and T. J. Maier. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? Journal of Field Ornithology 70:257–262.

Kirby, R. E., and L. M. Cowardin. 1986. Spring and summer survival of female mallards from northcentral Minnesota. Journal of Wildlife Management 50:38–43.

Knutson, M. G., and E. E. Klaas. 1997. Declines in abundance and species richness of birds following a major flood on the Mississippi River. Auk 114:367-380.

Knutson, M. G., and E. E. Klaas. 1998. Floodplain forest loss and changes in forest community composition and structure in the upper Mississippi River: a wildlife habitat at risk. Natural Areas Journal 18:138-150.

Knutson, M. G., J. R. Sauer, D. A. Olsen, M. J . Mossman, L. M. Hemesath, and M. J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. Conservation Biology 13:1437-1446.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit. Ecology 52:2-22.

Ladd, W. N., Jr. 1990. Status of wood ducks in the Central Flyway. Pages 121-126 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium, St. Louis, Missouri, USA.

Leonard, J. P., M. G. Anderson, H. H. Prince, and R. B. Emery. 1996. Survival and movements of canvasback ducklings. Journal of Wildlife Management 60:863-874.

Leopold, F. 1951. A study nesting wood ducks in Iowa. Condor 53:209-220.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35: 213-245.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504-1514.

Long, J. S. 1997. Regression models for categorical and limited dependent variables. Sage Publications, Thousand Oaks, California, USA.

Lowney, M. S., and E. P. Hill. 1989. Wood duck nest sites in bottomland hardwood forests of Mississippi. Journal of Wildlife Management 53:378-382.

Major, P. D., and R. L. Hager. 1996. A portable swim-in wood duck trap. Illinois Department of Natural Resources preliminary report, Alton, USA.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-532.

MathSoft. 1997. S-PLUS 4 guide to statistics. Data Analysis Products Division. MathSoft, Seattle, Washington, USA.

McGilvrey, F. B. 1968. A guide to wood duck production habitat requirements. Bureau Sport Fisheries Wildlife, Resource Publication 60. Washington, D.C., USA.

McGraw, J. B., and J. Antonovics. 1983. Experimental ecology of Dryas octopetala ecotypes. Journal of Ecology 71:899-912.

McPherson, R. J., T. W. Arnold, L. M. Armstrong, and C. J. Schwarz. 2003. Estimating the nest-success rate and the number of nests initiated by radio marked mallards. Journal of Wildlife Management 67:843-851.

Mech, L. D. 1983. Handbook of animal radiotracking, University of Minnesota Press, Minneapolis, USA.

Merino, S., and J. Potti. 1995. Pied flycatchers prefer to nest in clean nest boxes in an area with detrimental nest ectoparasites. Condor 97:828-831.

Mielke, P. W., Jr., and K. J. Berry. 2001. Permutation methods: a distance function approach. Springer Verlag, New York, New York, USA.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, New York, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife habitat relationships: concepts and applications. University of Wisconsin Press, Madison, USA.

Nagel, R. E. 1969. Predation on eggs in simulated nests and tree cavity abundance in wood duck nesting habitat. Thesis, Iowa State University, Ames, USA.

Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. Journal of Wildlife Management 46:535-540.

Nichols, J. D., S. L. Stokes, J. E. Hines, and M. J. Conroy. 1982. Additional comments on the assumption of homogenous survival rates in modern bird banding estimation models. Journal of Wildlife Management 46:953-962.

Nichols, J. D., and F. A. Johnson. 1990. Wood duck population dynamics: a review. Pages 83-105 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15:167-175.

Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific northwest. Journal of Wildlife Management 54:18-27.

North, P. M. 1985. A computer modelling study of the population dynamics of the screech owl. Ecological Modelling 30:105-143.

Picman, J. 1988. Experimental study of predation on eggs of ground-nesting birds: effect of habitats and nest distribution. Condor 90:124-131.

Pollock, K. H., and D. G. Raveling. 1982. Assumptions of modern banding-recovery models, with emphasis on heterogenous survival rates. Journal of Wildlife Management 46:88-98.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Prince, H. H. 1965. The breeding ecology of wood duck (Aix sponsa L.) and common goldeneye (Bucephala clangula L.) in central New Brunswick. Thesis, University New Brunswick, Fredericton, Canada.

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

Purcell, K. L., J. Verner, and L. W. Oring. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114:646-656.

Reese, K. P., and J. T. Ratti. 1988. Edge effects: a concept under scrutiny. Transactions of the North American Wildlife and Natural Resource Conference 53:127-136.

Reeves, H. M. 1990. The wood duck: some historical and cultural aspects. Pages 3-12 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Rendell, W. B., and R. J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. Condor 91:875-885.

Rendell, W. B., and N. A. M. Verbeek. 1996. Old nest material in nest boxes of tree swallows: effects on nest-site choice and nest building. Auk 113:319-328.

Ringelman, J. K., and J. R. Longcore. 1983. Survival of female black ducks, *Anas rubripes*, during the breeding season. Canadian Field-Naturalist 97:62-65.

Robb, J. R. 1986. The importance of nesting cavities and brood habitat to wood duck production. Thesis, Ohio State University, Columbus, USA.

Robb, J. R., and T. A. Bookhout. 1990. Female and juvenile wood duck survival and movements in Indiana. Pages 179-184 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Robb, J. R., and T. A. Bookhout. 1995. Factors influencing wood duck use of natural cavities. Journal of Wildlife Management 59:372-383.

Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075-1085.

Robertson, B. A., and R. L. Hutto. 2007. Is selectively harvested forest an ecological trap for olive-sided flycatchers? Condor 109:109-121.

Robertson, P. A., M. D. MacKenzie, and L. F. Elliott. 1984. Gradient analysis and classification of the woody vegetation for four sites in southern Illinois and adjacent Missouri. Vegetatio 58:87-104.

Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and nesting success of migratory birds. Science 267:1987-1990.

Robinson, S. K., and S. F. Morse. 2000. Conservation insights from demographics studies of migratory songbirds in the American Midwest. Pages 225-232 *in* R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, editors. Strategies for bird conservation: the Partners in Flight planning process. Proceedings of the third Partners in Flight workshop. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Rodgers, A. R., and A. P. Carr. 1998. Home range extension users manual. Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

Rogers, A. 1968. Matrix analysis of interregional population growth and distribution. University of California Press, Berkeley and Los Angeles, USA.

Rogers, A. 1985. Regional population projection models. Sage Publications, Beverly Hills, California, USA.

Rohwer, F. C., and M. G. Anderson. 1988. Female biased philopatry, monogamy, and timing of pair formation in migratory waterfowl. Pages 187-221 *in* R. F. Johnson, editor. Current Ornithology, Volume 5. Plenum Press, New York, New York, USA.

Rotella, J. J., and J. T. Ratti. 1992. Mallard brood movements and wetland selection in southwestern Manitoba. Journal of Wildlife Management 56:508-515.

Rothstein, S. I. 1973. The niche-variation model - is it valid? American Naturalist 107:598-620.

Rothstein, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 109:161-176.

Roy Nielsen, C. L., R. J. Gates, and P. G. Parker. 2006. Intraspecific nest parasitism of wood ducks in natural cavities: comparisons with nest boxes. Journal of Wildlife Management 70:835-843.

Roy Nielsen, C. L., R. J. Gates, and E. H. Zwicker. 2007. Projected availability of natural cavities for wood ducks in southern Illinois. Journal of Wildlife Management 71:875-883.

Ryan, D. C. 1995. Breeding Biology of wood ducks nesting in southern Illinois. Thesis, Southern Illinois University, Carbondale, USA.

Ryan, D. C., R. J. Kawula, and R. J. Gates. 1998. Breeding biology of wood ducks using natural cavities in southern Illinois. Journal of Wildlife Management 62:112-122.

Saracco, J. F., and J. A. Collazo. 1999. Predation on artificial nests along three edge types in a North Carolina bottomland hardwood forest. Wilson Bulletin 111:541-549.

Savard, J. P. L., and J. M. Eadie. 1989. Survival and breeding philopatry in Barrow's and common goldeneyes. Condor 91:198-203.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17: 474-480.

Schwegman, J. E. 1973. The natural divisions of Illinois. Illinois Natural Preserves Commission, Rockford, USA.

Selle, A. T. 1998. Annual variation in breeding productivity of natural cavity nesting wood ducks in southern Illinois. Thesis, Southern Illinois University, Carbondale, USA.

Semel, B., and P. W. Sherman. 1992. Use of clutch size to infer brood parasitism in wood ducks. Journal of Wildlife Management 56:495-499.

Simpson, J. W., T. Yerkes, T. D. Nudds, and B. D. Smith. 2007. Effects of habitat on mallard duckling survival in the Great Lakes region. Journal of Wildlife Management 71:1885-1891.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. Midcontinent Ecological Science Center, National Biological Survey, Fort Collins, Colorado, USA.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, New York, USA.

Soulliere, G. J. 1986. Cost and significance of a wood duck nest-house program in Wisconsin: an evaluation. Wildlife Society Bulletin 14:391-395.

Soulliere, G. J. 1988. Density of suitable wood duck nest cavities in a northern hardwood forest. Journal of Wildlife Management 52:86-89.

Stuewer, F. W. 1943. Small entrance to a wood duck nest. Journal of Wildlife Management 7:236.

Stewart, P. A. 1979. Radial dispersal of wood ducks after the nesting season and before fall migration. North American Bird Bander 4:1-3.

Storaas, T. 1988. A comparison of losses in artificial and naturally occurring capercaillie nests. Journal of Wildlife Management 52:123-126.

Suloway, L., and M. Hubbel. 1994. Wetland resources of Illinois: an analysis and atlas. Illinois Natural History Survey Special Publication 15, Springfield, Illinois, USA.

Talent, L. G., R. L. Jarvis, and G. L. Krapu. 1983. Survival of mallard broods in south-central North Dakota. Condor 85: 74-78.

Teels, B. M. 1975. Waterfowl production and utilization along the proposed route of the Tennessee-Tombigbee Waterway. Dissertation, Mississippi State University, Starkville, Mississippi, USA.

Thomas, C. D., and T. M. Jones. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. Journal of Animal Ecology 62:472-481.

Trost, R. E. 1990. Relationship between harvest and survival rates of wood ducks in eastern North America, 1966-84. Pages 367-370 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. Proceedings of the 1988 North American Wood Duck Symposium. St. Louis, Missouri, USA.

Twedt, D. J., and C. R. Loesch. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. Journal of Biogeography 26:1215-1224.

Utsey, F. M., and G. R. Hepp. 1997. Frequency of nest box maintenance: effects on wood duck nesting in South Carolina. Journal of Wildlife Management 61:801-807.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Weddle, C. B. 2000. Effects of ectoparasites on nestling body mass in the house sparrow. Condor 102:684-687.

Werner, P. A., and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipascus sylestris* Huds.). Ecology 58:1103-1111.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 465(Supplement):120-139.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Willebrand, T., and V. Marcström. 1988. On the danger of using dummy nests to study predation. Auk 105:378-379.

Wilson, R. R., and R. J. Cooper. 1998. Acadian flycatcher nest placement: does placement influence reproductive success? Condor 100:673-679.

Wilson, S. E., and C. K. Nielsen. 2007. Habitat characteristics of raccoon daytime resting sites in southern Illinois. American Midland Naturalist 157:175-186.

Wisdom. M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302-312.

Yerkes, T. 2000. Influence of female age and body mass on brood and duckling survival, number of surviving ducklings, and brood movements in redheads. Condor 102:926-929.

Zwicker, E. H. 1999. Availability and use of tree cavities by wood ducks nesting in southern Illinois. Thesis, Southern Illinois University, Carbondale, USA.

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