INFLUENCE OF HABITAT CONDITIONS ON NESTING ACTIVITY OF WOOD DUCKS (AIX SPONSA) IN TREE CAVITIES

A Thesis

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By

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ABSTRACT

Wood duck breeding biology has largely been studied in artificial nest boxes, but environmental influences on nesting biology must be studied in the context within which wood ducks evolved (i.e. natural tree cavities). Previous work suggested that intra- and inter-seasonal changes in abundance of invertebrate foods and/or accessibility of tree cavities may affect nesting season length and the breeding chronology of wood duck hens. This study examined the relationships of intra-seasonal and annual variation in invertebrate food abundance and leaf emergence with nesting chronology, nesting effort, and nest parasitism rates in a southern Illinois' wood duck population that nests in natural cavities. Nest chronology, nesting effort, and parasitism rates were studied during 1994 – 1998 and 2001 – 2002. I modeled wetland conditions with local precipitation and stage of the Mississippi River. Wetland invertebrate food abundance was measured by sweep-net sampling in seasonal and semi-permanent wetlands in 2001 and 2002. Invertebrate sampling was completed during four nesting periods (egg laying, late egg laying/early incubation, incubation/ early hatch, hatch) during 2001 – 2002. Weekly leaf emergence in 2001 and 2002 was measured with a Model-A Spherical Densiometer, from the onset of leaf emergence through the period of maximum upper story leaf coverage. Annual nesting effort of radiomarked hens known to incubate clutches ranged from 42% - 70% throughout the study. Clutch sizes >14 (indicative of nest parasitism) ranged from 8% -

43% during the study and varied inversely with nesting effort. High nesting effort was observed in years with the most stable water levels during egg laying and incubation. Invertebrate biomass did not differ throughout the 2001 ($P = 0.758$) and 2002 ($P = 0.167$) nesting seasons. During hatch, densities in 2002 were 1.7 times higher than egg laying and incubation/early hatch; however did not differ from late egg laying/early incubation ($P = 0.047$). Mean invertebrate densities were not significantly different ($P = 0.869$) during 2001. Two commonly consumed invertebrates known to occur during nest initiation and hatch, *Isopoda* and *Diptera* (primarily *Chironomidae*), were 10.2% and 18.4% more numerous during the egg laying and hatch ($P < 0.01$), respectively. Leaf emergence in floodplain and upland habitats commenced during the week of 13-April in 2001 and 2002. Rates of leaf emergence did not differ between forest types in 2001 ($P = 0.998$) and across-year upland habitat ($P = 0.396$) comparisons. Forest types in 2002 ($P = 0.006$) and across-year floodplain habitat ($P = 0.007$) comparisons were significantly different. Data suggests that hens must arrive early on the breeding grounds in order to build reserves for egg laying when the appropriate invertebrate communities persist at elevated levels and before cavities become concealed in a dense forest canopy.

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CHAPTER 1

INTRODUCTION

Environmental conditions influence nesting activity of wood ducks, however those most relevant include rainfall or flood pulse, food resources, and cavity availability and dispersion (Selle 1999; Drobney and Fredrickson 1985; Bellrose and Holm 1994; Robb and Bookout 1995). Specifically, habitat conditions on breeding grounds have been shown to affect a variety of prairie-nesting waterfowl species throughout their respective breeding seasons (Bluhm 1992). Dry conditions are generally most dramatic under severe drought, where most breeders do not breed at all or emigrate from the area (Rogers 1964). Higher numbers of prairie-nesting ducks, mallards (*Anas platyrhynchos*) and redheads (*Aythya americana*), are forced to abandon established nests (Krapu et al. 1983, Low 1945) or forego additional nesting attempts (Krapu et. al. 1983) when water levels decline during the nesting period. Conversely, wet conditions have the most influence on earlier nesting activity (Krapu et al. 1983) and result in increased nest productivity (Vrtiska and Frederick 1993).

Breeding patterns of waterfowl has caused researchers to ask how habitat conditions are associated with the timing and chronology of nesting. Nest initiation in all avian species may be timed so that the period of maximum nutritional demand coincides with the peak of food abundance (Rowher 1992). Altricial birds may time reproduction so that egg hatching coincides with peak food abundance (Lack 1947, Rowher 1992). Lack (1947) concluded that post-hatch care may limit clutch size in altricial birds, since clutch size does not depend on the female's nutritional status during egg-laying. Therefore, difficulty in feeding altricial young may be a limiting factor in clutch size (Lack 1947). However, precocial birds, like temperate nesting waterfowl, require adequate food availability upon arrival to breeding grounds and during the hatching period for young (Rowher 1992). The process of building reserves for the demanding periods of egg development and incubation by breeding females has been considered the more important variable since young are self-feeding in waterfowl species. Nevertheless, adequate food availability may ultimately direct the timing and chronology of nesting activity in precocial species.

Krapu et al. (1983) mentioned that condition of wetlands on the breeding grounds of waterfowl can have substantial effects on the availability and abundance of nutritional resources, like aquatic invertebrates (Krapu 1981, Drobney and Fredrickson 1985). The timing of drought was found to directly affect the availability of invertebrate communities for breeding blue-winged teal (Swanson et al. 1974). On the contrary, the presence of water on the breeding grounds may also impact overall nesting strategies (Vrtiska and Frederick 1993, Selle 1999). Therefore, access to resources during periods of extreme or severe habitat conditions may be influencing nesting chronology.

Wood duck are opportunistic foragers, but they are seasonally dependent on invertebrates for protein acquisition during egg-laying (Bellrose and Holm 1994). Hens prefer to forage for invertebrates in shallow (i.e. ≤ 20 cm) seasonal wetlands during egg-laying (Drobney 1990). Seasonal dependence on invertebrates is facilitated by "moving territories" that allow hens to respond to unpredictable spatial and temporal shifts in aquatic invertebrate populations. If a sudden increase in water depth dilutes preferred or familiar feeding sites, then the availability of invertebrates in seasonal wetlands may take several days to become available to laying hens. Therefore, the social adaptation of moving territories is crucial for wood duck hens because the search for protein ultimately regulates the depletion rate of fat reserves, critical during incubation (Drobney and Fredrickson 1985).

Visibility of suitable nest sites may also influence reproductive chronology in cavity-nesting ducks. Dense leaf cover has been considered as a possible limiting factor in natural cavity-dependent species (Snyder 1977, Semel and Sherman 1995). Robb and Bookhout (1995) suggested that cavity visibility, as well as availability, are primary limitations in cavity selection and use by wood ducks. However, Zwicker (1999) found shorter nesting seasons in cavity-nesting wood ducks despite the abundance of suitable cavities. Cavity- nesting wood ducks selected forest with higher basal areas, possibly to increase their chances of finding available suitable cavities (Robb and Bookhout 1995, Yetter et al. 1999). Zwicker (1999) also found hens in floodplain forested habitats may be selecting suitable nest cavities with lower nest site visual obstruction.

Research has invariably recognized the relationship between habitat condition and nesting strategies. The importance of breeding experience, age, nest site availability and visibility, and population density (Bellrose et al. 1964, Heusmann 1975, Semel et al. 1988, Eadie and Fryxell 1992, Hepp and Kennamer 1993, and Eadie et al. 1998) should be recognized when considering the effect of habitat conditions, particularly with regard to wood duck breeding strategies. Wood ducks exhibit four alternative nesting strategies (Clawson et al. 1979): (1) laying and incubating their own clutch, (2) parasitizing nests, (3) parasitic laying followed by incubating their own clutch, or (4) foregoing nesting altogether (Clawson et al. 1979, Sayler 1992, and Bellrose and Holm 1994). Vrtiska and Frederick (1993) found brood sizes of wood duck hens were larger during a flood year, suggesting that parasitism rates may have been higher during periods of adverse habitat conditions. Furthermore, Semel and Sherman (1995) found that more concealed nest boxes had more stable, moderate rates of parasitism, increased egg hatchability, similar reproductive success, and shorter nesting seasons.

Selle (1999) suggested that wood duck hens alter reproductive strategies during years of large spring flood events. Primary evidence remains in the correlation found between annual rates of nest parasitism, 8-43%, and nesting effort, 40-72% (Selle 1999) during variable annual flood pulses. Sudden rises in water level (> 1m in < 1 week) were associated with decreased nesting effort and increased intraspecific nest parasitism (Selle

1999). Although high water levels create more abundant shallow areas, they may deepen previously used feeding sites. Consequently, newly flooded areas may require several days to develop invertebrate populations that are necessary for protein and calcium requirements of egg-laying and incubating hens (Drobney 1982). Alternatively, Zwicker (1999) has discounted limited nest site availability as an influence on nesting effort. However, tree cavity visibility in floodplain habitats was higher in percent visual obstruction between used than unused.

Previous empirical and anecdotal evidence suggests that nesting activity could be a function of both variation in limited invertebrate food abundance in shallow wetlands due to fluctuating water levels and nest accessibility due to increasing visual obscurity. As a result, wood ducks may alter the timing, onset, and termination of reproduction in response to difficulty in locating abundant macro-invertebrates and suitable nest sites. The primary goal of my study was to understand how the availability of food resources influences the wood duck nesting chronology. Secondarily, understanding that many factors may influence a breeding wood duck population, it seemed apparent to understand how visual obstruction may influence a cavity nesting population. I addressed these goals by examining two fundamental questions. (1) How does invertebrate food abundance change throughout the nesting season? I hypothesized that invertebrate food abundance would be greatest during egg-laying, the period of maximal nutritional demand for breeding wood duck populations. (2) How does the timing of leaf emergence relate to nesting chronology? I hypothesized that the onset of leaf emergence would coincide with the decline in nest initiation; potentially acting as one limiting factor in the duration and timing of nest initiation. (3) How does the timing and magnitude of flood pulses (i.e. water levels) relate to nesting effort (e.g. breeding propensity and nest parasitism)? I hypothesized that large fluctuation in water levels during egg-laying would be inversely related to the proportion of hens that incubate nests and positively related to nest parasitism rates.

In order to address my research questions, I have incorporated nest chronology, productivity, breeding propensity, and parasitism data collected in 1994 – 1998 and 2001 - 2002 by Ryan (1996), Selle (1999), Zwicker (1999), Roy et. al (2006), and Gates (unpublished). All data were collected at Union County Conservation Area (CA), LaRue-Pine Hills Research Natural Area (RNA), and Oakwood Bottoms in 1994 – 1997, Union County CA and LaRue-Pine Hills RNA in 1998, and Union County CA in 2001 - 2002.

CHAPTER 2

STUDY AREA AND METHODS

STUDY AREA

The study area consisted of 6,089 ha of Mississippi River floodplain and adjacent upland forest, including LaRue-Pine Hills Research Natural Area (RNA), Union County CA and adjacent Shawnee National Forest (SNF) in Jackson and Union Counties, Illinois. General study area boundaries were defined by nest locations of radio-marked wood duck hens during 1993-1997 (Zwicker 1999) and included both upland and floodplain habitats.

LaRue-Pine Hills RNA (2,289 ha) included the Mississippi River bluff line that separates floodplain habitat (LaRue Swamp) from the adjacent upland forest (Pine Hills). Dominant tree species in the floodplain were oaks (*Quercus spp*.) and hickories (*Carya spp*.) (Zwicker 1999). Upland areas were predominantly red oak (*Quercus rubra*), black oak (*Quercus velutina*), white oak (*Quercus alba*) and hickory. Other important cavity producing tree species in both areas included American sycamore (*Platanus occidentalis*) and American beech (*Fagus grandifolia*).

Union County CA (3,800 ha) has been managed to provide migration and wintering habitat for waterfowl, primarily Canada Geese (*Branta canadensis*). Numerous temporary, seasonal, semi-permanent, and permanent wetlands were distributed across the Mississippi River floodplain. Approximately 39% of the area was cultivated at Union County CA, the remaining area consisted primarily of lowland forest (33%) and wetlands (28%) (IDNR, 2000). Common tree species included cottonwood (*Populus deltoides*), sweetgum (*Liquidambar styraciflua*), American sycamore, American beech, and maples (*Acer spp.*) (Zwicker 1999). The adjacent SNF was characterized by rolling hills, ridgetops, and steep bluffs. Hickory and oak dominated much of the forests, however, past logging has allowed the growth of various species such as beech, maple, and sycamore.

METHODS

Capture and radiomarking

Female wood ducks were captured with portable and permanent swim-in traps on Union County CA. Hens were captured and handled in accordance with Animal Care Protocols at The Ohio State University (00A0001). All hens were banded with a serially numbered No. 5 U.S. Fish and Wildlife Service aluminum leg bands. Radio-transmitters (7.5 - 9.0 g) were attached to Herculite (Herculite Products, York, Pennsylvania, USA) fabric bibs (Montgomery 1985) and placed on laying hens. Hens were radio-marked from 4 April – 8 May 2001 and 14 March – 13 May 2002. In 2001 and 2002, female reproductive condition was determined by examining the cloaca. Hens with measurements of the cloaca opening ≥ 10 mm in diameter were considered laying hens.

Radio-marked females were followed with VHF telemetry equipment and hand-held Yagi antennas (Mech 1983) to confirm nesting activity throughout the breeding season or until the transmitters expired. Hens were located throughout the day, commencing at sunrise through 17:00-18:00 hours, until nesting behavior was confirmed. Tracking was most intensive in the morning hours when most egg laying activity occurs (Clawson et al. 1979, Bellrose and Holm 1994). A visual contact was made with birds when possible or movement had ceased for >3 days. These hens were then flushed, tracked to nest trees, or their radios were recovered. Radio-marked hens were located at least 2 times per week until completion of breeding season.

Nesting ecology

Brood surveys. -- Field surveys and incidental sightings of wood duck broods concurrent with other field activities were conducted throughout the breeding season. Sightings commenced at sunrise and terminated at sunset. Records were kept on duckling age class (Gollop and Marshal 1954), minimum brood size, place of sighting, and adult presence.

Nesting effort and radio telemetry.-- Nesting effort was determined by classifying the proportion of non-migrant radio-marked hens that remained alive on the study area during the nesting season and were tracked to a suitable nest tree. Radio-marked hens determined as migrants, radio failures, or hens that died before or during the nesting season were not included in nesting effort calculations**.** Nesting effort was not calculated in 2001 and 2002, since radio transmitters were placed on hens believed to be depositing eggs [>10mm cloaca measurement]. Radio-marked hens remaining >3 days in the same tree were considered to be active nesting hens. Trees used by radio-marked hens were climbed to confirm the presence and fate of a nest attempt. Nesting attempts were considered successful upon finding the presence of hatched egg shell and membranes or by later brood observation. Unsuccessful nesting attempts included visually destroyed or unhatched eggs, hens found with an abbreviated incubation period and no brood, or post-incubation movement patterns different from successful hens. Radio-marked hens were tracked through June during all years to detect late or second nesting attempts.

Nest site and clutch data.-- Approximately 50 known tree cavities were located and considered safe to climb. These trees were located by random plot survey, incidental observations, and following radio-marked hens (Ryan et al. 1998, Zwicker 1999, Roy et al. 2006). Climbable nest trees were given three separate designations: (1) tree cavities used by currently radiomarked hens, (2) tree cavities used in prior project years, and (3) those discovered incidentally during other field activities. Hereafter these nest types will be respectively referred to as new, reclimbed, and incidental. However, reclimbed and incidental nests have been combined for analysis.

All known nest trees were accessed using ropes and tree ascenders, or when necessary, tree spikes. Records of clutch size and hatch date were collected during all years. Rates of nest success were recorded through multiple visits (i.e. 30 days) to each nest tree in 2001 and 2002. Abandoned or partially predated clutches were taken for embryo dissection (Bellrose and Holm 1994) to determine, more accurately, the date of nest initiation. Clutch sizes of >14 eggs were considered to have been parasitized nests (Semel and Sherman 1992).

Back-dating procedure.-- Nesting chronology was determined by backdating from the observed brood ages acquired during observational surveys (Bellrose and Holm 1994). Brood ages were estimated from the midpoints of duckling ages at the beginning and end of each plumage subclass (Bellrose and Holm 1994). Dates of nest initiation were back-dated using brood age, an additional 30 days for incubation, and 12 days for egg laying (Bellrose and Holm 1994). A quartile distribution of nest initiation dates was constructed based on the observed brood's plumage class in all years. Similar procedures were used in 2001 and 2002 for determining new and reclimbed nesting chronologies. Data from successive re-climbs or via radio telemetry on particular nest events was used to determine exact or mid-point chronology dates for abandoned or predated clutches, when possible. All backdating procedures used 1 day for each egg recorded in the known clutch size (Bellrose 1980). Knowledge of clutch sizes < 12 eggs (Semel and Sherman 1992), days of incubation, and precise hatch dates were used to more precisely determine nest initiation dates.

Habitat Conditions

Water Levels.-- Water depths were measured by Selle (1999) in 10 semi-permanent and 10 seasonally flooded wetland forests, according to the National Wetlands Inventory (NWI), at Union County CA during 1996 and 1997. All measurements were taken in flooded wetland forest transects known to be used by breeding wood ducks (Kawula 1998, Ryan 1996). The measured water depths from the Mississippi River stage and local precipitation were used to model water depths on transects at Union County CA. River stage from the Mississippi River (1 km west of Union County CA) was obtained from the gauging station at Thebes, Illinois. (U.S. Geological Survey, unpublished). Local precipitation was obtained from the Anna/Jonesboro Water Treatment Plant (13 - 15 km east of Union County CA) in Jonesboro, Illinois. The mean weekly stages of the Mississippi River and local precipitation were calculated for input into water level models.

Multiple linear regression was used to develop a statistical model to relate surface water depths of wetlands on Union County CA to daily local precipitation levels and river stage. A cumulative weekly average of measured water depths was calculated from transects located on semi-permanent and forested seasonal wetlands at Union County CA. Regression models for each year were cross-validated using local precipitation and river stage data from the other year. The final model was chosen based on the coefficient of determination (R^2) and measured water depths relative to the 95% confidence interval of predicted water levels. Total variance (s^2) and flood pulses of >15 cm in < 2 weeks each year were used to characterize variation in water levels during the nesting period. Annual range of water fluctuation and weekly pulses were calculated within the nesting period. The nesting period was defined as the period of time that encompassed 90 – 95 % of all breeding hens. The best model was used to quantify changes in water levels for 1993 – 1998 and 2001 – 2002.

Invertebrate Sampling.-- Invertebrate samples were collected weekly from 9 April – 6 June 2001 and 16 March – 17 May 2002 on 4 (Figure 2.1) and 7 wetlands (Figure 2.2), respectively, where Selle (1999) monitored water-levels. Sampling was conducted with a sweep net in water depths of ≤ 30 cm (Drobney 1990), using a net size of 1,500 cm^3. Samples were collected by scraping the wetland bottom with one net stroke, holding the net rim flush against the bottom, then quickly pulling the net upward through the water column. A second sample was taken up-wind, 15 - 20 m, avoiding the disturbed area from the first sample. Sampling was conducted in close proximity to the previous week's location to minimize spatial variability, due to weekly water level fluctuation. Samples were preserved in 70% percent ethanol and appropriately labeled.

Sorting of invertebrates from organic debris was facilitated by staining each sample with rose bengal stain at a concentration of 100mg/L (Mason and Yevich 1967). Samples were stained for 24 hours to enhance the stain coloration of invertebrates, and then strained through #5 and #60 sieves, respectively. Larger twigs, wood, stems, and leaves were inspected and removed from invertebrate samples. Invertebrates were removed from debris and preserved in 70% percent ethanol. Samples were subsampled for composition by classifying 100 invertebrates to the level of Phylum, Class, Order, or Family. The level of classification varied with the importance of invertebrates encountered and known to occur in the diet of breeding wood duck hens (Bellrose and Holm 1994, Drobney and Frederickson 1979). Weekly percent occurrence was determined by averaging together both samples within each wetland. Weekly samples were classified according to the nesting activity during the period of collection based on the overall nesting chronology (1994 – 1998, 2001 – 2002).

Samples were oven dried at 60 ^{o}C and weighed until constant dry mass (24 – 48 hr) to the nearest microgram (μg). The total sample biomass and density for each wetland was calculated by averaging the two collected samples. The weekly mean biomass was used to calculate weekly mean densities (weight * volume) within each wetland. Based on the nesting chronology (2001 – 2002), weekly samples were pooled according to four different nesting periods of collection. These nesting periods were classified as egg laying, late egg laying/early incubation, incubation/early hatch, and hatch.

Differences in mean invertebrate biomass and density among nesting activity periods within 2001 and 2002 were determined using 2–way Analysis of Variance (ANOVA). Significant differences were separated using the Ryan-Einot-Gabriel-Welsch

(REGWQ) Multiple Range Test (SAS 1990). The same procedure was used to determine differences in mean biomass and density between nesting periods in 2001 and 2002.

The variation in mean percent occurrence of knowingly important invertebrate groups within each year was identified using 2–way ANOVA. Significant differences were separated using the REGWQ Multiple Range Test.

Leaf Emergence.-- Weekly leaf emergence in 2001 and 2002 was measured with a Model-A Spherical Densiometer, from the onset of leaf emergence through the period of maximum upper story leaf coverage. Habitats that did not contain suitable tree cavities (agricultural land, open water, or forest clearcuts <50 years old) were not sampled. Five selected floodplain and upland sites were measured within the study boundaries in 2001 (Figure 2.1). Readings were taken on ten selected floodplain and upland sites in 2002 (Figure 2.2). All readings were taken at a 1 m height, recording the average rate of leaf emergence in the canopy from each of four cardinal directions. Readings were plotted as percent visual obstruction emerged in weekly increments over the course of the breeding season.

A simple linear regression analysis, with data transformation, was used to compare daily rate of change in leaf emergence. Leaf emergence values were transformed with the following odds ratio equation: TEMERGE = (EMERGE / 1 - EMERGE); where TEMERGE = transformed leaf emergence value, EMERGE = actual percent of leaf emergence. Linearization of transformed values were compared using a simple linear regression analysis to determine whether differences existed between 2001 upland and floodplain habitats, 2002 upland and floodplain habitats, 2001 and 2002 upland habitats, and 2001 and 2002 floodplain habitats. Daily rate of change in leaf emergence was estimated from the slope coefficient for julian date. The slope can be interpreted as the daily rate of change in the rate of leaf cover to non-leaf cover (e.g. odds ratio).

Data analysis.-- Statistical Analysis System (SAS Institute 1990) and R (R Development Core Team 2006) were used to perform all statistical tests. All tests were considered statistically significant at $P \leq 0.05$.

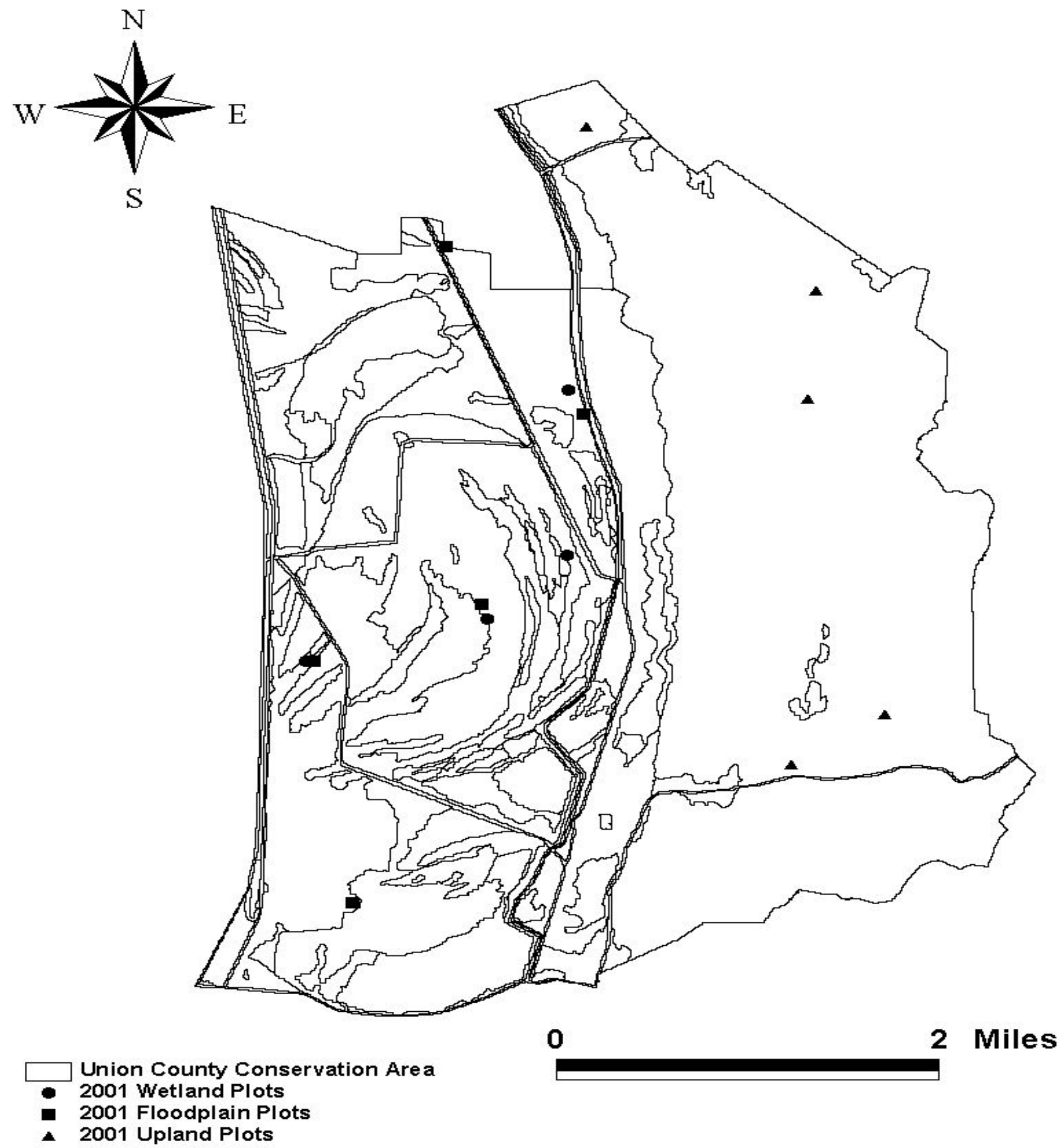


Figure 2.1. Locations of wetland invertebrate sampling and floodplain and upland leaf emergence study plots at Union County Conservation Area in southern Illinois during 2001.

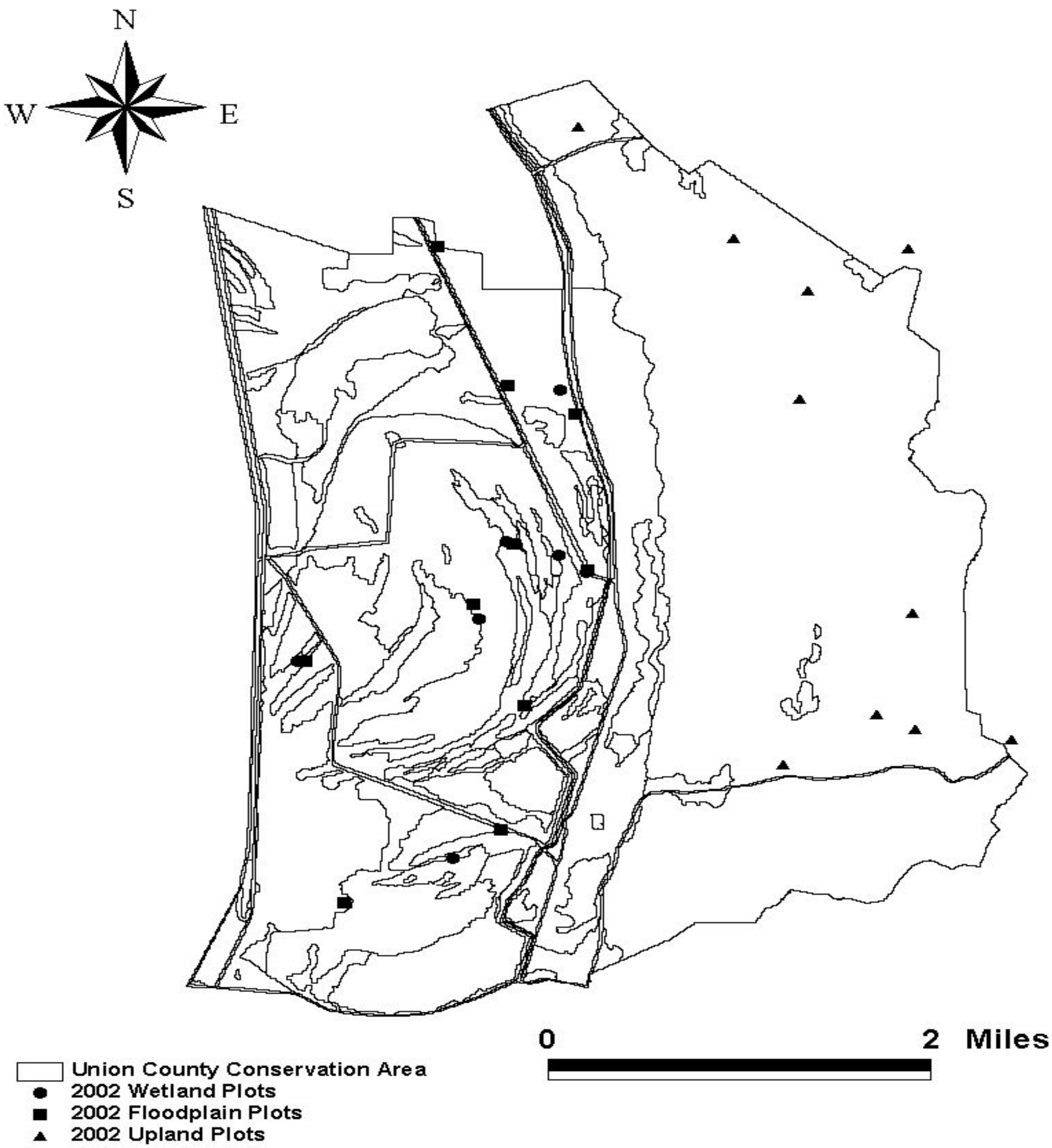


Figure 2.2. Locations of wetland invertebrate sampling and floodplain and upland leaf emergence study plots at Union County Conservation Area in southern Illinois during 2002.

CHAPTER 3

RESULTS

CAPTURE AND RADIO-MARKING

Radio-transmitters were placed on 42 hens (30 adult, 12 juveniles) in 1994, 52 hens (41 adults, 11 juveniles) in 1995, 45 hens (29 adults, 16 juveniles) in 1996, 51 hens (35 adults, 16 juveniles) in 1997, 46 hens (28 adults, 18 juveniles) in 1998, 14 hens (11 adults, 3 juveniles) in 2001, and 31 hens (27 adults, 4 juveniles) in 2002. Radio-marked hens were captured within 57 (1994), 53 (1995), 48 (1996), 56 (1997), 42 (1998), 34 (2001), and 60 (2002) days. Trapping in 1994 – 1995 and 1998 was completed in < 2 months. Hens were trapped over a period > 2 months in 1996 – 1997 and 2001 – 2002. Twelve hens were radio-marked in multiple years from 1993 – 1998 and 2001 – 2002.

NEST CHRONOLOGY

Reclimbed and incidental nest trees

Hens nesting in previously used cavities during 2001 and 2002 initiated nests over 112 and 103 days, respectively. Nest initiation ranged from 9 March – 20 May in 2001 (n = 15) and 3 March – 8 May in 2002 (n = 13). Incubation encompassed 21 March - 30 May in 2001 (n = 15) and 13 March – 19 May in 2002 (n = 13). Hatch ranged from 20 April – 29 June in 2001 (n = 6) and 30 April – 14 June in 2002 (n = 7).

Brood Observation

The nesting season (first egg laid - last egg hatched) based on brood observation ranged from 91 days in 1994 and 142 days in 1998 (Table 3.1). Nests were initiated between 49 days in 1994 and 100 days in 1998. The stages of nest initiation (Figure 3.1) and hatch (Figure 3.2) during 2001 and 2002 demonstrated peaks similar to 1994 – 1998. Nest initiation peaked on the week of 31 March, during all years (Figure 3.3).

Radio-marked hens

Radio-marked hens nested over a period of 77 days (30 March – 15 June) in 2001 to 126 days (16 March – 20 July) in 1996. Females initiated nests during 5 March – 9 June during 1994 – 1998 and 2001 – 2002. Nest initiation ranged from 18 March – 29 May in 2001 – 2002 (n = 37). The chronology of incubation spanned 28 March – 8 June in 2001 – 2002 (n = 35). The hatching chronology ranged from 1 May – 4 July in 2001 - 2002 (n = 20). More than 99 % of radio-marked hens nested within the observed dates of nest initiation from brood observation during all years (Figure 3.4).

Radio-marked hens (0 of 76) were not found to initiate multiple nest attempts during 1993 – 1998 (Selle 1999, Gates unpublished), however I did detect re-nesting attempts in 5 of 9 hens (56%) after failed nest attempts in 2001 – 2002. All five hens nested within the same habitat type (floodplain or upland).

Twelve individual hens were radio-marked in more than one year. Nine of 12 hens (75%) were found with a nest in at least two years. Eight of the nine hens (89%)

were found within the same habitat type. One nesting hen was known to have occupied the same tree cavity in consecutive years. Of the three remaining hens, there were two juveniles and one adult. The two juveniles did not nest in their first year, but nested as adults. The other adult hen was never found with a nest.

Chronologies of brood observations, reclimbed nest trees, and radio-marked hens when combined, spanned 91 – 142 days from 1994 – 1998 and 2001 – 2002.

NESTING EFFORT AND PARASITISM

Ninety-seven of 235 hens were confirmed to have nested in 1994 – 1998 (Table 3.2). Nesting efforts ranged between 42% - 70%; while rates of parasitism ranged from 8% - 43% during 1994 – 1998 and 2001 – 2002 (Figure 3.5). Although nesting effort was not calculated in 2001 – 2002, nest attempts were confirmed in 35 of 45 hens (78%).

HABITAT CONDITIONS

Water Levels

The following three models developed to predict water depths at Union County CA were:

Equation 1 - 1996; $Y = -20.7627 + 1.2555\ X_1 + 1.0191\ X_2$,

Equation 2 - 1997; $Y = -10.8831 + 0.8254\ X_1 + 0.1503\ X_2$,

Equation 3 - Combined 1996/1997; $Y = -19.3758 + 1.1345\ X_1 + 1.3428\ X_2$,

where Y = predicted water depth, X_1 = weekly mean Mississippi River Stage at Thebes,

X_2 = weekly total precipitation at Jonesboro, Illinois. The R^2 values were 0.93, 0.93, 0.88 for respective equations 1, 2, and 3.

Validation was completed on all three models. The 1996 and 1997 models were cross-validated with the other year's precipitation and river stage data. A 95 % C.I. for the 1996 model contained 22% of the measured water depths in 1997. A 95% C.I. for the 1997 model contained 44% of the 1996 measured water depths. Although a cross-validation could not be completed on the combined year model, 83% of the measured water depths in 1996 and 1997 were within the 95% confidence interval (Figure 3.6). The combined year model was selected due to a R^2 and the results of the model validation.

Annual Comparisons.-- The predicted water depths at Union County CA demonstrated the annual occurrence of flood pulses throughout the period of nest initiation during 1994 – 1998 and 2001 – 2002 (Figure 3.7). Variance of weekly mean water measurements during egg laying and incubation stages (depicted by mean quartile distribution of known nesting hens) were used to characterize how wetland fluctuation influences the wood duck's breeding season (Figure 3.8). Water depths appeared most variable in 1994 (s^2 = 47.33), 1996 (s^2 = 64.19), and 2002 (s^2 = 55.42) when compared to 1995(s^2 = 27.82), 1997 (s^2 = 7.14), 1998 (s^2 = 27.03), and 2001 (s^2 = 11.21). The 1994 and 1996 nesting seasons demonstrated water pulses of >15 cm in < 2 weeks (Table 3.3). Of the annual flood events occurring when hens were initiating nests in all years, the magnitude of flood events was greatest in 1994, 1996, and 2002.

Invertebrate sampling

Pooled data within nesting season collection periods (egg laying, late egg laying/early incubation, incubation/early hatch, hatch) showed no deviation in mean invertebrate biomass and density in 2001 and 2002 ($P > 0.05$). No difference was detected in between year comparisons of 2001 and 2002 individual nesting season periods for mean invertebrate biomass ($P = 0.12$ - .0.69) or densities ($P = 0.13 – 0.95$). Mean invertebrate biomass during nesting season collection periods ranged from 0.661 – 0.099 µg in 2001 ($F_{2,17} = 0.28$, $P = 0.76$) and 0.062 – 0.100 µg in 2002 ($F_{3,65} = 1.74$, $P = 0.17$) (Figure 3.9). Similarly, mean invertebrate densities during nesting season periods (0.0791 – 0.110µg/cm^3) showed no significant difference in 2001 ($F_{2,17} = 0.14$, $P = 0.87$) (Figure 3.10). However, mean invertebrate densities between nesting periods differed in 2002 ($F_{3,65} = 2.79$, P = 0.05) (Figure 3.10). Densities in 2002 during hatch were 1.7 times higher than egg laying and incubation/early hatch; however did not differ with late egg laying/early incubation.

Invertebrate food items with notable mean percent occurrence throughout 2001 (Figure 3.11) and 2002 (Figure 3.12) collection periods were *Copepoda*, *Cladocera*, *Isopoda*, *Diptera*, *Oligocheta*, and *Ostracoda*. Other notable food items present in samples across 2001 – 2002 included *Amphipoda*, *Nematoda*, *Pulmonata* (*Planorbidae*, *Physidae*, unidentified), *Conchostraca*, and *Coleoptera* (larval and adult). Of the 6 invertebrate food items, only *Cladocera* and *Oligocheta* had a significant difference in mean percent occurrence (P = 0.02, 0.01, respectively) throughout the nesting season periods. *Cladocera* and *Oligocheta* were at least 19.8% and 5.5% more abundant during incubation/early hatch and late egg/early incubation, respectively. Except for extrapolating trends, sample size may not be adequate for a meaningful statistical comparison during 2001. Most notable taxa in 2001 during late egg-laying/early incubation included *Copepoda* and *Isopoda*; while *Diptera* and *Ostracoda* were most prevalent during hatching. A significant difference in *Copepoda, Isopoda, Diptera, Oligocheta, Ostracoda* ($F_{3, 65}$ = 14.83, 6.79, 10.62, 10.51, 6.84, P < 0.01, respectively) was measured in mean percent occurrence across the nesting season collection periods during 2002. *Copepoda* and *Isopoda* were 27.9% and 10.2%, respectively, more numerous during the egg-laying than the hatch ($F_{3, 65}$ = 14.83, 6.79, P < 0.01). Contrarily, *Oligocheta* and *Diptera* (primarily *Chironomidae*) species were 22.8% and 18.4%, respectively, most prevalent during hatch compared to egg-laying ($F_{3, 65}$ = 10.62, 10.51, P < 0.01). Ostracoda were at least 2 times more numerous during late egg-laying/early incubation than other nesting season periods ($F_{3, 65}$ = 6.84, P < 0.01).

Leaf Emergence

Leaf emergence in floodplain and upland habitats commenced during the week of 13-April in 2001 (Figure 3.13) and 2002 (Figure 3.14). Leaf-on in both years was > 90% complete by 5 – May in both years. The percent leaf emergence surpassed 25% and 50% in floodplain and upland habitats during the weeks of 13-April and 20-April in 2001, respectively. However, the percent of leaf emergence in 2002 exceeded 25% and 50% in the both habitats during the week of 27-April.

The following regression models predict the rate of leaf emergence at Union County CA:

Equation 1 – Upland – Y = 1.1674 X – 126.86

Equation 2 – Floodplain – Y = 0.7308 X – 77.34

Equation 3 – 2001 – Y = 0.8278 X – 87.57

Equation 4 – 2002 – Y = 1.0583 X – 115.43

where Y = transformed leaf emergence value, and X = julian date. R^2 values were 0.91, 0.96, 0.94, 0.84, respectively.

The comparison between 2001 floodplain (0.75) and upland (0.90) habitats demonstrated similar rates of leaf emergence (0.15 daily rate of change in odds ratio, $F_{10,11} = 0.131$, $P = 1.00$); however rate of leaf emergence in 2002 upland (1.37) habitat was significantly faster than 2002 floodplain (0.74) habitat (0.63 daily rate of change in odds ratio, $F_{10,11} = 5.16$, $P < 0.01$). A difference in the rate of leaf emergence in the 2001 and 2002 upland habitats was not detected (0.46 daily rate of change in odds ratio, $F_{10,11} = 1.17$, $P = 0.40$); but between year comparison of floodplain habitats demonstrated a significant difference in the rate of leaf emergence (0.01 daily rate of change in odds ratio, $F_{10,11} = 5.00$, $P < 0.01$).

Nesting Season	Julian Date: Nest Initiation Start - End	Julian Date: Incubation Start - End	Julian Date: Hatch Start - End	Length of Nesting Season (Days)	Broods Observed
1994	76 – 125	88 – 137	118 - 167	91	59
1995	59 – 144	71 – 156	101 - 186	127	70
1996	67 – 128	79 – 140	109 - 170	103	102
1997	59 – 132	71 – 144	101 - 174	115	103
1998	52 – 152	64 – 164	94 - 194	142	108
2001	51 – 110	63 – 122	93 - 152	101	10
2002	50 – 122	62 – 134	92 - 164	114	46

Table 3.1. Duration of wood duck nesting dates as determined by aging broods (1994 – 2002) and re-climbing known nest trees (2001 – 2002) at Union County Conservation Area and LaRue Swamp Research Natural Area in southern Illinois during springs of 1994 – 2002. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

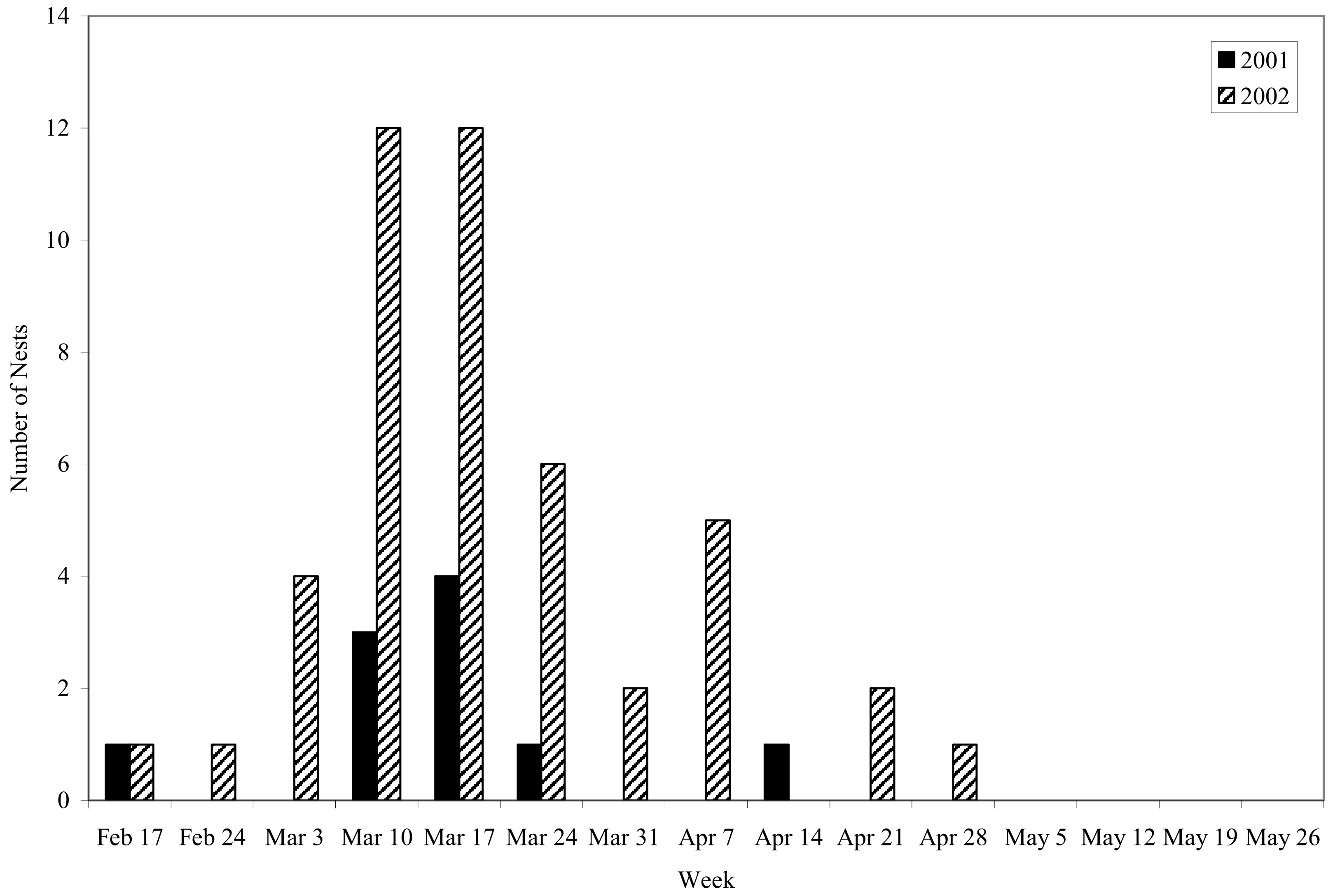
Hen Fate	Total 1994 No.	1994 %	1995 No.	1995 %	1996 No.	1996 %	1997 No.	1997 %	1998 No.	1998 %	2001 No.	2001 %	2002 No.	2002 %	All Years No.	All Years %
Nested	12	29	24	46	14	30	23	45	24	52	12	86	24	77	133	47
Resident, no nest	13	31	15	29	19	42	10	19	16	35	1	7	2	6	76	27
Migrant	6	14	10	20	9	20	9	18	4	9	-	-	-	-	38	14
Died	6	14	2	4	3	7	4	8	2	4	1	7	1	3	19	7
Radio-failed/lost	5	12	-	-	-	-	5	10	-	-	-	-	3	10	13	5
Unknown	-	-	-	-	-	-	-	-	-	-	-	-	1	3	1	0
Total	42	100	51	100	45	100	51	100	46	100	14	100	31	100	280	100

Table 3.2. Fates (no.,%) of wood duck hens radio-marked at Union County Conservation Area, Oakwood Bottoms Greentree Reservoir, and LaRue Pine Hills Research Natural Area during springs 1994 - 1998 and 2001 – 2002. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

Nesting Season	Range (cm)	Variance (s^2)	Coefficient of Variation (%)	2 Wk Maximum Water Pulse (cm)	1 Wk Maximum Water Pulse (cm)	Nesting Effort (%)	Nest Parasitism (%)
1994	17.40	47.33	43.12	16.24	11.43	48	43
1995	12.31	27.82	66.53	10.96	8.31	63	18
1996	23.97	64.19	141.80	22.16	13.23	42	31
1997	7.42	7.14	14.93	7.40	3.80	70	8
1998	17.60	27.03	27.98	9.95	6.01	60	14
2001	11.59	11.21	28.44	6.46	6.90	-	8
2002	25.10	55.42	85.80	11.03	6.35	-	23

Table 3.3. Characterization of yearly water fluctuations in relationship to the nesting wood duck hens (>90% of laying hens) at Union County Conservation Area using the combined year model.

Figure 3.1. Weekly distribution of nests initiated by wood ducks on Union County Conservation Area (2001 - 2002) in southern Illinois by observing wood duck broods. Data are based on range midpoints of estimated hatch dates based on plumage classes recorded when broods were observed during spring breeding seasons.



2001
2002
Number of Nests
0
2
4
6
8
10
12
14
Feb 17
Feb 24
Mar 3
Mar 10
Mar 17
Mar 24
Mar 31
Apr 7
Apr 14
Apr 21
Apr 28
May 5
May 12
May 19
May 26
Week

Figure 3.2. Weekly distribution of hatched nests by wood ducks on Union County Conservation Area (2001 – 2002) in southern Illinois by observing wood duck broods. Data are based on range midpoints of estimated hatch dates based on plumage classes recorded when broods were observed during spring breeding seasons.

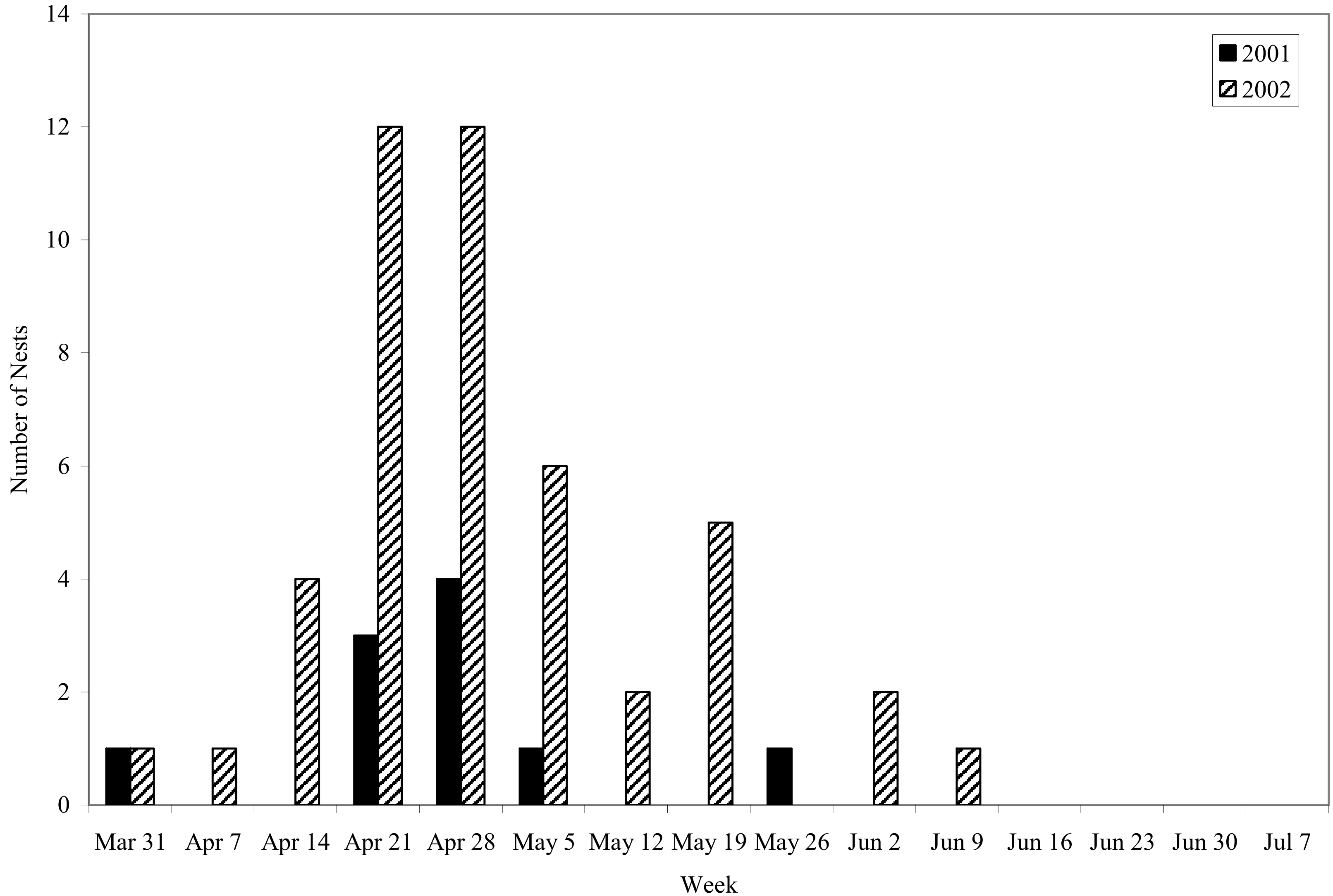

14
12
10
8
6
4
2
0
Number of Nests
2001
2002
Mar 31
Apr 7
Apr 14
Apr 21
Apr 28
May 5
May 12
May 19
May 26
Jun 2
Jun 9
Jun 16
Jun 23
Jun 30
Jul 7
Week

Figure 3.3. Weekly distribution of nests initiated by wood ducks on Union County Conservation Area (1994 – 1998 and 2001 – 2002) and LaRue-Pine Hills Research Natural Area (1994 – 1998) in southern Illinois by observing wood duck broods. Data are based on range midpoints of estimated hatch dates based on plumage classes recorded when broods were observed during spring breeding seasons. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

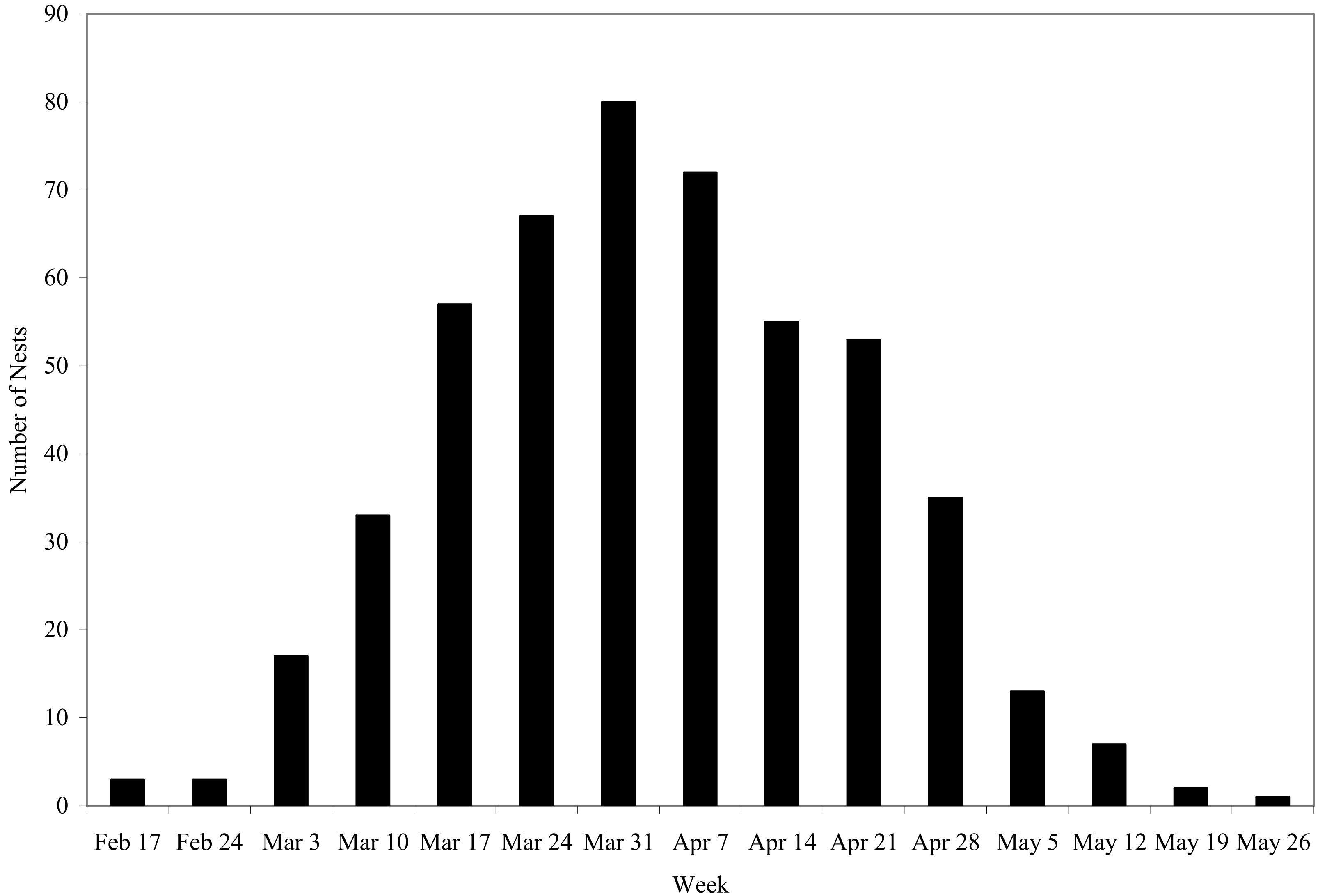

90
80
70
60
50
40
30
20
10
0
Number of Nests
Feb 17
Feb 24
Mar 3
Mar 10
Mar 17
Mar 24
Mar 31
Apr 7
Apr 14
Apr 21
Apr 28
May 5
May 12
May 19
May 26
Week

Figure 3.4. Frequency distribution of nest initiation dates by week for radio-marked wood duck hens and brood observation at Union County Conservation Area (1994 – 1998 and 2001 – 2002) and LaRue-Pine Hills Research Natural Area (1994 – 1998) in southern Illinois. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

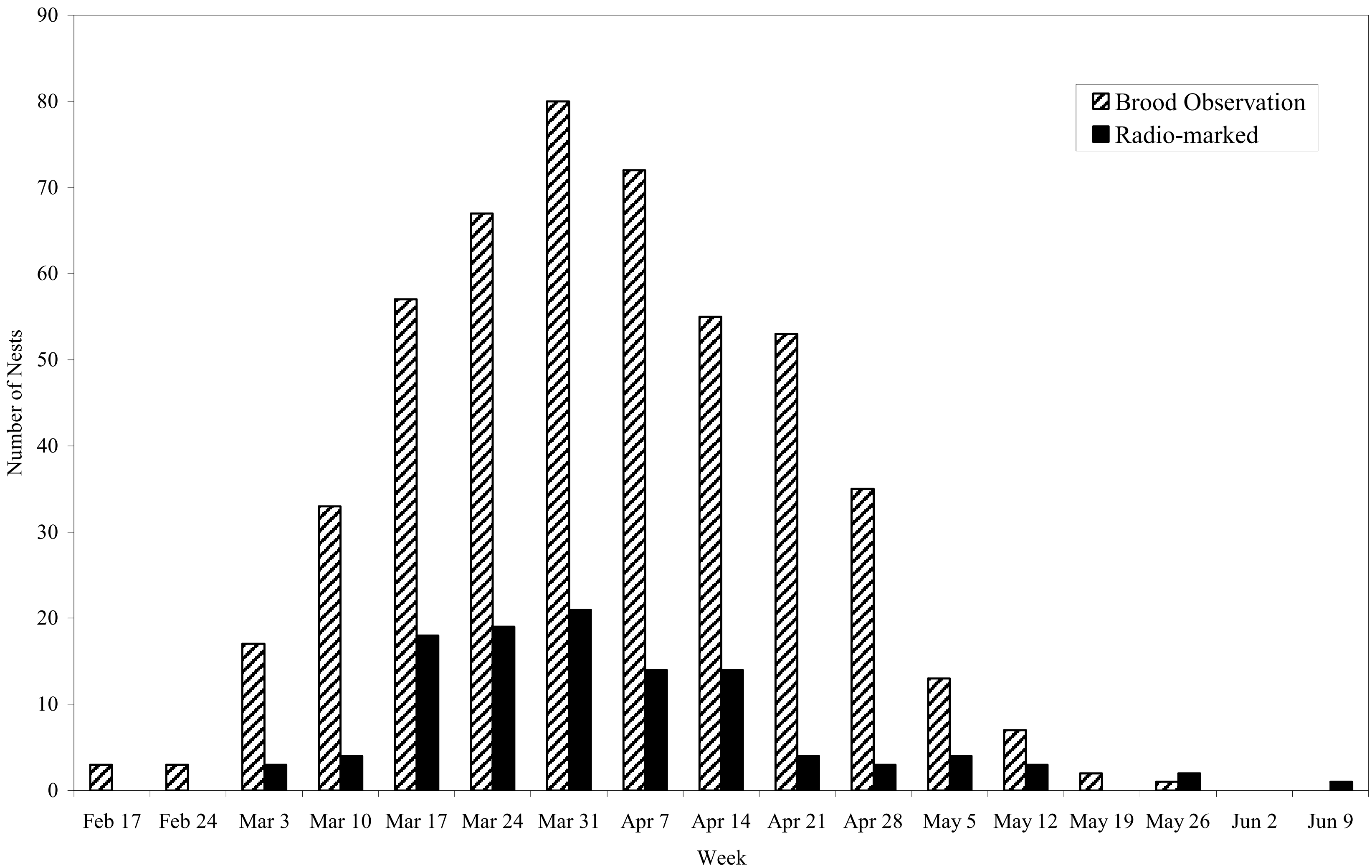
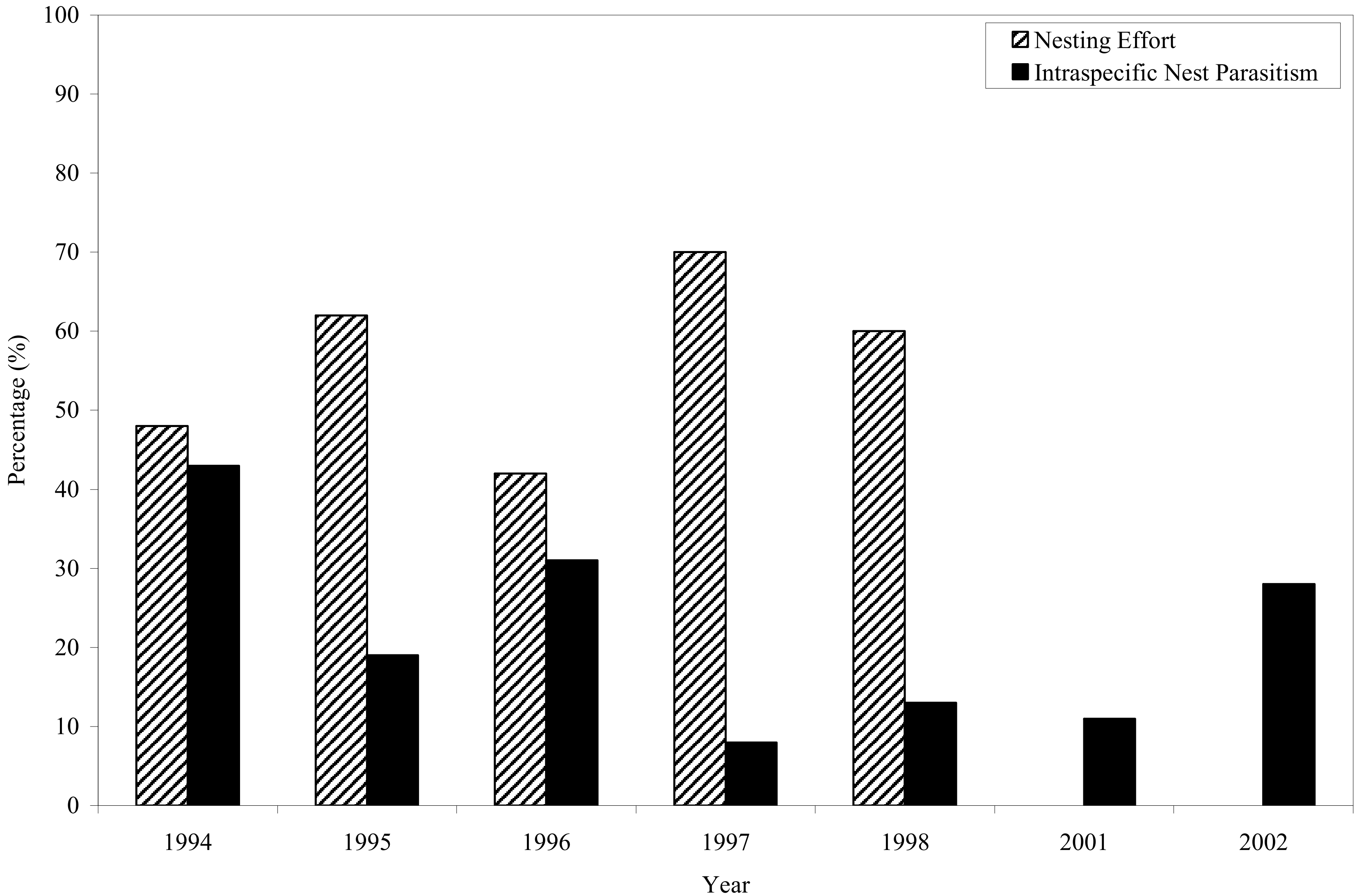

Brood Observation
Radio-marked
Number of Nests
0
10
20
30
40
50
60
70
80
90
Feb 17
Feb 24
Mar 3
Mar 10
Mar 17
Mar 24
Mar 31
Apr 7
Apr 14
Apr 21
Apr 28
May 5
May 12
May 19
May 26
Jun 2
Jun 9
Week

Figure 3.5. Rates of nesting effort and intraspecific nest parasitism at Union County Conservation Area (1994 – 1998 and 2001 – 2002) and LaRue-Pine Hills Research Natural Area (1994 – 1998) in southern Illinios. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).


Nesting Effort
Intraspecific Nest Parasitism
Percentage (%)
100
90
80
70
60
50
40
30
20
10
0
1994
1995
1996
1997
1998
2001
2002
Year

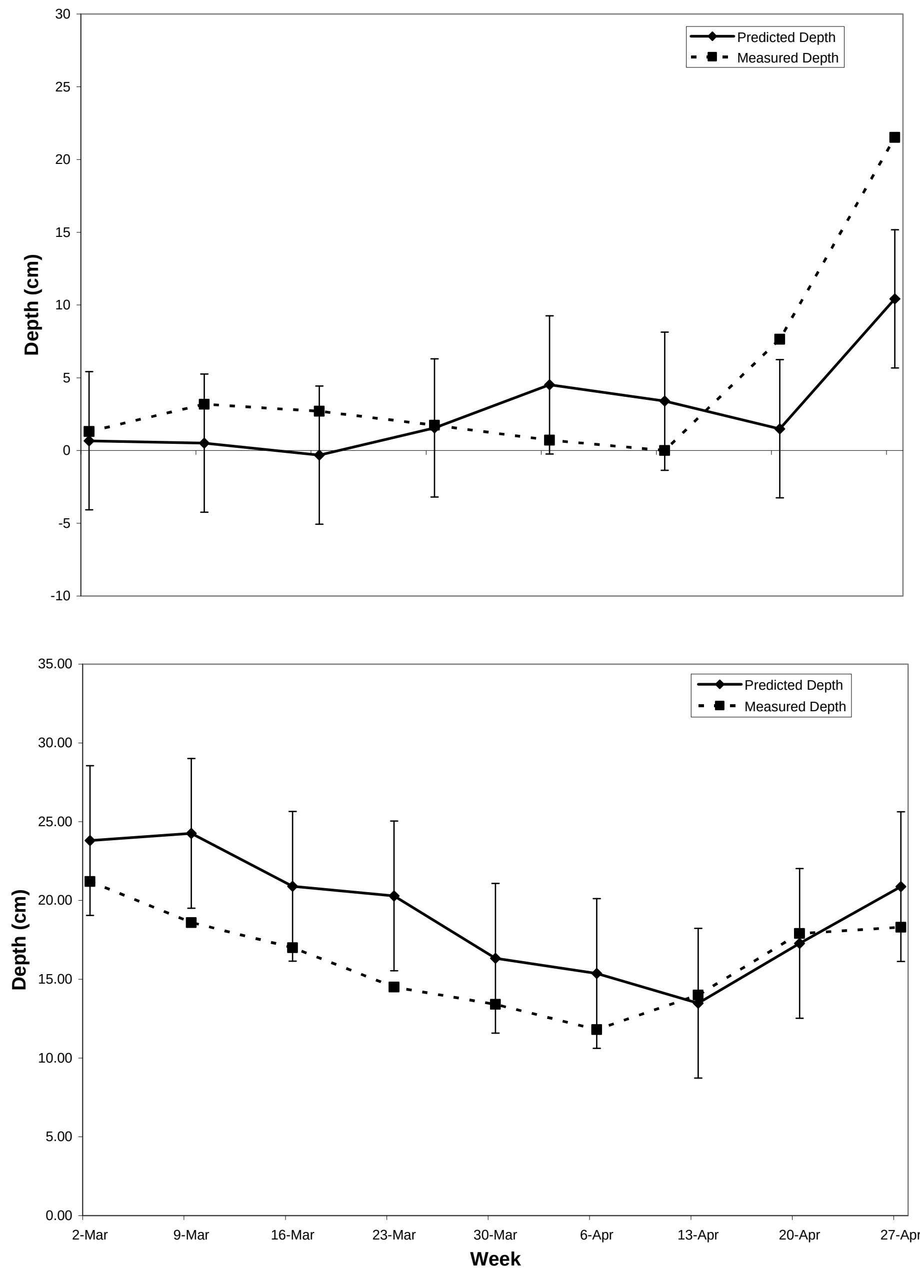
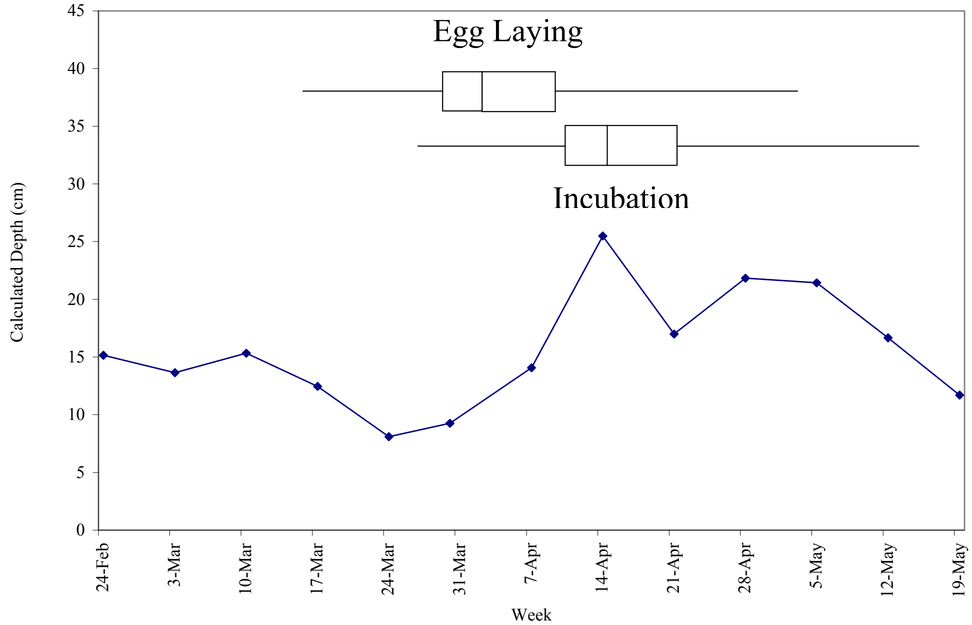


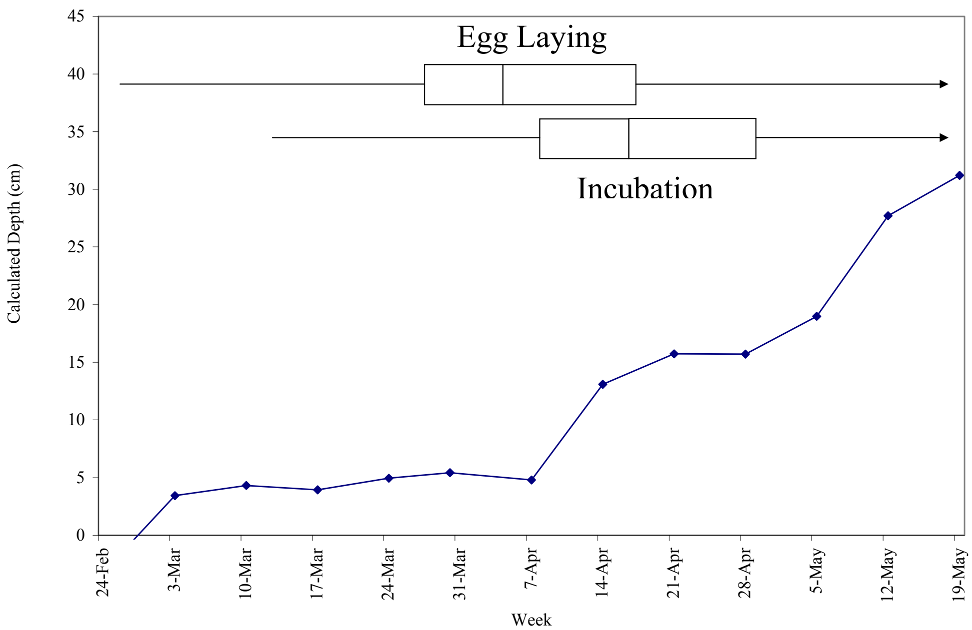
Figure 3.6. Validation of predicted mean water depths using a combined year regression model on transects with seasonal and semi-permanent forested wetlands at Union County Conservation Area in southern Illinois during 1996 (top) and 1997 (bottom).

Figure 3.7. Predicted mean water depths in relation to the spring breeding season of wood duck hens at Union County Conservation Area in southern Illinois during 1994 – 1998 and 2001 – 2002. Egg laying and incubation (depicted by mean quartile distribution) were determined from back-dated ages of broods observed at Union County Conservation Area (1994 – 1998, 2001 – 2002) and LaRue Swamp Research Natural Area (1994 – 1997) in southern Illinois. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

1994



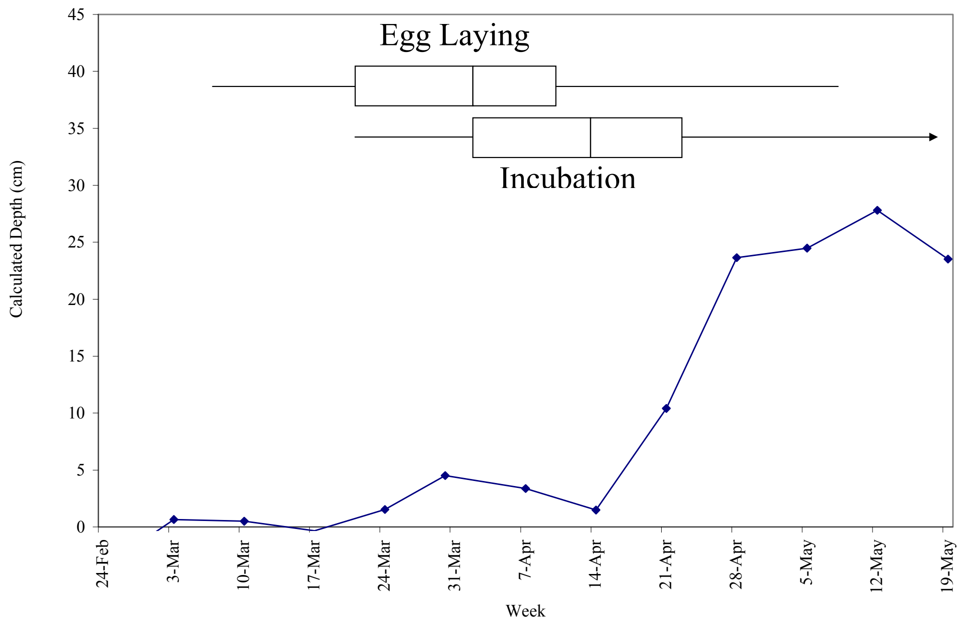
1995



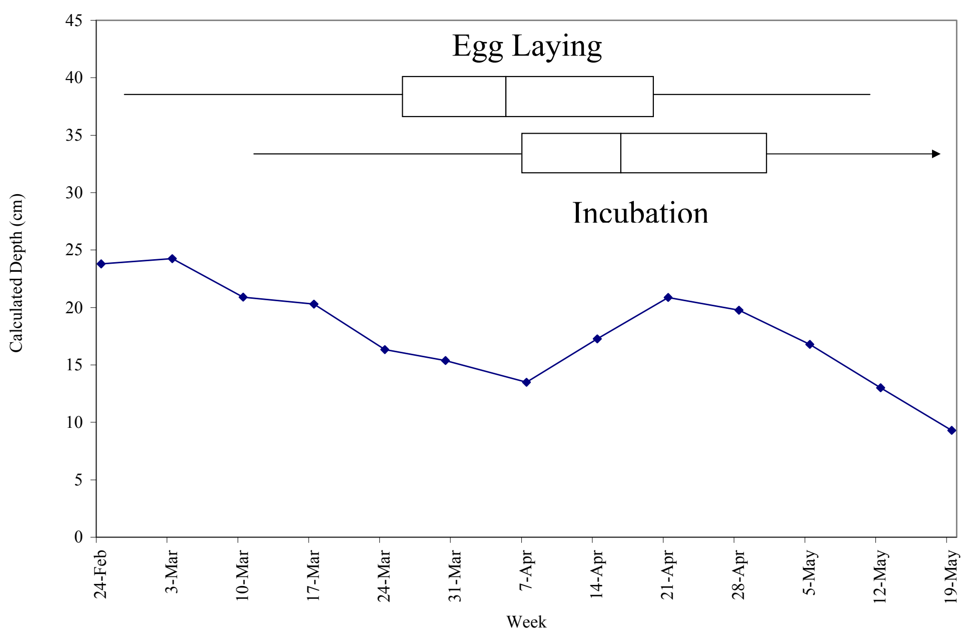
(Continued)

Figure 3.7: Continued

1996

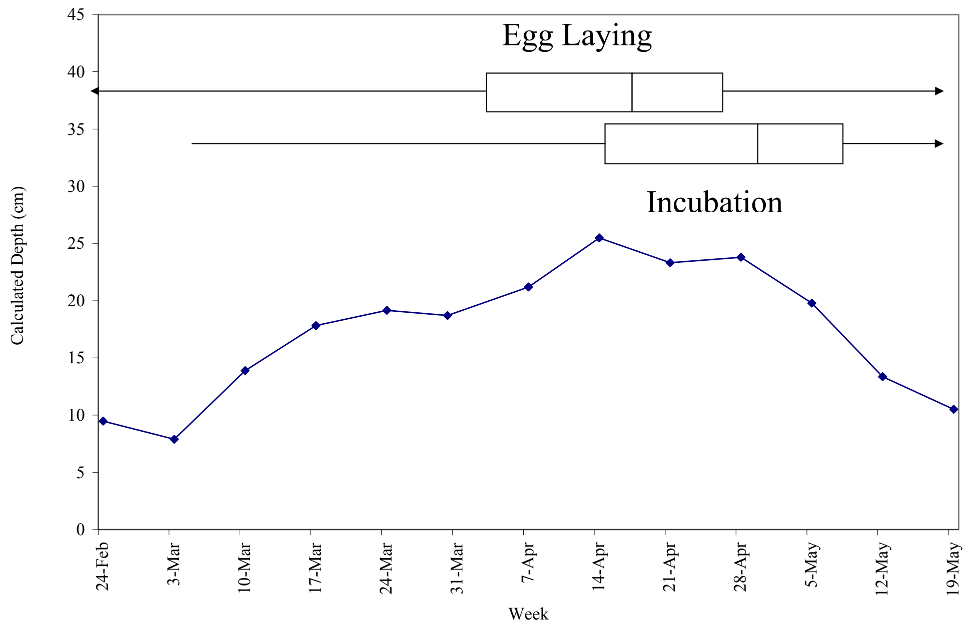


1997

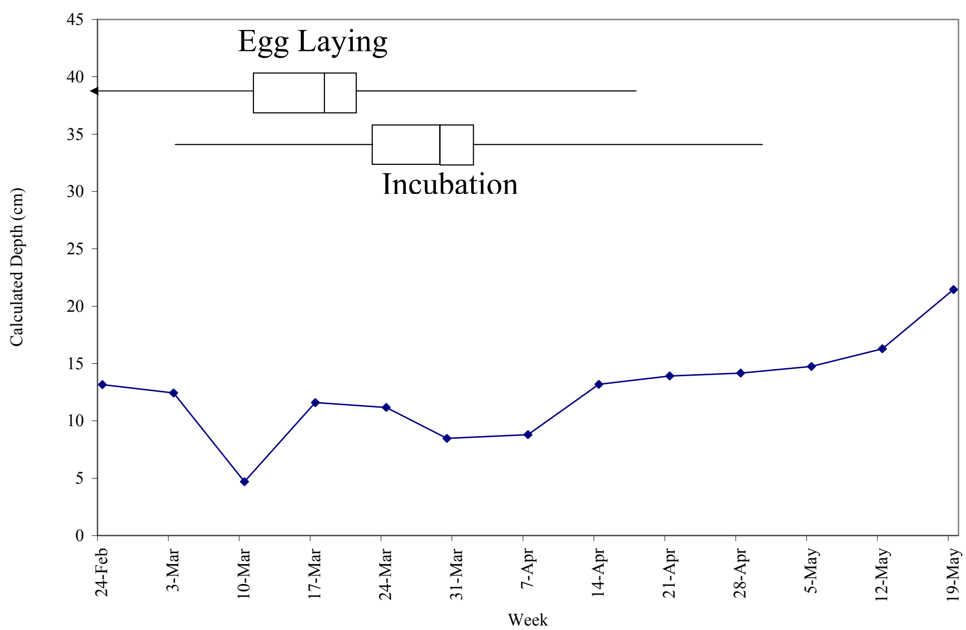


(Continued)

Figure 3.7: Continued 1998



2001



(Continued)

Figure 3.7: Continued

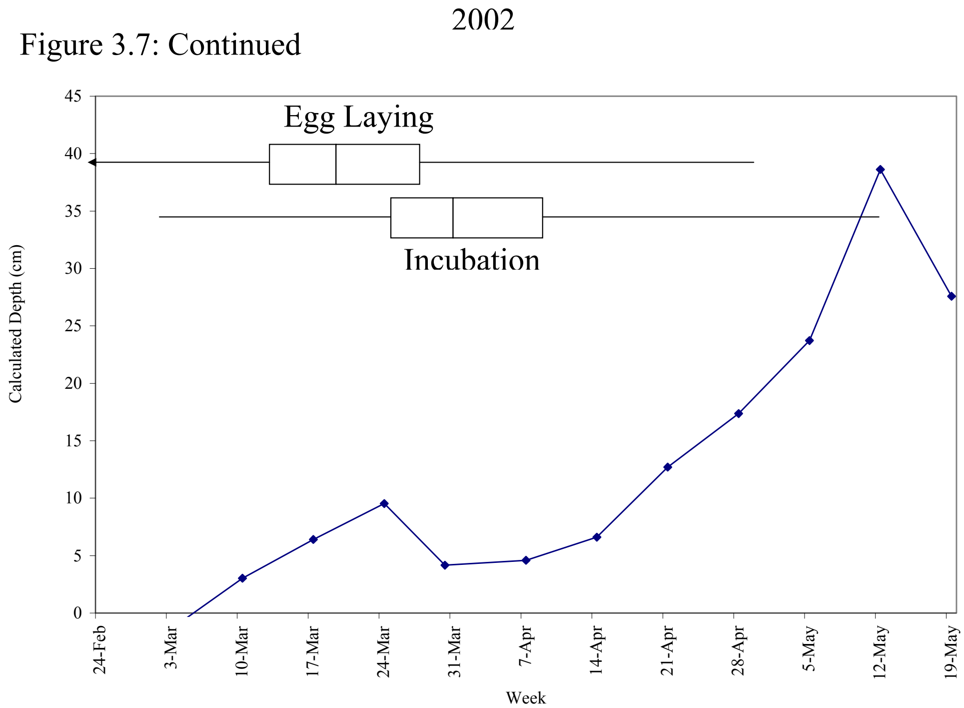


Figure 3.8. Variance of weekly mean predicted water depths and timing of flood pulses in relation to nesting wood ducks hens observed through brood surveys at Union County Conservation Area (1994 – 1998 and 2001 – 2002) and LaRue Swamp Research Natural Area (1994 – 1998) in southern Illinois. Data from 1994 – 1998 was collected by Ryan (1996), Selle (1999), Zwicker (1999), and Gates (unpublished).

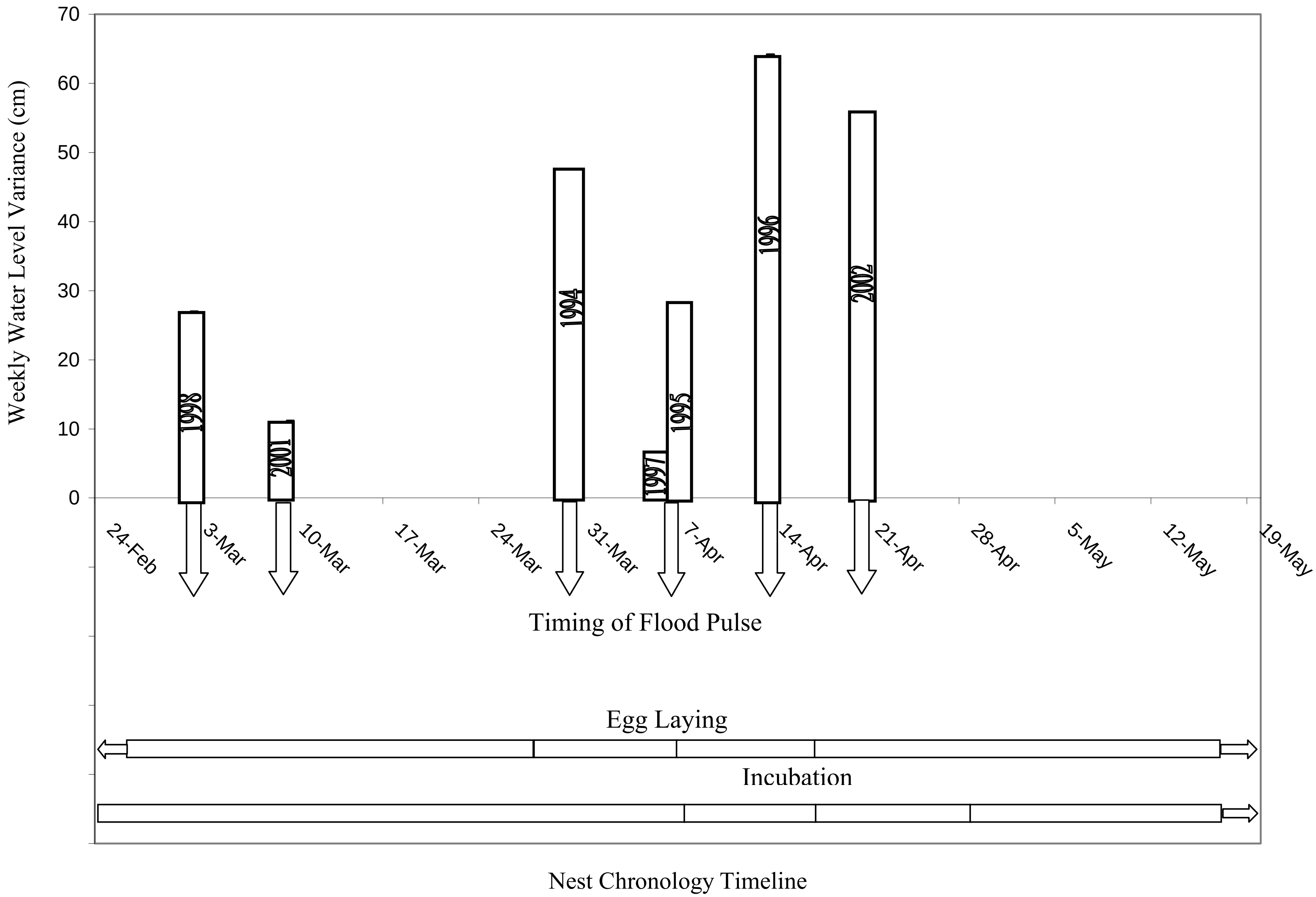
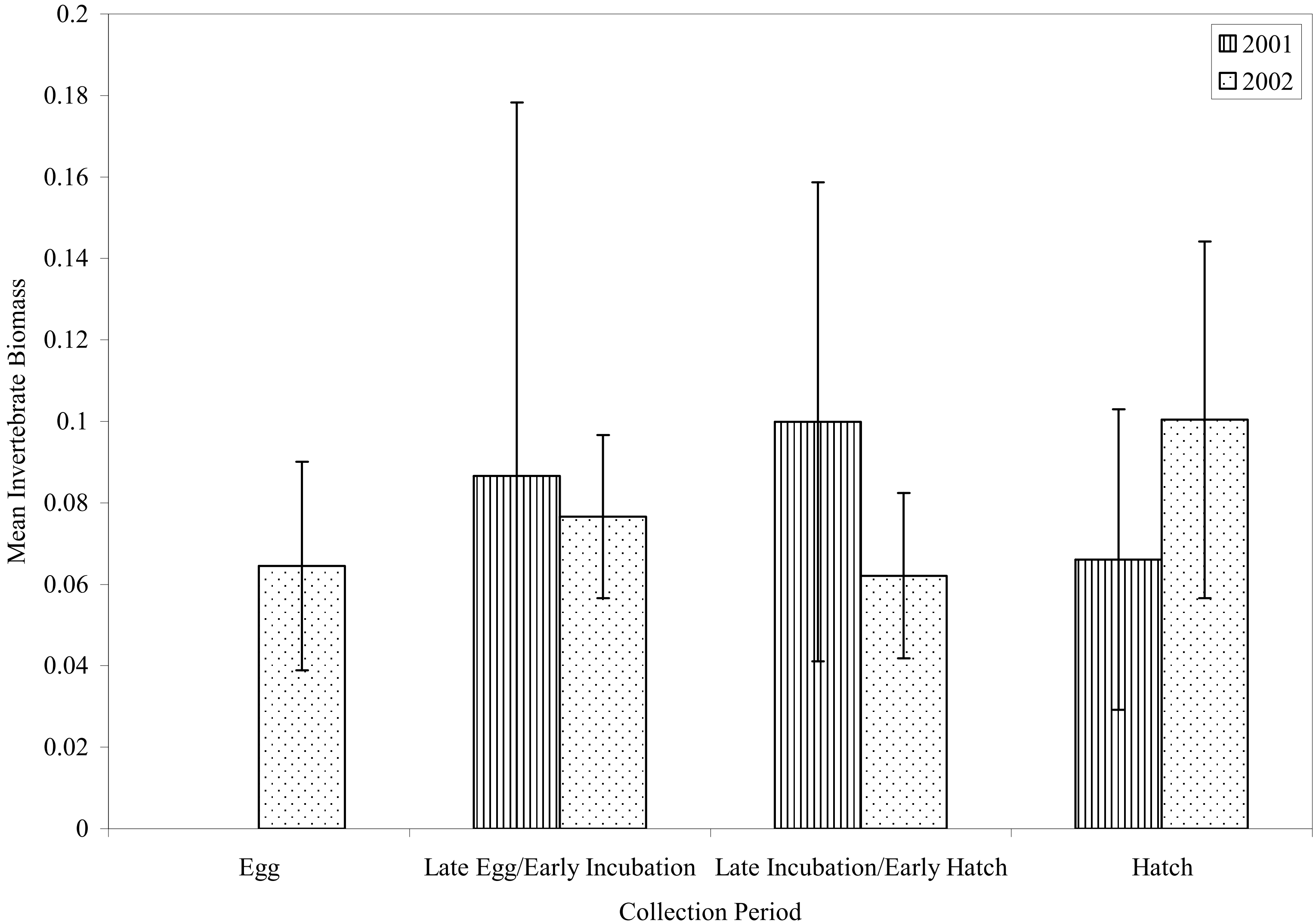
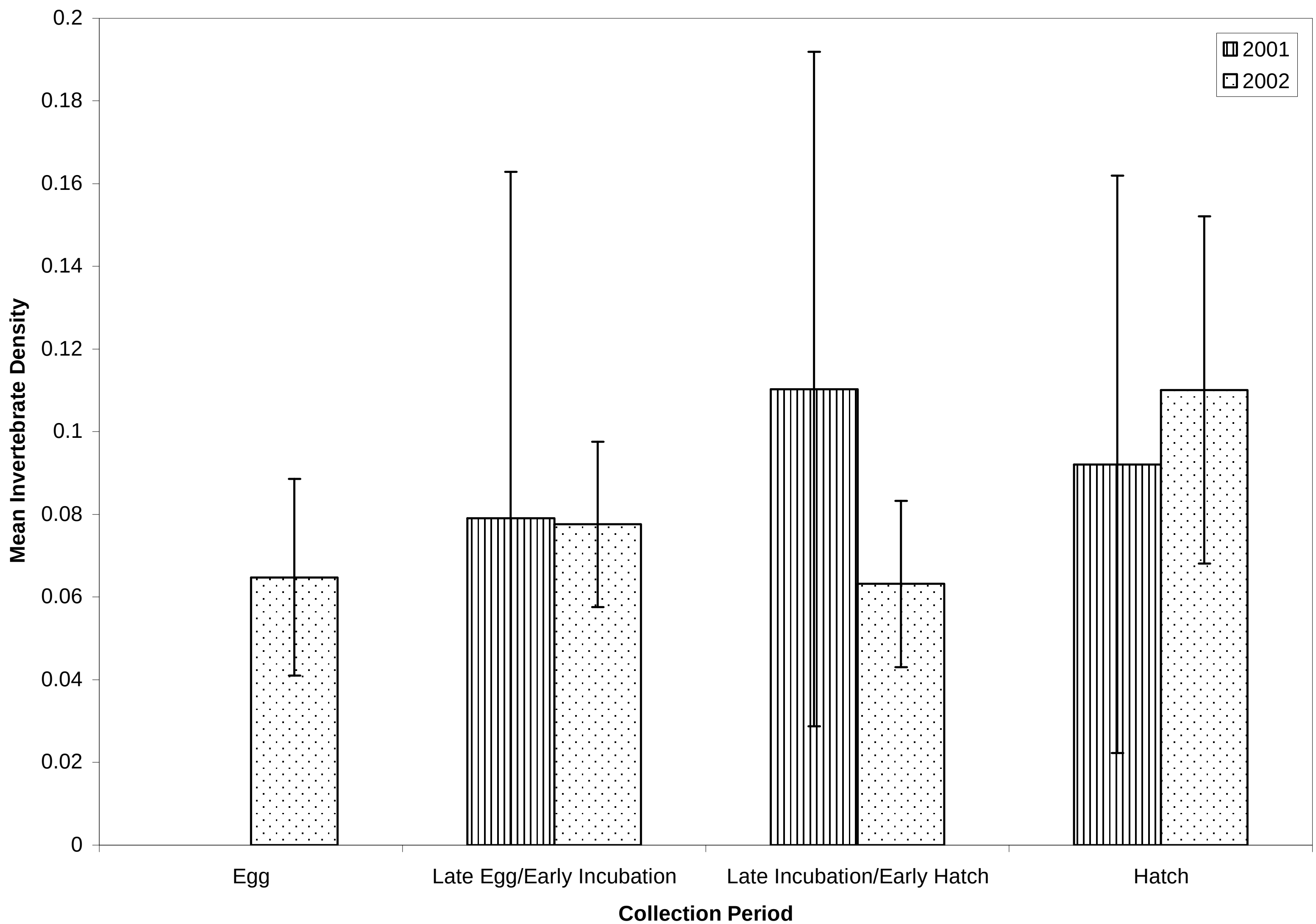

Weekly Water Level Variance (cm)
70
60
50
40
30
20
10
0
1998
2001
1994
1997
1995
1996
2002
24-Feb
3-Mar
10-Mar
17-Mar
24-Mar
31-Mar
7-Apr
14-Apr
21-Apr
28-Apr
5-May
12-May
19-May
Timing of Flood Pulse
Egg Laying
Incubation
Nest Chronology Timeline

Figure 3.9. Mean biomass (95% C.I.) of invertebrate species during 2001 - 2002 in relation to periods of the nesting season as determined by brood observations completed on Union County Conservation Area (2001 - 2002) in southern Illinois.



0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Mean Invertebrate Biomass
2001
2002
Egg
Late Egg/Early Incubation
Late Incubation/Early Hatch
Hatch
Collection Period

Figure 3.10. Mean density (95% C.I.) of invertebrate species during 2001 - 2002 in relation to periods of the nesting season as determined by brood observations completed on Union County Conservation Area (2001 - 2002) in southern Illinois.



Mean Invertebrate Density
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
2001
2002
Egg
Late Egg/Early Incubation
Late Incubation/Early Hatch
Hatch
Collection Period

Figure 3.11. Mean percent occurrence of invertebrate species during 2001 in relation to periods of the nesting season as determined by brood observations completed on Union County Conservation Area (2001 - 2002) in southern Illinois. Significant differences in mean percent occurrence of invertebrate food items, determined by REGWQ analysis, were denoted by a letter change.

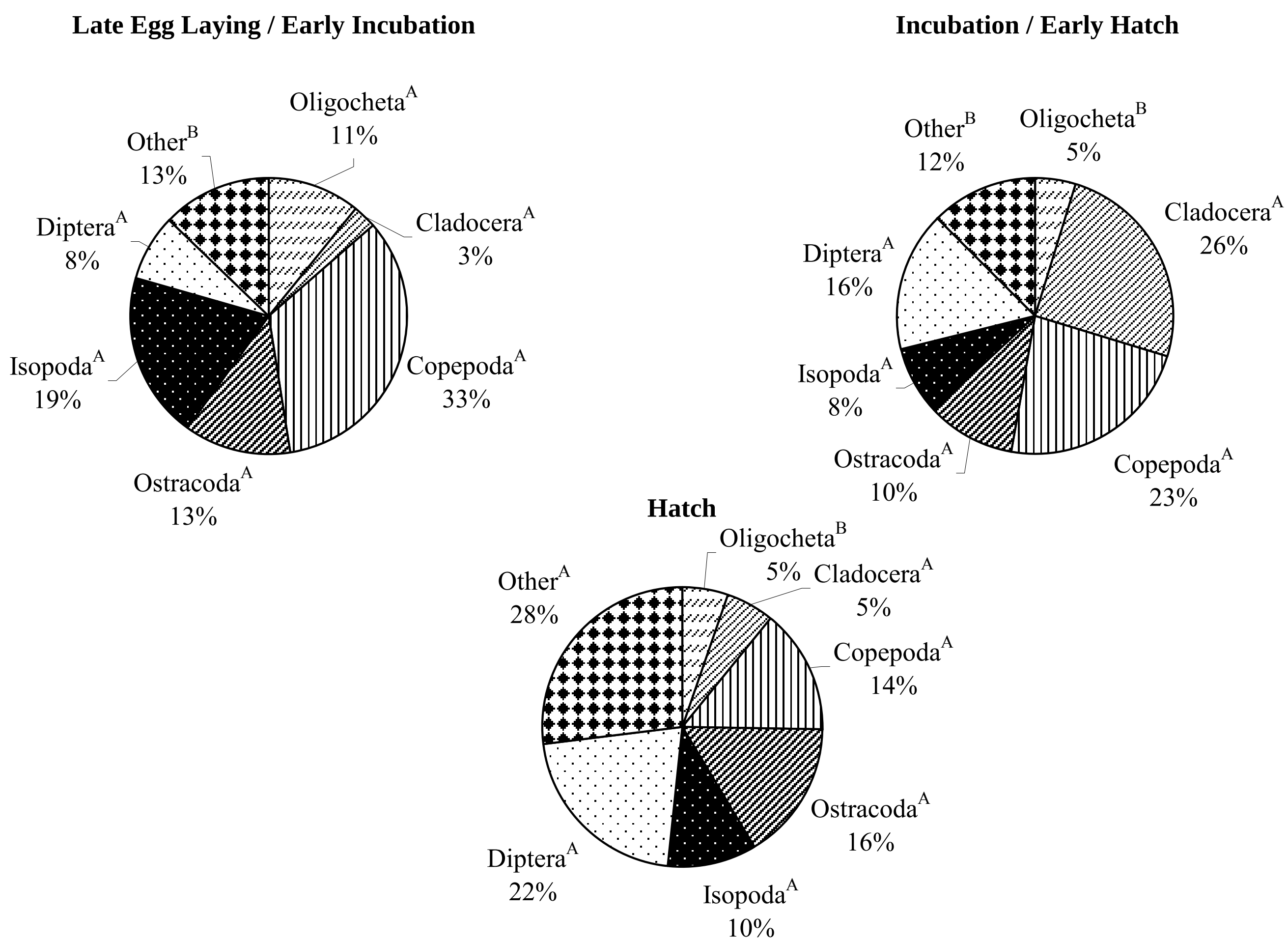
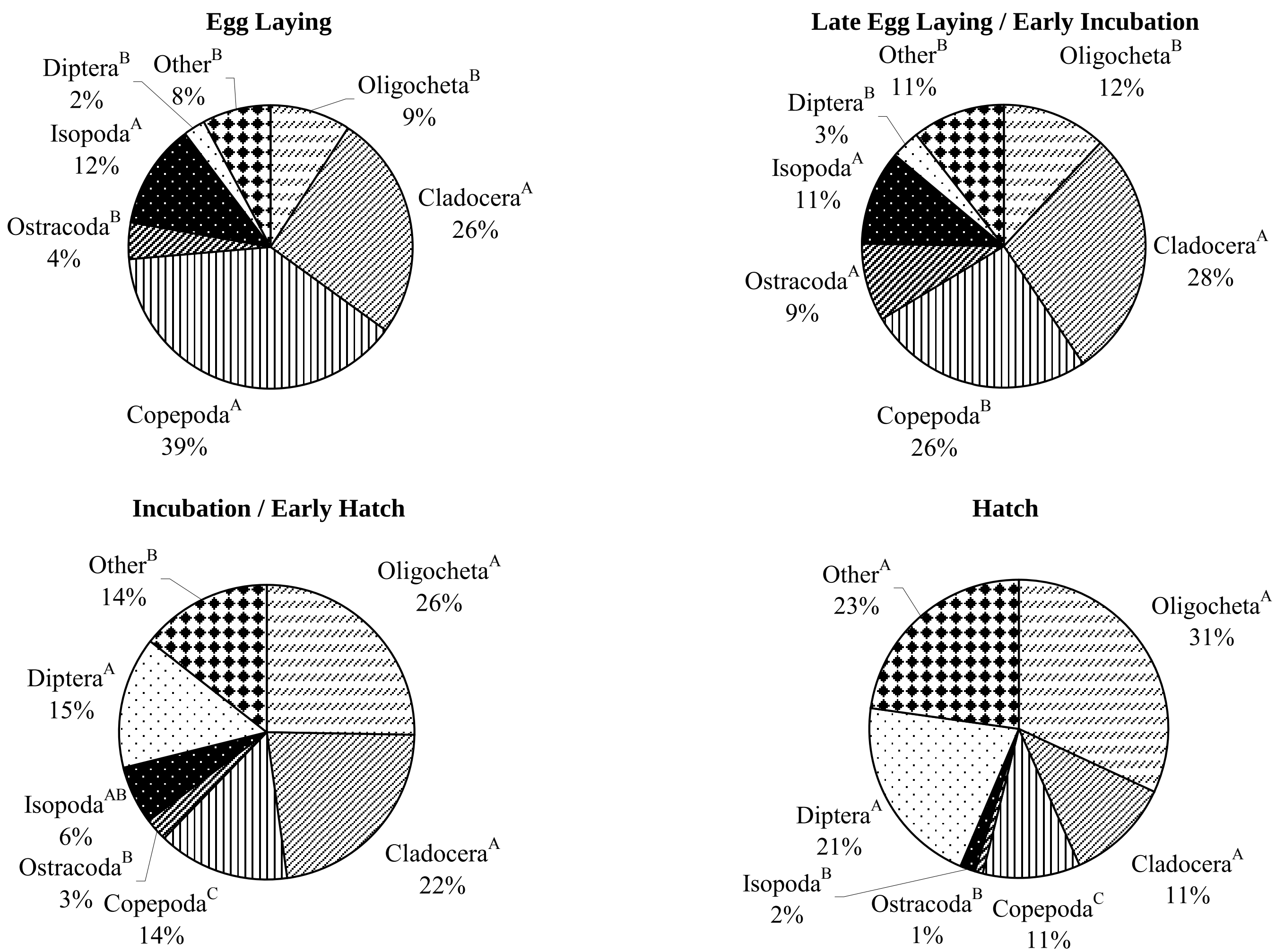
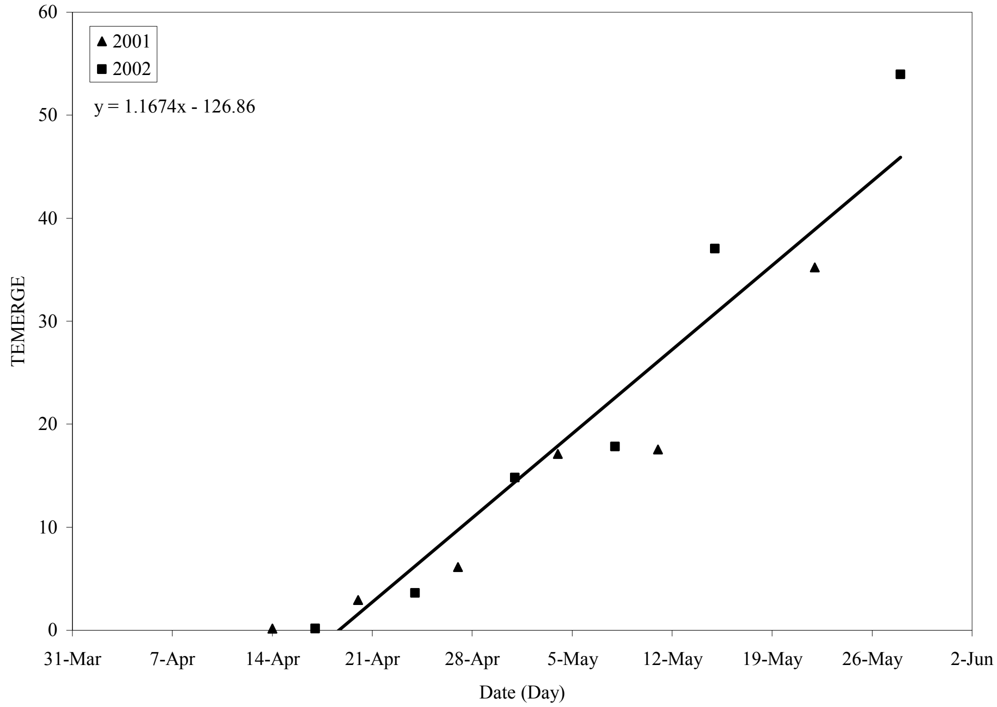

Late Egg Laying / Early Incubation
Oligocheta^A 11%
Cladocera^A 3%
Copepoda^A 33%
Ostracoda^A 13%
Isopoda^A 19%
Diptera^A 8%
Other^B 13%
Incubation / Early Hatch
Oligocheta^B 5%
Cladocera^A 26%
Copepoda^A 23%
Ostracoda^A 10%
Isopoda^A 8%
Diptera^A 16%
Other^B 12%
Hatch
Oligocheta^B 5%
Cladocera^A 5%
Copepoda^A 14%
Ostracoda^A 16%
Isopoda^A 10%
Diptera^A 22%
Other^A 28%

Figure 3.12. Mean percent occurrence of invertebrate species during 2002 in relation to periods of the nesting season as determined by brood observations completed on Union County Conservation Area (2001 - 2002) in southern Illinois. Significant differences in mean percent occurrence of invertebrate food items, determined by REGWQ analysis, were denoted by a letter change.

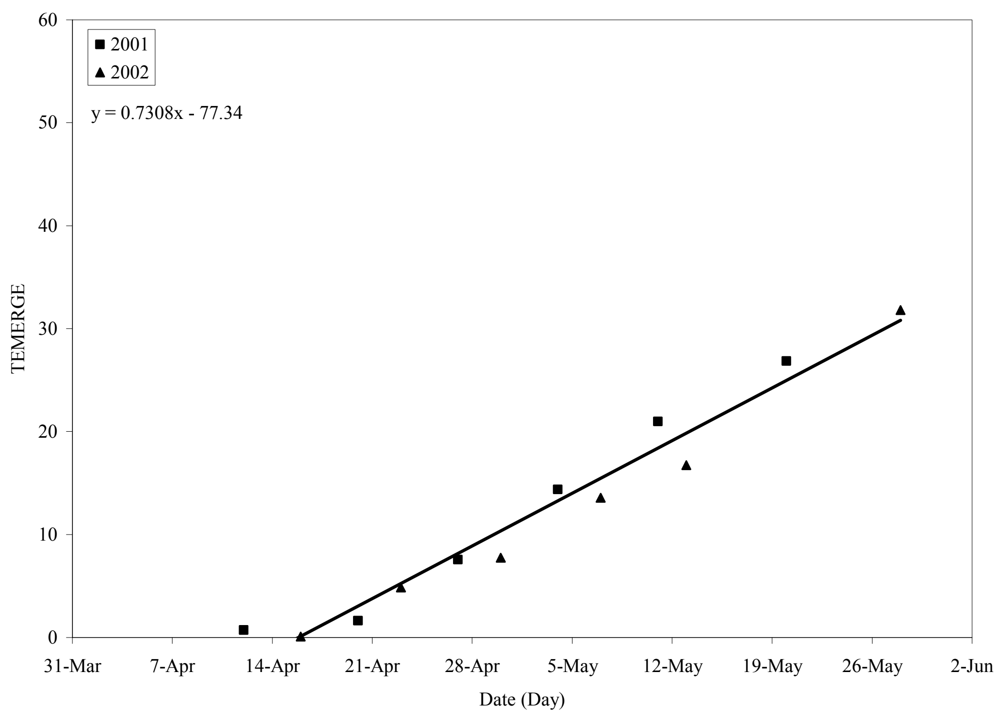


Egg Laying
Diptera^B 2%
Other^B 8%
Oligocheta^B 9%
Isopoda^A 12%
Cladocera^A 26%
Ostracoda^B 4%
Copepoda^A 39%
Late Egg Laying / Early Incubation
Other^B 11%
Oligocheta^B 12%
Diptera^B 3%
Isopoda^A 11%
Cladocera^A 28%
Ostracoda^A 9%
Copepoda^B 26%
Incubation / Early Hatch
Other^B 14%
Oligocheta^A 26%
Diptera^A 15%
Isopoda^AB 6%
Ostracoda^B 3%
Copepoda^C 14%
Cladocera^A 22%
Hatch
Other^A 23%
Oligocheta^A 31%
Diptera^A 21%
Isopoda^B 2%
Ostracoda^B 1%
Copepoda^C 11%
Cladocera^A 11%

Figure 3.13. Between year comparison of leaf emergence in upland (top) and floodplain (bottom) habitats at the Union County Conservation Area in southern Illinois during 2001 and 2002.

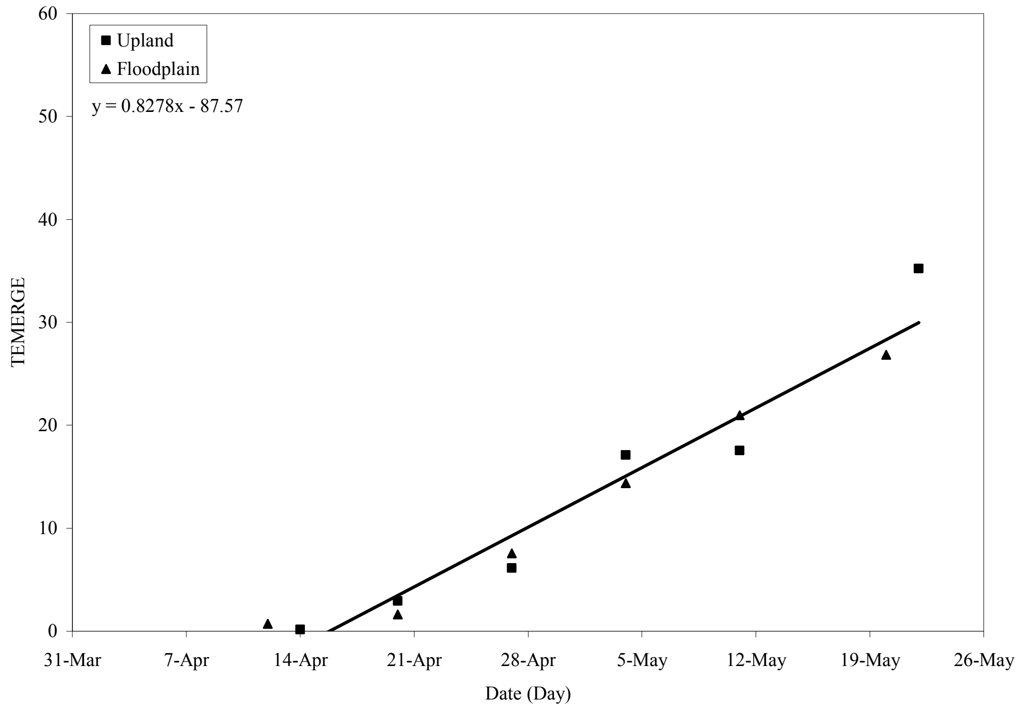


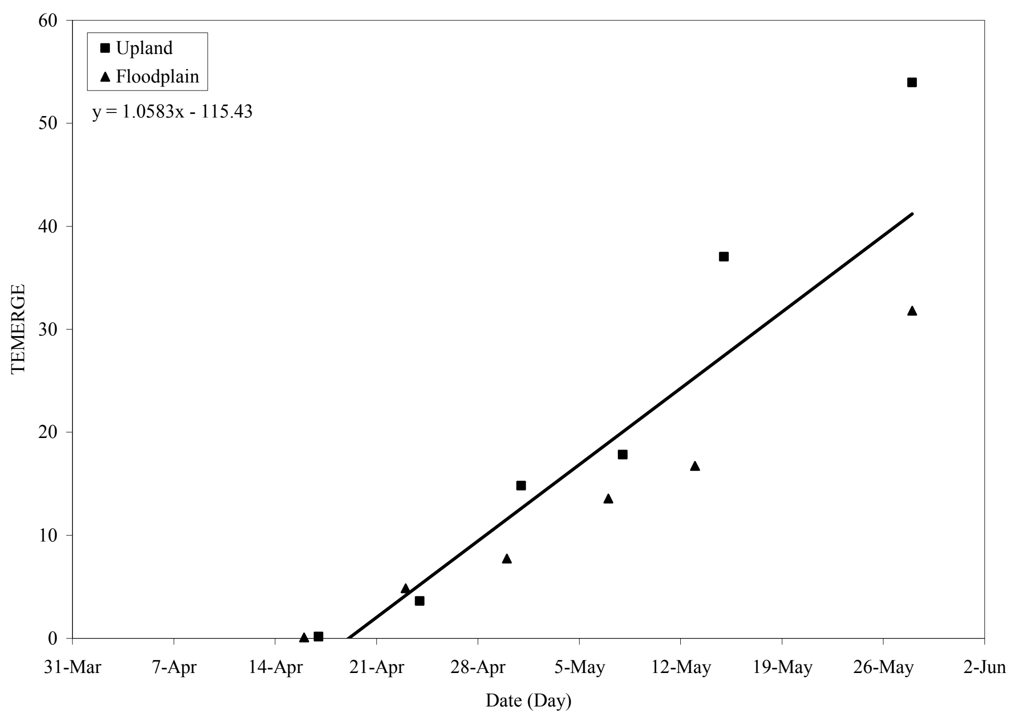
60
50
40
30
20
10
0
TEMERGE
2001
2002
y = 1.1674x - 126.86
31-Mar
7-Apr
14-Apr
21-Apr
28-Apr
5-May
12-May
19-May
26-May
2-Jun
Date (Day)



60
50
40
30
20
10
0
TEMERGE
2001
2002
y = 0.7308x - 77.34
31-Mar
7-Apr
14-Apr
21-Apr
28-Apr
5-May
12-May
19-May
26-May
2-Jun
Date (Day)

Figure 3.14. Within year comparison of leaf emergence in upland and floodplain habitats during 2001 (top) and 2002 (bottom) at the Union County Conservation Area in southern Illinois.


Upland
Floodplain
y = 0.8278x - 87.57
TEMERGE
0
10
20
30
40
50
60
31-Mar
7-Apr
14-Apr
21-Apr
28-Apr
5-May
12-May
19-May
26-May
Date (Day)


Upland
Floodplain
y = 1.0583x - 115.43
TEMERGE
0
10
20
30
40
50
60
31-Mar
7-Apr
14-Apr
21-Apr
28-Apr
5-May
12-May
19-May
26-May
2-Jun
Date (Day)

CHAPTER 4

DISCUSSION AND CONCLUSION

DISCUSSION

Nesting Activity

Nesting season length was variable from 91- 142 days, but considerably shorter than artificial nest box populations (Clawson et. al 1979). Bellrose and Holm (1994) noted that variability in wood duck nest initiation changes with latitude. In more southern latitudes, hens may initiate nests beginning in late January and early February throughout late June and early July. My study population began initiating nest in late February through middle June. The period of nest initiation for wood ducks in southern Illinois was considerably shorter (49 – 85 days) in every year except 1998 (100 days). Frederickson and Hansen (1983) found wood duck populations began nesting at similar dates in artificial structures; however they had an extended period of nest initiation that spanned 101 days. The shorter nesting season may be an indication of how environmental variables confine the nesting season for natural cavity nesting wood ducks to an optimal time window.

Observation of broods showed a 3-week peak nest initiation period was evident during 1994 – 1998 and 2001 – 2002. Bellrose and Holm (1994) mentioned that a majority of adult wood duck hens in a population generally initiate nests over the course of a 15 – 20 day period, followed by subsequent peaks of after hatch year, re-nesting, and double-brooded hens. However, re-nesting or double brooding was not detected in my study population, although nearly 132 radio-marked hens were known to nest during 1994 – 1998. However, in 2001 – 2002, 5 of 9 (56%) hens with failed nest attempts were confirmed to have re-nested, with 100% re-nesting in the same habitat type. Furthermore, of the hens tracked over multiple years, 8 of 9 (89%) nested within the same habitats in each year. The familiarity with nest site location and habitat selection may lend evidence toward a limiting factor in cavity nesting wood duck nest initiation.

Nesting effort (48% - 70%) in southern Illinois varied considerably between years (Ryan et. al 1998, Selle 1999, Gates unpubished). DNA analysis of the clutch size revealed that annual parasitism rates approached 61% - 100% over the course of my study (Roy et. al 2006); however, Semel and Sherman (1992) have shown that nesting hens appear capable of successfully laying, incubating, and rearing clutch sizes up to 13 eggs. Therefore the intensity of parasitism may be more influential on breeding propensity. Intense rates of parasitism showed a drastically reduced but highly variable range, from 8% - 43%, coinciding inversely with the annual rates of nesting effort.

Habitat Conditions

Water Levels.-- Variable water level conditions during 1994 – 1998 and 2001 – 2002 were apparent when evaluating water level fluctuation. More precisely, the more pronounced flood pulses occurred in 1994, 1996, and 2002 nesting seasons when compared to 1995, 1997, 1998, and 2001. Severe water conditions (drought or flood) on the breeding grounds have been seen to influence waterfowl reproduction (Rogers 1964, Vrtiska and Frederick 1993). However, the "moving territories" of the wood ducks provides the ability for hens to be opportunistic and adaptable when yearly and annual variability in conditions persist during the breeding seasons. Based on this assumption, hens should not be limited in their ability to acquire the necessary invertebrates during egg-laying and incubation (Bellrose and Holm 1994). Although mere presence of water did not appear to influence nesting decisions, sudden increases in water level may have influenced the decision of hens to parasitize at more intense rates or forego nesting altogether during that season.

Selle (1999) theorized that the hydrology at Union County CA may have further influenced the results of mean transect measurements taken during 1996 and 1997. Since these transects were located in semi-permanent (deep water) and seasonal (shallow water) wetland basins, readings in semi-permanent basins were likely more sensitive to rain or water pulses from the Mississippi River than seasonal basins. Large pulses, whether rain or river driven, in water levels would be more extreme in deeper wetland basins than shallow wetlands that may be initially dry. Consequently, wood ducks hens feeding on invertebrates in these semi-permanent basins likely encountered even more water level fluctuation than indicated by predicted model depths.

Invertebrates and Leaf Emergence.-- Research has invariably recognized the importance that environmental variables have on waterfowl species, more specifically in the timing and acquisition of invertebrates and cavity visibility. Zwicker (1999) determined that cavity availability was not a limiting factor for nesting hens in the southern Illinois population. However, other causative factors may be associated with nesting chronology, effort, and parasitism.

The limited time window of my study suggests that overall invertebrate biomass does not peak during maximal nutritional demands for laying wood ducks. Still, the seasonal dependence upon invertebrates may be the first factor beyond limited cavity availability in southern Illinois that would affect a hen's ability to prepare for egg laying on the breeding grounds. Possibly, the most important factor may be accessing abundant populations of preferred invertebrates throughout the breeding season. Bellrose and Holm (1994) emphasized the occurrence of sowbug (*Isopoda*) and chironomid (*Diptera*) larvae in the diet of egg laying hens and brooding young, respectively. Both, *Isopoda* and *Diptera* (primarily *Chironmidae*), were numerically higher during those periods in 2001 and 2002; further substantiating that later arriving, un-conditioned hens, might be limited in their ability to access the shorter-life cycle invertebrates within an optimal time window at similar breeding latitudes.

Methods of sorting invertebrates may have further masked the overall importance of food abundance, biomass or density, in relation to individual invertebrate food items during the spring wood duck breeding season. *Isopoda* accounted for only 12.0% of invertebrates during egg-laying in 2002; whereas, the proportional weight (not measured) of *Isopoda* would likely have been much greater when compared with *Cladocera* and *Copepoda* species that were numerically represented in the sample as 25.8% and 38.6%, respectively. Smaller invertebrate species never have been seen as significant portions of a wood duck hen's diet, but should not be ruled out as a source of protein acquired accidentally through feeding.

Selle (1999) and Robb and Bookhout (1995) alluded to the difficultly that natural cavity nesting wood duck populations may face once leaves emerge during the spring breeding season. Although time of day, weather, size of over-story leaves, and loss of branches could all have affected the between year outcomes, the apparent consistency in the onset of leaf emergence between years provides evidence that visibility may be a confining factor present in a natural cavity nesting wood duck population every year. Greater than 90% of hens in 2001 – 2002, regardless of habitat, had already begun nest initiation before the onset of leaf emergence.

CONCLUSION

A complex interplay of habitat conditions has made it difficult to single out sole factors that affect the nest chronology of breeding wood ducks. In order to make logical and sound management prescriptions, we must first understand the way in which breeding wood duck hens evolved. However, the first tendency has been to view all wood duck intra-specific nest parasitism as detrimental to the population. Breeding wood duck hens may have evolved the alternative strategy of intra-specific nest parasitism in order to accommodate the more restricted laying windows created by annual habitat conditions in natural cavities.

As annual water level fluctuations changed during my study, so did rates of nesting effort and intra-specific nest parasitism rates, accordingly. More severe fluctuations in water levels were apparent in 1994, 1996, and 2002; as were the more intense rates of nest parasitism and lower rates of nesting effort. Similarly, more stable or moderate variation in water levels was apparent in other years (1995, 1997, 1998, and 2001); which corresponded with lower nest parasitism and higher rates of nesting effort. Presumably, fluctuating water levels may impose additional demands on nesting wood ducks during the process of invertebrate acquisition. In response to building the proper nutrient reserves within a time window that permits locating a suitable cavity, hens may opt to forego nest initiation and incubation in unfavorable conditions in order to realize future breeding benefits in years with more stable conditions. Semel and Sherman (1995) found that hens nesting in more concealed artificial nest structures had much shorter seasons compared to the traditional, highly visible artificial nesting structure. As leaves emerge, hens may become inefficient at nest prospecting due to reduced visibility in a natural setting. Therefore, with >90% concealment by 5 May, many juvenile, un-conditioned adults, re-nesting, and double-brooding hens may have difficultly locating a suitable nest site, although suitable resources (cavity availability, food resources, etc.) exist. This may cause hens to forego additional breeding opportunities or acquire reproductive benefits by parasitizing other laying wood ducks, thereby reducing the overall length of nesting seasons in natural cavities.

Waterfowl invest considerable time and energy in egg development and incubation, and consequently produce self-feeding young. Furthermore, wood duck females produce 12 egg clutches by storing fat reserves in developing follicles to reduce dietary requirements during egg laying over a 6-day pre-laying cycle (Drobney 1990). Although water level conditions differed between 2001 and 2002, biomass, density, and the type of invertebrate communities present appeared relatively stable. Therefore, the important factor may be the abundance of certain communities at critical stages such as egg laying and hatch. This suggests wood ducks may have adapted a social breeding system with moving territories in order to access invertebrate populations at critical points during the breeding season. In years like 1994, 1996, and 2002 that experience severe water level fluctuations during the breeding season, hens may be forced to salvage reproductive effort by nest parasitizing the remainder of developed eggs. More long term research is necessary to confirm the effect of flood pulses on particular invertebrate communities.

Wood duck breeding seasons may also be directed by a hen’s ability to locate unoccupied nests amongst a densely forested landscape. Although ample invertebrate biomass and density exist throughout the breeding season, hen's abilities to consume invertebrate populations for the demanding period of egg laying and incubation may be confined by their ability to find a nest site in a suitable cavity before leaf emergence in southern Illinois. Since most of the population had begun nest initiation before leaf emergence started in 2001 and 2002; wood ducks may in fact be limited in their chances to locate a nest site in a natural cavity environment. Therefore, this suggests that hens must arrive early on the breeding grounds in order to build reserves for egg laying when the appropriate invertebrate communities persist at elevated levels and before cavities become concealed in a dense forest canopy. Therefore, the apparently shorter overall nesting season in natural cavity populations, compared to artificial nest structures, may result from a combination of environmental factors.

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