

CHRONOLOGY OF PAIR FORMATION AND
BREEDING BIOLOGY IN THE WOOD DUCK

A Thesis
presented to
the Faculty of the Graduate School
University of Missouri-Columbia

In partial fulfillment
of the requirements for the degree
Master of Science

by
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May 1979

LOAN COPY

The undersigned, appointed by the Dean of the Graduate Faculty, have
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CHRONOLOGY OF PAIR FORMATION AND BREEDING BIOLOGY
IN THE WOOD DUCK

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Chapter I

INTRODUCTION

The annual behavioral cycle of the wood duck (Aix sponsa) has not been thoroughly investigated in the wild. An increase in the numbers of pairs throughout the fall indicates courtship activity may begin soon after completion of the prealternate molt. The timing of pair formation and the relationship of the breeding strategy to habitat are important in understanding the ecology of the wood duck. A study of courtship behavior and pair formation chronology can give insight to behavioral responses to an environment.

This study was designed to acquire information on pair formation and behavioral responses to environmental cues by pursuing the following objectives:

1. To determine chronology of pair formation by observation of courtship behavior throughout the year in the wild.
2. To determine strength of the pair bond in fall and spring including:
 - a. definition of a pair
 - b. interactions between pairs and groups of wood ducks
 - c. change in behavior patterns through the courtship period.
3. To determine existence or function of unpaired

males in spring.

4. To determine habitat use.

Chapter II

ACKNOWLEDGMENTS

I express my gratitude to my advisor, Dr. Leigh H. Fredrickson, for his guidance and encouragement throughout the study. I appreciate the comments and critical review of the thesis of Dr. T. S. Baskett, Dr. L. H. Fredrickson, and Dr. J. Faaborg, and am grateful to M. Armbruster for suggestions and editorial assistance. Thanks are given to J. Ware, G. Pogue, and L. Piest for assistance in pen repairs and field work, and to Duck Creek Wildlife Management Area personnel for assistance with equipment and in trapping wood ducks. Special appreciation is extended to M. Scherpelz and V. Cravens for their encouragement and support throughout the study.

The study was supported by funds from the Missouri Cooperative Wildlife Research Unit, Gaylord Memorial Laboratory, Edward K. Love Foundation, Sigma Xi, and Agricultural Experiment Station Project 170.

Chapter III

LITERATURE REVIEW

Wood ducks were near extinction in the early 1900's because of overharvest and loss of nesting habitat. Wood ducks increased in numbers under federal protection provided by the International Migratory Bird Treaty in 1918. By 1941 populations were high enough that a limited season was reinstated. Undoubtedly the increase in populations was partly in response to the regrowth of streamside trees with the concurrent formation of nesting cavities, and the widespread use of nest boxes in conjunction with the harvest restrictions.

The Breeding Cycle of the Wood Duck

Wood ducks are an integral part of the bottomland hardwood forest community. Important habitat components include areas of quiet backwaters with low, dense woody vegetation and temporarily flooded timber. Wood ducks nest in cavities along stream banks or adjacent to permanent and semipermanent waters. Nests are generally within 0.8 km (one half mile) of water but some may be 1.6 km (one mile) or more away. At the latitude of Duck Creek Wildlife Management Area migrating wood ducks usually arrive in February, and depending on weather conditions, initiate the first nests in late February or early March (Clawson 1975). The earliest arrivals on the breeding grounds are paired, and the

earliest nests are initiated by adults with previous experience (Grice and Rogers 1965). Female energy requirements for nesting influence activities of pairs in the spring. Before laying, a female must acquire enough lipid reserves to produce 12 eggs (Drobney 1977). Protein requirements are met through the daily dietary intake; thus, invertebrates are an important source of protein immediately before and during early egg laying. During this period the female spends 73 percent of the time feeding and 27 percent in maintenance and reproductive activities. Males spend 34 percent of the time feeding, 22 percent in maintenance and reproductive activities, and 44 percent in an alert posture (Drobney 1977). Alertness of the male allows the female to feed unmolested because the male watches for intruders or predators.

In southeastern Missouri hatching peaks in mid-April to mid-May, but some nests do not hatch until July (Clawson 1975). Shallow water areas with an abundance of invertebrates and aquatic plants, and protective cover such as American lotus (Nelumbo lutea) and buttonbush (Cephalanthus occidentalis) are important requirements for brood rearing (Grice and Rogers 1965). The female may remain with the young until flight stage, though females may abandon the young earlier (Gilmer et al. 1977). Some wood ducks begin molting in early summer and many adult birds have completed the prealternate molt by mid-September. Flooded timber offers an important source of food for migrating wood ducks in the fall (Grice and Rogers 1965). Wood ducks migrate south of Missouri by mid-November,

though a few may remain in the area during mild winters.

Behavior of Other Cairinini

The wood duck is a member of the subfamily Anatinae, tribe Cairinini, which has been classified between Tadornini (shelducks) and Anatini (dabbling ducks) (Johnsgard 1961). Many detailed behavior studies have involved the Anatini, but the Cairinini has been studied little. Cairinini occupy a more primitive (definition of "primitive" and advanced" follows Kear 1970) position in the Anatinae relative to the Anatini, and include perching ducks that have iridescent plumages and nest in cavities. It is the only tribe demonstrating orientating head movements before flight, and nystagmic head nodding with every other step rather than every step (Lorenz 1971). The larger Cairinini (including Plectropterus, Sarkidiornis, and some Cairina) appear to be less advanced than the smaller forms. The high incidence of rape and the weak pair bonds typical of these genera are interpreted as very primitive motor and behavioral characteristics (Lorenz 1971). Smaller Cairinini have stronger pair bonds and more highly developed courtship behavior.

The white-winged wood duck (Cairina scutulata) has strong family bonds. Larger groups with several families included are formed only during the dry season when water resources are limited (M. J. S. Mackenzie pers. comm.). Courtship occurs from late August until the breeding season in spring. Early fall courtship may be stimulated by the dominant male asserting himself in the presence of newly mature young in the family

group. Courtship may occur on water or in trees while birds are roosting. Adequate cover is important for normal courtship (M. J. S. Mackenzie pers. comm.).

The genus Aix exhibits a strong resemblance to the shelducks in behavior and morphology, except that birds of the former genus reach maturity in one year and have more complex repertoires of displays than the shelducks (Johnsgard 1961). Displays of Aix involve primitive and simple actions combined with the brilliant markings of the highly competitive male. Because the female chooses the male, females select for those males with the most effective releasers (Dilger and Johnsgard 1959), influencing the development of elaborate plumage and displays.

The mandarin duck (Aix galericulata) is the closest relative of the wood duck and the only other member of the genus Aix. Mandarin ducks occur naturally in forested habitat in southeastern Asia. They nest in tree cavities and have habits similar to the wood duck. Social display involving many males is very important in courtship, which occurs from autumn until May (Delacour 1956).

Behavior of the Wood Duck

Wood duck behavior, from a naturalistic viewpoint, was first described by Heinroth (1910). Later Lorenz (1951-1953) described the various display patterns more precisely, and then compared the displays with those of other Anatidae. Johnsgard (1961) used behavior reported by Heinroth and

Lorenz for taxonomic purposes to classify Anatidae. A description of wood duck vocalizations and courtship displays has been given by Heinroth (1910), Lorenz (1951-1953), and Johnsgard (1965:111), and include the following:

Vocalizations of Adult Wood Ducks

- Female: "Hauk"--call note, given when flying or swimming
 "Houi"--Coquette Call, given during courtship
 "Tetete"--given during nest searching
- Male: "Jiib"--call note, given when flying or swimming
 "Pfit"--given during Burp display
 "Jibjibjib"--given during nest searching

Displays

Pair Formation and Precopulation

- Female: Inciting, accompanied by the Coquette Call
- Male: Introductory Shake--occurs rarely
 Drinking
 Preen-Behind-the-Wing--moves "brass feather" always preceded by Drinking
 Burping--accompanied by vocalization "Pfit" --occurs rarely
 Chin-lifting
 shows white on chin
 performed alone or with Turn-the-Back-of-the-Head
 important--repeated often
 Turn-the-Back-of-the-Head--tail is tilted to one side
 female Inciting in conjunction with male
 Turn-the-Back-of-the-Head are important in pair maintenance
 Display Shake
 Wing-and-Tail-Flash
 Bill Jerk

Copulation

- Female: assumes the Prone position

Male: Faces
 swims around her with Bill-Dipping, Drinking,
 and pecking at her head, back, and tail
 Mounts and Treads

Postcopulation

Female: Bathes

Male: swims away rapidly a few feet
 Turn-the-Back-of-the-Head
 Faces female
 Wing-and-Tail-Flash (Korschgen and Fredrickson
 1976)

Little has been reported on aerial displays or pursuits. Females escape from unmated suitors more by diving and swimming than by flying (Heinroth 1910). Fall and winter courtship display are uncommon. Aggressive encounters during courtship between male wood ducks usually involve little more than two birds rushing alongside each other or an apparently harmless beating with the wings, with no bill contact. Lorenz (1951-1953) reported that males court one female in particular, with little social display as in mandarin ducks. Mutual preening of the mate's chin feathers may occur, and mutual feeding has been reported (Heinroth 1910, Korschgen 1972).

A recent study of behavior in captive wood ducks concentrated on courtship and pair formation, and behavioral differences in experienced and non-experienced males (Korschgen 1972). Captive adult male wood ducks in controlled situations have better orientations and posture exaggeration than yearling males, and exhibit a more complete repertoire of displays (Korschgen and Fredrickson 1976).

Wood duck courtship behavior in fall and winter is little known, but roost flight counts can be used as an indicator of activity and pairing. The incidence of two-bird flocks in North Carolina increased from 34 percent in October to 47 percent in January (Hester and Quay 1961). In southeastern Missouri paired wood ducks increased from 2.8 percent in August to 40.5 percent in October (Korschgen 1972). Apparently pair formation occurs during the fall and winter months.

Most published studies concern spring courtship behavior. Forbush (1912) stated that wood ducks in the South form pairs in December, January, or February. Courtship and copulation occur in North Carolina as early as 13 October (Hester and Dermid 1973). Fall courtship occurs in October to December in captive wood ducks in southeastern Missouri (Korschgen and Fredrickson 1976). Information is lacking on formation and strength of pair bonds through the courtship season.

The Pair Bond

A pair has been defined as a male and female which sleep, feed, and preen together, and the distance between them is smaller than the distance between either of them and any others of the same species (Lebret 1961). Occasionally trios have been reported in mallards (Anas platyrhynchos) (Lebret 1961, Wekdman 1956) and in captive wood ducks (Korschgen 1972). The association of an extra male tolerated by a pair is not fully understood. Excess males occur in many species of North American ducks, including both diving ducks and dabbling

ducks (Bellrose et al. 1961). Unpaired pintail (A. acuta) drakes often harass hens, and may serve as a source of fertilization for renesting attempts (Smith 1968). Pairs of most duck species are continually tested throughout pair formation by unpaired drakes (Weller 1965). Unpaired drake gadwalls (A. strepera) appear to recognize paired gadwalls in their activity centers as secure, and do not challenge them with aggressive behavior or harassment (Dwyer 1974). In many of the Anatini, pairs are territorial, and both the female and a general home range are defended (Sowls 1955). Pursuit (or defense) flights occur frequently in gadwalls (Dwyer 1974), mallards (Weidmann 1956), and blue-winged teals (A. discors) (Dzubin 1955). Defense of the territory may be important in minimizing predation through a lower nesting density, providing an adequate food supply for the female, or isolating the breeding pair (Hinde 1956, Hochbaum 1944).

Chronology of Pair Formation in Anatinae

Chronology of pair formation is an important element in analyzing pair formation, stability of pair bonds, and annual patterns of behavior. The principal advantage of pairing on the wintering grounds is that it allows the rapid initiation of breeding shortly after birds arrive at the nesting area (Orians 1969). Fall courtship is common in Anatini. In Maryland, black ducks (A. rubripes) formed pairs throughout the year, increasing from 10.5 percent paired in September to 90 percent in February (Stotts 1958).

Courtship in black ducks is less noisy in the fall than in the spring, and copulation is generally restricted to warm days. Copulation was not observed in winter, but occasional courtship displays were performed on sunny days (Trautman 1947). The period of pair formation is not clearly correlated with the frequency of copulation. In the mallard the most active period of display and copulation was October to November. Copulation in fall and winter strengthens bonds, but is relatively unimportant in pair formation (Johnsgard 1960).

Pairing begins on the wintering grounds in the wigeon (Anas americana), but the bonds are predominantly temporary associations that are tested by unpaired males (Soutiere et al. 1972). Courtship displays were observed infrequently from November through December and increased during January. Weather during January was not found to affect displays. After January an increase in rape attempts leading to courtship flights occurred. By this time copulation sequences were noted in those birds with well-established pair bonds (Soutiere et al. 1972). Captive green-winged teals (Anas crecca) at Delta, Manitoba display most actively from February to June, but records of display occur as early as August and September (McKinney 1965a).

Most courtship in the pintail occurs from mid-December to April. In captives, pairing occurs in September and October, but fall pairing is not expected in the wild, because the sexes tend to flock separately from September

until mid-December (Smith 1968). Copulation rarely occurs from January to February. Males become more aggressive near their mates from March through April, and copulation after arrival on the breeding grounds in April is associated with mate defense (Smith 1968).

Attainment of breeding plumage may affect the time of pairing. Blue-winged teals and cinnamon teals (Anas cyanoptera) acquire breeding plumage in September through December (adults earlier than first winter birds), pair by January and February, and lay eggs and raise broods from May through August. Northern shovelers (Anas clypeata) acquire breeding plumage in November through December and are paired by March. Pursuit flights are common during pairing and birds in alternate plumage are the most active. Early pairs are frequently unstable and firm bonds are distinguishable only after many weeks of pairing activity (McKinney 1970).

In the Aythyini, redheads (Aythya americana) begin courtship in December and January while ring-necked ducks (Aythya collaris) and lesser scaups (Aythya affinis) begin courtship and copulation in March (Weller 1965). The sequence of display and pairing correlates with the onset of breeding plumage and nesting. Redheads pair earlier than those species, including ring-necked ducks and lesser scaups, whose nests are parasitized by redheads. Thus redheads are in full breeding condition for early parasitic laying, and afterwards can nest and raise a brood. Mallards and pintails assume the adult plumage two months prior to divers, and nest one month

before canvasbacks (Aythya valisineria).

Eco-ethology

A knowledge of pair formation chronology and courtship displays is important in understanding the ecology of a species. A comparison of displays of the Steller's eider (Polysticta stelleri) and the Pacific eider (Somateria mollissima v.nigra) illustrates the effect of predation on the evolution of epigamic display. The smaller, more vulnerable Steller's eider feeds in densely-packed diving flocks and flies up steeply from the water at the approach of a bald eagle (Haliaeetus leucocephalus) or gyrfalcon (Falco rusticolus). Courting parties commonly exhibit preflight behavior, display movements are rapid and brief, and no loud calls accompany male displays (McKinney 1965b). The Pacific eider feeds in less dense diving flocks in more open waters and shows no response to birds of prey. Pre- and postcopulatory behavior includes conspicuous wing-flaps, slow, compound display movements, and loud calls (McKinney 1961). Predation was also the predominant factor influencing the nocturnal feeding and diurnal gregarious habits of the common teal (Anas crecca) in the camargue (Tamisier 1974).

Climate has a strong influence on the ecology and reproductive patterns of the waterfowl of the Falkland Islands. Crested ducks (Lophonetta specularoides) and Chilean teal (Anas f. flavirostris) nest in all months of the year. Territorial behavior and slow growth rates of the

young are characteristic of waterfowl in this mild climate. Eleven breeding anatids coexist in the relatively small area of the Falkland Islands by occupying both the herbivore and carnivore trophic niches and marine, estuary, freshwaters, and terrestrial habitat niches (Weller 1972).

Oldsquaws (Clangula hyemalis) at Churchill, Manitoba pair early, by mid-February, correlating with the shortness of the Arctic breeding season and the prolonged post-nuptial molt (Alison 1975). Males exhibit territorial behavior and short aerial pursuits, thus limiting local breeding population size to a density allowing the potential for the highest productivity for a given habitat.

Other aspects of breeding strategy are strongly influenced by the species' ecology. The habitat of permanent water areas rich in plankton dictate the time-consuming feeding habits of the shoveler. A restricted habitat also influences breeding behavior, which in the shoveler typically includes defense of discrete territories, Head-Pumping and calls as distant threat signals, strong pair bonds and frequent copulation (McKinney 1967). In contrast, the pintail travels widely between temporary pools and dispersed permanent water. The high mobility and open, sparsely-watered habitat affects the weak pair bonds, lack of hostility between paired males, and common rape attempts (McKinney 1965c). Paired male gadwalls in North Dakota show a decrease in tolerance to intruding males during prenesting and laying (Dwyer 1974).

As nesting approaches, three-bird chases increase in frequency, intensity, and length. Females feed 17 percent more than males during prenesting and 48 percent more during laying. Aggression by the male provides seclusion in activity centers for feeding, allowing the female to meet nesting energy requirements.

Chapter IV

MATERIALS AND METHODS

The study site was located on the Duck Creek State Wildlife Management Area and the adjacent Mingo National Wildlife Refuge located in Bollinger, Stoddard, and Wayne Counties in southeastern Missouri. Duck Creek Wildlife Management Area encompasses 2480 ha, including three pools of flooded lowland timber where water levels are manipulated throughout the year. Pool I is a 710 ha reservoir that provides water to flood the 527 ha of timber in Pools II and III for waterfowl hunting in the fall. Mingo National Wildlife Refuge is contiguous with the southern and western boundaries of Duck Creek Wildlife Management Area. Its 8400 ha include bottomland hardwoods with fluctuating water levels. Characteristic vegetation includes baldcypress (Taxodium distichum), water tupelo (Nyssa aquatica), overcup oak (Quercus lyrata), and ash (Fraxinus sp.) on lower sites, and elm (Ulmus spp.), red maple (Acer rubrum), sweetgum (Liquidambar styraciflua), willow oak (Q. phellos), pin oak (Q. palustris) and hickories (Carya spp.) on higher sites (Korte and Fredrickson 1977). Stands of buttonbush occur throughout the area. Beavers (Castor canadensis) are common and influence areas of flooding and water depths, thus creating habitat especially for older wood duck broods and for roosting. A nest box program on

Duck Creek Wildlife Management Area is used by approximately 200 breeding female wood ducks. The importance of cavity nesting is unknown.

Field Work

Observations in the field were conducted August through November 1976, August through November 1977 and January through May 1978. Field equipment included a tape recorder, binoculars, and a 35 mm Nikkormat camera with 300 mm and 600 mm lenses. Observations were made from a portable tree blind, while concealed in vegetation or while walking quietly through the study area. The following aspects of wood duck courtship activity were recorded:

- size of courting groups, sex of birds
- courtship display sequences, types of displays, copulations
- duration of sequences
- vocalizations of paired vs. unpaired birds
- documentation on film of any unusual or unreported display

Weather conditions including temperature, wind, and cloud cover at the time of all observations were noted.

Pen Work

A flight pen 45.6 m x 30.5 m x 3.6 m was used to supplement behavioral observations in natural situations. The surface area of the pen consisted of 50 percent land and 50 percent water about one half meter deep. A 1.1 m high plywood baffle around three sides of the pen reduced outside disturbances. An observation tower equipped with camera ports and one-way glass allowed an unobstructed view of the

entire pen. Pen-reared adult birds were used during the 1976 field season. Four male and four female wood ducks were introduced into the pen on 31 October 1976. Fall observations were terminated on 1 December when a mink (Mustela vison) destroyed the entire flock. Adult wild-trapped wood ducks from the Duck Creek Wildlife Management Area and Mingo National Wildlife Refuge were used to restock the flight pen during the 1977-1978 season. Four adult males and four adult females were introduced into the pen on 16 August. For individual identification, the penned birds were marked with colored nasal saddles of polyvinyl chloride tape (Sugden and Poston 1968). These birds were observed through the 1977-1978 breeding season.

Observations in the pen and the field were conducted for one- to five-hour periods between one-half hour before sunrise until 1100 and from 1400 until one-half hour after sunset. Checks were made periodically to determine activity levels during midday, when behavior was generally limited to loafing, preening, and foraging. Observations began both years on 29 August.

Analysis

Data from 1977-1978 were analyzed for group size, sex ratios, activities, and display rates. Observations during 1976 were not as detailed and complete, and were not included in the analysis. Activity patterns and courtship followed trends similar to 1977 data. Certain difficulties are

inherent in the observation and recording of courtship displays in the field. Most observation distances were over 40 m, with a great deal of dense vegetation between the observer and the ducks. Neither the entire group or any one member of the group remains in view for more than a minute at a time. From one to 30 wood ducks may be displaying at one time, and recording all displays of all males was rarely possible. Certain displays are imprecise and difficult to interpret at a distance, including Turn-the-Back-of-the-Head, Chin-lifting, and Facing.

Statistical analysis of the data included the Student's t-test, chi-square test, and Mann-Whitney U test (Sokal and Rohlf 1973, Conover 1971). Scientific names of plants are according to Steyermark (1963), waterfowl are according to Johnsgard (1965), other birds are according to A. O. U. (1957), and mammals are according to Walker (1964).

Chapter V

RESULTS

Field observations of 4934 wood ducks encountered on 1217 occasions were obtained between 29 August 1977 and 15 May 1978. A total of 638 groups and 763 pairs were observed. Courtship activity was observed on over 80 occasions in the field.

Vocalizations

Field observations suggest female vocalizations are important in coordinating social activity. For example, the Hawk call appears to announce a female's presence. The call is given regularly when females swim or fly into an area, or when a lone female is in a rising state of sexual excitement and approaches a group of males. The Coquette Call connotes a state of female sexual excitement and is given during a courtship sequence. Both feeding or loafing wood ducks may be stimulated by the call and begin courtship behavior. Both vocalizations are given most commonly during early morning hours and at sunset, and both calls carry well over open water or through timber. Males as far as one half mile away began swimming toward a female when she gave either call. A third vocalization, not previously described, is given during a high level of courtship activity and during sequences when a female is Inciting or Bill Jabbing.

The call is a soft, rapid "dihdihdih" and resembles a vocalization that I have heard only during nest searching. Vocalizations provided an index to the level of courtship activity.

The most common vocalization of the male wood duck was a drawn-out whistling "Jiib", that carried for short distances. Variations of this call express alertness or a warning. The "Pfit" vocalization of the Burp posture was heard rarely. A series of short, rapid "jibjibjib"s, resembling vocalizations I have heard during nest searching, was given during Inciting and Bill Jabbing, and indicated courtship of high intensity.

Display Sequences

A typical display sequence usually began with vocalizations or aggressive postures. Several males sat quietly on the water, each with the head pulled in toward the body, and slowly changed positions around the female. One or two males began whistling or gave Bill Jerks. The female gave the Hawk or Coquette Call, and males whistled with an increasing level of excitement until a female Incited or males began fighting. Following an aggressive confrontation between two males both usually Bathed. This usually lead to a session of preening the breast or back regions, or the birds fed, ending the display sequence. More vocalizations and aggressive postures followed as the level of sexual excitement increased again, and another display sequence began. Length of display

sequences ranged from 1 to 20 minutes, interspersed with 1 to 90 minutes of preening or feeding. Display sequences usually occurred in the early morning hours and around sunset, and occasionally mid-to-late afternoon. Courtship activity never occurred without accompanying vocalizations, thus a silent group of wood ducks exhibited no courtship activity.

New Displays

Fighting is an important functional component of courtship. A behavior pattern which I call the Rush is a form of fighting performed by both males and females at a high level of courtship activity. In Rushing the body is held low over the water in a prone position with the wings appressed to the body throughout the fight. A bird rushed with the bill open, accompanied by splashing by the feet. A female may assume the Prone position for as long as a minute before Rushing. The Prone posture followed by a Rush may be a form of Inciting. If a female Rushed a male, all other males present Rushed the same male. A female may also Rush another female, but this occurs rarely. Males Rushed each other, sometimes so vigorously that a male was driven from the courting party. During the fall females Rushed on 24 occasions and males on 30 occasions. In the spring females Rushed only once but males Rushed on 30 occasions. One distinct difference between fall and spring fighting is that physical contact or beating with the wings commonly

occurs in spring but not in fall.

A second important display I call the Bill Jab is performed by both males and females. The bill is jabbed repeatedly straight down at the water in front of the breast. Both sexes vocalize during the display: males with a rapid "jibjibjib" and females with a "dihdihdih", that rises in pitch and rapidity as intensity of displaying increases. The display connotes aggression and may be used at the beginning of a courtship sequence. In females the Bill Jab was observed 6 times in the fall and 25 times in the spring, and in males 39 times in the fall and 163 times in the spring. Both mated and unmated birds performed this display. If one bird Bill Jabbed others were stimulated to Bill Jab. Bill Jabbing by a female stimulated a male to defend her or to attack nearby males. During courtship in early fall Bill Jabbing had no directional component, and was seldom performed with other displays. The display appeared to function more in pair formation than in pair maintenance. During late fall and spring courtship Bill Jabbing by the females appeared to develop directional components that resembled Inciting, and was performed in conjunction with Turn-the-Back-of-the-Head by the male in pair maintenance situations.

I call a third unreported display the Supplanting Display. Twice during the fall a courting group was observed loafing and preening in an area of floating logs and large trees with stout, horizontal limbs. A female flew up to a branch,

followed by one or more males. Other males attempted to replace perched males by flying into them and knocking them off their perches. This then lead to another display sequence on the water.

Copulations

Copulations were observed 22 times in the flight pen and once in the field. Only three of the copulations occurred in the fall. All copulations involved paired birds that were isolated from other groups of birds. Females assumed the Prone position 118 times, but only 23 copulations occurred. In another attempt an unmated male was unsuccessful in mounting a mated female (Table 1). Rape was not observed. On one occasion four males chased a female that was swimming in the flight pen, but the outcome of the incident was unknown.

Male postcopulatory displays included Bathing, Preen-Behind-the-Wing, Wing-and-Tail-Flash, and Facing (Table 1). Once no postcopulatory displays were given because intruding males disturbed the pair. The mated male defended the female and attacked the intruders.

Nest Searching

Nest searching occurred throughout the morning from first light until 1000-1100 and from mid-afternoon (1500) until sunset. Wood ducks searched for nest sites in flooded and dry timber, and in open, flooded areas where

Table 1. Postcopulatory displays in male and female wood ducks.

Date	F Bathe	M Face	Wing-and-Tail-Flash	M Bathe	Preen-Behind-Wing
12 Nov.	X		X		
15 Dec.	X	X	X		
23 Feb.	X	X	X		
5 Mar.	X			X	
7 Mar.	X	X			
7 Mar.	X		X		
8 Mar.	X			X	
12 Mar.	X	X	X		
13 Mar.	(pair Rushed by intruding male)				X
16 Mar.	(pair Rushed by intruding male)				X
16 Mar.	X	X	X		
16 Mar.	X		X		
16 Mar.	(female threw off intruding dominant male)				
2 Apr.	X		partial		
2 Apr.	X	(intruding male usurped mated male)			
2 Apr.	X	X	X		
4 Apr.	X	X	X		
5 Apr.	X	X	partial	(interrupted by intruding male)	
19 Apr.	X	X			
19 Apr.	X	X	X		
2 May	X	X	partial		
*13 Oct.	X	X			X

* field observation Fall 1976

nest boxes were located 1-3 m high on poles or trees. A pair usually searched in a line parallel to roads, ditches, and openings, within 100 m of water.

Searching females paused and looked in all directions as they flew from tree to tree. Males followed females, but either swam or loafed near the base of the tree, or loafed in the tree while females were searching for cavities. Females gave a soft, rapid "dihdihdih" vocalization while the male whistled slowly or gave a soft, rapid "jibjibjib". A pair spent from 2 to 90 minutes in one tree, and over two hours at a time nest searching. Periods of nest searching were interspersed with feeding and loafing in flooded timber. Inspection and use of natural cavities was not observed.

Pairs had a general search pattern in relation to boxes. First the box was viewed from the water or ground surface, then the pair swam under the box. The hen flew onto the top of the box before entering. Each female spent 10-35 minutes inspecting the box, forming a nest bowl, or laying an egg. The hen then peered from the entrance for 2-15 minutes and then flew to the water where she was joined by her mate. The male usually remained in the general area, swimming, whistling, feeding, or loafing. Males were observed loafing on or under the boxes for as late as one week into incubation. Aggression and courtship occurred only when a pair was approached by another pair or a lone male.

Often 2-3 pairs fed or nest searched near each other with no apparent hostility.

Seasonal Changes in Courtship Activity

From August through September courtship activities were centered on Pool I in an area of open water 1-2 m deep. Large expanses of watershield (Brasenia schreberi) and American lotus provided food and cover. Wood ducks roosted in the lotus, and fed on sites with watershield until approximately 1000 hours and again after 1500. The 100 or so wood ducks that used the area formed loose groups that continually changed in size and composition throughout the day.

During Week 1 (30 August-5 September) activities were limited to foraging, loafing, and body maintenance. Encounters between individuals resulted in no reaction between birds, or a rapid Bill Jerk given as a greeting or mild aggression. Aggression was evident only when birds came closer than 30-50 cm to each other. Vocalizations other than an alarm note were rare. The Coquette Call and the Hawk call occurred less than four times in a morning, and sporadically during roost flights. Many birds were still in juvenal plumage and over 50 percent of the males were still in the prealternate molt.

By Week 2 (6-12 September) over 50 percent of the males were in alternate plumage. Activities included foraging, loafing, and maintenance activities. Aggression was limited to situations where high densities of birds occurred.

During Week 3 (13-19 September) over 90 percent of the males were in alternate plumage. Little change in activity was noted except for an increase in the level of alertness by males in alternate plumage. Molting males in loose feeding groups exhibited little aggression or alertness. In one 30-minute period a male in alternate plumage was in the alert posture 10 times, for approximately one minute each time. During the same period a molting male 25 m away was alert only once, for approximately 10 seconds.

The level of male responsiveness to courtship stimuli developed slowly. As the alternate plumage was attained, groups of loose "pseudo-pairs" formed from temporary associations between males and females. By Week 4 (20-26 September) all males were in the complete alternate plumage. Aggressive encounters increased. Courtship displays were first recorded on 21 September. This corresponded to temperature changes from a daily average of 33° C for 20 September to 23° C for 21 September, and overnight lows of 17° to 10° C respectively. The first display sequences observed included the Bill Jerk, Turn-the-Back-of-the-Head, Display Shake, Drinking, Preen-Behind-the-Wing, Prone position, and the Rush. On 23 September Inciting was first observed. Temporary associations of males and females became courting parties where pair bonds were continually tested. During this period "pairs" lasted from 10 minutes to one day. Females took an active part in courtship, vocalizing continually until other birds were stimulated to

display, or Inciting and causing males to defend her or attack each other.

During Weeks 5-6 (27 September-10 October) the first true pairs were evident. On 27 September Wing-and-Tail-Flash was first seen. During this period Pool II was flooded to a depth of 50-100 cm. Wood ducks ceased using the open water of Pool I in favor of the flooded timber in Pool II. Data were limited during this transition when wood ducks moved from Pool I to Pool II.

Courtship activity continued throughout October. Roost counts during Weeks 7-8 (11-24 October) revealed few wood ducks using the study area. During Weeks 9-10 (25 October-6 November) roost counts revealed a sharp rise to 1700 wood ducks followed by a rapid drop in numbers as the birds migrated from the area. Weeks 11-12 (7-20 November) had a decrease in activity as temperatures dropped and the water froze. Roost counts indicated an influx of migrating birds on 13 November when over 525 wood ducks passed through the area.

Waterfowl hunting season opened 15 November. Wood ducks on Pool II were always close enough to blinds to hear shots. During this period wood ducks were alert and extremely nervous, they vocalized less and they flushed readily. I had difficulty in observing a complete display sequence in the field, because of the constant disturbance from hunting. Vocalizations indicated that courtship occurred.

By Weeks 13-14 (21 November-4 December) the study

area was ice-covered, and except for a passage of 1500 wood ducks on 27 November, few birds used the area. During Weeks 15-17 (5-25 December) observations were limited to the captive birds in the flight pen, and courtship behavior was restricted to warmer, sunny days. Extended periods with temperatures below 5° C appeared to depress activity, though courtship occurred on one day when temperatures were near 0° C.

During January and February wood ducks were occasionally present in a loose group of approximately 50 birds. Courtship and vocalizations occurred on sunny days. During 1-13 March temperatures rose above 0° C and the ice and snow cover began melting. Wood ducks dispersed from flocks as pairs and in small groups. I saw nest searching activities for the first time on 14 March. Nest searching probably began about 1 March, because the earliest date of nest initiation was 12 March, and earliest date for incubation was 22 March. After 14 March most wood ducks were paired or were in small groups of 2-3 pairs.

Nest searching and nesting activities were obvious throughout April and into early May. I saw courtship on ten occasions (in three groups and seven pairs) after 1 April. In each situation a pair was approached by other pairs or males. One situation involved a pair approached by a group of courting blue-winged teals. The male wood duck displayed and assumed aggressive postures as the pair swam away from

the group. As males abandoned incubating females, the males tended to congregate in small groups of 1-5 birds, presumably before they started to molt. Incubating females spent increasingly longer periods on the nest with fewer, shorter feeding breaks, and thus were observed less often.

By 15 May few birds were seen; most females were incubating and males were beginning to molt. Pairs were observed occasionally throughout June, usually flying or feeding.

Activities of Captive Birds

Several problems arose with observations of the captive birds. Between September and February two females and two males died of unknown causes. In at least one case, a bird flew into the side of the pen and broke its neck. These birds were replaced with wild-trapped wood ducks, with a resulting change in the social status of all birds. Five of the eight wood ducks lost their nasal saddles. To avoid the stress of recapture and remarking, the birds were identified by scars on the mandibles and the size of the white eye patch in the females.

Courtship behavior in the captive birds in the flight pen paralleled field observations with the same increase in frequency of courtship sequences and in complexity of the sequences. Captivity often made behavioral interpretations difficult. For example, the first male to complete the prealternate molt was dominant over the other males, and often

seemed to restrict the courtship activity of other males and their access to females. This dominance was no longer apparent after the first two weeks of courtship when other males were in alternate plumage. Vocalizations were not as common in the flight pen as in the wild. The females did not vocalize at sunrise and sunset. Males vocalized regularly, though often in response to a disturbance outside the flight pen. Captive wood ducks in nearby pens vocalized throughout the day.

Evidence of pairing was observed by 1 October in two birds, but the strength of the pair bond in October through November is unknown. Male G, the dominant male, and Female R mutually preened on five occasions and often displayed near each other. Male G joined in all courtship sequences in the pen, and Female R copulated with Male N on 12 November. By February, Male G and Female R were spending an increasing amount of time together while they were feeding, preening, and loafing. Male W, a subdominant male, and Female W were paired by late February. In late May when Female R began incubating, Male G prevented Male W from approaching Female W. Male G and Female W were paired through late May into June.

All other birds were paired by late February, and females were nest searching by March. In only one of three nesting attempts were eggs incubated. The incubated clutch was initiated on 5 May and at least 2 hens laid a total of 10 eggs. Incubation began on 10 May, and 8 young hatched the week of 16-24 June.

Seasonal Changes in Pairing of Wild Wood Ducks

Pairs

Numbers of pairs were initially determined from daily observations of each bird's sex and behavior. Data from roost counts were not used in determining the numbers of paired birds. The first pairs were evident during September, when 5 percent of all birds were paired (Table 2). Pairs increased to 14 percent in October and 27 percent in November. Very few birds used the area in December and no estimate of paired birds was made. Four percent of all birds appeared to be paired during January and 13 percent in February. From mid-January to early March ice forced wood ducks into a small area of open water. Concentrations of birds on these small sites made pairs difficult to distinguish. In March after the ice melted and nesting activities began paired birds increased to 66 percent. A pairing peak (76 percent of all birds) was reached in April, coinciding with the peak of nest initiation. Paired birds decreased to 67 percent in May as males abandoned incubating females. All increases and decreases for spring and fall were significant ($P < 0.05$).

An uneven sex ratio could bias the estimates of percentage of birds paired; therefore, the percent of females paired was determined. Paired females increased from 18 percent in September to 60 percent in November (Table 2). Percent of females paired dropped to 45 during January and February, but then increased to 83 percent in March and 95 percent in May.

Table 2. Percentage of paired wood ducks and paired females in southeastern Missouri between 29 August 1977 and 15 May 1978.

Month	Total Numbers		Number Paired		Percent Paired	
	All Birds	Females	All Birds	Females	All Birds	Females
August	59	0	0	0	0	0
September	1436	256	72	36	5	18
October	487	60	68	34	14	67
November	232	52	62	31	27	60
December	6	0	0	0	0	0
January	448	22	20	10	4	46
February	379	56	50	25	13	45
March	1027	413	682	341	66	83
April	680	281	514	257	76	91
May	113	40	76	38	67	95

Groups

Group size, composition, and activity changed through the season. A group included any association of one or more wood ducks that was not a single pair. Group size decreased during the fall from 8.4 birds in August to 5.4 birds in November (Table 3). In January, when birds concentrated in small areas of open water, group sizes averaged 16.8. Group size decreased to 3.9 in March at the time the ice melted, and to 1.5 in May when most females were paired.

Groups were separated into non-displaying/non-vocalizing (NDV) and displaying and/or vocalizing (DV) categories. The NDV groups decreased from 8.5 in August to 4.25 in November, and from 22.4 in January to 1.46 in May. The DV groups changed from 8.0 in August to 10.5 in October and to 8.7 in November, and from 9.3 in January to 6.2 in March and to 4.0 in April. Differences (Mann Whitney U tests, $P < 0.05$) between sizes of DV groups (mean=9.30) and NDV groups (mean=6.59) occurred in the fall, August through December, and in the spring, January through May (means=13.8 and 4.05, respectively).

Group sizes are more variable in fall than in spring. A frequency distribution of group sizes illustrates the most common group size of non-vocalizing groups in the fall was 4, and of vocalizing groups was 4, 5, and 7 (Figure 1). During spring the most common group sizes were 1 bird for non-vocalizing groups and 3 for vocalizing groups.

Table 3. Average number of wood ducks in displaying, non-displaying, vocalizing, and non-vocalizing groups by month from 29 August 1977 to 15 May 1978.

Month	Display	Non-Display	Vocal	Non-Vocal	Total
August	0.00	8.43	8.00	8.50	8.43
September	9.45	6.76	8.96	6.74	7.01
October	7.57	8.10	10.50	7.05	8.04
November	16.25	3.97	8.66	4.25	5.41
December	0.00	6.00	6.00	0.00	6.00
January	11.87	19.05	9.27	22.40	16.85
February	33.20	8.20	26.00	6.37	12.68
March	0.00	3.95	6.25	3.87	3.95
April	4.50	2.04	4.00	2.03	2.09
May	0.00	1.46	0.00	1.46	1.46
Total					
Fall	9.90	6.74	9.30	6.59	7.05
Spring	18.00	4.22	13.80	4.05	4.86

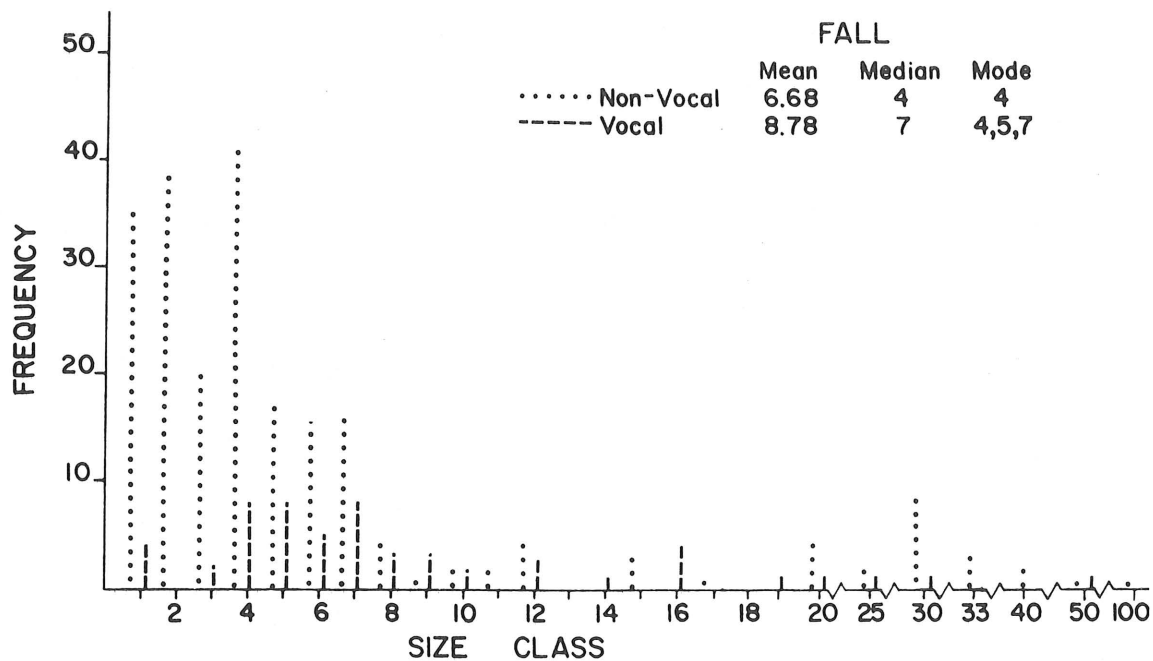
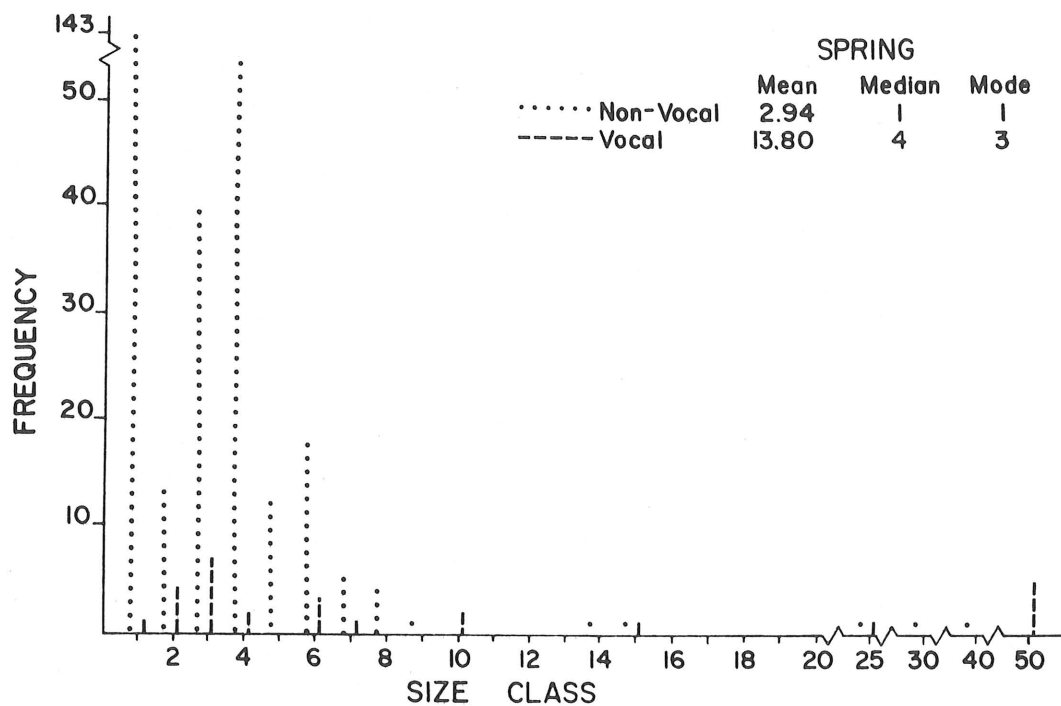


Figure 1. Size class distribution of vocalizing and non-vocalizing groups of wood ducks fall 1977 and spring 1978.

Sex Ratios

Sex ratios (males:females) increased throughout the fall and spring (Table 4). Displaying groups in fall and spring had higher ($\underline{P}<0.005$ and $\underline{P}<0.001$, respectively) sex ratios than non-displaying groups. Vocalizing groups also had higher ($\underline{P}<0.001$) sex ratios than non-vocalizing groups in fall and spring. A higher ($\underline{P}<0.001$) sex ratio occurred in spring than in fall for non-displaying, non-vocalizing, and overall averages of groups in all categories.

Unpaired Birds

Unpaired birds were censused by recording single birds and single-sex groups. During the fall 9 single females and 13 single males were observed (Table 5). Single-sex groups contained 50 females and 18 males. During the spring 48 single females and 90 single males were observed. Single-sex groups included 36 males and no females.

Activities of Groups and Pairs

Activities of groups and pairs differed throughout fall and spring. In the fall, displaying and vocalizing were more common by groups ($\underline{P}<0.005$ and $\underline{P}<0.01$, respectively) than by pairs (Table 6). Pairs avoided groups, perhaps to reduce harassment by unpaired males. Courtship activity was exhibited by pairs during copulation or in response to intruding birds. Spring groups all displayed more ($\underline{P}<0.001$) than pairs.

Table 4. Sex ratios in displaying, non-displaying, vocalizing, and non-vocalizing groups of wood ducks between August 1977 and May 1978.

Month	Display	Non-Display	Vocal	Non-Vocal	Total
September	1.94*+	0.81*	1.88	0.69	1.04
October	2.31+	1.68	2.50	1.38	1.94
November	3.42 Σ	1.87 Σ	3.00 Φ	1.67 Φ	2.55
December	--	--	--	--	--
January	4.00	2.00	3.75	2.00	2.78
February	1.87	2.25	1.80	7.10	1.97
March	--	1.38	2.43	1.30	1.38
April	2.00	2.04	1.75	2.06	2.04
May	--	7.25	--	7.25	7.25
Fall	2.24 Π	0.97 Π^{\wedge}	2.17 Π	0.80 ΠT	1.31 Δ
Spring	2.33 \S	1.79 \S^{\wedge}	2.20 ℓ	1.78 ℓT	1.88 Δ
Total	2.27 Ω	1.35 Ω	2.18 E	1.26 E	1.55

* + Σ Φ Π \S Ω \wedge Π ℓ E T Δ

refer to significant difference ($P < 0.001$) between two values, using X^2

Table 5. The occurrence of unpaired wood ducks singly and in single-sex groups, September 1977 through May 1978.

Month	Singles		Groups	
	F	M	F	M
September	6	8	50	14
October	0	1	0	4
November	3	4	0	0
December	0	0	0	0
January	1	6	0	2
February	0	3	0	2
March	18	28	0	0
April	26	42	0	20
May	3	11	0	12

Table 6. Activities of groups and pairs of wood ducks in southeastern Missouri Fall 1977 and Spring 1978.

Season	Condition	Number	<u>Displaying</u>		<u>Vocalizing</u>	
			No.	%	No.	%
Fall	Groups	199	31	15	54	27
Fall	Pairs	97	1	1	11	11
Spring	Groups	327	15	5	27	8
Spring	Pairs	666	7	1	82	12

Birds in groups displayed and vocalized more ($P < 0.001$) in the fall than in the spring. Activities of pairs were similar regardless of season. As the season progressed displays and vocalizations decreased concurrently as displaying groups became less common and the numbers in these groups decreased. In late spring few groups were involved in courtship activity. The prevalent activity was feeding or nest searching by groups of 2 or 3 pairs.

Display Rates

Display sequences were analyzed for changes in duration of each sequence through the season, number of displays per minute, and percent time spent displaying (Table 7). Minutes per sequence and percent time displaying increased from September through November. Sequences were longer ($P < 0.05$) in the fall than in the spring (1.89 vs. 1.0 minutes).

Weather

Courtship was observed at all times of the day and during all types of weather, but appeared to be inhibited when temperatures rose above about 30° C or fell below about -15° C. Wind stronger than about 24-32 kph (15-20 mph) inhibited activity, but its effects were difficult to interpret because birds may have used denser areas of timber where observations were difficult. Lack of open water during cold weather inhibited courtship in captive birds during February until open water was provided artificially. Abbreviated

Table 7. Display rates of courtship sequences observed
during field observations September 1977 to May 1978.

Month	No. of Sequences	Min. per Sequence	Displays per Minute	Percent Display Time
September	36	1.78	3.56	25
October	4	1.50	1.33	35
November	6	2.83	2.71	42
December	0	--	--	--
Fall Total	46	1.89	3.24	28
January	2	1.00	3.00	18
February	7	1.00	2.57	39
March	0	--	--	--
April	3	1.00	3.00	100
May	0	--	--	--
Spring	12	1.00	2.75	36

displays and very short (less than 15 seconds) display sequences were observed in captive birds standing on ice and snow.

Chapter VI

DISCUSSION

The relationships between pair formation, breeding strategy, and habitat characteristics can be demonstrated in a model (Figure 2). Three important habitat characteristics include limited numbers of cavities, dense vegetation, and fluctuating water levels. The energy requirements of the breeding female, combined with the habitat, influence the development of the breeding strategy and pair formation.

In a cavity-nesting species the number of available cavities can be a limiting factor. Early pairing is advantageous, allowing females to use available nest sites (Orians 1969). Fall courtship results in strong pair bonds lasting through the winter. The male is available to protect the female as she feeds, so she may meet energy requirements and be ready to nest when weather conditions become favorable in early spring. Adult males pair earlier than yearling males (Korschgen 1972), and after abandoning early nesting females are also available to fertilize females for renesting and second nesting attempts.

Courtship behavior reflects the stage of pair formation. Copulation functions in pair maintenance rather than in pair formation, as in the mallard (Johnsgard 1960). The change in female Bill Jabbing from an aggressive display to one associated with pair maintenance reflects the changes in

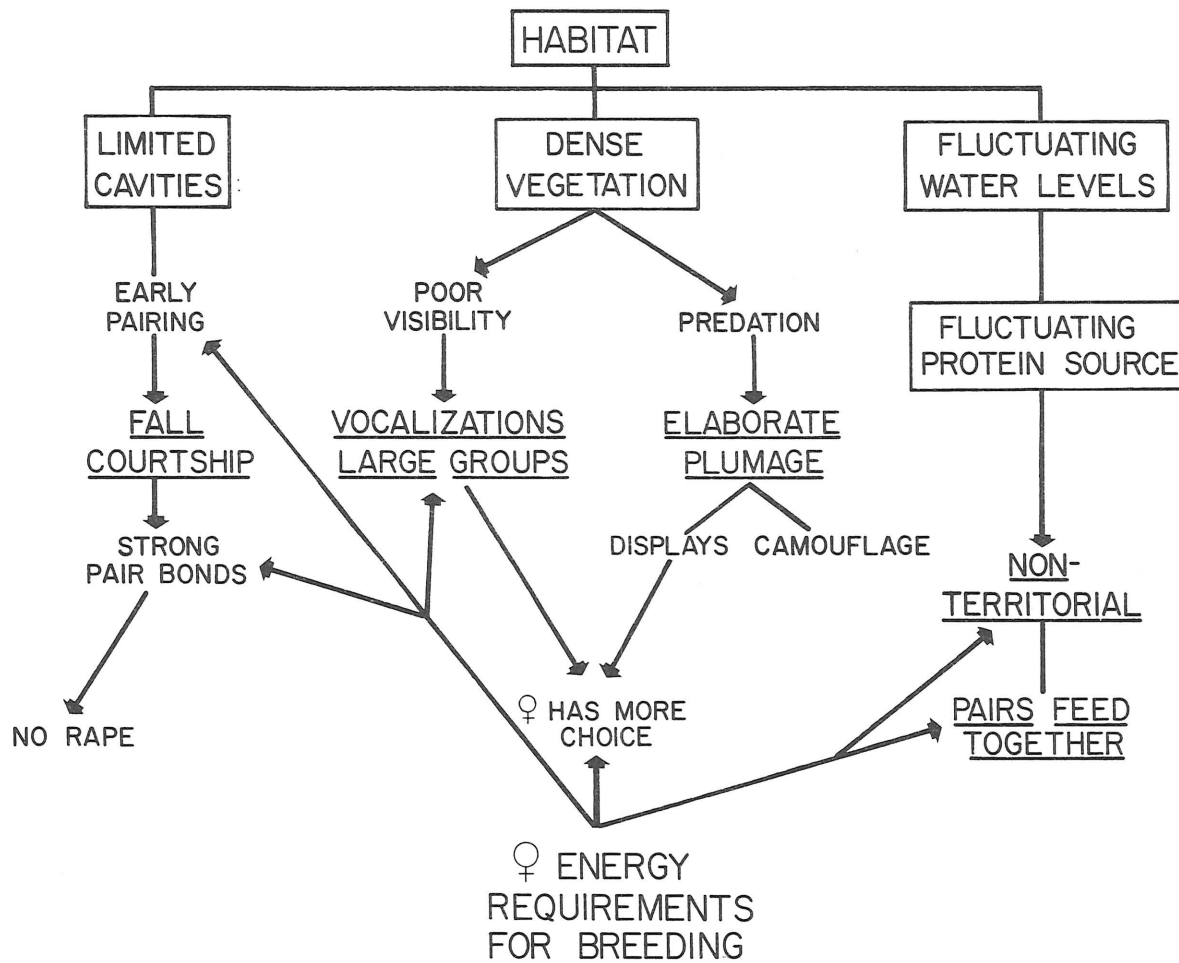


Figure 2. Model demonstrating relationship between pair formation, breeding strategy, and habitat characteristics.

female responses toward her mate and other males throughout the pair formation period. The Supplanting Display of the fall may be derived from spring nest searching, or may be similar to tendencies of white-winged wood ducks to begin display sequences in trees (M.J. S. Mackenzie pers. comm.).

In a densely vegetated habitat where visual signals are of limited value the importance of vocalizations in a gregarious species greatly increases. Vocalizations function to concentrate, orient, and synchronize birds for courtship activity. Female wood ducks attract males with vocalizations. In contrast, females of Anas species such as the mallard or pintail in more open habitats exhibit few attracting vocalizations since birds can be attracted by visual signals (Johnsgard 1965:167). As opposed to Lorenz's (1971) conclusion concerning courtship of wood ducks, I believe social display involving many males and females throughout the fall is important to wood duck pair formation, as in mandarin ducks and other anatids. Concentrations of courting birds result in large vocalizing and displaying groups that increase in size through the courtship season. An excess of males in the population results in higher sex ratios in vocalizing and displaying groups and an increase in sex ratios of all groups as increasingly more females become paired. During spring, vocalizations decrease, length of courtship sequences decreases, the number of groups displaying decreases, and group size decreases, allowing females the opportunity to feed unmolested and maintain proper breeding condition.

The function of elaborate male plumage in a species with no closely related sympatric species has caused some controversy. Dilger and Johnsgard (1959) theorize the female wood duck has an unrefined set of releasing mechanisms, responds slowly to courtship activity, and forms hybrids readily. Therefore males evolved elaborate plumage and courtship displays to stimulate females. In contrast to the theory, this study indicates the female takes an active part in courtship. Full alternate plumage and vigorous courtship activity are characteristic of a healthy male in full breeding condition. Differences in plumage, and timing, posture, and orientation of courtship displays, can be detected between yearling and adult male wood ducks (Korschgen and Fredrickson 1976). Females mate with adult males more readily than with yearlings. It is advantageous for a female to attract many males to her and to stimulate them to court, to provide her with a large selection of potential mates (Cox and LeBoeuf 1977). Loud, attracting female vocalizations insure a large number of choices at a low level of energy expenditure.

The male plumage has developed as a balance between being gaudy at short distances and yet camouflaged from predators in the dense vegetation. The white and irridescent feathers are cryptic when the disruptive color pattern is viewed in flooded timber with intermittent sunlight.

Territories in many species of anatids provide an area for a pair to nest or feed, isolation of a breeding pair to

reduce interference from other birds, and dispersion of nests to reduce predation (Welty 1975:226). The fluctuating water levels of the bottomland hardwood environment result in a fluctuating supply of protein for the female. To exploit the invertebrate food resources needed for egg production the wood duck must be highly mobile. The nesting and feeding habits of the wood duck do not require territories, since defense of a fluctuating food resource is energetically unfeasible (Brown 1964). Nesting density is regulated by nest cavity availability and the availability of a protein source. Territory in the wood duck is limited to male defense of the female and female defense of the nest site.

Pair bonds that are formed early allow the female to attain proper nutrition for breeding early in the season. When breeding condition is reached early females can use cavities before their competitors. Strong pair bonds insure the male is available to accompany the female during feeding periods before, and throughout laying and during early incubation. The pair bond in the wood duck differs from other anatids because of characteristics of the habitat and lack of territoriality. The male defends his mate from aggressive and sexual encounters, but allows other pairs to feed nearby after a minimum distance is established with aggressive postures. This tolerance enables many females to exploit the fluctuating invertebrate population. Members of a pair remain alert, attentive, and closer to each other

than to other birds, though members of two pairs may intermingle while feeding or nest searching.

Chapter VII

CONCLUSIONS

Pair formation chronology and courtship are adapted to a dynamic environment of dense vegetation with fluctuating water levels. Early pair formation allows exploitation of available nest sites, and strong pair bonds afford protection for the female while foraging to meet energy requirements for breeding. Development of courtship behavior has been influenced by the habitat characteristics. The ability to court in a variety of environmental conditions results in courtship occurring throughout the day, regardless of the portion of the habitat being used for feeding, preening, or loafing. Adaptability in a changing environment is an important component of the courtship and breeding strategy of the wood duck.

Chapter VIII

SUMMARY

Chronology of pair formation was studied by observation of courtship behavior throughout the year in the wild.

Courtship activities occurred from mid-September through April, in all types of weather except when winds exceeded about 32 kph and when temperatures rose above about 30° C or fell below about -15° C. When flooded timber was not available, courtship occurred in open water areas.

Female vocalizations are important in attracting males and initiating display sequences.

Three unreported behavior patterns are discussed.

Sixty percent of the females were paired by November, increasing to 95 percent in May.

Vocalizing and displaying groups were larger and had higher male:female sex ratios than non-vocalizing and non-displaying groups. Group size decreased in spring.

Groups displayed and vocalized more than pairs.

Pairs avoided groups, and vocalized or displayed rarely.

Length of courtship sequences and number of groups displaying decreased in spring.

Captive birds indicate pairs last throughout the winter. Serial polygamy may occur after a female begins incubation.

Copulations are important in pair maintenance and occur more in spring. Rape does not occur.

The male plumage stimulates females and offers a basis for choosing between potential mates, yet is cryptic in dense vegetation.

Extra males test pair bonds and along with paired males are available to fertilize females for renesting attempts.

A pair consists of a male and female that remain alert, attentive, and close to each other more than to other birds. The male defends the female from aggressive and sexual encounters but will tolerate intermingling with feeding or nest searching pairs.

Early pair bonds are favored by limited cavities and a fluctuating food source.

Energy requirements of the female for nesting favor strong pair bonds and non-territoriality.

A model is presented, illustrating the relationships between pair formation, breeding strategy, energetics of the breeding female, and habitat characteristics.

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