

WOOD DUCK DISPLAYS AND PAIRING CHRONOLOGY

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ABSTRACT.—Wood Ducks (*Aix sponsa*) in southeastern Missouri court and form pairs from September to May. Courtship bouts occurred in groups averaging 11.4 birds, with a male : female sex ratio of 2.24:1. Several new displays and vocalizations are described. The length of display sequences decreased from 1.9 min per sequence in the fall to 1.0 min per sequence in the spring. By 30 November, 60% of all females were paired. Early pair bonds appeared tenuous and were continually tested until nest-searching activities began in March. Birds in groups displayed and vocalized more than paired birds, and birds displayed and vocalized more in the fall than in the spring. Early pairing may be related to a bird's condition, success in obtaining a nesting site, and increased productivity. Received 15 January 1980, accepted 1 July 1981.

THE ethogram of the Wood Duck (*Aix sponsa*) is incomplete. A description of Wood Duck vocalizations and courtship displays is given by Heinroth (1910), Lorenz (1951–1953), and Johnsgard (1965: 111). Males court one female with little social display relative to *Anas* species (Lorenz 1951–1953). Forbush (1912) stated that Wood Duck pair formation in the southern U.S. occurs from December through February. Courtship and copulation have been recorded in North Carolina as early as 13 October (Hester and Dermid 1973: 38), however, and in southeastern Missouri captive Wood Ducks courted in the fall and spring (Korschgen and Fredrickson 1976). An increase in the number of pairs counted in roost flights through the fall indicated that courtship activity may begin soon after completion of the prealternate molt (Korschgen 1972). Information is lacking on the chronology of pair formation and strength of pair bonds, because most published studies have concerned only spring courtship behavior. This study was designed to determine the chronology and mechanism of pair formation in wild Wood Ducks observed throughout the year.

STUDY AREA AND METHODS

Study sites were on the Duck Creek Wildlife Management Area and the Mingo National Wildlife Ref-

uge in Bollinger, Stoddard, and Wayne counties in southeastern Missouri. Duck Creek encompasses 2,480 ha, including three pools of flooded timber where water levels are manipulated throughout the year. Mingo Refuge is contiguous with the southern and western boundaries of the Duck Creek Area. Its 8,745 ha include bottomland hardwoods with naturally fluctuating water levels. Characteristic vegetation has been described by Korte and Fredrickson (1977). Nest boxes on the Duck Creek Area are used by approximately 200 breeding female Wood Ducks. The nest boxes are also used by Hooded Mergansers (*Lophodytes cucullatus*). Earlier nesting by Hooded Mergansers relative to Wood Ducks decreases the likelihood of competition between the two species. The importance of nesting in natural cavities is unknown.

Field observations were conducted August–November 1976 and 1977, and January–May 1978. Wood Duck courtship was recorded from a portable tree blind or while I was concealed in vegetation or in the open. Records were kept on courting group sizes, sex ratios, displays, copulations, vocalizations, and weather conditions. A "group" included a single bird or any association of more than one Wood Duck that was not a single pair. Pairs were determined by male attentiveness to the female and female tolerance of the male. No birds were marked. Repetitive observations undoubtedly were made of groups or pairs.

Daily observations were conducted for 1–5-h periods from 0.5 h before sunrise until 1100 CST and from 1400 CST until 0.5 h after sunset, totalling over 1,000 h of observations. Fewer hours were spent observing in December and January, when cold temperatures and lack of open water reduced the number of Wood Ducks on the study area. Behavior during midday was monitored periodically and was generally limited to loafing, preening, and foraging.

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Groups of birds were separated into nondisplaying and displaying categories. Data were analyzed for group size using ANOVA, for sex ratios and activities using the Chi-square test, and for display rates using the Mann Whitney *U*-test (Sokal and Rohlf 1973, Conover 1971).

RESULTS

During field observations, 5,124 Wood Ducks were encountered on 1,217 occasions (635 groups and 763 pairs). Courtship was observed 82 times.

Display bouts.—Display bouts consisted of a series of display sequences in which the intensity of sexual excitement progressively increased. Courtship displays described by Lorenz (1951–1953) and Johnsgard (1965) were observed, including Drinking, Preen-Behind-the-Wing, Burping, Chin-lifting, Turn-the-back-of-the-head, Display Shake, Wing-and-Tail-Flash, and Inciting. The Introductory Shake was the only courtship display not observed.

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 displayed and 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 dorsum or of feeding, ending the display sequence. More vocalizations and aggressive postures followed as the level of sexual excitement increased again, and another display sequence began. The length of display sequences ranged from 1 to 20 min, interspersed with 1–90 min of preening or feeding. Display bouts 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.—Aggression is an important functional component of courtship. A behavior pattern that I call the Rush is a form of aggression performed by 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. A bird Rushed with the bill open, accompanied by splashing with 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 occurred rarely. Males Rushed each other, sometimes so vigorously that a male was driven from the courting party. The Rush appears to be synonymous with the Hunched Rush in the Ruddy Duck (*Oxyura jamaicensis*), as described by Johnsgard (1965). During the fall, females Rushed on 24 occasions and males on 30. In the spring, females Rushed only once, but males Rushed on 30 occasions. One distinct difference between fall and spring courtship is that physical contact or beating with the wings commonly occurs in spring but not in fall.

A second important display, which 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. The chin is not displayed, as it is in the Bill Jerk, Chin-lift, or Down-up. The display may have similarities to Water-twitching in the Mergini (Johnsgard 1965), except the head movement in Wood Ducks is vertical, with the bill pointed at the water, rather than lateral. Both sexes vocalize during the display: males with a rapid "jibjibjib" and females with a "dihdihdih" that rises in pitch and rapidity as the 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.

Vocalizations.—Two vocalizations, the Hawk and the Coquette Call, have been described for females by Lorenz (1951–1953) and are given commonly during early morning hours and at sunset. Both calls carry well over open water or through timber. Males as far as 0.8 km away react to these calls by swimming toward the calling female. The Hawk call appears to advertise a female's presence and is usually given when females swim or fly into an area or approach a group of males. The Coquette Call is given during courtship and appeared to stimulate other Wood Ducks to join a courting group. The "te-te-te" vocalization described by Lorenz (1951–1953) was heard during nest searching. A fourth vocalization, not described in the literature, is given during intense courtship activity and during sequences when a female is Inciting or Bill Jabbing. The call is a soft, rapid "dihdihdih" and resembles the "te-te-te" vocalization. The Hawk, Coquette Call, and "dihdihdih" vocalizations appeared to coordinate social activity, and I used them as an index to the intensity of courtship activity.

The most common vocalization of the male Wood Duck was a drawn-out whistling "Jiib," which carried for short distances. Variations of this call express alertness or a warning. The "Pfit" vocalization of the Burp posture was heard frequently. The "jibjibjib" vocalization was heard during nest-searching activities. These three vocalizations have been described by Lorenz (1951–1953). A variation of the "jibjibjib," not discussed in the literature, was given during Bill Jabbing and indicated courtship of high intensity.

Copulations.—Copulation was observed once in the fall, on 13 October, and involved an isolated pair. During simultaneous studies of wild-trapped Wood Ducks, copulation was observed twice in the fall and 20 times in the spring (Scherpelz 1979). All copulations involved paired birds that were isolated from other birds. Pre- and post-copulatory displays observed included all those described by Lorenz (1951–1953), Johnsgard (1965), and Korschgen and Fredrickson (1976). Pre-copulatory displays included the Prone position by the female and Facing, Bill-Dipping, and Drinking by the male. Post-copulatory displays included Bathing by the female and Turn-the-back-of-the-head, Facing, and Wing-and-Tail-Flash (Korschgen and Fredrickson 1976) by the male. Preen-Behind-the-Wing was observed,

along with Facing, as post-copulatory displays on 13 October. Females assumed the Prone position 118 times, but only 23 copulations occurred. In one attempt an unmated male was unsuccessful in mounting a mated female. Rape was not observed.

Seasonal changes in courtship activity.—During 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. Many hatching-year birds were still in juvenal plumage, and over 50% of all-aged males were still in the prealternate molt.

By 6–12 September, over 50% of the males were in full alternate plumage. Main activities still included foraging, loafing, and body maintenance. Aggression occurred only when birds were at high densities.

During 13–19 September, over 90% of the males were in alternate plumage. Little change in activity was noted except for an apparent increase in the level of alertness by males in alternate plumage. By 20–26 September, all males had completed the prealternate molt. As the alternate plumage was attained, aggressive encounters increased. Courtship displays were first recorded on 21 September. This corresponded to temperature changes from a daily high of 33°C for 20 September to 23°C for 21 September and overnight lows of 17° and 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 (Lorenz 1951–1953, Johnsgard 1965: 111), and the Rush. On 23 September, Inciting was first observed. Temporary associations of males and females became courting parties in which pair bonds appeared to be formed and continually tested. During this period, "pairs" lasted from 10 min to several hours. Though Wood Ducks were not marked, pairs in small groups could occasionally be identified throughout an observation period. Concurrent observations of wild-trapped, individually marked Wood Ducks substantiated changes within pairs. Females took an active part in courtship, vocalizing continually, and this seemed to stimulate other birds to display or become aggressive.

TABLE 1. Monthly occurrence of Wood Duck pairs in southeastern Missouri between 29 August 1977 and 15 May 1978.

Month	Total observed		Percentage paired	
	All birds	Females	All birds	Females
August	59	0	0	0
September	1,436	256	5	18
October	487	60	14	67
November	232	52	27	60
December	6	0	0	0
January	448	22	4	46
February	379	56	13	45
March	1,027	413	66	83
April	680	281	76	91
May	113	40	67	95

Courtship activity continued throughout the fall. By 21 November, the study area was ice-covered, and most birds departed.

During January and February, Wood Ducks were present occasionally in a loose group of approximately 50 birds. 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. The earliest date of egg laying was 12 March, and the earliest date for initiation of incubation was 22 March (Fredrickson, unpubl. data). After 14 March most Wood Ducks were paired or were in small groups of 2–3 pairs.

Nest searching and nesting activities occurred throughout April and into early May. I saw courtship on 10 occasions (in 3 groups and 7 pairs) between 1 April and 15 May. In each situation a pair was approached by other pairs or males, and the mated male responded to the intrusion with an aggressive courtship display.

Chronology of pair formation.—Paired birds increased from 5 to 27% of total birds between 1 September and 30 November (Table 1). From late November to early March, ice forced birds into small open-water areas, and this made pairs difficult to distinguish.

In mid-March when nesting activities began, 66% of the Wood Ducks were paired. During the peak of nest initiation in April (Fredrickson, unpubl. data), 76% of all Wood Ducks were paired, but pair counts decreased to 67% of total ducks in May, when pairs were separated during laying and incubation and males eventually abandoned incubating females.

TABLE 2. Duration of Wood Duck courtship sequences observed by month and season from September 1977 to May 1978 in southeastern Missouri.

Season	Month	Number of sequences	Minutes per sequence	Standard deviation
Fall	September	40	2.0	1.3
	October	6	1.3	0.816
	November	2	2.5	0.707
	December	0	—	—
	Total	48	1.9	1.245
Spring	January	2	1.0	0
	February	7	1.0	0
	March	0	—	—
	April	3	1.0	0
	May	0	—	—
	Total	12	1.0	0

Paired females increased from 18 to 60% between September and November. Over winter (January–February) only 45% of the females were paired, but by spring most were paired (March = 83%, May = 95%).

Seasonal changes in the duration of display sequences were noted (Table 2). The lengths of display sequences were longer in fall than in spring (1.9 vs. 1.0 min) (Mann Whitney *U*-test, $U = 150$, $P < 0.05$).

Group size fluctuated from 9.7 to 6.1 birds between August and November (Table 3). In February, when birds concentrated in small areas of open water, group sizes averaged 13.4. This decreased to 3.8 in March as more open water became available and to 1.5 in May when most females were paired and pairs were dispersed for nesting.

The size of nondisplaying groups fluctuated from 9.7 to 4.6 birds between August and November, rose in January and February, and subsequently declined after March (Table 3). A similar pattern occurred for displaying group sizes. Fall groups were significantly larger than those in spring (ANOVA, $F = 14.149$, $P < 0.0001$), and nondisplaying groups were significantly larger than those displaying (ANOVA, $F = 24.876$, $P < 0.0001$).

The ratio of males to females in Wood Duck groups increased throughout the fall and spring (Table 4). Displaying groups in fall had greater numbers of males ($\chi^2 = 24.736$, $P < 0.005$) than did nondisplaying groups. Vocalizing groups also had greater numbers of males ($\chi^2 = 37.843$, $P < 0.001$) than did nonvocalizing groups in fall. There were more males per

TABLE 3. Monthly and seasonal mean group sizes of displaying and nondisplaying Wood Ducks from 29 August 1977 to 15 May 1978 in southeastern Missouri.

Season	Month	Display			Nondisplay			Total	
		<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}
Fall	August	0	—	—	7	9.7	10.63	68	9.7
	September	20	9.5	6.36	175	6.8	10.31	195	7.0
	October	7	7.6	3.51	52	9.3	11.20	59	9.1
	November	4	16.3	9.88	27	4.6	5.36	31	6.1
	Total	31	9.9		261	7.1		292	7.4
Spring	January	8	11.9	17.26	27	5.9	11.51	35	7.3
	February	5	33.2	23.05	27	9.7	13.34	32	13.4
	March	0	—	—	133	3.8	5.14	133	3.8
	April	2	4.5	2.12	115	2.0	1.46	117	2.1
	May	0	0	—	26	1.5	0.86	26	1.5
	Total	15	18.0		327	3.6		342	4.2

female in spring than in fall for nondisplaying ($\chi^2 = 20.409$, $P < 0.001$), nonvocalizing ($\chi^2 = 28.478$, $P < 0.001$), and combined groups ($\chi^2 = 9.648$, $P < 0.005$) in all categories.

In the fall, displaying ($\chi^2 = 14.312$, $P < 0.001$) and vocalizing ($\chi^2 = 9.494$, $P < 0.005$) were more common in groups than in pairs (Table 5). Pairs avoided groups, perhaps to reduce harassment by unpaired males. Displays were performed by pairs during copulation or in response to intruding birds. Spring groups all displayed more ($\chi^2 = 12.658$, $P < 0.001$) than pairs.

Birds in groups displayed and vocalized more ($\chi^2 = 18.72$, $P < 0.001$) in fall than in spring. Activities of pairs were similar regardless of the season. As the season progressed, displays and vocalizations decreased 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.

DISCUSSION

Fall courtship is common in Anatini. In Maryland, Black Ducks (*Anas rubripes*) formed pairs throughout the year, increasing from 10.5% paired in September to 90% in February (Stotts 1958). In the Mallard (*Anas platyrhynchos*), the most active period of display and copulation was October–November. Copulation in fall and winter strengthens bonds but is relatively unimportant in pair formation (Johnsgard 1960). American Wigeon (*Anas americana*) females in Texas are 80% paired by March (Soutiere et al. 1972). Courtship displays

occurred infrequently from November through December and increased during January.

Attainment of breeding plumage may affect the time of pairing. Blue-winged Teal (*Anas discors*) and Cinnamon Teal (*Anas cyanoptera*) acquire alternate plumage in September through December (adults earlier than juveniles), pair by January and February, and lay first eggs in May. Northern Shovelers (*Anas clypeata*) acquire alternate plumage in November through December and are paired by March. Birds in alternate plumage are the most active courtiers. 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, whereas Ring-necked Ducks (*Aythya col-*

TABLE 4. Sex ratios (males:female) in displaying and nondisplaying groups of Wood Ducks between 29 August 1977 and 15 May 1978 in southeastern Missouri.

Season	Month	Dis- play	Non- display	Means
Fall	September	1.94	0.81	1.04
	October	2.31	1.68	1.94
	November	3.42	1.87	2.55
	December	—	—	—
	Mean	2.24	0.97	1.31
Spring	January	4.00	2.00	2.78
	February	1.87	2.25	1.97
	March	—	1.38	1.38
	April	2.00	2.04	2.04
	May	—	7.25	7.25
	Mean	2.33	1.79	2.88
Grand mean		2.27	1.35	1.55

TABLE 5. Social activities of groups and pairs of Wood Ducks in southeastern Missouri between Fall 1977 and Spring 1978.

Season	Bird status	Number ^a	Displaying		Vocalizing	
			Number	%	Number	%
Fall	Groups	199	31	15	54	27
	Pairs	97	1	1	11	11
Spring	Groups	328	15	5	27	8
	Pairs	666	7	1	82	12

^a Includes only observations after 20 September.

laris) and Lesser Scaup (*Aythya affinis*) do not begin to do so until March (Weller 1965). The sequence of display and pairing correlates with the attainment of alternate plumage and laying date.

Courtship and pair formation in the Wood Duck begin with the completion of the prealternate molt in the fall. Courtship activity occurs more in fall than in spring, as evidenced by larger courting groups, longer display sequences, and a greater frequency of sequences in the fall. Lack of open water from late November through early March and the resulting concentrated groups of Wood Ducks probably resulted in a low estimate of pairs. I believe most Wood Ducks are paired by late January. Copulation in winter appeared to function in the strengthening of pair bonds. Individually marked birds would indicate the stability of Wood Duck pair bonds formed at various stages over the winter.

In southeastern Missouri nest initiation may begin as early as late February or early March (Clawson et al. 1979). In Massachusetts the earliest arrivals on the breeding grounds are paired (Grice and Rogers 1965), and in Missouri the earliest nests are initiated by adults with previous experience (Fredrickson, unpubl. data). In a cavity-nesting species, the number of available cavities can be a limiting factor. Several studies have cited the scarcity of cavities suitable for Wood Duck nesting where artificial structures have not been erected (Grice and Rogers 1965, Weier 1966). Thus, one advantage of early pairing by Wood Ducks and other species is that it allows the selection of nest sites and rapid initiation of breeding shortly after birds arrive at the nesting area (Orians 1969).

Variability in the timing of pairing may be related to age, experience, or body condition of birds. Female Wood Ducks mate with adult

males more readily than with yearlings (Korschgen and Fredrickson 1976); thus, yearling males may pair later. The lower productivity rates and lack of breeding in yearling females (Heusmann 1975, Fredrickson, unpubl. data) may relate to inexperience or inadequate nutrition; these factors may also affect the timing of pair formation.

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On page 711 of J. Cracraft, 1981, *Toward a phylogenetic classification of the recent birds of the world (Class Aves)* (*Auk* 98: 681-714), the following references were inadvertently eliminated by the printer between the production of page proofs and the final published version:

- DEBEER, G. 1956. The evolution of ratites. *Bull. Brit. Mus. Nat. Hist. (Zool.)* 4: 57-70.
- DEBOER, L. E. M. 1980. Do the chromosomes of the kiwis provide evidence for a monophyletic origin of the ratites. *Nature* 287: 84-85.

A new edition of the "International registry of poultry genetic stocks; a directory of specialized lines and strains, mutations, breeds and varieties of chickens, Japanese Quail, and turkeys" has recently been published. It describes and gives sources for specialized lines and strains, mutations, and breeds and varieties of these species, presents a listing of the known genetic traits and their gene symbols, provides chromosome linkage maps, gives a description of chicken plumage colors grouped according to the *E* locus, and lists the addresses of breeders and suppliers. Copies may be obtained for \$3.00 (postpaid) from **Ralph G. Somes, Jr., Department of Nutritional Sciences, University of Connecticut, Storrs, Connecticut 06268.**