COMPARATIVE DISPLAYS OF YEARLING AND ADULT MALE WOOD DUCKS

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EXTENSIVE studies of the behavior of the Anatidae are limited principally to species in the tribes Anatini and Mergini. The Wood Duck (*Aix sponsa*) belongs to the tribe Cairinini; and only two primary technical sources describe its behavior. The first was Heinroth's (1910) investigation of courtship behavior. Later Lorenz (1951, 1952, 1953) studied Wood Duck behavior in more detail. He noted that drake Wood Ducks court one particular hen and seldom unite in a social display. Johnsgard (1965) compiled and condensed the reports of these two previous workers. Johnsgard modified behavior terminology to agree more nearly with the current waterfowl behavior nomenclature and to indicate any relationship in display patterns within the tribes of the Anatidae. We studied the fall and spring courtship behavior of Wood Ducks to describe the general form and duration of the epigamic displays and to determine if behavioral differences exist between nonexperienced males and males that had previous courtship experience.

The courtship movements of birds, especially waterfowl, represent actions that have become highly stereotyped. Signal movements occasionally have been seen in individuals the first time they were exposed to the appropriate stimulus situation. Such movements in gulls (Moynihan 1959) and Common Goldeneye ducks (*Bucephala clangula*) (Dane and Van der Kloot 1964) are at first more variable than when their signal function is developed. Dane and Van der Kloot noted that young male Goldeneyes, still in immature plumage, had different courtship actions from adult males. Courtship movements performed by first year males were "odd" and not stereotyped in form and were sometimes so different from adult actions that they were difficult to identify. Although aberrant in form, these actions were of normal duration.

Little information is available on whether a similar pattern is found in ducks that acquire the definitive alternate plumage and breed during their first year. Members of the genus *Anas* acquire the definite alternate plumage during the first year (Delacour 1956: 20). Juvenile Pintail (*Anas acuta*), Gadwall (*A. strepera*), and South American Green-winged (or Speckled) Teal (*A. flavirostris*) have display movements that are both atypical and lacking in adults (Kaltenhauser 1971).

METHODS

This study was conducted at the Gaylord Memorial Laboratory on the Duck Creek Wildlife Management Area, Puxico, Missouri. Two adjacent triangular pens,

30 feet (9 m) on a side with a 12-foot (3.6 m) high wire top, were used. A plywood wall 4 feet (1.2 m) high enclosed the perimeter of the two pens to isolate the birds visually. Each pen contained a shallow pool 10 feet (3 m) square. The birds were viewed through one-way glass from a two-story blind.

Film was exposed with a 16-mm Bolex camera equipped with a 400-foot (120 m) film magazine and a 25-mm and 75-mm lens. A constant film speed of 24 frames per sec was maintained by a battery powered motor. Film exposed at a speed less than 24 frames per sec was automatically fogged by a clapper attachment.

Descriptions of the display actions of male and female Wood Ducks are based on 4500 feet (1364 m) of 16-mm black and white movie film. Some of the accompanying prints were made directly from the negative film. Behavior sequences were analyzed by viewing the film through a projecto-editor. The duration of each movement was determined by counting the number of frames, each frame being equivalent to 0.04 second.

A flock of 88 Wood Ducks was maintained for this study, 35 of which were adults that had experienced a least one courtship cycle and were confined in one holding pen. The yearling females were penned with the adults. Yearling males were isolated visually from all other birds used in the study when they were less than 45 days old and before they had started to acquire their definitive alternate plumage. Individuals were marked with nasal saddles of polyvinyl chloride tape (Sugden and Poston 1968).

Observations began on 14 October 1971 and ended in mid-December 1971 when courtship activity diminished. Observations were resumed on 16 February 1972 and continued until 4 May. Filming and observing usually began at first light and continued until courtship activity diminished. Periodic observations of the birds during all daylight hours revealed no behavior patterns as intense as those early in the morning.

Groups of four males and one female were used to intensify interactions and competition in each experimental test. Drakes were introduced 1 or 2 days before hens to reduce fear reactions to the pen and to establish a hierarchy prior to contact with females. Displays were recorded by sex.

RESULTS

MATE SELECTION

Immediately after a hen was introduced into a pen, all four drakes showed awareness of her presence. One of the two birds highest in the hierarchy usually made the first contact with the hen and preened her back or head. If the female did not threaten the male as he preened her, the drake followed her. Usually only two of the four drakes indicated an active interest in the female and established the first indications of a pair bond within ½ h after her entrance into the pen. When the hen began comfort movements such as bathing, body shaking, tail-wagging, bill-dipping, and preening, the preferred drakes (males that the hen did not incite against) remained near her. Preferred drakes also defended the hen by aggressively pecking and chasing other drakes. Eventually the hen allowed only one of the preferred drakes to approach her closely as she made low intensity inciting movements towards other drakes. In all

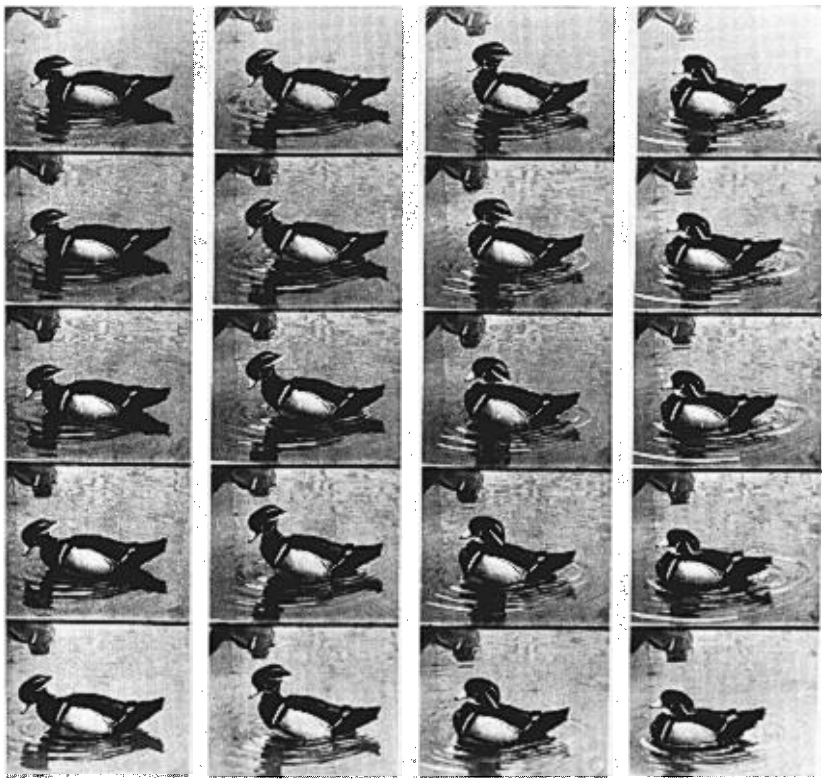

Fig. 1. Display shake by a yearling drake. The display starts at the upper left, continues in sequence in vertical columns and ends at lower right.

but one of eight pair formation experiments the hen chose the dominant drake as a mate.

Homosexual pair bonds formed between unmated yearling drakes. Drakes performed displays oriented towards each other. Bonds were developed between drakes to the extent that precopulatory displays and attempted mountings occurred.

Displays of the Male

Male pair maintenance displays were not important for mate selection but functioned to establish and maintain a pair bond. We observed no major displays by males that were not reported in the literature but recorded a variation of the preen-behind-the-wing display and the performance of displays in unreported situations. Males never performed displays in a simultaneous or synchronized manner. Specific male displays are

analyzed below. Duration of movements include both adult and yearling displays unless otherwise noted.

Display shake (Fig. 1).—Duration (mean 0.76 sec, $S_{\bar{x}} = 0.007$), 2 analyzed.

Most display shakes occurred during display bouts. Displays were performed by drakes either paired with the hen or involved in a trio with another drake and the hen. The drake oriented himself broadside to and within 2 feet of the female so that he faced her side.

The male prepares for this action by erecting the crest, lowering the head, and remaining motionless for several seconds. The display starts with an extending and lowering of the head. Once the head is extended anterior to the body, the breast is raised from the water and the white belly is exposed. The head is arched swiftly upwards and backwards. At the peak of the display the head is held high and the bill points downward so the chin is touching the neck, and the breast is still high out of the water. The display terminates when the bird lowers his head and the body resumes a normal swimming posture. A tail wag occasionally follows the display.

Preen-behind-the-wing.—Duration (mean 0.86 sec, $S_{\bar{x}} = 0.009$), 29 analyzed.

Preen-behind-the-wing is initiated with a stereotyped sequence of movements. The drake stops moving and then holds a posture for 1 to 2 sec with crest partially erected, head low, with bill resting on his breast. A ritualized drink then occurs. Water is held in the bill and often can be seen dribbling out as the head is raised to the normal position. The actual preen-behind-the-wing starts after a lapse of 0.40 to 0.75 sec. The display begins with a very fast lateral movement (0.10 sec) of the head. The orientation of the head-shaking movement is always such that the bill is pointed directly at the hen to which the display is performed. Possibly this movement is analogous to the directional bias noted in Mallards (*A. platyrhynchos*) because courting males tend to move their heads sideways towards the female during shaking movements (Simmons and Weidmann 1973). Water that was held in the bill from the preceding drink was thrown towards the hen on several occasions. Following the shaking movement, the drake returns his head to a normal position. Immediately he turns his head towards the hen as he reaches around to his back and always lifts the wing nearest the hen. The drake then reaches deep beneath the wing as the primaries are fanned to expose the white "frosting." The head returns to a normal position, and the wing is lowered onto the body.

Most adult drakes displayed preen-behind-the-wing in front of and perpendicular to the female (Fig. 2A). A Rayleigh test for distribution,

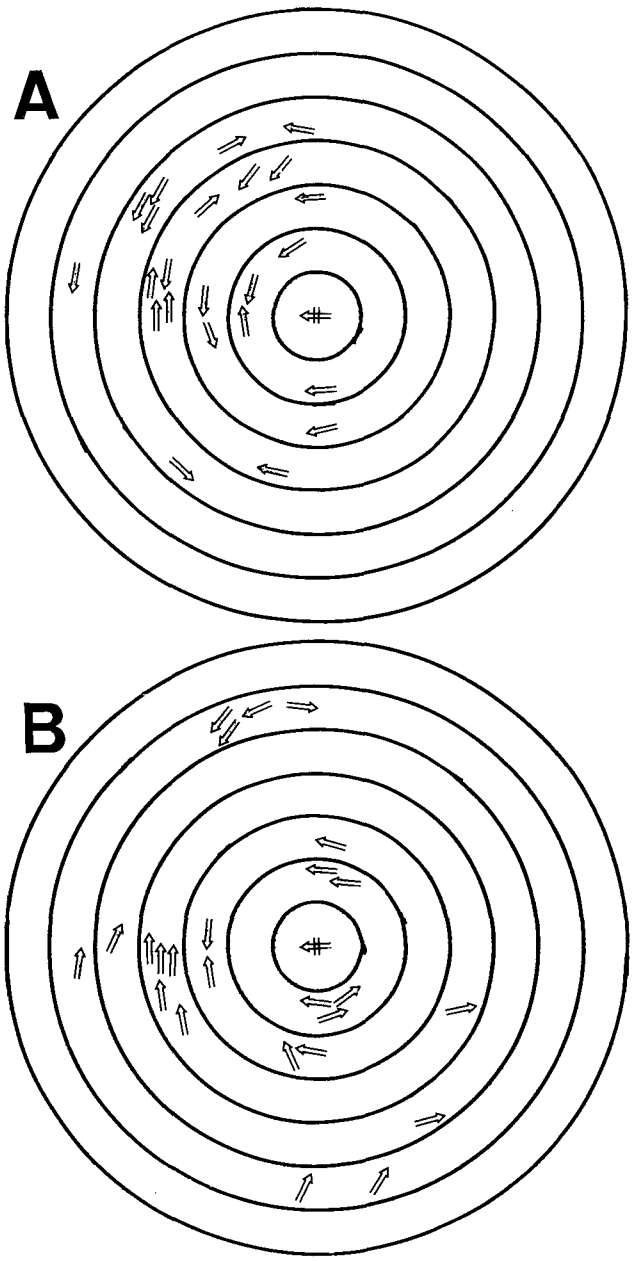

Fig. 2. Position of adult (A) and yearling (B) males (light arrows) in relation to the female (center arrow) when performing preen-behind-the-wing. Rings are 1 foot apart.

as described by Batschelet (1965), revealed that the display positions of adults are concentrated ($P < 0.01$). Some yearling drakes tended to perform farther away than adults and the Rayleigh test did not show a significant concentration of displays (Fig. 2B).

Preen-behind-the-wing normally occurred on water but did occur on land. The display was observed frequently in spring but was seen only twice during the fall.

In our experimental situation, paired males performed preen-behind-the-wing more frequently than did unpaired drakes. (This frequency was high because there were three unpaired drakes for each paired drake in the study.) Paired adults accounted for 43% of 39 preen-behind-the-wing displays. Likewise, paired yearlings performed 37% of 75 displays. The greater frequency of preen-behind-the-wing by paired males can be accounted for by the aggressiveness of the paired male because paired males often drove other males out of the pool before they could display.

Adult drakes frequently performed preen-behind-the-wing with the wing raised higher and primaries spread more than yearlings. Displays of yearlings lacked the exaggerated ritualized posture that was evident in the displays of adults.

Because preen-behind-the-wing did not occur during mate selection, we believe that this display strengthens and maintains the pair bond.

A variation of preen-behind-the-wing was noted. During this movement the drake orients his body and performs a drink exactly as in preen-behind-the-wing. A time lapse occurs between the drink and the start of the display, which is initiated with a fast lateral head shaking movement. The head is returned to the normal position and is turned immediately towards the side facing the female. Rather than reaching under a lifted wing, the male preens his back. The wing does not move from its normal position under the flank feathers. Seven of these movements had a duration of 1.57 sec, $S_{\bar{x}} = 0.19$. Possibly this movement is analogous to the preen-dorsally as Johnsgard (1965) described in many species of Anatinae.

Wing-and-tail-flash (Fig. 3).—Duration (mean 0.31 sec, $S_{\bar{x}} = 0.008$), 15 analyzed.

In wing-and-tail-flash, drakes orient themselves broadside to the female as in performing preen-behind-the-wing. The drake becomes motionless in the water and assumes a posture with head low and the bill on the chest. The crest is erected so that the feathers on the back of the head extend straight out and the bill is tipped downward exposing the entire crest. The pupil of the eye dilates, which decreases the amount of red color in the iris. The display action begins with a quick vertical forward lifting of the

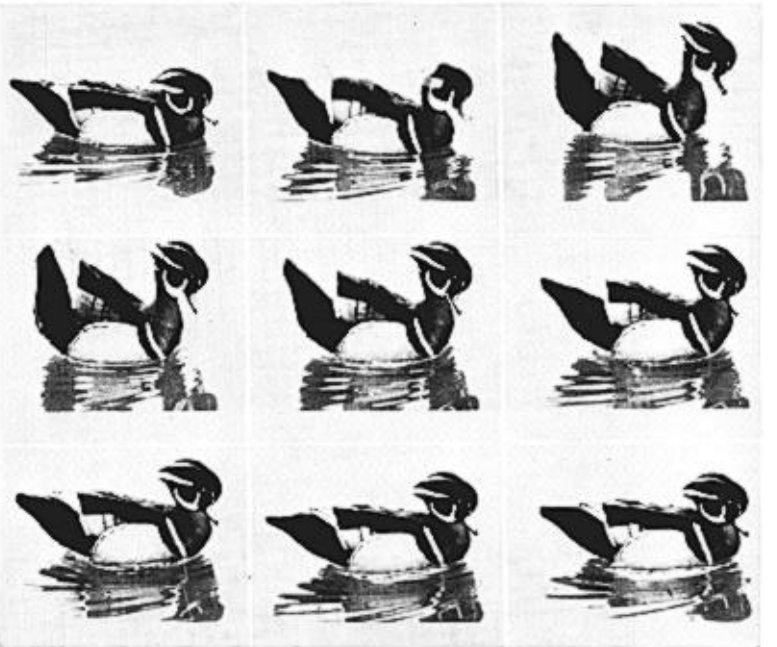

Fig. 3. Wing-and-tail-flash of an adult drake. The display starts at the upper left, continues in sequence in horizontal rows and ends at lower right.

head, so that the point of the crest on the back of the head is pointed upward. A gutteral vocalization is made as the neck is stretched. During the upward movement, the drake may point his bill towards the hen to which he is displaying. The slight head-shake towards the female, if it is a component of every wing-and-tail-flash display, is quite fast, lasting less than 0.04 sec. (No reference to a head-shake as a part of wing-and-tail-flash was found in the literature.) The wings are then lifted from the body and the tail is cocked vertically as the head rises. At the climax of the display the crest, wings, and tail form sharp pyramids projecting upward. Movement is so rapid that filmed sequences were blurred. The wings and tail are then lowered. The head is lowered at the same angle as when it is raised. At the end of the display the male once again assumes the initial posture. After the display the drake wags his tail and swims a short distance.

Paired adults performed 57% of 28 recorded displays and paired yearling males performed 52% of 59 displays. The social dominance of paired males again accounted for the more frequent performance because they prevented the subordinate males from displaying.

Bill-jerk.—Duration (mean 0.32 sec, $S_{\bar{x}} = 0.02$), 63 analyzed.

Bill-jerking is a simple rapid display performed from the swimming position. The display consists of an upward jerk of the bill during which the white chin is exposed to the hen. Occasionally two bill-jerks are performed in succession.

Bill-jerking by males occurred as a greeting and as a precopulatory display. A bill-jerk often was given as a greeting when a pair had been apart for a short time. In precopulatory situations as many as 20 bill-jerks were recorded as the drake swam around a hen that was in the prone position.

Eighteen adult displays had a mean duration of 0.35 sec, $S_{\bar{x}} = 0.05$; 45 yearling displays had a mean duration of 0.31 sec, $S_{\bar{x}} = 0.03$. The durations of these displays were not significantly different according to ages (t-test; $P > 0.05$).

Burp.—Duration (mean 0.23 sec, $S_{\bar{x}} = 0.03$), 7 analyzed.

The drake performs the burp display from a swimming position. The head is raised vertically and the crest is partially erected as the display is about to begin. The action is simple. The display starts with a rapid lateral head shake in which the bill is pointed at the female. A short "pfit" sound is emitted, and the crest is fully erected. The display is over when the crest and head are lowered.

Variations of the burp occurred, and at times the exact nature of the movement was undetermined. Occasionally the crest was held erect after the initial lateral head shake. One film record showed that the burp position was held for 11.25 sec. Two burping actions often were linked. The duration of the double burp was variable and considerably longer than the sum of two individual displays. Four such displays had a mean duration of 1.14 sec, $S_{\bar{x}} = 0.03$. Several burps often were given in succession, involving many lateral head shakes and the acompanying vocalization. On one occasion an unpaired yearling drake burped 23 times in succession.

Turning-the-back-of-the-head.—Turning-the-back-of-the-head is a ritualized movement that has not evolved a specific duration, as it is performed in conjunction with inciting by the female, which also has not evolved a specific time component. Under penned conditions, the duration also is limited by the size of the pool.

Turning-the-back-of-the-head was the most common male display. It was performed soon after the hen selected a mate and, apparently, functioned to strengthen the pair bond between two birds. The preferred drake responded to the female's inciting by swimming in front of her and performing this display.

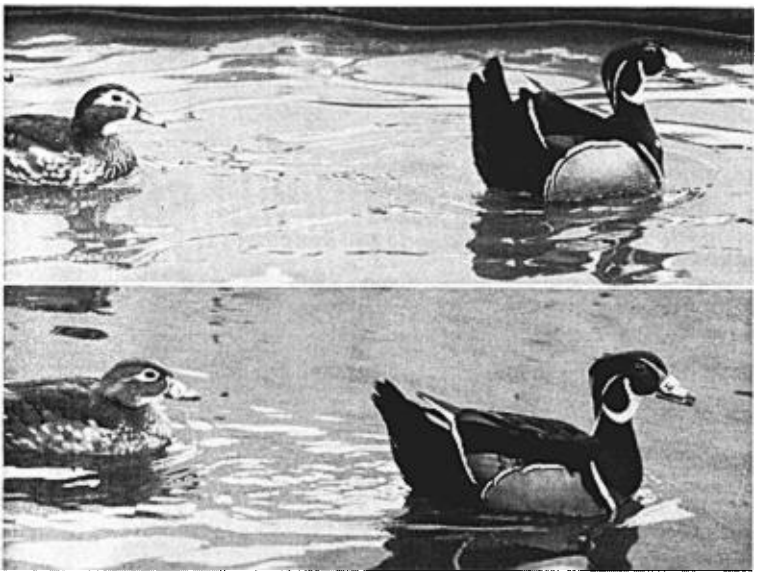

Fig. 4. Feather posture of adult (top) and yearling (bottom) drake Wood Ducks performing turning-the-back-of-the-head. Note the exaggerated posture of the adult male.

Adult drakes raised the wings and tail higher while turning-the-back-of-the-head than did yearlings (Fig. 4). Adult drakes had better orientation when performing the display as they were more frequently in front and to the side of inciting females than were yearling males.

Inciting.—Inciting by drakes is very similar to inciting by hens. The head is lowered over the shoulder and quick pecking movements are directed towards another bird. Paired drakes incited when the pair was preening or resting and when approached by an unpaired drake.

Displays of the Female

Female Wood Ducks perform relatively few displays. We observed a ritualized preen-behind-the-wing display, but found no such records for this species described in previous reports.

Inciting.—Inciting was the best indication that a pair bond had been formed. The combination of inciting by the female and turning-the-back-of-the-head by the male was the most important display in the formation and maintenance of a strong pair bond. The locomotive component of the combination of inciting and turning-the-back-of-the-head also tended to isolate the pair from other birds. These displays occurred on water and land when the pair came in contact with other birds.

The duration of this action is variable. The female may incite for the time it takes to make one or two pecking movements, or she may persist inciting for much longer, depending upon the aggressiveness of the hen and response of the intruding drake.

Bill-jerk.—Duration (mean 0.23 sec, $S_{\bar{x}} = 0.006$), 20 analyzed.

Male and female Wood Ducks have similar bill-jerking displays. Bill-jerks by females are performed as a sign of greeting and as a precopulatory display.

Precopulatory bill-jerking was used to synchronize the pair for copulation. In filmed precopulatory sequences, bill-jerks by drakes often were followed by bill-jerks by females less than half a second later. Females did not respond to all bill-jerks performed by males. Synchronous bill-jerking sometimes occurred before the female assumed the prone posture in preparation for copulation. Females in the prone posture occasionally rose partially to perform a bill-jerk if the male continued to drink and bill-jerk as he swam around her. The hen repeated the bill-jerking from the prone position until copulation occurred or until the drake or hen lost interest and swam away.

Preen-behind-the-wing.—Duration 1.00 sec, one analyzed.

Ritualized preen-behind-the-wing displays by females have been observed in several species of waterfowl (McKinney 1965). Both adult and yearling female Wood Ducks performed this display, which was not reported previously for Wood Ducks. In this study, three Wood Duck females performed the display 11 times. The hen stood on land 2 feet or less away from her drake when she took a drink, shook her head momentarily towards the drake, then preened the underside of her wing.

Preen-behind-the-wing was observed only when a pair was loafing or preening while standing near the edge of the pool. The birds were nearly always parallel to each other. Hens performed the display with the wing nearest the drake in 8 of 10 times that the action was watched closely.

PRECOPULATORY DISPLAYS

Yearling and adult pairs isolated themselves by chasing unmated birds out of the pool prior to preparation for copulation. The drake and hen swam slowly around in the pool and occasionally fed. Many times when the hen was dabbling on the surface of the water she assumed the prone position and the drake started bill-jerking and ritualized drinking.

Mutual bill-jerking and drinking by the drake excited and synchronized the pair for copulation. Precopulatory displays occurred for a few seconds or for several minutes. In a filmed sequence of 2-min duration, the drake performed 22 bill-jerks and 16 drinks and the hen bill-jerked 8 times.

Not every precopulatory sequence terminated with a successful mounting. In the pen situation, unpaired drakes often disturbed the pair. At other times, one member of the pair did not respond to precopulatory display and swam away. As many as five precopulatory sequences were counted before a pair copulated successfully.

If a drake failed to participate in a precopulatory sequence, the hen usually rose from the prone position, performed a bill-jerk, and immediately returned to the prone position. If a drake persisted in swimming away, she swam near him in the prone position and then swam towards another drake and incited vigorously. If the paired drake was responsive, he performed the turning-the-back-of-the-head. The hen again approached her mate and assumed the prone posture, and the precopulatory sequence continued. Drakes also tried to arouse a disinterested hen by inciting and threatening other males and repeatedly bill-jerking and drinking in front of her.

Precopulatory bathing by males was seen several times during this study. Although bathing is a common precopulatory display in many species of waterfowl, bathing by drake Wood Ducks was not reported previously in the literature. Two adult and two yearling drakes bathed in precopulatory sequences. In two of seven precopulatory sequences in which the male bathed, successful copulation followed.

Copulation.—A frame by frame analysis of filmed records of 12 copulations involving 3 adult and 2 yearling males revealed some dissimilarities in the form of precopulatory and postcopulatory actions. No major differences in the behavior of adult and yearling hens was observed.

Mounting.—Adult drakes mounted quickly and smoothly by swimming up behind the hen (Fig. 5) and did not have to readjust their position once on the hen's back. Young drakes approached the hen from the front or side. Young drakes that mounted in this manner had to reorient themselves while on top of the hen. This reorientation lengthened the time the drake spent on the hen's back. Both movement and length of time spent in reorientation disturbed the hen. In one unsuccessful copulatory sequence, a young drake mounted backwards but failed to reorient himself correctly before completing all the movements of mating.

Coition.—The drake wagged his tail until the hen raised and turned her tail to one side. Cloacal contact was made as the drake lowered and turned the underside of his tail towards the underside of the female's tail.

In contrast to precopulatory and postcopulatory actions, no major differences between the copulatory actions of adult and yearling birds were detected from filmed sequences. Durations of the time a drake treaded on the hen were measured from the time the drake grabbed the nape of the

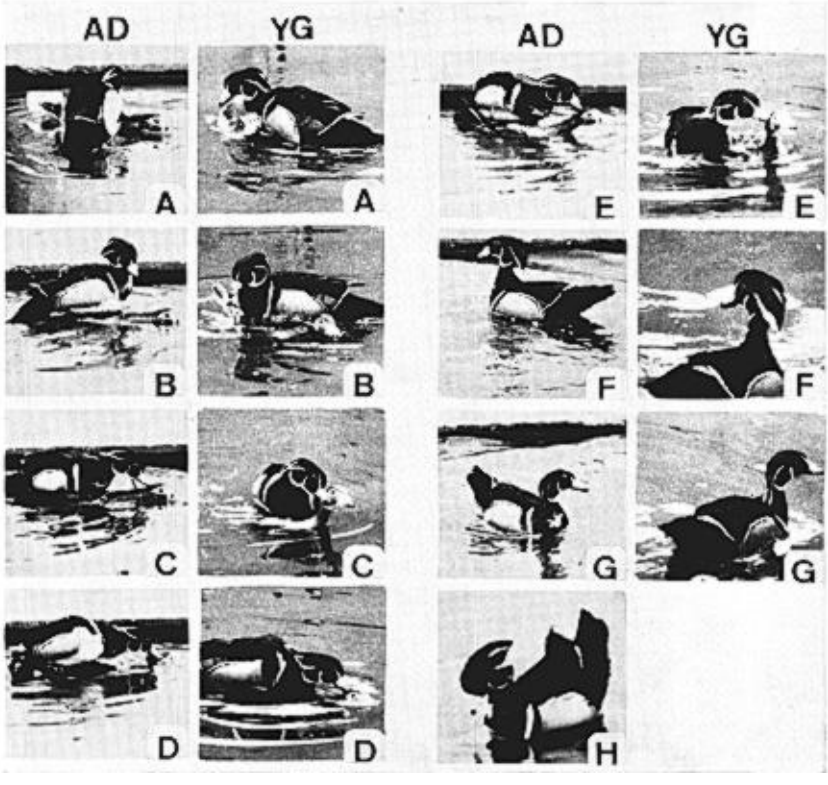

Fig. 5. Selected actions in a copulatory sequence of an adult (AD) and yearling (YG) drake paired to hens. A and B, mounting; C, nape hold; D, coition; E, dismounting; F, facing; G, postcopulatory turning-the-back-of-the-head; H, postcopulatory wing-and-tail-flash. Note the differences in the mounting orientation, and the performance of the postcopulatory wing-and-tail-flash by the adult male.

female until the hold was released. Drakes treaded hens for an average of 5.09 sec, $S_{\bar{x}} = 0.22$. A *t*-test revealed no significant differences in the copulatory interval between five adults and seven yearlings.

POSTCOPULATORY DISPLAYS

Both adult and yearling males performed facing and turning-the-back-of-the-head as postcopulatory displays. Only adult drakes performed the wing-and-tail-flash in postcopulatory situations.

Facing.—The drake continued to hold on to the hen's nape feathers as he dismounted. After dismounting, he released his hold and swam off a short distance and faced the hen as she bathed.

Adult and yearling drakes faced females in the same way. After swimming about 1.5 or 2 feet (0.5 m) away, the drake oriented himself parallel to the hen. He then raised the head and turned so that the bill pointed directly at the female, and usually erected the crest.

Yearling drakes faced the hen significantly longer than adults (t-test, $P < 0.05$). Two displays performed by an adult had a mean duration of 1.02 sec, $S_{\bar{x}} = 0.27$, whereas seven yearling displays performed by two males had a mean duration of 2.39 sec, $S_{\bar{x}} = 0.20$.

Turning-the-back-of-the-head.—The drake turned the head in the opposite direction to which he was facing to assume the proper orientation for turning-the-back-of-the-head. The form and posture of the postcopulatory turning-the-back-of-the-head was not as exaggerated as when the drake displayed in response to an inciting hen. The hen usually was still bathing as the drake performed the postcopulatory turning-the-back-of-the-head.

Wing-and-tail-flash.—The wing-and-tail-flash display has been noted only in the Wood Duck and Mandarin Duck (*Aix galericulata*) (Johnsgard 1965). The display has never been reported as part of the postcopulatory behavior of either of these species. In this study three adult drake Wood Ducks swam around in the pool for several seconds after turning-the-back-of-the-head. They assumed the display posture and performed a wing-and-tail-flash exactly as performed in pair maintenance. No wing-and-tail-flash followed eight copulations by yearling males.

Discussion

The form, duration, and orientation of displays performed by inexperienced male Wood Ducks parallels the situation in first year male Goldeneyes that lack the definitive alternate plumage. Despite the fact that Wood Ducks acquire their definitive alternate plumage during the first fall before courtship begins, slight plumage differences are known to exist between adults and yearlings of both sexes of Wood Ducks (Palmer 1972). In our Wood Duck study, the wing-and-tail-flash, preen-behind-the-wing, and turning-the-back-of-the-head displays performed by yearling drakes that lacked courtship experience were qualitatively different from adult displays. Inexperienced birds had different display orientation, lacked to some extent the ritualized postures, and failed to perform one postcopulatory display. Evidently young drakes develop display patterns resembling adult displays during the first courtship season. Whether this difference is related to learning or to maturation of the endocrine system is unknown, but the end result is the same regardless of the mechanism involved.

Because all yearling males used in this study were isolated from adult males and females during rearing, the influence of contact with ex-

perienced birds should be investigated. Ideally, a study of the behavior of both wild and captive birds should be conducted.

Age is a significant factor in many aspects of waterfowl ecology, but information is lacking regarding the relationship of age at first breeding to behavior, plumage, and reproduction. Many species of Mergini are known to have delayed maturity and do not breed until their third summer. For example, the age at which a Common Goldeneye attains the typical plumage and behavior of the species may be closely correlated with productivity. Dane and Van der Kloot (1964) noted that nonbreeding second-year Common Goldeneye drakes can be distinguished from adults on the basis of plumage characteristics and courtship behavior. Age may be more important than most waterfowl biologists believe, even for ducks that potentially breed when less than one year old. Yearling Lesser Scaup (*Aythya affinis*) obtain the breeding plumage later than most species, and yearlings often can be recognized on breeding grounds (Weller 1965). Yearling Lesser Scaup females are much less productive than older females because of poor nesting success and nonbreeding as shown in Trauger's (1971) studies. These factors may be closely associated with the lower productivity of yearling female Wood Ducks when compared to adults (Grice and Rogers 1965), and some yearling Wood Ducks apparently fail to nest at all. Most yearlings that did nest were not found to do so until the second half of the season.

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SUMMARY

Male Wood Ducks exhibited 10 ritualized displays, 8 of which were performed during pair formation and pair bond maintenance situations. The wing-and-tail-flash, preen-behind-the-wing, and turning-the-back-of-the-head displays by yearling drakes without previous display experience with adults of either sex were often different than displays of adult males. Inexperienced males had poorer orientation and less distinctive posturing than experienced adults. The display patterns of young drakes gradually develop to resemble displays of adults during the first courtship period.

Examination of filmed copulation sequences revealed that adult drakes consistently oriented themselves better and mounted females faster and smoother than yearling drakes. Postcopulatory displays of yearling drakes differed from adults in that the postcopulatory wing-and-tail-flash was completely lacking in the behavioral repertoire of inexperienced drakes.

Displays of female Wood Ducks were fewer in number than male displays. Females performed preen-behind-the-wing.

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