

CHRONOLOGY OF PAIR FORMATION IN SOME NEARCTIC *AYTHYA* (ANATIDAE)¹

MILTON W. WELLER

THE chronology of pair formation in ducks has been little studied in spite of sizable concentrations of waterfowl on wintering areas and relative ease of observation. This is, perhaps, a result of the rather deep-seated concept that pairing in birds occurs mainly in spring. It may be true that the intensity of courtship is more conspicuous in spring on migration stops and in breeding areas, because conflict situations are common and conspicuous aerial displays are more prevalent. However, it appears that many species arrive on the breeding areas paired, although the permanence of these pair bonds is unknown. It is well known that ducks in the Northern Hemisphere have a transient "winter" plumage ("basic" plumage of Humphrey and Parkes, 1959) which is shifted forward in the sequence to late summer and commonly is called the "eclipse" plumage. The breeding (or alternate) plumage then develops in fall or early winter. Obviously, this sequence must have evolved simultaneously with early pair formation in the Anatinae and in relation to the chronology of winter flocking.

In the North American members of the genus *Aythya* (the "pochards" or "inland divers"), some distinct differences are apparent in the comparative chronology of nesting. The usual sequence in these species appears to be: Canvasback (*A. valisineria*), followed very closely in most areas by the Ring-necked Duck (*A. collaris*), Redhead (*A. americana*), and still later by the Lesser Scaup (*A. affinis*) (Bent, 1923; Hochbaum, 1944; Mendall, 1958). Of special interest is the laying pattern of the Redhead, a semiparasitic bird. Some individuals start nesting as early as do Canvasbacks, but most start parasitic laying when Canvasbacks begin nesting and construct nests later in the season (Weller, 1959).

Although less is known of the sequence of plumages than of the sequence of nesting, it appears that there is less difference between species in the attainment of breeding plumages. The Lesser Scaup probably is the last to attain complete breeding plumage (especially in yearlings, which often are recognizable in spring migration and on breeding areas) while no dramatic difference seems to occur in the other three species. Redheads possibly precede Ring-necks and Canvasbacks (October versus November according to Bent, 1923; Mendall, 1958; and Weller, 1957). However, too little detailed information is available for comparable areas.

The purpose of this study was to determine whether differences in

¹ Journal Paper No. J-4843 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1504.

biology are reflected in the comparative chronology of pair formation. Preliminary observations of Redheads were made in southern Manitoba during the springs of 1953 and 1954, at Chesapeake Bay and Cayuga Lake during February and March of 1954, and at Spring Lake near Havana, Illinois, in March of 1957. Intensive observations of Redheads and other species on wintering areas were started during the winter of 1960. Southern Texas was selected for the study of wintering birds because of the concentrations of Redheads as well as smaller numbers of the other species of the genus *Aythya*. Brief observations of Ring-necked Ducks were made in southern Louisiana in early January of 1961. Some notes made on three dabbling ducks serve for comparison with the diving ducks: Pintails (*Anas acuta*) and Mottled Ducks (*A. fulvigula*) in Texas and Mallards (*A. platyrhynchos*) in Louisiana. Observations of divers were made in Iowa during the spring migration of 1961 and 1962 and in Michigan in 1963.

This project was financed by the Permanent Science Fund of the American Academy of Arts and Sciences of Boston, Massachusetts, and preliminary observations were supported by the Wildlife Management Institute through the Delta Waterfowl Research Station. The study was assisted greatly by the use of facilities of the Welder Wildlife Foundation of Sinton, Texas. Clarence Cottom and the late Bobby J. Wilks of the latter organization suggested study areas as did T. L. Clark of the Texas Game and Fish Commission and L. E. Beatty and E. B. Chamberlain of the U. S. Bureau of Sports Fisheries and Wildlife. Workers at the Laccasine National Wildlife Refuge in southern Louisiana were helpful in arranging for observation of Ring-necked Ducks and Mallards.

THE PAIRING PROCESS

Acquiring a mate appears to be a gradual process in most ducks and apparently starts in midwinter on the southern wintering areas. Pairing appears to be a result of many temporary associations within a flock of rather consistent members. Individual recognition is assumed. As sexual drives increase, pairs which remain together are "tested" constantly by aggressive unpaired and, possibly, paired males. Changes in mates probably are common early in the pairing periods, as noted in marked Mallards by Weidmann (1956). In species of *Aythya*, as in most ducks, the female plays a major role in the regulation of the pairing process, showing interest or lack of interest by leading, following, attacking, or fleeing. Johnsgard (1960b) has described the similarity of this type of behavior in species of *Anas* and *Aythya*.

Pairing displays are common in migration areas in the central United States and continue in the breeding areas. Whether these pairs remain together on the breeding areas and in migration is unknown, but pairs are conspicuous even in large flocks on wintering areas and in early migration.

Although many of these pairs may have only a temporary bond, the action clearly indicates the sexual stimulation essential to the permanent pairing process. This behavior differs markedly from that of individuals in flocks of one sex and flocks of both sexes in which no pair association exists.

CHRONOLOGY OF PAIRING

I attempted to measure the chronology of pairing quantitatively by determining the percentage of females which were associated with a male, regardless of the length of time of the association. This seemed to be the only way to record quickly the association of sexes in large flocks, since marking of birds was impractical. Obviously, some errors were due to chance association of males with females, but the obvious tolerance of females for males and the attraction of males to females was conspicuous. The duration of this bond was measured by observing "pairs" through a telescope and timing (by means of a stop-watch) the duration of the pair association. Such pairs were observed until: (1) they were lost from view among other birds, (2) members of the pair separated, or (3) observations were interrupted for some reason. In addition, notes were made on courtship to determine which displays were present in early pairing, whether aggressiveness between males was apparent, and whether copulation occurred.

Midwinter, 1960-61.—The first observations were made on Redheads during late December and early January, 1960-61, at the Laguna Atascosa Refuge near San Benito, Texas. Because the time of pairing was unknown, the time to initiate observations was a guess, but I considered it best to precede the display period rather than arrive after it had started. Surprisingly, I found that numerous pairs were already in evidence and that courtship parties were common among Redheads in this period. Most known displays, as described by Hochbaum (1944) for Canvasbacks and Johnsgard (1960b, 1961) for the genus *Aythya*, were noted except for aerial displays and copulation.

During the same period, 25 to 30 Canvasbacks were viewed at Sarita, Texas, and were predominantly females. However, males present were not seen to display. Several hundred Lesser Scaup were observed near Corpus Christi, Texas, for considerable periods. Scaup of both sexes were scattered as individuals and in small flocks of up to 30 birds but I observed no sexual activity.

Also, in early January, several refuges in southern Louisiana were visited to observe Ring-necked Ducks. A small number of Ring-necks was observed at Laccasine National Wildlife Refuge. The only display seen was the *head throw* by males. However, this display could not be related clearly to reproductive behavior. Moreover, in this particular situation, females

did not seem especially attached to males nor did males spend much time following females.

Late February–Early March, 1961.—Because of the status of pairing on the first trip to the wintering areas, I made a second trip during the last two weeks of February in an attempt to measure the rate of pair bond formation. Because of changes in water conditions and a major northward shift in the Redhead population, most observations were made near Corpus Christi, Texas. This may well have been a different flock, but courtship display was more intense and pairs were more in evidence than had been previously noted. However, aerial displays and copulation still were not witnessed.

Observations made on Lesser Scaup in February were more satisfactory than those of early January. Several hundred scaup were observed at close range and no evidence of pairs or displays was seen.

A few Canvasbacks were again observed in southern Texas and more males were in evidence than before. Males clearly showed more interest in females, but no intensive courtship activities were observed.

In the same period, about 40 Ring-necked Ducks were observed at the Welder Wildlife Refuge. During the day, birds were scattered about the lake and small groups of females were conspicuous, while males were in twos or threes. However, after sunset, the entire flock of Ring-necks moved, along with other ducks and coots, into a grove of trees, apparently to roost. In doing so, they all met and, on occasions, *head throws* were seen.

Thus, in late February, Lesser Scaup had not started pairing activities and Canvasbacks and Ring-necks showed only a slight attraction of males to females. Redheads, however, were strongly activated, and pairs made up a large percentage of the premigratory flock. Apparently, Lesser Scaup are still not actively courting in the southern United States even in mid-March. Observations in Louisiana by Frank McKinney (*in litt.*), of the Minnesota Museum of Natural History, indicated only one possible pair among 66 males and 22 females counted.

Spring, 1961–62.—Observations on pairing of Ring-necks, Lesser Scaup, and Redheads were made in central Iowa in late March and early April, 1961 and 1962. At that time, pairs of Redheads were conspicuous and lone hens were rare. Numerous Ring-necks and scaup were in pairs and courtship was seen commonly. Dr. John Rogers (*in litt.*), of the Gaylord Memorial Laboratory at Puxico, Missouri, made observations on Lesser Scaup in February of 1961 and found no pairing activity. But in Iowa in early April, not only were displays common, but I observed copulation in both Ring-necked Ducks and Lesser Scaup. Thus, courtship activity of Lesser Scaup and Ring-necks seemed to be of the same intensity in Iowa in early April as occurred in Redheads in Texas in early January. It ap-

TABLE 1

OBSERVATIONS ON THE PERCENTAGE OF FEMALE DUCKS PAIRED IN WINTER AND SPRING

<i>Species</i>	<i>Per cent of females paired</i>	<i>Number of females seen</i>	<i>Number of females paired</i>	<i>Number of females unpaired</i>	<i>Number of males unpaired</i>	<i>Locality</i>	<i>Month</i>
Mottled Duck	100	22	22	0	0	Texas	Dec.-Jan.
Mallard	90	31	28	3	6	Louisiana	January
Pintail	87	216	187	29	393	Texas	Dec.-Jan.
Redhead	35	709	249	460	733	Texas	Dec.-Jan.
	58	408	238	170	533	Texas	February
	84	37	31	6	19	Illinois	March
	89	27	24	3	31	Iowa	March-April
Ring-necked Duck	13	47	6	41	34	Texas-La.	January
	12	49	6	43	34	Texas	February
	55	172	94	78	149	Iowa	March-April
Lesser Scaup	9	35	3	32	119	Ill.-Missouri	December
	4	125	5	120	161	Texas-La.	Dec.-Jan.
	12	462	58	404	487	Texas	February
	17	166	29	137	185	Michigan	March
	56	259	146	113	427	Iowa	March-April
Canvasback	10	10	3	10	66	Ill.-Missouri	December
	0	48	0	48	59	Texas	January
	10	86	9	77	83	Texas	February
	4	27	1	26	61	Michigan	March
	41	19	8	11	41	Iowa	March-April

pears that, in Redheads and, probably, Canvasbacks, courtship starts on the wintering areas well ahead of similar activity in Lesser Scaup and possibly Ring-necks, which seem to start courtship in early migration. However, both copulation and aerial chases were common in all species by the time they arrived in central Iowa. It must be recognized, however, that not all flocks or even all birds in flocks are at the same stage in the reproductive cycle and that the origin of these flocks as well as their destinations were unknown. Moreover, Hochbaum (1944) has pointed out that early migrants often are paired birds.

Efforts to show "pairing" quantitatively are summarized in Table 1 and are compared, in Figure 1, with some data on dabbling ducks collected by other workers. Among Redheads, 35 per cent were "paired" during late December and early January, in comparison with 9 to 13 per cent in other divers and 87-100 per cent in dabbling ducks. By late February, 58 per cent of the Redheads were considered "paired," although little evidence of increased pair tendencies was noted among other divers. In spring migration at the latitude of Iowa and Illinois, 80 to 84 per cent of all female Redheads were "paired," and 41 to 55 per cent of other diving

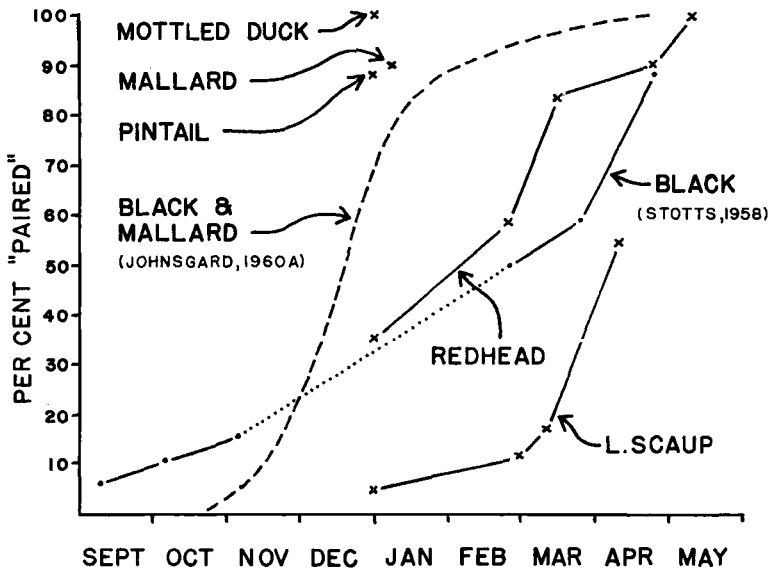


Figure 1. A comparison of data from this and other studies on the percentages of ducks "paired" at various times of the year.

ducks were "paired." Obviously, these figures are only a gross measure of sexual associations, but they demonstrate increased tolerance by females for the attention of males.

Limited observations on dabbling ducks demonstrate the significantly earlier pair formation in this group compared with that of pochards. Data here presented agree more closely with the estimates of Johnsgard (1960a) than with those of Stotts (1958). However, Stotts' observations were made in the field upon large flocks, and the lack of clear-cut sexual dimorphism in Black Ducks (*Anas rubripes*) limited observations. The general pattern presented here agrees with that of European species of *Anas* and *Aythya* shown by Bezzel (1959). Pairing of the Mallard occurred mainly from September through November, Tufted Ducks (*Aythya fuligula*) paired mainly in March, and Common Pochards (*Aythya ferina*) did not pair until May.

Another measure of the tendency of members of the pair to remain together is suggested by data on the duration of the pair relationship (Table 2). These data do suggest that the duration of the pair bond is longer for Redheads in March and April than in January and February. Of greater significance is that the duration of this bond in Redheads is more than three times that of the scaup at the same time.

TABLE 2
DURATION OF THE PAIR RELATIONSHIP IN FOUR SPECIES OF THE GENUS *AYTHYA*

<i>Species</i>	<i>December</i> <i>(Missouri-Illinois)</i>	<i>January-February</i> <i>(Texas-Louisiana)</i>	<i>March-April</i> <i>(Iowa)</i>
Redhead	—	9.9 ¹ (0.5-84) ² (33) ³	13.3 (4.0-22) (8)
Ring-neck	—	7.7 (1.0-22) (5)	12.2 (0.9-44.8) (19)
Canvasback	2.7 (0.4-5.0) (4)	1.9 (0.5-5.0) (16)	3.9 (1.7-5.0) (3)
Scaup	0.5 (0.1-1.2) (6)	3.2 (0.5-15) (16)	8.1 (0.3-44) (16)

¹ Average numbers of minutes.

² Range in minutes.

³ Sample size.

DISCUSSION

The observations on Canvasbacks and Ring-necked Ducks are not considered satisfactory because they involve small and somewhat isolated groups studied under conditions poor for observation. Some general observations in the Chesapeake Bay area in late February of 1954 indicated considerable courtship activity in Canvasbacks whereas relatively little was seen in Texas. However, the observations on Ring-necks agree generally with those of Zirrer (1945) who noted that some Ring-necks arrived in Wisconsin in pairs but that courtship was very intense in mid-April.

Although further observations are needed, the sequence of display and pairing seems generally correlated with the onset of breeding plumage and nesting. There is close agreement in data for Lesser Scaup while those for Canvasback and Ring-necks agree only in a more general way. Better data on chronology of nesting and plumage development of all species in the same area would help materially to clarify conclusions. The major exception is the pairing of the Redhead, which clearly is more nearly correlated with its establishment of home range on the breeding area and parasitic laying than with its major breeding period. Moreover, pairing activities in the Redhead seem to begin well in advance of those species which begin normal nesting at the time the Redhead lays parasitically. The relationship of this early courtship period to the parasitic habits of the Redhead is still obscure, but it suggests further abnormality in the reproductive cycle.

It is important to note that relatively little information is available on age of maturity in these species. Not all species acquire full breeding plumage as yearlings prior to the display period. This is especially conspicuous in Lesser Scaup which may be very brown in spring. Munro (1941) questioned whether yearling Lesser Scaup males mated in their first year but suggested that some females did. McKnight and Buss (1962) have presented some better evidence that some females do so. As in many

species of animals, it is probable that older and experienced males mate with most females and that yearling males rarely compete successfully. Moreover, the same situation may occur in the other divers, but it is less conspicuous because of less contrast between first and later breeding plumages.

Available data on dabbling ducks of the genus *Anas* suggests that pairing precedes that of the divers by several months. Males of Mallards and Pintails often assume their adult plumages in early fall, nearly two months prior to that of the divers, and nesting starts in early April or about one month prior to that of Canvasbacks. Thus, a general correlation exists in acquisition of breeding plumage, chronology of pairing, and initiation of nesting in both Anatini and Aythyini.

SUMMARY

Observations on four species of inland diving ducks (genus *Aythya*) demonstrated considerable difference in chronology of pairing. There was a general correlation between the comparative chronology of pairing, acquisition of breeding plumage, and initiation of nesting among most species but at least one irregularity seems to exist. Redheads, which normally follow Canvasbacks in initiation of nesting, preceded in courtship activities the Canvasbacks observed in this study. Compared with Redheads, Canvasbacks, and Ring-necked Ducks, Lesser Scaup were the last to start pairing activities and the last to nest. Limited observations on Ring-necks suggested that the pairing period was slightly later than that of Canvasbacks, as is their nesting period. Limited observations on three species of dabbling ducks (*Anas*) suggested a considerably earlier period of pairing in comparison with the divers.

LITERATURE CITED

- BENT, A. C. 1923. Life histories of North American wild fowl, Vol. 1. U. S. Natl. Mus., Bull. 126. 243 pp.
- BEZZEL, E. 1959. Beiträge zur Biologie der Geschlechter bei Entenvögeln. Anzeiger der Ornithologischen Gesellschaft im Bayern, **5**: 269-355.
- HOCHBAUM, H. A. 1944. The Canvasback on a prairie marsh. Amer. Wildl. Inst., Washington, D. C.
- HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk*, **76**: 1-31.
- JOHNSGARD, P. A. 1960a. A quantitative study of sexual behavior of Mallards and Black Ducks. *Wilson Bull.*, **72**: 133-155.
- JOHNSGARD, P. A. 1960b. Pair-formation mechanisms in *Anas* (Anatidae) and related genera. *Ibis*, **102**: 616-618.
- JOHNSGARD, P. A. 1961. The taxonomy of the Anatidae—a behavioural analysis. *Ibis*, **103**: 71-85.

- MCKNIGHT, D. E., AND I. O. BUSS. 1962. Evidence of breeding in yearling female Lesser Scaup. *J. Wildl. Mgmt.*, **26**: 328-329.
- MENDALL, H. L. 1958. The Ring-necked Duck in the northeast. *Univ. of Maine Bull.*, **60**: 1-317.
- MUNRO, J. A. 1941. Studies of waterfowl in British Columbia: Greater Scaup duck and Lesser Scaup duck. *Canadian J. Res. D*, **19**: 113-138.
- STOTTS, V. 1958. The time of pair formation in Black Ducks. *Trans. N. A. Wildl. Conf.*, **23**: 192-197.
- WEIDMANN, U. 1956. Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.), I. Das Aktionsystem. *Zeits. f. Tierpsychol.*, **13**: 208-271.
- WELLER, M. W. 1957. Growth, weights, and plumages of the Redhead (*Aythya americana*). *Wilson Bull.*, **69**: 5-38.
- WELLER, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.*, **29**: 333-365.
- ZIRNER, F. 1945. The Ring-necked Duck. *Passenger Pigeon*, **7**: 41-46.

Department of Zoology and Entomology, Iowa State University, Ames, Iowa.