Breeding Biology of the American Woodcock in Piedmont, North Carolina

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Abstract: Woodcock (*Scolapax minor*) were observed and collected in the Piedmont region of North Carolina, from November 1977 through June 1978 and from November 1978 through March 1979 for studies of their courtship behavior, reproductive physiology, and breeding chronology. Male courtship behavior began in early December and terminated in early June, with February and March having the greatest numbers of singing males. However, individual males spent more time on the singing grounds during March, April, and May. Testicular recrudescence was apparent by early January. Juvenile males produced sperm during their first breeding season. Two females were in the rapid stage of follicle development by 18 January which probably indicated imminent ovulation. However, it appears that successful reproduction did not occur until late March or early April, as evidenced by brood hatching dates. These hatching dates contrast with earlier breeding records from previous years. The severity of winter weather is suggested as a factor which determines when nesting is initiated by woodcock.

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Observations of male woodcock performing courtship flights in early December have been reported from several southeastern states (Glasgow 1958, Stamps and Doerr 1977, Roberts and Dimmick 1978, Roberts 1980, Roboski and Causey 1981). Stamps and Doerr (1977) reported several woodcock hens had completed clutches during January and February of 1975 and 1976 in North Carolina. Roboski and Causey (1981) also reported clutch completions during the first week of February during those years. However, since those winters were unusually mild in North Carolina, further investigation was war-

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ranted. The purpose of this study was to investigate the interrelationships of courtship behavior, reproductive physiology, and breeding chronology of the American woodcock in areas of Piedmont, North Carolina. Funding for this study was provided by the U.S. Department of the Interior, Fish and Wildlife Service Contract No. 14-16-004-3293 through the North Carolina Wildlife Resources Commission. The authors thank G. A. Ammann, F. Barick, and R. T. Stamps for assistance in collecting woodcock; J. P. Thaxton and C. Brockman for advice and assistance in preparing and interpreting slides of the testes; L. Morris, K. Gehweiler, Z. Erskine, and others for assistance in recording behavioral data; and J. D. Hair, T. R. Wentworth, and J. M. Whitsett for their review of the manuscript. This is paper No. 6795 of the Journal Series of the North Carolina Agricultural Research Service, North Carolina.

Methods

Singing ground surveys were conducted monthly from December through June 1977–1979 on 2 study areas near Raleigh, North Carolina, in a manner similar to guidelines published by the U.S. Fish and Wildlife Service (Martin 1962). One study area consisted of the Dorothea Dix State Farm and adjacent areas along Walnut Creek in south Raleigh; the other study area was the Carl Alwin Schenck Forest owned by North Carolina State University and located 3 km west of Raleigh on Richland Creek. The surveys were conducted on the first 2 days of each month, with the exception of the first trial surveys which were conducted on 15 and 16 December, when there was no precipitation or excessive wind. Surveys were conducted on foot by trained observers.

To determine if male woodcock were present, evening searches for singing males were conducted beginning on 20 November. Dusk courtship performances of singing male woodcock were monitored from 5 December 1978 to 2 June 1979. Eighty-three performances were monitored with the duration, number of courtship flights, number of cackle flights (Sheldon 1967), and the number of woodcock heard recorded. The study area on which the observation was to be made was randomly selected.

Woodcock were collected by shooting from diurnal coverts and singing grounds in Wake and Chatham counties from 15 November 1977 to 1 June 1978 and from 18 November 1978 to 30 March 1979.

Measurement of left testicle length and follicle diameters were taken using calipers. Linear regression analyses were used to determine trends in testicle and follicle growth. Follicles >4.0 mm were excluded from the analyses since they are assumed to be in the rapid growth stage preceding ovulation (Stamps and Doerr 1977). The effect of age (juvenile or adult) of the individual on testicle size was determined using analysis of variance procedures.

Testicles from the 1978–79 season were preserved in 10% formalin. Standard histological procedures (Hodges 1974) were utilized to prepare microscope slides of cross-sectioned testicles. A hemotoxylin-eosin stain was

used to differentiate stages of spermatogenesis. The slides were then scaled according to recognizable stages of spermatogenesis (Hodges 1974). Linear regression analyses were used to determine the relationships of spermatogenesis to left testicle size and date of collection.

Woodcock broods were located in Wake and Chatham counties using trained bird dogs. The age of the chicks was determined from bill-length measurements (Ammann 1970). Hatching dates were approximated by back dating from the age of the brood, and clutch completion dates were estimated by subtracting 21 days from the hatching date (Liscinsky 1972).

Weather data for the Raleigh-Durham area were obtained from the National Climatic Center in Asheville, N.C.

Results

Courtship Behavior of Males

The first observation of an evening courtship performance during the 1978–79 season was made on 5 December. Four males were performing on the study areas by mid-December (Fig. 1). The number of singing males increased to 10 at the first of February and to 25 at the first of March. However, most of the males observed at the beginning of March were apparently transitory. The number of males heard peenting by observers positioned at singing grounds also indicated February and March as months with high numbers of peenting males.

The duration of the courtship performance and the number of courtship flights per performance were greatest from March through May (Fig. 2). Singing males were most numerous during this period (Fig. 1). The duration of the performance and the number of courtship flights per performance were highly correlated ($r^2 = .82$). No significant differences in performance characteristics could be attributed to study area. The winter courtship performances, December through February, were brief, averaging 18 minutes (Fig. 2). The mean number of courtship flights per performance did not exceed 4 until March. Courtship behavior then increased, reaching a peak mean duration of 35 minutes in May although the mean number of courtship flights per performance peaked in March. Courtship activity terminated in June with only 1 performance being observed on either study area during that month.

The mean number of cackle flights per performance peaked in January (Fig. 2), suggesting that territorial relationships were being established. The mean number of cackle flights increased slightly in March, which coincided with the presence of many transitory males.

Reproductive Condition of Males

Stamps and Doerr (1977), Whiting and Boggus (1982), and Roberts (1980) reported that testicular enlargement occurred in woodcock during the winter. In the present study, 55 males collected during the 1977–78 and

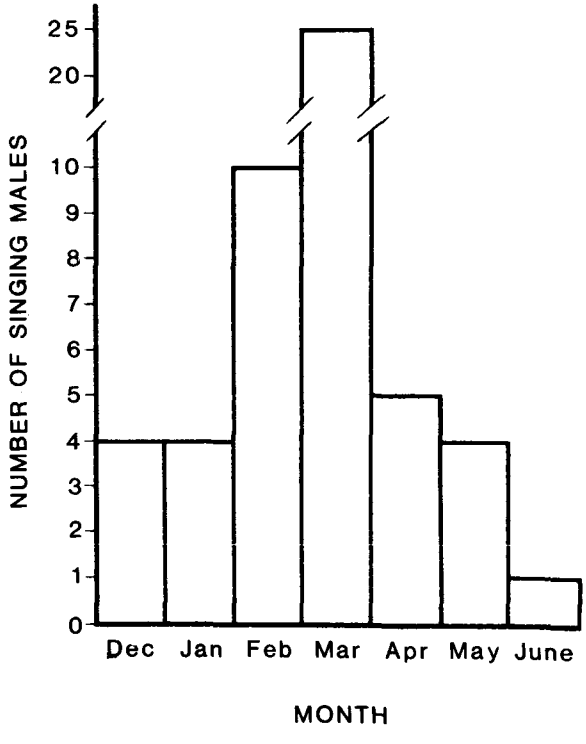

Figure 1. The number of singing male woodcock heard on survey routes on the two study areas during the 1978–79 season.

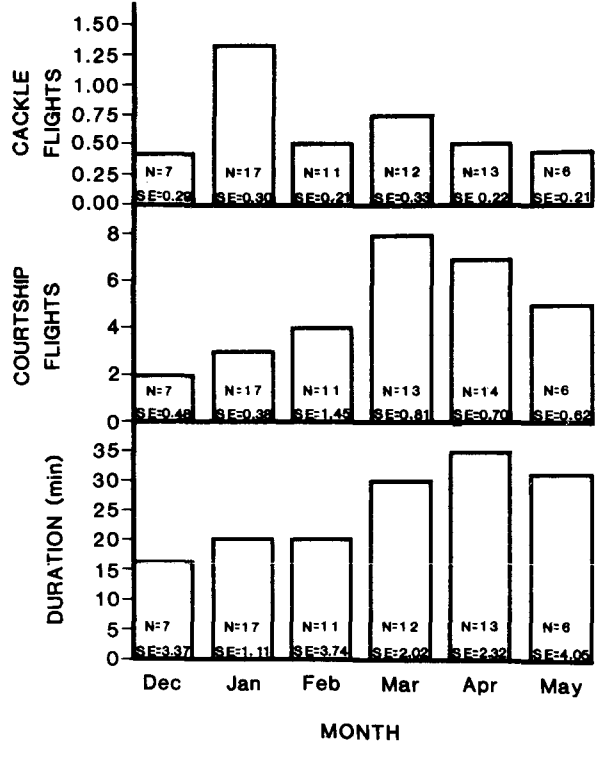

Figure 2. A comparison of the mean duration of courtship performances, the mean number of courtship flights per performance, and the mean number of cackle flights per performance by month.

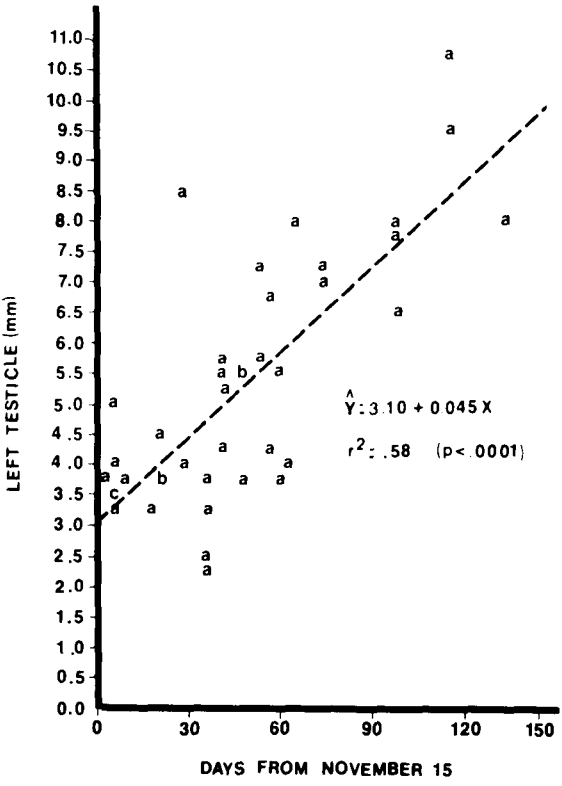

Figure 3. Linear regression of left testicle length against date for woodcock collected in piedmont North Carolina during the 1977–78 and 1978–79 seasons. (Legend: a = 1 observation, b = 2 observations, c = 3 observations)

1978–79 seasons possessed left testicles ranging from 2.25 to 11.60 mm in length (Fig. 3). A significant trend of increasing testicle length existed over the collection period, 15 November to 2 June ($F = 92.03$; 54 df; $P < 0.0001$) (Fig. 3). Testicular enlargement became apparent by early January in the majority of the birds. However, the population exhibited high variability, and 1 individual possessed a left testicle 8.45 mm in length on 15 December. Large testicle sizes persisted through May although singing activity ceased by early June.

The age of individual woodcock accounted for a significant amount of the variation in testicle length. An apparent difference in mean testicle length between adults (6.20 mm ± 0.40 SE) and juveniles (5.05 mm ± 0.42 SE) approached statistical significance ($P = 0.087$) after variation attributable to the date of collection was removed. Whiting and Boggus (1982) also reported a significant difference in Texas, but Roberts (1980) reported no difference in February in Tennessee.

Microscopic examination of sectioned testicles from 21 males collected during the 1978–79 season revealed a seasonal cycle of spermatogenesis (Fig. 4). The majority of testicles examined from November and December

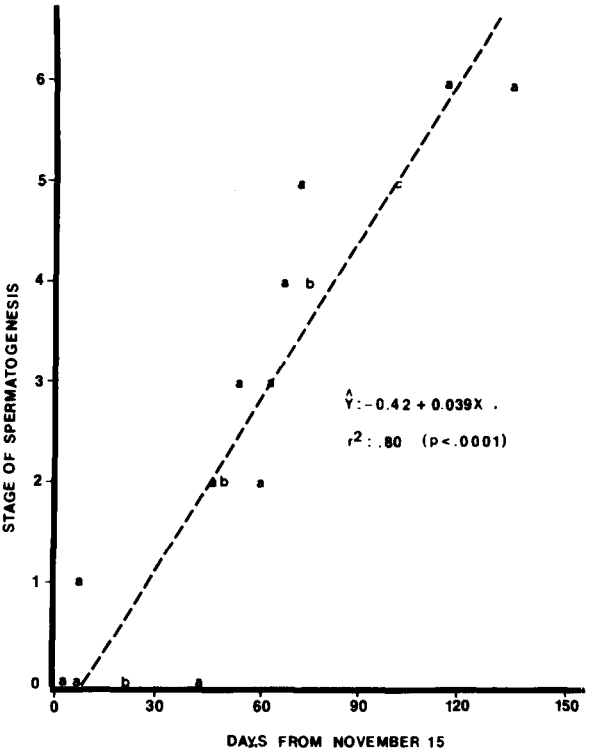

Figure 4. Linear regression of the stage of spermatogenesis against date for woodcock collected during the 1978–79 season. The stages of spermatogenesis are: 0 – interstitial cells pycnotic, no active germ cells; 1 – interstitial cells surrounding seminiferous tubules, spermatogonia prevalent; 2 – primary and secondary spermatocytes present, spermatids absent; 3 – lumen developing, spermatids present; 4 – spermatozoan production beginning, few spermatozoa present; 5 – full sperm production; 6 – interstitial cells becoming pycnotic, no spermatogonia.

had no active germ cells and contained pycnotic interstitial cells (Stage 0). The cycle began with interstitial cells migrating to surround enlarging seminiferous tubules. Spermatogonia were soon prevalent (Stage 1), and they proceeded to become spermatocytes (Stage 2) by late December or early January. The lumen developed and spermatids were present (Stage 3) in early January. Production of spermatozoa was just beginning (Stage 4) by mid- to late January. Full sperm production (Stage 5) was first seen on 28 January. Both adult and juvenile males were found to be producing sperm by that date. Some testicles >8 mm in length were nearing the completion of the cycle at this time. The production of spermatogonia had been halted in some of these testicles, but those germ cells already produced were continuing through spermatogenesis (Stage 6). Cessation of spermatogonia production was observed as early as

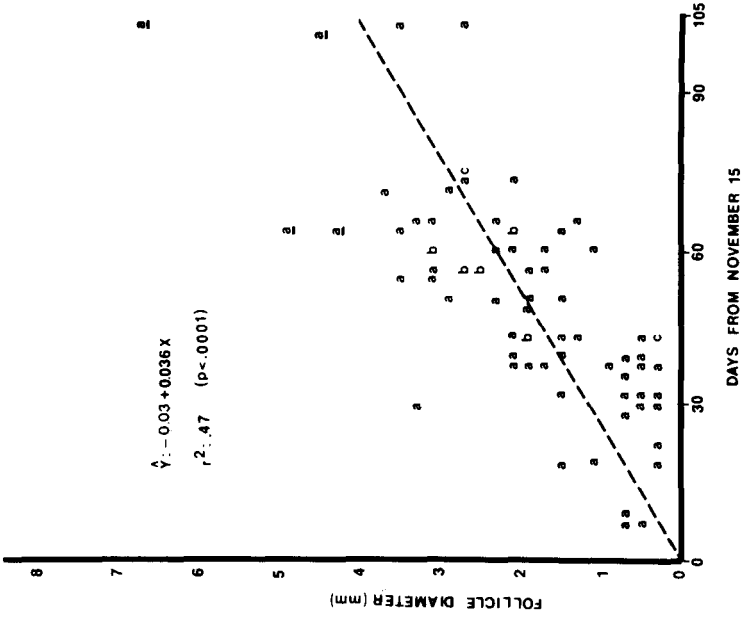

Figure 6. Linear regression of ovarian follicle diameters <4.0 mm over date.

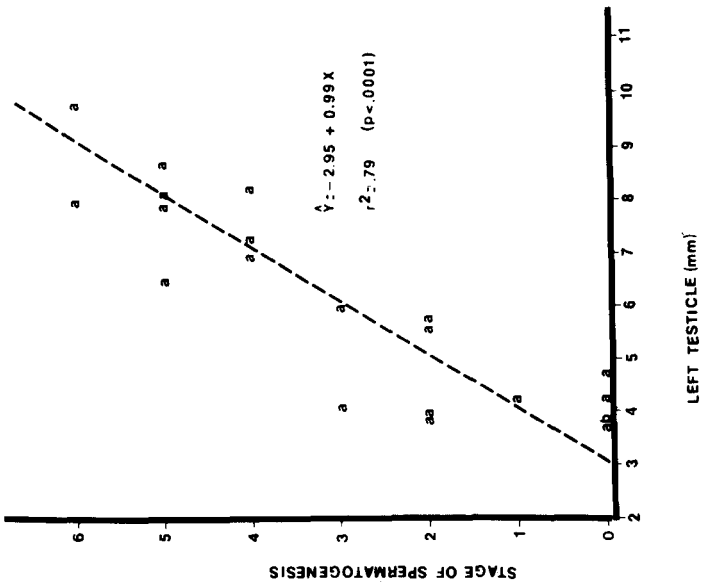

Figure 5. Linear regression of the stage of spermatogenesis against the length of the left testicle for woodcock collected during the 1978–79 season.

Table 1. Summary of heating degree days[a] and snowfall in the Raleigh-Durham area for years during which woodcock reproduction was studied.

Year	Heating degree days				
	Dec	Jan	Feb	Mar	Totals
1974–75	668 (tr.)[b]	651 (tr.)	589 (tr.)	553 (1.5)	2,461 (1.5)
1975–76	705 (tr.)	843 (0.4)	426 (tr.)	300 (0.0)	2,274 (1.0)
1977–78	768 (tr.)	914 (tr.)	883 (22.9)	514 (4.0)	3,079 (26.9)
1978–79	627 (0.0)	793 (1.0)	792 (43.7)	398 (0.0)	2,610 (44.7)

[a] Heating degree day is departure of mean daily temperature from base temperature of 65° F. For a day with 70° F high and 50° F low, the mean is 60° F, or 5 heating degree days.
[b] (tr.) indicates trace amounts of snowfall (<0.025 cm); other values in parenthesis are cm of snowfall.

15 March, but males containing sperm were present throughout the collection period.

The stage of spermatogenesis was related significantly to the length of the left testicle ($F = 66.57$; 20 df; $P < 0.0001$) (Fig. 5). The smallest testicle examined which contained sperm measured 6.5 mm in length; the largest testicle examined which did not contain sperm measured 5.9 mm in length; and the earliest testicle examined microscopically which contained sperm (Stage 4) was collected on 23 January.

Reproductive Condition of Females

Data collected from 76 female woodcock revealed that the diameter of the largest ovarian follicle increased at a slow linear rate from 15 November until at least 18 January during 1977–78 and 1978–79 ($r^2 = .47$; $F = 60.92$; $P < 0.0001$) (Fig. 6). Only 4 females contained follicles measuring ≥4.0 mm in diameter (Fig. 6). These follicles were excluded from the linear regression analysis since they are in the size class that Stamps and Doerr (1977) specu-

Table 2. The hatching and clutch completion dates for woodcock broods located in 1978 and 1979.

Brood	Year	Clutch completion date	Hatching date
1	1979	10 Mar	31 Mar
2	1979	10 Mar	31 Mar
3	1979	19 Mar	1 Apr
4	1979	19 Mar	1 Apr
5	1979	15 Mar	5 Apr
6	1979	16 Mar	6 Apr
7	1979	20 Mar	10 Apr
8	1979	20 Mar	10 Apr
9	1978	24 Mar	14 Apr
10	1978	25 Mar	15 Apr
11	1978	27 Mar	17 Apr

lated to be undergoing rapid development preceding ovulation. The small number of woodcock containing follicles >4.0 mm is undoubtedly influenced by the lack of an adequate sample from February. Collection efforts continued through February, but very few woodcock were flushed until the last week of the month during either collection period, possibly due to severe weather (Table 1).

Eleven woodcock broods were located in Wake County during this study. The estimated hatching dates of these broods ranged from 31 March until 17 April (Table 2). Thus, the earliest estimated clutch completion date for this study is 10 March. Coverts were searched during February and March (both seasons) without locating any earlier broods. However, a more intensive effort utilizing better-trained dogs was not initiated until the first 2 weeks of April. Therefore, the possibility of earlier hatching dates is not absolutely precluded; but the broods which were located indicate March as the time when successful nesting took place during the 1977–78 and 1978–79 seasons.

Discussion

Although male woodcock were observed performing courtship flights in early December, many males were just beginning to undergo interstitial cell development at this time. However, a great deal of variability in testicle length (Fig. 3) existed within the population, which raises the possibility that a few males in more advanced stages of recrudescence than those examined were responsible for the early December courtship flights. This hypothesis was further supported by the small number of males performing at this time (Fig. 1). If this courtship behavior is under androgenic control, males with developed interstitial cells (Stage 1) (Fig. 4) should be capable of this behavior since interstitial cells have been shown to be a probable site of androgen production (Woods and Domm 1966, Sturkie 1976). These males, with the possible exception of 1 collected on 15 December, probably were not capable of sperm production until late January.

Much variability in testicle size exists for each collection period, but it is possible that the size of the testicle remained constant with respect to sperm production; i.e., testicles of a particular size were at the same stage. Although Johnson (1961) could not predict stages of spermatogenesis from testicle sizes and weights in mallards (*Anas platyrhynchos*) due to overlap between categories, Woodward et al. (1978) successfully related the size and weight of the left testicle to stages of spermatogenesis in the chukar partridge (*Alectoris graeca chukar*). Roberts (1980) showed that 97% of the left testicles ≥6 mm in length were from sexually mature woodcock. Since testicles in stages 3 and below of spermatogenesis do not overlap in size with stages 4 and above in the present study, the authors suggest that left testicles measuring ≥6.5 mm in length were probably producing viable sperm with the possible exception of

the testicles of males at the end of the breeding season before testicular regression occurred.

Two female woodcock collected in late January (1 in each season) possessed follicles measuring >4.0 mm in diameter (Fig. 6) which would suggest that these females were in or were rapidly approaching breeding condition. However, from estimated clutch completion dates (Table 2), it appeared that successful reproduction did not take place until later in the year. The interpretation of these data is complicated by the lack of an adequate sample during February. Woodcock were largely absent from coverts for the first 3 weeks of February in both winters. Unusual snows blanketed the ground during February of both winters of this study (Table 1). This severe weather may have caused a delay in follicle development, or follicle development may have taken place in another geographic region.

Apparently, woodcock did not reproduce successfully in Piedmont, North Carolina, until early March, after the February snows (Table 2). Thus, the severity of the winter may affect the timing of successful woodcock nesting in North Carolina. Stamps and Doerr (1977) reported a daily rate of testicle growth of 0.053 mm per day, as calculated from their 9-day rate during the mild 1974–75 and 1975–76 winters in North Carolina. Their rate compares with a rate of 0.038 mm per day in the present study. They also reported clutch completion dates of late January and early February, while the earliest clutch completion date of successful nesting in the present study was 10 March. These differences may be due to variability in the severity of winter weather. Testicular growth was apparently slower, and clutch completion dates of successful nests were apparently much later during the more severe winters. Thus, the authors suggest that the woodcock in Piedmont, North Carolina, is an opportunistic breeder able to take advantage of mild weather or adjust to accommodate more severe winters. These findings support those of Walker and Causey (1982) who hypothesized that mean January temperatures were important in the timing of woodcock reproduction in Alabama. Further investigations into the reproductive physiology of woodcock over a wider geographic range are needed to delineate more precisely the relationship of the woodcock nesting activities to winter weather.

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