the feces fall free to the ground. In this case, however, the lower nest protruded beyond the upper nest and accumulated a hard layer of urate left by droppings from above. By the time the chicks in the upper nest were 18 days old, their accumulated excrement had partially obstructed their own nest opening. The parents were apparently no longer able to enter the upper nest although they continued feeding their chicks through the opening as usual. At 23 days, the mature chicks tried to leave the nest but were able to fit only their heads through the reduced opening, a semicircle of 2-cm radius. The brood in the lower nest fledged normally.

The following day, parental feeding had ceased at the upper nest so I chipped away the solidified guano and freed the young. All four chicks were of normal weight and wing length; however, one had died the previous day. The three live chicks had dried excrement on their throat feathers but flew away readily. Without my intervention the remaining chicks presumably would have died shortly.

Suboptimal nest placement often confers fitness costs to the builders, directly through early nest collapse or indirectly through the energetic costs of collecting extra mud. The surprising result of this incident was the much greater cost to the pair nesting above. Although this outcome was predictable to human observers when the nestlings were only half grown, the parent swallows made no attempt to renest, extend the existing entrance tube, or scrape away the accumulating guano. I can only guess that this problem is sufficiently new, i.e., a side effect of nesting on man-made structures, or rare, that selection has been insufficient to render a solution.—PHILIP K. STODDARD, *Animal Behavior Program, Psychology Dept., NI-25, Univ. Washington, Seattle, Washington 98195.* *Accepted 15 Feb. 1983.*

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Reproductive behavior and pairing chronology in wintering dabbling ducks.—In dabbling ducks (Anatini), pair bond formation generally occurs prior to spring migration. Autumn and winter pairing chronology has been reported for some species (Weller, Auk 82: 227–235, 1965; Soutiere et al., J. Wildl. Manage. 36:752–758, 1972; Armbruster, Auk 99: 116–122, 1982), but until recently quantitative descriptions of reproductive behavior in wintering waterfowl were lacking (Paulus, The winter ecology of the Gadwall in Louisiana, M.S. thesis, Univ. North Dakota, Grand Forks, North Dakota, 1980; Afton and Sayler, Can. Field-Nat. 96:295–300, 1982), with the exception of Johnsgard's (Wilson Bull. 72:133–155, 1960) comparative study of Mallards (*Anas platyrhynchos*) and Black Ducks (*A. rubripes*).

The objective of this study was to quantitatively describe courtship behavior of dabbling ducks during autumn and winter. Emphasis was placed on determining chronology of pair bond formation, estimating proportion of time allocated to reproductive behavior and describing the pattern of courtship activity.

Study area and methods.—The study was conducted from October through February in 1978–79 and 1979–80 on Bodie Island, part of the Cape Hatteras National Seashore, Dare Co., North Carolina. Six species were studied: Gadwall (*Anas strepera*), Black Duck, American Wigeon (*A. americana*), Northern Shoveler (*A. clypeata*), Pintail (*A. acuta*), and Green-winged Teal (*A. crecca carolinensis*).

Data on reproductive behavior were compiled using both focal individual and ad libitum sampling (Altmann, Behaviour 49:227–265, 1974). With focal individual sampling, we attempted to observe each species once during each hour from sunrise to sunset every month from November through February. During 1-h sample periods, 10 focal individuals were selected and observed for 5 min each. Observations of behavior were recorded continuously with a cassette tape recorder. Each sample provided a record of the frequency of all behav-

TABLE 1

MEAN (±SE) PERCENT TIME ALLOCATED TO REPRODUCTIVE BEHAVIOR, 1978–79 AND 1979–80

Species	Nov.	Dec.	Jan.	Feb.	P^a
	N = 17.0[b]	N = 19.2	N = 15.8	N = 15.8	
Gadwall	2.2 (0.8)	0.9 (0.5)	0.4 (0.2)	0.04 (0.04)	<0.01
	N = 13.3	N = 18.3	N = 15.8	N = 7.5	
Black Duck	2.4 (0.9)	0.3 (0.1)	1.0 (0.6)	2.0 (1.2)	NS
	N = 18.3	N = 11.2	N = 6.4		
Wigeon	0.4 (0.3)	1.0 (0.8)	0.6 (0.5)	—	NS
	N = 16.7	N = 18.7	N = 15.1	N = 13.3	
Shoveler	0.0	0.1 (0.1)	0.2 (0.1)	0.7 (0.6)	NS
	N = 16.7	N = 18.7	N = 15.8	N = 11.7	
Pintail	0.0	0.5 (0.2)	2.6 (1.1)	1.4 (0.8)	<0.01
	N = 19.2	N = 19.2	N = 15.0	N = 15.8	
Green-winged Teal	0.0	0.7 (0.4)	5.4 (1.6)	1.2 (0.6)	<0.001

[a] ANOVA on rank transformed data.
[b] Total hours of observation using focal individual sampling.

iors, including reproductive behaviors, and time spent performing each. Ad lib sampling was used during periods when focal samples were not employed and aided the overall description of courtship activity. Observations in October consisted entirely of ad lib samples, but this sampling technique was used secondarily in other months.

Classification of reproductive behaviors follows previous studies (Lorenz, Avic. Mag. 57, 58, 59, 1951–1953; Johnsgard 1960; Johnsgard, Handbook of Waterfowl Behavior, Cornell Univ. Press, Ithaca, New York, 1965; McKinney, Wilson Bull. 77:112–121, 1965; Smith, Auk 85:381–396, 1968; McKinney, Living Bird 9:29–64, 1970) with the following exceptions: (1) all displays that involved preening ("preen-behind-the-wing," "preen dorsally," and "belly preen") were placed under the general heading "preening"; (2) displays of "head shake," "head flick," "tail wag," "bill dip," "drink," and "wing flap" were assembled under the heading "maintenance"; and (3) all displays involving copulatory behavior (pre- and postcopulatory displays) were placed under "copulatory behavior." "Swimming" by individuals within courting groups was considered reproductive behavior. Birds used swimming primarily to position themselves for display, and a more accurate estimate of time allocated to reproductive activity was obtained by including it.

To estimate pairing chronology, a random sample of females from each species was selected monthly and the proportion of paired females was determined. Several criteria were used to determine pair status. The best criterion was sustained proximity to a member of the opposite sex, but other behaviors, such as female "inciting," following of a particular male by a female, and male defense of the female were also used as indicators of pair bond formation. Females were observed for 5 min before assessing and recording pair status.

Percent time allocated to reproductive behavior was calculated for 1-h sample periods and mean percents tabulated for each month. Yearly estimates were combined for analysis. Statistical analysis of percent time spent in reproductive behavior was performed using

TABLE 2

PERCENT TIME SPENT IN REPRODUCTIVE BEHAVIORS AND DISPLAYS BY MALE AND FEMALE GADWALL WINTERING AT BODIE ISLAND, NORTH CAROLINA

Reproductive behaviors	Nov.		Dec.		Jan.	
	M	F	M	F	M	F
Swimming	47.9	60.0	59.3	92.0	71.4	43.5
Burp	20.1	—	21.0	—	9.5	—
Introductory shake	1.8	—	0.0	—	0.0	—
Grunt-whistle	3.2	—	3.5	—	4.8	—
HUTU-TTF	1.0	—	2.3	—	4.8	—
Preening	0.0	0.0	0.0	0.0	0.0	4.3
Maintenance	16.0	0.6	11.6	2.0	9.5	8.7
Jump flight	5.0	0.0	2.3	0.0	0.0	0.0
Inciting	—	39.4	—	6.0	—	43.5
Copulatory behavior	5.0	0.0	0.0	0.0	0.0	0.0
Total[a]	18.2	6.7	7.2	4.2	1.7	1.9

[a] Time observed (min).

standard parametric procedures (*t*-test and ANOVA) after rank transformation of data (Conover and Iman, Am. Stat. 35:124–133, 1981).

Results.—Data are based on 354.5 h of focal individual sampling. Proportion of time allocated to reproductive behavior varied significantly among months for Gadwall, Green-winged Teal, and Pintail but not for the other species (Table 1). Proportion of time spent each month in reproductive behavior did not differ significantly ($P > 0.05$) by sex for any species.

Gadwall.—Courtship activity for Gadwalls was observed initially in late October, but displays performed suggested that courtship began earlier. For instance, females incited and were aggressive to single males, indicating that females in early courting groups were paired. Males performed a wide range of displays including "burp," "introductory shake," "grunt-whistle," and "head-up-tail-up turn-to-female" (HUTU-TTF). HUTU-TTF is characteristic of courtship activity of intermediate intensity (Johnsgard 1960). Gadwalls also engaged in "courtship flights," and based on our observations of other species, this behavior usually occurred late in the pairing process as competition among males intensified.

Proportion of time spent in reproductive behavior was greatest in November and decreased thereafter (Table 1). In November, males performed burping most frequently and inciting was the most frequent of female displays (Table 2). "Jump flights" and aggression among courting males were also common. Approximately 92% of female Gadwalls had formed pair bonds in November (Table 3). Copulation occurred initially on 9 November.

In late winter, time spent in reproductive behavior decreased, but intensity of courtship remained high as courtship was initiated primarily by unpaired males. Although copulations were not recorded during focal samples in late winter, copulatory behavior by paired individuals was not uncommon at this time and probably served to strengthen pair bonds (see Johnsgard 1960).

Black Duck.—Black Ducks participated in courtship behavior in early October. Males displayed to females with grunt-whistle, HUTU-TTF and "nodswimming" and females were

TABLE 3
MONTHLY ESTIMATES OF THE PERCENT OF FEMALES THAT HAD FORMED PAIR BONDS, 1979–80

Species	Month			
	Nov.	Dec.	Jan.	Feb.
Black Duck	N = 30 96.7	N = 50 98.0	N = 45 100.0	N = 10 100.0
Gadwall	N = 49 91.8	N = 50 96.0	N = 45 97.8	N = 40 100.0
Wigeon	N = 33 84.1	N = 17 70.6	N = 91 84.6	—
Shoveler	N = 48 8.3	N = 42 43.0	N = 38 65.8	N = 30 96.7
Pintail	N = 47 0.0	N = 45 9.0	N = 45 84.4	N = 30 100.0
Green-winged Teal	N = 49 2.0	N = 46 0.0	N = 41 31.7	N = 44 79.5

observed inciting and nodswimming. Paired individuals were common in October, indicating that courtship activity commenced sometime before our observations.

Proportion of time spent in courtship did not change significantly from November through February (Table 1). In November, males performed displays of every intensity and inciting was performed regularly by females in courting groups (Table 4). Copulatory behavior also was recorded. Approximately 97% of females were paired in November (Table 3). Black Ducks initiated courtship and began pairing earlier than any other species studied.

Intensity of courtship remained high throughout December, January, and February. Pair bonds were stable, however, and single males were never successful in breaking up pairs.

Wigeon.—In late October, male Wigeon in alternate plumage displayed with burps, "folded-wings-raised-high-overhead" (FWRHO), and jump flights. Some females in courtship groups incited, so formation of pair bonds had begun. Even though reproductive behavior was not common at this time, displays performed suggested that courtship activity was initiated previous to our observations.

Proportion of time spent in courtship did not change significantly by month (Table 1). In November, courtship activity frequently was characterized by aggression among males. Females displayed with "chinlifting" and inciting, and common male displays were maintenance (8.3%), preening (6.2%), introductory shake (2.1%), and FWRHO (2.1%). Approximately 84% of females were paired in November (Table 3). In December, males performed burping (33.3%) most frequently, followed by maintenance (12.8%) and FWRHO (7.3%); females primarily incited. Jump flights were also common in December (4.0%). In January, females principally incited and the most common male displays were preening (18.7%), maintenance (11.6%), and FWRHO (3.1%). Gradual dispersal of individuals from the study area made it impossible to obtain a full record of courtship throughout winter.

Shoveler.—Reproductive behavior by Shovelers was rarely observed during periods of focal

TABLE 4

PERCENT TIME SPENT IN REPRODUCTIVE BEHAVIORS AND DISPLAYS BY MALE AND FEMALE BLACK DUCKS WINTERING AT BODIE ISLAND, NORTH CAROLINA

Reproductive behaviors	Nov.		Dec.		Jan.		Feb.	
	M	F	M	F	M	F	M	F
Swimming	75.2	44.1	64.3	3.8	77.7	14.8	75.4	59.7
Burp	0.9	—	0.0	—	1.7	—	1.7	—
Introductory shake	2.1	—	0.0	—	1.7	—	1.7	—
Grunt-whistle	2.1	—	0.0	—	1.7	—	0.8	—
HUTU-TTF	1.2	—	0.0	—	1.7	—	1.7	—
Down up	1.8	—	0.0	—	0.0	—	0.0	—
Nodswimming	4.3	23.6	0.0	42.3	1.7	68.5	7.0	0.0
Preening	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0
Maintenance	11.5	2.4	0.0	0.0	13.8	1.9	8.3	6.0
Jump flight	0.9	0.0	14.3	0.0	0.0	0.0	1.7	0.0
Inciting	—	26.8	—	50.0	—	14.8	—	34.3
Copulatory behavior	0.0	3.1	21.4	3.8	0.0	0.0	0.0	0.0
Total[a]	9.4	10.6	2.3	2.2	4.8	4.5	4.7	5.2

[a] Time observed (min).

individual sampling (Table 1); however, ad lib sampling greatly aided description of pairing activity. Only males in alternate plumage displayed to females. In early November 6% (N = 36) of males were in alternate plumage and no courtship was recorded during this month (Table 1). Some females were paired in November (Table 3); however, because courtship was rarely observed, development of these associations was unclear.

Courtship groups occurred initially in early December. Aggression among courting males was infrequent and male displays consisted of jump flight and "head dip." Intensity of courtship was low and groups soon dispersed. Courtship activity became more frequent in late December. Most males were in alternate plumage and displayed most frequently with jump flights. In January, jump flights remained the most prevalent male display and aggression among males in courtship groups was frequent. Approximately 66% of females were paired in January. Copulatory behavior occurred initially on 17 January, and all major displays described by McKinney (1970) had been observed by the end of the month. In February, over 95% of females were paired. Pair bonds were stable and attempts made by unpaired males to disturb established pair bonds were unsuccessful.

Pintail.—Most males attained alternate plumage in mid-November and initiated courtship by swimming up to females and burping. Females showed no interest in these males and continued their regular activities; males soon dispersed. Reproductive activity occurred in ad lib sampling but courtship was not recorded in focal samples during November. No females were paired in November (Table 3).

Pintail courtship activity continued at low frequency and intensity into December. Males circled females while burping; females usually showed no interest and males stopped displaying. In the second week, courtship behavior was still infrequent but it intensified as burp, grunt-whistle, and HUTU-TTF displays were performed by males. Nodswimming was the most common female display (Table 5). Courtship behavior became more frequent in

TABLE 5

PERCENT TIME SPENT IN REPRODUCTIVE BEHAVIORS AND DISPLAYS BY MALE AND FEMALE PINTAIL WINTERING AT BODIE ISLAND, NORTH CAROLINA

Reproductive behaviors	Dec.		Jan.		Feb.	
	M	F	M	F	M	F
Swimming	45.3	13.6	56.2	56.3	57.4	50.0
Burp	42.2	—	17.2	—	21.7	—
Introductory shake	0.0	—	1.5	—	3.0	—
Grunt-whistle	0.0	—	1.0	—	0.0	—
HUTU-TTF	0.0	—	0.5	—	0.0	—
Down up	0.0	—	0.0	—	0.9	—
Nodswimming	0.0	54.6	1.5	2.9	1.7	0.0
Preening	0.0	0.0	1.5	0.0	0.9	0.0
Maintenance	12.5	9.1	10.0	2.5	13.9	0.0
Jump flight	0.0	0.0	6.4	0.5	0.5	0.0
Inciting	—	22.7	—	34.9	—	50.0
Copulatory behavior	0.0	0.0	4.4	2.9	0.0	0.0
Total[a]	5.3	1.8	16.9	8.6	9.6	0.1

[a] Time observed (min).

late December. Low intensity displays still were most common for both sexes, but some females were observed inciting, indicating pair bonds were beginning to form.

Proportion of time spent in reproductive behavior was greatest in January (Table 1). Males used displays of every intensity, and females were inciting more often and nodswimming less (Table 5). High intensity behaviors such as jump flights and copulatory behavior were performed. Approximately 85% of females were paired in January (Table 3).

Proportion of time spent in courtship decreased in February. During this period, courtship was initiated by unpaired males. If approached by unpaired males, paired males usually attempted to lead the female away as she incited but they sometimes also attacked the intruding males.

Green-winged Teal.—Courtship activity by Green-winged Teal was observed first in November during ad lib sampling but did not occur in focal samples until December. In November, males in alternate plumage displayed with low intensity burps and grunt-whistles only after they had been excited in some manner.

Courtship activity increased in December, but intensity and frequency of courtship behavior in this month varied during the two years of study. In 1978, intensity of courtship increased during the first week of December. Male courtship consisted of low and intermediate intensity displays (burp, grunt-whistle, and HUTU-TTF) while females performed nodswimming and maintenance displays. Courtship flights were observed in the second week of December and more intense reproductive activity continued throughout the month. Few females had paired by the end of December.

In contrast, reproductive activity was infrequent throughout December 1979. Reproductive behavior was observed only after birds had been excited and consisted of burps and grunt-whistles. Individuals displayed briefly and soon dispersed. Like the previous year, few females had formed pair bonds by the end of the month (Table 3).

TABLE 6

PERCENT TIME SPENT IN REPRODUCTIVE BEHAVIORS AND DISPLAYS BY MALE AND FEMALE GREEN-WINGED TEAL WINTERING AT BODIE ISLAND, NORTH CAROLINA

Reproductive behaviors	Dec.		Jan.		Feb.	
	M	F	M	F	M	F
Swimming	52.5	60.7	63.3	58.7	79.1	62.0
Burp	5.0	—	7.9	—	3.3	—
Introductory shake	0.5	—	2.5	—	2.2	—
Grunt-whistle	3.0	—	1.8	—	2.2	—
HUTU-TTF	3.0	—	0.8	—	1.1	—
Down up	0.0	—	0.8	—	0.0	—
Bill up	0.0	—	0.2	—	0.0	—
Turn-back-of-head	0.0	—	0.4	—	0.0	—
Bridling	0.0	—	0.2	—	2.2	—
Nodswimming	6.9	35.7	10.9	20.9	1.1	19.0
Preening	17.7	0.0	0.7	1.0	0.0	0.0
Maintenance	11.4	3.6	10.5	3.1	8.8	0.0
Inciting	—	0.0	—	16.3	—	19.0
Total[a]	8.4	4.7	36.7	8.2	7.6	1.7

[a] Time observed (min).

In both years, proportion of time spent in reproductive behavior by Green-winged Teal was greatest during January (Table 1). Aggression was common among males in courtship parties. Males performed displays of every intensity, including high intensity "down-up" and "bridling" while inciting was performed initially by females (Table 6). During January approximately 32% of females were paired. Copulatory behavior occurred during January in 1979 but not in 1980. In February, proportion of time spent in reproductive activity decreased (Table 1), but intensity of courtship remained high. Proportion of paired females increased in February, and by early March approximately 80% of female Green-winged Teal were paired.

Discussion.—This study is the first to quantify and compare reproductive behavior of several species of waterfowl during winter at a single location. Considerable variation in timing of courtship activity occurred among species. Initiation of reproductive behavior was related closely to attainment of alternate plumage. Species which developed alternate plumage late (e.g., Green-winged Teal, Pintail) began courtship later and paired later. Weller (1965) also concluded that chronology of courtship activity and eventual pair bond formation in the genus *Aythya* was closely linked to development of alternate plumage. This same trend has been reported for other species of waterfowl as well (McKinney 1970, Armbruster 1982).

A general pattern of reproductive behavior occurred in wintering dabbling ducks from initiation of the pairing process until most females were paired. At first, courtship activity was infrequent and males performed displays of low intensity (e.g., burp, grunt-whistle, introductory shake). Females often were not receptive to early courtship attempts, and this lack of receptivity seemed to deter and shorten male display. In addition, few aggressive interactions among courting males were observed. As pairing continued, courtship activity

increased in intensity. Courtship at this time frequently was characterized by aggression among males, courtship flights, jump flights, and copulatory behavior. In addition, males performed a greater diversity of displays, and females displayed most often by inciting. Reproductive behavior continued at this high level until most females had paired. At this time, frequency of courtship usually declined but intensity of display remained unchanged. Late in the pairing process, attempts by single males to disrupt established pair bonds were never successful.

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Expectable decline of forest bird populations in severe and mild winters.—In an earlier paper (Graber and Graber, Wilson Bull. 91:88–103, 1979) we described the change of bird numbers in three habitats in southern Illinois between early winter (26 December–7 January) and late winter (3–18 February) during 1976–77, an especially cold winter with heavy snow. On average, bird populations that season declined about 58% in mature bottomland forest, and 66% in mature upland forest, but increased slightly (9%) in urban residential habitat. We attributed the change to mortality and local movements of birds. Those observations posed two other questions of interest to us: (1) How would populations vary in a mild winter? and (2) Is there a predictable rate of change during the winter season?—important questions for those who census birds.

Methods.—To find the answers we censused, using the same methods on some of the same areas, early (26 December–11 January) and late (25 January–15 February) winter in 1977–78 (another severe winter) and 1979–80 (a mild winter). The relative severity of those winters is indicated in Table 1. Our attempts to acquire data early and late in the winters of 1978–79 and 1981–82 were frustrated by floods and ice storms. Within the seasonal limits posed by the study, we censused every day that weather permitted. The periods of censusing were chosen to avoid early and late migration. We varied coverage of habitats in the different years to consider different problems concerned with the census. In 1977–78, to consider population variability, we censused seven bottomland forest areas (Nos. 1, 2, 6, 8, 10, and two forests at No. 11 in Fig. 1 of Graber and Graber [1979]). The variability shown (Table 2) includes variation from the census method and from the habitats as well as the populations. For that reason and because of the small number of areas that could be censused in the time available, the standard errors are large. Differences between early winter and late winter populations (all native species) in the seven bottomland forest areas were significant ($t = 2.72$, df = 12, $P < 0.02$).

Because it is important to know whether decline in numbers of birds represents mortality or movement to other habitats, we censused representative areas of the principal arboreal habitats in southern and central Illinois. In the mild winter of 1979–80 (Table 3), in addition to mature bottomland (No. 10 in Fig. 1 of Graber and Graber [1979]) and mature upland forest (Warbluff Forest, 10 km N, Golconda, Pope County), we censused upland forest-edge