## SOCIAL BEHAVIOR OF BREEDING GADWALLS IN NORTH DAKOTA

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RESPONSES of duck pairs encountering other ducks were categorized by McKinney (1965a) as displays, attack, escape and avoidance, sexual pursuit, and sociability. Gadwalls (*Anas strepera*) show all these responses on the breeding grounds, and characteristic behavior patterns occur depending on the reproductive state of the birds involved. The responses of paired ducks to unpaired males on the breeding grounds have not been described for the Gadwall or any other species. The function of aerial flights (McKinney 1965a) is also confused in the literature. The objectives of this paper are to describe the responses of paired breeding Gadwalls to other Gadwall pairs and unmated drakes and to discuss the possible reasons for the type of spacing behavior Gadwall pairs exhibit.

#### STUDY AREA AND METHODS

The 36-square-mile study area is in south central North Dakota, 6 miles south of Medina. The topography results from extensive stagnation of the last ice sheet and consists mainly of stagnation moraine with smaller patches of perched lacustrine plain and glacial outwash (Winters 1963). The land is characterized by numerous low hills interspersed with small undrained depressions that contain wetlands of various sizes and types. The number of wetland basins per square mile ranges from 5 to 30 with an average size of about 4 acres. According to the classification of Stewart and Kantrud (1971), 10% of the wetlands are ephemeral, 33% temporary, 35% seasonal, and 15% semipermanent. Three permanent lakes over 50 acres in size and several dugouts and fens occur on the area. Approximately 40% of the land is grazed pasture and 60% is farmed for small grains.

Data for this paper were gathered during 1972 and 1973 by visual study of marked and unmarked Gadwall pairs and unmated drakes. Ducks were trapped at baited shoreline sites and marked with back-mounted radio packages (Dwyer 1972) and/ or nasal saddles. Transmitter signals were used primarily to locate birds quickly for periods of extended visual observation. Studies on seven pairs and three unmated drake Gadwalls that were marked during the prenesting period showed that members of pairs spend virtually 100% of the time together. Therefore for purposes of this study, I considered a drake unmated if he was absent from a female for 5 min or longer during the prenesting period. Unmated drakes showed no tendency to remain at any specific location and were quite mobile.

Intraspecific social responses of Gadwalls on the breeding grounds are described for the spring arrival, prenesting, and laying to early incubation periods (Table 1). Responses of marked pairs to other pairs and unmated drakes were correlated to the stage of the breeding cycle when nests of the marked females were found and the laying or incubation stage determined. During the breeding season the reproductive states of individual birds overlap in any local population, but Gadwalls seem to be more synchronized in the start of breeding than other duck species

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Interaction between	Responses			
	Spring arrival	Prenesting	Laying	
Pair-pair	Chin-lift Threat	3-bird flight Chin-lift	3-bird flight Chin-lift	
Pair-unmated drake	Chin-lift	Chin-lift	Chin-lift	
	Threat Inciting	Threat Inciting	Threat Preening-behind- the-wing	
	Courtship displays Courtship flight	Courtship displays Preening-behind- the-wing	the wing	
	Preening-behind- the-wing			
Paired drake²- pair	—	-	3-bird flight Chin-lift	
Paired drake <sup>2</sup> - lone drake <sup>3</sup>		—	Chin-lift Fighting Preening-behind- the-wing	

TABLE 1					
Summary of Responses of Gadwalls to Conspecifics During Three Time Periods of the Breeding Season <sup>1</sup>					

<sup>1</sup> Exact quantitative data on frequencies or sequences of these responses were not gathered in this study. <sup>2</sup> Hen at next.

<sup>3</sup> Either paired or unpaired drake.

(Duebbert 1958, Bezzel 1962, Oring 1969). Thus data from interactions between unmarked pairs were usable because most birds were in the same reproductive state at any particular time. Behavior patterns resulting from interactions were quite consistent during any one time period.

A sex ratio and breeding chronology survey was conducted weekly on a sample group of 24 potholes during April and May of both 1972 and 1973. Observations of flights and behavioral interactions were written directly as notes or dictated to a portable tape recorder. Flights involving both marked and unmarked birds were timed with a stopwatch or the second hand of a wristwatch. Three-bird flights were timed from initiation of the flight to the breakoff point of the pursuing male.

In 1973 a metronome timing device (Wiens et al. 1970) set at a 15-sec interval was used to establish a sampling interval for time budget studies of Gadwall pairs. The activity of both members of a pair was coded directly on a columnar form each time the tone sounded. Two 1-h sampling periods were picked at random for each of three separate time periods of the day, 0600 to 1100, 1100 to 1600 and 1600 to 2100. I tried to watch a pair each day for 1 h in each of the three time periods, but succeeded in only about half of these attempts.

I succeeded in observing unmarked pairs of Gadwalls for purposes of time budget analysis during 34.8 h in the prenesting period. I watched two other pairs for 23.4 additional h during the laying period. Both drakes of these two pairs were identifiable by plumage characters, and I confirmed that the females were nesting by watching them fly to the nest site in the early morning while the drake remained at the activity center alone. I also gathered 6 h of data on the two paired drakes while their females were at the nest.

Three pairs of Gadwalls were introduced into a flight pen similar to that used by McKinney (1967) on 1 May 1973 and watched for 6 to 10 h per week until the hens were incubating. This procedure yielded information on vocalizations and permitted better interpretation of some behavior patterns seen in the wild.

## **RESULTS AND DISCUSSION**

Lorenz (1953) first described the courtship behavior of the Gadwall. Gates (1958) elaborated on Lorenz's descriptions and related some displays to social situations in which they occur. Both Gates (1958) and Johnsgard (1965) illustrated displays. Displays characteristically given by paired Gadwalls to conspecifics on the breeding grounds are: preening-behind-the-wing, chin-lifting, and inciting. Courtship displays most often given by unmated drakes on the breeding grounds include burp, grunt-whistle, head-up-tail-up, down-up, and turn-back-of-head. Displays involved in copulatory behavior are not discussed.

#### Spring Arrival Period

Small flocks of paired Gadwalls began to arrive at the study area during the first week of April 1972 and the fourth week of March 1973. Among these early arrivals sex ratios were almost equal, and this ratio continued through the peak of migration in April. Numbers declined in early May, and the sex ratio became much more imbalanced in favor of males, primarily because many transient pairs left the area.

Duebbert (1966) working at J. Clark Salyer National Wildlife Refuge in northern North Dakota noted average spring arrival dates of Gadwalls to be about the same as in this study and showing a similar early season sex ratio. Gates (1962) found two major influxes of birds through his study tract in Ogden Bay, Utah. Many of the early arrivals were unpaired, and an unequal sex ratio prevailed among them. The second group of birds to arrive there was composed almost entirely of mated pairs.

Gadwall pairs usually arrive on their breeding grounds as much as a month or more before egg-laying begins (Gates 1962, Duebbert 1966, Oring 1969). A similar interval occurred in this study. This long residency before nesting begins allows many opportunities for social interactions between pairs. McKinney (1965a) pointed out that social responses play an important role in determining patterns of pair spacing.

Pairs of Gadwalls were usually seen in the company of other species including Redheads (*Aythya americana*), Canvasbacks (*A. valisineria*), American Wigeon (*Anas americana*), and American Coots (*Fulica americana*). The spatial pattern of pairs in the flocks appeared to conform to

Condor's (1949) concept of "individual distance." During April of both years, when the sex ratio did not exceed 1.2 males per female, hostile interactions between pairs usually consisted of open-bill threat movements by males, mutual chin-lift postures by pairs, and avoidance responses by other birds during feeding activities. Early in May when smaller groups of pairs were present on potholes, very short three-bird chases (female of a pair chased by a paired male and followed by her mate) became common.

In flock situations paired hens are sometimes approached by unpaired males who attempt to court them. The hen incites and alternately chinlifts in unison with her mate. Pairs seem vulnerable to unmated drakes at this time and are sometimes harassed for long periods as the drakes perform the complete repertoire of the species' courtship displays. Sometimes the drakes press the hen too closely, and she takes flight followed by her mate and the courting drakes. Other drakes in the vicinity that appear to be unmated are immediately attracted by the sight and sounds of the flight and a swift erratic display flight ensues involving a changing number of drakes and lasting several minutes. First one, then another drake maneuvers to catch up with the hen, sets his wings, thrusts his head up and back, and utters the harsh nasal sound characteristic of the burp display. Much fighting between males takes place in the air behind the hen as the paired male tries to drive the other drakes away. The female gives the inciting call (Lebret 1958) during the flight as she tries to elude the pursuing drakes. Upon returning to a pond, the female incites against the remaining drakes, and the pair moves away.

Wüst (1960) and Gates (1958) describe courtship flights that derive from swim courtship during pair formation in the fall and winter. Neither author distinguishes these flights from spring courtship flights involving an already paired hen. Dzubin (1957) describes Mallard (*Anas platyrhynchos*) spring courtship flights that seem essentially the same as in the Gadwall in that they are caused by encounters between loosely paired hens and unmated drakes, but Mallard flights lack the ingredient of male-to-male aggression so characteristic of Gadwall flights. Lebret (1955) describes how intraspecific encounters of unmated drakes and pairs of several species, including Gadwalls, give rise to courting flights in the winter. He also mentions that spring courtship flights are no different than those in the winter except they occur less frequently because most birds are paired.

#### PRENESTING PERIOD

The prenesting period begins when pairs from flocks of Gadwalls have dispersed to smaller wetlands. At this time two categories of pairs are distinguishable. One group has already selected one or more preferred feeding and loafing spots, called activity centers or core areas (Gates 1958), where they spend virtually the entire day. The other group consists of those pairs actively seeking such centers. Mated drakes initiate most three-bird chases, so characteristic of this period, from activity centers.

Responses of mated drakes to pairs.—Throughout the prenesting period the degree of intraspecific tolerance mated drakes exhibit steadily decreases. Early in the prenesting period paired drakes usually tolerate other pairs to within 20 to 30 yards with no aggression. But when a pair approaches closer, the resident drake immediately becomes alert, swims rapidly toward the approaching pair for approximately one-half the distance separating them, and then flies the remaining distance. He lands close to the hen, assumes the chin-lift posture, and gives a rapid burplike call. The hen immediately takes flight chased by the resident drake and followed by her drake. During the chase, the female's mate continually tries to position himself between the attacker and his mate.

Later in the prenesting period, the attacking drake flies at the hen on the water and sometimes lands directly on her. At this time a paired drake's attack threshold is lower, and he will chase pairs flying overhead or those that approach to within 50 to 60 yards. Also at this time, hens aware of mated drakes flying at them take flight before the drake can approach them too closely.

The frequency, intensity, and length of three-bird chases all increase as nesting approaches. The peak of chasing activity occurs during the second week of May when pairs are establishing themselves at activity centers (Fig. 1). Chases increase in length until about the last week in May and first week of June when most hens are laying (Fig. 1). In 1972 one marked drake's chases lasted from 5 to 20 sec 3 weeks prior to nesting (seven chases), 15 to 30 sec 2 weeks prior to nesting (five chases) and 30 to 50 sec the week before and during early laying (seven chases).

A drake whose hen is being chased readily attacks the pursuing drake in the air as his hen gives the inciting call. During early prenesting this male-to-male aggression is usually enough to deter the pursuer, and he returns to his hen. Later the pursuits are so vigorous that the drake of the pursued hen rarely catches up to the pursuer before the chase ends. The hen gives the inciting call much more rapidly during these high intensity chases as she frantically maneuvers to escape the pursuing drake.

The pursuing drake gives one or more burp calls as he glides back to the site from which he initiated the attack and also burps as he swims back to his hen. The burp may function as a recognition call whereby the hen can recognize her approaching drake. In over 150 three-bird



WEEK

Figure 1. Number of Gadwall three-bird chases recorded during 12 h of observation per week and average duration of flights in seconds during 1973.

chases, I have never seen a paired drake fail to give the burp display on completion of the flight.

Unpaired males occasionally fly up to follow three-bird chases and may display to the hen in the air. They do not burp when returning to a pond and may break off in midflight to follow other birds.

Responses of pairs to unmated drakes.—The sex ratio of Gadwalls on the study area in 1972 averaged 1.6 males per female during the first 3 weeks of May. In 1973 there were 1.3 males per female present during the same period. These unmated drakes frequently associated in groups of two or three and attempted to associate with mated pairs.

While pairs are selecting an activity center, they are sometimes approached by unmated drakes. Pairs usually tolerate an unmated drake to within a few yards with no aggression, but when the unmated male approaches closer, the mated male swims between his hen and the intruder and chin-lifts. If the intruder persists, the pair chin-lifts in unison, and the hen incites against him. Occasionally two unmated drakes approach and try to court a hen. This situation elicits inciting by the hen coupled with chin-lifting by her mate and alternating with mutual chin-lifting by the pair. The paired drake threatens each approaching drake after the hen incites against him. The hen at times

is much more aggressive in these situations than her mate. I have rarely seen these encounters result in a courting flight as occurs regularly during flock situations in the spring arrival period.

After pairs have selected activity centers, they appear more secure from the harassment of unmated males. A chin-lift by the mated male is enough to make unmated males stop their approach. I theorize that unmated males recognize pairs at activity centers as secure.

The actions of unpaired males change quite rapidly. After several minutes of harassing a pair, they may stop and begin to feed and allow the pair to move away. The high frequency of preening-behind-the-wing by unmated males during the harassment of a pair may show conflicting tendencies to associate with the pair and to retreat from the pair's threats. Members of the pair also preen-behind-the-wing at this time. McKinney (1965b) has shown that ritualized preening movements occur during and after hostile encounters in the Anatidae. Ritualized preening and drinking movements also occur as displays in courtship (Gates 1958, von de Wall 1965).

## LAYING TO EARLY INCUBATION PERIOD

Response of mated drakes to pairs.—Pairs spend virtually all their time at one or two activity centers (Gates 1958, Dwyer pers. obs.). Mated drakes chase hens of other pairs from the general vicinity of the activity center as described in the section on prenesting. Three-bird flights are lengthy until the midpoint of the laying period, when male aggression seems to taper off and the flights become shorter. During laying of the first half of the clutch, the four paired drakes under observation usually did not leave the activity center while their hens were at the nest. They remained very alert and gave the burp display often. Time budget analysis shows that a mated drake alone on an activity center spends over 5% of the time giving the burp display. He also makes short, low flights over the general vicinity of the nest giving the burp call.

A drake seems preoccupied during his hen's absence and he does not initiate as many pursuits against other pairs as when his hen is present (Gates 1958). The few three-bird flights I have seen initiated by males alone at activity centers lasted approximately half as long as flights when the hen was present. As laying progresses, the drake spends more time away from the activity center. He associates peacefully with other males, and pairs treat him as an unmated drake.

Hens in the late laying or incubation stage sometimes become involved in chases that involve more than one pursuing male. These flights usually occur when a female returns to her activity center from the nest and her mate is not there. She is then vulnerable to other paired males who are usually associating in small groups at this time. Gates (1958) called these flights "harrying chases." They are long and may last over 4 min. I have seen only six of these flights, and none resulted in rape of the female as occurs regularly in the Mallard or Pintail (*Anas acuta*). Gates (1958) saw attempted rape in only two out of many Gadwall "harrying chases" he watched. The great amount of male-to-male aggression in the flights or the fact that the extra males drop out of the flight after varying lengths of time may prevent rape from occurring.

Responses of mated drakes to other drakes.—When pairs are together in activity centers mated drakes tolerate lone drakes to within a short distance. A chin-lift or threat posture by a mated drake is enough to make a lone drake retreat. No harassment of pairs by unmated drakes occurs as in the early prenesting period.

When a drake is alone on his activity center, he is hostile to other lone drakes who approach. Chin-lifting and sometimes bill grabbing and pushing are common for the first few days of laying. In all cases I have seen, the resident drake was the victor in these contests, and the other drake usually left the site. After the midpoint of laying, mated drakes seek out other lone drakes. Groups of several drakes feeding or loafing together are common at this time, but later in the day these same drakes may return to their activity centers and be reunited with their hens.

## SPACING BEHAVIOR IN THE GADWALL

Brown (1964) pointed out that competition for some essential ecological requisite is the most important factor in maintaining intraspecific aggression in a population. The type of territoriality or aggressive behavior that a species exhibits is probably the result of the kinds of ecological requisites that are in short supply (Brown 1964).

McKinney (1965a) reviewed the theories on the function of chasing in ducks and surmised that pair spacing tended to reduce predation rates because nests would probably be spaced. Siegfried (1968) in his paper on the Black Duck (*Anas sparsa*) of South Africa, speculated that the survival value of spacing in this species was based on a sparse food supply. Spacing, as Brown (1969) has pointed out, must be a secondary consequence of competition for some essential requirement, such as a foraging site. McKinney (1973) in a later paper modified his theory on the function of chasing to include the feeding requirements of female ducks during the breeding season. He concluded, without data on feeding rates, that it would be important for Northern Shoveler (*A. clypeata*) females to have assured feeding grounds during the prenesting, laying, and incubation periods.

	Stage of mate's breeding cycle		
	Prenesting	Laying	Early incubation
Amount of time paired male spends			
Alone on waiting area	0	XX	х
Associating with other males	0	X	XX
Attacking other pairs	XXX	XX	0
Attacking other males	$\mathbf{X}$	x	x
Attempting to rape strange females	0	0	x
Characteristics of pursuit flights			
Frequency of 3-bird flights by paired males	XXX	XX	х
Frequency of flights involving many males	X	x	X
Aggression between males in flight	XXX	x	х

# TABLE 2 Social Behavior and Some Characteristics of Pursuit Flights in the Gadwall<sup>1</sup>

<sup>1</sup> Table format adapted from McKinney (1965a). The ratings X, XX, XXX, (0 = absent), represent low, moderate, and high frequency of occurrence of the behavior pattern or characteristic. These approximate ratings are based on observations of marked birds.

Breeding female ducks, including Gadwalls, require a high-protein diet (Holm and Scott 1954) and consume aquatic invertebrates in much greater proportion before and during egg-laving than at other times of the year (Swanson and Nelson 1970, Swanson and Meyer 1974). Breeding hens probably also need an increased amount of feeding time to select this high quality diet. Several characteristics of Gadwall social behavior (Table 2) and general behavior provide evidence that chasing ensures the breeding hen an opportunity to utilize a needed food supply. Gates (1958) first described how a pair of Gadwalls spend the greater part of each day in one particular place. He emphasized that they used this site mainly for loafing or sleeping and occasionally for feeding. In this study I found that the greatest amount of feeding activity also takes place at the activity center. Time budget analyses of pairs during the prenesting and laying periods shows significantly greater (P <0.05) feeding rates by the females regardless of the time of day. On the average females spend 17% and 48% more time feeding than males during the prenesting period and laying period, respectively (Fig. 2). Bengtson (1972) showed that female Harlequin Ducks (Histrionicus histrionicus) spend 30% more time feeding than their mates prior to nesting.

As shown previously three-bird chases are most frequent when pairs select activity centers, but a male is aggressive toward other pairs and unmated drakes until his hen is well into laying. Thus a mated drake by protecting his female from unmated drakes intent on courtship may provide more time for her to feed unmolested. By protecting his female from the approach of pairs he eliminates competitors for the food source at the activity center. I theorize that the most important function of



Figure 2. Percentage of time pairs of Gadwalls spent feeding during the prenesting and laying periods. Males are indicated by crosshatching.

chasing is to protect the food supply and secondarily to provide for undisturbed feeding time. Young (1970) showed that Sheld-Ducks (*Tadorna tadorna*) most likely protect an adequate food supply as they do not establish their exclusive feeding areas where the snail density is below 30 snails/m<sup>2</sup>.

Orians (1971: 534) postulated that for birds living in habitats with a reasonably uniform distribution of food, "foraging time will be minimized" if no other individuals are feeding on the same food in the same area. Natural selection should favor behavior patterns that would eliminate other individuals as long as the energetic costs are not too great (Orians ibid.). Food resources in small wetlands vary in abundance owing to physical and chemical properties of each wetland. Once a paired female selects a spot, it could be advantageous for her mate to expel other Gadwalls from it to assure her food supply. She could then quickly build up her metabolic reserves for nesting with a minimum of disturbance.

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### Summary

The social behavior of the Gadwall on the breeding grounds in North Dakota is described in terms of the responses of mated drakes to other pairs and unmated drakes. During the spring arrival period, intraspecific aggression is limited to threat postures by paired males and avoidance responses by other birds. Spring courtship flights occur when paired hens are pressed by unpaired males who are displaying to them.

During the prenesting period the degree of intraspecific tolerance mated drakes exhibit steadily decreases. The chin-lift posture is the most important indication of aggressive tendencies in a mated drake. Mated drakes tolerate other pairs to within about 20 to 30 yards in the early prenesting period but chase them when they approach to within 50 to 60 yards or fly overhead as their hens near laying. The frequency, intensity, and length of three-bird chases all increase as the nesting perod approaches. Male-to-male aggression is common during three-bird flights. Nesting females are occasionally harassed by paired males, but rape appears to be very rare in contrast to the Mallard and Pintail.

While the hen lays the first half of the clutch, the drake remains at the activity center and is most aggressive toward other pairs while his mate is present. As laying progresses he spends more and more time away from the activity center and associates with other males. Time budget analyses shows that paired females spend 17% and 48% more time feeding than their mates during the time they are together in the prenesting and laying periods, respectively. A paired drake provides the seclusion necessary for this increased amount of feeding by chasing other Gadwalls from the vicinity of his female.

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