Dominance Relations, Resource Use, and Pairing Chronology of Gadwalls in Winter
Author(s): Stuart L. Paulus
Source: *The Auk*, Vol. 100, No. 4 (Oct., 1983), pp. 947-952
Published by: University of California Press on behalf of the American Ornithologists' Union
Stable URL: http://www.jstor.org/stable/4086423
Accessed: 14/12/2010 10:31

DOMINANCE RELATIONS, RESOURCE USE, AND PAIRING CHRONOLOGY OF GADWALLS IN WINTER

STUART L. PAULUS[1]

Biology Department, University of North Dakota, Grand Forks, North Dakota 58202 USA

ABSTRACT.—I studied pairing chronology and agonistic displays of Gadwalls (*Anas strepera*) and spatial associations among Gadwalls and other Anatinae in the coastal marshes of southwestern Louisiana from October 1977 through April 1978. Gadwalls began arriving in Louisiana in late September, but by mid-October 45% of females were paired and by late November 81% were paired. The percentage of paired females increased slowly to 90% in April. Bill threats were the predominant agonistic display of Gadwalls, accounting for 89% of all observations, while chasing (5.8%) and biting (5.2%) accounted for the remainder. Nearly all (91.1%) conflicts involved birds that had been feeding before the dispute. On average, Gadwalls spent 0.4% of their time in agonistic activities. Gadwalls preferred to associate with individuals of similar pair status. Paired Gadwalls were more likely to threaten other paired birds, and unpaired Gadwalls other unpaired birds, than they would individuals of the other pair status. Only 14% of disputes involving Gadwalls were with other Anatinae. Pairs were considered dominant over unpaired birds, as pairs won 81% ($P < 0.001$) of contests with unpaired birds. This study suggested that paired birds, because of their dominance, probably had greater access to preferred food resources and were more successful in meeting nutrient requirements than were unpaired birds. It also suggested that pairing chronology in Anatinae may be related to food choice and foraging strategies, those species feeding on poorer-quality foods forming pairs earlier, as individuals attempt to optimize their allocation of time for feeding and other activities. *Received 30 April 1982, resubmitted 4 October 1982, accepted 11 April 1983.*

THE presence of over 6 million waterfowl in Louisiana during winter (Novara et al. 1981) increases the likelihood of competition among these birds for limited resources and has probably influenced the evolution of aggressive displays by wintering waterfowl and the development of dominance hierarchies (Raveling 1970, Patterson 1977). The result is that dominant individuals probably have access to preferred resources, while subordinates are displaced into suboptimal habitats (Fretwell 1972). Dominants may be better able to obtain adequate resources for maintenance than subordinates and therefore experience greater survivorship in winter if resource availability is a limiting factor.

Gadwalls (*Anas strepera*) rely almost entirely upon a diet of leafy aquatic vegetation and algae (Paulus 1982) and spend over 63% of their time feeding to meet nutritional needs in winter (Paulus 1980). Feeding habitats used by Gadwalls vary depending upon food types available and their abundance, distribution and quality. Although Gadwalls spend only 0.4% of their time in agonistic activities (Paulus 1980), development of dominance relations may be useful in limiting agonistic interactions and influencing the distribution of individuals throughout coastal marshes. Although rigid rank orders seem impractical in large flocks (Wynne-Edwards 1962), Raveling (1970) attributed the competitive success of Canada Geese (*Branta canadensis*) during the nonbreeding season, to pair status, family size, and intensity of threat posture. Among Bewick's Swans (*Cygnus columbianus bewickii*; Scott 1980) and Common Goldeneyes (*Bucephela clangula*; Afton and Sayler 1982), birds with mates were more successful in agressive encounters and foraged more efficiently than unpaired birds.

This paper describes the types and frequencies of agonistic displays and the development of rank order in Gadwalls and the spatial associations among Gadwalls and other Anatinae. Because most Gadwalls formed pairs in winter, I examine dominance relations among paired and unpaired Gadwalls and discuss how

[1] Present address: Department of Zoology-Entomology, Auburn University, Auburn, Alabama 36849 USA.

TABLE 1. Relative frequency of agonistic displays of Gadwalls in Louisiana in winter. Values are percentages of displays observed for a given pairing class.

Type of display	Initiator of display		
	Pairs ($n = 437$)	Unpaired male ($n = 57$)	Unpaired female ($n = 61$)
Bill threat	91.8	77.2	80.3
Chase	5.7	8.8	3.3
Bite	2.5	14.0	16.4

TABLE 2. Total number of agonistic interactions between paired and unpaired Gadwalls in Louisiana in winter.

Loser of conflict	Winner of conflict		
	Pairs	Unpaired male	Unpaired female
Pairs	300	13	10
Unpaired male	67	18	35
Unpaired female	34	24	13

these relations may influence pairing chronology and resource use by Gadwalls in winter.

STUDY AREA AND METHODS

This study was conducted in coastal southwestern Louisiana on Rockefeller and Marsh Island state wildlife refuges and on privately owned lands within 13 km of Rockefeller Wildlife Refuge (Paulus 1982). Using focal analysis sampling procedures (Altmann 1974, Paulus 1980), I collected data on agonistic behaviors and spatial relationships of Gadwalls concurrently with observations on activity budgets from October 1977 through April 1978. Observations were made with a 15–40× spotting scope and 7× binoculars. Activities were observed during 1-h sampling periods randomly selected during the day and during nonrandom periods at night under clear to partly cloudy skies when the moon was between the first and last quarter. Nocturnal observations were limited to Gadwalls within 30 m of the observer.

All aggressive intra- and interspecific encounters involving Gadwalls were recorded and divided into three categories: (1) *bill threats*—an open-beak display usually accompanied by a cackling sound, the bill raised slightly upward from horizontal and toward another bird; (2) *chasing*—one bird rushing at another and forcing it to swim or fly away rapidly; and (3) *biting*—one bird grabbing another with its beak. More subtle avoidance behaviors were observed during the study, such as one bird moving away from the other as it approached, but, because they were difficult to detect consistently, these behaviors were not included in the analysis. The species, sex, and pair status of individuals involved in agonistic interactions were recorded. At 1-min intervals, the distance between a paired or unpaired Gadwall and the nearest bird and the species, sex, and pair status of the focal bird were recorded. From these data, intra- and interspecific associations involving Gadwalls were determined.

Pairing chronology was determined from the percentage of females judged to be closely associated with males. Weller (1965) noted that chance or temporary associations were a potential source of error. On many occasions, even widely separated (15 m or more) Gadwalls later resumed close associations, and I judged these to be paired. Error in judgment was reduced by restricting the paired category to those birds (1) mutually avoiding or threatening other birds, (2) exhibiting consistent synchronization of activities, especially locomotion, and (3) remaining within 2 m of each other during most of the observation period. In my judgement, these methods of determining pair status can be used for most species of Anatinae wintering along the Gulf Coast but are most reliable when they are applied to individuals or small- to moderate-sized flocks and when sufficient time is available for careful analysis.

Chi-square analysis of contingency tables (Snedecor and Cochran 1976: 250) was used to analyze frequencies of agonistic interactions and associations involving Gadwalls. When χ^2 analysis indicated rejection of the hypothesis of independence, Goodman's (1964) simultaneous confidence-interval procedure was used to identify those associations that were significant.

RESULTS

Gadwalls began arriving in Louisiana in late September, and by mid-October over 300,000 Gadwalls were estimated to be present along coastal southwestern Louisiana (H. A. Bateman, unpubl. repts. Louisiana Wildl. and Fish. Comm., 1977–1978). Pair formation among Gadwalls apparently began during fall migration or on the breeding grounds, as well as on the wintering grounds, as 45% ($n = 384$) of females were paired by mid-October. Pairing occurred rapidly, such that by late November 81% ($n = 736$) of females were paired. This percentage increased slowly during the remainder of the study, and by April 90% ($n = 1,589$) of females were paired.

From a total of 165.5 h of diurnal and 65.5 h of nocturnal observations, I found that bill threats were the predominant agonistic display

TABLE 3. Total number of associations among paired and unpaired Gadwalls and other Anatinae in Louisiana in winter.

Individual observed	Nearest neighbor			
	Pair	Unpaired male	Unpaired female	Other Anatinae
Pair	1,726	433	125	840
Unpaired male	396	145	71	161
Unpaired female	164	228	117	180

of both paired and unpaired Gadwalls (Table 1). Chasing comprised a similar percentage of agonistic displays of paired and unpaired birds, but unpaired birds were observed biting other individuals at a level 5 times that of pairs ($P < 0.001$).

Nearly all conflicts (91.1%, $n = 372$) were between individuals that were feeding before the dispute. Only 0.5% of agonistic activities were recorded between Gadwalls involved in courtship activities, an amount similar to the mean amount of time spent by Gadwalls (0.3%) in courtship behaviors during the entire study. The remaining conflicts involved birds engaged in resting (2.7%), comfort (2.4%), alert (2.2%), or locomotor (1.1%) activities at the time of the dispute. Agonistic activities lasted only a few seconds, and, except when chased, the retreating individual usually moved only a few meters away. Mean distance between individuals when threat displays were initiated was 0.7 m ($n = 498$), whereas mean distance maintained between individuals for all activities was 1.9 m ($n = 3{,}405$). The percentage of time allocated to agonistic activities by Gadwalls was greatest during October and November, when threat behaviors comprised 0.8% ($n = 42.0$ h) and 0.9% ($n = 8.4$ h) of time spent by paired and unpaired Gadwalls, respectively. During the rest of the study, paired ($n = 151.2$ h) and unpaired ($n = 38.5$ h) Gadwalls spent, on average, 0.3% of their time in agonistic activities.

Gadwalls were more likely to threaten other Gadwalls of similar pair status than individuals of the other pair status ($P < 0.001$; Table 2). This may have been influenced by the fact that Gadwalls preferred to associate with members of similar pair status ($\chi^2 = 378.0$, df = 6, $P < 0.001$) during activities (Table 3). Although pairs were associated with unpaired males in proportion to that predicted by chi-square analysis ($P > 0.05$), unpaired females were associated more often with other unpaired birds than with pairs ($P < 0.001$). Only 14% ($n = 87$) of disputes involving Gadwalls were with other Anatinae, and most of these (77%) were with American Wigeon (*Anas americana*), which often used the same feeding areas as Gadwalls. Although the arrangement of paired and unpaired Gadwalls within the flock was not quantified, unpaired birds usually remained on the perimeter of the flock during observations, and it was not uncommon to observe unpaired female Gadwalls feeding with wigeon, away from the main Gadwall flock.

Pairs were considered dominant to unpaired birds, because pairs won 84% of contests with unpaired males ($n = 80$, $P < 0.001$) and 78% ($n = 45$, $P < 0.001$) with unpaired females. In interactions involving unpaired birds, males and females were judged equally dominant, as males won 24 and females 35 ($P > 0.05$) of contests involving unpaired birds of each sex.

DISCUSSION

Previous studies of North American waterfowl have suggested that pairing chronology is related to time of nest initiation (Weller 1965, Soutiere et al. 1972, Armbruster 1982). However, Gadwalls, which are late nesters (Gates 1958, Bellrose 1978: 215), initiate pairing activities earlier in winter than do earlier nesting ducks. Although over 80% of female Gadwalls were paired by late November, this level was not reached by Mallards (*Anas platyrhynchos*), Northern Pintails (*Anas acuta*), or American Black Ducks (*Anas rubripes*) until December or January and not by diving ducks (*Aythya*) until early spring (Johnsgard 1960, Weller 1965). From this study, I believe that diet choice and foraging strategies also may play an important role in determing rate of pair formation.

Paired Gadwalls were dominant in most agonistic encounters with unpaired birds. Numerous studies have stressed that dominants forage more efficiently and are better able to survive food shortages than are subordinates (Smith 1976, Patterson 1977, Caraco 1979), because subordinates are forced into marginal habitat as flock size increases. Gadwalls spent over 60% of their time feeding on a diet comprised of 95% leafy aquatic vegetation and algae in Louisiana in winter (Paulus 1980, 1982),

TABLE 4. Timing of pairing and nesting in relation to diet in North American Anatinae.

Species	Period of peak pairing activity	Period of peak nesting activity[a]	Major food groups consumed in winter[a]
Anas strepera	October–November[b]	May–June[a]	Aquatic vegetation, algae[b]
Anas americana	November–December[c]	May–June	Aquatic vegetation, algae, seeds
Anas platyrhynchos	November–December[d]	April–May	Seeds, aquatic vegetation
Anas acuta	November–December[d]	April–May	Seeds, aquatic vegetation
Anas rubripes	November–December[e]	April–May	Aquatic plants, invertebrates, seeds
Anas clypeata	January–February[a]	May–June	Plankton, invertebrates, algae
Anas crecca carolinensis	February–March[a]	May–June	Seeds, invertebrates
Aythya americana	February–March[a]	May–June	Aquatic plants, invertebrates[f]
Aythya valisineria	March–April[d]	April–May	Aquatic plants, invertebrates
Aythya affinis	March–April[d]	May–June	Invertebrates, seeds, vegetation

[a] From Bellrose (1978) unless otherwise noted.
[b] From Paulus (1980, 1982).
[c] From Soutiere et al. (1972) and Paulus (unpubl. data).
[d] From Weller (1965).
[e] From Johnsgard (1960).
[f] From Cornelius (1977).

and food preference depended both on quality and quantity of available foods. Most conflicts involving Gadwalls occurred while birds fed, and, although agonistic activities recorded in this study comprised only 0.4% of the total activity budget, threat displays, as well as more subtle avoidance behaviors, were important in determining the spatial distribution and access to food resources of flock members. The precise distribution of flock members was not recorded in this study. An analysis of spatial associations, however, indicated that individuals usually associated with members of similar pair status, and observations during activity-budget periods suggested that unpaired birds usually remained on the perimeter of the flock (Paulus 1980). Because Gadwalls maintained an average distance of 1.9 m between individuals, birds of lower dominance status in large flocks would be far removed from the central flock location, where food quality and quantity are presumably greatest.

Most foods used by Gadwalls were relatively abundant in fall but varied in quality. The primary energetic requirements of Gadwalls in fall were for molt, maintenance, and lipid deposition. If the quality of food intake varied among Gadwalls, with paired Gadwalls more likely to obtain highest quality foods, paired birds would be more successful than unpaired birds in meeting energetic requiements, and they would be in better condition as winter approached. As food supplies diminished over winter, Gadwalls selected foods of lower quality (Paulus 1982). Under these conditions, the higher priority in food choice of paired birds could be an important survival advantage. Other factors probably also determined success in resource acquisition among individuals, however, because most birds were paired by this time.

If pairs are more successful than unpaired birds in obtaining nutrients and, subsequently, are more likely to be in better condition and survive periods of stress during winter, then why do not all Anatinae pair at similar rates or earlier than do Gadwalls? Previous studies, as well as this one, have shown that feeding is the predominant activity of wintering ducks (Tamisier 1976, Paulus 1980, Jorde 1981), but individuals must also spend time in other activities, including plumage maintenance, resting, courtship, and pair-bond maintenance. The diets of most other ducks wintering along the Gulf Coast contain a greater proportion of seeds or invertebrates (Harmon 1962, Cornelius 1977, Bellrose 1978). Because these foods are a more concentrated source of nutrients or of a higher caloric content than leafy vegetation or algae (Sugden 1973, Driver et al. 1974, Paulus 1982), species consuming these foods are expected to spend less time feeding than Gadwalls to meet nutritional needs. Tamisier (1976) observed in coastal Louisiana that Northern Pintails and Green-winged Teal (*Anas crecca carolinensis*),

whose diets are composed predominantly of seeds, spent about 50% of their time feeding. Gadwalls also spent less time feeding when consuming foods of higher quality (Paulus 1980).

I suggest that, as foraging-time requirements increase and time available for other activities decreases, selection favors individuals that are able to reduce their foraging time while fulfilling nutrient requirements. Pair formation and related dominance may allow individuals access to higher quality foods and thus reduce the time needed to forage. For species whose diets are of a higher quality than that of Gadwalls, individuals may be able to meet their nutrient requirements and have sufficient time for other activities, regardless of pair status, as long as food supplies remain plentiful. As food supplies diminish, however, individuals forming pairs may be better prepared than unpaired birds to maintain a balance in their allocation of time for various activities.

Data currently available on diets and timing of pair formation in Anatinae seem to support the hypothesis that pairing activities occur later in winter in species whose diets contain more seed or animal matter than leafy vegetation (Table 4). Testing this hypothesis will require more information, however, about timing of pair formation in Anatinae and the ability of individuals to defend specific food types and a greater understanding of those components of the habitat most important to wintering ducks. Food choice and feeding strategies are two of probably many potential factors influencing pairing chronology in waterfowl, including age and sex composition of the population, migration chronology, age of sexual maturity, physiological condition, latitude of major wintering areas, and date of nest initiation. If resources are limited on the wintering grounds, however, dominant, paired individuals are expected to have greater survivorship.

Acknowledgments

I am grateful to R. Crawford, T. Joanen, L. McNease, K. Paulus, D. Trauger, and W. Wrenn for their help during all phases of the study. I also thank C. D. Ankney, R. Bailey, R. Blohm, D. Raveling, K. Reinecke, and an anonymous reviewer for reviewing earlier versions of this manuscript. Financial assistance was provided by U.S. Fish and Wildlife Service, Louisiana Department of Wildlife and Fisheries, University of North Dakota, and The Society of Sigma Xi.

Literature Cited

Afton, A. D., & R. D. Sayler. 1982. Social courtship and pairbonding of Common Goldeneyes, *Bucephela clangula*, wintering in Minnesota. Can. Field-Natur. 96: 295–300.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227–267.

Armbruster, J. S. 1982. Wood Duck displays and pairing chronology. Auk 99: 116–122.

Bellrose, F. C. 1978. Ducks, geese and swans of North America. Harrisburg, Pennsylvania, Stackpole Books.

Caraco, T. 1979. Time budgeting and group size: a theory. Ecology 60: 611–617.

Cornelius, S. E. 1977. Food and resource utilization by wintering Redheads on lower Laguna Madre. J. Wildl. Mgmt. 41: 374–385.

Driver, E. A., L. G. Sugden, & R. J. Kovach. 1974. Calorific, chemical and physical values of potential duck foods. Freshwater Biol. 4: 281–292.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. No. 5. Princeton, New Jersey, Princeton Univ. Press.

Gates, J. M. 1958. A study of the breeding behavior of Gadwall in northern Utah. Unpublished M.S. thesis. Logan, Utah, Utah State Univ.

Goodman, L. A. 1964. Simultaneous confidence limits for cross-product ratios in contigency tables. J. Royal Statistical Soc., Ser. B. 26: 86–102.

Harmon, B. G. 1962. Mollusks as food of Lesser Scaup along the Louisiana coast. Trans. 27th North Amer. Wildl. Conf. 27: 132–138.

Johnsgard, P. A. 1960. A quantitative study of sexual behavior of Mallards and Black Ducks. Wilson Bull. 72: 133–155.

Jorde, D. G. 1981. Winter and spring staging ecology of Mallards in south central Nebraska. Unpublished M.S. thesis. Grand Forks, North Dakota, Univ. North Dakota.

Novara, A. N., S. L. Rhoades, B. I. Hodges, & K. D. Norman. 1981. Waterfowl status report. 1978. Washington, D.C., U.S. Fish and Wildl. Serv. Spec. Rept. Wildl. No. 237.

Patterson, I. J. 1977. Aggression and dominance in winter flocks of Shelduck *Tadorna tadorna* (L.). Anim. Behav. 25: 447–459.

Paulus, S. L. 1980. The winter ecology of the Gadwall in Louisiana. Unpublished M.S. thesis. Grand Forks, North Dakota, Univ. North Dakota.

———. 1982. Feeding ecology of Gadwalls in Louisiana in winter. J. Wildl. Mgmt. 46: 71–79.

Raveling, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37: 291–319.

SCOTT, D. K. 1980. Functional aspects of the pair bond in winter in Bewick's Swans (*Cygnus columbianus bewickii*). Behav. Ecol. Sociobiol. 7: 323–327.

SMITH, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93: 95–107.

SNEDECOR, G. W., & W. G. COCHRAN. 1976. Statistical methods. Ames, Iowa, Iowa State College Press.

SOUTIERE, E. C., H. S. MYRICK, & E. G. BOLEN. 1972. Chronology and behavior of American Widgeon wintering in Texas. J. Wildl. Mgmt. 36: 752–758.

SUGDEN, L. G. 1973. Metabolizable energy of wild duck foods. Can. Wildl. Serv. Prog. Notes 35. Saskatoon, Saskatchewan, Can. Wildl. Serv.

TAMISIER, A. 1976. Diurnal activities of Green-winged Teal and Pintail wintering in Louisiana. Wildfowl 27: 19–32.

WELLER, M. W. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). Auk 82: 227–235.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. New York, Hafner Co.

The **Association of Pacific Systematists** was officially formed in February 1983 and is now soliciting membership applications. The Association will be an organization for and of systematists in the Pacific. News concerning research efforts and opportunities in the Pacific will be distributed in a Newsletter. Annual dues are $5.00. Inquiries should be directed to **S. H. Sohmer, Department of Botany, Bernice P. Bishop Museum, P.O. Box 19000-A, Honolulu, Hawaii 96819.**

The **North American Loon Fund** announces two grant programs for support of new or current research, management, or education projects that may yield useful information for Common Loon conservation in North America. The Robert J. Lurtsema Research Award consists of a $1,000 stipend available annually for a suitable research project focused on a member of the Family Gaviidae. Preference will be given to students and independent researchers with limited availability of other funding. The second program offers modest grants in support of research, management, or educational projects directly related to the conservation of Common Loons as a breeding species. Proposals in the range of $500 to $3,000 are mostly likely to be considered for funding. Guidelines are available from **North American Loon Fund Grants Committee, North American Loon Fund, Meredith, New Hampshire 03253.** Deadline for submission of proposals is **31 January 1984.**