# WINTER FORAGING BEHAVIOR AND AGGRESSION OF DIVING DUCKS IN SOUTH CAROLINA[a]

WILLIAM C. ALEXANDER, Department of Zoology, Clemson University, Clemson, SC 29631
JAY D. HAIR[b], Department of Entomology and Economic Zoology, Clemson University, Clemson, SC 29631

*Abstract*: The diving times, diving distances, foraging rates, intraspecific and interspecific interactions between canvasbacks (*Aythya valisineria*), ring-necked ducks (*A. collaris*), lesser scaup (*A. affinis*) and redheads (*A. americana*) were studied on coastal winter habitats in South Carolina. Diving times, distances and foraging rates varied between habitats of different water depths and between species, but with few exceptions not between sexes. Canvasbacks were the dominant birds and actively defended foraging sites against other birds, particularly ringnecks. During late winter when food resources were presumed limited, male canvasbacks excluded females from preferred foraging sites. Temporal and/or spatial segregation of habitats between sexes of the other species was not demonstrated. Exclusion of individuals from optimal winter foraging areas may have significant implications affecting population dynamics of waterfowl.

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Nesting management and ecology of most species of waterfowl in North America are well documented (Johnsgard 1975, Bellrose 1976, Palmer 1976). Research during the nonbreeding period of the year has dealt primarily with evaluations of band returns, food habits analysis, patterns of migration and a variety of mortality factors (Anderson 1959, Bellrose 1959, Geis 1959, Bellrose et al. 1961, Thompson 1973, Stott and Olson 1973, inter alia). Only a limited number of studies have been conducted on the behavioral characteristics of waterfowl during the winter period (Weller 1965, Raveling 1970, Soutiere et al. 1972). Correspondingly, the importance of the winter period, exclusive of hunting mortality, on the population dynamics of waterfowl is not well documented.

Studies on other groups of birds, however, have indicated that in terms of survival the winter may be the most critical period of the year (Lack 1954, 1966 and Fretwell 1972). Dominance by certain members of a population may cause subordinate individuals to be dispersed into suboptimum habitats (Fretwell 1969), which may increase their susceptibility to various decimating factors.

The southeastern United States is an important wintering area for waterfowl (Bellrose 1976). In recent years the population levels of several species of diving ducks (*Aythya* spp.) have declined (Trauger 1974, Bellrose 1976). For some species the quality of traditional winter habitats (i.e. Chesapeake Bay) has deteriorated, which may result in more birds wintering farther south (Perry 1974, 1975).

The overall objective of this study was to investigate winter habitat utilization by canvasbacks, ring-necked ducks, lesser scaup and redheads. This report represents a preliminary comparison of the foraging strategies and behavioral interactions between these species during their co-occurrence on coastal impoundments in South Carolina.

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## MATERIALS AND METHODS

This study was conducted during the winters of 1975-76 and 1976-77 on 4 impoundments near Georgetown, S. C.: (1) a 12 ha freshwater impoundment (2.0 m deep) at Huntington Beach State Park; (2) 2 freshwater impoundments, Fairfield pond (8 ha,

[a]Technical contribution No. 1503, South Carolina Agricultural Experiment Station, Clemson.

[b]Present address: Department of Zoology, North Carolina State University, Raleigh, N.C. 27650.

2.0 m), and Middleton pond (13 ha, 1.0 m); and (3) 1 brackish water impoundment, Bridge pond (12 ha, 0.5 m), at Arcadia Plantation. Banana water lily (*Nymphae mexicana*) was the predominant aquatic vegetation on the freshwater impoundments; the brackish water impoundment was characterized by widgeongrass (*Ruppia maritima*).

Several species of birds utilized all impoundments during the winter period. Other than the subject species, the most important were mallards (*Anas platyrhynchos*), black ducks (*A. rubripes*), pintails (*A. acuta*), wigeons (*A. americana*), gadwalls (A. *strepera*) shovelers (*A. clypeata*), and coots (*Fulica americana*).

Behavior of the 4 species studied was recorded daily during 1 of 4 40 minute intervals spaced 3 hours apart. Intervals were shifted on a daily basis to include all portions of the diurnal period. Species were assigned to observation intervals by using a table of random numbers (Steel and Torrie 1960). During each interval, behavioral data were coded, recorded on a tape recorder and later transcribed to fortran coding forms.

The 40 min observation intervals were divided into 8 sample periods in which a focal individual (Altmann 1974) was observed continuously for 5 minutes. The focal individual was selected randomly by directing a spotting scope towards a flock and selecting the bird nearest the center of the field. Where feasible, equal numbers of males and females were selected as focal individuals. Throughout the 5 min sample period, each behavioral event (Altmann 1974) performed by the focal individual was recorded in sequence.

The distance moved underwater by foraging birds was estimated in bird-body-lengths (chest to tail while sitting on water) from the point of diving to the point of surfacing and was timed with a stopwatch. Foraging rates for each bird were determined by the number of dives, or tip-ups, per 5 min interval.

Statistical analysis followed Steel and Torrie (1960) using the statistical analysis system (SAS) developed by Barr and Goodnight (Service 1972).

## RESULTS

The population levels of each species fluctuated throughout the winter period. On a daily basis, ringnecks had the highest average abundance (1,000, all values approximate), followed by canvasbacks (300), lesser scaup (75) and redheads (50). With the exception of Fairfield pond (which had only ringnecks and canvasbacks), all 4 species of diving ducks were observed concurrently during the diurnal period on all impoundments. Behavioral activities observed included foraging, resting, courtship, general maintenance behavior and interactions within and between species.

## BEHAVIORAL CHARACTERISTICS

### *Ringnecks*

Diving times of ringnecks varied with water depth (Table 1). Mean diving times of

Table 1. Mean diving time by four species of diving ducks on South Carolina coastal impoundments.

| *Mean Depth (m):* | *Huntington Beach (2.0)* | *Fairfield (2.0)* | *Middleton (1.5)* | *Bridge (0.5)* |
|---|---|---|---|---|
| Ringneck | 16.0[a] (±3.1)[b] | 14.3 (± 4.35) | 11.2 (± 3.9) | |
| | 114[c] (8.2-23.5)[d] | 1,821 (2.1-26.5) | 102 (3.4-20.6) | ——— |
| Canvasback | 14.8 (± 3.3) | 15.3 (± 3.63) | 13.9 (± 3.6) | 13.1 (± 4.9) |
| | 106 (6.8-24.0) | 1,167 (3.0-26.0) | 924 (3.2-26.6) | 20 (4.3-19.5) |
| Lesser Scaup | | | 6.32 (± 0.6) | 16.6 (± 4.8) |
| | ——— | ——— | 5 (5.8-7.0) | 165 (4.5-28.7) |
| Redhead | 15.0 (± 3.7) | | 11.0 (± 3.8) | 7.2 (± 2.7)[e] |
| | 75 (6.8-21.0) | ——— | 132 (3.0-20.4) | 68 (1.4-14.4) |

[a]mean diving time in seconds.
[b]one standard deviation.
[c]number of dives.
[d]range of diving times in seconds.
[e]mean tipping time in seconds.

ringnecks ranged from 16.0 sec at Huntington Beach (2 m) to 11.2 sec. at Middleton pond (1 m) and they moved an average of 3 body lengths while diving (Table 2). On

Table 2. Mean distances moved under water by four species of diving duck while foraging on South Carolina coastal impoundments.

| *Species* | *N* | *Mean*[a] (± *S. D.*) |
|---|---|---|
| Ringneck | 61 | 2.98 (2.84) |
| Canvasback | 67 | 0.96 (0.84) |
| Lesser scaup | 78 | 16.12 (11.49) |
| Redhead | 74 | 0.77 (0.93) |

[a]units were estimated as bird-body-lengths (chest to tail while on water).

Fairfield pond (where most foraging activity was observed) ringnecks had an average foraging rate of 5.5 dives per min interval (Table 3). There were no significant differences in diving times, distances moved or foraging rates between males and females.

Aggressive encounters between foraging ringnecks occurred frequently. On the study area male ringnecks outnumbered females by a ratio of 3:1. Although these sex ratio differences were accounted for in calculating expected frequencies of interactions between individuals, there were still significant differences in interactions between the male-male, female-female and male-female components of the population. There were approximately half as many interactions between males as expected, but there were almost 4 times more interactions than expected between females ($X^2 = 243.27$, $p < .001$). In male-female interactions, male ringnecks won 91 percent of the encounters ($X^2 = 125.56$, $p < .001$).

Table 3. Mean winter foraging rates per five-minute interval for diving ducks on South Carolina coastal impoundments.

| *Impoundment* | *(depth)* | *Species* | *N* | *Mean*[a] (± *SD*) | *t-value*[b] |
|---|---|---|---|---|---|
| Huntington | (2.0m) | Canvasback | 16 | 1.7 (± 3.3) | 0.36[c] |
| Fairfield | (2.0m) | Ringneck | 415 | 5.5 (± 5.3) | 1.42[c] |
| | | Canvasback | 224 | 5.9 (± 5.0) | 0.21[c] |
| Middleton | (1.5m) | Canvasback | 360 | 4.2 (± 5.1) | 3.03[d] |
| | | Redhead | 44 | 0.3 (± 0.9) | 0.10[c] |
| Bridge | (0.5m) | Canvasback | 16 | 10.0 (± 7.4) | 0.19[c] |
| | | Redhead | 80 | 13.9 (±10.0) | 0.42[c] |
| | | Lesser scaup | 112 | 5.1 (± 6.3) | 0.36[c] |

[a]Mean frequency of feeding attempts per five-minute interval.

[b]Students t-test for sex differences in feeding rates within each species.

[c]Differences not significant at the .05 level.

[d]Differences highly significant ($P < .01$).

*Canvasbacks*

Diving times of canvasbacks also varied with depth of impoundment (Table 1). At Huntington Beach (2 m) the mean diving time for canvasbacks was 14.8 sec; at Bridge pond (0.5 m), the mean diving time was 13.1 sec. On the respective impoundments there were no significant differences in diving times between male and female canvasbacks.

Canvasbacks foraged over the entire area of each impoundment and established and defended individual foraging sites. These sites were characteristically small and the ducks

exhibited little lateral movement (less than 1 body length) from a particular site while diving (Table 2). Depending upon the depth of the water, the foraging rates of canvasbacks ranged from a mean of 1.7 (dives per 5 min interval) at Huntington Beach to 10.0 at Bridge pond (Table 3). On Middleton pond males fed more frequently than females but no differences between sexes occurred on the other impoundments (Table 3).

Observed aggressive encounters between canvasbacks totaled 471 and most occurred while foraging. Based on equal sex ratios (as determined by counts) and assuming random encounters between individuals, there were significantly more interactions between the male-male component of the population and fewer between the female-female component than would be expected by chance ($X^2 = 18.64$, $p < .001$). Males won 158 of 250 encounters with female canvasbacks ($X^2 = 17.42$, $p < .001$) which suggested that male canvasbacks were dominant over females during the winter period.

The importance of this dominance relationship was examined further by comparing changes in the ratios of male to female canvasbacks in an area of Middleton pond where the apparent preferred food (banana water lily) was concentrated (determined by visual observations). From 1 November 1976 to 31 January 1977 the sex ratios on the impoundment varied, but overall there was an equal ratio (1:1.1) of male to female canvasbacks (Table 4). During the same period of time there were almost 3 times as many males as there were females (2.8:1) in the area where food was concentrated. As the season progressed, and presumably the available food supply declined in abundance, the males in this area increased from 40 percent (1:1.5) in early November to 100 percent (9:0) by mid-January (Table 4). There was no evidence of habitat segregation between sexes demonstrated by any of the other species of diving ducks during this same period of time.

Table 4. Seasonal comparison of overall sex ratios of canvasbacks on Middleton pond with sex ratios for the area where food was concentrated.

| | *Overall* | | | *Concentrated Food Source* | | | | |
|---|---|---|---|---|---|---|---|---|
| *Period* | *Males* | *Females* | ($\frac{sex}{ratio}$) | *Males* | *Males* | *Females* | ($\frac{sex}{ratio}$) | *% Males* |
| (1976) | | | | | | | | |
| Nov. 1-Nov. 15 | 115 | 158 | (1:1.4) | 42 | 10 | 15 | (1:1.5) | 40 |
| Nov. 16- Nov. 30 | 179 | 192 | (1:1.1) | 48 | 50 | 36 | (1.4:1) | 58 |
| Dec. 1-Dec. 15 | 116 | 75 | (1.6:1) | 61 | 41 | 11 | (3.7:1) | 79 |
| Dec. 16-Dec. 31 | 83 | 55 | (1.5:1) | 60 | 45 | 8 | (5.6:1) | 85 |
| (1977) | | | | | | | | |
| Jan. 1-Jan. 15 | 166 | 168 | (1:1) | 42 | 54 | 6 | (9:1) | 90 |
| Jan. 16-Jan. 31 | 257 | 355 | (1:1.4) | 42 | 9 | 0 | (9:0) | 100 |

*Lesser Scaup*

Foraging behavior of lesser scaup was different from ringnecks and canvasbacks. Scaup did not defend a foraging site but swam individually, or in loose pairs, and dove while swimming. Consequently scaup had longer diving times on Bridge pond (the shallowest impoundment studied) than canvasbacks and redheads (Table 1) but shorter diving times on Middleton pond. Lesser scaup had lateral movements of approximately 16 body lengths while diving (Table 2) and reduced foraging rates (Table 3). Male and female scaup had no significant differences in diving times or foraging rates and only one aggressive encounter was observed between scaup. This suggests that during the winter period scaup were not an aggressive species.

*Redheads*

Redheads were the only species which foraged consistently in small groups (4 to 6 birds). Depending upon the habitat, they foraged either by tipping (like dabbling ducks) in shallow water or by diving. For example, on Bridge pond (0.5 m) the mean diving time of 7.2 sec was the time spent underwater while tipping. At Huntington Beach (2 m) the mean diving time of 15.0 sec reflects actual time spent underwater (Table 1). Whether tipping or diving there were no significant differences between sexes for the amount of time spent foraging. Although redheads exhibited little lateral movement while diving (Table 2) their foraging rates varied substantially between impoundments (Table 3).

Ten aggressive encounters were observed between male and female redheads, of which 6 were won by males. Similar to the situation with scaup, the significance of this is unknown, but suggests that these 2 species were less aggressive during the winter than either ringnecks or canvasbacks.

*Interspecific Interactions*

Interspecific interactions between the 4 species of diving ducks ranged from intense to no interactions. The greatest number of aggressive encounters (204) was observed

between canvasbacks and ringnecks, and occurred while foraging. Canvasbacks won over 98 percent (201/204) of these encounters. In general, after a canvasback dove, a ringneck dove in the same location. When they surfaced together canvasbacks chased the ringnecks, but when ringnecks surfaced at a distance of 2 to 3 m, they were not pursued by canvasbacks.

Ten encounters between foraging canvasbacks and redheads were observed. Similar to the above situation, canvasbacks were clearly dominant, winning 80 percent (8/10) of the encounters. Only 2 encounters between canvasbacks and scaup and 1 between redheads and scaup were observed, and none between ringnecks and redheads or ringnecks and scaup. On most occasions canvasbacks and ringnecks fed in close proximity to one another, whereas redheads and scaup had different foraging strategies and foraged in different parts of the impoundments.

## DISCUSSION

Coastal South Carolina overwinters large numbers of several species of waterfowl (Bellrose 1976) which frequently co-occur on some impoundments. The importance of the winter period and the mechanisms which permit the co-existence of multi-species waterfowl communities on relatively small impoundments has not been well documented. Lack (1954, 1966) and Fretwell (1972) have demonstrated that winter may be one of the most important periods of the year in terms of its impact on population dynamics of birds. MacArthur (1958) reported that several species of warblers (*Dendroica* spp.) were able to co-exist because they utilized different foraging strategies.

Our data support the hypothesis that the co-existence of waterfowl during the winter is due in part to differences in foraging strategies. Although several species of dabbling and diving ducks co-occurred on the same impoundments, there were few interactions between them. Of the 4 species of diving ducks, canvasbacks were the dominant species and established foraging sites which were defended actively against ringnecks and redheads. Scaup and redheads did not feed in close proximity to canvasbacks or ringnecks. Scaup foraged over large areas whereas redheads fed in small groups and were observed feeding frequently by tipping. Segregation in feeding behavior has been demonstrated previously for diving ducks during the summer months (Siegfried 1976). This is the first report, to our knowledge, of the occurrence of this phenomenon for diving ducks on winter habitats in North America.

Fretwell (1972) reported that dominance hierarchies during the winter period resulted in the dispersal of birds into 2 categories of habitats: (1) an "optimal habitat" in which dominant birds survive throughout the winter, and (2) a "fringe habitat" which is suboptimal and is inhabited by subordinate birds which may not survive the winter period. Jenkins et al. (1975) suggested that aggressive behavior during the winter was important in limiting the size of the subsequent breeding population of shelducks (*Tadorna tadorna*). They hypothesized that areas of good feeding were limited, that there was a dominance hierarchy in the winter flock and that subordinate birds were excluded from the best feeding areas. Patterson (1977), in a test of this hypothesis, concluded that a dominance hierarchy was present during the winter and that high-ranking male shelducks were older, arrived earlier from migration, were observed more frequently at feeding sites, and had higher reproductive success than low-ranking birds. Olson (1965), in a study of differential vulnerability to hunting of adult male, female and juvenile canvasbacks, reported that female and juvenile birds occurred in small flocks away from large groups of adult males and demonstrated greater flight activity.

Gauthreaux (1978), in a review of the ecological significance of dominance has pointed out that dominance must indicate priority, which in turn must be a result of individual behavior. The apparent priority of canvasbacks (particularly males) allowed them to forage for food resources that were presumably both limited in abundance and restricted in distribution over a given impoundment (determined by visual observations of distribution patterns of emergent forms of vegetation). When a female canvasback entered a foraging area of males she usually did not forage as frequently and consequently, had a significantly lower foraging rate. This agrees with Murton et al. (1971) who reported that subordinate wood pigeons (*Columba palumbus*) had lower feeding rates than dominant birds. They suggested that this was the result of subordinate birds spending a major portion of their potential foraging time looking out for dominant individuals. This ultimately resulted in losses in their weights and/or starvation.

Although our data suggested that dominance relationships were an important aspect of the coexistence of diving ducks during the winter in South Carolina, we have no data to evaluate the importance of this on their survival and/or subsequent reproductive suc-

cess. The implications are clear, however that if waterfowl partition their use of winter habitats by behavioral mechanisms, then subordinate individuals may be forced to utilize suboptimal habitats. This in turn may increase flight activity during the diurnal period and therefore, increase susceptibility to hunting pressure. Increased hunting pressure has been reported to cause waterfowl to use habitats not normally used (Kirby et al. 1976) and/or to change their feeding times from diurnal to nocturnal periods (Hochbaum 1960, Nilsson 1970). These are important points and their effects on the population dynamics of waterfowl should be addressed by future research on the ecology and management of waterfowl during the winter period.

## LITERATURE CITED


Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227-267.

Anderson, H. G. 1959. Food habits of migratory ducks in Illinois. Ill. Nat. Hist. Surv. Bull. 27:289-344.

Bellrose, F. C. 1959. Lead poisoning as a mortality factor in waterfowl populations. Ill. Nat. Hist. Surv. Bull. 27:235-288.

_____. 1976. Ducks, geese and swans of North America. Stackpole Books. Harrisburg, Penn. 543 pp.

_____, T. G. Scott, A. S. Hawkins, and J. B. Low. 1961. Sex ratios and age ratios in North American ducks. Ill Nat. Hist. Surv. Bull. 27:391-474.

Fretwell, S. D. 1969. Dominance behavior and winter habitat distribution in Juncos (*Junco hyemalis*). Bird-Banding 40:1-25.

_____. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton. 217 pp.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. In: Bateson, P. P. G., and P. H. Klopfer (Eds.). Perspectives in ethology. Vol. 3:17-54, Plenum Publ. Corp., N. Y.

Geis, A. D. 1959. Annual and shooting mortality estimates for the Canvasbacks. J. Wildl. Manage. 23:253-261.

Hochbaum, H. A. 1960. Travels and traditions of waterfowl. Univ. of Minn. Press, Minneapolis. 301 pp.

Jenkins, D., M. G. Murray, and P. Hall. 1975. Structure and regulation of a shelduck (*Tadorna tadorna* (L.)) population. J. Anim. Ecol. 44:201-231.

Johnsgard, P. A. 1975. Waterfowl of North America. Indiana Univ. Press. Bloomington. 575 pp.

Kirby, R., J. Riechmann, and M. Shough. 1976. A prelimiary report on Minnesota's innovative 1973 waterfowl season. Wildl. Soc. Bull. 4:55-63.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 pp.

_____. 1966. Population studies of birds. Claredon Press, Oxford. 341 pp.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology. 36:533-536.

Murton, R. K., A. J. Isaacson, and N. J. Westwood. 1971. The significance of gregarious feeding behavior and adrenal stress in a population of Wood-pigeons (*Columba palumbus*). J. Zool. 165-53-84.

Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos. 21:145-154.

Olson, D. O. 1965. Differential vulnerability of male and female canvasbacks to hunting. Trans. N. Amer. Wildl. and Nat. Res. Conf. 30:121-135.

Palmer, R. S. (ed.). 1976. Handbook of North American birds—waterfowl. Yale Univ. Press, New Haven. Vols. 2 & 3.

Patterson, I. J. 1977. Aggression and dominance in winter flocks of shelduck (*Tadorna*

Perry, M. C. 1974. Looking out for the canvasback, Part IV. Ducks Unlimited. 38:21. *tadorna* (L.)). Anim. Behav. 25:447-459.

_____. 1975. Looking out for the canvasback, Part V. Ducks Unlimited. 39:14.

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

Service, J. 1972. A user's guide to the statistical analysis system. N. C. State Univ., Raleigh, N. C. 260 pp.

Siegfried, W. R. 1976. Segregation in feeding behavior of four diving ducks in southern Manitoba. Can. J. Zool. 54:730-736.

Soutiere, E. C., H. S. Myrick, and E. G. Bolen. 1972. Chronology and behavior of American widgeon wintering in Texas. J. Wildl. Manage. 36:752-758.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, N. Y. 481 pp.

Stott, R. S., and D. P. Olson. 1973. Food-habit relationships of sea ducks on the New Hampshire coastline. Ecology. 54:996-1,007.

Thompson, D. 1973. Feeding ecology of diving ducks on Keokuk Pool, Mississippi River. J. Wildl. Manage. 37:367-381.

Trauger, D. L. 1974. Looking out for the canvasback, Part I. Ducks Unlimited. 38:12.

Weller, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk. 82:227-235.