DIFFERENTIAL USE OF FRESH WATER ENVIRONMENTS BY WINTERING WATERFOWL OF COASTAL TEXAS

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Species having similar life styles (Ralph 1975) characteristically occupy different ecological niches (Hutchinson 1957, 1965) within shared environments. Many workers have shown that this principle seems to be operative in avian communities (MacArthur 1958, Cody 1968, James 1971, Posey 1974, Whitmore 1975). Our study was conducted to determine how feeding flocks of wintering waterfowl coexisted in feeding site selection, what environmental factors that were measured were the most important in certain aspects of niche separation, and how the niches were arranged in the aquatic community at the study site.

METHODS AND MATERIALS

Study area.—Data were collected from early October through late December 1973 from 2 adjacent ox-bow lakes on the grounds of the Welder Wildlife Foundation in San Patricio County near Sinton, Texas. These fresh water lakes were up to 2.5 m deep but averaged about 1.5 m in the middle. A broad zone of semi-aquatic grasses (*Paspalum* and *Panicum*) occupied the perimeters and burhead (*Echinodorus rostratus*), southern cut-grass (*Leersia hexandra*), and bulrush (*Scirpus californicus*) occurred in isolated small patches. The transition zone from emergent semi-aquatic vegetation sometimes occurred over 90 m from shore, but was quite variable in position. Extensive floating or partly submerged patches of aquatic vegetation were dominated by southern naiad (*Najas guadalupensis*), star grass (*Heteranthera liebmannii*), musk grass (*Chara*), and duck weed (*Lemna perpusilla*).

Large numbers of waterfowl use the coastal region of southern Texas during the fall and winter months (Bellrose 1976) therefore, references to "wintering waterfowl" and "wintering grounds" throughout this paper are made on this basis. Most of the individuals of some species such as the Fulvous Whistling Duck and Blue-winged Teal have moved further south by late December or early January (Bennett 1938, Bellrose 1976) and may not be considered as truly wintering species of southern Texas. Nevertheless, these 2 species were included as they were present when the study was conducted.

Field methods.—The species studied were: Mottled Duck (*Anas fulvigula*), Pintail (*Anas acuta*), Gadwall (*Anas strepera*), American Wigeon (*Anas americana*), Northern Shoveler (*Anas clypeata*), Blue-winged Teal (*Anas discors*), Green-winged Teal (*Anas crecca*), Fulvous Whistling Duck (*Dendrocygna bicolor*), Redhead (*Aythya americana*), Canvasback (*Aythya valisineria*), Ring-necked Duck (*Aythya collaris*), Lesser Scaup (*Aythya affinis*), Ruddy Duck (*Oxyura jamaicensis*), and American Coot (*Fulica americana*).

To characterize the environments of feeding waterfowl flocks 20 factors were measured in the field comprising social, vegetational, physical, and chemical properties. *Social factors included*: total number of ducks in flock, number of species in flock, number in flock of species being sampled, number feeding of species being sampled, number of coots present in flock, and distance to neighboring flock (m). *Vegetational factors were*: % emergent vegetation, emergent vegetation height (cm), and % floating and/or submerged vegetation. *Physical factors were*: depth of water at feeding site (cm), distance of flock from shore (m), turbidity of water at feeding site (Jackson turbidity units), % cloud cover, and wind velocity (km/hr). *The chemical measurements of the water at feeding locations were*: pH, dissolved oxygen (ppm), total nitrogen (ppm), total phosphorous (ppm), total calcium (ppm), and conductivity (micromhos/cm).

Twenty-five samples of the 20 environmental factors were measured for each species. Feeding flocks were sampled at random and data collecting for each species was distributed as much as possible during the study period to eliminate time of sampling as a bias. Also, 60 random samples of the environmental factors (excluding social factors) were taken to determine the general nature of the habitat available in the aquatic environment at Welder. The random samples were selected by superimposing a grid on a map of the study area and using numbers from a random table as X and Y coordinates to designate approximate sample locations. Means and standard deviations of the factors measured in the study for each species and the random habitat samples are included in White (1975).

The feeding flocks of wintering waterfowl were studied regardless of size. Although loose mixed-species flocks often were encountered, the ducks tended to separate according to species. Therefore, the approximate center of each species flock within loose mixed flocks served as the sample point from which measurements were made. Sampling began at daylight and continued throughout the day. A canoe and hip boots were used in collecting data. Observations were made with binoculars and a telescope. Social factors were recorded from afar and the location of nearest neighboring flocks was noted before disturbing the ducks to measure other factors.

Flock-center locations were marked using a buoy and samples were taken within a radius of approximately 3 m from this point. Percentages of emergent vegetation and floating and/or submerged vegetation were estimated by making 50 random observations within the sampling perimeter using a sighting tube (Winkworth and Goodall 1962) and doubling the total sightings having plants intersected by crosshairs.

Water depth was measured with a meterstick or weighted nylon cord; distances to shore and to nearest neighboring flock were measured with a range finder; wind velocity was measured with an anemometer held at eye level; cloud cover was estimated. A water sample was taken at each site and analyzed at the end of the day for turbidity and chemical factors using a Hach water analysis kit.

Population densities of the waterfowl species included in this study were highly variable. For example, Pintails generally were much more abundant than Mottled Ducks, Canvasbacks, or Ruddy Ducks. Total numbers of the various species using the lakes at Welder varied from day to day since waterfowl are highly mobile and may cover a wide range of habitats. Certainly it is possible that on one or several occasions measurements were taken on the same individuals of a particular species. This should not bias the data (James 1971) since individuals of a species generally are indicative of that species as a whole. Population estimates for the 3 month period are not available per se, however see White (1975) for mean flock sizes based on 25 observations for each species.

Data analysis.—The IBM-360 Model 50 digital computer at the University of Arkansas was used for all data analyses. Principal component (PC) analysis (Morrison 1967) based on correlations between untransformed data was used to determine the environmental factors that varied the most in niche relationships. After transforming the data to minimize heteroscedasticity and non-normality (Box and Cox 1964, Andrews et al. 1971), multivariate analysis of variance (Cooley and Lohnes 1971) with a step-down procedure

(Bargman 1962) was used to determine how the species were arranged with respect to the environmental factors that were important in separating species. The canonical scores from the preceding analysis were subjected to 1-way analysis of variance with Duncan's multiple range test (Steel and Torrie 1960) to determine the degree of species environmental overlap.

RESULTS

The following PC analyses were conducted on the combined species data. The first included all of the 20 environmental factors measured in the study; the second involved only the 14 non-social factors (vegetational, physical, and chemical). In both analyses the initial principal components identified the combination of factors that described the greatest variation in the data sets. This represented the breadths and limits of the ecological niches based on the factors that were measured. Niche differences were evaluated using multivariate analysis of variance and associated procedures.

Overall relationships.—The PC analysis that included all of the 20 environmental factors measured in the study gave an overall account of niche structure for the species, including the social environment as a niche component. The first principal component (PC-I) of the combined data set for all species showed high correlation values for 4 social factors (Table 1). This indicated that waterfowl as a group varied the most in social activity. The second principal component (PC-II) showed high correlation values for water depth at feeding site, vegetational percentages, calcium content, and conductivity. Combinations of these factors characterize specific feeding sites. Together PC-I and PC-II accounted for 30% of the total environmental variance.

A 2-dimensional representation of the distribution of the ecological niches (Fig. 1) was produced by plotting the mean PC-I and PC-II scores (James 1971). Relative niche widths are shown by 1% confidence ellipses circumscribing the mean of each species data set. The ellipses are very small indicators of niche width; larger ellipses would tend to mask relationships due to broad overlap. Social activity, based on those social factors with high correlation values in Table 1, increases from left to right along the PC-I axis (Fig. 1). Water depth at feeding site and floating and/or submerged vegetation increase from top to bottom along the PC-II axis, whereas calcium and conductivity (high values equated to high productivity; Orians 1966, Russell-Hunter 1970) and emergent vegetation decrease in the same direction. Each species position within the total environmental space is determined by its individual responses to the definitive factors characterizing the space.

The Redhead and Canvasback were quite similar in response and exhibited the most social activity, whereas the Mottled Duck was the least social (Fig. 1). The Ruddy Duck and Gadwall generally occupied the deeper water with copious aquatic vegetation (Sincock 1963, Bellrose 1976) while at the other

TABLE 1

CORRELATIONS WITH FIRST AND SECOND PRINCIPAL COMPONENTS BASED ON ALL ENVIRONMENTAL FACTORS AND ON ALL EXCEPT THE SOCIAL ENVIRONMENT

	All Factors		All Except Social Factors			
	Combined Species Data		Combined Species Data		Random Samples	
Environmental Factors	PC-I	PC-II	PC-I	PC-II	PC-I	PC-II
Social						
1. Total number in flock	.81	.42				
2. Number of species in flock	.29	.34				
3. Number in flock of species being sampled	.83	.33				
4. Number feeding of species being sampled	.78	.36				
5. Number of coots in flock	.56	.02				
6. Distance to nearest neighbor flock	.17	.01				
Vegetational						
7. Percent emergent vegetation	-.50	.55	-.72	-.22	-.69	.50
8. Emergent vegetation height	-.40	.32	-.45	-.27	-.84	.14
9. Percent floating and/or submerged vegetation	.21	-.54	.60	-.21	-.19	-.79
Physical						
10. Depth of water at feeding site	.30	-.61	.67	.11	.68	-.14
11. Distance to shore	.27	-.34	.44	-.23	.68	-.14
12. Turbidity	-.10	.39	-.39	.38	-.19	.52
13. Percent cloud cover	.09	.06	.02	-.01	-.17	-.33
14. Wind velocity	-.07	.04	-.07	.26	.26	-.43
Chemical						
15. pH	.26	-.08	.20	.75	.53	.15
16. Dissolved oxygen	.18	-.22	.29	.76	.55	.51
17. Total nitrogen	-.02	-.05	.02	.48	-.37	.18
18. Total phosphorous	-.09	-.19	.09	.06	.05	.09
19. Total calcium	.05	.61	-.52	.16	.49	-.64
20. Conductivity	-.23	.73	-.77	.32	.16	.31

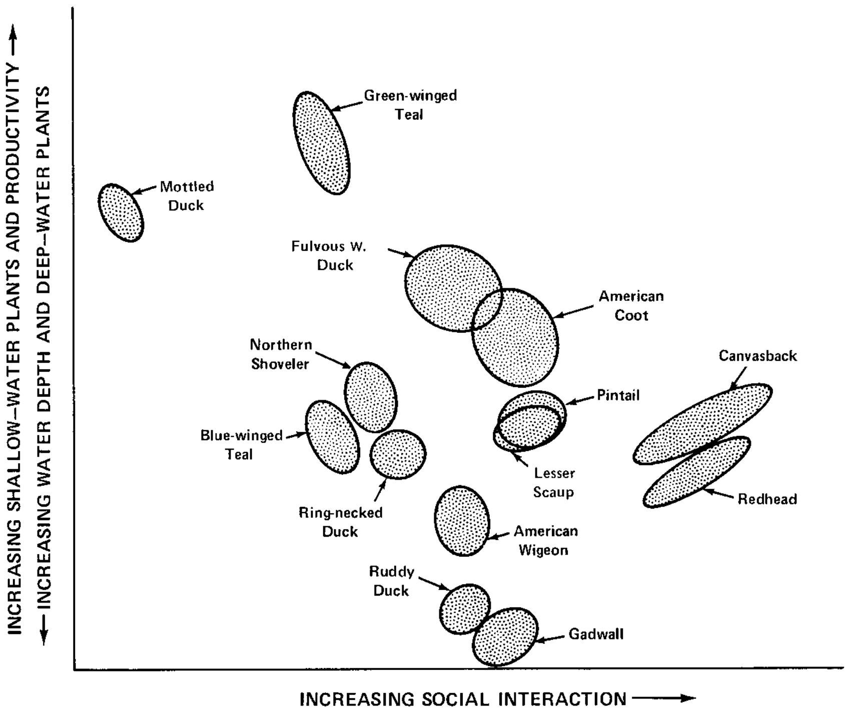

FIG. 1. Waterfowl ordination with 1% confidence ellipses based on species values and means for scores of the first (abscissa) and second (ordinate) principal components; social, vegetational, physical, and chemical environmental factors included in the analysis.

extreme the Green-winged Teal and Mottled Duck favored shallow productive waters with much emergent vegetation (Singleton 1968, Bellrose 1976). Grouped ellipses show similarities in mean niche characteristics of various waterfowl such as the closeness in the Blue-winged Teal, Northern Shoveler, and Ring-necked Duck. The American Coot and Fulvous Whistling Duck had the largest niche sizes, the Ring-necked Duck and Ruddy Duck the smallest. The Redhead and Canvasback were more specialized in feeding site than in breadth of social behavior, tending to be more social in shallower water.

Habitat relationships.—The PC analysis of the 14 non-social factors depicted the habitat space occupied by the whole waterfowl community and delineated the *realized habitat niches* (Hutchinson 1957, 1965) exhibited by the various species within this space. The first principal component (PC-I) showed that water depth at feeding site, vegetational percentages, calcium, and conductivity were the factors contributing to the most variability for waterfowl as a group (Table 1); these were the same factors identified by PC-II in the preceding

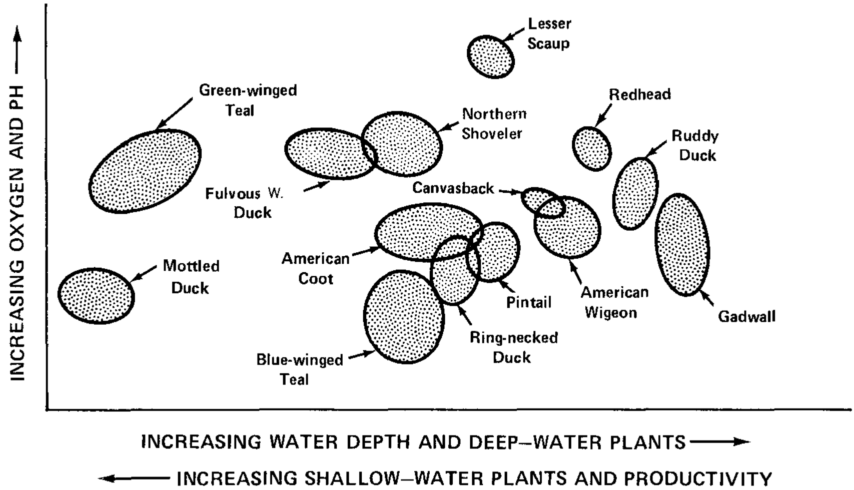

FIG. 2. Waterfowl ordination with 1% confidence ellipses based on species values and means for scores of the first (abscissa) and second (ordinate) principal components; only vegetational, physical, and chemical environmental factors included in the analysis.

analysis and characterized feeding site habitats. Oxygen content and pH were highly correlated with the second principal component (PC-II) and pertained to the nature of trophic activity in the water (Table 1). High pH and water oxygen levels are associated with sites dominated by photosynthesis in submerged plants. Sites dominated by organic decay are relatively low in oxygen and pH.

Waterfowl habitat preferences are shown in Fig. 2 with 1% confidence ellipses representing relative niche sizes. The sequence of species from left to right on the abscissa (PC-I) is similar to the equivalent PC-II from top to bottom on the ordinate in Fig. 1 (the slight differences being due to the elimination of social factor effects for the principal components in Fig. 2). With respect to PC-II (Fig. 2) the Lesser Scaup occupied sites with the highest pH and oxygen levels, the Mottled Duck and Blue-winged Teal at the opposite extreme. Interesting relationships occurred such as the Green-winged Teal favoring more photosynthesis dominated sites in shallow water compared to the Mottled Duck, while the Blue-winged Teal preferred decay dominated sites in deeper water. The Canvasback and Redhead had the smallest niche sizes with respect to habitat axes, both teals the largest. The 2 principal components described 35% of the total habitat variance.

Comparison of PC correlations for the random habitat samples (Table 1) with those from separate analyses of each waterfowl species (for the latter PC data consult White 1975) identified the species that responded directly to the existing habitat contrasted to those that made special habitat adjustments. The Mottled Duck, Green-winged Teal, Shoveler, American Wigeon, American Coot, Redhead, Canvasback, and Lesser Scaup exhibited moderate to high correlations for some or all of the factors that were highly correlated with PC-I for the random habitat samples (White 1975). Thus they responded directly to the range in habitat conditions that was available in the lakes studied. The other species, showing deviant PC correlations, selected special habitat conditions from the common conditions existing there. Even those that responded directly to the existing habitat were separated along the total habitat cline as was evidenced by the existence of different species means for habitat factors (White 1975). Principal components following PC-I differed progressively more among species, and between species and the random samples. This stressed the differing species specific habitat responses associated with the decreasing variance of the later PC's since essential requirements would tend to be constantly present and thus less variable.

Environmental differences.—Relative positions of waterfowl niches shown by PC analysis do not indicate whether species actually differ in responses, but employing multivariate analysis of variance showed that differences were significant ($\alpha = 0.05$). The latter analysis differs from PC analysis in computing new variables (canonical variables) which are linear functions of the original ones, but stressing those factors that effectively separate respective populations (Sokal and Rohlf 1969). An associated step-down analysis indicated that water depth at feeding site and % emergent vegetation, both important factors in the first canonical variable, were statistically significant in separating species. Vegetation height also was highly correlated with the first canonical variable. Floating and/or submerged vegetation and calcium content were highly correlated with the second canonical variable and thus were important in characterizing the species environments, but were not statistically significant in separating the species.

By plotting means of the first and second canonical variables for each species (James 1971), an ordination showing maximum separation is obtained (Fig. 3). The species ordering follows an environmental cline from shallow water on the left to deep water on the right with associated decreasing % emergent vegetation from left to right.

To determine which of the species overlapped in their requirements, the first canonical variable scores for all samples of each species were subjected to a common one-way analysis of variance with Duncan's multiple range test. Four distinct groups were significantly separated ($\alpha = 0.05$) from all others and each group was associated with a particular segment of the aquatic community (Fig. 4). Overlap in niche requirements among species along the

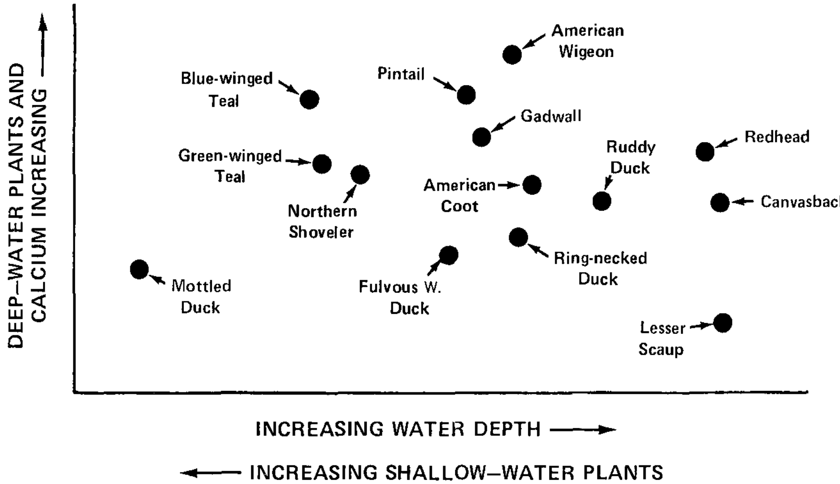

FIG. 3. Waterfowl ordination using means of the first and second canonical variables from multivariate analysis of variance, thus stressing factors that provide maximum separation among species.

cline is represented by the thin horizontal lines beneath the heavy ordination line.

Segment A (Fig. 4) represented very shallow water (1–30 cm) with abundant emergent vegetation near lake shorelines. The Mottled Duck occupied this part of the littoral zone and was never recorded elsewhere. Segment B contained 3 species (Blue-winged Teal, Green-winged Teal, and Northern Shoveler) and represented the part of the littoral zone having moderate amounts of semi-aquatic and aquatic vegetation with shallow to moderate water depths (30–88 cm). Segment C had abundant aquatic vegetation, sparse emergent vegetation, and moderate water depths (88–114 cm). Six species (Fulvous Whistling Duck, Pintail, Gadwall, American Wigeon, Ring-necked Duck, and American Coot) occupied this region mainly, but some overlap is seen between species in segments B and C. Thus the species in these subgroups were not as exclusive in requirements as was the shoreline restricted Mottled Duck. Segment D, representing open deep water (114–213 cm) with little emergent vegetation habitat was frequented by the Ruddy Duck, Redhead, Canvasback, and Lesser Scaup.

The general trend of the species ordering along a community transition is well illustrated in Fig. 5. The species arrangement on the abscissa is in the same order as in Figures 3 and 4, and the means for water depth at feeding site, % emergent vegetation, and % floating and/or submerged vegetation are plotted for each species (see White 1975 for tables giving mean values). The

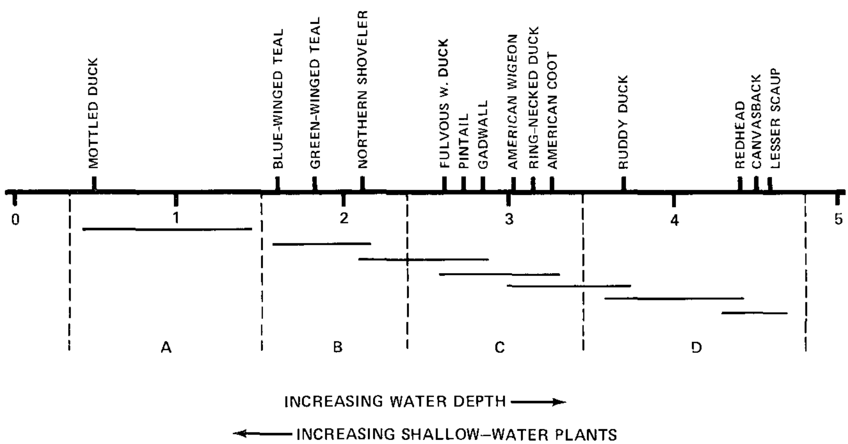

FIG. 4. Ordering of waterfowl determined by mean values of the first canonical variable (scale of values below heavy line). Each horizontal thin line underscores species subgroups that overlap in environmental characteristics. Capital letters (A, B, C, D) designate subgroups that were significantly different from one another (bracketing individual thin lines that do not overlap).

distinctiveness of environmental preferences (Weller 1975) for each subgroup is evident. Notice that puddle ducks are found in shallow to moderate water depths (Weller 1975), diving ducks in deep water, and the 2 groups are at opposite ends of the cline. The most species, 9 in 2 subgroups (B and C), are rather closely packed in the middle of the sequence (Fig. 4) where water depths are moderate (88–114 cm) and truly aquatic vegetation is greatest (Fig. 5).

The pattern of waterfowl preferences vs. habitat availability is shown by plotting the PC scores obtained from analyzing only the 60 random samples and establishing a 95% confidence ellipse based on these samples (Fig. 6). This represents most of the available habitat space at the study area on the Welder Foundation grounds (social factors not included in random samples). Increasing water depth and distance to shore from left to right on the abscissa (Fig. 6) and amount of emergent vegetation increasing in the opposite direction were highly correlated with PC-I (Table 1). Aquatic vegetation decreasing upward on the ordinate was highly correlated with PC-II. Together PC-I and PC-II accounted for 41% of the total variance. Directional cosines from the random samples PC analysis were used as weights to generate corresponding PC scores for each species. The means of these scores for each species plotted in Fig. 6 show that the species were clumped near the center of the available habitat space.

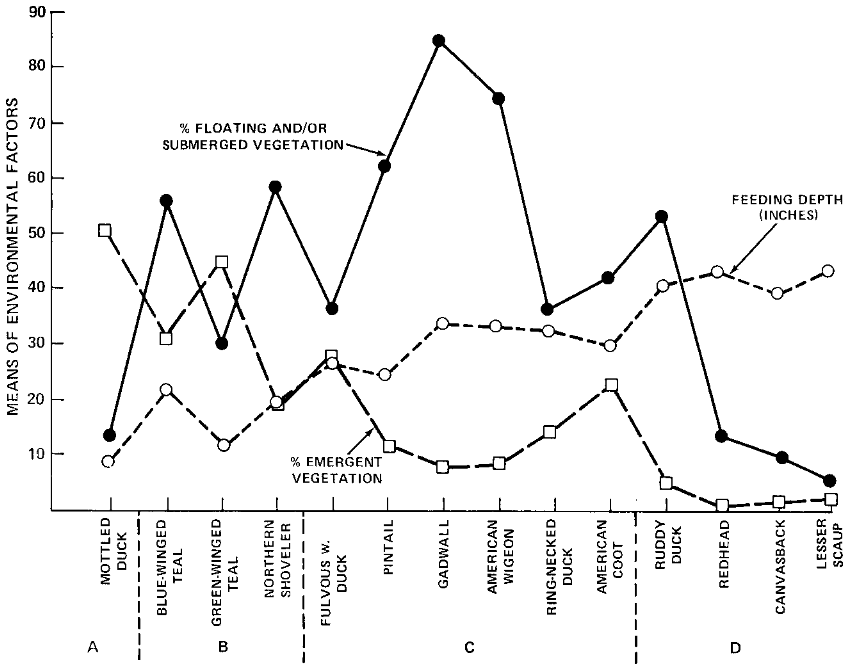

FIG. 5. Waterfowl environments represented by mean values for 3 environmental factors: water depth at feeding sites, % emergent vegetation, and % floating and/or submerged vegetation.

DISCUSSION

Recent multivariate studies of birds in various habitat types indicate that species may be arranged horizontally as well as vertically in response to vegetational characteristics. Grassland birds were distributed vertically in the tall vegetation by differences in feeding height and horizontally by differences in habitat preferences (Cody 1968). Forest birds were distributed vertically and horizontally along a continuum from forest edge to mature forest (James 1971) and old-field birds were scattered along a cline in shrubbiness habitat (Posey 1974). Our findings show that waterfowl too were distributed along an environmental cline, but an aquatic one rather than terrestrial. Social characteristics proved diagnostic too.

Despite much overlap in groups of waterfowl species, each species occupied a definite position with respect to sets of environmental factors ranging from very shallow water with abundant emergent vegetation to open deep water with little emergent vegetation of any kind (Figs. 3, 4, and 5). Water depth at feeding site and % emergent vegetation were the 2 factors that were significant

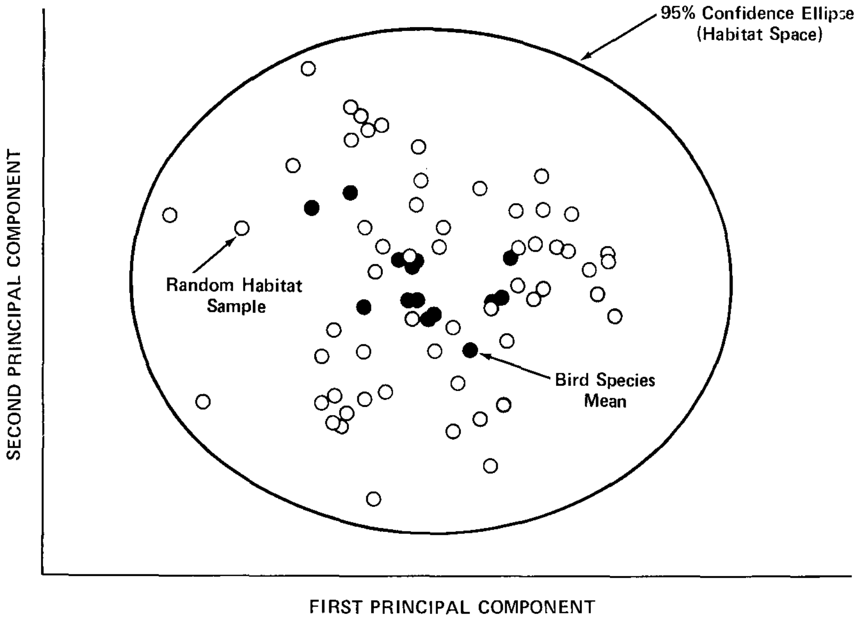

FIG. 6. Limits of the existing habitat space represented by the 95% confidence ellipse circumscribing the principal component values for the individual random samples (open circles). Mean values for the waterfowl species are superimposed (closed circles).

($\alpha = 0.05$) in separating species. Species richness and density were concentrated where aquatic vegetation was most prevalent (Figs. 4 and 5). Undoubtedly factors not measured in this study, such as food types (Weller 1972), feeding behavior (Lack 1971), and other aspects of food selection also are important in separating waterfowl environments, as is evidenced in other birds (Betts 1955, Root 1969, Shugart and Patten 1972).

Certainly the niche requirements for each species will shift from season to season (Wiens 1969) and care must be taken not to generalize for waterfowl wintering grounds as a whole. In fact it would be difficult, if not impossible, to determine the niche of a species in its entirety. However, the use of multivariate statistical methods provides important progress toward this end. These procedures produced a representative characterization and interpretation of the ecological niches of wintering waterfowl. Further, application of these or similar techniques may be useful in wetland management programs. In so doing it would be difficult to manage for or against particular species within a subgroup, such as within the subgroups identified in Fig. 4, because of broad overlap in habitat use by the grouped species.

SUMMARY

A comparative study of the environmental relationships among 14 species of wintering waterfowl was conducted at the Welder Wildlife Foundation, San Patricio County, near Sinton, Texas during the fall and early winter of 1973. Measurements of 20 environmental factors (social, vegetational, physical, and chemical) were subjected to multivariate statistical methods to determine certain niche characteristics and environmental relationships of waterfowl wintering in the aquatic community.

Each waterfowl species occupied a unique realized niche by responding to distinct combinations of environmental factors identified by principal component analysis. One percent confidence ellipses circumscribing the mean scores plotted for the first and second principal components gave an indication of relative niche width for each species. The waterfowl environments were significantly different interspecifically and water depth at feeding site and % emergent vegetation were most important in the separation. This was shown by subjecting the transformed data to multivariate analysis of variance with an associated step-down procedure. The species were distributed along a community cline extending from shallow water with abundant emergent vegetation to open deep water with little emergent vegetation of any kind. Four waterfowl subgroups were significantly separated along the cline, as indicated by one-way analysis of variance with Duncan's multiple range test. Clumping of the bird species toward the middle of the available habitat hyperspace was shown in a plot of the principal component scores for the random samples and individual species.

Naturally occurring relationships among waterfowl were clarified using principal component analysis and related multivariate procedures. These techniques may prove useful in wetland management for particular groups of waterfowl based on habitat preferences.

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