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RESOURCE PARTITIONING IN THE NORTH AMERICAN
GALLINULES IN SOUTHERN TEXAS

by

William W. Reagan

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Science

UTAH STATE UNIVERSITY
Logan, Utah

1977

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ABSTRACT

Resource Partitioning in the North American
Gallinules in Southern Texas

by

William W. Reagan, Master of Science

Utah State University, 1977

Major Professor: Dr. Jessop B. Low
Department: Wildlife Science

Data on the Common and Purple Gallinules at the Welder Wildlife Foundation in South Texas indicated that resource partitioning between the two birds occurred. The objectives of this study were: (1) to compare differences in daily activities; (2) to investigate nesting habits; and (3) to measure physical characteristics of the two birds.

Three methods of resource partitioning were utilized by the two gallinules. (1) Common Gallinules selected open water associated with sparse panicum and paspalum grasses while Purple Gallinules selected dense panicum and paspalum grasses. (2) Common Gallinules during migration and throughout the season shifted gradually from a sparse panicum and paspalum microhabitat to open water adjacent to sparse grasses. Purple Gallinules shifted from a sparse microhabitat during migration to an open panicum and paspalum microhabitat during courtship. However, during nesting, Purple Gallinules utilized a dense microhabitat. (3) Purple Gallinules placed nests in denser cover than Common Gallinules. Nests of Purple Gallinules were found at higher elevations above water than nests of Common Gallinules.

Different patterns of diurnal activity, choices of different food items, differences in feeding methods, and differences in physical characteristics were partitioning mechanism factors also investigated and found not to be utilized by the two gallinules.

(82 pages)

INTRODUCTION

Ecologists for many years have studied differences in the physical structure and behavior of similar coexisting species. Such data add to the total picture of evolutionary processes and speciation. Recently, emphasis has been placed on studies dealing with the methods by which ecologically similar species divide and coutilize the resources essential to their existence (Cody, 1968 and 1974; and Schoener, 1974).

The resource partitioning concept, the niche theory, and the competitive exclusion principle are directly related to each other (Hutchinson, 1957; Cody, 1968; and Schoener, 1974). The more recent concept, i.e., resource partitioning, however, is more clearly understood than are the complex and ambiguous niche theory and exclusion principles (Hardin, 1960; Patton, 1961; Whittaker, et al., 1973; Posey, 1974). The resource partitioning concept is concerned with understanding how and to what extent species divide shared resources (Ricklefs, 1973) and deals only with those measurable environmental variables coutilized by similar species (Cody, 1974). The niche concept, on the other hand, deals with all environmental variables (Hutchinson, 1957) and the competitive exclusion controversy focuses on why species are eliminated or coexist (Cody, 1974).

Cody (1968) describes a variety of resource division methods employed by similar coexisting species which reduces interspecific interactions. Coexisting species may differentiate horizontal and/or

vertical layers within a common habitat isolating the shared resources within the differentiated layers. If no differences are found in habitat selection, coexisting species may take different food items or differ in their feeding behavior. Coexisting species may breed at different times of the year or utilize the same habitat at different times of the day. Ricklefs (1966), however, found no differences in the temporal utilization of habitats among coexisting species. Thus, all observational studies pertaining to niche aspects and competitive exclusion describe to some degree those characteristics by which resources are utilized. An example of this is the classic study of MacArthur's (1958) work with five species of warblers that apparently shared the same ecological niche. His data showed that resources were partitioned by differences in microhabitat selection and feeding behavior. Others have described similar methods of dividing resources (Lack, 1946; Dixon, 1961; Croker, 1967; Pianka, 1969; Brown, 1973; and others).

Recent studies of birds nesting over bodies of water on the Rob and Bessie Welder Wildlife Foundation have indicated that the Purple Gallinule (*Porphyryula martinica*) and the Common Gallinule (*Gallinula chloropus*) utilize resources essential to their survival (Cottam, personal communication). Both birds apparently share the same nesting habitat, often nesting in close quarters of each other. Cases of nest parasitism and nest "take over" by both species were observed. Cottam (personal communication) was of the opinion that the Purple Gallinule requires slightly more dense habitat than does the Common Gallinule.

However, no quantitative data were available to verify this. The aspects of their feeding and reproductive behavior was not an objective of the above nesting study, but Gullion (1954) suggested that there is little difference in their breeding behavior. Bent's (1926) descriptions of Common Gallinule courtship displays differed only slightly from the accounts of Purple Gallinule courtship (Meanley, 1963). However, these descriptions are not detailed accounts. Bent (1926) also suggested that the two gallinules share similar food preferences.

An investigation was undertaken at the Rob and Bessie Welder Wildlife Foundation in southern Texas to determine whether Common and Purple Gallinules divide and utilize the resources that are apparently necessary for their reproductive success.

In order to investigate the manner of resource partitioning the following objectives were pursued:

1. To compare the daily activities between the Common and Purple Gallinules.
2. To investigate the nesting habits of the Common and Purple Gallinules.
3. To measure physical characteristics of the Common and Purple Gallinules.

STUDY AREA DESCRIPTIONS

Welder Wildlife Foundation

The Rob and Bessie Welder Wildlife Foundation, located at longitude $97^{\circ} 38'$ W. and at latitude $28^{\circ} 20'$ N. is bordered on the north by the Aransas River. Its eastern boundary is 7.8 kilometers from Copano Bay. The Foundation entrance is located on its western boundary, 13.3 kilometers northeast of Sinton, Texas, along U. S. Highway 77 (Figure 1). G. W. Thomas (in Gould, 1969) describes the area as a transitional zone between the South Texas Plains and the Gulf Coast Prairies and Marshes. Short springs turning gradually into long hot summers characterize the area and time of this study. The mean annual precipitation is 89.50 centimeters (Table 1). Two peaks of rainfall occur; one in April and May and the other in August and September. Precipitation can be highly variable due to the occasional occurrence of hurricanes and droughts.

Two ox-bow basins of the Aransas River served as study areas (Figure 2). Hereafter, the lakes will be referred to as Pollita Lake and Big Lake. A distance of 416 meters separates the two lakes.

Pollita Lake's surface area is approximately 32 hectares. It is 1,100 meters in length, and its widest point is not over 415 meters. When filled to capacity, Pollita Lake's deepest point is 1.83 meters.

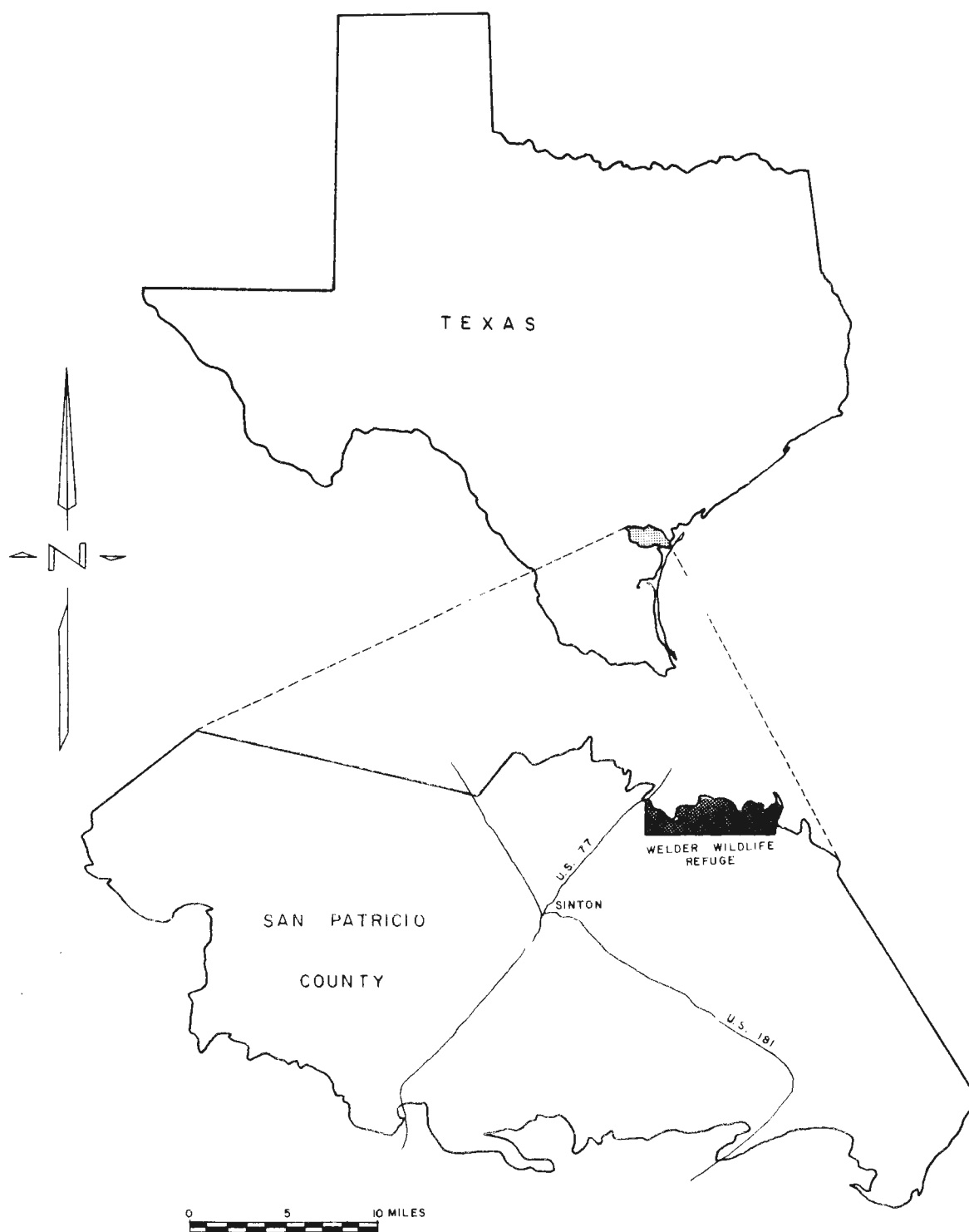


Figure 1. Welder Wildlife Foundation, San Patricio County, Texas.

Table 1. Rainfall at the Welder Wildlife Foundation, San Patricio County, Texas

	18 year average cm	1973 cm	1974 cm
January	4.30	6.35	6.47
February	6.60	4.60	0.00
March	2.35	3.30	4.90
First quarter	13.25	14.25	11.37
April	5.93	6.10	0.71
May	11.00	1.14	13.00
June	11.10	31.80	12.80
Second quarter	28.03	39.04	26.51
July	4.24	2.78	0.32
August	8.88	28.13	7.20
September	15.05	17.10	39.85
Third quarter	28.17	48.01	47.37
October	10.25	22.00	8.21
November	4.80	0.75	5.32
December	5.00	0.90	2.36
Fourth quarter	20.05	23.65	15.89
Annual total	89.50	124.95	101.14



Figure 2. Big and Pollita Lakes, Welder Wildlife Foundation, San Patricio County, Texas. Big Lake study area on left, Pollita Lake study area on right, and Aransas River in foreground. View looking south-southwest.

Big Lake covers 52 hectares and is the largest body of water on the Foundation. It approaches 1,666 meters in length, and its widest point is 833 meters. Like Pollita, Big Lake is shallow with a maximum depth of 1.98 to 2.14 meters. An earth dike cuts across the main body of the lake north and south. A drainage ditch connects the Aransas River and the lake on its eastern end.

Box and Chamrod (1966) describe sixteen separate plant communities on the Welder Foundation. Both lakes are surrounded by six of these communities. They are: chaparral-bristlegass community; halophyte-cactus community; huisache-buffalograss community; bunch-grass-annual forb community; huisache-bunchgrass community; and hackberry-anacua community.

Thick mats of paspalum (*Paspalum* spp.) and panicum (*Panicum* spp.) grass communities occur continuously around the periphery of the lakes (Figure 3). Fingerlike grass growths infrequently project into the water. Both lakes support stands of bulrush (*Scirpus californicus*), and cattail (*Typha latifolia* and *T. domingensis*). Lotus (*Nelumbo lutea*), the smaller water lilies (*Nymphaea* sp.), smartweed (*Polygonum* spp.), water stargrass (*Heteranthera dubia*), waternymph (*Najas guadalupensis*), Chara (*Chara* spp.), sedges (*Carex* spp.), devilweed aster (*Aster spinosus*), common arrowhead (*Sagittaria latifolia*), mosquito fern (*Azolla caroliniana*), duck weed (*Lemna minor*), coontail (*Ceratophyllum* spp.), and various species of algae occur in the lakes. Willows (*Salix* sp.) and small clumps of dead huisache (*Acacia farnesiana*) spot the lakes.



Figure 3. Primary gallinule study area in Big Lake, Welder Wildlife Foundation, San Patricio County, Texas. Note 12 meter observation tower at approximately 10:00 o'clock. View looking north-northeast.

Martheljohnni Swamp

The Martheljohnni Swamp, named after the private landowners, is located 20 kilometers southwest of Victoria, Texas, just off U.S. Highway 77. The area is privately owned, and the extent of the swamp is not known. However, the area used in this study is roughly 20 hectares. The swamp lies adjacent to the Guadalupe River. Annual late spring and early summer flooding keeps the swamp in a permanently wet condition. The average non-flooding depth is approximately one meter. Depths may exceed 3 meters when the river floods. The principle vegetational communities are bulrush (*Scirpus californicus*), common reed (*Phragmites communis*), and live oak anacua river bottom woods. The water surface is covered with water-hyacinth (*Eichornia crassipes*) and duck weed (*Lemna minor*). Few open areas free of vegetation exist (Figure 4).



Figure 4. Bulrush, common reed, water-hyacinth, and live oak-anacua communities of the Martheljohnni Swamp study area, Victoria County, Texas.

LITERATURE REVIEW

Resource partitioning, competitive exclusion, and the niche

The scope of literature dealing with resource partitioning is extremely broad and entangled. The interrelationship of resource partitioning with all aspects of niche, competitive exclusion, co-existence and habitat selection are obvious. In fact, any study dealing with interactions of two or more species will inevitably touch upon resource partitioning.

The phenomenon of two or more ecological homologous species dividing essential resources in order to coexist was first noted by Darwin (1859), when he pointed to the similarity of habits and habitats in congeneric species. The concept of the ecological niche which encompasses the resource partitioning theory was probably brought about by Grinnell (1904, p. 369). He states:

It is only by adaptations to different sorts of food, or modes of food getting that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other.

This statement precipitated perhaps the most controversial ecological theory yet known, the competitive exclusion principle (Hutchinson, 1965; Hardin, 1960) otherwise known as Gause's principle (Miller, 1967), Gause's axiom (Slobodkin, 1961), the Volterra-Gause principle

(Hutchinson, 1957), and the competitive displacement (DeBach, 1966). The concept was interpreted by some authors to adhere to the "all-or-none" law, and numerous arguments over its validity occurred. Most notable are Hardin (1960), Cole (1960), and Patton (1961) who content the theory is subject to dogma, and that the theory can neither be proved or disproved due to its application to circular reasoning. Their argument is that if two species are brought together and one is displaced, then the theory is proved. If they coexist, it is concluded that some unnoticed difference existed between them. Other authors (Savage, 1958; Herbert, 1958; and Ayala, 1972), purportedly proved and disproved the theory, depending on the degree of controls used during their experiments. In controlled experiments conducted on *Triboleum* species by Park and Lloyd (1955), alternating exclusion and coexistence between species resulted.

The principle, however, is accepted by many ecologists whose approach is not to prove or disprove the principle, but to distinguish between the factors that cause either exclusion or coexistence. DeBach (1966) and Miller (1967) have both written papers dealing with the principle and how it relates to the niche theory. The interrelations between competitive exclusion and the niche theory became apparent when Gause (1934) experimentally tested Volterra's (1926) competitive models.

Like the exclusion principle, the niche concept has had various definitions placed on it. Elton (1927) and Van Valen (1960) relate the niche to trophic levels. Weatherby (1963) defines an animal niche in

relation to all the foods available to it. Many authors relate niche to competition (Lotka, 1932; Herbert, 1958; Savage, 1958; Cole, 1960; Hardin, 1960; and Ayala, 1972). Shugart and Patton (1971) deal with niche in terms of habitat selection. The competitive models of Lotka (1932) and Volterra (1926) served as the base for the models concerning the niche. Hutchinson (1957), who first began to quantify the niche, views niche as an N-dimensional hyperspace defined by the N-parameters affecting the species in question. The model has since been expanded by MacArthur (1968, 1970) and Levins (1968) to include N-coexisting species. Arguments still continue concerning the exact definition of the niche. Recently, Whittaker et al. (1973) argued that Hutchinson was misinterpreted. Hutchinson contests that habitat is not separate from Niche. Whittaker et al. (1973) proposed to separate niche and habitat and have introduced a new term, ecotope, to include the range of habitat and niche. Posey (1974) refutes Whittaker et al. (1973), explaining the difficulty in separating habitat and niche.

Resource partitioning is a relatively new ecological concept, and though it is associated with the niche and the exclusion principle, it does not suffer the ambiguity of these two other concepts. The concept of resource partitioning and/or resource division is primarily associated with Code (1968) and Schoener (1974). Code concerned himself with the methods by which grassland bird communities divide their resources in order to coexist and reduce competition. He defined four methods as follows: (1) horizontal habitat selection; (2) vertical habitat selection; (3) food specialization; and (4) differences in

time of breeding for habitat utilization. Cody (1974) expanded on these methods when he states:

Coexistence is defined as the persistence of two species in the same habitat, and such coexistence is achieved by the evolution of some minimal degree of difference in resource use. By feeding on partially different foods, by taking foods at different heights or feeding sites, by locating foods with different feeding behavior, bird species can avoid competitive exclusion: these differences are called coexistence mechanisms.

Concerning the application of the resource partitioning concept, Cody further wrote:

The questions we should be asking as a consequence of Gause's results should not center on why the 'principle' is being 'violated,' but rather on how much overlap of resource use is tolerable? How does this overlap vary with resource predictability and density? To what extent are species distributions and abundances predictable from a knowledge of resource types and productivity? (p. 54)

Schoener (1974) considered the application of studies dealing with resource partitioning should give an idea of the limits interspecific competition place on the number of species that can coexist. Both Cody (1968) and Schoener (1974) used the hyperspace niche model of Hutchinson (1958) and applied the partitioning methods as the various axes of the hypervolume. The position of coexisting species within the hypervolume represents the degree to which all the partitioning methods are being utilized by individual species. Thus, MacArthur (1958), by describing the different niches of various warblers in north-eastern woods, also described the methods by which their resources were divided. This is a common procedure in almost all studies concerning niche diversity and overlap in coexisting species (Lack, 1946; Selander, 1966; Hespenheide, 1971; and others).

Gallinules

The majority of the literature on either the Common or Purple Gallinule deals with unusual sightings or nesting (Trautman, et al., 1964; Wauldbauer, 1964; Carber and King, 1970; and others). Simpson (1939) worked on the feeding habits of the Common Gallinule, and Bent's (1926) description of the foods of the Common and Purple Gallinule is not complete. The work of Howard (1940) on the Common Gallinule in England, and Gross and Van Tyne (1926) on the Purple Gallinule in the Canal Zone of Central America offer the greatest detail in description of nesting, territory, and to some extent the breeding displays of the two birds encountered thus far. Comparative studies and the accumulation of data where these two birds nest in the same area have not been reported.

METHODS

Daily activities

Observations were made from either a 12-meter tower or from a portable 3-meter blind (Figures 5 and 6), using a Bausch and Lomb Balscope Zoom 60 spotting scope mounted on a tripod. Data were collected after concealment in the tower or blind for 2 minutes. Beginning at a point closest to the tower or blind, scans were taken in a clock-wise direction for a variable length of time, along the periphery of the marsh; the center was then scanned. This constituted one scan. A 5-minute interval passed before another scan was initiated. The following data were collected for each gallinule sighted during a scan.

1. Date and time.
2. Species.
3. Sex and age class, if known.
4. Location within habitat.
5. Activity when spotted.

Sex and age were determined by using the methods of Gullion (1952). Activities included feeding, swimming, flying, inter and intraspecific territorial encounters, preening, resting, and calling.

Vegetation type

Data concerning the type of vegetation in which gallinules feed were collected at the same time and in the same manner as that of



Figure 5. Twelve meter observation tower.



Figure 6. Three meter portable blind.

'daily activities.' Five vegetational types recognized as feeding areas were as follows: (1) panicum and paspalum grass communities; (2) bulrush; (3) submergent vegetation; (4) lotus; and (5) cattail. Where mixtures of vegetation types occurred, the dominant vegetation was recorded. If more than one vegetation type was used in an interval, the most frequently used type was recorded.

Feeding zones

Data on feeding zones were collected in the same areas covered by the scans and according to the same procedures used for 'daily activities.' If more than one feeding zone was used during the time interval, the zone most frequently used was recorded. Feeding zones were defined by the location of individual feeding gallinules in a two-dimensional grid. The grid was divided into five vertical layers, based on variation of feeding activity from the normal sitting position and into four horizontal zones based on percentage of light admitted by cover. The normal sitting position is defined as posture held by gallinules when foraging undisturbed; head is erect, tail held horizontally, outer tail coverts are inconspicuous, and wings held close to the body. The percentage of light admitted by cover was determined by using a Weston Master II light meter. The light meter reading taken in full light (holding meter 17.8 cm above open water) was divided into the light meter reading taken at the location of feeding gallinules. The following feeding zones were defined:

1. Head is under water and feeding in open water or in 100 percent light admitted.

2. Head is under water and feeding 76 percent to 99 percent light admitted by cover.
3. Same as 1 except feeding in 51 percent to 76 percent light admitted by cover.
4. Same as 1 except feeding is in 0 percent to 50 percent light admitted by cover.
5. Eating food off the water surface with light admitted by cover 100 percent.
6. Same as 5 except feeding in 76 percent to 99 percent light admitted by cover.
7. Same as 5 except feeding in 51 percent to 75 percent light admitted by cover.
8. Same as 5 except feeding in 0 percent to 50 percent light admitted by cover.
9. Food items are obtained with normal reach of bill without leaving water or feeding on or below the water surface, light admitted by cover 100 percent.
10. Same as 9 except feeding in 76 percent to 99 percent light admitted by cover.
11. Same as 9 except feeding in 51 percent to 75 percent light admitted by cover.
12. Same as 9 except feeding in 0 percent to 50 percent light admitted by cover.
13. Obtained food located above the normal bill reach, accomplished by leaving the water or by using feet and beak to bring food items down, light admitted by cover 100 percent.

14. Same as 13 except feeding in 76 percent to 99 percent light admitted by cover.
15. Same as 13 except feeding in 51 percent to 75 percent light admitted by cover.
16. Same as 13 except feeding in 9 percent to 50 percent light admitted by cover.
17. Feeding out of water although food, while sitting in water is not above the normal bill length, light admitted by cover 100 percent.
18. Same as 17 except feeding in 76 percent to 99 percent light admitted by cover.
19. Same as 17 except feeding in 51 percent to 75 percent light admitted by cover.
20. Same as 17 except feeding in 0 percent to 50 percent light admitted by cover.

Changes in the surface area of the study area were also recorded. The extent of change in the surface area vegetation was determined by cutting out and weighing the panicum and paspalum grass community present in photographs taken of the study area in 1973 and 1974 (MacMahon, personal communication). The photographs were taken at the same time and in the same location each year.

Feeding methods

Different methods of searching for and obtaining food were recorded by observing individual gallinules at 5-minute intervals.

Food habits

Food utilized by the gallinules was determined by observing feeding gallinules. Further identification of food items was determined by observing food items consumed by a hand-reared Common and Purple Gallinule released in the study area. Data were recorded with a recognizable food item was consumed by a gallinule. Data were collected on the hand-reared gallinules by presenting an array of food items found in the study area to the birds and recording what items were consumed.

Temporal variation in microhabitat selection

Premigration period. The premigration period is the time preceding the Purple Gallinules' and non-resident Common Gallinules' arrival on the study area. To determine the placement of gallinules in the habitat, scans were made using the same procedure as for 'daily activities.' The location of a bird in the habitat was determined by its position in a two-dimensional grid. The grid was divided into two vertical layers, gallinules sitting or standing, and into four horizontal zones based on percentage of light admitted by cover. The following habitat subdivisions were defined:

1. Bird sitting in open water or in 100 percent light admitted.
2. Bird sitting on water with 76 percent to 99 percent light admitted by cover.
3. Bird sitting on water with 51 percent to 75 percent light admitted by cover.
4. Bird sitting on water with 0 percent to 50 percent light admitted by cover.
5. Bird standing on vegetation with 100 percent light admitted.
6. Bird standing on vegetation with 76 percent to 99 percent light admitted by cover.
7. Bird standing on vegetation with 51 percent to 75 percent light admitted by cover.
8. Bird standing on vegetation with 0% to 50% light admitted by cover.

Migration period. The same procedures were followed as for the premigration methods. To determine the onset and termination of the gallinules' migration period, censuses were taken by driving a 1,250 meter stretch of road peripheral to the study area and recording the number of gallinules seen on the lake. Eighteen censuses were conducted between April 10 and May 20, 1974.

Courtship period. The same procedures were followed as for the premigration methods. The courtship period was defined as the first observation of courtship displays to the termination of such displays.

Nesting and brood-rearing period. Gathering nesting and brood-rearing data followed the same procedures used for the premigration period. The nesting and brood-rearing period commenced when a nest

containing one egg was located. Brood-rearing was still in process when the field season ended.

Nesting parameters

Data on nest parameters were collected when at least one egg had been deposited. Nest locations included nests within and out of the immediate study area. Nests were located by patrolling Pollita and Big Lake in a canoe and searching the vegetation in which gallinules nest. A nest once located was marked by a 1.3 meter wooden lath 2 to 3 meters from the nest, bearing the nest number, date, species of nest, and the number of eggs in the nest. An example of gallinule nesting data sheet is shown in Figure 7. The 'density of vegetation' was measured with a Weston Master II light meter and given as the percentage of light admitted by cover. The density of the vegetation in which nests were located was determined by dividing the light meter reading in full light (holding the meter 17 cm above open water) into the meter reading taken at the rim level pointed to the center of the nest with eggs removed. The data on which the first egg was laid could be determined for uncompleted clutches by subtracting one day for each egg in the nest on the date of discovery. If the clutch was completed when first located, 15 days were subtracted from the date on which any one egg began to float broad end up where the natural air space occurs.

Nesting data, collected by Dr. Clarence Cottam dating to 1958, were made available to the writer. His data were incorporated into this study and compared with the nesting data collected during the project.

Physical characteristics

Measurements taken of physical characteristics from captured gallinules in the study area follow the methods of Pettingill (1956). Distances were measured with a metric Venior caliper and weights with a spring type gravity scale. The following measurements were recorded:

1. Wing, the distance in centimeters from the bend of the wing to the tip of the longest primary.
2. Tarsus, the distance in centimeters from the point of the joint at the base of the middle toe in front.
3. Bill length, the distance in centimeters from the tip of the upper mandible in a straight line to the base of the frontal shield.
4. Width at nares, the distance in centimeters of the width of the bill from the posterior margin of the external nares with bill shut.
5. Height at nares, the distance in centimeters from the lower mandible directly under the posterior margin of the external nares and to the culmen at the posterior margin of the external nares with the bill shut.
6. Toe length, the distance in centimeters from the point of the joint at the base of the middle toe in front to the tip of the most distal phalange.
7. Weight, measured in grams with a spring type gravity scale.

RESULTS AND DISCUSSION

Habitat segregation

Both Common and Purple gallinules utilized the panicum and paspalum grass community to a greater extent than any other plant community on the Welder Foundation. Common Gallinules utilized panicum and paspalum grasses for 90 percent of all feeding observations, and Purple Gallinules utilized panicum and paspalum grasses for 86 percent of all feeding observations. Other vegetational communities used by the two gallinules are listed in Table 2. A Chi-square test for independence comparing the use of panicum and paspalum grasses against all other vegetation used by the two gallinules resulted in a value of 0.83 ($\alpha 0.05 = 5.02$). This indicates that there are no significant differences in the habitat of the two gallinules on the Welder Foundation.

Cody (1974) and Schoener (1974) agree that the greater portion of coexisting animals partition resources through habitat separation. The smaller portion of coexisting species which do not experience habitat segregation divide resources by other mechanisms. Since the Common and Purple Gallinules were found to share the same habitat, I concluded that other partitioning mechanisms were being employed.

Table 2. Percentage of total feeding observations gallinules spent in different types of vegetation

Vegetation type	Common G. % N = 880	Purple G. % N = 54
Grasses*	90.2	86.3
Bulrush	0.1	0
Submergent vegetation	9.1	0
Lotus	0.6	0
Cattail	0	13.7

* Panicum and paspalum grasses.
N = number of observations.

Microhabitat segregation

The habitat of a species is generally defined as the place where an animal lives (Odum, 1971). When small differences within a given habitat are distinguished, the term microhabitat becomes operative (Odum, 1971). It is these small differences which define a microhabitat and are the primary concern of the partitioning concept. Microhabitat differentiation may take place through the partitioning of time, food and feeding behavior, and vertical and/or horizontal habitat selection (Cody, 1968).

Diurnal rhythm. Data concerning diurnal activity in 1973 numbered 1,007 observational samples on the Common Gallinule and 99 observational samples on the Purple Gallinule. For the Common Gallinule samples, 880 or 87 percent were feeding observations. The remaining 12 percent included such activities as swimming, inter and intraspecific

territorial encounters, preening, resting, calling, and incubation (Table 3).

Purple gallinules spent 55 percent of the daylight hours feeding, 10 percent of the observations were inter- and intraspecific territorial encounters, 9 percent were swimming, and 8 percent preening. The remaining 18 percent dealt with such activities as incubating, resting, and calling (Table 3).

Table 3. Percentage of observations relating to gallinule activities, 1973

Activity	Common G. % N = 1,007	Purple G. % N = 99
Feeding	87.4	54.6
Swimming	2.5	9.1
Flying	---	2.0
Encounters	4.2	10.1
Preening	4.6	8.1
Calling	0.1	3.0
Resting	0.7	5.1
Incubation	0.4	2.0
Unknown	0.1	6.1

N = number of observations

The high rate of inter- and intraspecific territorial encounters between the two birds observed suggests that the Purple Gallinule is more aggressive than the larger Common Gallinule. This however, is not the case. In all observed interspecific territorial encounters between the Common and Purple Gallinules, the Common Gallinule was the more aggressive. The high incidence of observed encounters in the Purple Gallinule is the result of observing a secretive bird performing a highly observable activity.

Both species of gallinules spent the greater portion of their diurnal activity in feeding. Cody (1974) theorizes that a resource partition mechanism that may be employed by similar coexisting species is to feed at different times. Ricklefs (1966), however, found that most coexisting birds have synchronous feeding periods.

Figure 8 compares the percentage of feeding observations of the two gallinules at 30-minute increments throughout the daylight hours. A Chi-square mean comparison value of 1.77 (α 0.05 - 21.9) indicates no significant differences were found in the feeding rhythms of the two gallinules. The results of the feeding data agrees with Ricklefs' (1966) findings that large overlap occurs in feeding times and with Cody's (1974) conclusion that time is not an important partitioning method.

Both gallinules are active feeders in the morning and evening. The lack of afternoon observations does not necessarily indicate a decrease in feeding activity; it simply means the gallinules are less observable in the afternoon. That is, during the hotter portion of

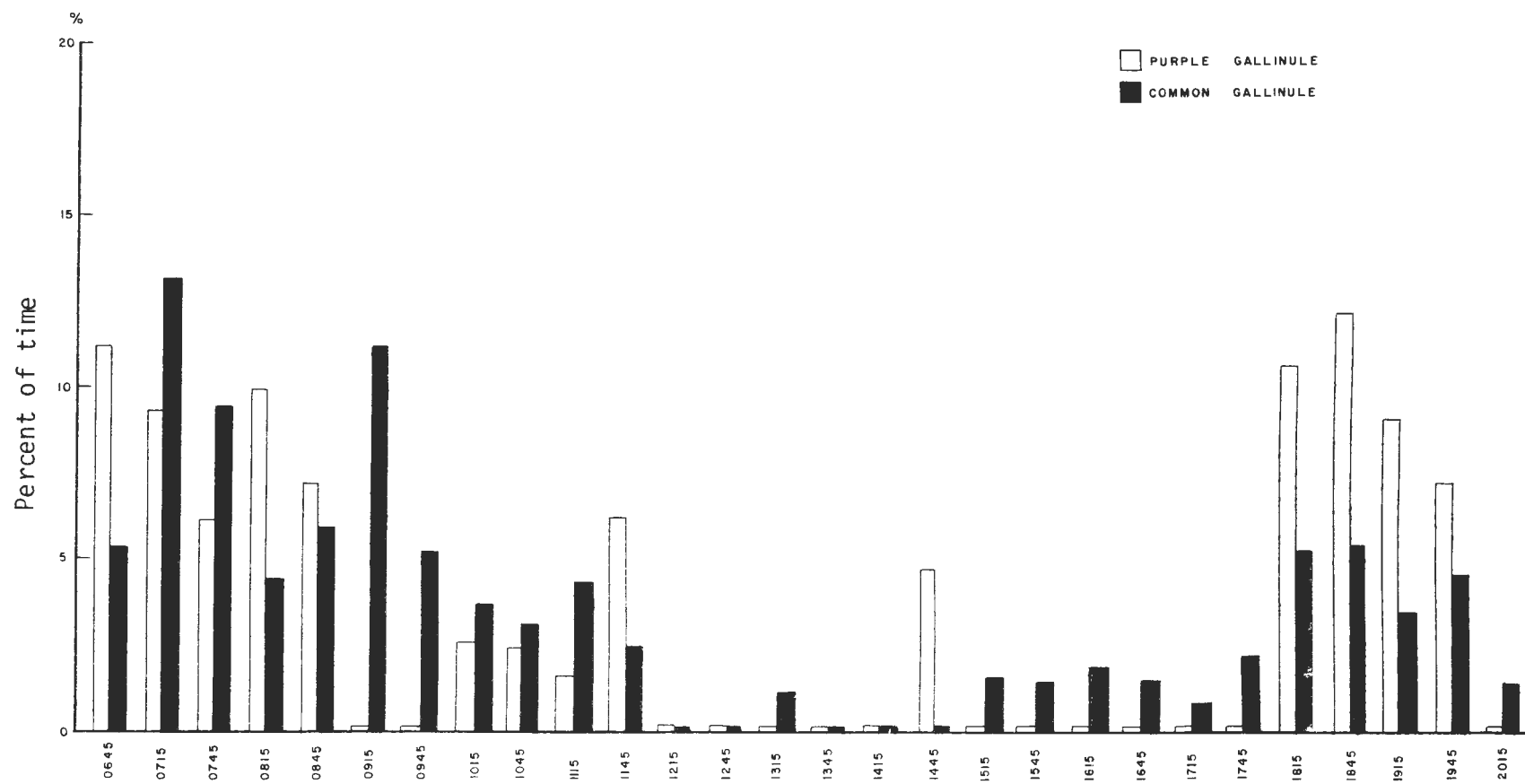


Figure 8. Percentage of time gallinules spent feeding throughout the daylight hours.

the day, both gallinules enter vegetation too dense to allow observation. Feeding may continue in this denser vegetation. However, if high temperature forces them out of optimal feeding habitat, it may be deduced that feeding is curtailed in the afternoon.

The disparity in samples between the Common Gallinule (1,007) and the Purple Gallinule (99) can be attributed not to the Purple's scarcity in relation to the Common Gallinule population but to the difficulty of observing Purple Gallinules. Many examples of Purple Gallinules entering dense panicum and paspalum grass clumps occurred throughout this study. These birds stayed in one clump of vegetation for the duration of a day's observation, rarely to be seen.

Feeding zones (vertical/horizontal habitat selection). Cody (1968) stated that a horizontal separation of feeding areas within the same habitat could enable coexisting species to reduce interactions. Another method of reducing interactions for shared resources is by vertical partitioning of feeding zones (Cody, 1974). MacArthur (1958) found that congeneric members of the family Parulidae coexisted by utilizing different vertical and horizontal components of trees and bushes.

Vertical and horizontal habitat selection between the Common and Purple Gallinules was studied by devising a two dimensional system for dividing their habitat. Five vertical parameters, based on variations of the feeding position, and four horizontal parameters, based on the density of cover, defined the system (see Feeding Zone Methods).

Tests for the analysis of variance show significant differences between the feeding zones utilized by the two gallinules during the

1973 ($F = 1,704.67 \quad \alpha .05 = 3.85$) and 1974 ($F = 1,597.60 \quad \alpha .05 = 3.85$) field seasons and the combined 1973-1974 field seasons. In 1973 Common Gallinules fed off the water surface in the open for 95 percent of all observations. A variety of other feeding zones were also used to a small extent (Table 4). Purple Gallinules, in 1973, utilized three feeding zones: 18 percent standing in sparse vegetation; 29 percent standing in dense vegetation (see Feeding Zone Methods, pp. 19-21 for definition of zones). Common Gallinules, during the 1974 field season, were associated with five feeding zones; 46 percent in open water; 15 percent on water in sparse vegetation; 8 percent standing in open vegetation; 29 percent standing in sparse vegetation; and 0.7 percent standing in moderately dense vegetation (Table 4). Purple Gallinules did not utilize the open water or water in sparse vegetation zones used by the Common Gallinules. Purple Gallinules during the same period made use of four zones: 22 percent standing in open vegetation; 29 percent standing in sparse vegetation; 16 percent standing in moderately dense vegetation; and 31 percent standing in dense vegetation (Table 4). I concluded that Common Gallinules selected open water adjacent to panicum and paspalum grass clumps while Purple Gallinules selected dense panicum and paspalum grasses in which to feed. Microhabitat selection therefore occurred in this fashion.

It was suspected that differences in intraspecific utilization of feeding zones existed between 1973 and 1974 for both species (Tables 5 and 6). Analysis of variance tests performed on intraspecific utilization of these feeding zones confirmed this suspicion (Table 7).

Table 4. Feeding zones of the Common and Purple Gallinules--expressed as a percentage of total feeding observations, 1973 and 1974

Feeding zone*	1973 Observations				1974 Observations			
	Common Gallinules	%	Purple Gallinules	%	Common Gallinules	%	Purple Gallinules	%
#5--open water	812	95.4	---	---	991	46.0	---	---
#6--on H ₂ O in sparse veg.	7	00.8	---	---	331	15.4	---	---
#7--on H ₂ O in mod. ² dense veg.	1	00.1	---	---	---	---	---	---
#10--normal bill reach in sparse veg.	1	00.1	---	---	---	---	---	---
#13--out of H ₂ O in open veg.	1	00.1	---	---	---	---	---	---
#14--out of H ₂ O in sparse veg.	1	00.1	---	---	---	---	---	---
#17--standing in open veg.	12	01.4	---	---	189	8.8	196	22.8
#18--standing in sparse veg.	12	01.4	9	18.8	628	29.2	253	29.5
#19--standing in mod. dense veg.	3	00.4	14	29.2	153	.07	138	16.1
#20--standing in dense veg.	1	00.1	25	52.1	---	---	272	31.7

* For definition of zones see feeding zone methods pp. 19-21.

Table 5. Feeding zones utilized by Common Gallinules in 1973 and 1974

Feeding zone*	1973		1974	
	observations	%	observations	%
#5--open water	812	95.4	991	46.0
#6--on H ₂ O in sparse veg.	7	0.8	331	15.4
#7--on H ₂ O in mod. dense veg.	1	0.1	---	---
#10--normal bill reach in sparse veg.	1	0.1	---	---
#13--out of H ₂ O in open veg.	1	0.1	---	---
#14--out of H ₂ O in sparse veg.	1	0.1	---	---
#17--standing in open veg.	12	1.4	189	8.8
#18--standing in sparse veg.	12	1.4	628	29.2
#19--standing in mod. dense veg.	3	0.4	15	0.7
#20--standing in dense veg.	1	0.1	---	---

* For definition of zones see Feeding Zone Methods pp. 19-21.

Table 6. Feeding zones utilized by Purple Gallinules in 1973 and 1974

Feeding zone*	1973		1974	
	observations	%	observations	%
#17--standing in open veg.	---	---	196	22.8
#18--standing in sparse veg.	9	18.8	253	29.5
#19--standing in mod. dense veg.	14	29.2	138	16.1
#20--standing in dense veg.	25	52.1	272	31.7

* For definition of zones see Feeding Zone Methods.

Table 7. Analysis of variance "F" test values for intraspecific utilization of feeding zones of gallinules between the 1973 and 1974 field seasons

	All data included		Minus premigration and migration data [†]	
	F value	$\alpha = .05$ value	F value	$\alpha = .05$ value
Common Gallinule	470.66*	3.84	26.54*	3.84
Purple Gallinule	20.21*	3.84	1.95*	3.84

* Significant at $\alpha = .05$ level.

[†] Purple Gallinule minus migration data only

There is an obvious reason for this deviation. In 1973, the migration of Purple Gallinules and nonresident Common Gallinules into the area had already taken place when data collection began. At the start of the 1974 field season only the resident Common Gallinules were present. Thus, a temporal shift in feeding zone utilization was suggested. This hypothesis was tested by deleting the 1974 gallinule premigration and migration data. By looking at Tables 8 and 9, it is evident that the intraspecific utilization of feeding zones between 1973 and 1974 coincide more closely when the 1974 premigration and migration data are deleted. However, an analysis of variance F value of 26.54 ($\alpha = .05 - 3.84$) still shows a significant difference existing between the Common Gallinules, although the significance is reduced by a factor of 18 (Table 9). Purple Gallinules, on the other hand, show no significant difference in feeding zone utilization when the migration data are deleted (Table 7). Thus, a temporal shift did take place and will be discussed later.

Table 8. Feeding zones utilized by Common Gallinules in 1973 and 1974 with premigration and migration data deleted

Feeding zone*	1973		1974	
	observations	%	observations	%
#5--open water	812	95.4	674	74.1
#6--on H ₂ O in sparse veg.	7	0.8	154	16.9
#7--on H ₂ O in mod. dense veg.	1	0.1	---	---
#10--normal bill reach in sparse veg.	1	0.1	---	---
#13--out of H ₂ O in open veg.	1	0.1	---	---
#14--out in H ₂ O in sparse veg.	1	0.1	---	---
#17--standing in open veg.	12	1.4	39	4.3
#18--standing in sparse veg.	12	1.4	42	4.6
#19--standing in mod. dense veg.	3	0.4	---	---
#20--standing in dense veg.	1	0.1	---	---

* For definition of zones see Feeding Zone Methods.

Table 9. Feeding zones utilized by Purple Gallinules in 1973 and 1974 with migration data deleted

Feeding zone*	1973		1974	
	observations	%	observations	%
#17--standing in open veg.	---	---	87	16.2
#18--standing in sparse veg.	9	18.8	41	7.6
#19--standing in mod. dense veg.	14	24.2	138	25.7
#20--standing in dense veg.	25	52.1	272	50.6

* For definition of zones see Feeding Zone Methods

Extreme variation in climatic conditions and its effect on the water level of Big Lake may also be a factor for the deviation in intraspecific feeding zone utilization. The precipitation between April and September of 1973 and 1974 is listed in Table 1. Before, during, and after the 1973 migration, only traces of precipitation were recorded (April and May). As a result, the lake level began to drop. By the time the gallinules arrives, the water level had dropped below the margins of the panicum and paspalum grasses--leaving little feeding and nesting habitat. By June 10, all vegetation used for nesting and feeding purposes (except bulrush stands) was completely above the lake's water level. By June 21, torrential rains filled the lake to its maximum level. On June 26 the lake went out of its banks, leaving a large portion of the habitable vegetation inundated. The Aransas River, on June 28, flooded into Big Lake. This condition persisted until July 3, after which the lake level returned to normal.

The 1974 season was considered normal, in that no drastic drop in water level or flooding occurred. However, a decrease of approximately 40 percent occurred in the surface area of the panicum and paspalum community between 1973 and 1974. There is no known reason for this decrease, but natural succession is suspected (Bolen, personal communication).

Food habits. Gallinules can be classified as omnivorous grazing animals. That is, most of their daily activity is devoted to feeding (Table 3), and their source of nutrition is highly variable. Food items were taken while participating in other activities such as preening, bathing, courtship, and territorial defense. The lake

ecosystem apparently provides food of abundant quantity and variety-- including floating debris, vegetation, insects and small freshwater vertebrates. Both gallinule species were observed taking all of these food items with no apparent selectivity.

Cody (1968) believed bird species are opportunistic and will take what they can get. He also considers stomach analysis unreliable as an index of coexistence. McAtee (1932) found, after analyzing eighty thousand bird stomachs, that the organisms contained within these stomachs were proportional to their availability. Because I agree with Cody's views on stomach analysis, and because of the opportunistic feeding nature of gallinules, the actual foods of the gallinules will not be discussed. The general omnivorous food habits of both gallinules is also noted by Bent (1926). Foods that both gallinules were observed taking are listed in Table 10. This list may be incomplete, for many food items taken could not be identified.

Feeding methods. Two or more similar coexisting species may divide the same food resources through differences in their feeding behavior (Hespenheide, 1971; Power, 1971; Karr, 1972; and Cody, 1974). Baker, et al. (1973), found that differences in foraging behavior in shorebirds were greater than food density was low.

Different foraging behavior by the Common and Purple Gallinules was found during this study. Of the 880 observations on Common Gallinules in 1973, 853 or 97 percent were of Common Gallinules feeding in the sitting position. In 1974, 92 percent of the total observations were also in the sitting position (Table 11); this was derived by

Table 10. Food items of the Common and Purple Gallinules at the
Welder Wildlife Foundation, San Patricio County, Texas

Common name	Scientific name
Animal foods	
Moth	Super Order Sphingoidae
Freshwater shrimp	Order Decapoda
Cricket	Family Gryllidae
Walking stick	Family Phasmidae
Water Strider	Family Gerridae
Giant Water bug	Family Belostomatidae
Waterscorpian	Family Nepidae
Cicada	Family Cicadidae
Leafhopper	Family Cicadellidae
Mosquito	Family Culicidae
Horse and deer fly	Family Tabanidae
Robber fly	Family Asilidae
Blow fly	Family Calliphoridae
Crab spider	Family Thomisidae
Wolf spider	Family Lycosidae
Orb-weaving spider	Family Araneidae
Top water minnow	Genus <i>Gambusia</i>
Plant foods	
	Species
Coontail	<i>Ceratophyllum</i> spp.
Lotus	<i>Nelumbo lutea</i>
Common water lily	<i>Nymphaea</i> spp.
Smartweed	<i>Polygonum</i> spp.
Water stargrass	<i>Heteranthera dubia</i>
Waternymph	<i>Najas guadalupensis</i>
Mosquito fern	<i>Azolla caroliniana</i>
Duck weed	<i>Lemna minor</i>
Water-hyacinth	<i>Eichornia crassipes</i>
Various species of algae	

Table 11. Different foraging methods used by gallinules at the Welder Wildlife Foundation, San Patricio County, Texas

	1973				1974			
	Standing (N* %)		Sitting (N %)		Standing (N %)		Sitting (N %)	
Common Gallinule	27	3.1	853	96.9	81	8.9	828	91.1
Purple Gallinule	52	96.3	2	3.7	538	100.0	0	0.0

* N = observation

deleting the premigration and migration data, so as to coincide more closely with the 1973 data. When the data are not deleted, a figure of 61 percent is determined. The remaining 39 percent concerns Common Gallinules feeding in the standing position.

Purple Gallinules, in contrast to Common Gallinules, were feeding while standing for 96 percent of the 1973 observations and for 100 percent of the 1974 observations (Table 11). Common and Purple Gallinules, as previously discussed, partition their resources through microhabitat selection. That is, Common Gallinules are generally associated with open water and sparse panicum and paspalum grasses, while Purple Gallinules select the denser portions of these grass communities. It seems natural, then, that Common Gallinules feed in a sitting position, since open water and sparse vegetation offer little substrate on which to stand. Along the same lines of reasoning, Purple Gallinules could hardly be expected to feed in the sitting position when the vegetation is too dense to allow it. Therefore, the differences

in feeding methods are not a method of partitioning resources, but is a consequence of horizontal microhabitat selection.

Temporal variation in microhabitat selection

Premigration. During the period between April 3 and April 17, 1974, fifty resident Common Gallinules inhabited the 52 hectare Big Lake. The location of these gallinules within the habitat was determined by devising a two-dimensional habitat grid based on two vertical parameters and four horizontal parameters. For definitions of zones see Temporal Variation in Microhabitat Selection methods. Of the 469 observations recorded, 328 or 70 percent were of common gallinules standing in vegetation (zones 5-7). Only 20 percent of the observations were of Common Gallinules sitting in open water (zone 1). Various other habitat zones were utilized to lesser degrees (Figure 9).

Migration. The first Purple Gallinules and additional Common Gallinules were seen on April 18, 1974. By May 12, 1974, a population of 84 adult Common and 28 adult Purple Gallinules were established on Big Lake. This population remained throughout the field season at a 3:1 ratio of Common to Purple Gallinules. The Purple Gallinules were found standing in sparse vegetation; 35 percent standing in open vegetation (zone 5); and 65 percent standing in sparse vegetation (zone 6) (Figure 9). Common Gallinules, on the other hand, shifted from 70 percent utilization of zones 507 (that is, standing in vegetation) during premigration to 57 percent (zone 7 was not used) during migration. An increase from 20 percent to 30 percent of Common Gallinules

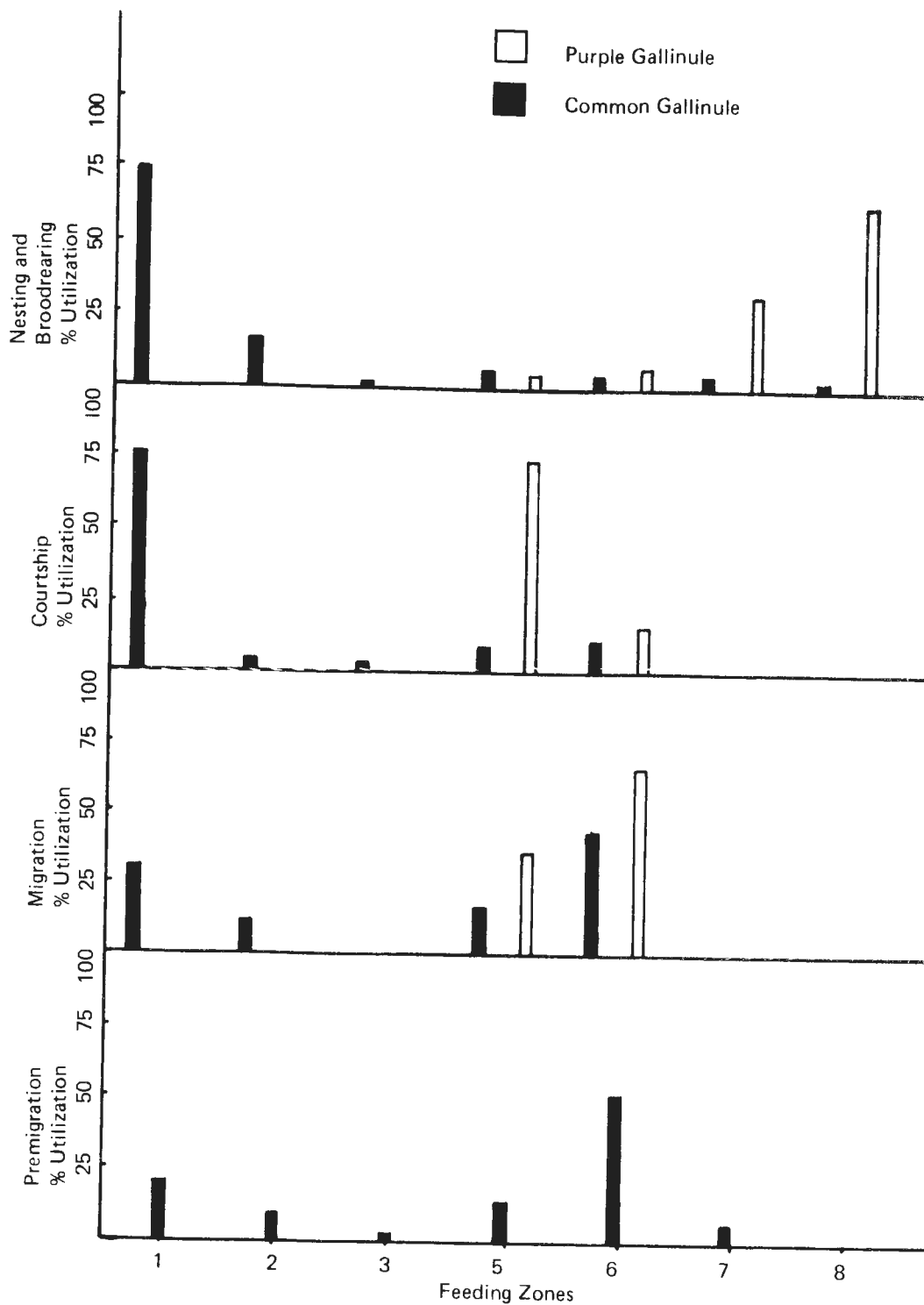


Figure 9. Habitat zones utilized by Common and Purple Gallinules during the premigration, migration, courtship, and nesting brood-rearing periods on the Weller Foundation, expressed as percentage of utilization.

sitting in open water was observed (Figure 9). Thus, with the influx of Purple and additional Common Gallinules, the Common Gallinule population began to shift to a more open micro-habitat (this shift deals with distances of 3 meters and less). Both resident and migrant Common Gallinules were involved in the shift.

Courtship. Courtship displays of both gallinules were first noted on May 10, 1974. By May 21, 1974, all gallinules in the study area were paired and courtship behavior had ended. Common Gallinule utilization of the open water zone (zone 1) continued to increase from 30 percent for the migration period to 75 percent (Figure 9). Habitat zones 5 and 6 experienced a decrease of use from 57 percent to 18 percent. The courtship displays of the Common Gallinule were performed while sitting in open water and this may be the reason for the increased usage of zone 1. Purple Gallinules likewise experienced a significant shift in microhabitat selection during courtship. Habitat zone 6 (standing in sparse vegetation) decreased in usage from 65 percent during migration to 16 percent during courtship. Likewise, in zone 5 (standing in open vegetation) utilization increased from 35 percent in migration period to 83 percent in courtship period (Figure 9).

Purple Gallinules arrived unpaired. With the commencement of courtship, solitary adults made themselves conspicuous by walking on top of the panicum and paspalum grass mats.

Nesting and brood-rearing. Nesting by both gallinule species was underway by June 5, 1974. Since there is a great deal of overlap in the nesting and brood-rearing periods of both species, and because there

were no further changes in microhabitat selection during these two periods, the nesting and brood-rearing data are combined.

The location of Common Gallinules in the open water zone (zone 1) resulted in insignificant changes (75 percent to 74 percent) between the courtship and nesting and brood-rearing period. However, the decrease observed in zones 6 and 5 (standing in sparse and open vegetation) 18 percent to 6 percent resulted in an increased use of zone 2 (sitting in sparse vegetation), 3 percent to 15 percent. Zone 7 (standing in moderately dense vegetation), after a period of non-use in the migration and courtship period experienced a 2 percent utilization during the nesting and brood-rearing period (Figure 9). Thus, a temporal change in microhabitat selection by Common Gallinules took place during the course of the 1974 field season. This change was from a utilization of sparse panicum and paspalum grasses, in which the gallinules were required to stand, to open water adjacent to panicum and paspalum grass clumps.

Purple Gallinules, during the courtship period, made themselves conspicuous on panicum and paspalum grass mats. However, as soon as they were mated, an immediate change in microhabitat selection took place. Habitat zone 5 (standing in open vegetation), which experienced an 83 percent utilization during courtship, abruptly declined to 2 percent usage. Zone 6 (standing in sparse vegetation) also declined from 16 percent to 5 percent utilization. Zones 7 (standing in moderately dense vegetation) and 8 (standing in dense vegetation), never before used, were suddenly heavily exploited by the Purple Gallinules during

nesting and brood-rearing; 30 percent for zone 7 and 63 percent for zone 8 (Figure 9). It is apparent that Purple Gallinules utilized a sparse open microhabitat in order to procure a mate. Once mated, they then rapidly made use of the denser panicum and paspalum grasses for the rest of the season.

Nesting parameters

Microhabitat selection, as described by Code (1968 and 1974) and Schoener (1974), also deals with differences in nest site selection within a homogeneous habitat as an indicator of resource partitioning.

During the course of this study, 38 nests of the Common Gallinule (22 in 1973 and 16 in 1974) and 22 nests of the Purple Gallinule (14 in 1973 and 8 in 1974) were located at the Welder Foundation. Figures 10 and 11 show that both species of gallinules exhibited synchrony in their breeding period and did not partition resources by breeding at different times of the year. The intraspecific deviation in times of nesting, as characterized in Figures 10 and 11, was most likely the result of seasonal climatic variation.

The similarity of the two species' habitat requirements for nesting is noted when examining the vegetation in which nests and nesting material were located. Common Gallinules had 77 percent and 93 percent of their nests located in panicum and paspalum in 1973 and 1974, respectfully. The number of Purple Gallinule nests located in panicum and paspalum amounted to 40 percent and 50 percent in 1973 and 1974, respectfully. Other vegetation used were cattail, bulrush, and aster (Table 19, in the appendix). Panicum and paspalum grasses

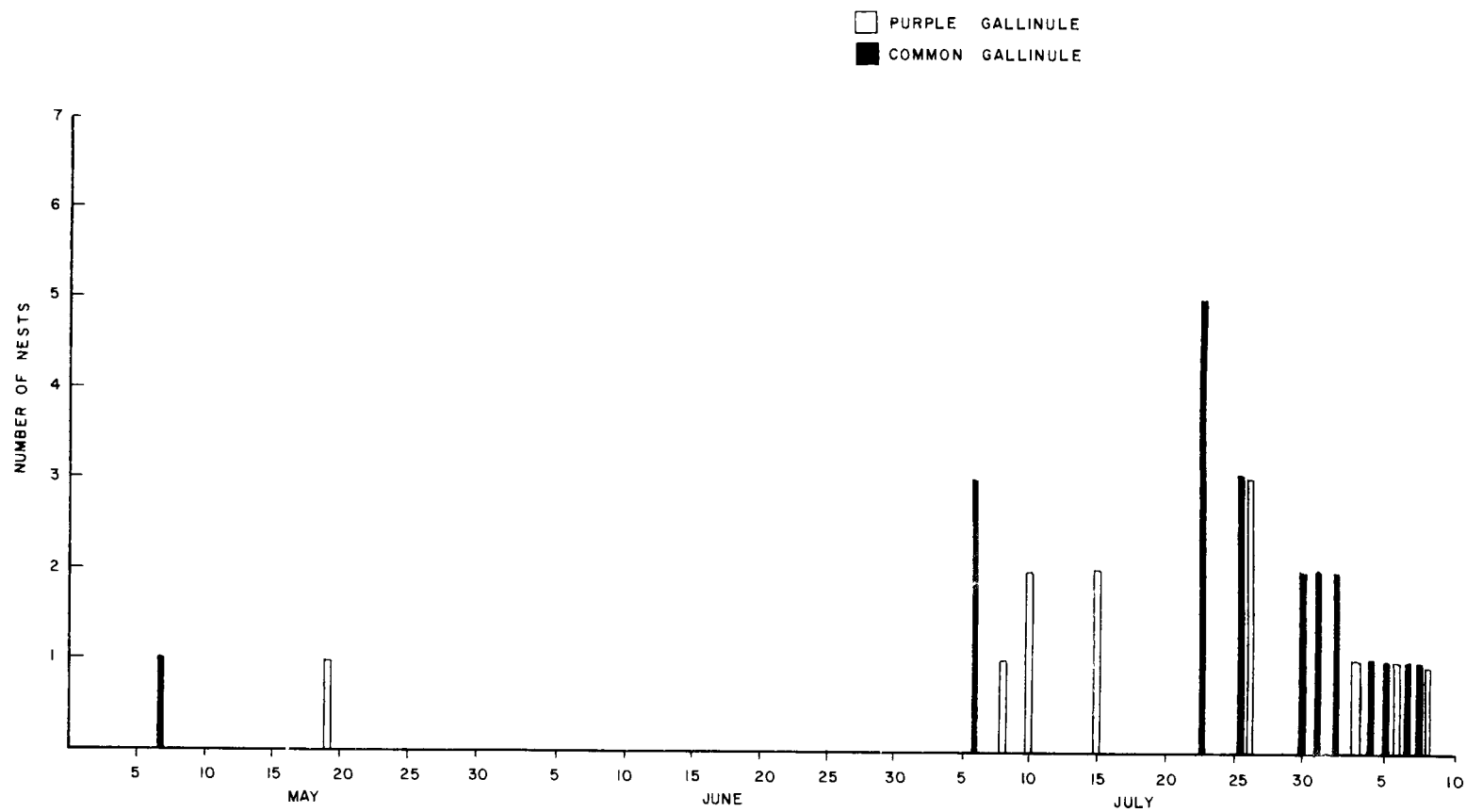


Figure 10. Distribution of gallinule nests over time in 1973--date marked is date first egg was layed.

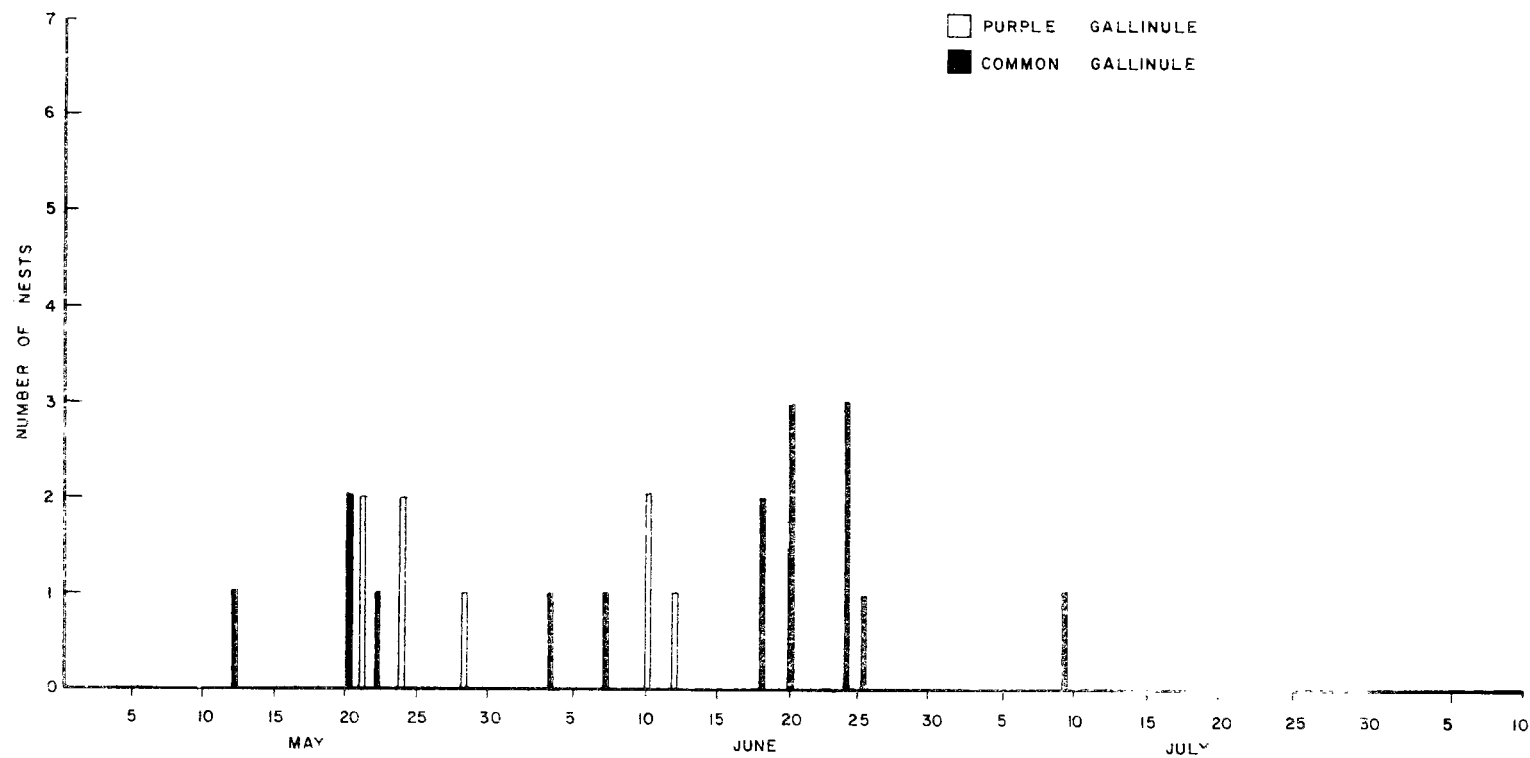


Figure 11. Distribution of gallinule nests over time in 1974--date marked is date first egg was layed.

were used as nesting material in 83 percent and 100 percent of the Common Gallinule nests in 1973 and 1974, respectively. Concerning Purple Gallinules, 50 percent of all nests were constructed of panicum and paspalum grasses in both 1973 and 1974 (Table 19). Analysis of variance tests were run on these two nest parameters. F test values of 0.5649 and 1.7100 ($\alpha .05 = 4.17$) for the 1973 and 1974 data on vegetation surrounding nests and values of 0.932 and 1.710 ($\alpha .05 = 4.2271$ and 4.170) for the 1973 and 1974 data on nesting material show no significant differences between these two nest site requirements. The 1961 data on nesting material and vegetation surrounding nests, on the other hand, shows a significant F test value of 4.48 ($\alpha .05 = 3.92$). However, this is the only year out of 7 years of data that shows significant differences between the gallinules (Table 20 in the Appendix).

The utilization of different nesting microhabitats by the two gallinules through vertical and horizontal habitat selection (Cody, 1968 and 1974) are made evident from the results of the 'density of cover' and 'nest height above water' parameters. In 1973, the mean density of the cover in which Common Gallinule nests were located was 92 percent light admitted by cover, and for Purple Gallinule nests, it was 80 percent light admitted by cover. In 1974, the mean cover density was 94 percent and 77 percent light admitted by cover for the Common and Purple Gallinule nests respectively (Tables 12 and 20). Analysis of variance test concerning cover density between the two gallinules yielded F test values of 4.3106 ($\alpha .05 = 4.2271$) and

Table 12. Nest cover density in which gallinule nests were located--expressed as percentage of light admitted by cover

Density range in percent	1973		1974	
	Common Gallinules	Purple Gallinules	Common Gallinules	Purple Gallinules
between 55-60	5.6	---	---	28.6
between 61-60	---	40.0	---	14.3
between 71-80	5.6	10.0	13.3	---
between 81-90	38.9	10.0	20.0	28.6
between 91-100	33.3	40.0	53.3	28.6
between 101-110	16.7	---	13.3	---

8.8095 ($\alpha .05 = 4.17$) for the 1973 and 1974 seasons, respectively. Thus, the two gallinules exhibited a horizontal selection in micro-habitats.

In the 1973-1974 data, and in all earlier data, Purple Gallinules selected higher nest sites than Common Gallinules (Tables 20 and 21 in the Appendix). The mean height of nests above water in 1973 was 11 cm and 39 cm for Common and Purple Gallinules respectively. In 1974, the mean nest height over water for Common and Purple Gallinules was 14 cm and 44 cm, respectively. Significant analysis of variance F test values of 8.410 and 11.499 ($\alpha .05 = 4.35$) for the 1973 and 1974 data were established. Significant values also resulted with the 1969 and 1972 data. Analysis of variance F test values of 2.66 ($\alpha .05 = 1.990$) for the 1969 data and 3.243 ($\alpha .05 = 1.982$) for the

1972 data were established. This evidence then gives credence to vertical partitioning by the Common and Purple Gallinules for nesting within the same habitat.

All other parameters studied, that is, distance from shore, distance to open water marginally, distance to open water medially, distance to closest point of open water, and water depth under nests, showed no significant differences between the two birds' nest requirements (Tables 13, 14, 15, 16, 20 and 22). However, the 1961 water depth data do show significant deviation between the two gallinules. This deviation may be explained, not through the choice of deeper water by Purple Gallinules for nest placement, but in the choice of surrounding vegetation (Table 18 in the Appendix). Purple Gallinules in 1961 placed 41 percent of their nests in bulrush, as compared to 13 percent for Common Gallinules. Panicum and paspalum grasses were utilized for nest placement by 67 percent of the Common Gallinules and 20 percent of the Purple Gallinules. The panicum and paspalum grass community is largely peripheral with respect to the lake and therefore it is in shallow water. The small bulrush community, on the other hand, is located in the deeper areas of the lake. The deviation in water depth, as it concerns gallinule nest placement, is a consequence of vegetational effect on nest site requirements.

Physical characteristics

In an earlier discussion of food habits, it was recognized that stomach content analyses can be biased as a criterion for coexistence. Cody (1974) believed an understanding of feeding methods and the

Table 13. Distance of gallinule nests from shore--expressed as percentage of total nests

Distance from shore in centimeters	1973		1974	
	Common Gallinules	Purple Gallinules	Common Gallinules	Purple Gallinules
greater than 1524	61.1	70.0	31.3	75.0
between 914.4-1523.9	27.8	10.0	43.8	0.0
between 304.8-914.3	11.1	30.0	25.0	25.0

Table 14. Distance of gallinule nests to open water marginally Big Lake, Welder Wildlife Foundation, Texas--expressed as percentage of total nests

Distance in centimeters	1973		1974	
	Common Gallinules	Purple Gallinules	Common Gallinules	Purple Gallinules
0-124.4	27.8	40.0	57.1	28.6
between 124.5-251.4	38.9	10.0	28.6	42.9
between 251.5-505.4	22.2	30.0	14.3	28.6
absence of open water	11.1	20.0		

Table 15. Distance of gallinule nests to open water medially on Big Lake, Welder Wildlife Foundation, Texas--expressed as percentage of total nests

Distance in centimeters	1973		1974	
	Common Gallinules	Purple Gallinules	Common Gallinules	Purple Gallinules
between 0-124.4	16.7	20.0	42.9	28.6
between 124.5-251.4	33.3	20.0	28.6	14.3
between 251.5-505.4	5.6	30.0	28.6	57.1
between 505.5-759.4	5.6	---	---	---
between 759.5-1013.4	5.6	---	---	---
between 1013.5-1267.4	5.6	20.0	---	---
between 1267.5-1521.4	---	---	---	---
between 1521.5-1775.4	5.6	---	---	---
greater than 1775.4	22.2	10.0	---	---

Table 16. Distance of gallinule nests to closest point of open water--expressed as percentage of total nests

Distance in centimeters	1973		1974	
	Common Gallinules	Purple Gallinules	Common Gallinules	Purple Gallinules
between 0-124.4	33.3	40.0	80.0	42.9
between 124.5-251.4	44.4	10.0	20.0	28.6
between 251.5-505.4	22.2	50.0	---	28.6

morphological characteristics of feeding appendages is adequate to infer the food and feeding determinants of resource partitioning. McAtee (1932) concluded that most birds are opportunistic feeders, taking food items that are available and manageable. Schoener (1965), on the other hand, suggested that body size is a better indicator of prey size than is bill morphology in birds. That is, the larger the body size, the larger the food item taken.

Measurements taken on Common and Purple Gallinules captured during the field study are given in Table 17. Common and Purple Gallinule sample sizes were too small to allow adequate statistical interpretation. Therefore, the conclusion drawn from the statistical results given below may not be a valid representation of the gallinule populations on the Welder Foundation.

Analysis of variance F test values of 0.140 ($\alpha .05 = 4.963$) show no significant differences in bill length. However, a significant value of 24.504 ($\alpha .05 = 4.963$) was found concerning the 'bill height at narea' measurements. The mean 'bill height at nares' of Common Gallinules was 9 mm and of Purple Gallinules was 11 mm. Cody (1968) found that among similar passerine species, birds with longer bills take longer food items, and birds with deeper bills take "harder" food items. This suggests that the two gallinules can take the same size food item, but that Purple Gallinules are more adapted to taking "harder" food items. A significant F test value was also found concerning body weight. Mean body weights of 322 g for Common

Table 17. Measurements in millimeters of Common and Purple Gallinules captured at the Welder Wildlife Foundation, San Patricio County, Texas

	Wing	Tarsus	Bill length	Width at nares	Height at nares	Toe length	Weight
Common Gallinules							
#1	190.0	531.0	31.0	6.0	10.0	65.0	370.0
#2	210.0	54.0	26.0	5.0	9.0	63.0	280.0
#3	219.0	51.0	27.0	6.0	9.0	68.0	235.0
#4	170.0	54.0	27.0	5.0	9.0	64.0	295.0
#5	180.0	60.0	28.0	6.0	10.0	69.0	350.0
#6	190.0	59.0	28.0	6.0	10.0	74.0	385.0
#7	183.0	57.0	31.0	6.0	10.0	65.0	370.0
#8	184.0	58.0	26.0	5.0	10.0	68.0	380.0
#9	194.0	51.0	27.0	5.5	9.0	63.0	235.0
	191.11	55.22	27.89	5.61	9.56	66.56	322.22
SD	15.12	3.38	1.90	0.49	0.53	3.57	61.60
Purple Gallinules							
#1	187	60.0	27.0	5.0	11.0	65.0	230.0
#2	183	68.0	27.0	6.0	11.0	69.0	205.0
#3	185	60.0	28.0	6.0	11.0	64.0	220.0
	185	62.67	27.33	5.67	11.0	66.0	218.33
SD	2	4.61	0.58	0.58	0	2.65	12.58

Gallinules and 218 g for Purple Gallinules suggests that Common Gallinules are capable of taking larger prey than are Purple Gallinules. That Common Gallinules may take larger food items and that Purple Gallinules may take "harder" food items was not observed. The methods of food manipulation by the two birds apparently compensated for the small but significant differences in the above measurements. It was observed with both birds that, if a food item once captured was too large to take whole, the gallinules used their feet to hold the item in place while tearing apart the item with their bills. Another method of reducing food items to edible size was by grasping the items in the bill and vigorously shaking the head. Thus, food size, once captured, is relatively unimportant to both gallinules.

CONCLUSIONS

Three partitioning mechanisms utilized by the Common and Purple Gallinules were found during this study.

1. The gallinules divided food resources by selecting different horizontal microhabitats. Common Gallinules fed in sparse panicum and paspalum grass clumps and in open water adjacent to peripheral panicum and paspalum grasses, whereas Purple Gallinules fed in denser panicum and paspalum grass clumps.

2. A seasonal variation in feeding zone utilization by both gallinules was observed throughout the study. Seasonal microhabitat selection varied for each species during the premigration, migration, courtship, and nesting and brood-rearing periods. Common Gallinules shifted gradually from a sparse to an open water microhabitat throughout the season. Purple Gallinules shifted from a sparse to an open to a dense microhabitat during the migration, courtship, nesting and brood-rearing periods respectively.

3. Common and Purple Gallinules partition nesting resources through both horizontal and vertical microhabitat selection. Purple Gallinules tend to nest in denser cover and at higher elevations than do Common Gallinules.

Partitioning mechanisms used by various species and investigated in this study were not used by the two gallinules.

1. Common and Purple Gallinules show synchronous overlap in daily activities. Therefore they do not divide their resources by performing activities at different times.

2. Common and Purple Gallinules are opportunistic feeders and take what is available and manageable. No differences were noted in food items taken.

3. Differences in feeding methods is a consequence of micro-habitat selection. Common Gallinules feed in the sitting position because they feed in open water, while Purple Gallinules must stand in dense panicum and paspalum grass in order to feed.

4. Despite the slight differences in bill height at the nares and in the birds' weights no significant differences in the size of food items taken were found.

SUMMARY

This study conducted between April and September 1973 and 1974 describes resource partitioning in the Common and Purple Gallinules at the Welder Wildlife Foundation in San Patricio County, Texas. The main objectives were: (1) describe differences of the two birds in their daily activities; (2) investigate nesting habits of the birds; and (3) compare physical characteristics of the birds.

Data collected on Purple and Common Gallinule included location within different types of vegetation, location during feeding, feeding behavior, and temporal changes in microhabitat selection. A 12 meter high observation tower and a 3 meter high portable blind were used for observations. Nests were located by using a canoe to search the vegetation in which gallinules nest.

The panicum and paspalum grass community on the peripheral margins of the lakes was the dominant vegetation used by both gallinules. No significant differences were found between Common and Purple Gallinules utilizing panicum and paspalum grasses.

Feeding occupied the greatest proportion of all daily activities in the two gallinule species. In 1973, Common Gallinules fed on the open water surface adjacent to panicum and paspalum grasses; in 1974, that figure was 74 percent. Purple Gallinules, during the study fed in dense panicum and paspalum grasses.

Both gallinules were observed taking floating debris, vegetation, insects, and small, fresh water vertebrates. The gallinules appeared to be taking what was available and manageable.

Different foraging methods were observed between the two birds. Purple Gallinules fed in a standing position, while Common Gallinules fed in a sitting position.

During the premigration period, Common Gallinules were observed to stand in sparse to moderately dense panicum and paspalum grasses 70 percent of the time; and sat in open water 30 percent of the time. During the migration period, Common Gallinules utilized vegetation 57 percent of the time and open water 30 percent of the time; while in the courtship period these birds were found in dense vegetation at first but later were found in open water.

Purple Gallinules, during migration, and courtship, utilized sparse panicum and paspalum grasses exclusively. During the nesting and brood-rearing period, Purple Gallinules utilized dense panicum and paspalum grasses.

Nesting periods coincided in both birds. Panicum and paspalum grass was the dominant vegetation in which both birds nested. Purple Gallinules nested at higher elevations and in denser cover within the same habitat. Both birds predominantly nested at distances greater than 15 meters from shore. Both gallinules nested at approximately the same distance to open water. The average depth of water under the gallinules' nests was the same.

Significant differences in the two birds' mean bill height at the nares were found, suggesting that Purple Gallinules with the greater height are more adapted to taking "harder" food items than are Common Gallinules. Significant differences in the two species' weight were also found. Despite the differences found in the mean bill height and the weights of the two birds, no differences in the type of food taken were found.

Three methods of dividing resources between the Common and Purple Gallinules were found in this study. (1) the gallinules differed in the microhabitat selected for feeding. Purple Gallinules fed in dense grasses, while Common Gallinules fed in open water and sparse grasses. (2) Seasonal variation in horizontal microhabitat selection between the species was observed. Common Gallinules shifted gradually from sparse panicum and paspalum to an open water and sparse grass microhabitat. Purple Gallinules utilized a sparse microhabitat during migration, an open microhabitat during courtship, and a dense microhabitat during nesting and brood-rearing. (3) Different horizontal and vertical microhabitat during the placement of nests showed that Purple Gallinules selected denser cover and placed their nests at higher elevations than did Common Gallinules.

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APPENDIX

Table 18. Vegetation in which gallinules nests were located--expressed as percentage of total nests in a given vegetation type

Vegetation	1961		1966		1968		1969		1972		1973		1974	
	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	#C.G. %	@P.G. %
panicum & paspalum	67.7	20.8	45.0	75.0	43.5	55.7	83.6	81.3	79.4	82.0	77.8	40.0	93.3	50.0
cattail	1.5	8.2	---	---	1.1	---	---	---	---	---	---	20.0	---	12.5
bulrush	13.8	41.7	---	---	10.9	16.5	2.7	3.1	13.5	5.5	11.1	20.0	---	12.5
astor	4.6	---	---	---	10.9	3.8	1.4	---	5.6	8.2	---	---	---	---
waterlilies	---	4.2	---	---	---	1.3	---	---	---	---	---	---	---	---
smartweed	---	---	---	---	---	---	1.4	9.4	---	---	---	---	---	---
eleocharis	6.2	---	---	---	4.3	---	---	---	---	---	---	---	---	---
huysache	---	---	---	---	6.5	1.3	1.4	---	---	---	---	---	---	---
p&p* and cattail	---	---	---	---	---	---	---	---	---	---	---	10.0	6.3	12.5
p&p and bulrush	---	---	---	---	---	2.5	---	---	---	---	---	---	---	---
p&p and aster	1.5	---	25.0	25.0	2.2	6.3	---	---	3.2	1.6	5.6	---	---	---
p&p and waterlilies	3.1	2.5	---	---	1.1	---	9.6	---	---	---	5.6	---	---	---
aster and cattail	---	---	---	---	---	---	---	---	---	---	---	---	---	12.5
aster and huysache	---	---	---	---	1.1	---	---	---	---	---	---	---	---	---
p&p and huysache	---	---	30.0	---	15.2	10.1	---	6.3	2.3	1.6	---	10.0	---	---
bulrush & smartweed	---	---	---	---	1.1	---	---	---	---	---	---	---	---	---
cut grass & huysache	---	---	---	---	1.1	---	---	---	---	---	---	---	---	---

*p&p = paspalum

#C.G. = Common Gallinule

@P.G. = Purple Gallinule

Table 19. Material from which gallinule nests were constructed--expressed as percentage of total nests located

Vegetation	1961		1966		1968		1969		1972		1973		1974	
	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	#C.G. %	@P.G. %
panicum & paspalum	67.7	20.8	45.0	75.0	43.5	55.7	83.6	81.3	75.4	82.0	83.3	50.0	100.0	50.0
cattail	1.5	8.3	---	---	1.1	---	---	---	---	---	---	10.0	---	12.5
bulrush	13.8	41.7	---	---	10.9	16.5	2.7	3.1	13.5	5.5	11.1	20.0	---	12.5
aster	4.6	---	---	---	10.9	3.8	1.4	---	5.6	8.2	---	---	---	---
waterlilies	---	4.2	---	---	---	1.3	---	---	---	---	---	---	---	---
smartweed	---	---	---	---	---	---	1.4	9.4	---	---	---	---	---	---
eleocharis	6.2	---	---	---	4.3	---	---	---	---	---	---	---	---	---
huisache	---	---	---	---	6.5	1.3	1.4	---	---	---	---	---	---	---
p&p* and cattail	---	---	---	---	---	---	---	---	---	---	---	10.0	---	12.5
p&p and bulrush	---	---	---	---	---	2.5	---	---	---	---	---	---	---	---
p&p and aster	1.5	---	25.0	25.0	2.2	6.3	---	---	3.2	1.6	5.6	---	---	---
p&p & waterlilies	3.1	2.5	---	---	1.1	---	9.6	---	---	---	---	---	---	---
aster and cattail	---	---	---	---	---	---	---	---	---	---	---	---	---	12.5
aster and huisache	---	---	30.0	---	15.2	10.1	---	6.3	2.3	1.6	---	---	---	---
bulrush & smartweed	---	---	---	---	1.1	---	---	---	---	---	---	---	---	---
cut grass & huisache	---	---	---	---	1.1	---	---	---	---	---	---	---	---	---

*
p&p = panicum and paspalum
#C.G. = Common Gallinule
@P.G. = Purple Gallinule

Table 20. Analysis of variance for nesting parameters of gallinules

Year	Number of nests		Distance from short	Vegetation around nests	Nest material	Cover density	Distance to open water marginally	Distance to open water medially	Distance to closest open water	Water depth	Nest height above water
	#C.G.	@P.G.									
1957	42	22	no data	no data	no data	no data	no data	no data	no data	no data	no data
1958	155	87	no data	no data	no data	no data	no data	no data	no data	no data	no data
1961	69	24	no data	*	*	*	no data	no data	no data	*	no sig.
1966	60	48	no data	no sig.	no sig.	no data	no data	no data	no data	no data	no data
1968	96	92	no data	no sig.	no sig.	no data	no data	no data	no data	no sig.	no sig.
1969	77	34	no data	no sig.	no sig.	no data	no data	no data	no data	no sig.	**
1972	130	64	no data	no sig.	no sig.	no data	no data	no data	no data	no sig.	**
1973	22	14	no sig.	no sig.	no sig.	*	no sig.	no sig.	no sig.	no sig.	*
1974	16	8	no sig.	no sig.	no sig.	*	no sig.	no sig.	no sig.	no sig.	**

* = Significant at .05 level

** = Significant at .01 level

= Common Gallinule

@ = Purple Gallinule

Table 21. Height of gallinule nests above water--expressed as percentage of total nests

Height in centimeters	1961		1968		1969		1972		1973		1974	
	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	#C.G. %	@P.G. %
0-5	---	---	---	---	---	---	---	---	---	---	6.7	---
5.1-10	---	---	17.0	15.2	7.4	3.6	---	---	77.8	40.0	46.7	---
10.1-15	---	10.0	26.8	24.1	53.7	28.6	48.6	25.0	11.1	10.1	26.7	28.6
15.1-20	---	---	23.1	20.3	20.4	25.0	38.3	37.5	---	---	6.7	14.3
20.1-25	---	---	22.0	21.5	5.6	10.7	4.7	15.6	5.6	---	---	---
25.1-30	---	---	8.5	11.4	---	---	2.8	4.7	---	---	---	---
30.1-35	---	30.0	---	---	11.1	14.3	0.9	4.7	---	10.0	6.7	---
35.1-40	---	---	---	3.8	---	---	0.9	1.6	---	---	---	14.3
40.1-45	---	---	1.2	1.3	---	---	---	1.6	---	---	6.7	---
45.1-50	---	20.0	---	1.3	---	10.7	0.9	---	5.6	---	---	---
50.1-55	---	---	---	1.3	---	---	---	---	---	10.0	---	---
55.1-60	---	---	---	---	---	---	0.9	---	---	---	---	14.3
60.1-65	---	30.0	---	---	---	3.6	0.9	1.6	---	10.0	---	---
65.1-70	---	---	---	---	---	---	---	---	---	---	---	---
70.1-75	---	---	---	---	---	---	---	---	---	---	---	---
75.1-80	---	---	---	---	1.9	---	0.9	3.1	---	---	---	---
80.1-85	---	---	---	---	---	---	---	---	---	10.0	---	14.3
85.1-90	---	---	---	---	---	---	---	---	---	---	---	14.3
90.1-95	---	10.0	---	---	---	---	---	1.6	---	---	---	---
95.1-100	---	---	---	---	---	---	---	---	---	---	---	---
100.1-105	---	---	---	---	---	---	---	---	---	---	---	---
105.1-110	---	---	---	---	---	3.6	---	1.6	---	---	---	---
110.1-115	---	---	---	---	---	---	---	1.6	---	---	---	---
115.1-120	---	---	---	---	---	---	---	---	---	---	---	---
120.1-125	---	---	1.2	---	---	---	---	---	---	10.0	---	---

#C.G. = Common Gallinule

@P.G. = Purple Gallinule

Table 22. Depth of water under gallinule nests--expressed as percentage of total nests

Water depth in centimeters	1961		1968		1969		1972		1973		1974	
	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	C.G. %	P.G. %	#C.G. %	@P.G. %
0-10	---	---	11.6	5.1	---	---	0.8	---	6.7	14.3	5.6	---
10.1-20	---	---	34.9	26.6	5.7	3.0	3.2	4.5	13.3	---	---	---
20.1-30	---	---	7.0	8.9	5.7	3.0	3.8	6.0	26.7	---	4.5	10.0
30.1-40	4.7	5.3	1.2	2.5	20.0	18.2	2.4	4.5	33.3	14.3	16.7	---
	23.2	---	10.5	6.3	22.9	24.2	8.7	9.0	13.3	28.6	11.1	10.0
50.1-60	4.7	---	3.5	6.3	1.4	3.0	20.6	23.9	6.7	42.9	33.3	20.0
60.1-70	16.3	26.3	1.2	3.8	7.1	12.1	19.8	23.9	---	---	5.6	30.0
70.1-80	16.3	5.8	2.3	7.6	6.1	12.1	10.3	10.4	---	---	---	---
80.1-90	---	---	3.5	1.3	---	---	8.7	3.4	---	---	---	---
90.1-100	18.6	21.1	7.0	3.8	17.1	15.2	8.7	4.5	---	---	11.1	10.0
100.1-110	7.0	10.5	4.7	8.9	7.1	3.0	4.0	3.0	---	---	---	10.0
110.1-120	4.7	5.3	4.7	---	---	---	2.4	3.0	---	---	---	---
120.1-130	4.7	26.3	7.0	15.2	5.7	2.9	0.8	1.5	---	---	---	---
130.1-140	---	---	1.2	3.8	---	---	---	---	---	---	5.6	---
140.1-150	---	---	---	---	---	---	4.0	---	---	---	5.6	---
150.1-160	---	---	---	---	---	---	2.4	3.0	---	---	---	10.0

#C.G. = Common Gallinule

@P.G. = Purple Gallinule

VITA

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