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FEEDING ECOLOGY OF THE PURPLE GALLINULE (*Porphyrula martinica*) IN THE CENTRAL LLANOS OF VENEZUELA

ECOLOGIA ALIMENTARIA DEL GALLITO AZUL (*Porphyrula martinica*) EN LOS LLANOS CENTRALES DE VENEZUELA

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ABSTRACT

The food habits of purple gallinules (*Porphyrula martinica*) were studied through direct observation in the Central Llanos of Venezuela during the rainy season of 1988, from August to December. Purple gallinules consumed an average 56.6% of plant foods and 31.1% of animal foods (12.3% unknown) Seeds were the most frequent and most abundant food in the diet for all months. Diet composition changed significantly through the rainy season in relation to changes on food resources availability and on the reproductive stage of the birds. Purple gallinules are opportunistic in their food habits being able to exploit a wide variety of foods when available but show preferences for some of them.

Key words: *Porphyrula martinica*, Venezuelan Llanos, food preferences, availability, phenology, diversıty, reproduction, opportunistic.

RESUMEN

Los hábitos alimentarios del gallito azul (*Porphyrula martinica*) fueron estudiados a través de observaciones directas en Los Llanos Centrales de Venezuela, durante la estación lluviosa de 1988, entre agosto y diciembre. Los gallitos azules consumieron en promedio 56,6% alimentos de origen vegetal y 31,1% de origen animal (12,3% no identificado). Las semillas fueron el alimento más frecuente y abundante en la dieta durante todos los meses. La composición de la dieta varió significativamente de un mes a otro, en relación a los cambios en la disponibilidad de recursos alimentarios y en la reproducción. Los gallitos azules son oportunistas en sus hábitos alimentarios siendo capaces de utilizar un amplio espectro de alimentos cuando están presentes, aunque muestran preferencias por algunos de ellos.

Palabras clave: *Porphyrula martinica*, Llanos venezolanos, diversidad, fenología, preferencias alimentarias, oportunista, reproducción, disponibilidad.

INTRODUCTION

The purple gallinule (*Porphyrula martinica*) is widely distributed in the neotropics from the southern United States to northern Argentina and inhabits freshwater wetlands, lowland lagoons and slow-flowing river margins (Blake 1977), the requirement being abundant marshy vegetation. Despite its abundance, its food habits are poorly documented, with only scarce records reported by Aguirre (1962) and Schubart *et al.* (1965). More detailed analysis have been performed by Mulholland and Percival (1982), who compared the food habits of common moorhens (*Gallinula chloropus*) and purple gallinules in north central Florida over an annual cycle.

Purple gallinules are very common in the Central Llanos of Venezuela when they breed during the rainy season. The llanos are extensive seasonal wetlands which support a highly diverse and abundant fauna. The vegetation consists mostly on plants adapted to soil saturation conditions (Ramia 1978). In spite of the abundance of purple gallinules in the llanos, little is known about their habits and behavior in these wetlands. This research determines the diet of the purple gallinule in Venezuelan Llanos during the rainy season, how diet changes over the season and if these changes are related to food resources availability and reproduction.

Natural wetlands in Venezuela have been gradually transformed into croplands, mainly rice fields, altering the natural pattern of habitat utilization of many birds. A detailed understanding on wetlands and how species use them will help maintain and control bird populations. Knowledge of purple gallinule food habits improves our understanding of its dietary and environmental requirements and of its role in the dynamics of these ecosystems.

METHODS

Study site

We conducted the field work in Fundo Pecuario Masaguaral, a cattle ranch on Guárico State, 50 Km south of Calabozo, from mid-August to mid-December during the rainy season of 1988. Masaguaral is located in the Central Llanos of Venezuela. The dominant features of the llanos are low relief and open grasslands, interrupted by gallery forests. The topography is nearly flat with heights up to 75 meters above sea level (Troth 1979). Four physiographic savanna units are found in Masaguaral: médano (fossil sandhill), banco (non-flooded, low ridge), bajío (moderately flooded lowlands) and estero (deeply flooded lowlands) (see Ramia 1967).

The climate of central Venezuela is markedly seasonal. The dry season lasts from December to March and the rainy season from May to October, with April and November as transition months. Average temperature and rainfall are 27° C and 1400 mm respectively. During the rainy season water level rises and river runoff fills up the low-lying depressions (esteros and bajíos), resulting in seasonal freshwater wetlands. Vegetation on these marshes consists mainly on soft-stemmed plants, grasses and sedges. Plants may emerge above water, float or be totally submerged. Plant communities on these marshes are very complex and their structure depend primarily on rainfall, morphology of the ground, soil and water level. Most of the species develop into dense colonies whose shape and size varies along the season (see Troth 1979).

Diet composition

We observed purple gallinules on a seasonal marsh of approximately 2.8 ha., which dried out completely during the dry season. Maximum water depth in the marsh was 71 cm.

We recorded food habits through focal observation of the birds using a 16-36x zoom telescope. Observations were conducted from 0630 h to 1100 h and from 1530 h to 1830 h., from two 6 m high scaffolds. We located feeding birds and recorded food handling time per item using a stopwatch. Food handling time was measured as the time elapsed from when the bird began to peck or pull a food item until it swallowed it, stopped pecking or began to manipulate another item.

We calculated the total food handling time per item for each month and for the entire season. We determined the relative abundance of each item in the diet as total food handling time per item divided by total food handling time for all items. The frequency of each food item (number of times the birds were seen feeding upon the item divided by the number of times the birds were seen feeding upon all items) was also calculated. A Spearman Rank Correlation ($\alpha < 0.05$) was used to compare the monthly diets (see Fritz 1974). Significant correlation coefficients indicate that a relationship exists between the diet composition of compared months (i. e., diet composition is the same).

Diet diversity

We estimated the diversity of the diet using the Hill numbers N_0, N_1 and N_2 (Hill 1973), where N_0 is the total number of species (richness), N_1 is the number of common species ($N_1 = \exp(H')$ where H' is Shannon's entropy) and N_2 is the number of very common species ($N_2 = 1/p_1^2 + p_2^2 + ... + p_n^2$ or the reciprocal of Simpson index). The ratio between common and total species was calculated as well ($E_{1.0} = N_1/N_0$). Evenness was estimated by the Hill's ratio modified by Alatalo (1981), $F_{2.1} = (N_2-1)/(N_1-1)$.

Food preferences

We analyzed food preferences for plant foods by calculating the ratio between the frequency of the item in the diet and its frequency in the habitat (see Sudgen 1992). Ratios which approximate 1.0 indicate that the item is used by the birds according to its abundance in the habitat (i.e., the item is neither preferred nor rejected). Ratios greater or less than one suggest preference or rejection respectively.

We determined plant species composition in the habitat using the technique suggested by Noon (1981) for non-forest habitats. We plotted twelve parallel transects 200 m long and 20 m apart on the marsh. Every ten meters along each transect a round plot (50 cm diameter) was set and the presence of each plant species was recorded. We registered the phenology of most plants but we did not estimate seed production over the rainy season. Additional information on phenology was obtained from Ramia (1978). Animal food availability in the habitat was not quantified.

Diet and reproduction

We separated the food items into two mayor food types, plant foods and animal foods, to determine if diet composition was correlated with reproduction. The relative abundance of food types consumed during each stage of the reproductive cycle was calculated and proportions for successive stages were compared (t test, $\alpha < 0.05$). We used Tárano unpublished data to estimate the duration and occurrence of each phase of the reproductive cycle (laying, incubation and posthatching) during the breeding season of 1988.

RESULTS

We followed 37 purple gallinules during 82 hours in 38 days of observation during the wet season of 1988. All birds observed were adults. Individuals in juvenile plumage were seen in December but observations on their diet were not included in the analyses.

Diet composition

Purple gallinules foraged on both plant and animal foods. Plant foods were positively identified to species and animal foods to class, and in some cases to order. Composition of the total diet (pooling all months) is presented in Table 1. Plant foods were exclusively seeds and fruits of aquatic plants and represented 56.6% of the total diet. Seeds of *Caperonia palustris*, *Thalia geniculata* and *Neptunia oleraceae* were the most abundant plant foods, accounting together for 39.2% of the total diet. Animal foods represented 31.1% and included invertebrates (arthropods and molluscs) and small vertebrates (fish). Arthropods (mainly insect adults and larvae) were the most important animal food being 26.4% of the diet.

Table 1. Total diet composition of purple gallinules in Central Llanos of Venezuela during the rainy season of 1988

Food Type	Family	Food Item	Relative abundance[a]	Frequency[b]
Plant:		Seeds:		
	Euphorbiacea	*Caperonia palustris*	15.73	0.45
	Ciperaceae	*Eleocharis interstincta*	3.39	0.11
	Ciperaceae	*Eleocharis mutata*	1.41	0.11
	Poaceae	*Hymenachne amplexicaules*	1.03	0.08
	Onagraceae	*Ludwigia helminthorryza*	3.66	0.16
	Onagraceae	*Ludwigia octovalvis*	1.57	0.18
	Fabaceae	*Neptunia oleraceae*	7.76	0.29
	Poaceae	*Oryza perennis*	2.92	0.05
	Marantaceae	*Thalia geniculata*	15.67	0.29
	Poaceae	Miscellaneous grasses	3.49	0.18
Animal:		Arthropods:		
		adults	21.30	0.58
		larvae	5.33	0.18
		Fish	2.35	0.05
		Molluscs	2.40	0.05
Unknown			12.26	
Totals			100.00	

[a] Total food handling time per item divided by total food handling time for all items

[b] Number of times the birds were seen feeding upon the item divided by the number of times the birds were seen feeding upon all items

Table 2. Monthly relative abundance[a] of plant and animal foods consumed by purple gallinules in Central Llanos of Venezuela during the rainy season of 1988.

Food Item	August n=10	September n=11	October n=7	November n=4	December n=5
Seeds:					
Caperonia palustris	23.69	24.50	0.26		
Eleocharis interstincta	17.93	0.18			
Eleocharis mutata		1.17			6.65
Hymenachne amplexicaules			6.10		
Ludwigia helminthorryza		3.20	11.82	3.02	
Ludwigia octovalvis	3.40				
Neptunia oleraceae		11.18	12.46		3.72
Oryza perennis	1.04		16.10		
Thalia geniculata		0.36	32.11	47.77	54.61
Miscellaneous grasses	8.86	2.88		4.00	
Arthropods					
adults	17.15	24.20	11.94	13.78	29.16
larvae	4.97	9.56			
Fish		0.41		35.43	
Molluscs			2.54		7.24
Unknown	26.36	16.42	1.96		1.86
Total	100.00	100.00	99.99	100.00	100.00

[a] Total food handling time per item divided by total food handling time for all items (%)

Monthly relative abundance and frequency of food items are presented in Table 2. Both estimates (abundance and frequency) produced similar results in terms of ranks given to each item (Spearman, r_s>0.79 p<0.01). Therefore, further analyses will be referred to the relative abundance. Plant foods were more abundant in all months except in November. Seeds of *C. palustris*, *Eleocharis interstincta* and *N. oleraceae* were the dominant plant foods on August and September. Water plantain seeds (*T. geniculata*) became the most abundant plant food from October to December. Arthropods were the main animal food during all months except November when fish dominated. Monthly diets by food items were not significantly related to one another all over the rainy season (Spearman, $-0.18 < r_s < 0.42$, $p > 0.10$).

Diet diversity

Diet diversity estimated through the total number of species (N_0), including both plant and animal foods, was maximum in September and

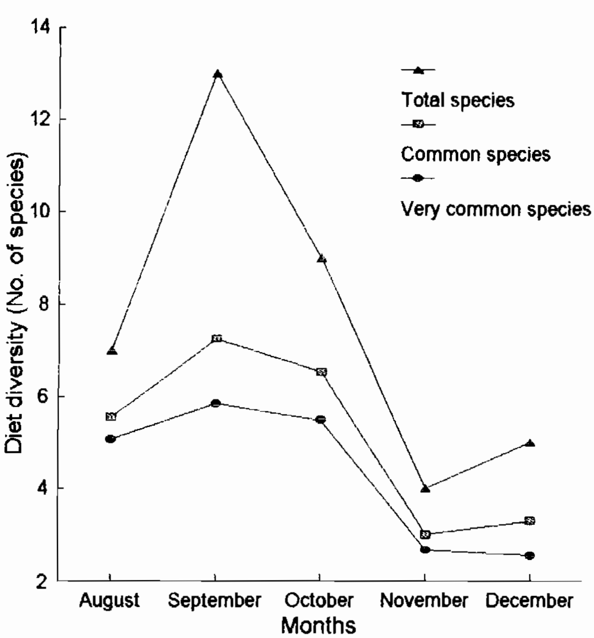

Figure 1. Monthly diversity of the diet of purple gallinules in Central Llanos of Venezuela during the rainy season of 1988. Diet diversity is measured as total number of species (N_0), number of common species (N_1) and number of very common species (N_2).

minimum in November (Figure 1). Number of common and very common species (N_1 and N_2 respectively) was similar from August to October but dropped in November. The ratio of common species to total species (N_1/N_0) was similar in August, October and November ($0.73 < E_{1,0} < 0.79$) but differed in September and December (0.56 and 0.66 respectively), which indicates that an important proportion of the diet consisted of relatively uncommon species, specially in September The evenness ($F_{2,1}$) was high from August to November (between 0.89 in November and 0.78 in September) but dropped abruptly in December (0.08) when the dry season commenced.

Food preferences

Plant species composition in the marsh was estimated in September and November. The ratios between the frequency of plant foods in the diet and in the habitat (Table 3) suggest that *C. palustris*, *N. oleraceae*, *Ludwigia octovalvis*, *T. geniculata* and grasses were slightly preferred. Sedges (*Eleocharis spp*) were rejected at the beginning of the rainy season but slightly preferred at the end.

Diet and reproduction

The reproductive activity of the purple gallinules during the rainy season followed a continuum from August to December. Some breeding pairs began laying by mid-July but most of them laid eggs in late August and in the first week of September, incubated during September, reared chicks from October to December and began migrating in late December (Tárano unpublished data).

Our records of feeding habits included both sexes. In purple gallinules males and females are alike. Males are slightly lager than females but size differences are not noticeable from the distance. Both pair members share the reproductive duties, such as defense of the territory, nest maintenance, incubation and feeding of the chicks (Hunter 1987, Tárano 1990).

Diet composition by food types on each stage of the reproductive cycle is shown in Figure 2. Plant

Table 3. Food preferences of purple gallinules in Central Llanos of Venezuela during the rainy season of 1988. Numbers represent selection ratios of plant foods consumed by the birds calculated by dividing the frequency of the item in the diet by its frequency in the habitat.

Food Item	September	December
Seeds:		
Caperonia palustris	1.73	
Eleocharis interstincta	0.46	
Eleocharis mutata	0.38	1.43
Ludwigia helminthorryza	0.49	
Ludwigia octovalvis	1.10	
Neptunia oleraceae	1.14	0.83
Thalia geniculata	0.10	2.33
Miscellaneous grasses	3.22	0.70

foods consumption increased significantly after incubation ($t=3.61$, $p<0.05$), while the proportion of animal foods did from laying to incubation ($t=2.55$, $p<0.05$).

DISCUSSION

The diet of the purple gallinule in the Central Llanos of Venezuela includes both plant and animal foods, but depends primarily on seeds. The composition of the diet changes significantly during the rainy season and this variation is related to food availability and perhaps to the reproductive condition of the birds as well.

Purple gallinules show a great ability to use a diverse array of foods (plant and animal). Mixed diets have several advantages, which are more striking in fluctuating environments such as the llanos. Birds with mixed diets can adjust themselves to changes in food resources abundance and diversity and meet their nutritional requirements more efficiently than birds with single diets (Bartonek and Hickey 1969, Landers *et al.* 1977, Sugden 1982). In addition, chemical analysis have shown that only a few foods can provide on their own all the nutritional needs of water birds (Sudgen 1982). Tárano unpublished observations in rice fields support the hypothesis that purple gallinules might seek mixed diets. Despite the fact that rice seeds were very abundant, purple gallinules also fed upon invertebrates (relative abundance up to 16.68%) and small vertebrates (frogs).

The proportions of plant and animal foods in the diet of purple gallinules in the llanos differ from those reported by Mulholland and Percival (1982) in south-central Florida (71% plant and 29% animal foods). These dissimilarities are expected given the differences in survey seasons and locations. Mulholland and Percival (1982) also reported the utilization of leaves, stems and petals of hydrilla (*Hydrilla verticillata*). It is possible that purple gallinules ate other plant foods besides seeds in the llanos. Occasionally we sighted the birds pulling the stems and roots of floating plants, but we could not identify what they were eating.

The relative abundance and diversity of foods utilized by purple gallinules in the llanos vary significantly during the rainy season. Because purple gallinules feed primarily upon seeds their diet should reflect the phenology of the aquatic plants. Fast growing emergent species developed soon after the first rains (e.g., *E. interstincta*, *C. palustris*). As water level rose, extensive floating clumps (e.g., *N. oleraceae*, *L. helminthorryza* and *Eichhornia crassipes*) covered the marsh. By the end of the rainy season, early plants dried while slow growing emergent species fruited (e.g., *T. geniculata*). This pattern of plant abundance and fruiting broadly corresponds to the changes observed in the composition of the diet (see Table 2).

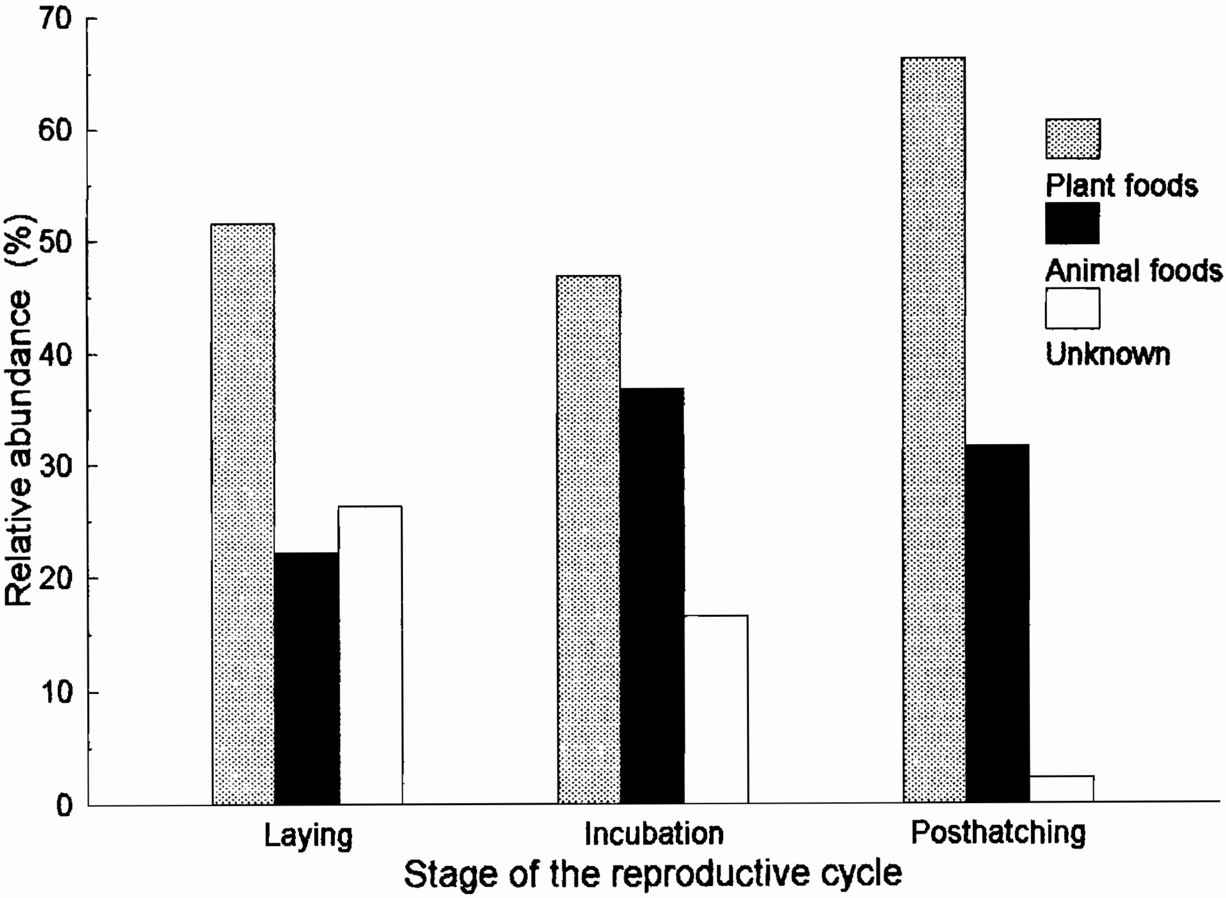

Figure 2. Relative abundance of plant and animal foods in the diet of purple gallinules during three stages of the reproductive cycle: laying, incubation and posthatching.

The rain triggers the reproduction of invertebrates, fish and amphibians (Wolda 1978). Many aquatic invertebrate eggs hatch after the first rains while many adults come to reproduce in the ponds. This pattern of invertebrate availability corresponds with consumption of arthropod larvae (Lepidoptera) and adults by purple gallinules at the onset of the rainy season (Table 2). High consumption of arthropods observed at the end of the rainy season was due to increased abundance of Coleoptera (Curculionidae) associated to water plantain leaves. Increasing numbers of Coleoptera and Hemiptera at the end of the rainy season have been documented by Wolda (1978) and Smythe (1990). Instead, occasional consumption of small vertebrates occurred as the drought approached. Fish were caught only when water level decreased making them easy prey for birds (Mago-Lecia 1978, Ayarzagüena *et al.* 1981). Snails are also difficult to catch by relatively short-legged, short-beaked birds like purple gallinules, because they sink when water is disturbed. Purple gallinules also lack a strong beak to break snail shells or to separate the operculum. Only once did we see a bird eating a snail and it devoted a lot of time trying to get the body out of the shell.

Diet diversity also relates to food availability being high during the rains and dropping while the drought commences. Similarly, evenness is very low at the beginning of the drought when most plants are already dry. For instance, purple gallinules were feeding almost exclusively upon *T. geniculata* seeds in November and December. Interestingly diet diversity measured as total number of species (N_0) is remarkably high in September, just after the peak of rains, but 44% of these species are relatively uncommon (the ratio of common to total species is

0.56 in September). Again these results show that purple gallinules incorporate new foods on their diet as they become available, but suggest that besides food availability bird preferences influence diet composition as well (Table 3).

Optimal foraging theory predicts that animals will maximize their energy intake and minimize their time expenditure while foraging (Stephen and Krebs 1986). Analyzing food preferences in terms of biomass, we should expect that purple gallinules select the biggest and most nutritious seeds. In fact, *C. palustris* and *T. geniculata*, which are preferred by the birds (Table 3), produce the biggest seeds, 3.2 x 3.5 mm and 8 x 5.4 mm respectively compared to 1.5 x 2.3 mm of *E. interstincta* or 0.8 x 0.77 mm of *L. octovalvis* (see Anzola 1981 for more information on seed size and weight). Seed utilization might also correlate to nutrient composition. Sedges such as *Eleocharis* have hard coated seeds which are not easily digested (Bartonek and Hickey 1969) and their nutritional value may therefore be low by comparison to *C. palustris* or *T. geniculata* which lack such a coat.

We did not investigated availability of animal foods but our observations suggest that purple gallinules might select among them. We saw purple gallinules actively seeking larvae and adult arthropods. Birds sought lepidopteran larvae by sweeping folded leaves with their beaks. These larvae enveloped themselves by folding the leaves of their host plant prior to metamorphosis. Birds also spent a lot of time walking through water hyacinth clumps (*Eichhornia crassipes*), whose seeds were not eaten, but which harbored many arthropods such as spiders, dragonflies, ants and other insects.

Purple gallinules migrate to the llanos at the dawn of the rainy season and begin reproduction soon after arrival (Thomas 1979). In the rainy season of 1988 birds were first seen in July and several pairs began to lay two weeks after arrival (Tárano personal observation), suggesting that they were in good nutritional condition.

Fluctuations of animal and plant foods on the diet of purple gallinules during reproduction might correlate with nutritional requirements. For instance, animal foods are important sources of protein, calcium and other nutrients required for egg formation (Krapu 1974a). Therefore we would expect that animal foods were more important during laying. Our results did not support this prediction entirely because animal food intake increased during incubation. This result may be due to sub-sampling during laying (we began recording food habits when several females had already laid) or to changes in animal food availability. However the increase in animal food proportion during incubation might be correlated to renesting. Birds attempting to renest must meet their protein and fat requirements from daily food intake (Krapu 1974a, Swanson and Meyer 1977). During our study two pairs lost their nests while incubating and renested two weeks later. The increase of plant food consumption during posthatching might be related to restoring fat reserves depleted during incubation (e.g., Krapu 1974b) and maintaining body weight after breeding (Holm and Scott 1974). Further research must be directed to analyze food quality in order to relate it to food selection and nutritional requirements during reproduction.

In summary, purple gallinules are opportunistic in their food habits exploiting a wide variety of foods according to their abundance and availability, but show preferences for some foods as well. These preferences could be partially related to foods chemical composition, digestibility and nutritional requirements during reproduction. Purple gallinules are expected to be opportunistic considering the characteristics of their habitat. The rainy season is highly predictable in the llanos but the amount of rain and the duration of the season varies from year to year. The birds which use these habitats should be able to respond to this variable water regime. Thus they must be flexible and opportunistic in their general behavior specifically in their food habits.

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