

# FLOODED FALLOW RICEFIELDS AND THE STRUCTURE OF BIRD COMMUNITIES

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## ABSTRACT

The interaction of abiotic and biotic factors, their intensity, and the mechanisms by which these factors affect population dynamics are crucial data for understanding how ecological communities work. Tropical grasslands with standing water have a higher bird species diversity (BSD) than those without; habitat characteristics thought responsible for this effect were evaluated in four fallow ricefields. A three-year-old flooded fallow field had the highest BSD, while an unflooded three-year-old had the same BSD as a six-month-old flooded field. The other six-month unflooded field had the lowest BSD. Aquatic birds accounted for 76% and 83% of the diversity in the three-year and six-month-old flooded fields, respectively. In contrast, water birds accounted for 0% (three-year) and 27% (six-month) of the diversity in the two unflooded fields. There were significant linear relationships between the dependent variables (BSD) and on water depth, light intensity, plant height, and vegetation density, respectively. The strength of the relationships accrued in descending order. Although vegetation density was the best predictor of community BSD, aquatic bird diversity was predicted by percent of area flooded, and water depth. The prediction that the presence of water increases BSD was corroborated.

## INTRODUCTION

Community ecologists focus on deciphering patterns that characterize natural assemblages of species, elucidating causal agents of these patterns, and demonstrating their generality in nature (Wiens 1983). Bird community structure is a reflection of habitat selection (Lack 1937; Hilden 1965) because most birds have specific requirements for feeding, courting, mating, reproduction, and other important survival activities. Many avian species do so with such specificity that their presence in a particular habitat makes them useful indicators of environmental change. The juxtaposition of various habitat types is dictated by varying combinations of overlapping gradients of abiotic factors. These factors include topography, soil mineral content, pH, soil type, and moisture regimes, which in turn affect the patchy

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distribution of vegetation. Vegetation, standing and running water, and topography produce the kind of habitat patchiness which is most apparent to us. They add dimension and variety to the landscape. These landscape components are the substrate on which terrestrial and aquatic birds act out their ecological roles.

Habitat structure has long been shown to be a major determinant of bird community structure because bird species diversity (BSD) tends to increase as a function of vegetation complexity (MacArthur & MacArthur 1961; Karr & Roth 1971; Wiens 1974; Willson 1974; Roth 1979; Wiens 1983). However, variability in BSD/habitat relationships cannot be explained by vegetation complexity alone (Roth 1977; Karr 1983; Osborne et al. 1983; Wiens 1983). I attempted to elucidate other factors influencing avian community structure in flooded and unflooded fallow ricefields in Guyana, South America, from January to March 1984. The bleak economic conditions gripping third world countries made it possible to conduct this comparative study because marginal agricultural lands were removed and continue to be removed from production. I was especially interested in testing Karr's (1968) prediction that the presence of water increases bird diversity. I also wanted to demonstrate that ecological and recreational values are enhanced by allowing succession to proceed on marginal, inundated agricultural lands.

#### STUDY SITES

Field work was conducted at four 2 ha locations on coastal Guyana at Turkeyen ( $6^{\circ} 49'N$ ,  $58^{\circ} 8'W$ ) and neighboring Cumming's Lodge about 6.4 km east of Georgetown, the capital (Figure 1). These sites are on

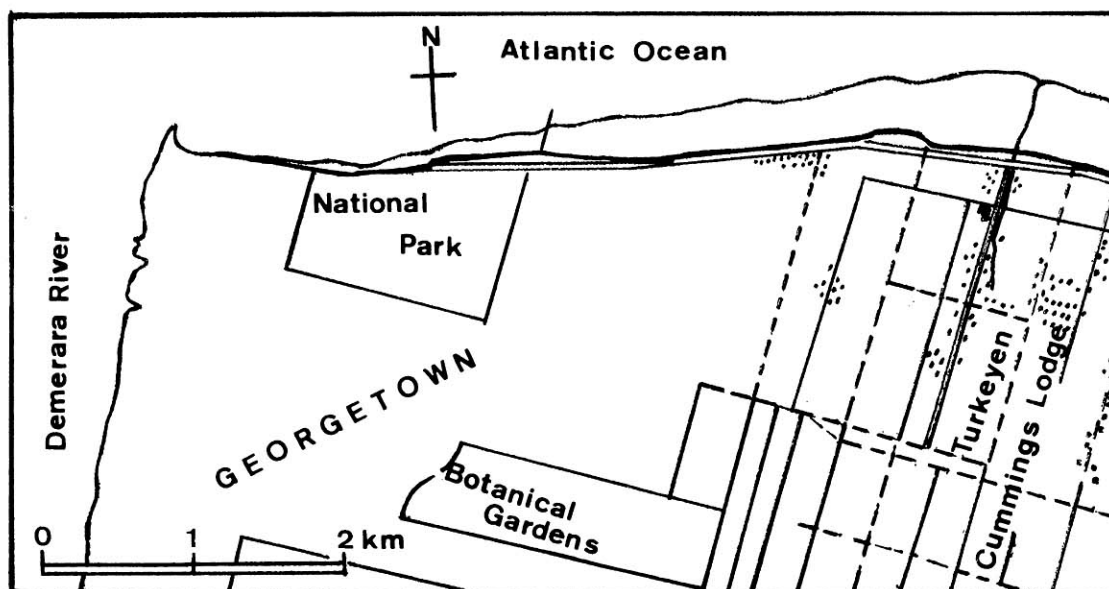


Figure 1. Northern Guyana showing the locations of Turkeyen and Cumming's Lodge. After the Directorate of Overseas Surveys, Fifth Edition, sheets (20/NE, 21/NW), 1965).

the eroded coastal flood plain with several drainage canals dissecting the landscape. These canals discharge water into the Atlantic Ocean to the north. Annual precipitation exceeds 2,250 mm (Giglioli 1959), but during my sampling period only 201 mm of rainfall fell during the three months. Mean yearly temperature is 27° C, while mean annual relative humidity is 82% (Giglioli 1959). Detailed descriptions of geology, flora and fauna of Guyana's coast are available in Harrison et al. (1913), Pain (1950), Snyder (1966), and Poonai (1970).

## MATERIAL AND METHODS

### Habitat Sampling

Two three-year, and two six-month-old 2 ha fallow fields were sampled to obtain quantitative estimates of five habitat variables. One of each field age class was flooded and one was unflooded. Each 2 ha sample plot was part of the interior of larger fields. This was done to minimize the influence of edge effect. A modification of the point quadrat random sampling method (Wiens 1968) was utilized along transects established at 50 m intervals. Twenty-five samples were taken in each field.

Three random numbers were used to locate the sample units (Wiens 1969). The first random number indicated how far (in meters) to travel along a transect. The second was used to determine the side of the transect to sample. Thus, when this number ended with an odd digit, I worked on the left of the transect, and when it ended in an even digit, I sampled the right side. The third random number dictated the distance to travel perpendicular to the transect to locate the sample unit (Wiens 1969).

After sample units were located, a 1 m<sup>2</sup> quadrat was lowered into place. A 2.5 m long metal rod 4.5 mm in diameter, marked at 100 mm intervals was placed vertically into the vegetation, 30 mm in from each corner of the quadrat. At each point, I recorded the presence or absence of each vegetation physiognomic type, i.e. (1) gramoid or narrow leaf herbaceous plants; (2) forb or broad leaf herbaceous plants; (3) woody vegetation; and (4) no vegetation present. The number of contacts of vegetation at each 100 mm height increment was recorded to quantify vegetation density (complexity) (Wiens 1969). Plant heights and water depths were also recorded at each point.

Vertical light penetration (footcandles) were recorded as an index of vegetation density. Sampling was done between 1030 and 1330 hours (Guyana Standard Time), to ensure some verticality in light penetration (Wiens 1969). Readings were made above the vegetation (open sky) and at 200 mm above ground level, or just above the water surface when the 100 mm marker was submerged. These data were converted to percent open-sky intensity.

## Bird Census, Foraging Guild Construction and Diversity

In order to evaluate the influence of habitat structure on avian community composition, I conducted transect counts of all diurnal year-round resident birds utilizing the fields between sunrise and 0930 hours. Counts were made twice weekly from January to March 1984.

Each bird species was assigned to a foraging guild consisting of a three digit number (ABC). This is a modification of Willson's (1974) scheme to better represent tropical conditions as follows: A. PRIMARY FOOD HABITS: 1. frugivore, 2. granivore, 3. insectivore, 4. omnivore, 5. nectivore, 6. carnivore, 7. scavenger. B. FORAGING SUBSTRATE: 1. ground, 2. low plant elevation (0-1 m), 3. middle elevation (1-6 m), 4. high elevation (> 6 m), 5. bark, 6. flower, 7. termitorium, 8. water, 9. air. C. FORAGING BEHAVIOR: 1. ground peck, 2. foliage glean, 3. flower probe, 4. mud probe, 5. bark drill, 6. dabble, 7. sally, 8. dive, 9. strike.

The Shannon-Wiener function (Shannon & Weaver 1949) was calculated to estimate BSD ( $H'_S$ ), and foraging guild diversity ( $H'_{FG}$ ):

$$H'_S = - \sum_{i=1}^S p_i \log_n p_i$$

where  $H'_S$  is the amount of diversity in a group of S species of  $H'_{FG}$  is the diversity of a sample of foraging guild types; S is the number of species;  $p_i$  is the fraction of the whole sample composed of species i, n is the base of logarithm used (here it is the natural logarithm or base e).

A separate diversity index was calculated for all birds that used water as their foraging substrate (water birds), i.e., birds with eight as the middle digit of their foraging guild number (see Appendix). The diversity of these water birds ( $H'_{WB}$ ) was compared to community BSD to evaluate the importance of water in structuring avian communities in fallow ricefields (see Osborne et al. 1983).

## RESULTS

### Habitat Structure

Both flooded fields were dominated by gramoid vegetation which comprised 69% cover in the three-year-old, and 78% in the six-month-old field. Forbs contributed 17% and 12%, while woody vegetation accounted for 6% and 2%, respectively. Eight percent of each field was unvegetated. Unflooded fields were also dominated by gramoids, which contributed 62% cover in the three-year-old and 78% in the six-month-

old fields. Forbs provided 12% and 10%, woody plants covered 23% and 4%, and 3% and 8% was without vegetation in these two unflooded fields, respectively. Gramoid forms appeared to become less dominant in the three-year-old fields, being replaced by forbs and woody vegetation, especially in the unflooded field.

**Table 1.** Measurements (mean  $\pm$  one standard deviation) of habitat characteristics for four fallow 2 ha ricefields on coastal Guyana, January-March 1984.

Parameter	Sites			
	3-YR F <sup>1</sup>	3-YR D <sup>2</sup>	6-MTH F <sup>1</sup>	6-MTH D <sup>2</sup>
Water Depth (mm)	200 $\pm$ 173	5 $\pm$ 12	109 $\pm$ 70	4 $\pm$ 10
Plant Height (mm)	760 $\pm$ 378	530 $\pm$ 286	309 $\pm$ 210	206 $\pm$ 278
Vegetation Density (contacts/100 mm)	6 $\pm$ 2	4 $\pm$ 3	3 $\pm$ 3	1 $\pm$ 2
Light Intensity (% open sky)	57 $\pm$ 24	54 $\pm$ 22	74 $\pm$ 16	84 $\pm$ 16
Percent Flooded	80 $\pm$ 5	15 $\pm$ 2	86 $\pm$ 3	14 $\pm$ 1

<sup>1</sup>Flooded

<sup>2</sup>Unflooded

Qualitatively, all of the sites looked different, and these differences were reflected in quantitative measurements (Table 1). Comparisons of mean water depth indicated significant differences among sites ( $P < 0.01$ , Mann-Whitney U Test), except for the comparison between the three-year- and six-month-old unflooded fields [ $P = 0.89$ , Mann-Whitney U Test (Table 1)]. Comparisons of plant height at all sites (Table 1) showed significant differences ( $P < 0.01$ , Mann-Whitney U Test). Light intensity (Table 1) comparisons indicated differences among the three-year-old flooded, and six-month-old flooded and unflooded fields, and three-year-old unflooded and six-month-old flooded and unflooded fields ( $P \leq 0.05$ , Mann-Whitney U Test). There were no differences between the two three-year-old fields [ $P = 0.18$ , Mann-Whitney U Test (Table 1)]. Comparisons of vegetation density (Table 1) indicated no significant differences except for that between the three-year-old flooded and six-month-old dry fields ( $P < 0.05$ , Mann-Whitney U Test). Finally, comparisons of percent area flooded (Table 1) indicated significant differences for the three-year- and six-month-old flooded fields contrasted with the two unflooded fields ( $P < 0.01$ , Mann-Whitney U Test).

## Bird Community Structure and Organization

The qualitative and quantitative habitat differences in the four fields (Table 1) were reflected in differences in bird community structure and organization (Table 2).

Table 2. Bird community characteristics of four fallow 2 ha ricefields on coastal Guyana, January-March 1984.

Parameter	Sites			
	3-YR F <sup>1</sup>	3-YR D <sup>2</sup>	6-MTH F <sup>1</sup>	6-MTH D <sup>2</sup>
Species Richness	33	27	20	11
Guilds	18	16	13	7
Individuals	273	180	180	159
H'S	3.1	2.8	2.8	2.2
H'FG	3.8	3.6	3.1	2.2
H'WB	2.4	0	2.3	0.6

<sup>1</sup>Flooded

<sup>2</sup>Unflooded

There were significant statistical differences in avian community composition for all sites in terms of species richness and number of individuals [ $P < 0.05$ , Mann-Whitney U Test (Table 2)], except for the comparison between three-year-old dry and six-month flooded fields. Also, there were no differences in the number of guilds (Table 2) for comparisons between three-year-old flooded and unflooded fields, three-year- and six-month-old flooded fields, and three-year-old dry and six-month-old flooded fields ( $P > 0.05$ , Mann-Whitney U Test). However, significant differences existed between three-year-old flooded and six-month-old dry fields, three-year- and six-month-old dry fields, and between the two six-month-old fields ( $P < 0.05$ , Mann-Whitney U Test).

All sites had relatively high BSDs and foraging guild diversities with both three-year-old fields having the highest indices (Table 2). It is notable that the six-month-old flooded field had the same BSD as the three-year-old unflooded field, but a lower foraging guild diversity index (Table 2). Birds that used water as their foraging substrate accounted for most of the diversity of the two flooded fields (Table 2). Water birds contributed 76% and 83% of the diversity for the three-year- and six-month-old flooded fields respectively, but



contributed 0% and 27% to the community diversity of the three-year- and six-month-old unflooded fields (Table 2).

Analysis of the ability of habitat parameters to predict three bird species diversity indices indicated that water depth, light intensity, plant height, and especially vegetation density were good predictors of community BSD (Table 3). The best predictors of bird foraging guild diversity were plant height, vegetation density, and light intensity, while water depth and percent area flooded predicted water bird diversity (Table 3).

Table 3. Regressions of three bird species diversity indices on habitat characteristics on coastal Guyana, January-March 1984.

Diversity Index on Habitat Parameters		$r^2$	$y=ax+b$
$H_S^1$	Water Depth	0.55*	$y=0.003 \cdot x + 2.47$
	Plant Height	0.85*	$y=0.001 \cdot x + 2.07$
	Vegetation Density	0.96*	$y=0.177 \cdot x + 2.08$
	Light Intensity	0.76*	$y=-0.023 \cdot x + 4.23$
	Percent Flooded	0.36	$y=0.006 \cdot x + 2.43$
$H_{FG}^1$	Water Depth	0.33	$y=0.004 \cdot x + 2.83$
	Plant Height	0.83*	$y=0.003 \cdot x + 2.00$
	Vegetation Density	0.90*	$y=0.327 \cdot x + 2.03$
	Light Intensity	0.90*	$y=0.048 \cdot x + 6.38$
	Percent Flooded	0.19	$y=0.008 \cdot x + 2.80$
$H_{WB}^1$	Water Depth	0.83*	$y=0.012 \cdot x + 0.40$
	Plant Height	0.09	$y=0.002 \cdot x + 0.66$
	Vegetation Density	0.20	$y=0.258 \cdot x + 0.42$
	Light Intensity	0.0004	$y=0.002 \cdot x + 1.22$
	Percent Flooded	0.94*	$y=0.030 \cdot x + 0.12$

\*Significant at  $P < 0.05$

## DISCUSSION

In this study birds preferred the inundated fallow fields irrespective of the time elapsed since last cultivation. The three-year-old flooded field had 18% more species, 22% more guilds, and 34% more individuals than the three-year-old dry field. Similarly, the six-month-old flooded field was occupied by 45% more species, supported 46% more guilds, and 12% more individuals than its unflooded counterpart. Furthermore, the three-year-old unflooded field with its significantly greater vegetational complexity supported 26% more species and 7% more guilds, but exhibited no differences in the number of individuals or

community BSD, compared to the six-month-old inundated field. Thus, Karr's (1968) prediction that the presence of water increases avian species diversity is supported.

Only one BSD data set is known for tropical wetlands. BSD in the three-year-old flooded field was 3.1 and is similar to the 3.2 recorded for a 1.3 ha two-year-old fallow ricefield censused by me during 1974 and reported in Osborne et al. (1983). However, the latter index included a southern migrant, the Forked-tailed Flycatcher (Muscivora tyrannus), while the present index consists of data on year-round residents. Although Wiens (1983) cautions about the pitfalls of comparing BSDs from different geographical localities, it is interesting to note that the unflooded three-year-old field had a similar BSD (2.6) as African grasslands (Karr 1976). The general pattern of biotic diversity being higher in the tropics holds since BSDs measured during this study exceed those (1.5-1.6) reported for temperate North (Wiens 1969) and South American (0.7-1.3) grasslands (Cody 1966). Tropical moist forest have the highest avian species diversity indices, but they are not much higher than the estimates for tropical fallow wetlands in this study. For example, Howell (1971) recorded a BSD of 3.6 in Nicaragua, Karr (1971) 3.7, and Karr and Roth (1971) 3.5 in Panama, and Lovejoy (1974) recorded 3.9 in Belem, Brazil.

There were qualitative differences in guild structure of the aquatic bird communities occupying the three-year- and six-month-old flooded fields. Open habitat shorebirds (Scolopacidae) occupied the six-month field and were not found in the three-year-old field. Both wet habitats shared several species of herons (Ardeidae), Snail Kites (Rostrhamus sociabilis) and Limpkins (Aramus guarauna) among others. Herons have food preferences that include fish, frogs and tadpoles, while kites and Limpkins specialize on apple snails (Pomacea dolioides). These food habits suggest that standing water enhances avian community diversity by providing access to additional aquatic food resources not available in the two unflooded habitats.

Other species found mostly in the three-year-old fields prefer to build their nests over water (Haverschmidt 1968). These species include the Pale-breasted Spinetail (Synallaxis albens), Yellow-throated Spinetail (Certhiaxis cinnamomea), Pied Water-Tyrant (Fluvicola pica), and White-headed Marsh-Tyrant (Arundicola leucocephala). A total of 22 individuals of the aforementioned species occupied the three-year-old field, and only five Pied Water-Tyrants lived in the six-month-old wet field. These findings suggest that all of the above species except Pied Water-Tyrants require some vegetational complexity. It also seems reasonable to conclude that water may provide relatively safer nesting sites not available in similarly structured but dry habitats.

Wetlands provide considerable amounts of animal protein for human consumption, particularly in Guyana. I have observed hundreds of people harvesting birds, including herons, whistling ducks, Limpkins, Purple Gallinules, Wattled Jacanas, shore birds, and Red-breasted



Blackbirds, in addition to several fish species, apple snails, and fresh water shrimp from inundated fallow ricefields. This role is critical because increasing numbers of Guyanese do not have the economic resources to obtain protein from the marketplace. By allowing marginal agricultural lands on coastal Guyana to undergo ecological succession, human survival, ecological and recreational values can be enhanced.

In North America and elsewhere, modifications of the methods described in this study could prove useful for obtaining quick evaluations of the functioning of the relatively few remaining but imperiled wetlands.

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# APPENDIX

Bird Species, their foraging guild numbers and sites on coastal Guyana, January-March 1984.

Species	Foraging Guild	Site
Striated Heron	<u>Butorides striatus</u> 689 3-YR F <sup>2</sup>	6-MTH F <sup>2</sup>
Little Blue Heron	<u>Florida caerula</u> 689 3-YR F	
Cattle Egret	<u>Bubulcus ibis</u> 329 3-YR F	6-MTH D <sup>3</sup> 6-MTH F 6-MTH D <sup>3</sup>
Great Egret	<u>Casmerodius albus</u> 689 3-YR F	6-MTH F
Snowy Egret	<u>Egretta thula</u> 689 3-YR F	6-MTH F
Tricolored Heron	<u>Hydranassa tricolor</u> 689 3-YR F	6-MTH F
Bl.-cr. Night-Heron	<u>Nycticorax nycticorax</u> 689 3-YR F	
B.B. Whist. Duck	<u>D. autumnalis</u> 286 3-YR F	6-MTH F 6-MTH D
Black Vulture	<u>Coragyps atratus</u> 711	3-YR D
Ylw.-hd. Vulture	<u>Cathartes Burrovianus</u> 711	3-YR D
Snail Kite	<u>Rostrhamus sociabilis</u> 688 3-YR F	6-MTH F
White-Tailed Hawk	<u>Buteo albicaudatus</u> 618	6-MTH F
Gray Hawk	<u>Buteo nitidus</u> 618	3-YR D
Savana Hawk	<u>H. meridionalis</u> 618	3-YR D
Long-wing. Harrier	<u>Circus buffoni</u> 618 3-YR F	
Ylw.-hd. Caracara	<u>Milvago chimachima</u> 618	3-YR D
Crested Caracara	<u>Polyborus plancus</u> 711 3-YR F	3-YR D 6-MTH F 6-MTH D
Limpkin	<u>Aramus guarauna</u> 484 3-YR F	6-MTH F
Purple Gallinule	<u>Porphyryla martinica</u> 482 3-YR F	
Wattle Jacana	<u>Jacana jacana</u> 482 3-YR F	3-YR D 6-MTH F 6-MTH D
Southern Lapwing	<u>Vanellus chilensis</u> 481	6-MTH F
Solitary Sandpiper	<u>Tringa solitaria</u> 484	6-MTH F
Greater Yellowlegs	<u>Tringa melandleuca</u> 484	6-MTH F
Spotted Sandpiper	<u>Actitis macularia</u> 481	6-MTH F
Common Stilt	<u>H. himantopus</u> 384 3-HR F	6-MTH F

Eared Dove	<u>Zenaida</u>						
	<u>auriculata</u>	211				6-MTH D	
Ruddy	<u>Columbina</u>						
Grnd.-Dove	<u>talpacoti</u>	211				6-MTH D	
Br.-thr.	<u>Aratinga</u>						
Parakeet	<u>pertinax</u>	132		3-YR D			
Smooth-Bil.Ani	<u>crotophaga ani</u>	312	3-YR F	3-YR D			
Striped Cuckoo	<u>Tapera naevia</u>	322	3-YR F	3-YR D			
Bl.-throated							
Mango	<u>A. nigricollis</u>	523		3-YR D			
Wh.-tail.	<u>Polytmus</u>						
Gldthroat	<u>guainumbi</u>	523	3-YR F	3-YR D			
Pale-br.	<u>Synallaxis</u>						
Spinetail	<u>albescens</u>	322	3-YR F	3-YR D			
Ylw.-thr.	<u>Certhiaixis</u>						
Spinetail	<u>cinnamomea</u>	312	3-YR F	3-YR D			
Pied Water-							
Tyrant	<u>Fluvicola pica</u>	322	3-YR F	3-YR D	6-MTH F		
Wh.-hd.							
Marsh-Tyr.	<u>A. leucocephala</u>	382	3-YR F				
Tropical	<u>T.</u>						
Kingbird	<u>melancholicus</u>	437	3-YR F	3-YR D			
Rust-mgd.	<u>Myiozetetes</u>						
Flcatcher	<u>cayanensis</u>	322	3-YR F	3-YR D			
Great	<u>Pitangus</u>						
Kiskadee	<u>sulphuratus</u>	432	3-YR F	3-YR D			
Cm. Tody-	<u>Todirostrum</u>						
Flcatcher	<u>cinereum</u>	432	3-YR F	3-YR D			
Ylw.-bellied	<u>Elaenia</u>						
Elaenia	<u>Flavogaster</u>	337	3-YR F	3-YR D			
Shiny Cowbird	<u>Molothrus</u>						
	<u>bonariensis</u>	411	3-YR F				
Carib Grackle	<u>Quiscalus</u>						
	<u>lugubris</u>	411	3-YR F	3-YR D	6-MTH F	6-MTH D	
Ylw.-hooded	<u>Agelaius</u>						
Blbird	<u>icterocephalus</u>	411	3-YR F				
Yellow Oriole	<u>Icterus</u>						
	<u>nigrogularis</u>	432		3-YR D			
Red-br.	<u>Leistes</u>						
Blackbird	<u>militaris</u>	411	3-YR F	3-YR D		6-MTH D	
Red-capped	<u>Paroaria</u>						
Cardinal	<u>gularis</u>	222		3-YR D			
Blue-bl.	<u>Volatina</u>						
Grassquit	<u>jacarina</u>	222	3-YR F	3-YR D	6-MTH F	6-MTH D	
Variable	<u>Sporophila</u>						
Seed eater	<u>americana</u>	222				6-MTH D	
Ruddy-br.							
Seed eater	<u>S. minuta</u>	222	3-YR F	3-YR D	6-MTH	F6-	
MTH D							

<sup>1</sup>English and scientific names taken from Meyer de Schauensee (1966)

<sup>2</sup>Flooded

<sup>3</sup>Dry