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THE AVIAN COMMUNITY STRUCTURE OF A BOLIVIAN SAVANNA ON THE EDGE OF THE CERRADO SYSTEM

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ABSTRACT. The avian community structure of a Bolivian savanna on the edge of the Cerrado ecosystem was studied during August and September 1994, using line-transects. The avifauna of two habitats, wet campo and dense campo, is described in detail. A third habitat, wooded savanna, is identified, but only briefly described due to limited survey effort. The diversity of these habitats is compared to data from other tropical studies. Areas of wet campo contained the greatest density of birds, but were characterized by a relatively simple bird community, formed primarily of granivorous, ground-gleaning species. Dense campo habitats, characterised by greater vegetation cover, supported a higher diversity of foraging guilds, including frugivores, insectivores and omnivores, exhibiting a variety of foraging strata and behaviours. Consequently, this habitat contained the greatest number of species. Bird species diversity was therefore related to vegetation structure and niche availability.
Key words: Avifauna, Bolivia, Cerrado, Diversity, Foraging guild, Savanna.

Estructura de la comunidad de aves de una sabana boliviana al borde del ecosistema del Cerrado.

RESUMEN: Se estudió la estructura de una comunidad de aves en una sabana boliviana al borde del Cerrado, entre Agosto y septiembre de 1994, usando transectas de línea.La avifauna de dos hábitats, llamados campo húmedo y campo denso, se describe en detalle. Se identificó un tercer hábitat, la sabana arbolada, pero sólo se describe brevemente. La diversidad de los hábitats se comparó con otros sitios tropicales. Las áreas de campo húmedo tuvieron la mayor densidad de aves, pero en una comunidad relativamente simple, formada principalmente por granívoros que forrajeban en el suelo. El campo denso, con una mayor cobertura vegetal, tuvo mas diversidad de gremios de forrajeo, incluyendo frugívoros, insectívoros y omnívoros, los que mostraron variadas conductas y sitios de alimentación. Consecuentemente este hábitat contuvo el mayor número de especies. La diversidad de aves estuvo correlacionada con la estructura de la vegetación y abundancia de nichos.
Palabras clave: avifauna, Bolivia, cerrado, diversidad, gremios tróficos, sabana.

INTRODUCTION

The Cerrado ecosystem covers 1.8 million km^2 of central Brazil and extreme eastern Bolivia (Cavalcanti 1988), and includes a wide range of habitats (Goodland 1971; Eiten 1978). Many bird species are surprisingly local (Haffer 1985), and Cracraft (1985) outlines the region as an area of endemism. This is one of the most endangered environments in South America (Cavalcanti 1988; Ridgely and Tudor 1989) and a wide range of cerrado birds are of conservation concern (Collar et al. 1994; Stotz et al. 1996). It is therefore important to collect quantitative information regarding the composition of cerrado avian communities.

The methods for analysing community characteristics are well established (Shannon and Weaver 1949; Pielou 1966), and a number of studies have been conducted in the tropics. Typically, areas of forest contain the greatest avian diversity (cf. Tramer 1969; Karr 1971; Terborgh & Weske 1969), whilst grassland and savanna habitats support fewer species (cf. Krueger and Johnson 1996; Karr 1976; Howell 1971), due to the lack of vegetation height and habitat homogeneity (Willson 1974). Indeed, the richness of grassland bird communities is a function of habitat diversity (Cody 1981), with vegetation height, density and structure the most important factors regulating avian distribution (Cody 1968; Karr and Roth 1971; Folse 1982).

This paper summarises the results of five weeks of avian surveys of a seasonally inundated savanna

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on the western edge of the cerrado ecosystem. The composition of bird communities in separate habitats is compared, and differences related to foliage density and food availability.

METHODS AND MATERIALS

The work was undertaken at Los Fierros (14°30' S, 61°10' W) in the Noel Kempff Mercado National Park, Santa Cruz Department, Bolivia. The National Park contains some of the largest remaining areas of pristine campo and cerrado habitats (Bates et al. 1992), including Los Fierros, a 200 km² area of seasonally inundated termite mound savanna surrounded by lowland tropical forest.

The study area, encompassing the northern quarter of the savanna, was composed of three distinct habitats. The most widespread was wet campo, consisting of short (< 50 cm tall) grass with occasional herbaceous plants. Shrubs and small trees formed clusters around termite mounds. More heavily vegetated areas were labelled dense campo. Characterized by a proliferant ground flora of grass and herbaceous plants, with widespread bushes and small trees, the structure of this habitat approached that of campo cerrado (cf. Goodland 1971). Finally, patches of cerrado woodland and forest islands, collectively termed wooded savanna, covered a small area. Fire damage had defoliated shrubs and trees in some parts of this habitat. To provide some measure of vegetation structure, foliage density was quantified in each habitat using 100 randomly positioned quadrats, 4 m² in area. Percentage vegetation cover within the quadrats was estimated at half-metre height intervals, as measured by eye.

Between 20 August and 26 September 1994, transects spaced at 500 m intervals were used to survey the avifauna. Each transect was walked once by two observers between the hours of 06:00 and 09:30, at a speed of approximately 1 km hr^{-1} for 2.4 to 4 km, as measured by pacing. All birds within 20 m of the transect were recorded (Pommeroy 1991). In total, 25 transects were censused, covering 79.6 km, of which 54 % was in wet campo, 40 % in dense campo and 6 % in wooded savanna.

Individual transects contained different proportions of each habitat, and so cannot be regarded as replicates. Consequently, data for each habitat was pooled across transects. Sightings from line-transects were used to calculate avian diversity for each habitat using the Shannon-Wiener function ($H' = -\sum^{s} p_i \ln p_i$), where s is the number of categories, and pi is the proportion of observations in the ith category (Shannon and Weaver 1949). Two measures of the evenness of distribution of abundance were also calculated for each habitat; (J' = H'/H max) (Pielou 1966) a widely used index, but one with limitations (James et al. 1981), and Alatalo's modified Hill's ratio ($F_{2,1} = (N_2 - 1) / (N_1 - 1)$, where $N_2 = 1/\sum p_i^2$, and $N_1 = \exp H'$) as calibrated by Molinari (1989). Relative abundance curves were also used to describe graphically the evenness in wet campo and dense campo habitats (James et al. 1981). Due to the small size of the sample from wooded savanna, this habitat was not considered further in the statistical analysis. To compare the diversity scores between wet campo and dense campo, the data was artificially split into 5 km lengths of transect for each habitat, providing 8 and 6 replicates respectively. An independent samples t-test was used to compare the difference between the two mean values. All analysis was conducted using MEGA-STATS (M. Hounsome, Manchester University 1992).

Accumulative abundance curves were modelled for both wet campo and dense campo habitats, using logarithmic curves. These curves allow species richness in the two habitats to be compared, irrespective of survey effort, by extrapolation to a constant end point.

The main foraging guild of each species, at the time of the study, was determined from field observations and published data (cf. Isler and Isler 1987; Ridgely and Tudor 1989, 1994; Davis 1993; Sick 1993). These were categorized into three components; primary food habits: (1) frugivore, (2) granivore, (3) insectivore, (4) omnivore, (5) nectivore, (6) carnivore; most commonly used stratum: (1) ground, (2) low (0 - 1 m) vegetation, (3) middle (1 - 6 m) vegetation, (4) high (> 6 m) vegetation, (5) air; and foraging behaviour: (1) ground-glean, (2) foliage-glean, (3) bark-glean, (4) flower-probe, (5) sally, (6) aerial-sweep, (7) strike. From these components, each species was given a three-digit number representing the foraging guild to which it had been assigned (adapted from Willson 1974; Osborne et al. 1983).

RESULTS

A total of 62 bird species were recorded from line-transects. These are listed in Appendix 1, giving the number of sightings of each species in each habitat. Cryptic species may have been under-recorded. Caprimulgidae, *Chaetura spp. and Elaenia spp.* have each been treated as one group because of identification difficulties. This may result in a slight under-estimate of diversity. In addition, the abundance of *Sporophila spp.* which formed extensive mixed flocks composed primarily of birds in unidentifiable 'female-type' plumage, was calculated from the pro-

portions of males identified in each habitat (see Pearce-Higgins 1996).

Table 1 summarises the community characteristics of each habitat. The community with the greatest diversity was dense campo, followed by wooded savanna, and finally wet campo, although the latter habitat supported a greater density of birds. The diversity of the wet campo and dense campo communities differed significantly ($t = -3.828$, $df = 12$, $p = 0.002$). The accumulative abundance curves presented in Figure 1, further illustrate this pattern of community shallower in the dense campo habitat. The wet campo avifauna was indeed dominated by a small number of species, with the three most abundant comprising 62.6 % of the birds seen (*Volatinia jacarina* 33.2 %, *Sporophila ruficollis* 18.2 % and *Leistes superciliaris* 11.2 %). The equivalent species from the dense campo community constituted 42.7 % of the birds seen (*Schistochlamys melanopis* 18.4 %, *Streptoprocne zonaris* 14.1 % and *Elaenia spp.* 10.2 %).

These patterns of abundance can be related to foliage density, used as an indication of habitat structu-

Table 1. Avian community characteristics of the three habitats surveyed at Los Fierros, assessed using line-transects.

Variables	Wet campo	Dense campo	Wooded savanna
Transect length (km.)	43.3	31.7	4.6
Transect area (ha)	173.2	126.8	18.4
Total no. species seen	36	49	16
Total no. birds seen	1328	537	27
Bird density (birds/ha)	7.67	4.24	1.47
Species diversity (H')	2.26	3.08	2.67
Evenness of abundance (J')	0.63	0.79	0.96
Calibration of Alatalo's index (G 2,1)	0.18	0.47	0.73

species diversity (dense campo, regression, $R^2 = 95.9$ %, $n = 32$, $t = 26.599$, $p < 0.001$; wet campo, regression, $R^2 = 95.5$ %, $n = 43$, $t = 29.101$, $p < 0.001$). Dense campo, with an expected end point of 51 species after 43 km of transects had a higher species diversity than wet campo (37 species), for the same survey effort. Data was insufficient to model diversity in wooded savanna habitats in this way.

The reasons for this clear pattern in diversity are given by the indices measuring evenness of abundance (J', G 2,1) (Table 1). A low value, approaching zero, indicates that a community is dominated by a small number of very common species, as seen in the wet campo avifauna, whereas the higher values for dense campo and especially wooded savanna demonstrate a more even distribution of abundance across the species, and consequently a greater community diversity. This is illustrated by the relative abundance curves presented for wet campo and dense campo habitats in Figure 2. Although both habitats contained a small number of common species, the decline in abundance from common to rare species is re (Figure 3). Areas of dense campo contained a vigorous ground layer and many small shrubs, providing a high foliage density at low levels. In contrast, quadrats in wet campo often contained sparsely vegetated ground, with an impoverished flora. The habitat with the greatest foliage density was therefore dense campo, and supported the richest bird community, whilst areas of wet campo, with the lowest density of foliage, had the least diverse avifauna.

Figure 4 summarises the occurrence of foraging guilds in each habitat, from the number of individuals seen. Areas of wet campo were dominated by granivorous, ground-feeding, ground-gleaning birds, of which 9 species were recorded. Although sixteen insectivorous species were seen, primarily low and mid-level foliage gleaners, none were particularly abundant. In contrast, the dense campo community consisted primarily of insectivorous, aerial-sweepers (6 species) and mid-level salliers (6 species), with a large component of omnivorous, mid-level foliage-gleaners (4 species). Five species of high-level, foliage-gleaning frugivores were also frequent.

Figure 1. Fitted accumulative abundance curves for wet campo(broken line) and dense campo (solid line) habitats, modelling the increases in the number of species recorded with transect distance. The raw data are plotted (triangles, wet campo; circles, dense campo) to demonstrate the goodness of fit for each curve. Values of B (regression coefficient) are also given.

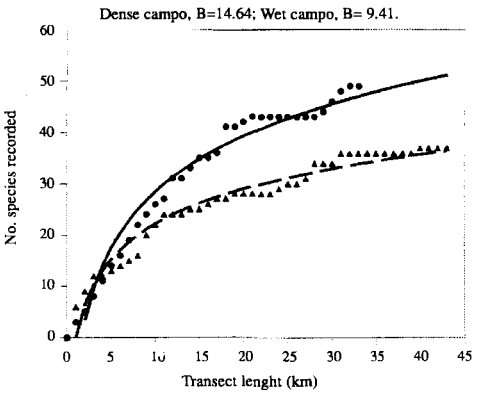


Figure 3. Lineal profile of foliage density in wet campo (broken line) and dense campo (solid line) habitats.Vegetation density was assessed at half-metre height intervals using 100 quadrats in each habitat.

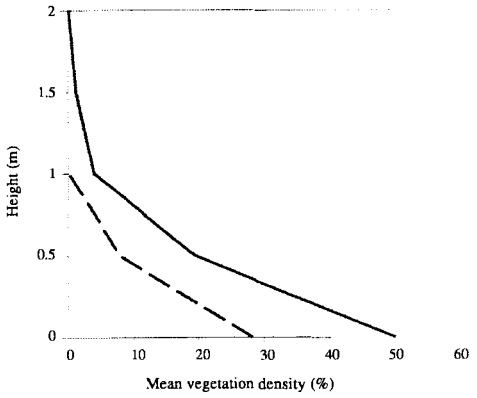


Figure 2. Relative abundance curves for wet campo (triangles) and dense campo (circles). Log percentage composition is plotted for each species in rank order. The stepness of the relationship indicates the evenness of the community, with steep declines in abundance indicative of a community dominated by few species.

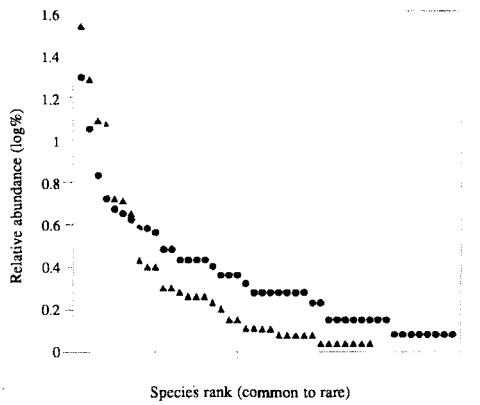
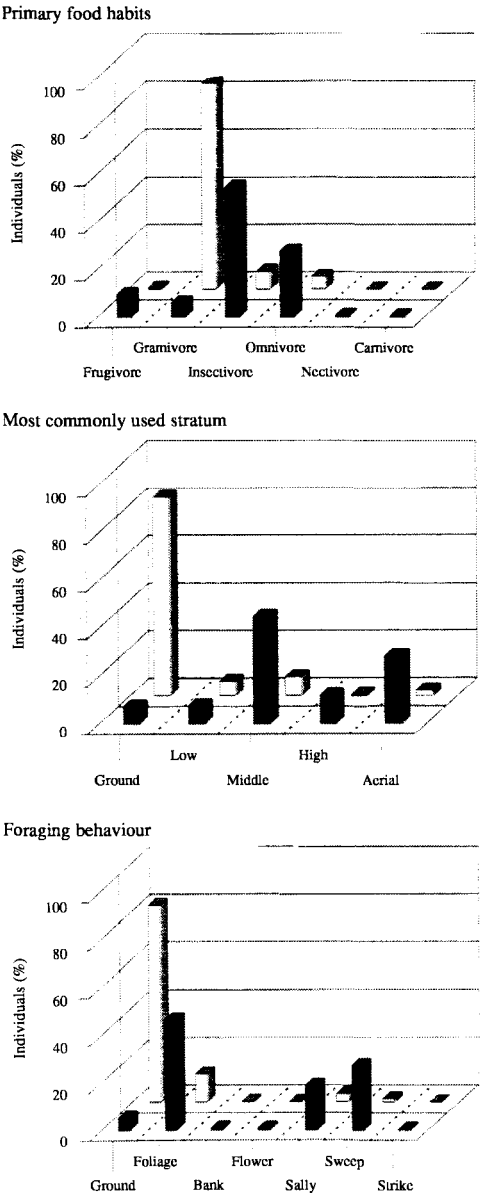


Figure 4. A description of the avian community structure of each habitat at Los Fierros, using foraging guilds. Species were allocated to a particular guild and community composition calculated from the number of individuals in each guild recorded from a particular habitat.



DISCUSSION

Although this analysis is not a complete account of the avifauna of Los Fierros, being based on just 38 days of research during August and September, it does provide a quantitative description of the bird communities surveyed. Consequently, it is possible to compare the diversity scores from this study, with

other published figures, thus providing an indication of the diversity of cerrado habitats. Certainly the wet campo habitat (H' = 2.26) appears more diverse than Puerto Rican grassland habitats (H' = 0.51 - 2.17) and Panamanian grassland areas (H' = 0.76 - 1.85. McArthur et al. 1966), but slightly less so than African tropical grasslands, (H' = 2.63. Karr 1976). Savanna converted to rice production in Guyana yielded figures of H' = 3.22 and J' = 0.94 (Osborne et al. 1983), although the community was enhanced by the presence of water. The diversity of dense campo (H' = 3.08) was similar to that of secondary growth in Peru (H' = 3.08. Terborgh and Weske 1969), bush grassland (H' = 3.09) and wooded grassland (H' = 2.95) in Uganda (Krueger and Johnson 1996), although greater than scrub in Puerto Rico (H' = 1.95) and Panama (H' = 2.43. MacArthur et al. 1966). Another study of Panamanian shrubland produced scores of H' = 3.46 - 3.73 (Karr and Roth 1971). The diversity of wooded savanna was lower than most of these values for tropical scrub and wooded grassland, although this may have been due to limited sample effort.

The importance of vegetation height, plant biomass and percentage cover in regulating avian distribution and diversity has long been recognized (MacArthur 1964; Willson 1974; Cody 1981; Folse 1982), and is further supported by this study. A comparison between wet campo, a relatively homogeneous and open habitat and dense campo, with a more varied and dense vegetation structure has shown marked divisions in the composition of the savanna avifauna. Despite bird density being highest in wet campo areas, bird species diversity was greatest in dense campo. This pattern reflects the number of species recorded in different habitats at Concepción, Bolivia, by Davis (1993), who found scrub-like habitats to have the highest diversity, with more open areas and wooded savanna, supporting fewer species.

The importance of the contrasting habitats for different species was highlighted by the analysis of guild structure. Extensive flocks of *Columbina spp.*, Emberizidae and *Leistes superciliaris* foraged on the abundant grass seed in wet campo areas, and produced the high bird density. Consequently, the wet campo community was composed primarily of granivorous, ground gleaning species (guild 211). Similarly, Davis (1993) found open areas of disturbed cerrado to support more granivorous species than dense cerrado. Seed availability was much reduced in other habitats (see Pearce-Higgins 1996), where fruit and insect prey were probably more abundant, due to the density of shrubs and small trees. Consequently, large numbers of frugivorous, insectivorous and omnivorous species were supported by dense campo. The greater availability of middle and high level vegetation layers allowed a broader range of niches to be exploited; for example, insectivorous, mid-level, salliers (guild 335) including *Elaenia spp., Pyrocephalus rubinus* and *Tyrannus melancholicus*; omnivorous, mid-level, foliage-gleaners (guild 432) such as *Crotophaga ani, Turdus amaurochalinus* and *Schistochlamys melanopis*; and frugivorous, high-level, foliage-gleaners (guild 142) like *Columba cayennensis, Amazona aestiva* and *Amazona ochrocephala.* Many insectivorous, aerial sweepers (guild 356) such as Caprimulgidae, Apodidae and Hirundinidae also preyed on the abundant insects. Furthermore, the availability of cover in dense campo was potentially important to species such as *Crypturellus parvirostris* and *Formicivora rufa.* Although little sampled, it appears that the community structure of wooded savanna was similar to that of dense campo, but perhaps with a greater emphasis on ground foragers, such as Tinamidae and *Melanopareia torquata,* and high-level frugivores. Mid-level foragers were less frequent, possibly as a result of the partially defoliated shrub layer, although sample sizes are small. Differences in bird diversity between the three habitats can therefore be related to the abundance of individual species, influenced by niche availability in each habitat.

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Appendix 1. The number of birds recorded from line-transects in each habitat. Transect lengths were as follows: wet campo, 43.3 km; dense campo, 31.7 km; wooded savanna, 4.6 km. Foraging guilds are also given for each species seen: primary food habits, (1) frugivore, (2) granivore, (3) insectivore, (4) omnivore, (5) nectivore, (6) carnivore; most commonly used stratum: (1) ground, (2) low (0 - 1 m) vegetation, (3) middle (1 - 6 m) vegetation, (4) high (> 6 m) vegetation, (5) air; foraging behaviour: (1) ground-glean, (2) foliage-glean, (3) bark-glean, (4) flower-probe, (5) sally, (6) aerial-sweep, (7) strike.

Species or family	Guild	Wet campo	Dense campo	Wooded savanna	Total
Crypturellus parvirostris	412	4	5	3	12
Rhynchotus rufescens	412	1		1	2
Cathartes aura	611	1	1		2

Species or family	Guild	Wet campo	Dense campo	Wooded savanna	Total
Gampsonyx swainsonii	617		1		1
Buterogallus meridionalis	617	1			1
Caracara plancus	611		1		1
Micropygia schomburgkii	311	2			2
Columba speciosa	142			1	1
Columba cayennensis	142	5	23		28
Columbina minuta	211	19			19
Columbina talpacoti	211	10		1	11
Aratinga leucophthalmus	142		2		2
Amazona aestiva	142		10		10
Amazona ochrocephala	142		15	2	17
Crotophaga ani	432		6		6
Bubo virginianus	617		1		1
Caprimulgidae unknown	356		7	3	10
Streptoprocne zonaris	356		76		76
Chaetura spp.	356		20		20
Tachornis squamata	356		3		3
Trochilidae unknown	534		3		3
Heliactin cornuta	534	1	1		2
Chelidoptera tenebrosa	345		1		1
Ramphastos toco	142	2	2	1	5
Dryocopus lineatus	333			1	1
Lepidocolaptes angustirostris	333	4	5		9
Synallaxis albescens	322	13	5		18
Thamnophilus doliatus	322		9		9
Formicivora rufa	322		7	2	9
Melanopareia torquata	312	4	2	3	9
Suiriri suiriri	335	3	5		8
Elaenia spp.	335	20	55	2	77
Euscarthmus meloryphus	322	1			1
Tyrannulet unknown	332	1			1
Pyrocephalus rubinus	335	12	17		29
Xolmis cinerea	355	3	2	1	6
Tyrannus melancholicus	335	1	15	1	17
Tyrannus savana	355	10	4		14
Megarynchus pitangua	335		1	1	2
Myiodynastes maculatus	335		1	2	3
Cyclarhis gujanensis	332		2		2
Turdus amaurochalinus	432	2	19		21
Mimus saturninus	311	4	9		13
Troglodytes aedon	322	5	5		10
Polioptila dumicola	332		2		2
Tachycineta leucorrhoa	356	8	7		15
Progne chalybea	356	9	31		40
Hirundo rustica	356		2		2
Parula pitiayumi	343		2		2
Ammodramus humeralis	211	23	1		24
Schistochlamys melanopis	432	47	99	2	148
Cypsnagra hirundinacea	432	13	11		24
Thraupis sayaca	442		5		5
Emberizoides herbicola	222	58	14		72

Species or family	Guild	Wet campo	Dense campo	Wooded savanna	Total
Volatinia jacarina	211	440	5		445
Sporophila caerulescens	222		1		1
Sporophila nigrorufa	211	11			11
Sporophila hypoxantha	211	143			143
Sporophila ruficollis	211	241	12		253
Sporophila hypochroma	211	55			55
Icterus cayanensis	442		4		4
Leistes superciliaris	211	148			148
TOTAL		1328	537	27	1892