



Estimation of the Food Consumption of Fish-Eating Birds in the Seasonally-Flooded Savannas (Llanos) of Alto Apure, Venezuela

by

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Presented by K. PETRUSEWICZ on July 14, 1979

Summary. The study was carried out in savannas of south-western Venezuela (7 20 N, 69° 15' W). It was found that the density of fish-eating birds during the dry season (December–April) in managed savannas, where the water level is raised and many small artificial ponds (so-called prestamos) are created, is twice as high as in the natural savannas (Table I). In the rainy season (May–November), the fish-eating birds catch 10–25 kg fish per ha and 12–60 kg/ha in the dry season in the managed savannas (Table II). From the artificial water ponds (prestamos) formed in the areas where earth was taken to build dikes, these birds catch 18–500 kg/ha of fish, depending on fish densities, the dry season (Table III). The deepest ponds, never drying out (category III), have the highest fish densities (1279 kg/ha), and about one-third of the fish population is caught by birds. From shallower ponds (categories II and I), drying out during the dry season and with a smaller fish density, even all fish can be taken by the birds. Herons, storks and cormorants are the most important fish consumers in managed savannas (Figs 1 and 2).

The purpose of the present study was to determine the potential impact of birds on fishes in seasonally-flooded tropical savannas under managed conditions.

The study area is located in the so-called low llanos of south-western Venezuela, in the State of Apure near the small town of Mantecal (lat. 7 20' N, long. 69 15' W and altitude 74–79 m a.s.l.). The terrain is extremely flat with a slight slope of 0.02‰ to the east. The landscape is a mosaic of three physiographic units called: (1) “banco” (gallery forest along the rivers or isolated woodplots, 1 to 2 m higher than the surrounding areas and not normally inundated)—covering 29‰ of the region of Mantecal; (2) “bajío” (low, flat and wide plain covered with semi-aquatic grasses under water during the rainy season)—covering 44‰ of the region, and (3) “estero” (shallow and wide temporary ponds)—covering 27‰ of the region [8]. Alternation of dry (December–April) and rainy season (May–November) and high constant temperature (mean temperature 26.6 C) are the most important

features of the climate [12]. In order to lessen seasonal variation in water conditions, a water control system was developed [1, 9]. It consists of a network of dikes that divide the terrain into isolated areas of approximately 4000 ha each. One of them was selected as the study area and named Modulo Experimental. Due to the natural slope, rain water accumulates in the lower section, which is used as a reservoir for the dry season, whereas the higher side is not flooded. In managed savannas the inundation was deeper and longer-lasting than on "natural" savannas [8]. Besides natural ponds, or "esteros", artificial ponds, or "prestamos", were formed where earth was taken to build the dikes. By the end of the dry season, water remained only in the deeper esteros and prestamos.

The study was conducted from December 1975 to May 1979 in the Modulo Experimental. Birds were censused from a car driven at constant speed along an 11.8 km census strip. Censuses were conducted twice per day (morning and afternoon) once or twice a month. All birds within 200 m on each side of the census belt were counted. Prestamos, esteros, bajios and bancos occurred on both sides of the census road. The area of every prestamo included in the census belt was measured. The prestamos were divided into three categories depending on how long the water remained during the dry season (I completely dry in February-March; II partly but never completely dry; III deep and full of water at the end of dry season). On one side of the census road there were the managed savannas (Modulo Experimental) and on the other the "natural", not managed savannas.

The consumption of birds was estimated by computing the existence metabolism (M) from the regression $M = a + bt$ (p. 201) [6], where $a = 4.142 W^{0.5444}$ (p. 143, regression No. 5.35) [6]; $b = 0.2761 W^{0.2818}$ (p. 141, regression No. 5.21) [6]. Weight (W) of birds was obtained from the study area and from literature. The average monthly temperatures from Mantecal were used as the t values. We obtained the daily energy budget from regression No. 5.67 (p. 181) [6]. The digestibility index of 85% was used for most fish-eating birds [3]. For *Mycteria americana*, we used digestibility index of 79% [5]. Caloric content of food (fresh fish) was estimated to be 1.1 Kcal/g [3, 5]. In this way we estimated the birds' daily consumption under the climatic conditions of the study area. The energy cost of egg production was added to the daily consumption of *M. americana*, *Casmerodius albus* and *Ardea cocoi*, using regression No. 5.52 (p. 166) [6]. For estimating food consumed by nestlings we used the data from Tomlinson [11] for *C. albus*, from Junor [4] for *A. cocoi* (data for nestling of *A. cinerea* No. 586-07748), and from Kahl [5] for *M. americana*. Per cent of total food consumed composed of fishes was from the literature and our own observations. From March to October 1978 we made 39 hours of observations of feeding herons and storks. We used field glasses (50 × 10, 50 × 12, 50 × 40) to categorize and estimate the size of prey.

Results

Population densities. Among 187 species of birds so far reported from the study area, at least 25 are fish-eating. In this paper we analyse the 20 most common species. In general, fishes are more important as food for aquatic birds in the tropics than in temperate regions [10]. The population density of most species of fish-eating birds was higher on managed than on "natural" savannas, especially during the dry season (Table I). The differences were greatest for storks, *M. americana*, as well as *Egretta thula* feed in open water while other storks and herons feed in wet meadows (bajio), the edges of esteros and prestamos, all these biotope being more widespread in the dry season on managed savannas than on the "natural" ones. Only Kingfishers, Darters and *Anhinga anhinga* had higher densities on "natural" savannas than on managed savannas. Most species of fish-eating birds were more common during the dry season than during the rain season both on managed and on "natural" savannas. However, the most common species, *C. albus*, was more abundant in the rainy season, perhaps because of its breeding phenology (Table I). During the dry season managed savannas attracted fish-eating birds from other areas which did not offer suitable feeding grounds.

Consumption of fishes by birds in all biotopes. Rainy season. During the rainy season 90% of the entire census belt was flooded, therefore we increased by about 10% the amount of fishes eaten by birds per 1 ha of census belt covered by water. During the peak of the rainy season a maximum of 2417 ha of the Modulo Experimental was covered with water. The consumption of fishes by birds during the rainy season on the managed side of the census belt was 26.2 kg/ha in 1976 and 11.6 kg/ha in 1978 (Table II). Therefore, the consumption of fishes by birds on the entire surface of Modulo Experimental during the rainy season was $26.2 \times 2417 = 63325$ kg in 1976 and $11.6 \times 2417 = 28037$ kg in 1978.

The most common and, therefore, the most important fish-eating bird during the rainy season was *C. albus* which in both years (1976, 1978) ate more than 50% of the fish consumed by birds (Fig. 1). After the breeding season, during August, September and October, flocks of hundreds of young birds of this species fed on Modulo Experimental. *Phalacrocorax olivaceus* and *Anhinga anhinga* were fishing almost exclusively on both sides of the sluice gate. When the sluice gate was open, as much as 200 kg fishes per night escaped from Modulo Experimental [2]. According to rough estimates, *A. anhinga* and *P. olivaceus* caught 3382 kg of fishes in 1976 and 1262 in 1978 on both sides of gate during the rainy season.

In this season, birds were catching fish when the water level was decreasing, which was directly related to precipitation, evaporation and water manipulation by man (opening or closing the sluice gate). The water level

TABLE I

The average yearly density of the birds (individuals/km²) calculated from monthly densities (December 1975 to November 1978) along the entire census belt

Species	Dry period Dec-Apr			Rainy period May-Nov			"natural"	managed
	savanna		managed	savanna		managed	dry	dry
	"natural"	managed	"natural"	"natural"	managed	"natural"	rainy	rainy
	$\bar{x} \pm S.D.$	$\bar{x} \pm S.D.$		$\bar{x} \pm S.D.$	$\bar{x} \pm S.D.$			
<i>Jabiru mycteria</i> (Licht.)	0.1 ± 0.3	0.6 ± 2.4	6.0	1.9 ± 5.2	1.6 ± 4.3	0.8	0.1	0.4
<i>Euxenura maguari</i> (Gmel.)	0.4 ± 0.4	1.6 ± 3.1	4.0	2.4 ± 2.7	1.7 ± 2.0	0.7	0.2	1.0
<i>Mycteria americana</i> L.	2.6 ± 7.6	9.9 ± 21.8	3.8	1.8 ± 3.7	5.6 ± 1.6	3.4	1.4	1.7
<i>Egretta thula</i> (Molina)	4.5 ± 4.2	15.3 ± 24.7	3.4	1.9 ± 1.9	7.9 ± 23.8	4.1	2.3	1.9
<i>Florida caerulea</i> (L.)	5.9 ± 10.1	19.0 ± 25.8	3.2	3.0 ± 6.8	3.0 ± 3.0	1.0	1.9	6.3
<i>Tigrisoma lineatum</i> Bodd.	3.7 ± 3.1	10.4 ± 16.4	2.8	1.1 ± 1.2	1.3 ± 2.1	1.1	3.4	8.0
<i>Ardea cocoi</i> L.	4.5 ± 2.7	9.8 ± 10.1	2.2	5.9 ± 7.8	6.9 ± 9.3	1.2	0.7	1.4
<i>Casmerodius albus</i> (L.)	12.6 ± 11.4	25.7 ± 17.0	2.0	23.8 ± 21.7	47.6 ± 86.1	2.0	0.5	0.5
<i>Butorides striatus</i> (L.)	5.4 ± 8.7	10.9 ± 12.1	2.0	1.9 ± 2.2	1.6 ± 1.8	0.8	2.8	6.9
<i>Rynchops nigra</i> L.	0.05 ± 0.1	0.1 ± 0.3	2.0	2.3 ± 0.5	0.0	—	0.02	—
<i>Sterna + Phetusa</i>	1.3 ± 1.8	2.0 ± 1.8	1.5	0.0	2.3 ± 0.7	—	—	0.8
<i>Phalacrocorax olivaceus</i> Humb.	4.5 ± 4.5	5.4 ± 7.6	1.2	3.1 ± 3.6	1.5 ± 1.8	0.5	1.4	3.6
<i>Nycticorax nycticorax</i> (L.)	4.9 ± 5.7	5.7 ± 5.1	1.1	2.1 ± 4.1	2.0 ± 2.9	0.9	2.3	2.8
<i>Chloroceryle americana</i> (Gm.)	3.7 ± 0.7	4.2 ± 1.1	1.1	0.1 ± 1.1	0.1 ± 0.2	1.0	37.0	42.0
<i>Ajaia ajaja</i> (L.)	4.6 ± 6.0	4.2 ± 6.5	0.9	1.3 ± 2.2	0.9 ± 1.9	0.8	3.6	4.6
<i>Anhinga anhinga</i> (L.)	3.4 ± 4.9	2.5 ± 3.4	0.7	8.2 ± 2.3	1.6 ± 1.8	0.2	0.4	0.3
<i>Chloroceryle aenea</i> (Pallas)	0.3 ± 0.6	0.1 ± 0.1	0.3	0.0	0.03 ± 0.1	—	—	3.3
<i>Ceryle torquata</i> (L.)	0.6 ± 0.8	0.06 ± 0.1	0.1	0.3 ± 0.4	1.0 ± 0.2	3.3	2.0	0.1
<i>Busarellus nigricollis</i> (Lath.)	0.3 ± 0.7	0.06 ± 0.2	0.02	0.02 ± 0.06	0.0	—	15.0	—
	$\bar{x} = 2.1 \pm 1.7$			$P < 0.001$			$\bar{x} = 1.2 \pm 1.0$	

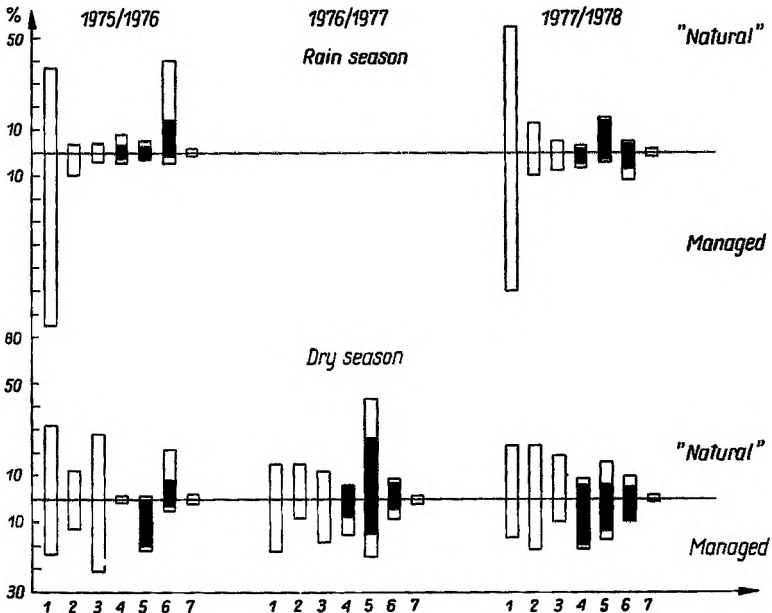


Fig. 1. Per cent (%) of consumption of fishes (fresh weight) by various species of birds in the entire census belt, on the "natural" and managed sides (Modulo Experimental)

1—*Casmerodius albus*; 2—*Ardea cocoi*; 3—*Egretta thula*, *Florida caerulea*, *Nycticorax nycticorax*, *Tigrisoma lineatum*, *Butorides striatus*; 4—*Euxenura maguari* (shaded); *Jariba myceteria*; 5—*Mycteria americana* (shaded), *Ajaja ajaja*; 6—*Phalacrocorax olivaceus* (shaded); *Anhinga anhinga*; 7—*Sterna superciliosa*, *Phaethusa simplex*, *Chloroceryle americana*, *C. h. aenea*, *Ceryle torquata*, *Busarellus nigricollis*

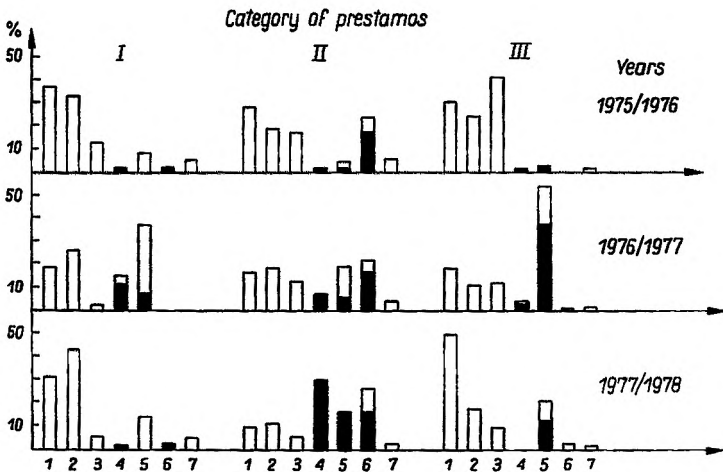


Fig. 2. Per cent (%) of consumption of fishes (fresh weight) by various species of birds on prestamos during the dry season (December–April)

For the key to the species of birds see explanations to Fig. 1

decrease usually begins in September-October when the birds can easily catch fishes on shallow esteros and bajios.

Dry season. At the end of the dry season, less than 50% of the census belt is under water. For this reason we doubled the number of fishes caught by birds on 1 ha of the entire census belt (Table II). During the dry season managed savannas were attractive feeding ground for all species of herons, storks, cormorants, darters, terns, skimmers and kingfishers (Table I, Fig. 1).

At the end of the dry season water covered only 320.0 ha of the area of Modulo Experimental. The consumption of fishes by birds during the dry season of 1975/76 was 59.6 kg/ha (see Table II). i.e. $59.6 \times 320.0 = 19072$ kg in 1975/76 for the total surface of Modulo Experimental. Calculating in the same way for 1976/77 and 1977/78 we obtained 13606 kg and 6464 kg, respectively. This means that the number of kilograms of fishes eaten by birds in the dry season on the entire surface of Modulo Experimental is 4.3-4.5 that in the rainy season.

Consumption of fishes by birds on selected biotope: prestamos. The amount of fishes caught by birds during the dry season in prestamos was directly linked with the biomass of fishes living there.*) Standing crop of biomass

TABLE II

Total consumption of fishes by birds (kg/ha) on census belt covered with water data for the entire census belt in parentheses. For explanations see text

Biotopes	Years	1975/1976	1976/1977	1977/1978
Managed savanna	Rainy season	26.2 (23.6)	-	11.6 (10.4)
"Natural" savanna	(May-November)	14.7 (13.2)	-	20.4 (18.4)
Managed savanna	Dry season	59.6 (29.8)	42.8 (21.4)	20.2 (10.1)
"Natural" savanna	(December-April)	25.8 (12.9)	23.8 (11.9)	12.0 (6.0)

TABLE III

Consumption of fishes by birds during the dry season on prestamos (kg/ha)

Category of <i>prestamos</i>	Years		
	1975/1976	1976/1977	1977/1978
I	30.2	40.2	18.2
II	52.3	49.0	78.9
III	491.2	404.7	247.3

*) During the rainy season prestamos are too deep for herons and storks to feed.

of fishes was in February 1977 1279 kg/ha for prestamos of category III and a dozen or so for category I [2]. The most common fish-eating birds on prestamos category I (shallow, completely drying in mid-dry season without bushes and trees) were *C. albus*, *A. cocoi* and in 1976/77 also *Ajaia ajaja* (Fig. 2). On intermediate prestamos (category II) other herons were also common in addition to the above-mentioned species. The sluice gate is situated in the area of prestamos of category II, and so, in this area, *P. olivaceous* and *A. anhinga* were common, feeding exclusively near the sluice gate (see above). In 1977/78, on prestamos category II storks were also important predators of fishes (Fig. 2). The prestamos of category III, deepest and richest in fishes, were in 1975/76 almost exclusively feeding places for herons. However, in the following year *M. americana* and *A. ajaja* also fed there (Fig. 2). The fish consumption by birds in prestamos category III was about 10 times greater than in poor, completely drying prestamos of category I ($P < 0.05$, Table III). In prestamos of category III the birds were catching about 32% of the biomass of fishes during the dry season of 1977. The standing crop of fishes at prestamos of category III was as high as 1279 kg ha in February [2] and consumption of fishes by birds was 404.7 kg ha (see Table III), i.e. $404.7 / 1279.0 \times 100 = 31.6\%$. In prestamos of category II and especially of category I, the pressure of birds on fishes can be higher and birds can kill nearly 100% of the fishes. We observed many times big flocks containing hundreds of fish-eating birds on drying prestamos and esteros. The killing of up to 90% of the standing stock of fish by the birds in a drying pond can save the rest of fishes from death by asphyxiation [7].

The sharp decrease of fish consumption by birds in the 1977/78 dry season and in 1978 was connected with the drainage of almost all water through the gate and the consequent general drying of all of the Modulo Experimental which caused a reduction of fish stock (Tables II, III). The prestamos of category II were situated outside of the Modulo Experimental. According to visual observations, the most common prey of birds among big fishes were: *Gymnotus carapo* (L.), *Serrasalmus notatus* (Lütken) and *Hoplias malabricus* (Bloch).

In summary, we can conclude that under conditions of managed savannas (llanos), birds can be an important factor in controlling the levels of fish populations.

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Я. Пиновски, Л. Г. Моралес, Н. Пачеко, К. А. Добровольски, Б. Пиновска, **Определение величины потребления пищи рыбоядными птицами на временно заливных саваннах (Льянос) в район Альто Апуре (Венесуэла)**

Установлено, что в юго-восточной части Венесуэлы (7 20' И, 69 15') после повышения уровня воды и создания множества новых мелких водохранилищ (т. наз. престамо) плотность рыбоядных птиц на мелиорированных саваннах оказалась вдвое больше чем на естественных (Таблица I). Рыбоядные птицы на мелиорированных саваннах в дождливое время года (май-ноябрь) добывают от 10 до 25 кг/гектар рыбы, а в сухое время от 12 до 60 кг/гектар (Таблица II). Из искусственных водоемов, возникших в результате выгребания земли для сооружения дамбы (насыпи) в сухое время птицы добывают от 18 до 500 кг гектар рыбы в зависимости от общего количества рыбы (Таблица III). В крупнейших, никогда не высыхающих водоемах (кат. 3), плотность рыбы самая большая (1279 кг/гектар); из таких именно водоемов птицы потребляют 1/3 всей популяции. Из мелких водохранилищ (кат. 2 и 1) с меньшей численностью рыб и при том высыхающих в сухое время, птицы могут вылавливать даже все рыбы. Цапли, аисты и кормораны являются главными консументами рыбы в условиях исследуемого района (рис. 1, 2).

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The purpose of the present study was to determine the potential impact of birds on fishes in seasonally flooded tropical savannas under managed conditions.

The study area is located in the so-called low llanos of southwestern Venezuela, in the State of Apure near the small town of Mantecal (lat. 7° 20' N, long. 69° 15' W and altitude 74–79 m a.s.l.). The terrain is extremely flat with a slight slope of 0.02% to the east. The landscape is a mosaic of three physiographic units called: (1) “banco” (gallery forest along the rivers or isolated woodplots, 1 to 2 m higher than the surrounding areas and not normally inundated) — covering 29% of the region of Mantecal; (2) “bajío” (low, flat and wide plain covered with semi-aquatic grasses under water during the rainy season) covering 44% of the region; and (3) “estero” (shallow and wide temporary ponds) — covering 27% of the region [8]. Alternation of dry (December–April) and rainy season (May–November) and high constant temperature (mean temperature 26.6°C) are the most important

features of the climate [12]. In order to lessen seasonal variation in water conditions, a water-control system was developed [1.9]. It consists of a network of dikes that divide the terrain into isolated areas of approximately 4000 ha each. One of them was selected as the study area and named *Modulo Experimental*. Due to the natural slope, rainwater accumulates in the lower section, which is used as a reservoir for the dry season, whereas the higher side is not flooded. In managed savannas the inundation was deeper and longer-lasting than on “natural” savannas [8]. Besides natural ponds, or “esteros”, artificial ponds, or “prestamos”, were formed where earth was taken to build the dikes. By the end of the dry season, water remained only in the deeper esteros and prestamos.

The study was conducted from December 1975 to May 1979 in the Modulo Experimental. Birds were censused from a car driven at constant speed along an 11.8-km census strip. Censuses were conducted twice per day (morning and afternoon) once or twice a month. All birds within 200 m of each side of the census belt were counted. Prestamos, esteros, bajios and bancos occurred on both sides of the census road. The area of every prestamo included in the census belt was measured. The prestamos were divided into three categories depending on how long the water remained during the dry season (I: completely dry in February–March: II: partly but never completely dry: III: deep and full of water at the end of dry season). On one side of the census road there were the managed savannas (Modulo Experimental) and on the other the “natural”, not managed savannas.

The consumption of birds was estimated by computing the existence metabolism (M) from the regression $M = a + bt$ (p. 201) [6], where $a = 4.142 W^{0.5444}$ (p. 143, regression No. 5.35) [6]; $b = 0.2761 W^{0.2818}$ (p. 141, regression No. 5.21) [6]. Weight (W) of birds was obtained from the study area and from literature. The average monthly temperatures from Mantecal were used as the t values. We obtained the daily energy budget from regression No. 5.67 (p. 181) [6]. The digestibility index of 85% was used for most fish-eating birds [3]. For *Mycteria americana*, we used digestibility index of 79% [5]. Caloric content of food (fresh fish) was estimated to be 1.1 Kcal/g [3, 5]. In this way we estimated the birds' daily consumption under the climatic conditions of the study area. The energy cost of egg production was added to the daily consumption of *M. americana*, *Casmerodius albus* and *Ardea cocoi*, using regression No. 5.52 (p. 166) [6]. For estimating food consumed by nestlings we used the data from Tomlinson [11] for *C. albus*, from Junor [4] for *A. cocoi* (data for nestling of *A. cinerea* No. 586-07748), and from Kahl [5] for *M. americana*. Percent of total food consumed composed of fishes was from the literature and our own observations. From March to October 1978 we made 39 hours of observations of feeding herons and storks. We used field glasses (50 × 10, 50 × 12, 50 × 40) to categorize and estimate the size of prey.

Results

Population densities. Among 187 species of birds so far reported from the study area, at least 25 are fish-eating. In this paper we analyze the 20 most-common species. In general, fishes are more important as food for aquatic birds in the tropics than in temperate regions [10]. The population density of most species of fish-eating birds was higher on managed than on "natural" savannas, especially during the dry season (Table I). The differences were greatest for storks. *M. americana*, as well as *Egretta thula* feed in open water while other storks and herons feed in wet meadows (bajio), the edges of esteros and prestamos, all these biotope being more widespread in the dry season on managed savannas than on the "natural" ones. Only Kingfishers, Darters and *Ajaia ajaja* had higher densities on "natural" savannas than on managed savannas. Most species of fish-eating birds were more common during the dry season than during the rain season both on managed and on "natural" savannas. However, the most common species, *C. albus*, was more abundant in the rainy season, perhaps because of its breeding phenology (Table I). During the dry season, managed savannas attracted fish-eating birds from other areas which did not offer suitable feeding grounds.

Consumption of fishes by birds in all biotopes. Rainy season. During the rainy season 90% of the entire census belt was flooded; therefore we increased by about 10% the amount of fishes eaten by birds per 1 ha of census belt covered by water. During the peak of the rainy season a maximum of 2417 ha of the Modulo Experimental was covered with water. The consumption of fishes by birds during the rainy season on the managed side of the census belt was 26.2 kg/ha in 1976 and 11.6 kg/ha in 1978 (Table II). Therefore, the consumption of fishes by birds on the entire surface of Modulo Experimental during the rainy season was $26.2 \times 2417 = 63\,325$ kg in 1976 and $11.6 \times 2417 = 28\,037$ kg in 1978.

The most common and, therefore, the most important fish-eating bird during the rainy season was *C. albus*, which in both years (1976, 1978) ate more than 50% of the fish consumed by birds (Fig. 1). After the breeding season, during August, September and October, flocks of hundreds of young birds of this species fed on Modulo Experimental. *Phalacrocorax olivaceus* and *Anhinga anhinga* were fishing almost exclusively on both sides of the sluice gate. When the sluice gate was open, as much as 200 kg fishes per night escaped from Modulo Experimental [2]. According to rough estimates, *A. anhinga* and *P. olivaceus* caught 3382 kg of fishes in 1976 and 1262 in 1978 on both sides of gate during the rainy season.

In this season, birds were catching fish when the water level was decreasing, which was directly related to precipitation, evaporation and water manipulation by man (opening or closing the sluice gate). The water level

TABLE I

The average yearly density of the birds (individuals/km²) calculated from monthly densities (December 1975 to November 1978) along the entire census belt

Species	Dry period Dec–Apr			Rainy period May–Nov			“natural”	managed
	savanna		managed	savanna		managed	dry rainy	dry rainy
	“natural”	managed	“natural”	“natural”	managed	“natural”		
	$x \pm$ S.D.	$x \pm$ S.D.		$x \pm$ S.D.	$x \pm$ S.D.			
<i>Jabiru mycteria</i> (Licht.)	0.1 ± 0.3	0.6 ± 2.4	6.0	1.9 ± 5.2	1.6 ± 4.3	0.8	0.1	0.4
<i>Euxenura maguari</i> (Gmel.)	0.4 ± 0.4	1.6 ± 3.1	4.0	2.4 ± 2.7	1.7 ± 2.0	0.7	0.2	1.0
<i>Mycteria americana</i> L.	2.6 ± 7.6	9.9 ± 21.8	3.8	1.8 ± 3.7	5.6 ± 1.6	3.4	1.4	1.7
<i>Egretta thula</i> (Molina)	4.5 ± 4.2	15.3 ± 24.7	3.4	1.9 ± 1.9	7.9 ± 23.8	4.1	2.3	1.9
<i>Florida caerulea</i> (L.)	5.9 ± 10.1	19.0 ± 25.8	3.2	3.0 ± 6.8	3.0 ± 3.0	1.0	1.9	6.3
<i>Tigrisoma lineatum</i> Bodd.	3.7 ± 3.1	10.4 ± 16.4	2.8	1.1 ± 1.2	1.3 ± 2.1	1.1	3.4	8.0
<i>Ardea cocoi</i> L.	4.5 ± 2.7	9.8 ± 10.1	2.2	5.9 ± 7.8	6.9 ± 9.3	1.2	0.7	1.4
<i>Casmerodius albus</i> (L.)	12.6 ± 11.4	25.7 ± 17.0	2.0	23.8 ± 21.7	47.6 ± 86.1	2.0	0.5	0.5
<i>Butorides striatus</i> (L.)	5.4 ± 8.7	10.9 ± 12.1	2.0	1.9 ± 2.2	1.6 ± 1.8	0.8	2.8	6.9
<i>Rynchops nigra</i> L.	0.05 ± 0.1	0.1 ± 0.3	2.0	2.3 ± 0.5	0.0	—	0.02	—
<i>Sterna + Phaetusa</i>	1.3 ± 1.8	2.0 ± 1.8	1.5	0.0	2.3 ± 0.7	—	—	0.8
<i>Phalacrocorax olivaceus</i> Humb.	4.5 ± 4.5	5.4 ± 7.6	1.2	3.1 ± 3.6	1.5 ± 1.8	0.5	1.4	3.6
<i>Nycticorax nycticorax</i> (L.)	4.9 ± 5.7	5.7 ± 5.1	1.1	2.1 ± 4.1	2.0 ± 2.9	0.9	2.3	2.8
<i>Chloroceryle americana</i> (Gm.)	3.7 ± 0.7	4.2 ± 1.1	1.1	0.1 ± 1.1	0.1 ± 0.2	1.0	37.0	42.0
<i>Ajaia ajaja</i> (L.)	4.6 ± 6.0	4.2 ± 6.5	0.9	1.3 ± 2.2	0.9 ± 1.9	0.8	3.6	4.6
<i>Anhinga anhinga</i> (L.)	3.4 ± 4.9	2.5 ± 3.4	0.7	8.2 ± 2.3	1.6 ± 1.8	0.2	0.4	0.3
<i>Chloroceryle aenea</i> (Pallas)	0.3 ± 0.6	0.1 ± 0.1	0.3	0.0	0.03 ± 0.1	—	—	3.3
<i>Ceryle torquata</i> (L.)	0.6 ± 0.8	0.06 ± 0.1	0.1	0.3 ± 0.4	1.0 ± 0.2	3.3	2.0	0.1
<i>Busarellus nigricollis</i> (Lath.)	0.3 ± 0.7	0.06 ± 0.2	0.02	0.02 ± 0.06	0.0	-	15.0	-
			$x = 2.1 + 1.7$	$P < 0.001$	$x = 1.2 \pm 1.0$			

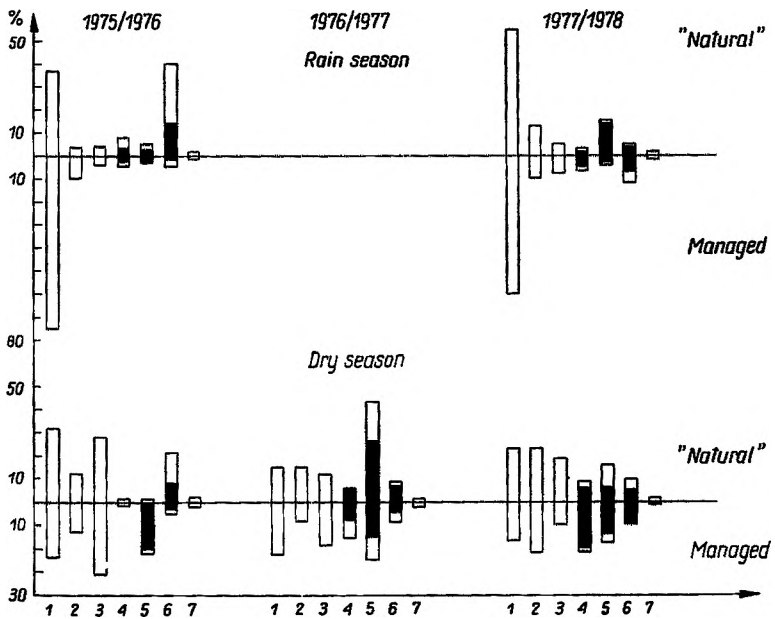


Fig. 1. Percent (%) of consumption of fishes (fresh weight) by various species of birds in the entire census belt, on the "natural" and managed sides (Modulo Experimental)

1 — *Casmerodius albus*; 2 — *Ardea cocoi*; 3 — *Egretta thula*, *Florida caerulea*, *Nycticorax nycticorax*, *Tigrisoma lineatum*, *Butorides striatus*; 4 — *Euxenura maguari* (shaded), *Jabiru mycteria*; 5 — *Mycteria americana* (shaded). *Ajaia ajaja*; 6. *Phalacrocorax olivaceus* (shaded), *Anhinga anhinga*; 7. *Sterna superciliaris*, *Phaetusa simplex*, *Chloroceryle americana*, *Ch. aenea*, *Ceryle torquata*, *Busarellus nigricollis*.

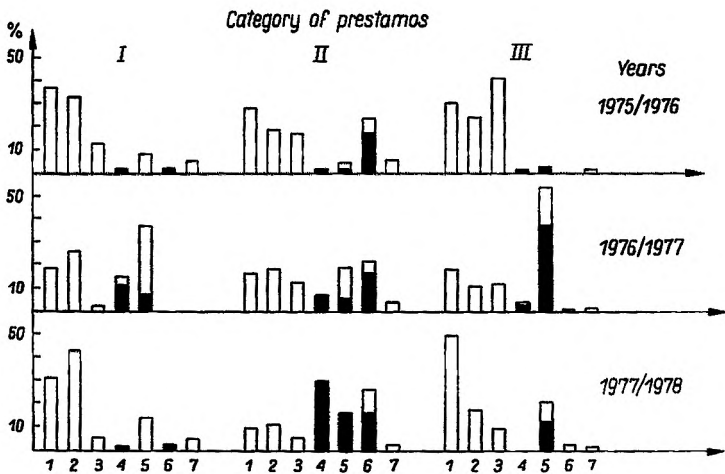


Fig. 2. Percent (%) of consumption of fishes (fresh weight) by various species of birds on prestamos during the dry season (December–April)

For the key to the species of birds see explanations to Fig. 1.

decrease usually begins in September--October when the birds can easily catch fishes on shallow esteros and bajios.

Dry season. At the end of the dry season, less than 50%, of the census belt is under water. For this reason we doubled the number of fishes caught by birds on 1 ha of the entire census belt (Table II). During the dry season managed savannas were attractive feeding ground for all species of herons, storks, cormorants, darters, terns, skimmers and kingfishers (Table I. Fig. 1).

At the end of the dry season water covered only 320.0 ha of the area of Modulo Experimental. The consumption of fishes by birds during the dry season of 1975/76 was 59.6 kg ha (see Table II). i.e. $59.6 \times 320.0 = 19072$ kg in 1975/76 for the total surface of Modulo Experimental. Calculating in the same way for 1976/77 and 1977/78 we obtained 13606 kg and 6464 kg, respectively. This means that the number of kilograms of fishes eaten by birds in the dry season on the entire surface of Modulo Experimental is 4.3-4.5 that in the rainy season.

Consumption of fishes by birds on selected biotope: prestamos. The amount of fishes caught by birds during the dry season in prestamos was directly linked with the biomass of fishes living there. *) Standing crop of biomass

TABLE II

Total consumption of fishes by birds (kg/ha) on census belt covered with water data for the entire census belt in parentheses. For explanations see text

Biotopes	Years	1975/1976	1976/1977	1977/1978
Managed savanna	Rainy season	26.2 (23.6)	-	11.6 (10.4)
"Natural" savanna	(May-November)	14.7 (13.2)	-	20.4 (18.4)
Managed savanna	Dry season	59.6 (29.8)	42.8 (21.4)	20.2 (10.1)
"Natural" savanna	(December -April)	25.8 (12.9)	23.8 (11.9)	12.0 (6.0)

TABLE III

Consumption of fishes by birds during the dry season on prestamos (kg/ha)

Category of <i>prestamos</i>	Years		
	1975/1976	1976/1977	1977/1978
I	30.2	40.2	18.2
II	52.3	49.0	78.9
III	491.2	404.7	247.3

*) During the rainy season prestamos are too deep for herons and storks to feed.

of fishes was in February 1977 1279 kg/ha for prestamos of category III and a dozen or so for category I [2]. The most common fish-eating birds on prestamos category I (shallow, completely drying in mid-dry season without bushes and trees) were *C. albus*, *A. cocoi* and in 1976/77 also *Ajaia ajaja* (Fig. 2). On intermediate prestamos (category II) other herons were also common in addition to the above-mentioned species. The sluice gate is situated in the area of prestamos of category II, and so, in this area, *P. olivaceous* and *A. anhinga* were common, feeding exclusively near the sluice gate (see above). In 1977/78, on prestamos category II, storks were also important predators of fishes (Fig. 2). The prestamos of category III, deepest and richest in fishes, were in 1975/76 almost exclusively feeding places for herons. However, in the following year *M. americana* and *A. ajaja* also fed there (Fig. 2). The fish consumption by birds in prestamos category III was about 10 times greater than in poor, completely drying prestamos of category I ($P < 0.05$, Table III). In prestamos of category III the birds were catching about 32% of the biomass of fishes during the dry season of 1977. The standing crop of fishes at prestamos of category III was as high as 1279 kg ha in February [2] and consumption of fishes by birds was 404.7 kg ha (see Table III), i.e. $404.7/1279.0 \times 100 = 31.6\%$. In prestamos of category II and especially of category I, the pressure of birds on fishes can be higher and birds can kill nearly 100% of the fishes. We observed many times big flocks containing hundreds of fish-eating birds on drying prestamos and esteros. The killing of up to 90% of the standing stock of fish by the birds in a drying pond can save the rest of fishes from death by asphyxiation [7].

The sharp decrease of fish consumption by birds in the 1977/78 dry season and in 1978 was connected with the drainage of almost all water through the gate and the consequent general drying of all of the Modulo Experimental, which caused a reduction of fish stock (Tables II, III). The prestamos of category II were situated outside of the Modulo Experimental. According to visual observations, the most common prey of birds among big fishes were: *Gymnotus carapo* (L.), *Serrasalmus notatus* (Lütken) and *Hoplias malabricus* (Bloch).

In summary, we can conclude that under conditions of managed savannas (llanos), birds can be an important factor in controlling the levels of fish populations.

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