The Auk 111(3):643–651, 1994

ECOLOGY OF THE FOLIVOROUS HOATZIN (*OPISTHOCOMUS HOAZIN*) ON THE VENEZUELAN PLAINS

M. G. DOMÍNGUEZ-BELLO,[1] F. MICHELANGELI,[1] M. C. RUIZ,[1] A. GARCÍA,[1] AND E. RODRÍGUEZ[2]

[1]*Laboratorio de Fisiología Gastrointestinal, Centro de Biofísica y Bioquímica, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; and*
[2]*Laboratory of Phytochemistry and Toxicology, Department of Developmental and Cell Biology, University of California, Irvine, USA*

ABSTRACT.—The Hoatzin (*Opisthocomus hoazin*) is the only avian folivore known to have fermentative digestion in the crop. We compare results on nesting, growth, and feeding in Piñero Ranch, Cojedes State, Venezuela, with results from another location in the Venezuelan plains. The Hoatzin nests in trees abundant in the habitat. Nests containing two eggs were predominant. Growth rate of chicks was linear over the nesting period (5.68 g/day). The diet of the Hoatzin consisted of young leaves and twigs of some of the most abundant trees in its habitat. Although there are no reports on the phytochemistry of dietary plants, families to which these plants belong include plants known to contain secondary compounds. The crop, which functions as a mediator in plant-Hoatzin interactions and as a detoxification chamber, deserves further study. *Received 4 November 1992, accepted 13 November 1993.*

THE HOATZIN (*Opisthocomus hoazin*), a folivorous bird that inhabits riverain forests in South America, is peculiar in many respects. A cooperatively breeding bird, with young having special swimming and climbing abilities (Grimmer 1962), the Hoatzin is the only avian folivore with pre-gastric fermentation (Grajal et al. 1989). The first reports on the Hoatzin date from the 17th century (Hernández 1651, cited by Strahl 1985), but only in the late 19th and early 20th centuries did more precise anatomical descriptions appear (Young 1888, Böker 1929). The claws on the chick wings (Fig. 1), unlike those in other birds, are functional and of high adaptive value for the young. The Hoatzin is the only species in the family Opisthocomidae (Cuculiformes; Sibley et al. 1988).

The Hoatzin nests on branches of trees over water courses, and the incubation of eggs for 30 to 31 days is performed by male and female breeders, and sometimes by nonbreeder helpers of the group (Strahl 1988, Vander Werf and Strahl 1990).

We present results that provide comparative data on ecological aspects (nesting, growth, and diet) relevant to the study of the nutritional strategy of the Hoatzin. Such information provides a basis for physiological and microbiological studies that might clarify the evolution of the Hoatzin's unusual fermentative digestion.

METHODS

Our study was performed at Hato Piñero, a cattle ranch and wildlife reserve in Cojedes State, central Venezuela (Fig. 2). The dominant landscape is open *Trachipogon* savannas, which flood during the rainy season (May–October), and gallery forests along water courses. We divided the study site, San Jerónimo Creek, into northern and southern sections (indicated by a bridge crossing the creek; Fig. 2) because in the southern section the gallery forest has been narrowed by deforestation.

Field observations were made from September through November 1990, during a year with a late-ending rainy season. We conducted a survey along the left shore of the southern section of the creek of the tree species on 48 linear and consecutive 100-m transects (Smith 1974; Fig. 2). Data were used to rank the frequencies of tree species (as percentage of transects containing the trees). An indication of diversity (D) was obtained,

$$D = S/N, \qquad (1)$$

where S is an average number of species found in the transects (sum of transects containing each tree/total number of transects) and N is the total number of species found in all 48 transects (Acevedo 1989).

We conducted a survey of nests along 7 km of the

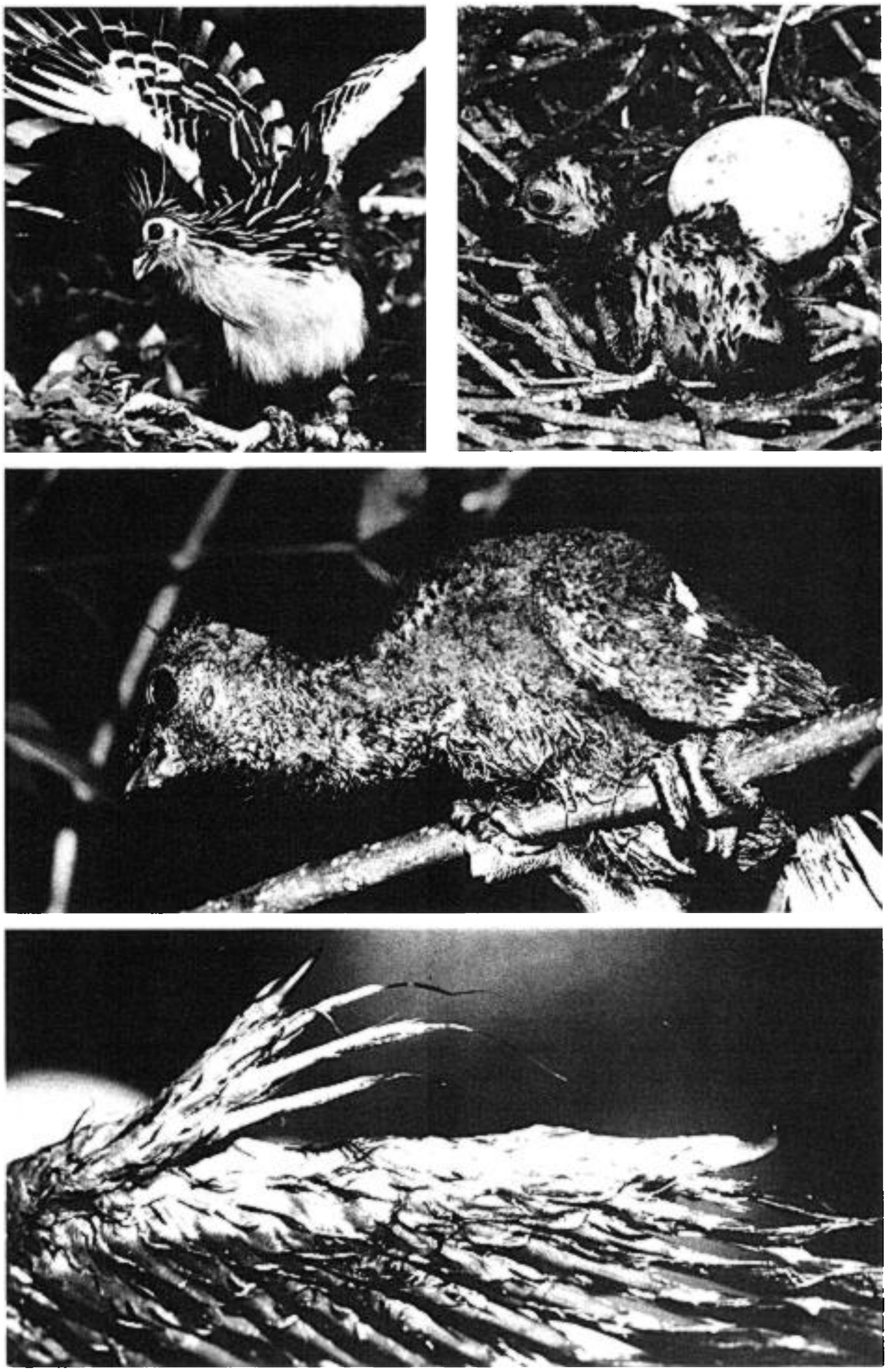

Fig. 1. (Upper left) Hoatzin in the wild, showing nest-defense behavior of adult. (Upper right) Nest of clutch size 2 with a newborn chick and an egg. (Middle) Typical perching posture of chick. (Lower) Wing claws on young.

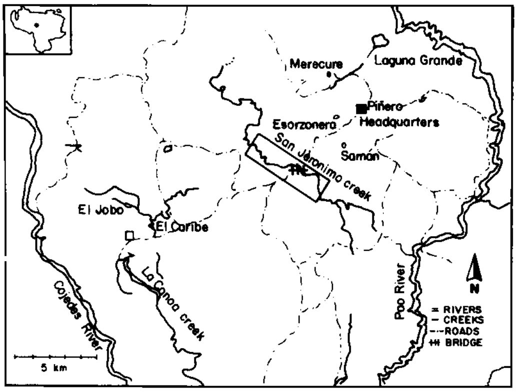

Fig. 2. Map of Piñero Ranch showing study site (in box).

river (both sections of river), recording clutch sizes and the tree species in which nests were located. Nest activity was monitored for the surveyed nests.

Chicks were weighed until such time that we could no longer find the birds in the nests, either due to predation or because the young had fledged. Data of nest height, clutch size, body masses, and growth rate of chicks were compared with results from other studies in a different location of the Venezuelan plains, using a Student's t-test, after testing equality of variances (Montgomery 1976).

During the breeding season, we recorded the tree species used as food by Hoatzins at San Jerónimo Creek and other locations on the Piñero Ranch. We supplemented these data with information gathered during the following dry season.

Results

Nesting.—Along the 4.8 km of transects, 66 tree species were recorded. The first 100 m contained more than 40% of the total species of trees (Fig. 3). Over 90% of tree species were found within 2.5 km, indicating that the transect of 4.8 km was representative of the forest. A minimal sampling-transect length would be about 3 km, after which the curve levels off (Vareschi 1986). Tree diversity (D) was 0.32, which indicates that each transect contained about 29% of total tree species. The relationship between the cumulative percentage of tree species (Y) and length of the transect (X) is multiplicative, and the regression fits the model,

$$Y = aX^b, \qquad (2)$$

with an a (in the log-log equation; Fig. 3) of 74.4 and b of 0.2 (r = 0.98; SE of slope = 0.04).

The main species are listed in Table 1. There

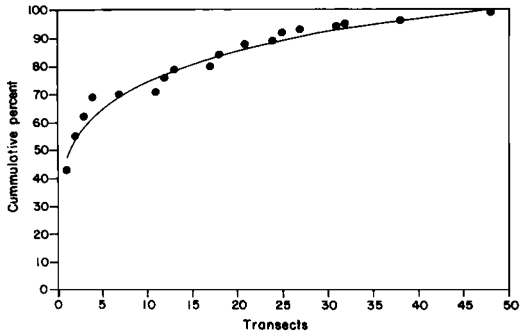

Fig. 3. Cumulative species richness along 100-m transects (n = 48) located along southern section of creek. $Y = 74.4X^{0.2}$ (r = 0.98).

was an exponential relationship between the number of intervals containing a tree species (Y) and the species rank (X). The regression (Fig. 4) fits the model,

$$Y = ab^x, \qquad (3)$$

with an a (in the semilog equation; Fig. 4) of 67.36 and b of 0.94 (r = −0.98; SE of slope = 0.23).

Nests of Hoatzins were found on the most abundant species of trees (Fig. 5). There were 250 nests along the 7 km studied and only about 33% were active (e.g. containing eggs or chicks). We found 1.2 active nests per 100 m. Trees with ranks 3, 7, and 9 (*Machaerium* sp., *Trichilia unifoliata*, and an unidentified Anonaceae, respectively; Table 1) supported over 40% of the nests. The proportion of active nests was higher along the southern section of the creek (Fig. 5; 40.8 vs. 25.4% active nests for southern and northern sections, respectively). In addition, nests from

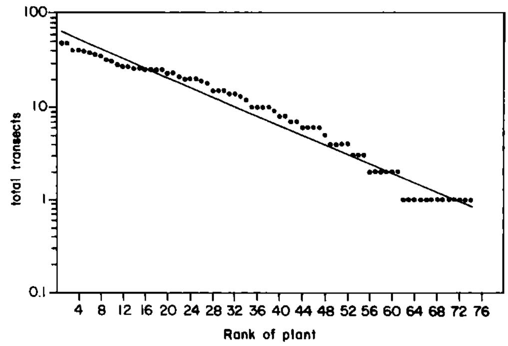

Fig. 4. Frequency of tree species (n = 66) on transects (n = 48). ln Y = 4.22 − 0.06X (r = 0.98). For tree species, see Table 1.

TABLE 1. Tree species found along 4.8 km of transects on southern bank of San Gerónimo Creek, Piñero Ranch, Venzuela.

Rank and frequency (%)[a]	Family	Species	Local name
1 (100.0)	Polygonaceae	*Coccoloba* sp.	Uvero
2 (97.9)	Lecythidaceae	*Lecythis ollaria*	Coco e mono
3 (83.3)	Papilionaceae	*Machaerium* sp.	Menudito
4 (83.3)	Flacourtiaceae	*Caesaria* sp.	Fruto Palomo
5 (81.3)	Sterculiaceae	*Guazuma tormentosa*	Guacimo
6 (79.2)	Cucurbitaceae	*Luffa operculata*	Esponjilla
7 (75.0)	Meliaceae	*Trichilia unifoliata*	Cochinito
8 (72.9)	Leguminosae (Mimosaceae)	*Acacia maracranta*	Cuji
9 (66.7)	Anonaceae	Not identified	Anoncillo
10 (64.6)	Leguminosae (Papilionaceae)	*Pterocarpus* sp.	Drago
11 (58.3)	Combretaceae	*Combretum fructicosum*	Melero
12 (56.3)	Leguminosae (Mimosaceae)	*Pithecellobium ligustrinum*	Orore
13 (56.3)	Lecythidaceae	*Couropita guianensis*	Bejuco, taparon
14 (54.2)	Sapindaceae	*Serjania paniculata*	Zarcillo
15 (54.2)	Combretaceae	*Terminalia catappa*	Almendroan
16 (52.1)	Polygonaceae	*Ruprechtia* sp.	Palo de agua
17 (52.1)	Rubiaceae	*Genipa americana*	Caruto
18 (52.1)	Capparidaceae	*Capparis odoratissima*	Olivo
19 (52.1)	Rhamnaceae	*Zyzyphus* sp.	Limoncillo
20 (47.9)	Dilleniaceae	*Tetracera volubilis*	Chaparrillo
21 (47.9)	Papilionaceae	Not identified	Aranagato
22 (43.8)	Anacardiacea	*Astronium graveolens*	Gateao
23 (41.7)	Erythroxylaceae	Not identified	Jallito
24 (41.6)	Cactaceae	*Cereus hexagonus*	Cardon
25 (41.6)	Leguminosae (Mimosaceae)	*Pithecelobium saman*	Saman
26 (39.6)	Leguminosae	*Acacia glomerosa*	Tiamo
27 (37.5)	Combretaceae	*Combretum alternifolium*	Gueica
28 (31.3)	Myrtaceae	*Psidium* sp.	Guayabo
29 (31.3)	Boragineaceae	*Cordia collococa*	Candelero
30 (31.3)	Euphorbiaceae	*Sapium* sp.	Lechero
31 (21.2)	Not identified		Mangle negro
32 (29.2)	Leguminosae (Mimosaceae)	*Mimosa pigra*	Mora
33 (27.1)	Bromeliaceae	*Bromelia* sp.	Maya
34 (25.0)	Anonaceae	*Anonna jahnii*	Manirito
35 (20.8)	Leguminosae (Mimosaceae)	*Inga spuria*	Guamo
36 (20.8)	Sterculiaceae	*Sterculia apelata*	Camoruco
37 (20.8)	Leguminosae (Mimosaceae)	*Pithecellobium pistaciaefolium*	Vera macho
38 (20.8)	Connaraceae	*Connarus* sp.	Picoeguaro
39 (18.8)	Caesalpiniaceae	*Caesalpinia coriara*	Dividive
40 (16.7)	Not identified		Canoito
41 (16.7)	Combretaceae	*Combretum frangulaefolium*	Guayabito
42 (14.6)	Papilionaceae	*Piscidia carthagenensis*	Jebe
43 (14.6)	Not identified		Pagueno
44 (12.5)	Moraceae	*Seracea sprucei*	Charo
45 (12.5)	Not identified		Palo de agua
46 (12.5)	Euphorbiaceae	Not identified	Mangle
47 (12.5)	Not identified		Espinacolora
48 (12.5)	Sapindaceae	Not identified	Parapara
49 (8.3)	Asclepiadeceae	Not identified	Orosul
50 (8.3)	Palmae	*Copernicia tectorum*	Palma llanera
51 (8.3)	Caesalpiniaceae	*Copaifera officianalis*	Aceite
52 (8.3)	Nyctaginaceae	*Pisonia macranthocarpa*	Pegopego
(<7.0)	14 additional species (<7% each)		

[a] Rank and frequency (%) based on percent of 48 transects containing tree species.

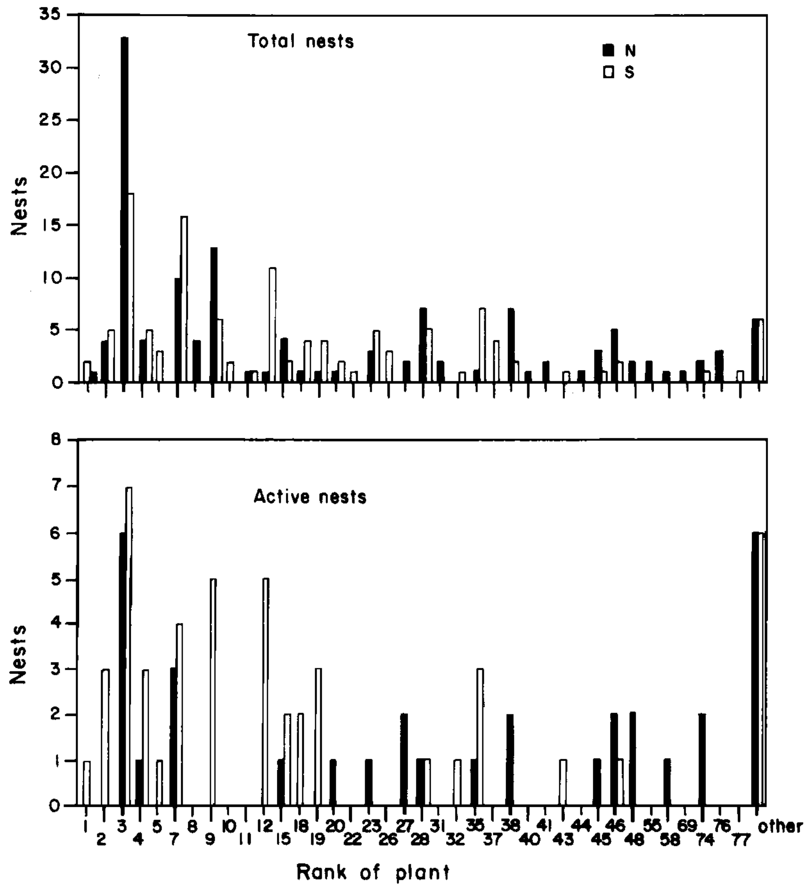

Fig. 5. Numbers of total and active nests in trees along northern (N) and southern (S) sections of creek. Total number of nests was 250 (130 N + 120 S), of which 82 (33 N + 49 S) were active. For tree species, see Table 1.

the southern section of the creek were set in higher branches ($\bar{x}$ = 2.52 ± SE of 0.10 m and 3.10 ± 0.10 m above creek water level for northern [n = 120] and southern [n = 114] sections, respectively; $P < 0.01$).

Eggs were laid one day apart, with hatching after 32 to 34 days of incubation. The clutch size was 2 in 54% of the nests (Fig. 6). Clutch size of one and three were found in 20 and 25% of the nests, respectively. Average clutch size was 2.06 ± 0.075 (n = 81). The southern section of the creek had 90 eggs in 49 nests, while the northern section had 45 eggs in 33 nests. The number of nests with a clutch size of three was higher in the southern than in the northern section (14 vs. 1, respectively; Fig. 6).

When nests were lost, it was usually due to predation on all eggs or chicks, regardless of clutch size. Of 135 eggs laid in 82 monitored nests, only 37 (27%) hatched before being taken by a predator. Hatching success was higher in the southern than in the northern section (31% vs. 16%, respectively).

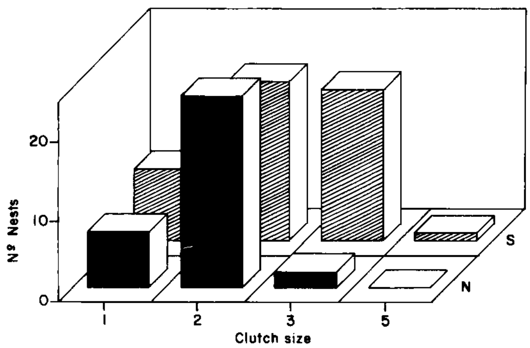

Fig. 6. Clutch sizes in nests along northern and southern sections of creek.

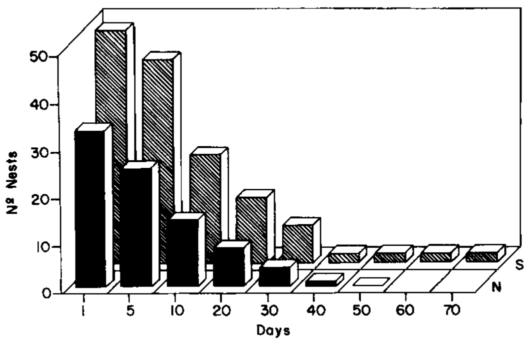

Fig. 7. Activity in nests along northern (N) and southern (S) sections of creek. Total number of active nests was 82 (33 N + 49 S).

The lengths of time nests were active (i.e. contained eggs or chicks) are summarized in Figure 7. Nests from the southern section of the creek remained active longer than those in the northern section. Trees containing the nests that were active the longest were among the commonest and most frequently used for nesting.

Diet and growth.—There were two peaks of feeding activity during the day, around sunrise and sunset. During the study period, mostly the rainy season, birds consumed the young stems and shoots of various tree species. The main trees eaten were *Coccoloba* sp., *Machaerium* sp., *Combretum* sp., *Pithecellobium* sp., and *Couropita* sp. (ranked 1, 3, 11, 12 and 13, respectively; Table 2).

Miscellaneous observations, made later, indicated seasonal dietary differences related to the availability of plant parts. At the end of the dry season (when trees have few leaves and no shoots), the Hoatzins were seen consuming flowers and buds from *Guazuma* (ranked 5 in Table 1). In the transition between dry and rainy seasons, the birds increased the consumption of leaves from *Acacia maracranta, Pterocarpus* sp., *Machaerium* sp. and an unidentified Anonaceae (ranked 8, 10, 3, and 9, respectively; Table 1). During the dry season, birds were observed drinking water from the creek; they perched on branches just above the water or on the ground at the shore. During the breeding season the water from the creeks was rich with green algae in suspension.

Chicks were fed regurgitated material from adults for as long as two months, after which the young could feed independently and were able to scramble or fly away from the nest to other branches. Body masses of chicks less than 24-h old averaged 19.0 ± 0.49 g ($n = 7$). Chicks were born with no yolk to be absorbed. Growth rates of chicks were not significantly affected by the number of chicks sharing the nest ($P > 0.01$). The linear regression of body mass of chicks on age (Fig. 8) indicates a daily gain in body mass of 5.63 g/day. The fitted line of mass data indicates a body mass at hatching of 9.61 g (intercept), which differs from the measurements in youngest animals (19.0 g), recorded

TABLE 2. Main tree species in diet of Hoatzin along with reported toxic compounds in plants.[a]

Species	Toxic compounds
Combretaceae	
Combretum sp.[1,2]	Phenols, tannins, saponins[4]
Compositae	
Mikania congesta[2]	Phenols, terpenoids[4]
Cucurbitaceae	
Luffa operculata[1]	Not available
Euphorbiaceae	
Margaritaria nobilis[2]	Phenols, saponins, tannins[4]
Leguminosae	
Acacia sp. (Mimosaceae)[1,2,3]	Catechol, phenols, saponins, alkaloids, protease inhibitor[6,7]
Albizzia polycephala (Mimosaceae)[2]	Saponins, flavonoids[8]
Entada polystachya (Mimosaceae)[2]	Saponins, phenols[4]
Inga sp. (Mimosaceae)[1]	Phenols, alkaloids, saponins, sterols[7]
Lonchocarpus cruciarubierae (Papilionaceae)[1,2,3]	Phenols[4]
Pithecellobium ligustrinum (Mimosaceae)[1]	Saponins, phenols, djenkolic acid, mimosine[4,5]
Lecythidaceae	
Couropita guianensis[1,2]	Tannins[8]
Myrtaceae	
Myrtus sp.[2]	Saponins, phenols[4]
Rutaceae	
Zanthoxylum culantrillo[2,3]	Phenols, culantramine, culantraminol, rotenone[4,6]
Sterculiaceae	
Guazuma sp.[1,2,3]	Phenols,[4] sterols, tannins[8]
Vitaceae	
Cissus sicyoides[2]	Tannins[8]

[a] References as follows: (1) this work; (2) Schmitz 1987; (3) Grajal et al. 1989; (4) Torres 1988; (5) D'Mello 1989; (6) Blohm 1962; (7) Galindo et al. 1989; (8) E. Rodriguez unpubl. data.

about 24 h after hatching. The increase in body mass due to growth and gut contents may explain this difference. The adult average body mass was 695.7 ± 17.46 g (n = 9).

Discussion

Vegetation and nesting.—The Hoatzin nested in the most frequently encountered trees along the water courses. The most frequent tree species in other habitats used by the Hoatzin differ from those we found. Strahl (1985) and Schmitz (1987) reported trees abundant in Masaguaral Ranch that are scarce in Piñero Ranch: *Pseudonamonis* (Papilonaceae), *Psychotria* (Rubiaceae), *Mimosa* (Fabaceae), *Clonodia* (Malpighiaceae), and *Mikania* (Asteraceae). Other genera are common in both places: *Guazuma* (Sterculiaceae), *Coccoloba* (Polygonaceae), *Acacia* (Fabaceae), and *Combretum* (Combretaceae).

Sites for nesting appeared to be related directly to the frequency of tree species in the habitat (Fig. 5). This coincides with reports of nesting in Masaguaral Ranch (Strahl 1985). While menudito (*Machaerium* sp.), cuji (*Acacia*), anoncillo (an Anonaceae), and orore (*Pithicellobium* sp.) trees were the main ones chosen for nesting in Piñero, Strahl (1985) reported *Acacia, Lonchocarpus, Myrtus,* and *Coccoloba* as the most commonly used trees for nesting in Masaguaral Ranch.

The fact that some of the most dominant species in our study were not preferentially chosen for nesting (e.g. *Coccoloba* sp., *Guazuma tormentosa, Pterocarpus* sp., and *Combretum fructicosum;* ranked 1, 5, 10, and 11, respectively) may be related to the structure of the tree canopy. Tree canopies that provide suitable branches for supporting the nests over the watercourse, allowing access for the Hoatzin but limiting that of predators, could enhance nest success and chick survival. The higher nest success on the southern section of the creek may be related to the wider gallery forest in the northern section, which favored the presence of arboreal predators. We observed nest predation by the wedge-capped capuchin monkey (*Cebus olivaceus*), which was often found along the northern section of the creek, and by the taira (*Eira barbara*). In Masaguaral, the main predator was reported to be the wedge-capped capuchin monkey; other predators included avian raptors, piranhas (*Serrasalmus* sp.), caimans (*Caiman crocodilus*), and boa constrictors (*Boa constrictor;* Strahl 1985). In

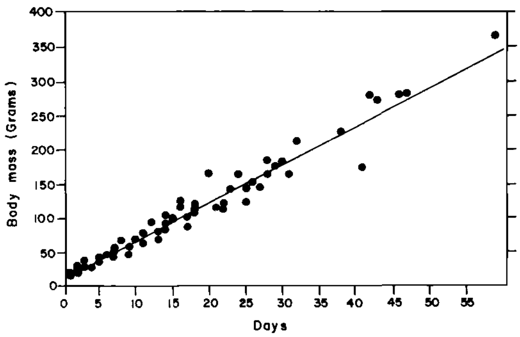

Fig. 8. Growth of chicks up to 59 days as indicated by body mass. $Y = 9.61 + 5.63X$ ($r = 0.98$).

our study, hatching success was 27%. Strahl (1985) reported a nest success (proportion of chicks reared to independence) of 35% on Masaguaral Ranch in 1982–1983. Renesting was observed in our study and was also reported by Strahl (1985) to occur up to six times if nesting attempts were unsuccessful (Strahl 1985).

In our study, eggs were laid one day apart and hatched after 32 to 34 days of incubation, longer than the 31 days reported by Strahl (1985). Clutch sizes were similar to those reported in Masaguaral (Strahl 1985; $P < 0.1$; $\bar{x} = 2.06 \pm 0.08$ [$n = 81$] and 2.20 ± 0.05 [$n = 238$] for Piñero and Masaguaral, respectively).

Growth and diet.—Average masses of chicks within the first 24 h from hatching in this study (19 g) were similar to those reported by Strahl (1985) at Masaguaral Ranch (19.2 g; $P < 0.1$). Growth of chicks in Piñero was independent of the number of young sharing the nests, with an average daily gain of 5.7 g. Although we were not able to make statistical comparisons of growth rates for chicks in Piñero and Masaguaral ranches, Strahl (1985) reported higher growth rates (6.8–7.6 g/day), although adult average body masses were similar in the two locations ($P < 0.1$; Grajal 1991).

The Hoatzin is one of the few avian folivores (Morton 1978). It lives on young leaves and shoots of the most common trees in its habitat, surely influenced by their nutritional value (nutritive components and content of antinutritional compounds). It is likely that diet selection maximizes the supply of soluble tree-cell components, as is done by most small herbivores (Parra 1978), and overcomes the nutritional constraints imposed by phytotoxins.

The Hoatzin has a lower metabolic rate than that predicted for its body mass (Grajal 1991), which together with its digestive adaptations seems to allow the bird to overcome the theoretical incompatibility between flight energetics, body mass, and folivorous habits. The presumably toxic nature of the Hoatzin's diet suggests a role of the crop in dietary detoxification. Small pregastric fermenters are known to be poor cell-wall digestors (Hume and Warner 1980) and to choose young leaves with higher cell contents and lower cell-wall components, so that they act as specialist or concentrate feeders. However, some young leaves of trees could contain higher concentrations of small-molecular-weight secondary compounds than mature leaves, presumably as a defense against herbivores (Janzen 1979). Some mammal concentrate feeders, like the koala (*Phascolarctos cinereus*), are able to handle toxic dietary compounds (Cork et al. 1983), while generalist herbivores (such as domestic ruminants) appear more influenced in their food choices by energy/nutrient availability (Belovsky 1986). Generalist herbivores such as cattle and sheep, have been shown to degrade dietary toxins in the rumen (Gutierrez et al. 1958, Domínguez-Bello and Stewart 1990), but the extent of this activity in smaller herbivores, and in particular in the Hoatzin, is unknown.

There are at least two possibilities that may condition the dietary choices of the Hoatzin: (1) a crop microbiota with a biochemically wide spectrum that detoxifies different toxins from chemically and phylogenetically heterogeneous trees; or (2) a crop microbiota limited in biochemical activities for detoxification of a chemically homogeneous group of trees.

Studies by our group have yielded preliminary results on the microbial composition of the Hoatzin's crop and their biochemical activities (Domínguez-Bello et al. 1993). Phytochemical studies of the diet of the Hoatzin are now in progress. More investigations are necessary to yield insights into the ecology of gut microbial communities and their hosts, as well as concerning the evolution of pregastric fermentation.

ACKNOWLEDGMENTS

We are grateful to: A. J. Branger and the personnel of Hato Piñero for their valuable support; Francisco Delascio for identification of plants; A. Grajal and F. A. Michelangeli for fruitful discussions; and L. R. Pericchi for statistical assistance. We acknowledge travel support from the Office of Academic Affairs, University of California, Irvine. This project was partially financed by Fundación Polar, CONICIT (S1-2152) and the International Foundation for Science (B-1030).

LITERATURE CITED

ACEVEDO, M. F. 1989. Diversidad de plantas en los cerros Marahuaca, Huachamacare y Duida. Acta Terramaris 1:21-32.

BELOVSKY, G. E. 1986. Generalists herbivore foraging and its role in competitive interactions. Am. Zool. 26:51-69.

BLOHM, E. 1962. Poisonous trees from Venezuela. Harvard Univ. Press, Cambridge, Massachusetts.

BÖKER, H. 1929. Flugvermögen und kropf bei *Opisthocomus crisatus* und *Stringops habroptilus*. Gegenbaurs Morphol. Jahrb. 63:152-207.

CORK, S. J., I. D. HUME, AND T. J. DAWSON. 1983. Digestion and metabolism of a natural foliar diet (*Eucalyptus punctata*) by an arboreal marsupial, the koala (*Phascolarctos cinereus*). J. Comp. Phys. B 153:181-190.

D'MELLO, J. P. F. 1989. Toxic amino acids. Pages 29-50 *in* Anti-nutritional factors, potentially toxic substances in trees (J. P. F. D'Mello, C. M. Duffus, and J. H. Duffus, Eds.). Association of Applied Biologists, Warwick, United Kingdom.

DOMÍNGUEZ-BELLO, M. G., AND C. S. STEWART. 1990. Degradation of mimosine, 2,3 dihydroxypyridine and 3 hydroxy 4 (1H) pyridone by bacteria from the rumen of sheep in Venezuela. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 73:283-290.

DOMÍNGUEZ-BELLO, M. G., M. LOVERA, P. SUAREZ, AND F. MICHELANGELI. 1993. Microbial inhabitants in the crop of the Hoatzin (*Opisthocomus hoazin*): The only foregut fermenter avian. Physiol. Zool. 66: 374-383.

GALINDO, W. F., M. ROSALES, E. MURGUEITO, AND J. LARRAHONDO. 1989. Sustancias antinutricionales en las hojas de guamo, nacedero y matarratón. Invest. Pecuaria Desarr. Rural 1:37.

GRAJAL, A. 1991. Nutritional ecology and digestive physiology of the Hoatzin, *Opisthocomus hoazin*, a folivorous bird with foregut fermentation. Ph.D. dissertation, Univ. Florida, Gainesville.

GRAJAL, A., S. D. STRAHL, R. PARRA, M. G. DOMINGUEZ, AND A. NEHER. 1989. Foregut fermentation in the Hoatzin, a Neotropical avian folivore. Science 245:1131-1134.

GRIMMER, J. L. 1962. Strange little world of the Hoatzin. Natl. Geogr. 122:391-401.

GUTIERREZ, J., R. E. DAVIS, AND I. L. LINDHAL. 1958. Dissimilation of alfalfa saponin by rumen bacteria. Science 127:335.

HUME, I. D., AND A. C. I. WARNER. 1980. Evolution of microbial digestion in mammals. Pages 665-684 *in* Digestive physiology and metabolism in ruminants (Y. Ruckebusche and P. Thivend, Eds.). Avi Publishers, Westport, Connecticut.

JANZEN, D. H. 1979. New horizons in the biology of trees defenses. Pages 331–350 *in* Herbivores, their interactions with secondary trees metabolites (G. A. Rosenthal and D. H. Janzen, Eds.). Academic Press, New York.

MONTGOMERY, D. C. 1976. Design and analysis of experiments. John Wiley and Sons, New York.

MORTON, E. S. 1978. Avian arboreal folivores: Why not? Pages 123–130 *in* The ecology of arboreal folivores (G. G. Montomery, Ed.). Smithsonian Institution Press, Washington, D.C.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 205–229 *in* The ecology of arboreal folivores. (G. G. Montomery, Ed.). Smithsonian Institution Press, Washington, D.C.

SCHMITZ, A. 1987. Algunos aspectos de la dieta y del sistema social de las chenchenas (*Opisthocomus hoazin*) durante la estación seca en los llanos venezolanos. B.Sc. thesis, Univ. Simón Bolívar, Caracas, Venezuela.

SIBLEY, C. G., J. E. AHLQUIST, AND B. L. MONROE, JR. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. Auk 105:409–423.

SMITH, R. L. 1974. Ecology and field biology. Harper and Row, New York.

STRAHL, S. D. 1985. The behavior and socio-ecology of the Hoatzin, *Opisthocomus hoazin* in the Llanos of Venezuela. Ph.D. thesis, Univ. New York at Albany, Albany.

STRAHL, S. D. 1988. The social organization and behaviour of the Hoatzin *Opisthocomus hoazin* in central Venezuela. Ibis 130:483–502.

TORRES, L. 1988. Caracterización de los compuestos secundarios presentes en los componentes de la dieta de la chenchena (*Opisthocomus hoazin*) (Aves, Cuculiformes) en los Llanos de Venezuela. B.Sc. thesis, Univ. Central de Venezuela, Caracas.

VANDER WERF, E., AND S. D. STRAHL. 1990. Effects of unit size and territory defense on communal nest care in the Hoatzin. Auk 107:626–628.

VARESCHI, V. 1986. Cinco breves ensayos ecologicos acerca de la Selva Virgen de Rancho Grande. Pages 171–187 *in* La Selva Nublada de Rancho Grande, Parque Nacional Henry Pitier (O. Hubber, Ed.). Fondo Editorial Acta Cientifica Venezolana, Caracas.

YOUNG, C. G. 1888. On the habits and anatomy of *Opisthocomus crisatus*, Illig. Notes from the Leyden Museum 10:169–175.