UNIVERSITY OF MICHIGAN
MUSEUM OF ZOOLOGY

Miscellaneous Publications No. 19

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Ramphastos brevicarinatus

BY
JOSSELYN VAN TYNE

ANN ARBOR, MICHIGAN
PUBLISHED BY THE UNIVERSITY
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ALEXANDER G. RUTHVEN,
Director of the Museum of Zoology,
University of Michigan.

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THE LIFE HISTORY OF THE TOUCAN, *RAMPHASTOS BREVICARINATUS*[1]

By Josselyn Van Tyne

Introduction

The birds of tropical America, by their great abundance and diversity, their many amazing eccentricities and specializations of structure and habit, well merit the special attention they have received from ornithologists. The history of the explorations and publications which have made them known to us, from Gould, Lafresnaye, and Swainson to Salvin and Godman, Lawrence, Sclater, and others, is a fascinating one. The description and naming of the multitudinous new species may have been the privilege some called it, but it might be equally well termed the drudgery of ornithology. But it had to come first. Without a sound taxonomic foundation upon which to build, the more attractive study of the habits, specializations, and interrelations of these birds would be quite impossible. However, these pioneers in the field could not, for lack of time and facilities, do more than mention briefly some of the most striking of these problems. For the most part they had to struggle along, describing new species and revising their classification, hampered always by poor and insufficient material and the many delays resulting from the difficulties of tropical collecting. We, who now profit by their work, have good cause to wonder at the soundness of their conclusions based upon such inadequate collections.

Even now, the voluminous literature of ornithology is strangely lacking in detailed life history studies of single species of birds. These studies are absolutely fundamental and we can get nowhere without basing our results largely upon such work. Accurate conclusions cannot be reached without sufficient facts upon which to base them. Yet we go ahead cheerfully, making wise generalizations about the "controlling factors" in distribution, the "adaptive and non-adaptive characters" in taxonomy, and even the "beneficial and injurious" species in economic ornithology, with only a scanty knowledge of the facts involved. Until we know much more fully the life histories of the various species, our most important generalizations must remain, as they are, highly theoretical.

The first well-rounded life histories of single species of American birds were those recently published by Dr. Alfred O. Gross. His studies of the dickcissel and of the black-crowned night heron opened a new phase of

[1] A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

ornithological work in America. Hitherto nothing of the sort had been attempted in the even more attractive field of neotropical ornithology because of the obstacles presented by the climate and other local conditions. However, with the recent establishment of the Barro Colorado Biological Station in Panama, it has become possible for the zoologist to carry on detailed life histories of neotropical birds without the difficulties and dangers formerly attendant upon any such endeavor. This study was a direct result of the establishment of that Station and, without its facilities, could not have been carried out.

Knowing the importance of the family of toucans (Ramphastidae) as one of the most striking and distinctive of all of the exclusively neotropical groups of birds, and realizing how little was known of their life histories, I decided that I could not use my opportunity to work at the newly established Station better than to make a detailed study of one of the toucans. *Ramphastos brevicarinatus* was chosen because of its greater abundance and availability. I have endeavored to make as detailed a study as possible of the life cycle of this toucan, its habits and distribution, together with other facts which seemed necessary to an adequate knowledge of the bird.

The field work upon which this study is based was conducted at the Barro Colorado Biological Station in the Panama Canal Zone. In the course of the investigation I made three trips to Panama and worked at the Station for periods of two, three, and six months between the following dates: June 24 to August 21, 1925; February 28 to May 20, 1926; and February 24 to August 21, 1927.

Acknowledgments: In the course of this study I have become indebted to many without whose aid I would have been greatly handicapped.

It was at the suggestion of Dr. Alexander G. Ruthven that the investigation was begun and, without his support and advice, it would not have been completed.

In my field associates I have been particularly fortunate. During the first season's work I had the benefit of the companionship of Dr. Alfred O. Gross, whose life history studies have opened a new field in the ornithology of North America. In the second field season, when the greater part of this material was secured, I had the active help of Frederick M. Gaige, whose skill and resourcefulness in the field I have never seen equaled. During the first month of the 1927 season, Walter E. Hastings was with me at the laboratory and assisted me in many ways.

Throughout my work at the Station I received the constant cooperation of the Custodian, James Zetek, and his aide, Ignacio Molino, Jr. Through March of 1927 I had the pleasure of association with Dr. Frank M. Chapman and frequently profited by his unrivaled knowledge of neotropical birds.

Dr. Thomas Barbour, to whom the Barro Colorado Station owes its existence, has given me assistance of every sort. I wish to acknowledge here my great obligation to him.

The photographs reproduced in this paper, with the exceptions noted below, were taken by the author. However, figures 1, 2, and 7 are from photographs by Walter E. Hastings and figures 6, 8, and 18 are from photographs by Alfred O. Gross. The two drawings of the nestling heel-pads (figs. 12 and 13) were made by Miss Grace Eager.

NOMENCLATURE

It has proved somewhat of a problem to decide what scientific name should be used in designating the subject of this study. The biological facts are as follows. The form studied ranges from Colombia through Central America to Honduras and a slightly different but representative form ranges from Honduras through Guatemala and southern Mexico. The two forms probably intergrade, though I have not personally examined intermediate specimens. The facts concerning the nomenclature involved are less clear. In current usage the northern form is called *Ramphastos piscivorus piscivorus* Linnaeus and the southern, *Ramphastos piscivorus brevicarinatus* (Gould), but the name *piscivorus* of Linnaeus is based on Edwards (Natural History of Birds, I, pl. 64), who figured a bird with a white throat and a bill quite unlike this species. Dr. C. E. Hellmayr writes me that he calls the northern form *Ramphastos sulfuratus* Lesson (Traité d'Orn., livr. 3, July, 1830, p. 173–Mexico) of which he has seen the type.

Since it seems to me that a life history study is a poor place to introduce nomenclatorial innovations, I have decided to use simply the more brief form *Ramphastos brevicarinatus*, which cannot possibly be misunderstood, and to make no attempt to decide either the subspecific relationships or the possible "reformed" nomenclature which might be applied.

The following references include the principal synonymy of the bird discussed in this paper and will serve to bring out in brief form its taxonomic history.

Ramphastos brevicarinatus Gould, Monogr. Ramphast., 2d., 1854, pl. 3 and text (Panama; coll. J. Gould).
Cassin, Proc. Acad. Nat. Sci. Phila., 1867, p. 103.
Bradbourne and Chubb, Birds of South America, I, p. 156.
Rhamphastos brevicarinatus Sclater, Cat. Birds Brit. Mus., XIX, 1891, p. 126.
Salvin and Godman, Biol. Centr.-Amer., Aves, II, 1896, p. 553.
Carriker, Ann. Carnegie Mus., VI, 1910, p. 572.
[*Rhamphastos*] *brevicarinatus* Sharpe, Hand-list, II, 1900, p. 189.
Burhynchus brevicarinatus Heine and Reichenow, Nom. Mus. Hein. Orn., 1890, p. 228.
Ramphastos approximans Cabanis, Jour. für Ornith., no. 59, Sept., 1862, p. 333.

Rhamphastos carinatus (not of Swainson) Lawrence, Ann. Lyc. Nat. Hist. N. Y., VII, 1861, p. 299.

Salvin and Godman, Ibis, 1879, p. 206.

[*Rhamphastos*] *carinatus* Sclater and Salvin, Nom. Avium Neotr., 1873, p. 108 (part).

Ramphastos piscivorus (not of Linné) Lawrence, Ann. Lyc. Nat. Hist. N. Y., VIII, 1865, p. 183.

Ramphastos tocard (not of Vieillot) Salvin and Godman, Ibis, 1879, p. 206.

Ramphastos piscivorus brevicarinatus Ridgway, Bull. U. S. Nat. Mus., no. 50, Part VI, 1914, p. 334.

Chapman, Bull. Amer. Mus. Nat. Hist., XXXVI, 1917, p. 328.

Cory, Field Mus. Nat. Hist., Zool. Ser. XIII, 1919, p. 361.

Native Names: In Panama all toucans are indiscriminately called "*pico féo*" (ugly beak) and are known to every one. In Costa Rica, Underwood (1896, p. 445) writes that "its familiar name is '*cuni*,'" while the Calverts (1917, p. 254) report that the native name there is "*curre grande.*" Gould (1834) says *Ramphastos piscivorus* "is called *Pito canoa* by the inhabitants of Mexico;" which, is doubtless an error for *Pico de canoa,* as reported by Ferrari-perez (1887, p. 163). The latter also gives *Tucan de cuello amarillo* as a native Mexican name, but this sounds suspiciously like a book name. In many parts of South America this species and others of the genus are known as "*Dios te de*" (God gives it to thee). This was doubtless first applied to *Ramphastos swainsonii* which throws back its head and utters a three-syllable call which might easily be so rendered. The name may then have spread to *R. brevicarinatus* and others because of their similar appearance. Another version of this is the name "*Predicadores*" (preachers) reported by Goodfellow (1900, p. 173) and others.

DESCRIPTION

Adults (sexes alike except in size): Pileum and hind neck black, the latter strongly washed with maroon; upper tail-coverts white; the rest of the back, wings, and tail glossy greenish black; malar and auricular regions, throat, upper breast, and small spot between the eye and nostril Lemon Chrome[2] or Lemon Yellow; the convex lower margin of the yellow breast edged with a band of Brazil Red, five to twelve millimeters broad; under tail-coverts Brazil Red (black basally); rest of underparts slightly greenish black; iris Olive Yellow to Neva Green; bare orbital skin Yellow Green about the eye to Lemon Yellow above and posteriorly; bill Light Greenish Yellow along the culmen to Yellow Green toward the tomia and on the basal third of the mandible; terminal fourth of the bill Maroon; wedge-shaped lateral area on the tomial half of the maxilla Orange Chrome; remainder of mandible Pale Cerulean Blue; bill margined basally by a

[2] All color names capitalized in this paper are from Ridgway's "Color Standards and Color Nomenclature," 1912.

sharply defined black line about two millimeters wide; feet Pale Methyl Blue, becoming Pale Sulfate Green on upper tarsi; soles of feet Clay Color to Isabella Color; claws black.

Juvenal: Similar to adults except as follows: all contour feathers much more soft and lax; red of breast and under tail-coverts decidedly duller; the red breast band more diffused over the black of the lower breast; the black body feathers a dull brownish black, those of the belly tipped with red; less maroon on the nape feathers. Soft parts (from the time of leaving the nest up to the molt of the juvenal plumage): Iris Light Paynes Gray, becoming Lime Green; orbital skin Viridine Yellow (Bright Green Yellow about nostrils), becoming Pale Nile Blue below the eye; maxilla Apple Green centrally to Olive Yellow on culmen and anterior part, becoming Yellow Green centrally to Sulphur Yellow on culmen; lateral wedge-shaped area Light Ochraceous Orange, becoming Capucine Yellow; terminal fourth of bill Light English Red, becoming Light Brazil Red; mandible Mignonette Green, becoming Light Glaucus Blue on anterior part and Rivage Green toward the base; no sharply defined black line at the base of the bill, but instead a broader blackish area nearly ten millimeters in width at first and becoming more restricted by the end of the juvenal period; tarsi and feet Columbia Blue, with many of the large scutella of the tarsus blackened centrally in the younger birds.

Adult male: Length (in the flesh), 535–580 mm. (554); wing, 198–205 (202.3); tail, 148–166 (157.1); culmen, 139–147 (142.5); weight, 410–452 grams (427.1).

Adult female: Length (in the flesh), 505–535 mm. (520); wing, 194–200 (196.5); tail, 141–158 (151); culmen, 119–132 (124.4); weight, 337–405 grams (380.5).

The above measurements are from eleven males and ten females, all collected on Barro Colorado Island and sexed by myself. After measuring all of the adult specimens in the National Museum, the American Museum of Natural History and the Museum of Comparative Zoology, fifty-seven skins in all, I decided not to use those measurements here, for I found many specimens that were obviously wrongly sexed, and averages based upon these would have been misleading. It seemed better to use only the much smaller series, all of which were from the same locality and all sexed by myself.

In measuring, I have followed the methods used by H. F. Witherby (Practical Handbook of British Birds, 1920, vol. I, p. XIII). Measuring the arc of the wing instead of the chord is not the usual American method but is, I am convinced, much more precise, especially in the case of a bird with as "rounded" a wing as Ramphastos. All measurements were made before skinning and are expressed in millimeters and grams.

The above description is based on tweny-one normal adult specimens which I collected in the Canal Zone, the type locality of *brevicarinatus*. In spite of great care in checking this series, taken in nearly every month from February to September, I find extremely little variation in the colors of the "soft parts." However, Gould (1834, p. 3) wrote, "The bill of toucans varies much in color, and is subject to variation in this respect, even in the same species, according to the age of the individual." Further, concerning "*R. carinatus*" (which then included the present *brevicarinatus*) he says "it is easy to observe that the original colour is very different in different individuals, whence I am led to conclude that the colours of the beak are greatly influenced by the season of the year and are doubtless in the finest and most brilliant state during the time of pairing." This is a rather natural supposition and it is interesting to find that Darwin, when working on his theory of sexual selection, inquired about such variation in toucans. On June 3, 1868, he wrote to F. Muller (Darwin and Seward–1903, vol. 2, p. 83): "Here is another point: have you any Toucans? if so, ask any trustworthy hunter whether the beaks of the males, or of both sexes, are more brightly coloured during the breeding season than at other times of the year." Ridgway (1914, p. 334) also found a great variation in the colors of the soft parts and described it with some exactness. However, two of his five specimens were "cage birds of unknown locality" and therefore cannot be relied upon. No cage birds that I have seen were normally colored. Their bills were duller and many other abnormalities of color were noticeable. Two more of Ridgway's five specimens were "from eastern Nicaragua" and, I suspect, also cage birds (he does not say). The fifth was a freshly killed, wild Costa Rican bird and it is perhaps significant that this is the only one of the five that I would call normally colored as compared with the Panama bird.

In the coloration of the yellow throat and breast feathers there is a most interesting variation. Normally the yellow of the throat is very uniform. Among some twenty-five skins from the Canal Zone, the only variation is a slight dullness in birds of very worn plumage, but three specimens (out of more than sixty) examined in other collections show a striking difference in the yellow of the throat. The Lemon Yellow of the normal bird is replaced by a much richer and more orange color. This cannot even be approximated in Ridgway's Color Key (1912), but is exactly matched by the yellow of the breast of the prothonotary warbler (*Protonotaria citrea*). The Museum of Comparative Zoölogy has a pair of these birds (Nos. 121066 and 121064) taken at Tenorio, Costa Rica, on January 30, 1908, and I noted a similar specimen from Costa Rica in the National Museum. Cassin (1867, p. 103) in his revision of the toucans,

described such a specimen in the collection of the Academy of Natural Sciences of Philadelphia and thought this "probably" a specific character of use in separating *brevicarinatus* from *approximans*. It is, then, apparently of regular occurrence and may be a reversion to a more primitive condition, for an examination of the species of Ramphastos suggests strongly a course of evolution from the orange colored breast (*ariel*) to the white (*toco*).

A sexual variation has been described, but I find no difference between the sexes except in size. However, the male is so much larger than the female, especially in the proportions of the bill, that the two sexes can usually be recognized in the field.

MOLT

As in many other Picarian birds, the young of this toucan has no natal down. The juvenal plumage is slow in developing, but the young bird is fairly well covered when it leaves the nest at the age of about forty-five days. The juvenal plumage is soon lost by an incomplete molt which apparently begins within a month after the young bird leaves the nest. The post-juvenal molt involves all of the body plumage except the remiges and rectrices, which are retained until the first post-nuptial molt when all feathers are normally changed. Thereafter there is but the single annual molt, the post-nuptial. Nesting in Panama takes place in the dry season (February–May) and the general molting period begins toward the end of this season. Late May and early June finds most toucans molting heavily. There is considerable individual variation in the exact time of molting and this so extends the period of molt that many were still molting during the last of August, the latest date I was in the field. It is difficult therefore to judge the length of time required for an individual to complete its molt, but it is evidently a rather slow process.

The method and order of molt is remarkably regular. The molt begins at the first or proximal primaries and almost immediately afterwards in the body plumage. The molt of the body plumage usually appears first on the head, but soon breaks out in the various tracts over all the body. No very definite order was observable within these tracts. The molt of the primaries continues rapidly outward in regular sequence. The molt of their major upper coverts is carried out in the same order, but several places ahead of their respective primaries, while the major lower coverts are lost at exactly the same time or shortly after their primaries. The molt of the secondaries begins with the loss of the first (or distal) one, and at about the same time the fifth or sixth primary is molted. The molt of the secondaries then proceeds inward rapidly, but with less regularity than is the case with the primaries. The tertials begin to molt about the

same time as the first secondaries and are completed before them because they are fewer in number.

In their method of tail molt toucans are nearly unique among birds. Instead of molting the rectrices in regular order, beginning with the central pair and progressing outward, they exactly reverse this and molt the tail from the outer toward the central feathers. Beebe (1916, p. 74) first described this and called it the "centripetal type" of tail molt. He also recorded this type of molting in a tropical woodpecker (Celeus) and in certain pheasants. I am not aware of its occurrence outside of these groups. The tail molt begins simultaneously with the molt of the second primary and proceeds so rapidly that it is usually completed by the time the sixth primary is molted. The upper and lower tail coverts molt at the same time as the tail, but seem to follow no particular order.

The molt of the remiges and rectrices is usually very symmetrical; corresponding feathers on the two sides are lost at exactly the same time.

PTERYLOSIS

A study of the pterylosis of *Ramphastos brevicarinatus* has brought out a number of interesting facts. The only published drawing of the feather tracts of a toucan is Nitzsch's (Sclater, 1867, pl. V) figure of *Ramphastos erythrorhynchus* [=*monilis*] and the tracts of *R. brevicarinatus* prove to be essentially similar. In the following particulars, however, this species differs from Nitzsch's figure. In *Ramphastos brevicarinatus* both the anterior and the posterior sections of the dorsal tract are narrower. Also, the outer limb of the femoral tract (to use Nitzsch's terminology) does not join the dorsal tract, but stops short before even reaching the posterior end of the inner limb of the femoral tract. The crural tracts are in the form of three definite rows of feathers extending length-wise along the leg and merging as they approach the heel.

Although Ridgway (1914, p. 327) followed Nitzsch in stating that the contour feathers of the Ramphastidae lack the aftershaft, this is not the case, for the aftershaft is actually well developed, as Miller (1924a, p. 2) has already pointed out. In *R. brevicarinatus* it is often nearly as long as the feather itself. In a typical example before me, the base of the aftershaft consists of a solid shaft more than a centimeter in length, while the remaining four centimeters are composed of long delicate filaments. The occurrence of the aftershaft is of considerable interest because its presence or absence is one of the best taxonomic characters found in the feather structure of birds.

As stated by Miller (1915, p. 133), toucans are eutaxic. He also listed this species as having a vestigial eleventh primary, but this I fail to find even after careful examination of the most favorable material.

Clark (1918) has called attention to the extraordinary number of major upper tail-coverts in toucans. In *Ramphastos cuvieri* he found twenty or twenty-two coverts for the ten tail feathers, instead of the usual condition of one covert for each tail feather. I find that the usual number in *Ramphastos brevicarinatus* is sixteen, or eight on each side, but of thirteen specimens examined, four had nine coverts on a side and one had seven. A fifteenth specimen had eight on the right side and nine on the left. With the hope of finding some explanation of this anomalous condition, I examined also the two other species of toucan which I collected. Eight specimens of the closely related *Ramphastos swainsonii* had eight coverts on a side, but an examination of the more primitive *Pteroglossus torquatus* revealed an intermediate condition, more like the normal in other birds. From their condition I am led to believe that the apparent tail-coverts in Ramphastos are not the original tail-coverts, but are merely the lower ends of the paired dorsal feather tracts which have taken over the function of coverts. Close against the base of the tail feathers, I found what appear to be the vestiges of the former tail-coverts. In Pteroglossus these are more prominent than in Ramphastos. Also, in Pteroglossus the two dorsal feather tracts merge without the slightest change into the "tail-coverts" so that it is quite impossible to determine the number of coverts. Even in Ramphastos the white "tail-coverts" form a perfect continuation of the dorsal feather tracts and are only set off by their color and their somewhat different form. These are not sharp differentiations, for at the point of transition there are frequently feathers which are half the color of the dorsal tract and half the color of the "tail-coverts."

If this is the correct interpretation, we not only have a most interesting example of the methods of evolution of feather tracts, but also a logical explanation of the large number of coverts and the even more strange variation in their number.

ANATOMY

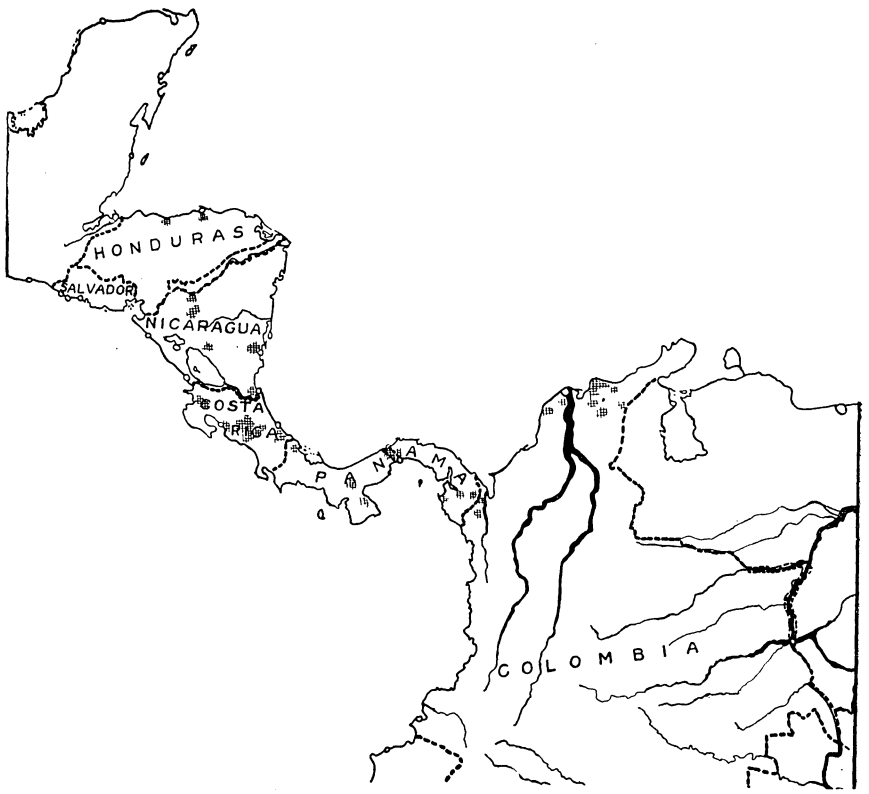
There is an excellent account of the anatomy of the toucan by Sir Richard Owen in Gould's Monograph of the Toucans, but there are a few points which may well be added here.

Although both Sir Richard Owen and later Hans Gadow stated that there was no gall bladder in toucans, it actually reaches an extraordinary development in this family. In *Ramphastos brevicarinatus* it is very long and tubular, as much as 60 mm. long and only about 4 mm. in diameter. Forbes (1882) points out that the only other birds with a gall bladder of this type are the Capitonidae and the Picidae, a further evidence of the close relationship between these three families.

Friedmann (1927) has recently called attention to the testicular asymmetry of birds and, following Riddle, has attempted to correlate this with the sex ratio. In breeding males of many wild birds the left testis is much larger than the right and there is evidence that in some cases this condition is correlated with an excess of males in the population. Since Friedmann had no data on toucans, it seems worthy of record here that, in *Ramphastos brevicarinatus, Ramphastos swainsonii,* and *Pteroglossus torquatus,* I found the left testis always much larger than the right in specimens examined at all times of the year. Nevertheless, it is quite certain that in toucans there is no great disparity of numbers between the sexes.

DISTRIBUTION

Honduras (Ceiba, mouth of Rio Roman) through Nicaragua (Bluefields, Greytown, Jalapa, La Libertad, Los Sabalos, Matagalpa, San Emilis, San Rafael del Norte, Pena Blanca, Rio Escondido, Zapatera), Costa Rica (Aguacate, Angostura, Atalanta, Bonilla, Candelaria Mts., Cariblanco de Sarapiqui, Cartago, Cuabre, Dota Mts., El Hogar, Grecia, Guacimo, Guaitil,



Map showing distribution of *Ramphastos brevicarinatus*

Guayabo, Juan Vinas, La Gloria, Machuca, Miravalles, Monte Verdi, Naranjo de Cartago, Orosi, San José, Sipurio, Talamanca, Tenorio, Tucurriqui, Turrialba), Panama (Almirante, Barro Colorado Island, Chitre, El Real, Gatun, Laguna del Pita, Loma del Leon, New Culebra, Rio Chilibre, Rio Jesusito, Santa Fé de Veragua, Tapalisa) to Colombia (Barranquilla, Bonda, Cacagualito, Cincinnati, Don Diego, Fundacion, La Concepcion, La Tigrera, Las Vegas, Manaure, Minca, Pueblo Viejo, Rio Salaqui, Santa Marta, Soatata, Turbaco).

Carriker (1910, p. 572) writes that "the Costa Rican range of this species covers the whole of the highland portion of the country up to perhaps 4,000 feet, and down on both slopes to near sea-level. In lower altitudes it is found in company with *R. tocard* [*swainsonii*], but in smaller numbers. I believe it to be more abundant on the higher portions of the Caribbean slope than on the Pacific slope at any point. It inhabits only the heavy forest, seldom, if ever, going out into the open and sparsely wooded district, as do some of the other species of the family in Costa Rica."

My only experience with the species was in Panama where I found it very common in the rain forest in the Canal Zone. In a similar forest on the Jesusito River ten miles from Garachiné, it was also fairly common when I was there in June, 1927. Kennard (1928, p. 453) states that at Almirante it was "occasionally seen at sea level, but commoner above 2,000 feet." Goldman (1920, p. 32), in his discussion of the life zones of Panama, lists this species as characteristic of the Humid Lower Tropical Zone. W. C. Allee (1926) has attempted to describe the ecological conditions on Barro Colorado Island and in his first paper will be found a valuable account of his measurements of some of the physical factors in the environment. Unfortunately, his second paper, dealing with the distribution of the animals, seems to be neither accurate nor adequate.

In the Santa Marta region of Colombia, Todd and Carriker (1922, p. 233) write "this handsome large toucan is found in all parts of the Tropical Zone, from sea-level up to about 5,000 feet, wherever the forest is sufficiently dense. In the drier portion of the lowlands it keeps to the woodland along the narrow valleys of the various streams." Apparently 5,000 feet is the highest altitude reached by the species in any part of its range. Bangs (1898, p. 157) records one specimen collected by W. W. Brown at Pueblo Viejo at "about 8,000 feet," but this is an error as shown by Carriker (Todd & Carriker 1922, p. 35), who refers to Brown's work at Pueblo Viejo which "he [Brown] gives as having an altitude of 8,000 feet, while as a matter of fact it is only about 2,000 feet above the sea."

I can find no evidence that *Ramphastos brevicarinatus* ranges beyond Colombia, although Ridgway (1914, p. 335) and later Cory (1919, p. 361)

included "Venezuela to Trinidad" in the range of the species. Ridgway seems to have based this upon Finsch (1870, p. 585) for he added, "specimens from Venezuela and Trinidad not seen by me." However, Finsch never intended to record the species from Trinidad. He merely injected in the midst of his faunal list some side remarks on the synonymy of certain extralimital toucans which included *Ramphastos brevicarinatus*. There is apparently no published record of the occurrence of the species in Venezuela and I find no specimens in any American museum.

In the forested areas of the Canal Zone and especially on Barro Colorado Island, where most of this work was done, *Ramphastos brevicarinatus* is a very common bird. It is not only the commonest species of toucan, but it is without doubt the most abundant large bird in the jungle. Since no such statement could convey much to one unfamiliar with the region, or be of much use for future comparison, I have made a special effort to secure an accurate determination of the actual numbers in a given area. This is very difficult in a dense tropical forest but, given sufficient time, a rather accurate determination can be made. During the nesting season when the birds were most localized, I studied a square area one quarter of a mile on a side. With the aid of a detailed map of the island, the area chosen was accurately measured. This area was then intensively studied and the breeding pairs of toucans located. It was not possible to find all the nests but they could be located within a small radius. In this rectangle, one fourth of a mile on a side, there were four pairs of *Ramphastos brevicarinatus,* three pairs of *Pteroglossus torquatus,* and two pairs of *Ramphastos swainsonii.* As closely as could be estimated this also gave a very fair average for Barro Colorado Island in general. At least this seemed to hold for all of the big forest. For the second growth forest, these numbers should be somewhat reduced.

GENERAL HABITS

The flight of the toucan is simple and direct but very weak. Flight is accomplished by rapid strokes of the short rounded wings, interrupted at regular intervals by an upward flip followed by a short glide. After every six to ten strokes there is a short glide on outstretched wings. While in flight the feet are drawn up forward. The enormous beak extends forward, tilted slightly downward, and gives the bird a very unbalanced appearance when on the wing. Dr. Thomas Barbour (1922) aptly compared them with "tiny bow heavy airplanes as they flapped and then sailed, often for long distances, high over the forest."

Their powers of flight are quite adequate for their normal life in the heavy forest, but when they fly out across a clearing and are attacked by

some Tyrant-flycatcher (such as Myiozetetes or Megarynchus), their weakness on the wing is very apparent. The toucan in such a predicament can only hasten slightly or swerve a little away from its tormenter and finally, in desperation, dive steeply into the shelter of the nearest trees. They usually confine themselves to short flights over the forest, but on several occasions I saw single toucans come flying in to Barro Colorado Island across a mile of open lake. At such times they flew seventy-five to a hundred feet above the water. Perhaps this distance marks the very limit of their ability, for the Penards (1910, p. 3) describe the species of Ramphastos in Dutch Guiana as very feeble on the wing. They even tell of toucans starting to fly across "the broad savanna of a river" and failing, because of sheer weakness of wing, to reach the forest on the far side. They describe the toucan starting out high in the air to fly directly across the savanna, gradually falling lower and lower until it finally strikes the open ground or the water.

Although one of the noisiest birds in the jungle, this toucan has ordinarily but a single note, a shrill, frog-like *cree* which it repeats over and over with monotonous regularity. While uttering this note the bird usually goes through an odd series of motions. By these motions the notes are set off into series of about five to seven notes, though the series follow each other with such regularity that the punctuation can only be seen and cannot be detected by ear. At the beginning of each series of notes the toucan jerks its head and tail up and assumes a very sprightly attitude. Then with each succeeding note the head and tail are dropped a bit until, at about the sixth note, the head and tail are jerked back to the top and the process repeated without any break. Usually the calling bird swings from side to side at the same time. That is, it may swing to the right at the first note, then to the left at the second, and so on through the series. This swinging and bobbing motion nearly always accompanies the calling, especially when the toucan is excited. Sometimes, however, when a toucan calls from a dead tree top at sunrise or sunset it may sit almost motionless while doing so. Of course the motions, even when performed, are at times slighted or varied somewhat. When starting to croak, it seems to take the toucan a half minute or so to become warmed to the task. It begins with a low *crr, crr, crr,* which works up to a louder *cra, cra, cra* and finally to the shrill *cree, cree, cree.* This note which I have rendered as *cree* is a shrill note reminding me very much of a northern Hyla (*Hyla crucifer*) although louder. Or, it may be compared with the similar shrill note of the common domestic Guinea hen which it also greatly resembles.

The voice of the toucan is quite loud and may readily be heard more than half a mile across the open. The rate of calling is as regular as a

metronome and varies on different occasions between ninety and a hundred notes to the minute, though I have heard toucans calling as rapidly as a hundred and sixteen to the minute. When a pair, or several of a flock of toucans, "croak" at the same time they do not call in unison. The slight individual differences in the rate of calling bring them first together and then gradually into discord again.

The only other note I have heard the species utter is a low mechanical rattle. The noise is very like that which might be produced by clattering the mandibles together. It is of short duration, consisting usually of but eight or ten notes. I did not discover this note until I worked from a blind placed close beside an occupied nest, for the rattle is so low that it would be inaudible fifty feet away. However, the noise is actually produced vocally and is used frequently about the nest. In captivity, I understand, this is the only note the toucan gives.

As described beyond in the account of the nest life, the young are very noisy, keeping up an almost constant rasping call.

The adult toucans are most active vocally during the early part of the breeding season but even during the height of the molting season they are still noisy. As several observers (Todd & Carriker, 1922, p. 233; Dearborn, 1907, p. 90) have noted, these toucans call most frequently in the morning and evening. However, they continue calling all through the day and may be heard regularly even at noon on the hottest days. They do not seem to be early risers and the first calls are not heard until sunrise or about five minutes before, long after the general chorus of bird-song in the jungle has begun. On clear evenings they cease calling at sunset and hurry off to their roosting holes, while on cloudy days their retirement is correspondingly hastened. I have never heard them call at night.

In the literature, the voices of this species and *R. swainsonii* have been completely confused. The latter species never gives the *cree* note of *R. brevicarinatus,* but has instead a totally different, gull-like squawk which the natives render as *dios- te- de.* Nevertheless, our best authorities have confused them. Richmond (1894, p. 518) says, "both of these species [ie., *R. swainsonii* and *R. brevicarinatus*] make a curious croaking noise * * * *. It is the only note I have heard them utter." Carriker (1910, p. 573) similarly writes of *R. brevicarinatus,* "Their notes and habits are about the same as those of *R. tocard* [=*R. swainsonii*]." Ridgway, however, differentiated between them. He writes (1922, p. 322) "Frequently one hears a peculiar rasping sound, as if someone were drawing the end of a stick quickly, three times in succession across the ridges of an ordinary washboard, or the woven rattan slats of a chair bottom. This is the call of two species of toucan (*Ramphastos brevicarinatus* and *Selenidera*

spectabilis); and although these two species belong to very different genera and are utterly unlike in appearance, I could never tell, from the sound alone, which was producing it. Another toucan (*Ramphastos tocard*) [= *swainsonii*] has altogether different notes."

Small parties of toucans were observed a number of times acting in a peculiar manner which could only be interpreted as play. As an illustration I give the following excerpts from my notes. "Barro Colorado, April 18, 1926: While paddling along the shore north of the Laboratory just before sunset this evening I saw fourteen toucans (*R. brevicarinatus*) scattered about in a big leafless tree on the edge of the jungle. Two appeared to be fencing. They stood in one spot and fenced with their bills for a half minute or so, rested, and were at it again. Presently they flew off into the forest and I then noticed two others that had now begun to fence. Then one of these flew away and the remaining one picked a new opponent and fell to fencing again. Soon the toucans began flying off into the jungle to the west, but one or two more contests took place before the last of them followed the flock. They did not move about much while fencing, although sometimes one climbed above the other as though to gain an advantage. They fenced with and against each other's beaks and seemed never to strike at the body. There was a fairly rapid give and take."

On the evening of April 24, 1927, I made further notes on a flock of eight that came into a big tree in the Laboratory clearing a little before sunset. "They kept moving actively about the branches but to no apparent purpose except that some seemed to approach others which fled away from them. For a moment two stopped and engaged in a brief fencing duel, the bills clattering loudly against each other. A little later four of them began to croak, but soon stopped and then all flew off together."

On April 27th (7 A. M.) I observed "two, doubtless a pair, sitting close together in a dead tree top preening their feathers. Then they playfully fenced softly with their bills for about a half minute." This last instance was to me strongly reminiscent of the way a pair of parrots will playfully tussle with their beaks.

The only published mention of such habits I have found is that by Goodfellow (1900, p. 129), who describes thus a flock of Ramphastos playing in Ecuador, "How I feasted my eyes on them as they gamboled among the branches of the great trees above us. I say gamboled, for that is what they were doing, chasing each other from branch to branch and snapping their beaks and making a peculiar rattling noise in their throats. One would throw a fruit into the air and before it could catch it again, another would seize it without any intention of swallowing it, but pass

it on like boys would a ball. I have never seen any other birds play together like a number of Toucans will, and on many occasions since I have watched them doing the same thing.'' Although this observer was writing for a rather popular audience and may possibly have embroidered a trifle upon his tale, yet what he saw was surely play, very much like some that I have myself witnessed. Playing, then, is apparently a regular habit among adult toucans of the genus Ramphastos. Although it may occasionally have some sexual significance, I believe that this is usually not the case.

It is always difficult to learn the roosting habits of birds and, in spite of every effort, I was not able to add much to our knowledge of this phase of the toucan's life. All Ramphastos toucans watched from the Laboratory flew off at sunset out of sight over the western forest. From the scanty information I was able to secure from natives and others, I strongly suspect that these big toucans roost in small flocks in hollow trees, and I actually found such a communal roosting hole of a smaller species of toucan (*Pteroglossus torquatus*) at the very edge of the Laboratory clearing. The cavity used was an old woodpecker hole some six feet from the top of a twenty-foot dead tree stub (Pl. II, Fig. 4). The hole had probably been made by a pileated woodpecker (*Ceophloeus lineatus*) and seemed rather small for birds the size of toucans, but on the evening of March 20, 1926, I watched four Pteroglossus fly down in rapid succession and disappear into the hole. For several nights afterward three or four of the little toucans regularly roosted there. As they entered the hole they could be seen to jerk their long tails back flat against their backs, thus saving much valuable space. In fact, I believe the extraordinary posture assumed by sleeping toucans (as described below) is directly correlated with their hole-nesting habit and more particularly with the communal roosting habit, for the habit of folding the tail flat against the back must aid their movements greatly in a confined space, and compensate in a measure for the awkwardly long beak.

The roosting posture has long been known from captive birds. Indeed, the best description ever given of this is that published by Broderip more than a hundred years ago (1825, p. 488). He described the roosting of a captive toucan (*Ramphastos monilis*) as follows: ''When he settles himself on his roost, he sits a short time with his tail retroverted, so as to make an acute angle with the line of his back; he then turns his bill over his right shoulder, nestling it in the soft plumage of his back, (on which last the under mandible rests), till the bill is so entirely covered that no trace of it is visible. When disturbed, he did not drop his tail, but almost immediately returned his bill to the comfortable nidus from

which, on being disturbed, he had withdrawn it. He broke, a short time ago, some of his tail feathers, and the proprietor informed me, that before that accident, the bird, when at roost, retroverted his tail so entirely, that the upper surface of the tail feathers lay flat over, and came in contact with the plumage of the back; so that the bird bore the appearance of a ball of feathers, to which, indeed, when I saw him at rest, *after* his accident, he bore a very considerable resemblance. The proprietor informs me that he always roosts in the same way."

The following year Vigors (1826, p. 480) described and figured this posture as assumed by a captive toucan in his possession. His bird was the type specimen of *Ramphastos ariel.*

FOOD

Very little information has been published on the food and the feeding habits of toucans, and much of this is conflicting. The Penards (1910, p. 4) and other very reliable authorities have said that the food of toucans consists entirely of fruit, while others have accepted Azara's statements and consider them carnivorous or at least omnivorous. I shall describe here the feeding habits of *Ramphastos brevicarinatus* only, but I may add parenthetically that the data I have on *Ramphastos swainsonii* and *Pteroglossus torquatus* indicates very similar feeding habits.

In addition to many field observations, I have examined the stomachs of twenty-four birds collected on Barro Colorado Island. All of these contained some fruit, and nineteen contained only fruit. Animal matter as well as fruit was found in the remaining five, but in only two cases did it constitute as much as half of the stomach contents.

The identification of the fruits eaten has proved rather difficult, but I believe that the eight species listed below include most of the important food plants of this toucan. All of the plant identifications were made by Dr. Paul C. Standley at the National Herbarium.

Astrocaryum polystachyum Wendl. (Phoenicaceae).

Iriartea exorrhiza Mart. (Phoenicaceae). A common palm.

Ficus sp. (Moraceae).

Virola panamensis (Hemsl.) (Myristicaceae). A very important food.

Cnestidium rufescens Planch. (Connaraceae). A common woody vine producing abundant red berries in the dry season.

Protium sessiliflorum (Rose) Standley (Burseraceae). A common tree with white fruits eagerly sought by all toucans.

Salacia sp. (Hippocrateaceae). Fruits in the wet season.

Cupania Seemanii Triana & Planch. (Sapindaceae). A common tree. (See Pl. I., Fig. 2.)

All of the above are important food plants.

Mr. F. M. Gaige has identified for me the animal matter found in the remaining five stomachs. One of them contained only fruit and a single ant (*Leptothorax* sp.) of a kind frequently found about fruit and so doubtless taken accidentally with it by the toucan. Of the four stomachs containing significant animal remains, two contained a large spider (Lycossidae) each and two contained a large cicada each. In addition to the usual fruit, one stomach contained fragments of a coleopteran and an ant (*Cryptocerus umbraculatus*). No animal matter was found in any of the other stomachs examined. It seems probable that cicadas are regularly eaten by toucans, for the only insect found in the stomachs of a series of *Ramphastos swainsonii* was another of these large cicadas. The number of stomachs studied is rather small, but it may possibly be significant that those which contained animal matter were all taken in the rainy season.

We have it from several authorities (as Gould, 1854, pp. 13, 15) that toucans prey upon the nestling young of other birds. None of these reports are very definite, but the story comes from several independent sources and there may well be some truth in it. I never saw any evidence of such habits myself, but Mr. R. R. Benson, who has done extensive bird collecting in Panama, says that he has seen toucans pulling out fledglings of the smaller woodpeckers and eating them. I have not as yet been able to secure from him any further details.

Hallinan (1924, p. 314) reports that the stomachs of two collected in the Canal Zone in November and January contained only "fruit fragments."

In December, 1927, Dr. A. O. Gross collected three females and a male at the United Fruit Company plantation at Monte Verdi, Costa Rica, and sent the stomachs to me for examination. One was gorged with bananas and the other three contained wild fruits which could not be identified. None of them contained any animal matter. The manager of the plantation stated that the toucans were very fond of bananas. Fortunately this is of no economic importance, because all of the bananas which are to be utilized commercially are cut when still green and only the fruit too small or poor to use is left in the plantations. The discards ripen on the trees or on the ground and become the favorite food of many birds and mammals.

The food of the nestling toucans I shall take up later in the discussion of the nest life.

The feeding habits of toucans may often be studied by watching near one of their favorite species of food tree which is in full fruit. During the early part of the morning especially, a small flock of toucans may

wander in to feed. They come straggling in, one or two at a time, until eight or ten or more have arrived. Larger groups are probably formed by the meeting of two flocks, for I have seen as many as twenty of this one species feeding in the same tree. Moving with long bouncing leaps out to the ends of the branches where the fruit is borne, each bird is soon busily gulping down the fruit. Here its huge beak certainly serves the useful purpose of increasing the bird's reach. Clinging with its stout zygodactyl feet to the outermost branch that will bear its weight, the toucan reaches out in every direction and may secure all the fruit within a very considerable radius without shifting its position. The fruits are seized between the tips of the mandibles and tossed back with an upward jerk of the head and then swallowed whole. Or, in some cases (as with the fruits of *Cupania Seemanii*) the outer husk is skillfully removed before the fruit is swallowed. It is difficult to see just how this is managed, but it is done very quickly with the mandibles alone. Often, very small berries are eaten and these are handled with equal skill with the fine tips of the mandibles. The fruits are not broken or crushed but are swallowed whole, even when they are great tough palm nuts three centimeters in diameter. Palm nuts and many other of their favorite fruits have large stony pits a centimeter or two in diameter but these fruits are swallowed intact like all the rest. The fleshy pulp is the part of the fruit used and, after this is digested off, the hard pit is regurgitated and ejected through the mouth. Numbers of such pits the size of large marbles are ejected by the toucans while incubating and come to form the lining of the nest.

Since toucans are common in this forest and live largely on fruit, they may be of considerable importance in the wide dispersal of the seeds of forest trees.

I have never happened to see wild toucans come down to the water to drink, but captive birds are very fond of water and require a rather large amount. Dr. Wetmore (1926, p. 210) observed the big *Ramphastos toco* drinking from a forest stream. He writes, "on one occasion one descended to a perch on a tree root fully 15 inches above the inky water of a lowland stream in order to drink. It bent over gingerly, hesitating several times before dipping the tip of the bill in the water, a caution directed by the presence of savage fish and *jacarés* (alligators). When a few drops of water had been secured the head was thrown back and the fluid swallowed."

Much has been said about the "fierce struggle for existence" in the tropical jungles and a life history study such as this might well be expected to show more definitely just where the results of keen competition are felt. Few factors are as important in the life of an animal as the food supply. It is therefore of particular interest to find that this has apparently no

restrictive effect upon this toucan. Its food consists largely of fruit, of which there is certainly a very large supply at all times of the year. Fruiting plants of many kinds are abundant and, in spite of many other species that share this food with the toucans, a large excess is always left to fall to the ground.

BREEDING HABITS

In spite of the abundance of toucans in most tropical American forests, their nests are rarely found. Carriker, in all of his experience in Costa Rica and Colombia, apparently never found the nest of a Ramphastos. The Penards in Guiana wrote that they had never seen the eggs or young of any toucan. This is probably due to the fact that toucans are very shy and suspicious in the vicinity of their nests and the nests themselves, because of their situation in natural tree cavities, are very difficult to locate. Also, the nests are frequently at great heights from the ground and quite inaccessible.

In spite of strenuous efforts throughout two breeding seasons, I was able to find but five nests of this species. All were in natural cavities in large trees (*Cupania Seemanii, Hura crepitans,* and *Inga* sp.) but their positions varied greatly. One was over ninety feet above the ground (Pl. II, Fig. 3), while others were seventy, forty, twenty-one, and nine feet high. In fact, the actual nest cavity of the lowest one (Pl. III, Fig. 5) was only three feet above the ground, but the entrance hole was six feet above the nest. In the other four nests the cavity was three to sixteen inches below the entrance hole. In three of the nests, the entrance hole was only three and a quarter inches in diameter, barely large enough for the birds to squeeze through (Pl. IV, Fig. 8). In fact I twice saw male toucans stick momentarily when they became alarmed and tried to make a too hasty exit. The entrance holes of the other two nests were about twice as large. The toucans do no excavating, merely cleaning out the loose débris in the natural free cavities and laying their eggs without any nest lining whatever.

In a nest of this type the incubating bird is of course completely concealed, thereby removing any need for protective coloration of the bird itself. It is doubtless this very fact which has permitted the toucans to develop the brilliant coloration in both sexes, for a large and conspicuously marked bird like a toucan could not possibly survive in a less protected nesting site

On April 4, 1926, I first found the eggs of this species. Since then I have found two more sets. The eggs are dull white in color and are curiously sculptured with irregular pitted grooves extending lengthwise

along the egg and becoming most prominent at the large end. At the small end of the egg they become less distinct or disappear entirely. The yolk is of a rich orange color and this gives a suffusion of pink to the fresh egg which is lacking after it has been blown. As shown by the measurements and by the photograph (Pl. IV., Fig. 7), the eggs are very rounded in shape, with one end but slightly more pointed than the other. The number of eggs in the nests found were one, three and four. A fourth nest when found, contained a single young one only a few days old.

Number in set	Long diameter in millimeters	Short diameter in millimeters	Weight in grams
4	38.5	28	[3]
1	40.5	29	17.0
3	38.	30	17.4
	39.	30	17.8
	39.	30	18.0

There appears to be no previous authentic account of the eggs of this toucan. However, what may have been the eggs of this bird are described by Todd and Carriker (1922, p. 233) in their account of the birds of the Santa Marta region of Colombia. Their description is as follows: "A set of two eggs, taken from a 'nest in a large hollow tree,' are in the Smith collection, labeled Bonda, May 12. They are soiled white in color, and measure 35 x 27.5, which seems small for the size of the bird." But the identification is not very certain, as the authors themselves state (p. 38), "The really unfortunate part about this collection, however, would appear to be the unsatisfactory identification. The skins sent as 'markers' for the determination of the nests and eggs are in no case the parent birds, but merely specimens supposed by the collector to belong to the same species. The risk of error was thus considerable * * * *. An examination of the set of nests and eggs sent to the Carnegie Museum discloses numerous discrepancies, * * * *." I would suggest that the eggs they described were perhaps those of the smaller *Pteroglossus torquatus*. The only toucan egg described in the British Museum catalogue of birds' eggs is that of *Pteroglossus flavirostris* (Oates and Reid, 1903, vol. III, p. 137) previously described by Ihering and by Nehrkorn. Ihering (1900, p. 262) has also described an egg supposed to be that of *Ramphastos ariel*. A third species of toucan egg previously described and the only one ever figured is that of *Ramphastos monilis* by Beebe (1917, p. 195).

Apparently each nest cavity is used year after year by the same pair of toucans, and long before the time for egg laying, the pair returns to the

[3] This set of four eggs hatched before the rest of the measurements could be taken.

hole and occupies it. In several cases I observed this re-occupation of the nest hole a month or even six weeks before the eggs were finally laid. The number of suitable natural tree cavities is so small compared with the toucan population that this early preemption of the nest site may have the important function of assuring the pair of a safe place to nest when the proper time comes. They do not use it as a roosting place, but hang about almost constantly during the day. In the rainy season several inches of rotten wood and débris accumulate in the bottom of the cavity and the toucans now clean this all out, leaving only a few chips to line the nest. They also begin to bring small green leaves, up to two and three inches in length, into the nest. Nearly every day a fresh green leaf or two is left in the nest and when the leaves dry up they are frequently carried away again. I could see no reason for this habit and can only call attention to the fact that certain hawks and other birds have a similar custom. The only other accretions in the nest cavity at this time are fruit seeds and pits resulting from the toucans' habit of disgorging the pits of fruits which form their food. Like the pellets of owls, these pits are disgorged at irregular intervals between meals and soon they line the whole nest cavity. As a result the eggs are later laid and the young reared in a nest with a "cobble-stone" lining of fruit pits the size of large marbles.

The sense of ownership is very strong at this period and human intruders are frequently scolded quite strenuously by both birds. However, there is not as much anxiety shown as after the arrival of the eggs and young and, after croaking a few minutes, the pair usually fly quietly away and desert the nest for several hours. If undisturbed, they spend a large part of the day sitting quietly in the entrance hole or on a branch nearby.

In the single instance in which I was able to follow closely the laying of a set of eggs, they were laid one each day on three consecutive days. The last one was laid early on the morning of April 24, 1927. Both sexes are almost constantly near the nest at this time and go in and out of the nest cavity frequently, but incubation does not begin until the set is complete. At about the same time I was able, by chance, to observe the female at another nest actually in the act of laying an egg. The nest had been used the previous season and, in order to be able to study the progress of things, I had made, at the level of the nest, an artificial window which I kept plugged when not in use. The nest cavity itself was less than four feet above the ground but the entrance hole used by the birds was about six feet higher. Since the toucans were showing every sign of using the cavity again in the season of 1927, I kept it under close observation. When I approached at 9:30 on the morning of April 23rd the male flew from the nest hole and began to croak in alarm from a nearby tree. Assuming that

the nest was now empty, I took out the plug and was amazed to find the female on the nest. She was alarmed but refused to leave the nest or even move when touched. Her position was doubtless the usual one assumed by toucans on the nest. Although the cavity was eight inches in diameter, there was not room for either the bill or tail in a horizontal position. The bill was pointed almost directly upward with the tip against the wall of the cavity in front of and above the sitting bird. The tail was rested similarly against the rear wall and not folded down upon the back as might be supposed from the position taken by toucans when roosting. Finally, I raised the sitting bird a little and could see the white egg projecting from the cloaca. But this was evidently too much of an intrusion for, as the plug was replaced in the "window," she was heard scrambling up the nearly vertical shaft to the entrance hole where she then appeared and flew out to join the male in croaking at the intruder. A reexamination of the empty nest cavity showed that she had not completed the laying of the egg. The pair continued to use the nest but did not begin egg laying again for several days and then the unusually early rainy season began and prevented further nesting operations.

All my attention was then devoted to the previously mentioned nest with three eggs. A blind had already been placed near the nest and there I spent many hours watching the nest life of the unsuspecting toucans. In the blind, mosquitoes and ticks were rather troublesome, but this was more than compensated for by the opportunity it offered to watch these splendid birds going naturally about their nesting activities. The nest (Pl. III, Fig. 6 and Pl. IV, Fig. 8) was twenty feet above the ground in a natural cavity of a Gorgojo tree (*Cupania Seemani*). The heavy jungle about it is fairly well shown in the photograph. The blind, situated at that time across a narrow ravine, was on a level with the nest and commanded an excellent view of its surroundings.

Both toucans sometimes left the nest locality, but not for long. Usually within fifteen or twenty minutes one of them would be seen returning. This was sometimes heralded by a short period of croaking from a neighboring tree top. Then the returning bird would fly into the top of the nest tree and, after a short pause, come deliberately down to the nest by short flights from one liana or branch to another. Often there was a pause of several minutes on a favorite liana just in front of the nest hole while the bird peered slowly about and up and down with that strange deliberative air which only toucans have. Then, if all seemed safe, it would fly to the hole and cling to the rim for a moment with its great beak in the nest but with head and eyes still outside and, after a final look around, clamber into the hole. Both sexes shared in the duties of incubation and relieved each other

frequently. During the first few days of incubation, when these observations were made, they were surprisingly restless and frequently stayed on the nest only twenty minutes to an hour before being relieved, or left without being relieved. They were clearly not alarmed about anything, but seemed merely to be bored with the unaccustomed monotony. Several times during a shift the sitting bird would appear at the entrance and hang its great beak straight down from the hole for minutes at a time while gazing idly about. Finally it would withdraw into the nest again only to repeat the process a little later. Or, it would sometimes come entirely out and sit on the nearest liana and preen itself thoroughly before returning.

Several authors have expressed the theory that the toucan must use its powerful beak to defend its home against marauding monkeys or snakes. For instance, Belt (1874, p. 197) wrote, "I believe that the principal use of the long sharp bill of the toucan is also that of a weapon with which to defend itself against its enemies, especially when nesting in the hole of a tree. Any predatory animal must face this formidable beak if seeking to force an entrance to the nest; . . ." Doubtless a toucan *could* use its beak very effectively from the shelter of a hole, but these birds and others which I watched showed not the slightest tendency to do so. They have very good hearing and quickly detect the approach of danger, but their invariable reaction is to scramble out of the hole, fly up into the branches above and then, if the danger is a real one, they begin to croak in alarm. This invariably brings the mate upon the scene and the two continue to bob and croak as long as the danger remains. Once a panic-striken agouti, dashing up the ravine past the nest, brought the sitting bird out in alarm, but when she saw the animal disappearing up the ravine, she quietly began to preen herself and soon returned to the nest. When, however, the danger proved real, the bird always sought the higher branches and croaked in protest. It was interesting to note that small birds were allowed to feed close to the nest without interference and even large species were usually not molested. Once a great curassow (*Crax globicera*) walked directly across the nest without causing alarm. *Ramphastos swainsonii,* a closely related toucan, sometimes chanced fairly near the nest without being disturbed, but I never saw a strange toucan of the same species near a nest and feel sure that they are not tolerated within the nest "territory."

When leaving the nest they would again go up to the higher branches before flying off, but instead of flying up to the top of the tree, they usually climbed the lianas, progressing by a series of jumps until they reached the desired altitude.

As already stated, the two sexes frequently relieved each other at the nest. No ceremony of any kind attended the nest relief. The relieving

bird merely flew down and lit in front of the nest hole. Whereupon the sitting bird came out and flew away while the relieving bird immediately took its place on the eggs.

Because of the unusual rainy season which finally destroyed the nests I had under observation in 1927, I was unable to determine the length of the incubation period.

On April 2, 1926, I found the first nest of *Ramphastos brevicarinatus*. It was in a natural cavity seven meters from the ground in a Gorgojo tree (*Cupania Seemani*) and contained four eggs. All four eggs hatched on April 5 and the egg shells were immediately removed by the old birds. The details of the hatching process could not be adequately observed, but apparently did not differ from the usual method. The constant calling, so characteristic of young toucans, was remarkable from the first. As early as the first pipping of the egg shell, the young bird could be heard constantly repeating its low rasping note.

When newly hatched, the young toucans presented a very strange appearance. The many obstacles in the way of tropical forest photography prevented my securing a satisfactory picture during the first few days, but the accompanying photograph (Pl. V, Fig. 9) taken at the age of ten days shows with but slight change the appearance of the recently hatched young. They were entirely naked and of a pinkish flesh color at first. Within a few hours this changed to a peculiar golden hue which was retained until the feathers began to cover the body nearly a month later.

Several morphological peculiarities were noticeable. The head was large in proportion, and the bill, though not disproportionately long, was rather broad and heavy. The lower mandible was the longer, jutting out two millimeters beyond the tip of the upper. This persisted for some time and not until the tenth day were the two mandibles equal in length. I am at a loss to understand what significance this may have, but it is certainly very different from the usual condition found in other birds. In the hornbill, however, Shelford (1899) has described and figured a similar condition, and in view of the parallelism between the hornbills and the toucans it may be desirable to compare further the condition of the nestlings of the two. The young hornbill, Shelford states, has no egg tooth, while the young toucan has a well-developed one. In general the bill of the newly hatched toucan seems to be more like the adult form than is that of the young hornbill. Also, the young toucan has far more highly developed heel-pads than has the hornbill. The unusual length of the pygidium of the adult toucan was foreshadowed from the very first by a marked development in the young and it was even held customarily at a sharp angle with the body in the manner so characteristic of the adult.

During the first few days the young toucans were very weak and helpless, resting on the tripod formed by the heel-pads and the abdomen, but only able to raise their heads for a few seconds at a time. When disturbed or alarmed in any way they pushed out vigorously with their strong heel-pads and moved away backwards regardless of the source of the alarm.

The most striking feature of the nestling toucan is the presence of these well-formed heel-pads. The joint between the tibio-tarsus and the tarso-metatarsus is covered with a thick horny pad, studded with strong projecting tubercles (Pl. VI, Figs. 12 and 13). The pad is roughly oval in shape, and measures about 22 mm. in length and 11 mm. in width. Around the outer edge is set a ring of nine or ten strong, cusp-like tubercles ranging in size from the largest at the anterior (or distal) end to much smaller ones at the posterior end. The pad is a definite, well-defined structure, not a mere callosity of the integument. The tubercles are arranged in a definite manner and their number is constant, except that the smallest is sometimes absent, leaving but nine. After the young bird has left the nest the heel-pads gradually become loosened and are sloughed off, leaving on the heel of the adult no trace of their former presence. The heel-pads are usually shed before the molt of the juvenal plumage.

The heel-pad of nestling toucans was first described by Seth-Smith (1913), who figured a young *Selenidera maculirostris* which was hatched in the Zoological Gardens of the Zoological Society of London, the only toucan ever hatched in captivity. His drawings are not very detailed, but apparently show a heel-pad similar to that in Ramphastos, although less specialized in form. The tubercles are not confined to the outer edge, but cover the pad in a more irregular fashion, and the whole pad seems to be more fused with the integument and not as sharply defined as in Ramphastos.

A few years later Beebe (1917, p. 204) found the young of *Pteroglossus aracari* in Guiana and published drawings of the heel-pad in this species. As would be expected in this more specialized toucan, the heel-pads are more highly developed and approach very closely the type found in Ramphastos. That is, the tubercles are here largely confined to the periphery and the pad is more sharply differentiated.

Still more recently, Gyldenstope (1917, p. 3) has described and illustrated the heel-pads of *Pteroglossus torquatus,* but his figures are not of much use because they are based upon dried skins of well-grown birds in which the heel-pads were worn and badly distorted by drying.

The heel-pads of Ramphastos, the most highly evolved genus of toucans, have not before been described or figured.

Although the morphology of nestling heel-pads has been correctly described by several writers, yet some rather strange guesses have been made

with regard to their function. Seth-Smith even said they enabled "it to climb up the sides of the hollow cavity in a tree in which it is hatched." This would, of course, be a physical impossibility and would not be of the slightest use even if it were possible. The nestling does not leave the nest until it is strong and well feathered and can scramble out the same way its parents do. The function of the heel-pads is, I believe, simply to form a pair of substitute feet during the long period of helpless nest life.

Young birds may be roughly grouped into two classes, altricial and praecocial. The praecocial young are hatched thickly covered with down, with their eyes open, and able to run about almost immediately. From this type a graded series leads to the altricial type which are hatched naked, blind, and helpless. The toucan apparently marks the farthest point to which the altricial type has evolved. The praecocial type is evidently the primitive type of nestling, for all of the more primitive groups of birds, such as the grebes, gulls, rails, and pheasants have praecocial young, while all passerine birds have altrical young. If we classified birds according to the condition of their young, we should have to place the toucans at the climax of the system. The toucan nestling is hatched naked, blind, and very helpless. The eyes do not even open for three weeks, and the young one is very weak and awkward much longer than that. The feet are quite useless, but, by shortening the leverage and using its heel instead, it is able to sit up within a day or two. As shown in the accompanying photographs, the young toucan rests on a tripod formed by its abdomen and the two legs. The spiked pads protect the exposed heel joint from the rough, unlined nest cavity and even form a sufficiently roughened point of vantage so that the nestling can stump about rather actively.

Even before hatching, the fourth toe of the nestling toucan was turned backward, paired with the first toe and opposed to the second and third, just as in the adult, while in nestling parrots of the same age I found that the toes had not yet assumed the adult position.

The wings were very small and feeble at first, but the thumb was large and prominent. Only the slightest indication of the future position of the flight feathers could be observed. By the fourth day, the pattern of the feather tracts of the body was visible and the ten tail feathers had become a row of little spikes a millimeter or two in length. Thus the tail feathers made a start before the wing feathers, but at this point they ceased to grow and made no further progress for more than three weeks. The wing feathers made no growth during the first two weeks but at fifteen days they began to push forth and then grew rapidly. It was interesting to find that there was no retardation of the growth of the inner primaries such as Chapin (1921) has described in woodpeckers.

At the age of fourteen days all of the feather tracts had become well marked, with the ventral tracts and the major upper secondary coverts most conspicuous. The following day the remiges, especially the primaries, had suddenly begun to grow and from that time on their growth was constant and rapid. Indeed, throughout the development period of the nestlings it was a striking fact that changes in mental as well as physical growth appeared very suddenly. For instance, on the eighteenth day all of the nestlings began to flap their wings vigorously. They had never done it before, but from that day on it was an important part of their activity. A day earlier they had suddenly evinced a desire to seize in their mouths and try to swallow anything that came within reach. Their eyes had not yet opened, but they were very active and constantly grabbed at my fingers, making it very difficult to handle them while taking their daily measurements. By the nineteenth day the secondaries had also begun a rapid growth, but still the rectrices remained the little spikes produced in the first three days after hatching. At twenty days the contour feathers over all the body except on the head, broke through the skin and began to grow rapidly, while within two or three days the capital tract also started its growth. Then the eyes began to open, but this was a slow process and it was several days before they had opened enough to permit vision. At the same time the voices of the nestlings changed abruptly. Instead of the almost constant buzzing or rasping note, they now uttered, when disturbed or hungry, a low harsh *wraa, wraa, wraa.* On the twenty-third day the tail feathers suddenly began to grow and thereafter progressed rapidly. The following day the remiges and the upper coverts of the secondaries began to unsheath, but, as well shown in figures 14 and 15, the primary coverts were still very small and undeveloped. By the thirty-third day the feathers began coming out rapidly all over the body and even the red feathers of the lower throat were plainly visible. At the same time the tail finally began to make rapid growth. The young birds were then very active and showed more fear than at any previous time. During the next two or three days they rapidly became more easily frightened and would dodge actively when I reached to pick them up. At this point I was interested to find that a young bird kept as a control, which I had never handled or taken from the nest, was hardly more wild when taken up than other young which I had handled and measured daily. Its measurements also checked closely with those of the young which I handled daily for five weeks.

In addition to the daily routine of measuring and photographing the young toucans, I wished to observe the activities of the parent birds while feeding and caring for the young. For this a blind was necessary and fortunately the steep hillside on which the nest tree was located provided an

excellent position. Here a blind of saplings and burlap furnished a comfortable observation post within fifteen feet of the nest and but slightly below it. I spent many hours in the blind and came to know with some intimacy the home life of these splendid birds. They soon ignored the blind completely and came and went entirely unaware of my close proximity. Whenever they sighted me anywhere in the vicinity of the nest tree, they always dropped everything else and croaked in alarm until they saw me safely out of the neighborhood. But by approaching cautiously and entering the blind while they were away in search of food, I could study their habits at close range without disturbing them in the least.

Perhaps the nesting activities may be best described by quoting directly from my notes. For example, the following are one morning's notes exactly as written on April 27, 1926, when the young were twenty-three days old.

"Entered the blind at 8:30 A. M. The young can be heard calling almost constantly. An old bird is croaking in the distance. 9:03—the male came and lit on a liana near the nest. After peering about a few seconds he flew to the nest hole and clung to the entrance, woodpecker fashion. He stuck his head in, jerked it back to look around, then in again, etc., four or five times, very like a woodpecker. Finally he reached in and fed the young. After feeding them a berry, he flew to a branch nearby and then off east out of sight. The young were unusually noisy for several minutes afterwards. 9:10—the male arrived and then the female. The male had a berry in his bill and soon flew to the hole and, clinging there, fed it to the young. Then swinging his bill away from the hole and downward, he regurgitated another berry from his crop and fed this to the young. He then flew away and the female flew down to the hole with a berry in her bill, coming out head first a moment later without the berry. She flew to a nearby branch and brought up another berry from her crop, and, returning to the nest, fed it to the young from the entrance. Repeating the process a third time, she went into the nest and after a short delay emerged with some droppings in her bill and flew off with them. 9:20—male came and fed the young several fruits from the entrance in the usual way. 10:05—male came with a large fruit in his bill and perched for five minutes on his favorite liana near the nest hole. Then he flew to the hole, went in, and presently emerged head first and flew off. 10:11—the female came to the hole, reached a berry in to the young and then flew up to her favorite perch close by. Here she brought up another from her crop, took it to the entrance hole, fed the young and flew off. 10:35—female returned with a green crescent-shaped object which she fed the young from the entrance, and then successively regurgitated and fed to the young in turn another crescent-shaped object and two large red berries. The last time she went on into the hole, soon

came out with a big beakful of droppings and flew off. 11:00—I left the blind, and climbed to the nest and took out the young and gave them their daily measuring, etc. Left again before the old birds returned.''

With some variations, this was the regular routine. The young were fed very largely on fruit but sometimes animal matter was brought. When the young were twelve days old, I found in the nest the posterior fifty centimeters of a tree snake, *Oxybelis* (probably *accuminatus*). While I was watching the nest on the twenty-fourth day after hatching, I saw the male bring a small lizard which he had apparently just caught. Alighting near the nest he struck the lizard sharply on a limb several times and then flew down and fed it to the young birds from the entrance hole, after which he disgorged and fed them successively four large white fruits. When the young were thirty-six days old I found in the nest the body of a giant forest grasshopper (*Tropidacris*). With these three exceptions, I saw nothing but fruit brought to the young.

The young were never brooded during the day, but they seemed to require the protection provided by the nest hole and by close contact with each other for they always began to shiver soon after they were taken from the nest even though the outside temperature was over 80° Fahrenheit.

On the night of May 10th, when the young were thirty-six days old, the nest was broken into by some predacious animal, and the next morning I found it empty. Therefore, I was not able to determine the exact period of nest life of the young toucans, but from their known rate of growth and the measurements of young collected immediately after leaving the nest, I believe that they would have left the nest in ten days or at the age of about forty-five days.

There is certainly but a single brood raised in a season.

The principal facts of the reproductive cycle may be very briefly summarized as follows: *Ramphastos brevicarinatus* breeds only in the dry season and raises but a single brood, although probably remaining mated throughout the year. The nest is a natural cavity at almost any height in a forest tree and is apparently used year after year by the same pair of birds. One to four white eggs are laid and are incubated equally by both sexes. The young are hatched naked and are quite helpless in the nest for a long period. They are well adapted for this by the possession of elaborate heel-pads, a remarkable coenogenetic character. The young are fed by both parents and subsist largely on fruit. They are able to leave the nest at the age of about forty-five days.

ENEMIES

In any discussion of the life history of a species a knowledge of its enemies or of other factors controlling its increase is most important. It is

commonly assumed that some enemy or enemies actively preying upon it determine the abundance of an animal, but I doubt whether this is often true. In the case of *Ramphastos brevicarinatus* none of the enemies observed appear to be of great importance. A number of mammals of the Panama forest regularly prey upon birds and their eggs, and of these, the coati (*Nasua narica*) is certainly the most important at Barro Colorado. The nests of antbirds and other small birds were found to suffer severely from the raids of coatis, and on one occasion a toucan nest under my observation was certainly robbed by these agile climbers. But most of the toucan holes are too narrow and deep for the coati. The same obstacles, together with concealment, would also secure most toucan nests from the attacks of monkeys, another common enemy of nesting birds in that forest. Certain snakes are also a danger to many bird's nests and even to the birds themselves. I once found a large boa coiled about the entrance hole of a toucan nest and, if I had not removed it, the snake would doubtless have secured the eggs and perhaps the parent birds as well.

Several writers describe the toucans as mobbing hawks and owls after the manner of jays. I have never seen this happen and I suspect that it may not be very characteristic of the toucan. Twice only I saw a small mixed flock of toucans gathered about a hawk. They all kept within twenty feet or less of the hawk and followed it closely when it moved. However, they made no outcry or demonstration of any sort and were so perfectly peaceful in their actions that I was wholly at a loss to understand the meaning of the gathering. Because of their size and strength toucans are probably safe from the attacks of most birds of prey. As far as I can judge, none of these enemies are as important in controlling the increase of toucans as the available supply of nest sites, the parasites of the nestlings, and other such factors.

PARASITES

This species, like most toucans, was usually heavily infested with a variety of external parasites. All of the toucans I collected carried solid masses of feather mites (Proctophyllodinae) on the vanes of the flight feathers. Sometimes these were the only parasites found. But in most cases, there were three or four to more than a hundred Mallophaga of two species (*Philopterus cancellosus* and *Myrsidea vixtrix*) to be found on the head, throat and wings. The throat feathers were sometimes heavily incrusted with their eggs. A few ticks (Amblyomma) were nearly always found fastened on the bare skin of the face and throat. The only Hippoboscid fly seen was a single specimen of *Lynchia fusca* collected on a juvenal bird in August. It may be that they are most frequently found on young birds, for the only other Hippoboscid fly I ever saw on a toucan was on a young *Ramphastos swainsonii*.

Other Diptera were found to be parasitic on the nestling toucans. In the nest of four young I was observing in 1926 two were parasitized by dipterous larvae under the skin of the lower neck and back. There were two on one bird and one on the other. I first noticed the larvae when the nestlings were sixteen days old. At twenty-one days C. T. Greene of the National Museum, who happened to be at the Laboratory, cut out one of the larvae and reared it to maturity. At thirty-six days I extracted another one which was about to emerge. Mr. Greene has identified the adult as *Philornis pici*. The larvae appeared to cause the young birds no inconvenience and when in such small numbers they probably emerge without any real harm to their hosts. However, this genus of flies has sometimes been found in large numbers on nestling birds, greatly weakening them or even causing their death. Other larvae found among the debris in the bottom of the same nest were reared by Mr. Greene and identified as two species of scavengers, *Hermetia illucens* and *Milichiella* sp. From the very moment of hatching the same nestlings were heavily infested with small mites which have been determined to be *Liponyssus* (near *americanus* Banks).

In spite of rather careful examination, I found no internal parasites in any wild toucans I collected. However, Mrs. A. H. Bryan, of Ancon, tells me that captive toucans are often killed by tape-worms if allowed to eat meat.

In view of the specific host requirements of many parasites, it is interesting to note the other hosts used by some of these parasites. *Philopterus cancellosus* was first described from *Rhamphastos swainsonii* in Costa Rica. In my Panama collections it occurred on all three species of toucans collected: *Ramphastos swainsonii, R. brevicarinatus,* and *Pteroglossus torquatus. Myrsidea vixtrix* has been previously recorded from *Ramphastos swainsonii* in Colombia. The same tick seems to parasitize a great variety of birds. *Philornis pici,* the fly larva, had previously been found in a woodpecker (*Chryserpes striatus*) and a palm chat (*Dulus dominicus*) in Santo Domingo and Mr. Greene has so identified larvae which I collected from an adult wren (*Troglodytes musculus*) in the Canal Zone. So it appears that these Mallophaga are probably confined to toucans, but that the other parasites of *Ramphastos brevicarinatus* are less specific in their host requirements.

The above parasite identifications have been made for me as follows: the mites and lice by H. E. Ewing and G. F. Ferris, the ticks by F. C. Bishopp, and the flies by J. M. Aldrich and C. T. Greene.

PROTECTIVE COLORATION

Gerald Thayer (1909, p. 109), who was familiar with the toucans on the island of Trinidad, wrote concerning the protective effect of their

coloration as follows: "The toucans, also, with their great amount of sharply defined black, are best fitted for obliteration in the intermediate woodland realms, where darkly shadowed big branches and tree trunks contrast with sun-spots and gay vistas. But they are also tree-top birds, high-perchers, and their vividly patched costumes of course stand them in good stead in these situations also, in spite of the redundant black. This usually covers the head, back, wings and tail; while the underside is marked with big patches of bright color—red, orange, yellow, white—sometimes all four together—more or less blended into one another, but ending sharply against the black. The huge but almost weightless bill also is brilliantly adorned with yellow, white, or flaming orange, in bold bands and stripes, and the naked skin around the eye is usually bright colored—blue-purple, peacock-blue, or green. Truly, toucans are gorgeous birds! But it by no means follows that they are conspicuous in their native woods! Not even though they are vociferous and active, and often alight on exposed tree-top perches. Here or lower down in the forest, their gaudy 'ruptive' patterns 'break them all to pieces' and though the predator at whose approach they 'freeze' into rigid stillness may espy the black piece, or the red piece, or the yellow or blue piece, he is still far from sure to recognize his quarry, for none of these pieces has the form of a bird."

Ferry (1910, p. 266) also mentions the brilliant yellow throat patch: "This stands out in bold relief and seems utterly detached from the bird. It might be a yellow leaf or a piece of hanging fruit."

I should not wish to state dogmatically that there is no such thing as protective coloration among toucans, but, after nearly a year of field experience with this and two other species in Panama, I feel sure that it is of very slight importance. It is quite true that in many situations in a tropical jungle, if a toucan *does* sit quietly, the yellow throat and bill stand out alone and readily pass for a yellow fruit or leaf. But the actions of a toucan usually defeat any effect of protective coloration. At the first sign of danger, the toucan almost invariably begins to bob about on its perch and croak loudly, advertising its presence to all within a half mile or more.

I would summarize my conclusions thus: the toucan is not as conspicuous in the tropical jungle as one familiar only with northern birds might suppose, but, on the other hand, it seems extremely doubtful whether protective coloration has any real significance in the life of this species. This has been well stated by Chapman, our best authority on neotropical birds. Speaking of toucans and other brightly colored birds in the tropical and subtropical zones of Ecuador, he writes (1926, p. 132): "The essence of both habitats is luxuriant forest-growth in which color, assured of protection because of its comparative inconspicuousness or because of ever-present

opportunity for concealment, runs riot. * * * * Hummingbirds, Trogons, Toucans, Tanagers, and other brilliantly colored birds abound in each zone, not because of the characters which distinguish the zones, but because both zones possess the luxuriant forest-growth which, as a rule, is essential to the existence of brightly plumaged birds, just as a coral reef is essential to the existence of brightly colored fishes."

THE TOUCAN BILL AND ITS SIGNIFICANCE

The most striking fact about the toucan is the enormous size of its bill. Doubtless among the first natural objects brought back from the tropics of the New World were the bills of toucans. Indeed, the earliest record of the discovery of toucans is a description of the bird and its enormous beak by Oviedo in his Sumario de la Natural Historia de las Indias published in 1527. From very early times men have wondered why the toucan should have such a bill. Linnaeus and Buffon considered it a grave defect of nature and looked with pity on the poor overburdened creatures, but most writers have sought for some adaptive function and have usually found it. The list of conjectures covers most of the possibilities. Charles Waterton wrote to Traill from Guiana that the toucan's bill "contains a delicate net-work of bony matter" supporting a "great number of blood-vessels." From this Traill (1815) argued that the toucan bill was "an admirable contrivance of nature to increase the delicacy of the organ of smell." In this he was followed by Swainson and others. Then Sir Richard Owen studied the anatomy of the toucan bill and published an account in Gould's first monograph (1835) showing that the idea was untenable and advancing the theory that the extraordinary development of the toucan's bill compensated, by its great power of mastication, for the lack of grinding structures in the gizzard. This theory has had its followers ever since, although it seems to have no foundation in fact. Another theory was that of R. P. Stevens (1870), who stated positively that toucans use their great serrated beaks to saw off the deep corollas of flowers in order to obtain the insects therein. Shortly afterward, Belt (1874) in his famous book on Nicaragua made the much more plausible suggestion that the "principal use of the long sharp bill of the toucan is that of a weapon with which to defend itself against its enemies."

These are but a few of the ideas which have been put forth to explain the toucan's bill, but they will serve to indicate their range and variety. My own opinions on the subject are not as definite as I could wish, but at least they are based upon a certain amount of actual knowledge of the bird in the field, which most of my predecessors have lacked.

It has always been assumed that the great beak of the toucan must have *some* adaptive significance and that the only problem was to find for *what*

purpose it was adapted. But this seems to me to be an essentially unscientific method. It is surely false to assume that every character of every organism has an adaptive significance. With this in mind, I have endeavored not only to find the use to which the toucan bill is adapted, but also whether it has any particular adaptive significance. After the most careful study of the living bird in its natural habitat, and of its anatomy, I cannot believe that the enormous bill has any especial adaptive function. I have examined all of the various theories which have been put forth and I find that none of them will stand the test of critical examination. It seems hardly worth while to refute each one in detail for most of them have admittedly been mere guesses and none has received any particular support. It is obvious that hardly a size or shape of bill could be devised which would not have certain useful features in particular situations and in the case of the toucan there seem to me to be two such useful functions. As a means of defence the powerful beak is no mean weapon. I have attempted to pick up a wing-tipped toucan and learned at first hand the damage it can inflict. But nevertheless, it is too much to ask that we believe that the clumsy, slow-flying toucan maintains its great numbers in the face of serious competition from large predacious animals. I saw absolutely no evidence of such enemies and I feel convinced that the toucan population is controlled mainly by parasites, available nesting sites, and similar factors. A second useful function of the toucan's beak seems to be that it enables the bird to reach with greater ease some of the fruits which form its food, but this again can hardly be a very important factor because of the great abundance of fruit available without such reaching. It is probably an incidental convenience rather than an important adaptation.

In brief then, I feel that the bill of the toucan is not a special correlation of structure to function as in the case of the woodpeckers or grosbeaks, for instance, but is rather to be explained perhaps as the result of an orthogenetic evolution leading toward increased size of bill. There are a number of cases already recognized in which there has been a steady trend in evolution apparently without the guiding influence of natural selection, and it seems to me that this is probably another example of the unknown process or processes which we term orthogenesis.

SUMMARY

For the sake of convenience I may summarize very briefly the more important points brought out in this study as follows:

Ramphastos brevicarinatus is described in detail and certain variations noted. This species molts but once a year and its method of molt is peculiar in several respects. The feather tracts are described and the unique con-

dition of the tail-coverts discussed. Concerning the anatomy, only the peculiar gall bladder and the asymmetrical testes are described.

This species ranges throughout the tropical forest from Honduras to north-western Colombia.

In the Panama Canal Zone it is the most abundant large bird in the jungle.

The flight of this bird is simple and direct, but very weak.

The toucan's only call is a monotonous, frog-like croak.

The toucan has the habit of playing, which takes the form of mock fighting with the great beak.

The toucan apparently roosts in holes in trees, assuming a most extraordinary attitude which saves valuable space in the hole.

The food of this toucan is very largely fruit, together with a few large arthropods.

The food supply is always more than adequate, thus eliminating any competition at that point.

This toucan breeds in the dry season only, nesting in natural cavities at almost any height in a forest tree.

Both sexes share in the duties of incubation.

The young are hatched naked and are helpless for a long period.

The young are well adapted for their nest life by the possession of elaborate heel-pads, a remarkable coenogenetic character.

The young are fed by both parents and subsist largely on fruit.

The young leave the nest at the age of about forty-five days.

Several mammals and snakes prey upon this toucan, but its numbers are probably controlled more by the shortage of nest sites, the parasites of the nestlings, and other such factors.

A great variety of external parasites are described, but only those on the nestlings seem to be a serious drain on the species.

It has been claimed that toucans are protectively colored, but experience with the birds in their native forest seems to refute this.

The toucan's unique bill has several incidental uses but its great size probably has no real significance as an adaptation.

CONCLUSION

As shown by the data presented here *Ramphastos brevicarinatus* is one of the most specialized of the toucans, a very distinctive family of birds confined to tropical America. It is also one of the dominant and characteristic species of the tropical forest of Central America. However, its success seems to be due, not to highly specialized habits performed by its unique type of bill, but rather to its size, food, manner of nesting, and similar factors.

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PLATE I

Figure 1. Adult male toucan (*Ramphastos brevicarinatus*), a wing-tipped bird.
Figure 2. *Ramphastos brevicarinatus* feeding in a fruit tree.

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PLATE II

Figure 3. Nest of *Ramphastos brevicarinatus* ninety feet from the ground.
Figure 4. Communal roosting hole of *Pteroglossus torquatus*.

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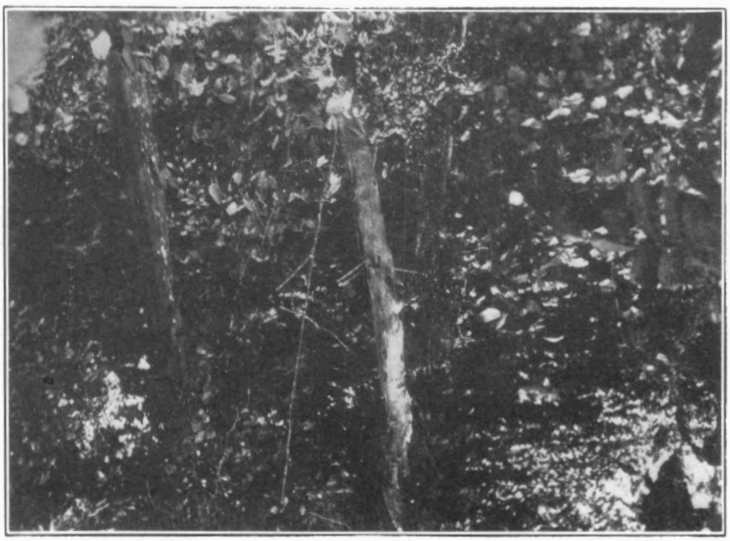

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PLATE III

Figure 5. Nest of *Ramphastos brevicarinatus* three feet from the ground.
Figure 6. Distant view of the toucan nest shown in Pl. IV, Fig. 8.

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PLATE IV

Figure 7. Set of eggs of *Ramphastos brevicarinatus* collected April 26, 1927, on Barro Colorado Island.

Figure 8. Entrance of nest shown on Pl. III, Fig. 6. The detailed study of the nest life of *Ramphastos brevicarinatus* was made at this nest.

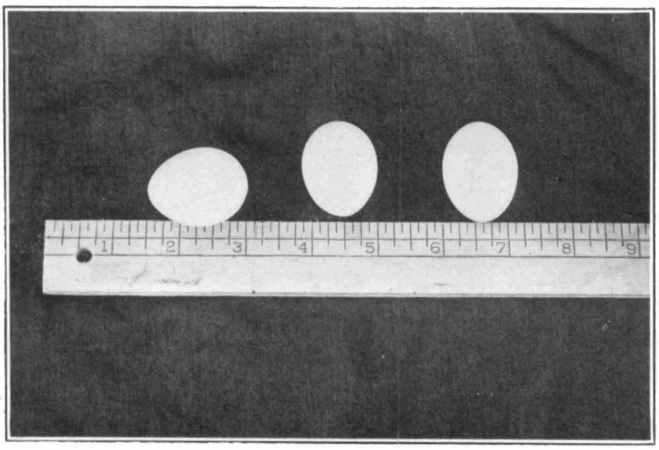

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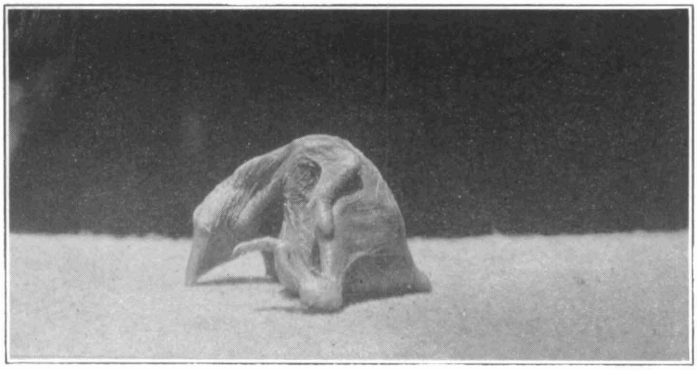
PLATE V

Figure 9. *Ramphastos brevicarinatus*—age ten days.
Figure 10. Same bird—age fifteen days.
Figure 11. Same bird—age sixteen days.



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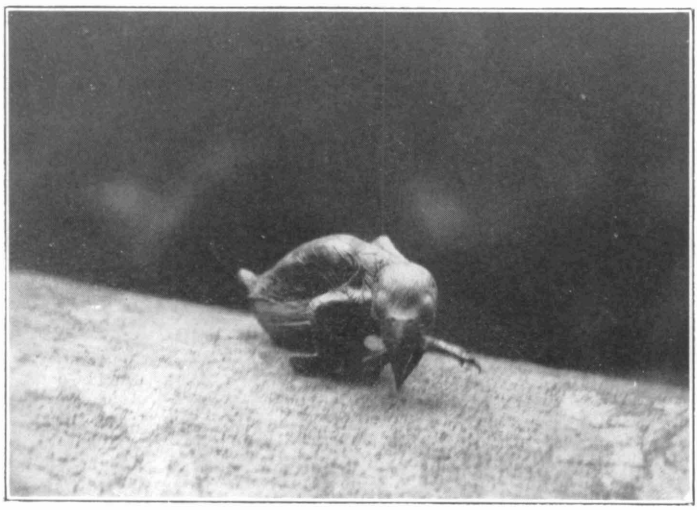

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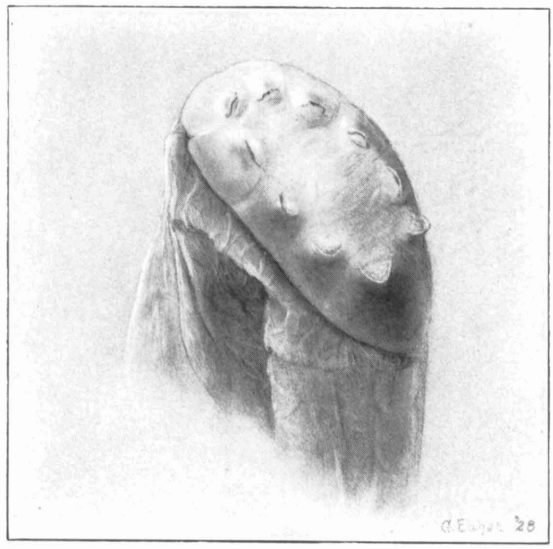
PLATE VI

Figure 12. Heel-pad of *Ramphastos brevicarinatus* viewed from below.

Figure 13. Side view of the right leg and heel-pad of *Ramphastos brevicarinatus.*



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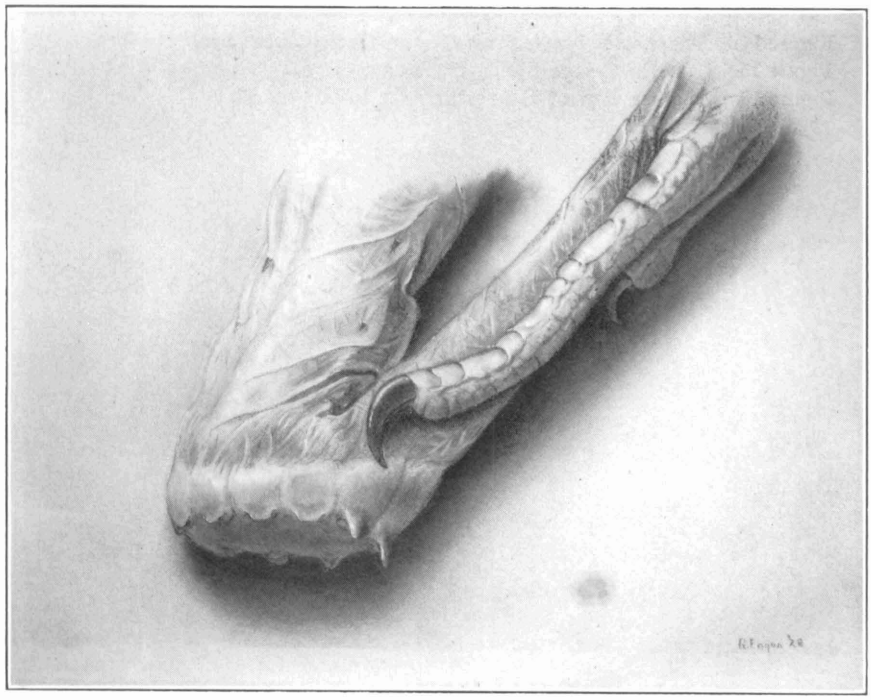

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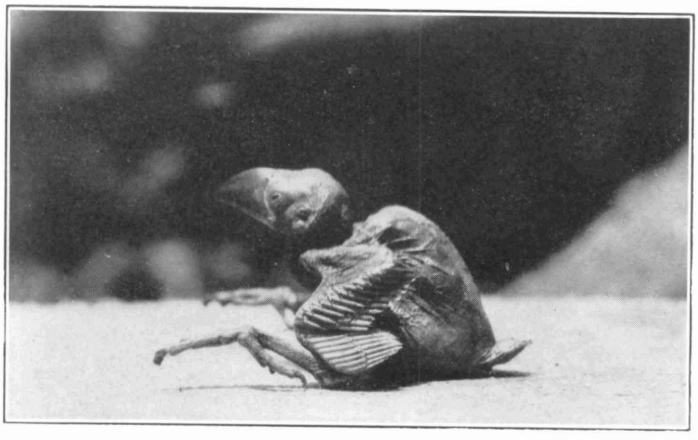
PLATE VII

Figure 14. *Ramphastos brevicarinatus*—age twenty-three days.
Figure 15. Same bird—age twenty-eight days.
Figure 16. Another view of the nestling shown in Fig. 15.



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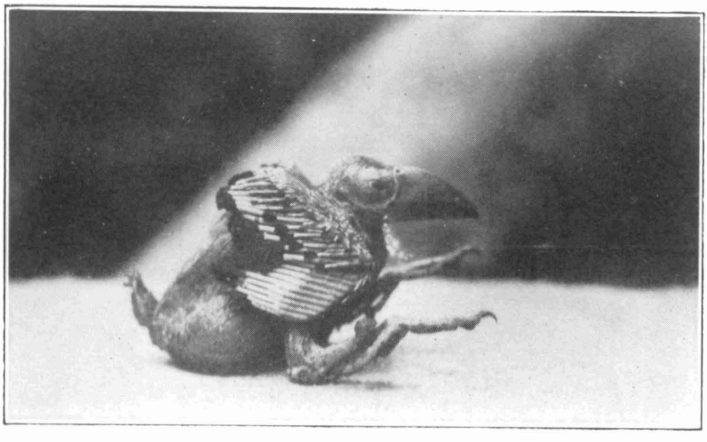

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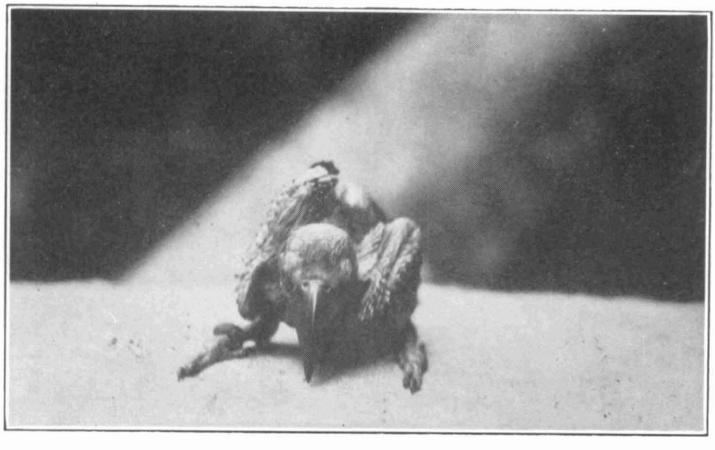

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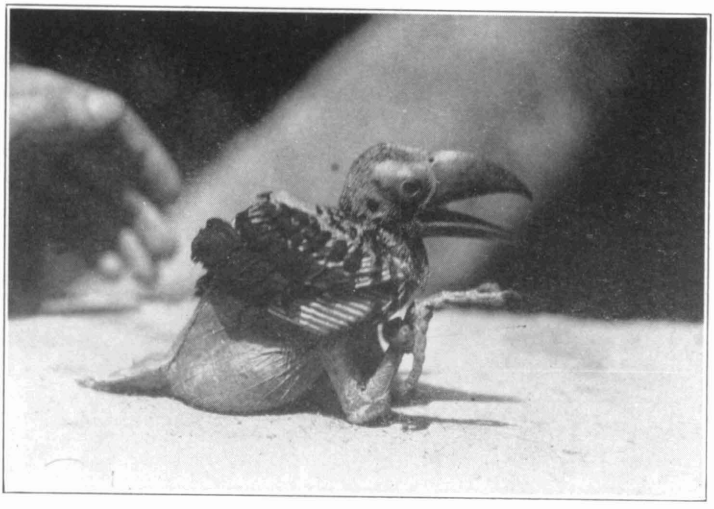
PLATE VIII

Figure 17. *Ramphastos brevicarinatus*—age thirty-two days.

Figure 18. Young *Ramphastos brevicarinatus* soon after leaving the nest (a captive bird).



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