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Understorey bird assemblages in various types of lowland tropical forest in Tambopata Reserve, SE Peru (with faunistic notes)

[with 1 text-fig.]

Zespoły ptaków dolnego piętra lasu tropikalnego Rezerwatu Tambopata w południowo-wschodnim Peru (z uwzględnieniem danych faunistycznych)

Abstract. Understorey bird assemblages were studied by means of mist-netting in three forest types representing a natural vegetation gradient: from the river (Upper Floodplain Forest) to the most elevated areas (Upland Forest type 2) that rise to 10 m above the seasonally flooded areas. The abundance of birds and relative wing length decreased, whereas species diversity and the degree of sedentariness increased along this gradient. The ant-followers were more common in upper forests, whereas hummingbirds and manakins were more abundant in floodplain forest.

CONTENTS

I. INTRODUCTION

The aim of the study was to describe the bird community in terms of species composition and abundance along an altitude and vegetation gradient. I was able to find very few papers devoted to these topics (Orians 1969, Karr 1971, Lovejoy 1974).

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II. STUDY AREA

The study was carried out during the period from 15 November 1985 to 12 February 1986, on 61 days, in the Tambopata Reserve, ca 30 km SW of Puerto Maldonado, Dpto. Madre de Dios, SE Peru (Fig. 1), during the first half of the rainy season. The reserve consists of 5000 hectares of natural, undisturbed forest and is situated at the confluence of the Rio Tambopata and its tributary, the Rio La Torre, at an average elevation of about 250 m. Annual precipitation reaches 1500—2000 mm, and mean annual temperature 18—24°C (cf. PARKER 1982). The study was done in four types of forest, which are described below.

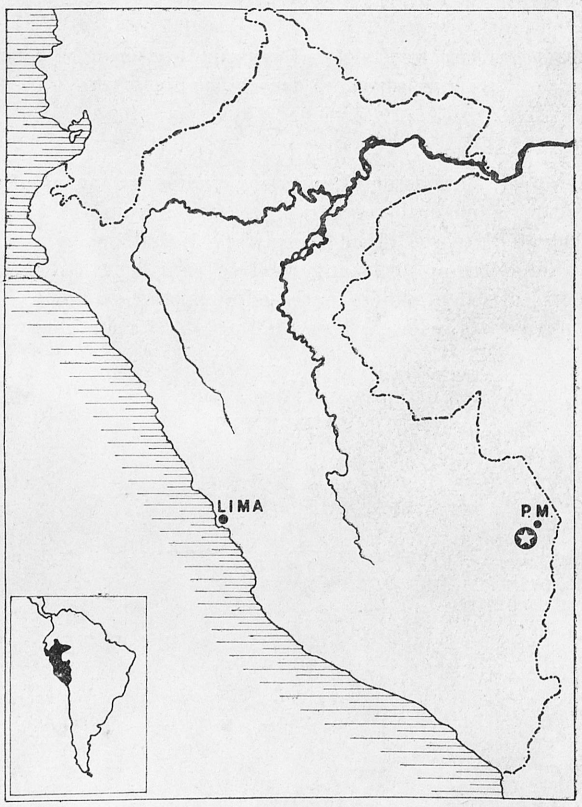

Fig. 1. The map of Peru and location of Tambopata Reserve (asterisk). P. M. — Puerto Maldonado

1. Lower Floodplain Forest (LF—PF). It is seasonally flooded by river waters, especially during the rainy season. The mist-nets were situated along the edge of *Cecropia* stand and small glade overgrown with herbaceous vegetation and shrubby second growth, with *Gynerium* cane, *Heliconia* and bamboo in the vicinity of a small oxbow pond. Only few and incomplete data were gathered here.

2. Upper Floodplain Forest (UF—PF). Along with the former type of forest it belongs to „Transitional Forest" but is flooded much less frequently. The canopy is uneven, averaging ca 30 m; palms are more abundant there (28% of total tree individuals) than in other forest types of the reserve. The dominant palm genus is *Iriartea*. Density of trees and vines (10 cm dbh or more in diameter) amounts to 540 per hectare (ERWIN 1984); the understorey was well developed. At the mist-netting plot small patches of secondary growth with *Heliconia* and bamboo also occurred. The site was close to the La Torre river.

3. Upland Forest, type 1 (UF—1). This forest stands on compact, reddish soil which drains poorly. During the rainy season it has standing puddles of water on the surface. It is rich in palms (22% total individuals); the dominant tree, however, is *Pouroma minor* (*Moraceae*). The number of trees and vines, 10 cm dbh in diameter or more, averages 585 per hectare (ERWIN 1984). The canopy is more continuous than that of transitional forest, and equally high. The forest stands on alluvial terraces that rise to 10 m above the seasonally flooded areas (PARKER 1982). The understorey is well developed. This type of forest is known also as „terra firme". The nets-site was situated ca 500 meters away from the river.

4. Upland Forest, type 2 (UF—2). The forest is situated on highest alluvial terraces on well-drained, sandy soils. Only 3% of trees were palms. The dominant hardwood tree genus is *Iryanthera* (*Mryisticaceae*). Density of trees and vines, 10 cm dbh in diameter or more averages 583 per hectare (ERWIN 1984). The average tree size is slighty smaller than in former forest type. Understorey was quite well developed. The study plot was situated ca 1.7 km away from the river.

There are three oxbows in the study area. The very large one is called Laguna Cococha and is situated at the border of reserve. Close to the tourist lodge are situated small Laguna Chica and very small oxbow called Marsh.

III. METHODS

The birds were mist-netted in constant locations, identified, colour-banded and released. Wing length and body weight were also measured. I used mist-nets ca 3.5 m high and 6—18 m long. At each study area I used rings of different colour. Recaptured individuals were provided with an additional ring. Very small birds, including all hummingbirds were marked by making excision on tail feathers. Nets were opened usually before sunrise and closed at various times of the day.

In Lower Floodplain Forest, due to difficulties caused by flooding by river waters, I mist-netted only 34 hours (7—9 and 29 November; 1, 2 and 20 December) caughting only 51 birds. So, these data were not included into the further considerations and they are only presented as Appendix 1.

In Upper Floodplain Forest I used 3—7 nets with the total length of 21—51 m for 170 net-hours. Netting days: 15, 16, 19, 21, 22, 23, 25, 26, 27, 28 and 29 November; 1, 2, 4, 7, 8, 10, 12, 17, 20, 22, 24, 28, and 30 December.

In Upland Forest, type 1, four mist-nets with total length of 72 m were used for 144 net-hours. Netting days: 15, 18, 21, 26, 27 and 31 December; 3, 5, 7, 9, 11, 12, 15, 17, 19, 20 and 21 January.

In Upland Forest, type 2, 7—11 mist-nets with total length 69—141 m were used for 159 net-hours. Netting days: 4, 6, 8, 14, 16, 18, 24, 25, 26, 28, 29 and 31 January; 2, 4, 5, 7, 9, 10, 11 and 12 February.

To compare avian abundance in various habitats I used the following index:

$$I_a = \frac{n}{h \times l} \times 100 \quad (1)$$

where n is the number of birds caught, h is the number of hours during which the mist-nets were open, and l is the total lenght of mist-nets (in m). The index was calculated for every day, and then the average value for all days at each site calculated.

To estimate diversity I used D index:

$$D = \frac{n_s}{n} \quad (2)$$

where n_s is the number of species, and n is the number of birds captured.

To estimate the degree of sedentariness I used the I_s index:

$$I_s = \frac{r}{n} \times 100 \quad (3)$$

where r is the number of first time recaptures, and n is the number of caught birds.

I also estimated the relative length of the wing, dividing the length of wing (mm) by the body weight (g).

For comparisons od bird assemblages between different study plots, SØRENSEN'S (1948) (SQ), and RENKONEN'S (1938) (Re) indexes were used (see Appendix 2).

The division of forest type applied here follows ERWIN (1984). Ant-followers were distinguished according to TERBORGH'S et al. (1984) paper.

Many authors (e.g. KARR 1981) stressed that the mist-net capture rates of different species are proportional not only to relative abundance but also to several other factors, including diet (MARTIN and KARR 1986). However, I think that this do not make illegitimate comparisons limited to my own data, taken in one locality during three months period. Mist-net capture rates of the same species between sites are proportional not only to relative abundance but also to vegetation structure and behaviour differences between various populations of this same species. However, all my nets were installed

among rather dense understorey vegetation, and the different net plots were too close to one another (minimum 400 m, maximum 3200 m) to support much different populations.

IV. FAUNISTIC NOTES

The region is told to be one of the richest in the world as regards the number of bird species, and many ornithologists made observations there, but only one faunistic paper was published (PARKER 1982). I suppose that some of my data are worth mentioning. The bird species mentioned below were selected on the ground of their relative rarity or limited distribution according to such sources as TACZANOWSKI (1884—1886), TERBORGH et al. (1984), HILTY and BROWN (1986). I also consider here species for which I gathered some data concerning breeding or biometry. For mist-netted birds I give wing length in mm (maximum chord method to nearest mm), and weight (g).

Anhinga *Anhinga anhinga* (LINNAEUS, 1766) — During the whole stay 1—7 birds were observed many times at Cococha and Laguna Chica.

Chestnut-billed Heron *Agamia agami* (GMELIN, 1789) — On 30 Oct. — one bird at old river bed.

Green Ibis *Mesembrinibis cayennensis* (GMELIN, 1789) — On 20 Oct. — one bird at oxbow.

Osprey *Pandion haliaetus* (LINNAEUS, 1758) — In December and January 2 birds seen several times at Cococha.

Hoatzin *Opisthocomus hoatzin* (MÜLLER, 1776) — Observed many times at oxbows: Laguna Chica and Lake Cococha. In the latter place usually flocks from several to dozen or so birds. On 23 Oct. a bird sitting on the nest which comprised two downy nestlings; on 14 Jan. I found the nest with the bird incubating two eggs which disappeared in next few days. Both nests were situated on bush-like plants standing in the water, ca 2 m above water level.

Azure Gallinule *Porphyrula flavirostris* (GMELIN, 1789) — Observed at Cococha, and on 29 Nov. at Laguna Chica — one bird with orange legs.

Sungrebe *Heliornis fulica* (BODDAERT, 1783) — In the end of October and November single birds on oxbow near "Swamp Trail" and Cococha.

Sunbittern *Eurypyga helias* (PALLAS, 1781) — In October and November. I saw single bird several times at the Rio Tambopata and Cococha. In January on several occassions I met one or two birds on "Main Trail" passing swamp forest. The behaviour of these birds suggested the presence of youngs.

Ruddy Quail-Dove *Geotrygon montana* (LINNAEUS, 1758) — Many times seen foraging on forest floor. On 14 Jan. I found a nest containing 2 eggs and incubating bird. It was made of leaves and situated on oblique small trunk 65 cm above the ground. The nest diameter was ca 18 cm. It was rather flat with small depression. The eggs were white (25.0 ×19.9 and 24.6 ×21.2 mm). Measurements of mist-netted birds: ♂♂ — 124, 128, 131, 132, 132, 132, 132, 133,

134, 138, 140 mm; 97, 108, 111, 112, 118, 119, 121, 122, 122, 127, 127 g; ♀♀ — 124, 125, 127, 128, 129, 129, 130, 132, 132, 134, 136, 137 mm; 99, 105, 108, 110, 114, 117, 119, 120, 121, 121, 122, 130 g.

Little Cuckoo *Piaya minuta* (VIEILLOT, 1817) — On 28 and 30 Dec. two birds caught at UF—PF (99 mm, 44 g; 103 mm, 36 g — wounded bird).

Spectacled Owl *Pulsatrix perspicillata* (LATHAM, 1790) — During the whole stay the characteristic voice of this bird was heard at lodge clearing.

Least Pygmy Owl *Glaucidium minutissimum* (WIED, 1821) — On 21 Nov. one bird caught at UF—PF. The owl attacked a netted hummingbird.

Rufous-breasted Hermit *Glaucis hirsuta* (GMELIN 1788) — One of the most, often mist-netted birds at LF—PF and UF—PF. No one caught in "terra firme" nets. The measurements of some birds: 57, 58, 61, 61, 61, 63 mm; 5.5, 5.5, 6, 6.5, 7, 7.5, 8, 8, 9 g.

White-bearded Hermit *Phaethornis hispidus* (GOULD, 1846) — One of the most often mist-netted birds, mainly at UF—PF. No one at UF—2. Out of 18 checked birds, 8 were in molt.

Needle-billed Hermit *Phaethornis philippi* (BOUCARD, 1847) — On 4 and 7 Feb. three birds were caught at UF—2. The measurements of one: 58 mm, 5 g, bill — 32.3 mm.

Reddish Hermit *Phaethornis ruber* (LINNAEUS, 1766) — Seen many times along "Main Trail". Single birds were caught in all types of forest. Measurements: 33, 35, 38 mm; 2, 2.5, 3 g.

Rufous Motmot *Baryphthenus martii* (SPIX, 1824) — Three birds were caught at UF—PF and UF—1. Measurements: 143, 149, 149 mm; 147, 161, 166 g; bill — 38.7, 40.5, 40.8 mm.

Bluish-fronted Jacamar *Galbula cayanescens* DEVILLE, 1849 — On 27 Nov. one bird caught in secondary growth by Rio La Torre. (76 mm, 26 g).

Chestnut-capped Puffbird *Bucco macrodactylus* (SPIX, 1824) — On 16 Nov. — 1 bird in UF—1.

Semi-collared Puffbird *Malacoptila semicincta* TODD, 1925 — On 5 Feb. two birds caught simultaneously in the same net at UF—2 (86 mm, 45.5 g; 88 mm, 42.5 g).

Gray-cheeked Nunlet *Nonnula ruficapilla* (TSCHUDI, 1844) — On 23 Dec. one bird in UF—PF close to the river.

Emerald Toucanet *Aulacorhynchus prasinus* (GOULD, 1834) — 25 Nov. — 1 bird at lodge clearing.

Brown-mandibled Aracari *Pteroglossus mariae* (FRASER, 1840) — Four and five birds caught simultaneously in one net at UF—1 and UF—2 (21 Dec. and 10 Feb.) Measurements: 121, 121, 121, 122, 123, 123, 124, 125, 127 mm; 128, 128, 134, 136, 137, 138, 139, 142, 146 g. Bill: 84.3, 88.5, 91.2, 91.3, 91.5, 92.1, 92.6, 93.3, 94.6 mm.

Curl-crested Aracari *Pteroglossus beauharnaesii* WAGLER, 1832 — Three birds mist-netted in UF—2 (16 Jan., 7 Feb.). Measurements: 138, 140, 143 mm; 184, 184, 194 g; bill: 94.2, 95.3, 95.4 mm.

Golden-collared Toucanet *Selenidera reinwardtii* (WAGLER, 1827) — Four birds caught at UF—1 and UF—2 (31 Dec. — 7 Feb.). Measurements: ♂♂ — 131, 131, 134 mm; 143.5, 170, 170.5 g; bill: 58.5, 64.5, 65.6 mm; ♀ — 121 mm, 149 g, bill — 55.4 mm.

Rufous-headed Woodpecker *Celeus spectabilis* SCLATER & SALVIN, 1880 — One bird caught at UF—PF on 17 Dec. (148 mm, 116 g).

Cream-coloured Woodpecker *Celeus flavus* (MÜLLER, 1776) — Met several times in UF—1 near clearing.

Wedge-billed Woodcreeper *Glyphorynchus spirurus* (VIEILLOT, 1819) — One of the more numerous bird in mist-nets, especially in UF—2. Measurements: 63, 64, 65, 66, 66, 66, 66, 67, 67, 67, 68, 68, 69, 69, 69, 70, 70, 70, 70, 70, 71, 71 mm; 12.5, 13.5, 14, 14, 14, 14, 14, 14.5, 14.5, 14.5, 15, 15, 15, 15.5, 15.5, 15.5, 15.5, 15.5, 15.5, 16, 16, 16.5, 17.5 g. Twelve out of 19 inspected birds were molting (mainly in January).

Red-billed Scythebill *Campylorhampus trochilirostris* (LICHTENSTEIN, 1820)— On 26 Nov. 1 bird caught in UF—PF (95 mm, 40.5 g, bill — 58.5 mm).

Pale-legged Hornero *Furnarius leucopus* SWAINSON, 1838 — A pair built the nest on *Cecropia* branch overhanging small oxbow close to the Rio La Torre. The nest was completed on 1st November. Two young bird left the nest between 13 and 21 December.

Peruvian Recurvebill *Simoxenops ucayalae* (CHAPMAN, 1928) — On 24 Dec. one bird caught in secondary growth by Rio La Torre (101 mm, 50 g, bill — 21.4 mm).

Ruddy Spinetail *Synallaxis rutilans* TEMMINCK, 1823 — In UF—2 four birds were caught. Measurements: 57, 58, 61, 64 mm; 18.5, 19.5, 19.5; 22.5 g.

Brown-rumped Foliage-gleaner *Automolus melanopezus* (SCLATER, 1858) — On 21 Dec. and 16 Jan. two birds were mist-netted at UF—1 and UF—2. The second one was molting (wing, tail and body feathers). Measurements: 75 mm, 31 and 32 g.

Bluish-slate Antshrike *Thamnomanes schistogynus* HELLMAYR, 1911 — 20 birds were caught, mainly in UF—1 and UF—2, but some also in second growth at Rio La Torre. Some individuals had brown underparts, including brown yellowish head (juveniles?). These birds were caught at the end of January, and in the beginning of February. Adult measurements: ♂♂ — 65, 66, 67, 67, 67, 67, 69, 69, 71 mm; 15.5, 16.5, 17, 17, 17.5, 19, 20 g; ♀♀ — 66, 68, 68, 69 mm; 16.5, 16.5, 16.5, 17 g.

White-throated Antbird *Gymnopithys salvini* (BERLEPSCH, 1901) — One of the most numerously caught birds (29 individuals), nearly exclusively in UF—1, and UF—2. 29 out of 32 checked (mainly December to Februrary) birds (including retraps) were molting. Measurements: ♂♂ — 68, 71, 71, 71, 71, 71, 72, 72, 72, 74 mm; 23.5, 25, 25.5, 26, 26.5, 26.5, 26.5, 27, 27, 27.5, g; ♀♀ — 69, 69, 71, 71, 71, 72, 72, 72, 73, 73, 73, 73, 74 mm; 24.5, 25.5, 25.5, 26, 26.5, 27, 27, 28, 29, 29, 29.5, 31 g.

Silvered Antbird *Sclateria naevia* (GMELIN, 1788) — Two birds caught in

UF—1 and UF—2. Measurements: ♂ — 65 mm, 21 g, bill 23.3 mm, tail and body feathers molting (28 Nov.); ♀ — 62 mm, 20.5 g, bill 18.9 mm, no molt (10 Feb.).

White-browed Antbird *Myrmoborus leucophrys* (TSCHUDI, 1844) — Seven birds were caught in UF—PF, and UF 1. Measurements: ♂♂ — 63, 63, 66, 66 mm; 18.5, 19, 20, 21, 22 g; ♀♀ — 60, 61 mm; 18.5, 20.5, g. Out of 6 checked birds, 3 were in molt (16 Nov. — 21 Jan.).

Black-faced Antbird *Myrmoborus myotherinus* (SPIX, 1825) — Seven birds were caught in UF—1 (1), and UF—2 (6). Measurements of 5 males: 60, 62, 63, 63, 64 mm; 18, 20, 21, 21.5, 25 g. Six out of 7 birds were in molt (4 Jan. — 7 Feb.).

Chestnut-tailed Antbird *Myrmeciza hemimelaena* SCLATER, 1857 — Five birds caught in UF—PF, UF—1, and UF—2. Measurements: ♂ — 54 mm, 16 g; ♀♀ — 5?, 53, 54, 56 mm; 15, 16, 16, 17.5, g. A bird checked on 22 Nov. was molting, three others (5 Jan. — 10 Feb.) were not.

Scale-backed Antbird *Hylophylax poecilonotus* (CABANIS, 1847) — Three birds were mist-netted on UF—1, and two on UF—2. Measurements: 66, 66, 67, 68, 68 mm; 17.5, 18.5, 20, 20, 20, g.

Black-spotted Bare-eye *Phlegopsis nigromaculata* (D'ORBIGNY & LAFRESNAYE, 1837) — Eight birds caught in UF—PF (2), and UF—1 (6). Measurements of some birds: 85, 86, 86, 89, 91 mm; 47, 47.5, 51, 53.5, 55 g. All six checked birds (4 Dec. — 17 Jan.) were molting. An adult bird with young (83 mm, 49 g) were caught simultaneously in the same net in UF—PF on 18 Dec. The bare skin round the eye was dark and indistinctive in the young. After 8 days the same two individuals were caught at the same spot. Another young (dark skin around eye) was caught on 17 Jan.

Band-tailed Manakin *Pipra fasciicauda* HELLMAYR, 1906 — Most numerous bird species in my mist-nets (73), caught mainly in LF—PF, UF—PF, and UF—1. On 19 Nov. and 18 Nov. I caught a female with brooding patch. Out of 80 birds checked (including retraps), only 22.5% were molting (mainly in January).

Fiery-capped Manakin *Machaeropterus pyrocephalus* (SCLATER, 1852). One of the most frequently caught bird species (32) in all four habitats. Out of 32 birds checked (21 Nov. — 9 Feb.) only two males (17 Jan. and 9 Feb.) and two females (12 Dec. and 9 Feb.) molted. Measurements: ♂♂ — 52, 52, 52, 53, 53, 53, 53, 53, 53, 54, 54, 54 mm; 9, 9.5, 9.5, 9.5, 9.5, 9.5, 9.5, 10, 10, 10, 10.5 g; ♀♀ — 48, 48, 49, 49, 49, 50, 50, 50, 50, 50, 50, 50, 51, 51, 51, 51, 51, 52, 52, 52 mm; 8.5, 9, 9, 9, 9, 9, 9, 9, 9.5, 9.5, 9.5, 9.5, 9.5, 9.5, 10, 10.5 g.

Red-headed Manakin *Pipra rubrocapilla* TEMMINCK, 1821 — Caught only in UF—2 (12). A bird with brooding patch caught on 6 Jan. It worn the female plumage through it had also several orange feathers on head. Measurements: ♂♂ — 58, 60, 61, 63 mm; 13, 13.5, 14, 15 g; ♀♀ — 59, 60, 60, 61, 61, 61 mm; 12.5, 12.5, 13, 14, 14, 14.5 g. Out of 11 checked birds (6 Jan. — 9 Feb.) only 2 were in molt.

Blue-crowned Manakin *Pipra coronata* SPIX, 1825 — Three following birds were mist-netted in UF—2. 24 Jan. ♀ — 56 mm, 10 g, no molt; 26 Jan. ♂ — 57 mm, 8.5 g, molting; 2 Feb. ♀ — 55 mm. 10 g, molting.

Thrush-like Manakin *Schiffornis turdinus* (WIED, 1831) — The measurements of four birds caught in UF—2 were as follows: 86, 87, 87, 89 mm; 30.5, 34, 34.5, 35.5 g. Two birds checked on 8 Jan. and 4 Feb. did not molt, and one (2 Feb.) molted.

Rusty-margined Flycatcher *Myiozetetes cayanensis* (LINNAEUS, 1766) — At the edge of rather small oxbow called Laguna Chica I found two occupied nests situated on small isolated bushes standing in the water. First nest contained two eggs, a single nestling hatched on 26 Nov. and fledged on 17 Dec. (after 22 days). On 29 Dec. (when 34 days old) I saw it (colour band) begging in the vicinity of nest. In the second nest, situated in vicinity, three eggs were laid, starting from 28 Now. They soon disappeared (predation ?). At the beginning of December the birds started to build a new nest (using material from the old one) but soon water in Rio La Torre rised unusually high and the whole area was flooded.

Large-headed Flatbill *Ramphotrigon megacephala* (SWAINSON, 1836) — On 18 Dec. one molting bird caught in UF—1 (61 mm, 15 g).

Flammulated Pygmy-Tyrant *Hemitriccus flammulatus* BERLEPSCH, 1901 — On 11 Feb. one no molting bird in UF—2.

Plain Tyrannulet *Inezia inornata* (SALVADORI, 1897) — On 20 Dec. one bird caught in UF—PF close to the Rio La Torre (55 mm, 12 g, bill — 13.3 mm, no molt).

Moustached Wren *Thryothorus genibarbis* SWAINSON, 1837 — On 2 Dec. one molting (tail feathers and wing coverts) bird was mist-netted at Rio La Torre in secondary growth (61 mm, bill — 16.4 mm).

Buff-breasted Wren *Thryothorus leucotis* LAFRESNAYE, 1845 — On 7 Nov. one bird (62 mm, 21 g, bill — 16.2 mm) was caught at the edge of *Cecropia* stands and *Heliconia* bushes close to the Rio La Torre. On 30 Dec. two molting birds (60 mm, 19.5 g, bill — 17.8 mm; 61 mm, 22.5 g) caught in UF—PF close to the secondary thickets with *Heliconia* and bamboo close to the river.

Lined Seedeater *Sporophila lineola* (LINNAEUS, 1758) — On 20 Dec. one male was caught in LF—PF (60 mm, 9.5 g).

V. BIRDS OF VARIOUS HABITATS

In Upper Floodplain Forest 215 birds of 71 species were caught (Table I). Most commonly captured species were: Band-tailed Manakin *Pipra fasciicauda*, White-bearded Hermit *Phaethornis hispidus*, Fiery-capped Manakin *Machaeropterus pyrocephalus*, and Ruddy Quail-Dove *Geotrygon montana*.

In Upland Forest, type 1, 199 birds of 57 species were captured (Table II). The most numerously captured were: Band-tailed Manakin *Pipra fasciicauda*,

White-throated Antbird *Gymnopithys salvini*, and Bluish-slate Antshrike *Thamnomanes schistogynus*.

In Upland Forest, type 2, 197 birds of 51 species were caught (Table III); the most commonly: White-throated Antbird *Gymnopithys salvini*, Wedge-billed Woodcreeper *Glyphorynchus spirurus*, and Red-headed Manakin *Pipra rubrocapilla*.

Comparison of understorey bird assemblages of different plots shows that there were some gradients to be seen in Table IV, going from the Upper Floodplain Forest to the Upland Forest, type 2. In the former the bird abundance and bird mobility (low tendency to be sedentary) were high. On the other hand, the Upland Forest, type 2, situated far from the river or other open space and

Table I

Birds caught in the Upper Floodplain Forest

Species	n	%	Species	n	%
1	2	3	4	5	6
Pipra fasciicauda Hellmayr, 1906	38	17.7	*Cyanocompsa cyanoides* (Lafresnaye, 1847)	3	1.4
Phaethornis hispidus (Gould, 1846)	21	9.8	*Piaya minuta* (Vieillot, 1817)	2	0.9
Machaeropterus pyrocephalus (Sclater, 1852)	16	7.4	*Florisuga mellivora* (Linnaeus, 1758)	2	0.9
Geotrygon montana (Linnaeus, 1758)	12	5.6	*Heliomaster longirostris* (Audebert & Vieillot, 1801)	2	0.9
Glyphorynchus spirurus (Vieillot, 1819)	6	2.8	*Baryphthengus martii* (Spix, 1824)	2	0.9
Terenotriccus erythrurus (Cabanis, 1847)	6	2.8	*Monasa nigrifrons* (Spix, 1824)	2	0.9
Saltator maximus (Müller, 1776)	6	2.8	*Nonnula ruficapilla* (Tschudi, 1844)	2	0.9
Glaucis hirsuta (Gmelin, 1788)	5	2.3	*Automolus rufipileatus* (Pelzeln, 1859)	2	0.9
Myrmoborus leucophrys (Tschudi, 1844)	5	2.3	*Xenops minutus* (Sparrman, 1788)	2	0.9
Thalurania furcata (Gmelin, 1788)	4	1.9	*Myrmotherula longipennis* Pelzeln, 1868	2	0.9
Threnetes leucurus (Linnaeus, 1766)	4	1.9	*Phlegopsis nigromaculata* (d'Orbigny & Lafresnaye, 1837)	2	0.9
Momotus momota (Linnaeus, 1766)	3	1.4	*Pipromorpha oeaginea* (Lichtenstein, 1823)	2	0.9
Xiphorhynchus guttatus (Lichtenstein, 1820)	3	1.4	*Rhynchocyclus olivaceus* (Temminck, 1820)	2	0.9
Thamnomanes schistogynus Hellmayr, 1911	3	1.4	*Leptopogon amaurocephalus* Tschudi, 1846	2	0.9
Formicarius analis (d'Orbigny & Lafresnaye, 1837)	3	1.4	*Corythopis torquata* Tschudi, 1844	2	0.9

1	2	3	4	5	6
Turdus ignobilis (Sclater, 1857)	3	1.4	*Cyphorhinus arada* (Hermann, 1783)	2	0.9
Habia rubica (Vieillot, 1817)	3	1.4	*Thryothorus leucotis* Lafresnaye, 1845	2	0.9
Paroaria gularis (Linnaeus, 1766)	3	1.4			
Represented by one individual (ca 0.5%): *Leptotila rufaxilla* (Richard & Bernard, 1792), *Glaucidium minutissimum* (Wied, 1821), *Phaethornis ruber* (Linnaeus, 1766), *Polyplancta aurescens* (Gould, 1846), *Chloroceryle americana* (Gmelin, 1788), *Galbula cyanescens* Deville, 1849, *Veniliornis passerinus* (Linnaeus, 1766), *Celeus spectabilis* Sclater & Salvin, 1880, *Xiphocolaptes promeropirhynchus* (Lesson, 1840), *Campylorhamphus trochilirostris* (Lichtenstein, 1820), *Automolus ochrolaemus* Tschudi, 1844, *Simoxenops ucayalae* (Chapman, 1928), *Gymnopithys salvini* (Berlepsch, 1901), *Myrmeciza hemimelaena* Sclater, 1857, *Hypocnemoides maculicauda* (Pelzeln, 1868), *Myrmeciza goeldii* (Snethlage, 1908), *Pygiptila stellaris* (Spix, 1825), *Thamnophilus doliatus* (Linnaeus, 1764), *Taraba major* (Vieillot, 1816), *Myrmotherula leucophthalma* (Pelzeln. 1868), *Myrmeciza atrothorax* (Boddaert, 1783), *Thamnophilus aethiops* Sclater, 1858, *Tyrannus melancholicus* Vieillot, 1819, *Zimmerius gracilipes* (Sclater & Salvin, 1867), *Ramphotrigon ruficauda* (Spix, 1825), *Todirostrum latirostre* (Pelzeln, 1868), *Pipromorpha macconnelli* Chubb, 1919, *Inezia inornata* (Salvadori, 1897), *Onychorhynchus coronatus* (Müller, 1776), *Thryothorus genibarbis* Swainson, 1837, *Catharus ustulatus* (Nattall, 1840), *Turdus amaurochalinus* (Cabanis, 1851), *Turdus hauxwelli* (Lawrence, 1869), *Cacicus solitarius* (Vieillot, 1816), *Psarocolius decumanus* (Pallas, 1769) and *Ramphocelus carbo* (Pallas, 1764)					
Total				215	100

Table II

Birds caught in the Upland Forest (type 1)

Species	n	%	Species	n	%
1	2	3	4	5	6
Pipra fasciicauda Hellmayr, 1906	27	13.6	*Hylophylax poecilonotus* (Cabanis, 1847)	3	1.5
Gymnopithys salvini (Berlepsch, 1901)	13	6.5	*Hypocnemis cantator* (Boddaert, 1783)	3	1.5
Thamnomanes schistogynus Hellmayr, 1911	10	5.0	*Formicarius colma* Boddaert, 1783	3	1.5
Geotrygon montana (Linnaeus, 1758)	8	4.0	*Xenops minutus* (Sparrman, 1788)	3	1.5
Glaphorynchus spirurus (Vieillot, 1819)	8	4.0	*Ramphotrigon ruficauda* (Spix, 1825)	3	1.5
Machaeropterus pyrocephalus (Sclater, 1852)	8	4.0	*Terenotriccus erythrurus* (Cabanis, 1847)	3	1.5
Chloroceryle aenea (Pallas, 1764)	6	3.0	*Cacicus cela* (Linnaeus, 1758)	3	1.5

1	2	3	4	5	6
Automolus ochrolaemus (Tschudi, 1844)	6	3.0	*Thalurania furcata* (Gmelin, 1788)	3	1.5
Myrmotherula hauxwelli (Sclater, 1857)	6	3.0	*Xiphorhynchus guttatus* (Lichtenstein, 1820)	3	1.5
Phlegopsis nigromaculata (D'Orbigny & Lafresnaye, 1837)	6	3.0	*Philydor pyrrhodes* (Cabanis, 1848)	3	1.5
Pteroglossus mariae (Fraser, 1840)	5	2.5	*Myrmoborus leucophrys* (Tschudi, 1844)	3	1.5
Myrmotherula axillaris (Vieillot, 1817)	5	2.5	*Myrmeciza hemimelaena* Sclater, 1857	3	1.5
Chloroceryle inda (Linnaeus, 1766)	4	2.0	*Rhynchocyclus olivaceus* (Temminck, 1820)	3	1.5
Myrmotherula leucophthalma (Pelzeln, 1868)	4	2.0	*Pipromorpha macconnelli* Chubb, 1919	3	1.5
Corythopis torquata Tschudi, 1844	4	2.0	*Attila spadiceus* (Gmelin, 1789)	3	1.5
Turdus albicollis (Vieillot, 1818)	4	2.0	*Cyphorhinus arada* (Hermann, 1783)	3	1.5
Phaethornis hispidus (Gould, 1846)	3	1.5			
Represented by one individual (ca 0.5%): *Selenidera reinwardtii* (Wagler, 1827), *Baryphthengus martii* (Spix, 1824), *Sittasomus griseicapillus* (Vieillot, 1818), *Dendrocincla merula* (Lichtenstein, 1818), *Automolus rufipileatus* (Pelzeln, 1859), *Automolus melanopezus* (Sclater, 1858), *Automolus infuscatus* (Sclater, 1856), *Philydor rufus* (Vieillot, 1818), *Granioleuca gutturata* (D'Orbigny & Lafresnaye, 1838), *Sclateria naevia* (Gmelin, 1788), *Myrmoborus myotherinus* (Spix, 1825), *Myrmotherula menetriesii* (D'Orbigny, 1839), *Myrmotherula longipennis* Pelzeln, 1868, *Myrmotherula ornata* (Sclater, 1853), *Thamnophilus aethiops* Sclater, 1858, *Laniocera hypopyrrha* (Vieillot, 1817), *Pipra chloromeros* Tschudi, 1844, *Ramphotrigon megacephala* (Swainson, 1836), *Hemitriccus flammulatus* Berlepsch, 1901, *Platyrinchus coronatus* Sclater, 1858, *Leptopogon amaurocephalus* Tschudi, 1846, *Pipromorpha oleaginea* (Lichtenstein, 1823), *Turdus ignobilis* (Sclater, 1857) and *Cyanocompsa cyanoides* (Lafresnaye, 1847)					
Total				199 ~	100

Table III

Birds caught in the Upland Forest (type 2)

Species	n	%	Species	n	%
1	2	3	4	5	6
Gymnopithys salvini (Berlepsch, 1901)	15	7.6	*Pteroglossus beauharnaesii* Wagler, 1832	3	1.5
Glyphorynchus spirurus (Vieillot, 1819)	15	7.6	*Pheathornis philippi* (Boucard, 1847)	3	1.5
Pipra rubrocapilla Temminck, 1821	14	7.1	*Xiphorhynchus guttatus* (Lichtenstein, 1820)	3	1.5
	11	5.6		3	1.5

1	2	3	4	5	6
Myrmotherula leucophthalma (Pelzeln, 1868)	9	4.6	*Automolus ochrolaemus* (Tschudi, 1840)	3	1.5
Myrmoborus myotherinus (Spix, 1825)	8	4.1	*Thamnophilus aethiops* Sclater, 1858	3	1.5
Thamnomanes schistogynus Hellmayr, 1911	7	3.6	*Pipra coronata* Spix, 1825	3	1.5
Myrmotherula axillaris (Vieillot, 1817)	7	3.6	*Pipra fasciicauda* Hellmayr, 1906	3	1.5
Machaeropterus pyrocephalus (Sclater, 1852)	6	3.0	*Terenotriccus erythrurus* (Cabanis, 1847)	3	1.5
Leptopogon amaurocephalus Tschudi, 1846	6	3.0	*Corythopis torquata* Tschudi, 1844	3	1.5
Turdus albicollis (Vieillot, 1818)	6	3.0	*Onychorhynchus coronatus* (Müller, 1776)	3	1.5
Thalurania furcata (Gmelin, 1788)	5	2.5	*Ramphotrigon ruficauda* (Spix, 1825)	3	1.5
Deconychura longicauda (Pelzeln, 1868)	5	2.5	*Phaethornis ruber* (Linnaeus, 1766)	2	1.0
Habia rubica (Vieillot, 1817)	5	2.5	*Malacoptila semicincta* Todd, 1925	2	1.0
Geotrygon montana (Linnaeus, 1758)	4	2.0	*Dendrocolaptes certhia* (Boddaert, 1783)	2	1.0
Pteroglossus mariae (Fraser, 1840)	4	2.0	*Xiphorhynchus spixii* (Lesson, 1830)	2	1.0
Xenops minutus (Sparrman, 1788)	4	2.0	*Automolus infuscatus* (Sclater, 1856)	2	1.0
Synallaxis rutilans Temminck, 1823	4	2.0	*Thamnophilus schistaceus* (d'Orbigny, 1835)	2	1.0
Formicarius colma Boddaert, 1783	4	2.0	*Hylophylax poecilonotus* (Cabanis, 1847)	2	1.0
Schiffornis turdinus (Wied, 1831)	4	2.0	*Myrmeciza hemimelaena* Sclater, 1857	2	1.0
Pipromorpha oleaginea (Lichtenstein, 1823)	4	2.0	*Myrmotherula hauxwelli* (Sclater, 1857)	2	1.0
Setenidera reinwardtii (Wagler, 1827)	3	1.5	*Microcercuius marginatus* (Sclater, 1855)	2	1.0
Represented by one individual (ca 0.5%): *Philydor pyrrhodes* (Cabanis, 1848), *Automolus melanopezus* (Sclater, 1858), *Myrmotherula longipennis* Pelzeln, 1868, *Myrmotherula menetriesii* (d'Orbigny, 1837), *Myrmotherula ornata* (Sclater, 1853), *Hemitriccus flammulatus* Berlepsch, 1901, *Catharus ustulatus* (Nuttall, 1840), *Cyanocompsa cyanoides* (Lafresnaye, 1847) and *Sclateria naevia* (Gmelin, 1788)					
			Total	197	100

standing on poorest soil, supported the understorey bird community which showed lowest abundance and highest species diversity and tendency to be stationary.

Comparison of bird assemblages both by means of qualitative SØRENSEN index and quantitative RENKONEN index (Table V) showed the strongest similarity between two type of forest standing on "terra firme".

In transitional forest the quantitative dominance of manakins and hummingbirds was recorded, while in "terra firme" forest, the dominant families comprised antbirds, and also woodcreepers and manakins. In the latter forests the ant-followers were relatively more abundant then in former forest type (Table VI).

Table IV

Parameters of bird assemblages in various forest type (I_a — abundance, D — diversity, I_s — sedentariness)

Index	Symbol of sample plot		
	UF-PF	UF-1	UF-2
I_a	(a) 3.7 **	1.9	(b) 1.4
D	3.03	3.29	3.86
I_s	(c) 9.0	10.8	(d) 17.4
Average wing/ weight index	(e) 4.46 *	3.84	(f) 3.94

Statistical significance (χ sq test): * $p < 0.02$, ** $p < 0.002$, ab — $p < 0.001$, cd — $p < 0.02$, ef — $p < p.05$

Table V

The similarities of bird assemblages observed in 3 forest types, calculated on the basis of SØRENSEN index (QS) and RENKONEN index (Re)

	UF-PE	UF-1	UF-2	Index
UF-PF		45.0	39.3	
UF-1	44.4		64.2	QS
UF-2	26.5	51.1		
Index	Re			

Table VI

Number of ant-follower individuals and forest type (% of total individuals)

Species	Habitat		
	UF-PF	UF-1	UF-2
Dendrocolaptes certhia (BODDAERT, 1783)	—	—	2
Dendrocincla merula (LICHTENSTEIN, 1818)	—	1	—
Gymnopithys salvini (BERLEPSCH, 1901)	1	13	15
Hylophylax poecilonota (CABANIS, 1847)	—	3	2
Myrmoborus myotherinus (SPIX, 1825)	—	1	8
Formicarius analis (D'ORBIGNY & LAFRESNAYE, 1837)	3	—	—
Phlegopsis nigromaculata (D'ORBIGNY & LAFRESNAYE, 1837)	2	6	—
Total	6 (2.8)	24 (12.6)	27 (13.7)
	$\chi^2 = 16.0$ $p < 0.001$		NS
		$\chi^2 = 18.2$ $p < 0.001$	

VI. DISCUSSION

The study concerns only the near-ground stratum (up to ca 3 m in height). This layer, in comparison to other strata, shows higher humidity, less light, more restricted temperature fluctuations, and reduced air circulation (ALLEE 1926 — after TERBORGH 1980). So this level represents a more or less definite unit, which justifies the treatment of its bird assemblages separately. The 662 captured bird individuals reported in this study were of 127 species, which indicates an unusual species richness (five individuals per species on average). For comparison in the Panamian lowland forest 3037 captures of 95 species were reported (KARR and FREEMARK 1983); ORIANS (1969) in four types of lowland forest in Costa Rica on the total of 5.6 ha, recorded 61 species. LOVEJOY (1974) for Amazon forest mentioned over 200 species per ca 15 000 captured birds. Moreover KARR (1980) found that species richness of the avifauna of tropical forest undergrowth is highest in Neotropics in comparison to Malaysia and Africa. The unusuall richness of the Tambopata Reserve avifauna has already been stressed by PARKER (1982), who mentioned that within 10 km of lodge clearing more than 515 bird species had been recorded.

The data suggests (Tables I—III) that there is considerable overlap of more numerous species between three of the studied forest types. So, the strong differences found between bird assemblages of various plots (Tables IV—V) are caused mainly by less numerous species. A similar overlap of most numerous

species in various habitats was reported from lower Amazon River forest (LOVEJOY 1974).

The relative low number of recaptures (75 out of 662 captures — 11.3%) probably confirms the high degree of nomadism in neotropical birds in comparison to temperate zone avifauna (KARR, 1971). This low recapture rate is perhaps even more striking if we take into consideration that at least a part of my study period (XI, XII) comprised a part of breeding season of some species as indicated by collected data concerning moult and fat deposits (DYRCZ, 1987a). I found also direct evidence of breeding (occupied nests, fledgelings, brooding patches) for Ruddy Quail-Dove *Geotrygon montana*, Pale-legged Hornero *Furnarius leucopus* (DYRCZ, 1987 b), Black-spotted Bare-eye *Phlegopsis nigromaculatus*, Black-faced Antthrush *Formicarius analis*, Ringed Antpipit *Corythopis torquata*, and Band-tailed Manakin *Pipra fasciicauda*.

Appendix 1

Birds caught in the Lower Floodplain Forest

Species	n	%
Glaucis hirsuta (GMELIN, 1788)	7	13.7
Pipra fasciicauda HELLMAYR, 1906	5	9.8
Ramphocelus carbo (PALLAS, 1764)	4	7.8
Furnarius leucopus SWAINSON, 1838	3	5.9
Polyplancta aurescens (GOULD, 1846)	2	3.9
Machaeropterus pyrocephalus (SCLATER, 1852)	2	3.9
Empidonax alnorum BREWSTER, 1895	2	3.9
Donacobius atricapillus (LINNAEUS, 1766)	2	3.9
Turdus ignobilis (SCLATER, 1857)	2	3.9
Represented by one individual (ca 2%): *Butorides striatus* (LINNAEUS, 1766), *Geotrygon montana* (LINNAEUS, 1758), *Florisuga mellivora* (LINNAEUS, 1758), *Phaethornis ruber* (LINNAEUS, 1758), *Xiphocolaptes promeropirhynchus* (LESSON, 1840), *Sittasomus griseicapillus* (VIEILLOT, 1818), *Synallaxis gujanensis* (GMELIN, 1789), *Taraba major* (VIEILLOT, 1816), *Myrmeciza atrothorax* (BODDAERT, 1783), *Cercomacra serva* (SCLATER, 1858), *Pitangus sulphuratus* (LAFRESNAYE, 1851), *Myiarchus tuberculifer* (D'ORBIGNY & LAFRESNAYE, 1837), *Contopus virens* (LINNAEUS, 1766), *Ochthornis littoralis* (PELZELN, 1868), *Stelgidopteryx ruficollis* (VIEILLOT, 1817), *Thryothorus leucotis* LAFRESNAYE, 1845, *Vireo olivaceus* (LINNAEUS, 1776), *Cacicus solitarius* (VIEILLOT, 1816), *Thraupis episcopus* (LINNAEUS, 1766), *Saltator maximus* (MÜLLER, 1776), *Sporophila lineola* (LINNAEUS, 1758), *Ammodramus aurifrons* (SPIX, 1825).		
Total	51	~100

Appendix 2

SØRENSEN index:

$$SQ = \frac{2c}{a+b} \times 100$$

where c is the number of species common for the two assemblages, a is the number of species in first assemblage, and b is number of species in second assemblage.

The RENKONEN index quantity can be evaluated by adding up the minimum quantities of percentage dominance (Re = Σ Dmin). Example:

	1st assemblage		2nd assemblage	
	n	%	n	%
(1) *Pipra fasciicauda*	15	68.2	2	9.1
(2) *Gymnopithys salvini*	4	18.2	4	18.2
(3) *Corythopis torquata*	3	13.6	16	72.7

Re = (1)9.1+(2)18.2+(3)13.6 = 40.9

If values of SØRENSEN index reach 80—95%, it means that the two assemblages are almost identical, and values within the range 60—80% denote clear similarity. In the case of RENKONEN index, values within the range 50—70% show clear similarity of assemblages and values above 70% may indicate that the samples belong to the same community (TOMIAŁOJĆ 1970).

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STRESZCZENIE

Badania prowadzono od połowy listopada 1985 do połowy lutego 1986 w południowo-wschodnim Peru, na terenie stanu Madre de Dios, w większości pokrytego naturalnym lasem tropikalnym. Obszar ten należy do zlewni Amazonki. Terenem badań był rezerwat Tambopata, położony ok. 30 km na SW od miasteczka Puerto Maldonado w widłach rzek Tambopata i La Torre, na wysokości około 250 m n.p.m. Obejmuje on głównie pierwotny las tropikalny. Roczna suma opadów wynosi tutaj 1500—2000 mm, a średnia temperatura roczna 18—24°C. Okres badań przypadł na pierwszą część pory deszczowej. Prowadzono je przy użyciu siatek stylonowych do połowu ptaków. Schwytane ptaki identyfikowano, znakowano, ważono, oceniano otłuszczenie i stopień pierzenia się, mierzono długość złożonego skrzydła i wypuszczano. Sieci były zainstalowane w trzech rodzajach lasu, odzwierciedlających gradient roślinności w miarę posuwania się od rzeki do wyżej położonych miejsc. Był to wyżej położony las zalewowy (Upper Floodplain Forest, UF—PF), las niezalewany typu 1 (Upland Forest, type 1; UF—1) i las niezalewany typu 2 (Upland Forest, type 2; UF—2). Ten ostatni położony był najwyżej (kilkanaście metrów nad poziomem rzeki) na piaszczystych glebach dawnych, aluwialnych teras rzecznych. Las UF—1, położony między dwoma pozostałymi, rósł na słabo przepuszczalnej glebie i w porze deszczowej tworzyły się tu rozległe kałuże i sadzawki. Poza tym wymienione rodzaje lasu różniły się składem gatunkowym roślin, struktura roślinności natomiast (np. wysokość drzew, obfitość podszycia) była zbliżona. W nisko położonym lesie zalewowym (Lower Floodplain Forest, LF—PF) prowadzono tylko sporatyczne obserwacje (Appendix 1).

Liczebność i względna długość skrzydła ptaków malała idąc od terenów przy rzece do UF—2 (Tabela IV), a zróżnicowanie gatunkowe i stopień osiadłości (wyrażony procentem retrapów) wzrastał. Wykaz ptaków schwytanych

w trzech rodzajach lasu przedstawiają tabele I—III. Różnice w składzie awifauny w różnych rodzajach lasu, oceniane na podstawie schwytań w sieci, dotyczyły przede wszystkim rzadszych gatunków, najczęściej chwytane natomiast dominowały we wszystkich trzech siedliskach. Awifauna odznaczała się niezwykle silnym zróżnicowaniem gatunkowym; 662 schwytane ptaki należały do 127 gatunków. Liczba retrapów (11.3%) była stosunkowo niska, sugerując znaczną mobilność ptaków, pomimo że dla ich części chwytanie przypadło na porę lęgową. Udział gatunków ptaków, towarzyszących kolumnom drapieżnych mrówek (ant-followers), wzrastał w miarę oddalania się od rzeki, kolibry (*Trochilidae*) i gorzyki (*Pipriade*) natomiast były częściej chwytane w lesie zalewowym.

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