

Birds of a Severely Hurricane-Damaged Atlantic Coast Rain Forest in Nicaragua¹

Tom Will

University of Michigan, Natural Science Building, Ann Arbor, Michigan 48109-1048, U.S.A.

ABSTRACT

On 22 October 1988 Hurricane Joan severely damaged 500,000 ha of lowland tropical rain forest in southeastern Nicaragua near Bluefields. An expedition in February 1989 detected virtually no birds in formerly forested sites, although standing trunks that had been snapped were resprouting and the forest appeared to be recovering. In March 1990 I observed birds along rivers and at a secondary forest site and surveyed and mist-netted birds at three sites reported to be largely mature forest before they were damaged by the hurricane. I recorded a total of 161 species throughout the hurricane-damaged region. In seven days at the regenerating forest sites, I recorded 113 species of birds, a species richness comparable to undamaged lowland forest I visited six months later near the Río Santa Cruz, Nicaragua. Mist net capture rates at the damaged sites suggested overall bird abundance similar to that of a comparable lowland rain forest at La Selva, Costa Rica, but the typical habitats of mist-netted frugivores differed significantly between the two areas: the hurricane-damaged sites had proportionately fewer captures of species typical of the forest interior. Most of the birds encountered in the hurricane-damaged forest were species typical of forest edge, forest canopy, and second-growth habitats; only 19 species were birds typical of the forest interior, and only two were exclusively so. Woodcreepers, forest antbirds, and furnariids, families characteristic of lowland rain forest, were notably absent or under-represented. Overall forest structure appeared to be important in determining the species composition of the reappearing bird community.

RESUMEN

El 22 de octubre de 1988, el huracán Juana provocó daños severos en 500,000 ha de un bosque muy húmedo tropical bajo al sureste de Nicaragua cerca Bluefields. Una expedición en febrero de 1989 casi no detectó pájaros en áreas previamente con bosque, a pesar de que los troncos de árboles partidos, que aún permanecían de pie, tenían rebrotes y el bosque aparentaba estar en recuperación. En marzo de 1990, yo observé pájaros a lo largo del río y en un lugar de bosque secundario y examiné y atrapé pájaros con redes en tres lugares que se habían reportado mayormente como bosque maduro antes de ser dañados por el huracán. Se registró un total de 161 especies a través de la región dañada por el huracán. En siete días en los lugares de bosque en recuperación, se registraron 113 especies de pájaros, una riqueza de especies comparable al bosque bajo no dañado que visité seis meses después cerca del Río Santa Cruz, Nicaragua. La tasa de captura en redes en los lugares afectados sugiere una abundancia de pájaros en general similar a la de un bosque muy húmedo tropical bajo en La Selva, Costa Rica, pero el ambiente típico donde se encuentran los frugívoros capturados, fue significativamente diferente entre las dos áreas: los lugares afectados por el huracán tuvieron proporcionalmente menos capturas de especies típicas del interior del bosque. La mayoría de los pájaros encontrados en el bosque afectado por el huracán fueron especies típicas del borde del bosque, el dosel y ambientes de crecimiento secundario: sólo 19 especies fueron pájaros típicos del interior del bosque, y sólo dos lo eran exclusivamente. Familias características de bosque muy húmedo bajo, como los trepadores, hormigueros, y horneros estuvieron notablemente ausentes o con poca representación. La estructura general del bosque aparentemente es importante para determinar la composición de especies en la comunidad de pájaros que reaparece.

HURRICANE JOAN HIT THE CARIBBEAN COASTAL city of Bluefields, Nicaragua, on 22 October 1988 with winds gusting to 290 km/hr (Cortes & Fonseca 1988). The storm severely damaged 500,000 ha of lowland tropical rain forest centered on a line from Bluefields to Rama, 50 km inland. Fewer than 20 percent of the trees in this region were left standing, and what had been canopy was strewn on

the ground as a deep and tangled litter (Yih *et al.* 1989, 1991; Boucher 1989).

One of the more spectacular effects of the hurricane that was mentioned repeatedly by local residents was the virtual absence of birds in the days following the storm and for several months afterward. In February 1989, in two weeks of field work at widely scattered sites throughout the region of damage, Yih *et al.* (1989) sighted only about 20 doves, 3 parrots, 2 toucans, 7 kingfishers, 5 flycatchers, and several groups that were more common: egrets, herons, and vultures. All of these were

¹ Received 22 January 1991, revision accepted 3 June 1991.

seen either along waterways or in agricultural areas. Alerted to the scarcity of birds, members of the expedition watched and listened intently for them in forest study areas. They heard none and saw only a single *Amazilia* hummingbird (Boucher 1989).

This study documents the presence of birds in the Bluefields region 16.5 months after Hurricane Joan. Unfortunately, there are no comparable baseline data available describing the avifauna prior to the hurricane. The only recent study is that of Howell (1957) from a second-growth forest 16 km W of Rama. Previous studies (Nutting 1884, Richmond 1894, Rendahl 1919) are all based on collections made in the 19th century. The fact that so little is currently known about the avifauna of southeastern Nicaragua is particularly lamentable because its forests comprise the largest tract of extant lowland tropical rain forest in all of Central America and therefore deserve the special concern of responsible ecologists, naturalists, and conservationists worldwide.

STUDY SITES AND METHODS

I visited the Bluefields, Nicaragua region 5–18 March 1990 as a member of an international team studying the regeneration of the hurricane-damaged forest. I recorded all birds sighted in transit on the waterways, but primary observations were concentrated at three forests and one second-growth study site.

Las Delicias (12°18'N, 83°52'W, elev. 30–60 m), about 17 km NW of Kukra Hill, was visited 6–9 March. La Fonseca (12°16'N, 83°58'W, elev. 20–40 m), visited 16–18 March, is 12 km W of Las Delicias and about 3 km E of the agricultural cooperative Carlos Fonseca on the Río Kama. La Bodega (11°52'N, 83°58'W, elevation 10–20 m), visited 11–14 March, is located 500 m from the bank of the Río Kukra about 33 km by river from its mouth on Bluefields Bay. All three forest sites were primarily mature *terra firme* rain forest before the hurricane, but La Bodega differs in its proximity to the river and its inclusion of seasonally inundated *Pterocarpus* swamp. At Las Delicias and La Bodega, 80.5 percent of the trees were severely damaged (snapped = 53.2%, windthrown = 27.3%) by the hurricane, but by February 1989, 77 percent were resprouting from the base of fallen trunks or by epicormic branching. Tree seedling species composition was similar to that of adults (Yih *et al.* 1991, Vandermeer *et al.* 1990b). By March 1990 the overall death rate of adult trees was estimated at 45 percent, including those directly killed by the

hurricane (Vandermeer *et al.* 1990a). A fourth site, El Kama, visited on 6 March and again 15–17 March, is situated on the W bank of the Río Kama, approximately 5 km S of La Fonseca. It comprises a mosaic of river edge, pasture, agricultural fields, low scrub, young second growth, and older second growth.

At each site, with binoculars or by voice, I identified birds during all daylight hours and recorded vocalizations for later identification, confirmation, or to lure birds into view with playback. I walked on whatever trails were available, penetrating the forest wherever possible. The forest "interior" (a euphemism, since there was no canopy) was extremely difficult to reach due to the ubiquitous litter of fallen trunks and limbs, the dense tangle of vines, and new sprouting vegetation. For estimates of avian abundance, I opened between three and seven 2.6 × 12 m mist nets from ≈0600 to ≈1000 hr on the second and third mornings at each forest site (only one morning at La Fonseca). I used mostly 36 mm mesh nets with one 30 mm or 71 mm net set along existing or modified trails. I checked nets every 30 minutes and color-banded resident birds or feather-clipped migrants and hummingbirds to identify recaptured individuals.

Mist net capture rates were compared with those of Levey (1988a, b) at La Selva, a lowland rain forest in Costa Rica 180 km to the south. I also compared the species list from my study with birds which I recorded over a similar period of 7 days (30 August to 5 September 1990) at La Lupe (11°7'N, 84°22'W, elev. 80–160 m), a site 110 km SW of Bluefields near the Río Santa Cruz, 12.5 km NNE of El Castillo, Río San Juan, Nicaragua. La Lupe was not damaged by the hurricane and comprises mostly mature *terra firme* rain forest selectively logged in 1985–86, patches of uncut primary forest, and forest edge and second growth. In overall structure it resembles mature rain forest, since the crowns of many of the large trees (*e.g.*, *Dipteryx panamensis*) have been left intact, but it also shares some characteristics with the hurricane-damaged forest, notably an understory littered with fallen branches and dense new vegetation. To compare distributions of birds by typical habitats, I used the classification in Stiles (1983) for La Selva. Species that were listed as occurring in several habitats were placed in mutually exclusive categories based on the most mature forest category in which they are typically found, in the order: mature forest interior, interior of old second growth, forest canopy, forest edge, young second growth, and scrub and pasture.

RESULTS

In the 12 field and travel days of the study, I recorded 161 species of birds in the region (Appendix A). The total for all terrestrial habitats, excluding aquatic birds, was 130 species over 8.5 days. Excluding species seen in transit, at the second growth site of El Kama, and at or above a forest pond at La Bodega, I recorded 105 terrestrial species in the recovering forest over a 7-day period. Using identical observation methods, I recorded 112 non-aquatic species over 7 days in undamaged rain forest at La Lupe (T. Will, pers. obs.). Excluding migrants and transients from both lists (since the surveys were done at different times, March *vs.* September), the comparison is 90 species in the hurricane-damaged forest *vs.* 98 at the undamaged site. If more open pasture habitat is included, there were 130 species at the hurricane-damaged sites compared with 122 at La Lupe (109 *vs.* 107, respectively, without migrants). Thus, depending on whether more open habitats and/or migrants are included, the hurricane-damaged sites near Bluefields appear from 6.5 percent richer in bird species to 8.2 percent less rich than a similarly surveyed, undamaged forested area. The distribution of species (migrants excluded) typical of mature forest/old second-growth interior, forest canopy, forest edge, and young second growth/pasture was similar at both sites (test of independence, $\chi^2_3 = 6.24$, $P > .05$).

Of the 105 nonaquatic species at the three forest sites, 19 (18%) were birds typically found in the interior of tropical forest ("Fi" in Appendix A). Of these, only Slaty-breasted Tinamou and Song Wren are more or less birds of the forest interior exclusively (they also are found in closed canopy old second growth). The other 17 species are also often found at the forest edge (including light gaps), in older second growth, or in tree plantations. Of the 105 forest site species, 21 (20%) were birds of open pasture, low scrub, and young second growth—not at all typical of forest. Thirty-six (34%) of the forest site species were birds typical of the forest canopy. With the exception of Great Green Macaw, all of these are also commonly found in other habitats, notably forest edge, old second growth, and tree plantations. An additional 24 species (23%) were typical of forest edge, including light gaps of various ages, but not of forest canopy; many of these are also found in older second growth and tree plantations. The distribution of species typical of mature forest/old second-growth interior, forest canopy, forest edge, and young second growth/pasture found at the three forest sites differed significantly from

that found at the predominantly second-growth/pasture site of El Kama (test of independence, $\chi^2_3 = 9.57$, $P < .025$); El Kama had proportionately fewer forest interior and more young second-growth/pasture species.

At the three hurricane-damaged forest sites, I captured a total of 52 individuals of 30 species in 113.5 net-hours, an average of 0.458 birds per net-hour (numerals in Appendix A). In lowland rain forest at La Selva, Costa Rica, Levey (1988a) captured an average of 0.237 birds per net-hour in forest gaps over all months of the year (0.195 in gaps and intact forest combined). Because tropical bird abundance can vary considerably from month to month (Karr 1976, Levey 1988b), it is more enlightening to compare only March captures, where the Levey (1988b) data were available only for frugivores in intact forest, mature forest gaps, and second growth. I used Levey's (1988b) dietary classification for my captures (Appendix A) and recorded 0.282 frugivore captures per net-hour as compared with 0.125 for the Levey (1988b) study in March at La Selva. Although there are differences in habitat, in the magnitude of the studies (114 *vs.* ≈ 1042 March net-hours), and in the duration of net set (until ≈ 1000 *vs.* ≈ 1400 hr) that make comparison less than ideal, the contrast provides no evidence of low overall bird abundance in the hurricane-damaged Nicaraguan forest. However, the distributions of number of frugivore captures typical of mature forest/old second-growth interior, forest canopy/edge, and young second growth were significantly different between La Selva and the hurricane-damaged sites (test of independence, $\chi^2_3 = 13.3$, $P < .005$). Frugivores typically found in the forest interior were proportionately less abundant while edge and scrub birds were more abundant in the Nicaraguan forest samples.

DISCUSSION

Sixteen months after Hurricane Joan, neither overall bird species richness nor abundance appeared to be unusually depressed at study sites in the damaged Nicaraguan rain forest—a situation radically different from the virtual absence of birds reported four months after the hurricane by Yih *et al.* (1989). Although none of the researchers on the February 1989 expedition were trained ornithologists, they all were ecologists or naturalists with much tropical experience. Their perceptions should not be taken lightly, especially as the scarcity of birds was a common theme among local residents, many of whom were quite familiar with the local avifauna

and capable of identifying many birds to species both visually and by vocalization. But without evidence of massive mortality or displacement or comparable mist net sampling in the months immediately following the forest destruction, it is not possible to assess the magnitude of the direct effects of the hurricane on the avifauna. Birds may have been killed outright by the high winds and debris or blown away—or many birds may have survived the storm and concentrated in local patches, singing less and remaining inconspicuous in the tangles of fallen debris.

The fact that the hurricane damaged so vast an area coupled with the relative abundance of birds detected 16.5 months later suggests that many birds probably did survive the storm and afterward wandered locally as regenerating patches of forest became available. Similar strong hurricanes in forests of Jamaica (J. Wunderle, pers. comm.), Mexico, and Puerto Rico appear to have resulted in little direct mortality of birds, but drastic declines in populations of nectarivores and frugivores in Mexico after Gilbert (Lynch 1991) and in Puerto Rico (Waide 1991) and the Virgin Islands (Askins & Ewert 1991) after Hugo, suggest that loss of food resources results in subsequent local movement. The data from this study also suggest that birds reappear as food resources become available in the regenerating forest. Yih *et al.* (1991) found virtually no pioneer tree species in the forest study sites in February 1989, but by March 1990 bird-dispersed species like *Cecropia* and fruiting shrubs were common on several of the transects (Vandermeer *et al.* 1990a)—along with the frugivorous birds that were so conspicuously absent a year before.

The reappearance of birds in the Nicaraguan hurricane-damaged forest seems to be closely linked to the availability of structurally suitable habitat. The first species to become conspicuous after the hurricane were birds of less damaged agricultural zones and waterways (Yih *et al.* 1989). By March 1990 the regenerating forest sites resembled expanses of dense second-growth understory, but they differed from young secondary forest in having a tree species composition similar to that of mature forest (Yih *et al.* 1991) and in the presence of numerous large resprouting trunks which nonetheless lacked the spreading crowns of mature forest

trees. Thus, it is not too surprising that most of the birds noted on the regenerating sites were species typical of forest canopy, forest edge, and second-growth sites and that there were proportionately more net captures of frugivores typical of forest edge and young second-growth habitats than at La Selva. Lynch (1991) noted a similar influx of field- and shrub-associated species in Mexico after Hurricane Gilbert. In the distribution of species by typical habitats, the Nicaraguan hurricane-damaged forest sites were similar to selectively logged forest at La Lupe, but they still had proportionately more species typical of the forest interior and fewer species typical of scrub and young second-growth habitats than the largely second-growth site of El Kama. Intermediate in structure and tree species composition between mature forest and second growth, the hurricane-damaged forest sites in March 1990 appeared to support an avifauna intermediate between one characteristic of mature rain forest and one characteristic of second-growth forest. This suggests an hypothesis of close linkage between overall forest structure and the species composition of the bird community. As the forest continues to regenerate (Vandermeer *et al.* 1990a), forest interior birds should become more evident. This prediction assumes that there was sufficient variation in the extent of hurricane damage throughout the region to have provided the necessary refugia to sustain populations of the more uncommon forest species.

ACKNOWLEDGMENTS

The Nicaraguan Center for Research and Documentation of the Atlantic Coast (CIDCA) and its director, Galio Gurdian, and the Division of Natural Resources (DIRENA) of the Southern Atlantic Autonomous Region and its director, Jorge Brooks, were indispensable to the success of the project. I thank my companions on the expedition for their support and Nat Wheelwright for assistance at La Bodega. Doug Levey, Joe Wunderle, Robert Waide, and an anonymous reviewer made insightful suggestions for improving the manuscript. The work was supported by NSF grant number BSR-8917688 to John Vandermeer. The study at La Lupe was done under the auspices of the UCA/CATIE/SAREC project, "Desarrollo de sistemas de producción sostenible para el aprovechamiento de los bosques tropicales húmedos en la zona del Río San Juan, Nicaragua." It would not have been possible without the gracious assistance of the many people involved in the project, especially Alejandro Mejía, César Sabogal, Jan Salick, and Rigoberto Obando.

LITERATURE CITED

- ASKINS, R. A., AND D. N. EWERT. 1991. Impact of Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. *Biotropica* 23: 481–487.

- BOUCHER, D. H. 1989. When the hurricane destroyed the rain forest. *Biology Digest* 16: 11–18.
- CORTES DOMÍNGUEZ, G., AND R. FONSECA LÓPEZ. 1988. *El Ojo Maldito*. Editorial Nueva Nicaragua, Managua, Nicaragua.
- HOWELL, T. R. 1957. Birds of a second-growth rain forest area of Nicaragua. *Condor* 59: 73–111.
- KARR, J. R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *Am. Nat.* 110: 973–994.
- LEVEY, D. J. 1988a. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076–1089.
- . 1988b. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- LYNCH, J. F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica* 23: 488–496.
- NUTTING, C. C. 1884. On a collection of birds from Nicaragua. *Proc. U.S. Nat. Mus.* (1883) 6: 372–410.
- REHND AHL, H. 1919. Notes on a collection of birds from Panama, Costa Rica, and Nicaragua. *Ark. Zool.* (Band 12) 8: 1–36.
- RICHMOND, C. W. 1894. Notes on a collection of birds from eastern Nicaragua and the Rio Frio, Costa Rica, with a description of a supposed new trogon. *Proc. U.S. Nat. Mus.* (1893) 16: 479–532.
- STILES, F. G. 1983. Birds. *In* D. H. Janzen (Ed.). *Costa Rican natural history*, pp. 502–544. University of Chicago Press, Chicago, Illinois.
- , AND A. F. SKUTCH. 1989. *A guide to the birds of Costa Rica*. Cornell University Press, Ithaca, New York.
- VANDERMEER, J., D. BOUCHER, I. PERFECTO, L. ROTH, T. WILL, AND W. K. YIH. 1990a. El bosque devastado de Bluefields: segunda expedición. *Wani* 8: 60–73. Centro de Investigaciones y Documentación de la Costa Atlántica (CIDCA), Managua, Nicaragua.
- , N. ZAMORA, K. YIH, AND D. BOUCHER. 1990b. Regeneración inicial en una selva tropical en la costa caribeña de Nicaragua después del huracán Juana. *Rev. Biol. Trop.* 38: 347–359.
- WAIDE, R. B. 1991. The effects of Hurricane Hugo on bird populations in the Luquillo Experimental Forest. *Biotropica* 23: 475–480.
- YIH, K., D. H. BOUCHER, J. H. VANDERMEER, AND N. ZAMORA. 1989. Efectos ecológicos del huracán Joan en el bosque tropical húmedo del sureste de Nicaragua a los cuatro meses: posibilidades de regeneración del bosque y recomendaciones. Centro de Investigaciones y Documentación de la Costa Atlántica (CIDCA), Managua, Nicaragua.
- , ———, ———, AND ———. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica* 23: 106–113.

Appendix A

Species of birds noted in the vicinity of Bluefields, Nicaragua, 5–18 March 1990. Birds seen along waterways are indicated under RIOS; those recorded at El Kama are listed under KAMA. The three forest sites of Las Delicias, La Fonseca, and La Bodega are designated as DEL, FON, and BOD, respectively. Numerals in the columns indicate mist-net captures.

Scientific name ^a	English common name ^a	Habitat ^b	Diet ^c	RIOS	Forest sites ^d		
					KAMA	DEL	FON BOD
<i>Crypturellus soui</i>	Little Tinamou	Fe, S	F/G		x	fc	x fc
<i>Crypturellus boucardi</i>	Slaty-breasted Tinamou	Fi, oS	F/G			x	
<i>Pelecanus occidentalis</i>	Brown Pelican	A	P	fc			
<i>Phalacrocorax olivaceus</i>	Olivaceous Cormorant	A	P	fc			
<i>Anhinga anhinga</i>	Anhinga	A	P	fc			
<i>Fregata magnificens</i>	Magnificent Frigatebird	A	P	fc			
<i>Tigrisoma mexicanum</i>	Bare-throated Tiger-Heron	A	Pr				(x)
<i>Nycticorax nycticorax</i> **	Black-crowned Night-Heron**	A	Pr		x		
<i>Bubulcus ibis</i>	Cattle Egret	P	I	c	x		
<i>Butorides striatus</i> **	Green-backed Heron**	A	Pr	fc			(x)
<i>Egretta caerulea</i> *	Little Blue Heron*	A	P	vc			(x)
<i>Egretta tricolor</i> *	Tricolored Heron*	A	P	c			
<i>Egretta thula</i> *	Snowy Egret*	A	P	c			
<i>Casmerodius albus</i> **	Great Egret**	A	Pr	vc			
<i>Ardea herodias</i> *	Great Blue Heron*	A	Pr	fc			(x)
<i>Mycteria americana</i>	Wood Stork	A	P	vc	x		(fc)
<i>Ayaia ajaja</i>	Roseate Spoonbill	A	P, I	x			(x)
<i>Cairina moschata</i>	Muscovy Duck	A	G	x			(x)
<i>Cathartes aura</i>	Turkey Vulture	O	C	c	c	c	c
<i>Coragyps atratus</i>	Black Vulture	O	C, Fp	c	c	c	c
<i>Pandion haliaetus</i> *	Osprey*	A	P	fc	x	x	x
<i>Elanoides forficatus</i> ^e	American Swallow-tailed Kite ^e	O	Pr	x			
<i>Elanus caeruleus</i>	Black-shouldered Kite	P	Pr			x	
<i>Harporhynchus bidentatus</i>	Double-toothed Kite	Fe, Fe	Pr			x	
<i>Leucopternis semiplumbea</i>	Semiplumbeous Hawk	Fi, Fe, oS, Fp	Pr	x			x
<i>Leucopternis albigollis</i>	White Hawk	Fe, Fe	Pr	x			
<i>Buteogallus anthracinus</i>	Common Black-Hawk	Fe	Pr	x			x
<i>Buteo nitidus</i>	Gray Hawk	Fe	Pr	x			
<i>Buteo magnirostris</i>	Roadside Hawk	yS	Pr				
<i>Buteo platypterus</i> *	Broad-winged Hawk*	Fe	Pr		x		
<i>Spizaetus tyrannus</i>	Black Hawk-Eagle	Fe, S	Pr		x		
<i>Herpetotheres cachimans</i>	Laughing Falcon	Fe, S, Fp	Pr				x
<i>Falco sparverius</i> *	American Kestrel*	P	Pr		x		

Appendix A

Continued.

Scientific name ^a	English common name ^a	Habitat ^b	Diet ^c	RIOS	KAMA	Forest sites ^d		
						DEL	FON	BOD
<i>Ortalis cinereiceps</i>	Gray-headed Chachalaca	yS	Fh					x
<i>Penelope purpurascens</i>	Crested Guan	Fi, Fe, oS, Fp	Fh					x
<i>Laterallus albigularis</i>	White-throated Crane	A, P	I, G		x			
<i>Helminis fulica</i>	Sungrebe	A	I, Pr	fc				
<i>Jacana spinosa</i>	Northern Jacana	A, P	I, Pr, G	fc				
<i>Actitis macularia</i> *	Spotted Sandpiper*	A	I, Pr	fc				
<i>Larus atricilla</i> *	Laughing Gull*	A	Pr	c				
<i>Sterna maxima</i> *	Royal Tern*	A	P	fc				
<i>Columba spectiosa</i>	Scaled Pigeon	Fc, Fe, Fp	Fh		fc		fc	fc
<i>Columba nigrirostris</i>	Short-billed Pigeon	Fc, Fe, oS, Fp	Fh			x		
<i>Columbina talpacoti</i>	Ruddy Ground-Dove	P	F/G		x			
<i>Claravis pretiosa</i>	Blue Ground-Dove	P, yS	G	fc			fc 2	
<i>Leptotila cassinii</i>	Gray-chested Dove	Fe, oS, Fp	F/G				x	x
<i>Ara ambigua</i>	Great Green Macaw	Fc	Fh			x		
<i>Aratinga finchi</i>	Crimson-fronted Parakeet	P	Fh	fc				fc
<i>Aratinga nana</i>	Olive-throated Parakeet	Fe, oS, Fp	Fh		fc	c	fc	fc
<i>Brotheria jugularis</i>	Orange-chinned Parakeet	P, yS	F/G		fc	fc		x
<i>Pionopitta baematoris</i>	Brown-hooded Parrot	Fc, Fe, S, Fp	F/G	x	fc	fc		
<i>Pionus senilis</i>	White-crowned Parrot	Fc, Fe, S, Fp	F/G	x	fc		x	fc
<i>Amazona autumnalis</i>	Red-lore Amazon	Fc, Fe, Fp	F/G		c	c	fc	fc
<i>Amazona farina</i>	Mealy Amazon	Fc, Fe, Fp	F/G		fc	c		fc
<i>Piaya cayana</i>	Squirrel Cuckoo	Fe, yS, Fp	I			fc 1	x	fc 1
<i>Crotophaga sulcirostris</i>	Groove-billed Ani	P, yS	I, Fp	c	c			
<i>Tapera naevia</i>	Striped Cuckoo	P	I		x			
<i>Otus guatemalae</i>	Vermiculated Screech-Owl	Fi, Fe	I			x		x
<i>Pulsatrix perspicillata</i>	Spectacled Owl	Fi, Fe, Fp	Pr					x
<i>Ciccaba virgata</i>	Mottled Owl	Fe, oS, Fp	Pr		x			
<i>Nyctibius grandis</i>	Great Potoo	Fc, Fe	I			x		
<i>Chordeiles acutipennis</i> **	Lesser Nighthawk**	P	I	fc				
<i>Nyctidromus albigollis</i>	Pauraque	P, yS	I		c		fc	fc
<i>Chaetura cinereiventris</i>	Gray-rumped Swift	O	I	fc	fc		fc 2	fc
<i>Glaucidis aenea</i>	Bronzy Hermit	Fe, yS	N		fc			
<i>Phaethornis longuemareus</i>	Little Hermit	Fi, Fe, oS	N			fc 2		
<i>Florisuga mellivora</i>	White-necked Jacobin	Fi, Fe, oS, Fp	N		x			
<i>Thalurania colombica</i>	Crowned Woodnymph	Fi, Fe, S, Fp	N		x	fc 1		

Appendix A

Continued.

Scientific name ^a	English common name ^a	Habitat ^b	Diet ^c	RIOS	KAMA	Forest sites ^d		
						DEL	FON	BOD
<i>Hylocharis eliciae</i>	Blue-throated Goldentail	Fe, oS	N			fc 1	fc 2	1
<i>Amazilia tzacatl</i>	Rufous-tailed Hummingbird	yS	N			x	x	fc 2
<i>Trogon masena</i>	Slaty-tailed Trogon	Fc, Fe, oS, Fp	Fp					
<i>Trogon melanoccephalus</i>	Black-headed Trogon	Fc, Fe, oS	Fp		x		x	
<i>Ceryle torquata</i>	Ringed Kingfisher	A	P	c				(x)
<i>Ceryle alcyon</i> *	Belted Kingfisher*	A	P	fc				
<i>Chloroceryle amazona</i>	Amazon Kingfisher	A	P	c				
<i>Chloroceryle americana</i>	Green Kingfisher	A	P	fc				
<i>Chloroceryle aenea</i>	American Pygmy Kingfisher	A, Fi, Fe	P					1
<i>Electron platyrrhynchum</i>	Broad-billed Motmot	Fc, Fe, oS	Fp			x		
<i>Baryphthengus martii</i>	Rufous Motmot	Fc, Fe, oS	Fp			fc	x	
<i>Bucco macrorhynchos</i>	White-necked Puffbird	Fc, Fe, oS	I, Pr			x		
<i>Pteroglossus torquatus</i>	Collared Aracari	Fc, Fe, oS, Fp	Fp	x		x		
<i>Ramphastos sulfuratus</i>	Keel-billed Toucan	Fc, Fe, oS, Fp	Fp			fc	x	x
<i>Ramphastos swainsonii</i>	Chestnut-mandibled Toucan	Fc, Fe, oS, Fp	Fp	x		fc		x
<i>Melanerpes pucherani</i>	Black-cheeked Woodpecker	Fc, Fe, oS, Fp	I, Fp	x				x
<i>Dryocopus lineatus</i>	Lineated Woodpecker	Fe, oS	I		x			x
<i>Campephilus guatemalensis</i>	Pale-billed Woodpecker	Fc, Fe, oS, Fp	I			x		
<i>Dendrocincla fuliginosa</i>	Plain-brown Woodcreeper	Fi, Fe	I				x	
<i>Cymbilaimus lineatus</i>	Fasciated Antshrike	Fe, S, Fp	I	x				
<i>Taraba major</i>	Great Antshrike	yS	I					
<i>Thamnophilus doliatus</i>	Barred Antshrike	yS	I		x	x		
<i>Thamnophilus punctatus</i>	Slaty Antshrike	Fi, Fe, oS, Fp	I		x	x		fc
<i>Cercomacra tyrannina</i>	Dusky Antbird	Fe, oS	I			fc		x
<i>Myrmeciza exul</i>	Chestnut-backed Antbird	Fi, Fe, oS	I			fc		fc
<i>Hylophylax naevioides</i>	Spotted Antbird	Fi, Fe	I				x	
<i>Tityra semifasciata</i>	Masked Tityra	Fc, Fe, oS, Fp	Fp		x	fc		x
<i>Carpodectes nitidus</i>	Snowy Cotinga	Fc, Fe, Fp	Fh		x	x		x
<i>Pipra mentalis</i>	Red-capped Manakin	Fi, Fe, oS	Fh			c 2		fc 1
<i>Manacus candei</i>	White-collared Manakin	Fe, oS	Fh		fc	fc 1		c 1
<i>Colonia colonus</i>	Long-tailed Tyrant	Fc, Fe, Fp, P	I		x			
<i>Tyrannus tyrannus</i> †	Eastern Kingbird†	Fe, oS, Fp	Fp		x			
<i>Tyrannus melancholicus</i>	Tropical Kingbird	P, yS	Fp	c	fc			
<i>Megarhynchus pitangus</i>	Boat-billed Flycatcher	Fc, Fe, oS, Fp	Fp		x		x	
<i>Artibeus spadicreus</i>	Bright-rumped Atrila	Fc, Fe, oS, Fp	Fp	x		fc	fc	fc

Appendix A

Continued.

Scientific name ^a	English common name ^a	Habitat ^b	Diet ^c	RIOS	KAMA	Forest sites ^d		
						DEL	FON	BOD
<i>Myiozetetes similis</i>	Social Flycatcher	P, yS	Fp	fc	fc			
<i>Pitangus sulphuratus</i>	Great Kiskadee	P	Fp	c	fc			
<i>Rhytipterna boleythra</i>	Rufous Mourner	Fc, Fe, oS, Fp	Fp				1	
<i>Myiarchus crinitus</i> *	Great Crested Flycatcher*	Fc, Fe, oS, Fp	Fp		x	x		x
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	Fe, oS, Fp	Fp		x		1	x
<i>Contopus cinereus</i>	Tropical Pewee	P, yS	I		x			
<i>Oncotoma cinereigulare</i>	Northern Bentbill	Fe, oS	I				x	
<i>Elaenia flavogaster</i>	Yellow-bellied Elaenia	P, yS	Fp		x		x	
<i>Mionectes oleagineus</i>	Ochre-bellied Flycatcher	Fi, Fe, oS, Fp	Fp			1		
<i>Progne subis</i> †	Purple Martin†	O	I	x	fc	fc	c	
<i>Progne chalybea</i>	Gray-breasted Martin	P	I	fc				
<i>Tachycineta albilinea</i>	Mangrove Swallow	A	I	vc				
<i>Cyanocorax morio</i>	Brown Jay	yS	Fp			x		
<i>Thryothorus thoracicus</i>	Stripe-breasted Wren	Fe, oS, Fp	I		fc			x
<i>Thryothorus nigricapillus</i>	Bay Wren	Fe, oS	I		fc	x		fc
<i>Troglodytes aedon</i>	House Wren	yS	I		fc	fc		
<i>Cypborhinus phaeocephalus</i>	Song Wren	Fi, oS	I					x
<i>Dumetella carolinensis</i> *	Gray Catbird*	yS	Fp		x	fc 2		fc 1
<i>Turdus grayi</i>	Clay-colored Robin	P, yS	Fp		fc			
<i>Hylocichla mustelina</i> *	Wood Thrush*	Fi, Fe, oS	Fp					1
<i>Polioptila plumbea</i>	Tropical Gnatcatcher	Fc, Fe, oS, Fp	I		fc	c		c
<i>Ramphocaelus melanurus</i>	Long-billed Gnatwren	Fe, oS	I		fc	1		
<i>Vireolanus pulchellus</i>	Green Shrike-Vireo	Fc, Fe, Fp	Fp		x			
<i>Vireo flavifrons</i> *	Yellow-throated Vireo*	Fc, Fe, oS, Fp	I		x	x		
<i>Vireo olivaceus</i> †	Red-eyed Vireo†	Fc, Fe, oS, Fp	Fp		x			
<i>Hylophilus decurtatus</i>	Lesser Greenlet	Fc, Fe, oS, Fp	Fp		fc	fc		c
<i>Vermivora pinus</i> *	Blue-winged Warbler*	yS	I			1	x	
<i>Vermivora peregrina</i> *	Tennessee Warbler*	Fe, yS, Fp	Fp		fc			
<i>Dendroica petechia</i> *	Yellow Warbler*	P, yS	I					
<i>Dendroica cerulea</i> †	Cerulean Warbler†	Fc, Fe, Fp	I		x			
<i>Dendroica pensylvanica</i> *	Chestnut-sided Warbler*	Fc, Fe, S, Fp	Fp		fc	fc 1		1
<i>Seiurus aurocapillus</i> *	Ovenbird*	Fe, oS	I					
<i>Seiurus noveboracensis</i> *	Northern Waterthrush*	Fe, S	I			1		1
<i>Oporornis formosus</i> *	Kentucky Warbler*	Fi, Fe, oS	I			1		
<i>Geothlypis poliocephala</i>	Gray-crowned Yellowthroat	P, yS	Fp				x	

Appendix A

Continued.

Scientific name ^a	English common name ^a	Habitat ^b	Diet ^c	RIOS	KAMA	Forest sites ^d			
						DEL	FON	BOD	
<i>Parocolinus montezuma</i>	Montezuma Oropendola	Fc, Fe, oS, Fp	Fp			fc	fc		
<i>Cactus uropygialis</i>	Scarlet-rumped Cacique	Fc, Fe, Fp	Fp			fc	fc		fc
<i>Quiscalus mexicanus</i>	Great-tailed Grackle	P		c					
<i>Icterus spurius</i> *	Orchard Oriole*	S			x				
<i>Icterus dominicensis</i>	Black-cowled Oriole	Fe, S, Fp	Fp		x				x
<i>Icterus galbula</i> *	Northern Oriole*	Fe, S, Fp	Fp		fc				fc
<i>Tangara larvata</i>	Golden-hooded Tanager	Fc, Fe, S	Fp		fc				fc
<i>Dacnis cayana</i>	Blue Dacnis	Fc, Fe, Fp	Fp			fc	x		
<i>Thraupis abbas</i>	Yellow-winged Tanager	S, Fp	Fp		x				
<i>Ramphocelus passerinii</i>	Scarlet-rumped Tanager	S	Fp	fc	c	c 2	c		c 1
<i>Piranga rubra</i> *	Summer Tanager*	Fc, Fe, oS, Fp	Fp		x				x
<i>Habia fuscicauda</i>	Red-throated Ant-Tanager	Fe, oS	Fp						1
<i>Salpator coerulescens</i>	Grayish Saltator	yS	Fp		x				
<i>Caryothraustes poliogaster</i>	Black-faced Grosbeak	Fe, oS, Fp	F/G		x				
<i>Pitylus grossus</i>	Slate-colored Grosbeak	Fc, Fe, Fp	F/G			1	fc		fc 1
<i>Cyanocampa cyanoides</i>	Blue-black Grosbeak	Fe, oS	F/G			1	1		
<i>Passerina cyanea</i> *	Indigo Bunting*	yS	F/G		x				
<i>Sporophila schistacea</i>	Slate-colored Seedeater	yS	G	fc	c		fc		
<i>Sporophila aurita corvina</i>	Variable Seedeater	P, yS	F/G		fc				
<i>Oryzoborus funereus</i>	Thick-billed Seed-Finch	yS, Fe	F/G		fc		fc 2		
<i>Volatinia jacarina</i>	Blue-black Grassquit	P, yS	F/G		fc		fc 2		
<i>Arremon aurantiostris</i>	Orange-billed Sparrow	Fi, Fe, oS	F/G		x	x			
<i>Arremonops contraintrix</i>	Black-striped Sparrow	yS, P	F/G		c	c 3	fc		c 1
Total species			161	48	78	62	54		65
Total less aquatic species			130		76	62	54		57
Total number of mist-net captures			52			20	17		15
Mist-net hours			113.5			28	31.5		54
Number of captures per net-hour			0.458			0.714	0.540		0.278
Frugivores per net-hour			0.282			0.429	0.349		0.167

^a Status: * = North American wintering migrant; ** = resident population + migrants; † = North American transients; ° = resident population migrating south. Taxonomic order and nomenclature based on Siles & Skutch (1989).

^b Typical habitat based on Siles (1983) for La Selva, Costa Rica: Fi = forest interior, Fc = forest canopy, Fe = forest edge, including light gaps, Fp = tree (e.g., cacao) plantations, arboreturns, etc.; oS = old second growth, with a more or less distinct canopy; yS = young second growth or low scrub; S = second growth in general; P = pastures and other open habitat; A = aquatic habitat; O = aerial, ranging above various habitats.

- ^c Diet classification after Levey (1988b) and Stiles & Skutch (1989): P = piscivore; Pr = predator (mainly of vertebrates); C = carrion; I = insectivore; Fh = heavy frugivore, Fp = partial frugivore (omnivore), F/G = frugivore/granivore; G = granivore; N = nectarivore.
- ^d Relative abundance of records: vc = very common, > 30 individuals noted daily; c = common, 10–30 individuals noted daily; fc = fairly common, 3–10 individuals noted daily (or < 30 individuals recorded once); x = present, or recorded infrequently. Numerals indicate mist-net captures. () = aquatic species excluded from certain analyses.