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## Habitat Selection and Foraging Ecology of Raptors in Amazonian Peru<sup>1</sup>

Scott K. Robinson

Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, U.S.A.

### ABSTRACT

Census results and observations of foraging tactics and diet were compiled for the 35 regularly occurring species of diurnal raptors in an 800-ha section of the lowland Manu National Park of southeastern Peru. Census results show that most forest raptors occurred across a broad array of successional stages. Population densities ranged from a high of one or two territories per 100 ha (e.g., *Micrastur* forest-falcons, double-toothed kite, *Harpagus bidentatus*) to lows of much less than one territory in the entire study area (e.g., large eagles). A species replacement apparently occurs in the genus *Leucopternis*, with the slate-colored hawk *L. schistacea* occupying flood plain forest and the white-browed hawk *L. kubli* occupying upland forest. All other congeners showed substantial overlap in habitat use. Based on observations by 35 researchers of over 400 prey items being carried and over 200 attacks, I divided raptors into several preliminary guilds. Forest raptors include seven species that hunt arthropods and small vertebrates from concealed perches (e.g., *Micrastur* forest-falcons, gray-headed kite, *Leptodon cayanensis*); seven species that hunt large birds and mammals either from concealed perches (e.g., ornate hawk-eagle, *Spizaetus ornatus*) or on long-range attacks on sites where birds or mammals aggregate (e.g., bicolored hawk, *Accipiter bicolor*); and several species with specialized diets of wasps (red-throated caracara, *Daptrius americanus*), snails (hook-billed kite, *Chondrohierax uncinatus*), and snakes (laughing falcon, *Herpetotheres cachinnans*). Species that hunt on the wing include four that feed mostly on flying insects and small vertebrates (two kites, the short-tailed hawk *Buteo brachyurus*, and the bat falcon *Falco ruficularis*), one that dives on perched vertebrates (zone-tailed hawk *Buteo albonotatus*), and two vultures that search for carrion. Raptors of open rivers, lakes, and marshes include a fish specialist (the osprey *Pandion haliaetus*), two snail specialist kites, a carrion-eating vulture, a *Buteo* that dives on arthropods and small vertebrates, and three species with extremely diverse diets (e.g., black-collared hawk, *Basarellus nigricollis*). Snail specialists tended to occur irregularly during the eleven field seasons of this study. Several raptors are known to influence the population dynamics of their prey species. Large forest-dwelling raptors such as the harpy and crested eagles are likely to require the largest preserves.

### RESUMEN

Resultados del censo y las observaciones de las tácticas de alimentación y dieta fueron recopiladas para las 35 especies de raptores diurnos que ocurrieron en 800 hectáreas dentro del Parque nacional Manu, al sudeste de Perú. Los resultados del censo indican que la mayoría de los raptores del bosque ocurrieron a través de una amplia serie de etapas sucesivas. Las densidades de población variaron de un máximo de 1 a 2 territorios por 100 hectáreas (ejemplo: *Micrastur*, *Harpagus bidentatus*), a mucho menos de un territorio en el área total de estudio (ejemplo: águilas grandes). Aparentemente, hay un reemplazo de especies en el género *Leucopternis*, donde el *L. schistacea* ocupa los valles formados por inundación y el *L. kubli* los terrenos elevados de bosque (terra firme). Todos los otros congéneres mostraron una considerable superposición en el uso de la región.

Basándose en observaciones hechas por 35 investigadores, de más de 400 presas transportadas y más de 200 ataques, he dividido los raptores en varios grupos preliminares. Los raptores del bosque incluyen siete especies que cazan artrópodos y pequeños vertebrados desde perchas escondidas (ejemplo: *Micrastur*, *Leptodon cayanensis*); siete especies que cazan pájaros grandes y mamíferos, ya sea desde perchas escondidas (*Spizaetus ornatus*), o en ataques a distancia en lugares donde pájaros o mamíferos se congregan (*Accipiter bicolor*); y varias especies con dietas especializadas de avispas (*Daptrius americanus*), caracoles (*Chondrohierax uncinatus*) y serpientes (*Herpetotheres cachinnans*). Las especies que cazan en vuelo incluyen cuatro que se alimentan principalmente de insectos voladores y pequeños vertebrados (*Ictinia*, *Elanoides*, *Buteo brachyurus* y *Falco ruficularis*); una que desciende sobre vertebrados en su percha (*Buteo albonotatus*); y dos *Cathartes* que buscan carroña. Los raptores de ríos, lagos y pantanos incluyen una especialista en pescado (*Pandion haliaetus*); dos que se especializan en caracoles; uno que come carroña; un *Buteo* que desciende sobre artrópodos y pequeños vertebrados; y tres especies con dietas extremadamente variadas (*Basarellus nigricollis*). Las especialistas en caracoles aparecieron muy irregularmente durante las once estaciones de este estudio. Se sabe que varios raptores influyen la dinámica de la población de las especies de sus víctimas. Los raptores grandes que habitan el bosque, como *Harpia* y *Morphnus*, necesitan los bosques más grandes.

*Key words:* Amazonian Peru; diet; diurnal raptors; Falconiformes; foraging tactics; guilds; habitat selection.

<sup>1</sup> Received 24 March 1993, revision accepted 16 December 1993.

THE LAST DECADE HAS SEEN A REEMERGENCE of interest in the role of predation in community organization and dynamics (Taylor 1984, Martin 1988, Terborgh 1988, Ricklefs 1989). Predation can exert a major influence on the reproductive success, habitat selection, population dynamics, life histories, and demographics of the species that make up a community (Taylor 1984). Martin (1988) hypothesized that the availability of safe nest sites may limit species coexistence. Oniki (1979, 1985) and Skutch (1985) have argued that nest predation is important in the life histories of most tropical forest birds. Populations of one of the commonest species of Amazonian forest birds may vary fivefold in response to recent attacks by nest predators (Robinson 1985). Munn (1985, 1986) has demonstrated how predators dictate the structure and organization of the huge multi-species flocks characteristic of much of Amazonia. Terborgh (1988) has further argued that large predators play a major role in regulating populations of medium-sized predators, which in turn affect populations of small prey species (Terborgh & Winter 1980, Soule *et al.* 1988). Thus, even though predators may have low population densities, they likely play a key role in community organization (Thiollay 1989).

Evidence that raptors are extremely vulnerable to habitat fragmentation and disturbance is growing. Small forest fragments lack many forest raptors in both the temperate zone (Robinson 1991) and in the tropics (Willis 1974, 1979; Leck 1979). Thiollay (1985c) and Whitacre *et al.* (1992) found that in disturbed habitats forest raptors are replaced by species characteristic of more open habitats. Thiollay (1989) argued that large home ranges and low population densities make raptors especially sensitive to habitat fragmentation, an argument seconded by Robinson and Wilcove (1989). Barro Colorado Island, which has lost many of its large raptors and cats, has extremely high levels of nest predation (Loiselle & Hoppes 1983; K. Sieving, pers. comm.), perhaps as a result of the lack of top predators, which prey on medium-sized predators.

Efforts to evaluate the impact of fragmentation on raptors and the impact of the loss of raptors on tropical communities have been hampered by the lack of data on raptor ecology (Thiollay 1980, 1985a, b, c; Whitacre & Thorstrom 1992). The low population densities, high diversity, and inconspicuous behavior of many raptors have made for a very slow accumulation of basic natural history data. Most of our understanding of raptor ecology comes from studies of single species, especially observations at single nests (*e.g.*, Beebe 1950, Rettig

1978, Bierregaard 1984). The only major studies at the community level have been done by Thiollay (1989) in French Guiana, who employed a team of observers working in huge plots (up to 10,000 ha) to quantify relative abundance, habitat selection, home range size, and diets of diurnal raptors, and the extensive studies in southern Mexico reported in Whitacre and Thorstrom (1992).

The purpose of the present study was to provide data comparable to those of Thiollay on habitat selection, population densities, hunting tactics, and diet of Amazonian raptors. In this paper, I have compiled my observations of raptors and those of 35 other researchers working at the Cocha Cashu Biological Station in the Manu National Park of southeastern Peru from 1973 through 1989. These observations include sightings of raptors attacking prey or carrying food and all data from an intensive census of the major habitats of the lowland sector of the Manu Park (Terborgh *et al.* 1990).

## STUDY AREA AND METHODS

The study site is in the 1.5 million-ha Manu National Park in the Department of Madre de Dios, southeastern Peru, at 71°19'W, 11°51'S. Except where noted, all observations were made within an 800-ha study area surrounding the Cocha Cashu Biological Station. The station is located on an oxbow lake (Cocha Cashu) of the Manu River and is 3–4 days by boat from the nearest road. The inaccessibility of the site has protected it from logging and systematic hunting. For this reason, the Manu Park has a full complement of species, including top predators and their prey, at natural population densities.

**MAJOR HABITATS.**—As the Manu River meanders across its flood plain, it creates a diverse mosaic of habitats, which have been described in detail by Terborgh (1983, 1985) and Robinson *et al.* (1990) and consequently are described only briefly here.

**River:** The stretch of habitat along the Manu River includes open water, steep eroded banks, and sandy beaches exposed during the dry season.

**Lakes:** The study area includes two oxbow lakes bordered by shrubby marshes and small trees.

**Pantanal:** A large (> 100 ha) open marshy area with scattered islands of trees and shrubs and numerous dead trees is located in the study area.

**Tessaria/Cane:** The first stage of riparian succession consists of narrow (< 50 m) belts of *Tessaria*, a treelike plant in the family Compositae,

and wider (up to 500 m) belts of *Gynerium*, a cane. Plants seldom exceed 10 m in height.

**Transitional forest:** The middle stages of riparian succession consist of forests that become taller and increasingly diverse as one moves further from the river. Canopy height ranges from 20 m at earlier stages of succession to 50 m by later stages. This habitat floods frequently and has an understory dominated by *Heliconia*.

**Mature flood plain forest:** This tall, diverse forest grows on high ground that seldom floods. Emergent trees reach 60 m and the understory is fairly open except around treefalls.

**Upland forests:** Areas above the current flood plain level consist of a mosaic of steep ravines, well-drained ridgetops and bamboo thickets. These ancient forests contain numerous vines, landslides, and treefall gaps.

**METHODS.**—This paper includes two kinds of data: census results and *ad lib* observations. Censuses were conducted in most major habitats, 1979–1986. Census plots and years were: mature flood plain forest (100 ha, 1982); transition forest (15 ha, 1982; 40 ha, 1984; 60 ha, 1985 and 1986); *Tes-saria*/Cane (3 ha, 1982; 5 ha, 1983; 6 ha, 1985 and 1986); upland forest (80 ha, 1985 and 1986); lake (30 ha, 1979–1985); and river (30 ha, 1982–1985). Plots in forested areas were censused using spot-map methods (Kendeigh 1944) along trails that were  $\leq 200$  m apart in each plot (Terborgh *et al.* 1990). Each trail was censused at least 20 times from August to November. Lakes were censused from canoes at least 20 times a year. We have not systematically censused pantanal habitats, but I have visited this habitat five times. Censuses were conducted by Theodore A. Parker III, John Terborgh, and Scott Robinson.

Our estimates of population densities are rather crude for raptors with territories much larger than our study plots. For rare, difficult-to-observe species, I augmented our census records with *ad lib* observations. Population density estimates are provided only for species known to reside year-round in the Cocha Cashu area. Migrants and vagrants (< 5 records) are treated separately.

*Ad lib* observations were recorded each time a raptor was observed attacking or carrying a prey item. During the 41 months I spent at the Biological Station (1979–1989), each time I observed a foraging raptor I recorded date, location, hunting tactics, and diet. My observations were biased towards lake margins, where I spent roughly 8000 hours studying colonies of the yellow-rumped cacique (*Ca-*

*cicus cela*) (Robinson 1985) and river margins where we observed many raptors during the 2–3 day boat trip to the station. All observations not followed by initials are my own. I also compiled the same data from sightings recorded by other scientists, including Dave Bolster (DB), Perri Eason (PE), Louise Emmons (LE), John Fitzpatrick (JF), Murray Gell-Mann (MG-M), Anne Goldizen (AG), Rolando Gutierrez (RG), Jon Herron (JH), Tom Hildebrand (TH), Charles Janson (CJ), Jennifer Leak (JL), Dave Lukas (DL), Carol Mitchell (CM), Debra Moskovits (DM), Charles A. Munn (CAM), Martha Brecht Munn (MBM), Ted Parker (TP), Ken Petren (KP), Nina Pierpont (NP), Leonides Quinones (LQ), Katherine Renton (KR), David Ricalde (DR), Lily Rodriguez (LR), Peter Sherman (PS), Margaret Symington (MS), John Terborgh (JT), Guisela Tesoro (GT), Bertina Torres (BT), Carel von Schaik (CV), Carol Walton (CW), Dave Willard (DW), and Pat Wright (PW).

Most observations are of raptors carrying prey across clearings. Captures of small inconspicuous prey items are therefore likely to be underrepresented in the data presented here. Supplementary dietary data were obtained from specimens from Amazonian Peru deposited in the Louisiana State University Museum of Natural Science (LSUMNS) and the Field Museum of Natural History (FMNH).

## RESULTS

**ABUNDANCE AND HABITAT SELECTION.**—Of the 43 Falconiforms (including vagrants and Cathartid vultures) recorded in the lowland sector of the Manu National Park, 35 either breed or regularly forage in the study area (Table 1). Of the eight remaining species, three are passage migrants that do not feed in the area (Mississippi kite [*Ictinia mississippiensis*], Swainson's hawk [*Buteo swainsoni*], and broad-winged hawk [*B. platypterus*]), and five are vagrants (*i.e.*, recorded fewer than five times from 1979 to 1989 (turkey vulture [*Cathartes aura*], pearl kite [*Gampsonyx swainsoni*], gray-bellied hawk [*Accipiter poliogaster*], crane hawk [*Geranospiza caerulescens*], and solitary eagle [*Harpohaliaetus solitarius*]). The orange-breasted falcon (*Falco deiroleucus*) has never been recorded within the National Park boundaries but has been observed along the nearby Alto Madre de Dios River (JWF, SR). Vagrants and passage migrants were excluded from further analyses.

Population densities of most forest-dwelling diurnal raptors appeared to be low. Only seven species were sufficiently common for territory mapping on

TABLE 1. *Habitat selection and estimated population densities of raptors in the Cocha Cashu area. For infrequently observed species, the number of sightings in each habitat is given in parentheses.*

Species	Abundance <sup>a</sup> in each habitat <sup>b</sup>						
	R	L	P <sup>c</sup>	T/C	TF	HGF	UF
King vulture ( <i>Sarcobambus papa</i> )	R	R	R	R	R	R	R
Black vulture ( <i>Coragyps atratus</i> )	U	R	R	R			
Turkey vulture ( <i>Cathartes aura</i> )	(2)	(1)	(5)				
Greater yellow-headed vulture ( <i>C. melambrotos</i> )	C	C	C	U	U	U	U
Pearl kite ( <i>Gampsonyx swainsonii</i> )			(1)				
American Swallow-tailed kite ( <i>Elanoides forficatus</i> )	U	U	U <sup>d</sup>	U	U	R	R
Gray-headed kite ( <i>Leptodon cayanensis</i> )		R	U	R	U	R	R
Hook-billed kite ( <i>Chondrobierax uncinatus</i> )			U		(8)		
Double-toothed kite ( <i>Harpagus bidentatus</i> )			R		U	C <sup>d</sup>	U
Plumbeous kite ( <i>Ictinia plumbea</i> )	C	C	C <sup>d</sup>	C	R <sup>d</sup>	R	R
Snail kite ( <i>Rostrhamus sociabilis</i> )		R	R				
Slender-billed kite ( <i>Helicolestes hamatus</i> )		(1)	U				
Bicolored hawk ( <i>Accipiter bicolor</i> )		R	U	R	R	R	R
Gray-bellied hawk ( <i>A. poliogaster</i> )							(1)
Tiny hawk ( <i>A. superciliosus</i> )			R		R	R	R
Zone-tailed hawk ( <i>Buteo albonotatus</i> )	R	R	U	R			
Short-tailed hawk ( <i>B. brachyurus</i> )	R	R	U	R	R	R	R
Roadside hawk ( <i>B. magnirostris</i> )	C	R	C <sup>d</sup>	C			
Slate-colored hawk ( <i>Leucopternis schistacea</i> )			R		U	U	
White-browed hawk ( <i>L. kubli</i> )							U <sup>d</sup>
Black-collared hawk ( <i>Busarellus nigricollis</i> )	R	C <sup>d</sup>	R				
Great black-hawk ( <i>Buteogallus urubitinga</i> )	U	U	U	R	R	R	
Crested eagle ( <i>Morphnus guianensis</i> )		(1)			(2)	(6)	(1)
Harpy eagle ( <i>Harpia harpyja</i> )		(1)	(1)		(4)	(11)	(3)
Black-and-white hawk-eagle ( <i>Spizastur melanoleuca</i> )	R	R	R	R	R	R	R
Ornate hawk-eagle ( <i>Spizaetus ornatus</i> )		R			R	R	R
Black hawk-eagle ( <i>S. tyrannus</i> )			R		R	R	R
Osprey ( <i>Pandion haliaetus</i> )	C	C					
Laughing falcon ( <i>Herpetotheres cachinnans</i> )		R	C <sup>d</sup>	R	U	U	R
Collared forest-falcon ( <i>Micrastur semitorquatus</i> )		R	R		U	U	U
Barred forest-falcon ( <i>M. ruficollis</i> )			R		C	C	
Lined forest-falcon ( <i>M. gilvicolis</i> )						C	C
Black caracara ( <i>Daptrius ater</i> )	C	C	C <sup>d</sup>	U	R		
Red-throated caracara ( <i>D. americana</i> )			U <sup>d</sup>		R	U	U
Bat falcon ( <i>Falco rufigularis</i> )	C	C	C <sup>d</sup>	C	U <sup>d</sup>	U <sup>d</sup>	U

<sup>a</sup> Abundance rankings: C = observed or heard on at least half of census visits; U = observed or heard once every 3–10 census visits; R = observed or heard less than once per 10 census visits. Numbers in parentheses refer to the total number of observations for very rare species.

<sup>b</sup> Habitats: R = River; L = Lake; P = Pantanal; T/C = *Tessaria*/Cane; TF = Transitional Forest; HGF = High Ground Forest; UF = Upland Forest.

<sup>c</sup> Based on only 5 censuses.

<sup>d</sup> Nests located.

the census plots, including double-toothed kite (three territories of 50–100 ha each), gray-headed kite (one territory of 50–80 ha), slate-colored hawk (two territories of 80–100 ha each), laughing falcon (one territory of 50–80 ha), barred forest-falcon (four territories of 40–50 ha each), and lined forest-falcon (four territories of 40–50 ha each). The rest of the species either had territories that were much larger than 100 ha (e.g., *Harpia harpyja*) or were strictly aerial and therefore difficult to census (three cathartid vultures, swallow-tailed kite, plumbeous kite, zone-tailed hawk, short-tailed hawk). The tiny hawk

was difficult to detect and may be much more common than our observations suggest. Harpy and crested eagles, king vultures, and black-and-white hawk-eagles appeared to have home ranges larger than the >800-ha area where most research was conducted in the Cocha Cashu area. Vultures probably did not defend territories, and I saw as many as eight adult king vultures simultaneously feeding on the same carcass.

Some raptors that occurred along rivers and lakes had high population densities. Ospreys, which occurred only as nonbreeders, averaged 1–2 indi-

viduals per oxbow lake (20–50 ha of open water) and also occurred along the river. Black-collared hawks averaged one pair per oxbow lake. Great black-hawks and black caracaras divided their time between the river and oxbow lakes and two pairs of each species occurred in the study area. Roadside hawks defended 2–4 km stretches along rivers and foraged mostly along beaches in *Tessaria* and rarely along oxbow lakes. Black vultures were found primarily along the river and less often along oxbow lakes; they were commonly found near native settlements.

The three species of snail-eating kites occurred irregularly. Of the 16 records of snail kites from 1979 to 1989, 12 were of juveniles (including one that resided for two months on a nearby oxbow lake), three were of pairs (none remained in the area for more than two weeks), and one was of a flock of 14 adults that visited Cocha Cashu for only half an hour before leaving. A group of three or four hook-billed kites was present in an area of transition forest during 1979 and 1980 but was not observed before or again until 1988 and 1989 when a group of 4 was observed in the pantanal, where they had not been observed previously (C. A. Munn, pers. comm., S. Robinson, pers. obs.). A pair of slender-billed kites moved into the pantanal in 1985 and was recorded through the end of the study.

The 200-ha pantanal habitat was by far the richest habitat for raptors in the study area. The combination of small wooded islands, open marshy areas, and isolated trees provided foraging and nesting opportunities for all but a few forest interior specialists. The pantanal was the only habitat where gray hawks and slender-billed kites were regularly recorded. The isolated trees were also used by at least eight species of raptors for nesting, including plumbeous, swallow-tailed and gray-headed kites, roadside hawk, laughing falcon, black and red-throated caracaras, and bat falcons.

**HUNTING TACTICS AND DIET.**—Table 2 summarizes data on hunting tactics and diets of the 31 species of raptor known to occur regularly in the Cocha Cashu area. Below are provided additional details on the data presented in Table 2 and the results compared with those from other sites.

**Vultures:** Our observations of king vultures are consistent with those of Houston (1984a, b), who proposed that this species locates carcasses by watching the activities of *Cathartes* vultures. Greater yellow-headed vultures soared fairly low (< 100 m) over the canopy and open areas and found small carcasses inside the forest (6 observations) and along

watercourses (15 observations feeding on dead fish). King vultures, on the other hand, soared very high and aggregated at large carcasses, including a giant armadillo (*Priodontes maximus*) and a black caiman (*Melanosuchus niger*). King vultures supplanted both black and greater yellow-headed vultures at carcasses. Black vultures were confined to more open habitats, frequently near human settlements, and supplanted greater yellow-headed vultures from dead fish on at least eight occasions along the edge of Cocha Cashu.

**American swallow-tailed kite:** This aerial species caught a variety of small insects on the wing (3 butterflies, 2 orthopterans, 23 unidentified) and in one instance was observed hovering and plucking fruit from a large canopy tree. Published reports suggest that swallow-tailed kites supplement their diet of aerial insects with fruit (Buskirk & Lechner 1978, Lemke 1979), nestling birds and other prey taken from surfaces (Skutch 1965, Snyder 1974, Lohrer & Lohrer 1984).

**Gray-headed kite:** All but two of the dietary observations were from a pair carrying food towards a presumed nest that I never located. Gray-headed kites were observed carrying 7 lizards (20–40 cm), 2 frogs, one orthopteran, one snake, two lepidopteran larvae, and one unidentified vertebrate. The seven lizards were slender with long (> 10 cm) tails. The five orthoptera were katydids (Tettigoniidae). These observations are consistent with those published elsewhere (Brown & Amadon 1968:214, Haverschmidt 1968:48, Voous 1969, Whitacre *et al.* 1992).

**Hook-billed kite:** No observations of this species foraging in the Cocha Cashu area were made. Presumably, hook-billed kites eat tree snails as they do elsewhere in their range (Smith & Temple 1982, Marroquín *et al.* 1992).

**Double-toothed kite:** The association of double-toothed kites and primate troops has been well-documented (Greenlaw 1967, Fontaine 1980, Boinski & Scott 1988). In the Cocha Cashu area, double-toothed kites followed troops of squirrel monkeys (*Saimiri sciureus*), brown capuchins (*Cebus apella*), and white-fronted capuchins (*C. albifrons*), which flush many large insects and lizards (Terborgh 1983). This species was never observed foraging independently of monkeys in the Cocha Cashu area. They were observed eating 13 large insects (2 moths and 11 orthopterans), and 2 lizards (one *Anolis* and one 35-cm unidentified). Most accounts of their diet also include insects (often specified as orthopterans, cicadas, and coleoptera) and small green lizards, including *Anolis* spp. Two dou-

TABLE 2. Summary of hunting tactics of raptors in the Manu National Park, Peru.

Species	Hunting tactics	Diet
Black vulture	Soared low, often near human settlements	Carcasses
King vulture	Soared very high (>100 m)	Large carcasses
Greater yellow-headed vulture	Soared 20–50 m over canopy	Carcasses
Swallow-tailed kite	Soared above canopy, caught prey on the wing	Insects, fruit
Grey-headed kite	Short (1–10 m) flights in upper canopy, short dives from branch to branch	Lizards, orthopterans, lepidoptera larvae, frogs, snake, unidentifiable vertebrate
Double-toothed kite	Followed monkey troops, dived on prey flushed by monkeys	Large insects, lizards
Plumbeous kite	Soared over open areas, caught flying insects in its talons	Lizards, orthopterans, lepidoptera larvae, frogs, snake, unidentified vertebrate
Snail kite	Perched and soared low (<10 m) over marshes, dives down to catch snails	<i>Pomacea</i> snails
Slender-billed kite	One pair observed foraging in shrubs along edge of a marsh	No observations
Bicolored hawk	Actively flew between concentrations of birds, especially in fruiting trees and along habitat margins	13 birds, 1 squirrel ( <i>Sciurus</i> )
Tiny hawk	Hunted high in the canopy, possibly follows flocks	No observations
Zone-tailed hawk	Soars 50–100 m over open areas, dived abruptly on prey below it	No successful attacks, dives at birds
Roadside hawk	Perched low (<10 m), dived on prey along the edges of clearings	Lizards, insects, snakes
Short-tailed hawk	Soared above canopy, sudden dives on birds	No observations
Slate-colored hawk	Mid-canopy in forest interior, occasionally followed monkeys, dives to ground	Lizards, snakes, orthopteran, moth
White-browed hawk	Unknown	No observations
Black-collared hawk	Shallow (<20 m) stoops to pluck prey near water surface or dives down into shallow water	Fish, snails, snakes, large frogs (>10 cm) mussels, arthropods, nestling bird
Great black-hawk	Attacked nests of colonial birds in trees and on beaches, reached into marshes, waded in shallow streams, walked along river banks	Nestling birds, eggs, adult birds, frog
Crested eagle	Long flying attacks through dense foliage in the forest interior, does not soar	Squirrel monkey
Harpy eagle	Long flying attacks through dense foliage in the forest interior; one attacked across a clearing, did not soar	Howler and squirrel monkeys, sloth
Black-and-white hawk-eagle	Long flying attacks through dense foliage and along edges	Bird
Ornate hawk-eagle	Attacked from concealed perches in canopy and along habitat edges, short (<50 m) attacks in trees and dived from dense cover to ground or shallow water	Birds, monkeys, rodents, snake

TABLE 2. *Continued.*

Species	Hunting tactics	Diet
Black hawk-eagle	Long (>50 m) flying attacks through forest; stooped down at prey in open areas	Squirrel, lizard, rodent
Osprey	Soars 50–100 m over lake, dived into water	Fish
Laughing falcon	No observations	Snakes
Collared forest-falcon	Attacked prey from a concealed perch, chased prey in open on long direct flights	Spix's guan
Barred forest-falcon	Attacked from concealed perches, often low (<10 m), followed army ants	Lizards, katydid
Lined forest-falcon	Attacked from concealed perches in understory	No observations
Red-throated caracara	No observations	Wasp (?) larvae
Black caracara	Attacked bird nests, ate carrion, searched canopy foliage for large insects, scavenged in camps	Nestlings, insects, carrion
Bat falcon	Aerial attacks on flying prey	Insects, birds, bats

ble-toothed kites collected near the Manu National Park in the FMNH contained the wing of a 4–5 cm orthopteran, 2 *Anolis* lizards, and a cockroach (Orthoptera: Blattidae). Two specimens from Peru in the collection of the LSUMNS contained “insect remains” Laughlin (1952) and Skutch (1965) have observed double-toothed kites foraging independently of monkeys.

Plumbeous kite: This raptor was observed catching only flying insects in the Cocha Cashu area, including 6 dragonflies, 3 orthopterans, 2 butterflies, and one moth. One individual caught and ate over 100 winged termites in a 15-minute period during a major emergence. Elsewhere, it has been observed eating small birds, snails, snakes, lizards, and frogs (Brown & Amadon 1968:255), some of which are caught on surfaces of trees (Marroquín *et al.* 1992). Skutch (1947), however, also found that plumbeous kites eat insects almost exclusively. One individual in the FMNH collected just outside the Manu National Park contained the remains of a Chrysomelid beetle. There were no records of plumbeous kites following monkeys as Ferrari (1990) observed in southeastern Brasil.

Snail kite: The irregular occurrence of snail kites suggests that the Cocha Cashu area represents marginal habitat for this species. Observations in the Manu Park (23 *Pomacea* caught by a juvenile, 6 by an adult) suggest that snail kites specialized on *Pomacea* snails caught in open marshy habitats and were nomadic as they are elsewhere in their range (Beissinger 1983, Snyder & Kale 1983).

Slender-billed kite: Haverschmidt (1959) reported that this species eats only large *Pomacea* tree snails, which it catches from low perches near water. This kite appears to hunt in dense shrubby areas along the edges of marshes in the Cocha Cashu area.

Bicolored hawk: Our observations of this species come mostly from the border of Cocha Cashu, where a pair apparently nested each year from 1979 through 1989. Bicolored hawks regularly attacked large concentrations of birds at fruiting and flowering trees, roosts, and colonies. They often made long-range (> 50 m) attacks rather than ambush prey from nearby concealed perches. An adult (presumably the same individual) regularly attacked a large flock of 150–200 Tui parakeets (*Brotogeris sanctithomae*) that was feeding in a *Ficus*. Each morning for at least 6 consecutive days, it flew towards the *Ficus* from the east between 0900 and 1030 and chased fleeing *Brotogeris*. On the fifth day, it caught one of the parakeets. Another attack on a flock of birds feeding in a *Cissus* vine resulted in the capture of a thrush-sized bird, possibly *Turdus ignobilis*. Bicolored hawks attacked yellow-rumped caciques in a flowering *Quararibea* tree (apparently unsuccessfully), in a fruiting *Coussapoa* (successfully: JL), and at cacique colonies (all 11 attacks were unsuccessful). A bicolored hawk was observed chasing an undulated tinamou (*Crypturellus undulatus*) across the Manu River (CW). The hawk caught its prey as soon as the tinamou reached the bank. A bicolored hawk was also observed catching a squirrel (*Sciurus* sp.) from the bole of a tree (JT). Elsewhere



in its range, bicolored hawks have been recorded eating mainly birds (Brown & Amadon 1968:534, Quixchán *et al.* 1992). Overall, bicolored hawks were seen catching or carrying 13 birds.

At least two juvenile bicolored hawks regularly attacked birds in the lakebed of Cocha Cashu. One of these juveniles visited the southern lakebed for 46 consecutive days when I observed it attacking chestnut-fronted macaws (*Ara severa*) 8 times; yellow-rumped caciques 13 times; russet-backed oropendolas (*Psarocolius angustifrons*) 23 times; a yellow-ridged toucan (*Ramphastos culminatus*), a boat-billed flycatcher (*Megarhynchus pitangua*), a purple gallinule (*Porphyryla martinica*), speckled chachalacas (*Ortalis guttata*) 4 times; pale-vented pigeons (*Columba cayannensis*) 5 times; a lettered aracari (*Pteroglossus inscriptus*); and a greater ani (*Crotophaga major*). None of these attacks was successful. Most attacks involved tail chases in which the prey either outdistanced or outmaneuvered the hawk. The purple gallinule escaped by diving repeatedly underwater whenever the hawk attacked. These chases may have functioned as practice, although neither juvenile was still being fed by an adult.

Tiny hawk: This rarely seen hawk seemed to forage exclusively in the upper canopy and has been observed catching a white-winged shrike-tanager (*Lanio versicolor*) in the nearby Rio Tambopata area of southeastern Peru (TAP). A bird collected just outside the Manu Park (FMNH) boundary contained the remains of unidentified insects (JF). Stiles (1978) suggested that tiny hawks may be hummingbird specialists.

Zone-tailed hawk: This species, which bears a striking resemblance to *Cathartes* vultures (Willis 1965), soared at or slightly above canopy level and dived down on prey. Most of our records were of attacks on birds, including three on yellow-rumped caciques and one on the tropical kingbird (*Tyrannus melancholicus*). This species was present only infrequently during 1979–1989, when it was observed on 27 of 1200 days on Cocha Cashu and 9 of 145 days on a nearby lake, which suggests that it may wander widely. Brown and Amadon (1968:600) and Zimmerman (1976) report a wide variety of prey items including lizards, frogs, fish, small mammals, and birds. All records were of adults.

Roadside hawk: Observations from the Manu area are consistent with literature accounts from other areas (Brown & Amadon 1968:574; Haverschmidt 1968:57; Marroquín & Moreno 1992). This species ate mostly large insects (3 orthopterans, 2 cicadas) and small vertebrates (1 snake, 7 lizards).

Four of the seven lizards reported were small (10–20 cm) *Ameiva* lizards caught on the ground. Individuals collected elsewhere in Peru contained the remains of three unidentified lizards and insect parts (LSUMNS). Groom (1992) found that roadside hawks also consume eggs and nestlings of sand-colored nighthawks (*Chordeiles rupestris*) along beaches of the Manu River. Marroquín and Moreno (1992) observed roadside hawks eating 15 rats, 14 lizards, 8 birds, 6 snakes, 9 insects and one frog in southern Mexico.

Short-tailed hawk: This species was rarely seen at Cocha Cashu, but has been observed diving at unidentified birds perched in the open on the tops of trees and attacking swallows and martins (*Progne* sp.) over open water. Elsewhere it attacks a variety of birds, many of which are caught on the wing (Ogden 1974). T. Parker (pers. comm.) has watched short-tailed hawks in Peru attacking white-collared swifts (*Streptoprocne zonaris*) in flight.

Slate-colored hawk: This little known forest hawk appears to have a diet typical of the genus *Leucopternis* (Brown & Amadon 1968:548). Of the five lizards it was observed carrying, four were slender with long (> 10 cm) tails (possibly in the family Teiidae) and the other may have been an Anole. Another was observed carrying a moth and there are two records of this species carrying a snake across a clearing. An individual following a troop of monkeys caught and ate a moth and an orthopteran. A slate-colored hawk was found perched on the ground holding a frog (CM).

White-browed hawk: There are no Cocha Cashu data on diet or hunting tactics for this poorly known species. Three birds in the collection at the LSUMNS contained the remains of an unidentified bird, two unidentified lizards, a "small snake," and a beetle.

Black-collared hawk: This sluggish bird foraged along the edge of oxbow lakes, where it caught prey from disparate taxonomic groups, including 11 fish, 5 snails, 4 mussels, 4 frogs, 3 large arthropods, and a nestling bird. Identifiable prey included a piranha, two *Leptodactylus* frogs (CC, KP, JL), three large *Pomacea* snails, an unidentified nestling or fledgling (possibly a purple gallinule) (RG, BT), and small (50–75 cm) snakes (TP, KP, JL, CC). When catching fish, black-collared hawks stooped in a shallow arc and grabbed fish from near the surface. When catching insects, snails, mussels, snakes, and frogs, black-collared hawks dived nearly straight down into shallow water and landed briefly before carrying prey to a perch. Willard (1985) also described the foraging ecology of this species.

**Great black-hawk:** This raptor used several distinct foraging tactics that made use of its long legs. Great black-hawks regularly attacked colonies of yellow-rumped caciques and russet-backed oropendolas (Robinson 1985). Their long legs could reach nests suspended well below branches. These hawks sometimes used their wings for support when reaching far below a perch. From 1979 to 1989 I observed 39 attacks on cacique and oropendola colonies during which 62 nestlings were consumed. Great black-hawks frequently walked upon open beaches and attacked colonies of sand-colored night-hawks (Groom 1992). I observed a great black-hawk walking from nest to nest in a nighthawk colony where it ate at least four small nestlings. Another great black-hawk approached the nest of a large-billed tern (*Phaetusa simplex*) but flew away without attacking, perhaps because it was distracted by the mobbing activities of the tern (see also Groom 1992). One hawk carried the remains of a frog when it was flushed from a stream. A bird in the collection at the LSUMNS contained fish vertebrae and crayfish that may have been captured by birds wading in streams. Great black-hawks are regularly observed walking along river banks, but no prey captures have been observed in this microhabitat. Great black-hawks sometimes perched in low shrubs or in marsh grass while searching for prey below them. They sometimes used their wings for support while reaching their talons deep in the marsh. Individuals foraging in dense shrubs have been observed eating eggs at five hoatzin (*Opisthocomus hoazin*) nests (JP, SR, RG). One great black-hawk was observed eating an adult hoatzin (RG) and another caught and killed a roadside hawk that was harassing it (TH).

Elsewhere, great black-hawks take a variety of vertebrate prey including crabs, snakes, lizards, small mammals, and frogs, as well as occasional large insects (Brown & Amadon 1968:559, Haverschmidt 1968:60, Whitacre *et al.* 1992) and attack bird nests (Olmos 1990).

**Crested eagle:** This rare species was observed five times attacking primate troops; one attack resulted in the capture of a squirrel monkey (*Saimiri sciureus*) (CM). All five attacks occurred at fruiting trees where monkeys were feeding. Elsewhere, crested eagles have been recorded taking birds (TAP), reptiles, including snakes, and some mammals (Bierregaard 1984). All of our observations came from primatologists and undoubtedly bias our data in favor of attacks on monkeys.

**Harpy eagle:** As is the case with the crested eagle, our observations reflect a probable bias toward

attacks on primates. Nine attacks on primate troops were documented (CJ, MS, CM; Eason 1989), seven at or near fruiting trees, two of which resulted in the capture of squirrel monkeys (CS, CJ). In most cases the harpy flew below the top of the canopy and maneuvered between the branches of canopy trees or along forest edges when approaching. Two other harpies were observed on the ground, one sitting on a red howler (*Alouatta seniculus*) (Sherman 1991) and the other on a three-toed sloth (*Bradypus variegatus*) (RG). Eason (1989) observed a gliding attack across a clearing on a troop of red howlers along the margin of Cocha Cashu. T. Parker (pers. comm.) also has observed a harpy eagle carrying a red howler at another site in southeastern Peru. Elsewhere in South America, harpy eagles have been recorded taking a wide variety of mostly arboreal mammals, especially sloths (Fowler & Cope 1964, Rettig 1978, Izor 1985) and adult male red howler monkeys (Peres 1990).

**Black-and-white hawk-eagle:** The only successful attack observed was on a blue-headed parrot (*Pionus menstruus*) captured at a mineral lick where hundreds of parrots were feeding (LQ). The eagle lunged into a tree and captured the parrot as it perched. Possibly the same black-and-white hawk-eagle was observed at least eight times (CAM, KR) attacking parrots in the vicinity of the mineral lick. Another individual attacked a group of hoatzins, but broke off the attack after the hoatzin it was chasing crashed into the water. A black-and-white hawk-eagle was also observed flying through a fruiting fig (*Ficus perforata*) where a mixed troop of squirrel and brown capuchin monkeys were foraging (CM). The monkeys reacted with alarm calls, and the eagle was unsuccessful. Black-and-white hawk-eagles have also been observed attacking colonies of russet-backed and crested (*Psarocolius oseryi*) oropendolas (JL, SR). In each attack, the hawk-eagle flew straight toward the nests and chased females as they left the nest. Presumably the same hawk-eagle was also observed attacking parrots from the canopy (KR). Elsewhere, black-and-white hawk-eagles take medium-to-large birds, small mammals, and reptiles (Grossman & Hamlet 1964:301). Willis (1988) observed this species hunting on the wing and diving down on prey. Our observations suggest that most attacks occur from the cover of the forest, although we frequently observed black-and-white hawk-eagles soaring high over the canopy.

**Ornate hawk-eagle:** This commonest eagle hunted by perching in dense foliage and flying horizontally or diving down at nearby prey. Ornate hawk-eagles have been observed twice diving from

concealed perches to the ground to catch wood-rats (*Proecomys* sp.) (JT, CM), and another was observed carrying a rat-sized (20–30 cm) rodent (KR). Ornate hawk-eagles also have been observed four times diving into shallow water to catch three purple gallinules (TAP, CAM, MG-M, SR) and a gray-necked wood-rail (*Aramides cajanea*) (DM). After three of these attacks, the eagle perched briefly in the water before carrying the prey into the forest. One of the gallinules was stolen by a white caiman (*Caiman crocodilus*) before the eagle could carry it back into the forest. An ornate hawk-eagle was also observed perched on the ground holding a 75-cm colubrid snake (RG). Ornate hawk-eagles have also been observed carrying a squirrel monkey (CS) and two saddle-backed tamarins (*Saguinus fuscicollis*) (JT, JWF). I have also observed three unsuccessful attacks on flocks of oropendolas foraging along the lake margin and three unsuccessful attacks on mixed colonies of oropendolas and yellow-rumped caciques. Additional unsuccessful attacks include an attack on ground-foraging pale-winged trumpeters (*Psophia leucoptera*) (PS), mixed monkey troops (CJ, CM), *Ara* macaws, *Brotogeris* and *Aratinga* parakeets foraging at a mineral lick (CC, KR), domestic chickens, and hoatzins (J. P. O'Neill, SR). Elsewhere, ornate hawk-eagles appear to eat primarily birds and small mammals, and have been known to attack large cracids (Lyon & Kuhnigk 1985, Klein *et al.* 1988, Montenegro *et al.* 1992).

**Black hawk-eagle:** This raptor has been observed carrying a large (30–35 cm) lizard and diving suddenly from the mid-canopy to capture a squirrel (*Sciurus* sp.) two m above the ground (LR). Black hawk-eagles have also been observed attacking macaws perched in a tree (KR) and carrying an unidentified rodent (KR). A large black raptor, possibly a black hawk-eagle, was observed eating a black-banded owl (*Ciccaba hubula*). Elsewhere, it has been observed eating birds, mammals (including bats), and reptiles (Smith 1970, French 1980:112, Funes *et al.* 1992).

**Osprey:** Willard (1985) gives an account of the fish selected by this species on Cocha Cashu. I have seen them catch 41 fish on Cocha Cashu.

**Laughing falcon:** All 16 observations were of laughing falcons carrying unidentified snakes 25 to 60 cm in length. No attacks on prey were observed for this species. Elsewhere, it has also been recorded eating small rodents, lizards, and arthropods (Skutch 1960, Brown & Amadon 1968:745–746, Guzmán & Orrego 1992).

**Collared forest-falcon:** This species appeared occasionally in the Cocha Cashu lakebed, where it was

observed attacking yellow-rumped caciques (12 attacks observed, 7 on flying caciques, 5 on individuals perched in colonies), and russet-backed oropendolas (*Psarocolius angustifrons*). In each attack, the cacique or the oropendola outmaneuvered the forest-falcon after brief tail chases and escaped into dense foliage. In between attacks, the collared forest-falcon(s) perched inconspicuously near colonies and waited until the caciques returned. The only successful attack was on an adult Spix's guan (*Penelope jacquacu*) (CM), which weighed at least 300 g more than the collared forest-falcon (S. Robinson and J. Fitzpatrick, pers. obs.). Observations at a nest (M. Silman, pers. comm.) in the Cocha Cashu area showed a diet consisting primarily of birds. Elsewhere, collared forest-falcons have been observed following army ants to catch flushed prey (Mays 1985) and eating birds, mammals, lizards, snakes, and insects often captured as the bird runs along the ground (Brown & Amadon 1968:752, Thorstrom *et al.* 1990). Rivera and Cordova (1992) found their diet to include 35 percent mammals, 27 percent birds and 15 percent amphibians in southern Mexico.

**Barred forest-falcon:** Even though this species is very common, there are few observations of it attacking prey, perhaps because barred forest-falcons forage inconspicuously in dense understory. Barred forest-falcons have twice been observed foraging at army ant swarms where one captured a large katydid (Orthoptera: Tettigoniidae). This species and the lined forest-falcon (see below) have also been observed attacking understory bird flocks (CAM). Another individual caught two *Ameiva* lizards 15–20 cm long along the edge of a small clearing. The falcon perched inconspicuously two m above the ground between attacks. Barred forest-falcons regularly attacked birds in mist nets. Four birds collected just outside the National Park boundary (FMNH) contained the remains of three small passerines (possibly a *Pipra* and two *Myrmotherula* antwrens), two small unidentified mammals, a large green beetle, a nematode head, and miscellaneous insect parts. Two of the birds may have been net kills because they had been eaten by falcons captured in mist nets, but the third came from an individual that had been shot away from mist net lines. A specimen in the LSUMNS had the remains of a beetle. Elsewhere, the barred forest-falcon is known to eat lizards, slugs, amphibians, and a variety of arthropods as well as birds (Brown & Amadon 1968:750, Schwartz 1972, Thorstrom *et al.* 1992). Remains at a nest in Guatemala in-

cluded mostly small (< 20 g) birds (Thorstrom *et al.* 1990).

Lined forest-falcon: No observations of successful attacks by this species have been recorded, although it has been observed attacking understory flocks (CAM). An individual collected just outside the Manu Park boundary contained the remains of a cockroach (Orthoptera: Blattidae) (FMNH). Three individuals collected elsewhere in Peru contained a lizard, a Hylid tree frog, insect parts, and the remains of a bird (LSUMNS). Elsewhere it has been observed following ants and eating nestlings (Schwartz 1972). Klein and Bierregaard (1988) hypothesize that lined forest-falcons eat a mixture of arthropods, lizards, and, occasionally, small birds.

Red-throated caracara: Even though red-throated caracaras were fairly common, the only foraging record is of a group eating small "grubs" from a branch (GT); these may have been wasp larvae. Elsewhere, red-throated caracaras eat wasp larvae, caterpillars, fruit, and palm seeds (Skutch 1959, Brown & Amadon 1968:728).

Black caracara: This conspicuous species eats a variety of prey along lakes and rivers. Most observations are of caracaras attacking bird nests. Black caracaras regularly attack colonies of yellow-rumped caciques, where they eat nestlings and eggs (Robinson 1985). Three attacks have also been observed on the nests of social flycatchers (*Myiozetetes similis*) (KP), but in each case, the flycatchers chased the caracaras away from nests with nestlings. Oropendolas also chased black caracaras out of colonies on 12 occasions.

Caracaras also regularly attacked nests on beaches. One family attacked a colony of sand-colored nighthawks, but caught only one nestling before leaving, probably as the result of the mobbing activities of pairs of black skimmers (*Rynchops nigra*), large-billed terns (*Phaetusa simplex*), and pied lapwings (*Hoploxypterus cayanus*). I saw a caracara carrying what appeared to be a nestling *Columba* pigeon. Groom (1992) describes interactions between black caracaras and beach-nesting birds in the Cocha Cashu area.

I have twice observed black caracaras catching large (4–7 cm) hairy caterpillars in canopy trees along the lake margin. Two of the six caterpillars caught were gleaned from nearby foliage by perched birds. The other four were too far to reach without flying and had to be plucked off leaves in short, stalling flights.

Black caracaras also scavenged in campsites and native settlements, where they were extremely tame. A trio of black caracaras also ate part of a dead fish

before being supplanted by a great yellow-headed vulture. Elsewhere, black caracaras are known to eat arthropods, palm fruits, small mammals, lizards and snakes (Grossman & Hamlet 1964, Brown & Amadon 1968:727).

Bat falcon: This species was active all day and attacks a wide variety of aerial prey in sudden stoops. At dusk, it has been observed stooping and catching a small (< 10 cm) insectivorous bat and a larger *Noctilio* bat low over that water (KP). Bat falcons have been observed stooping unsuccessfully at bats on 13 occasions and have been observed carrying four small (< 10 cm) and one large (15 cm) bat toward a presumed nest site. Bat falcons have also been observed diving into flocks of foraging sand-colored nighthawks on six occasions (CAM, CC). These attacks resulted in two captures; one other nighthawk broke the grip of the falcon and escaped before it was killed (CAM).

During the day, bat falcons attacked insects and birds, especially swallows. I have seen bat falcons stoop into concentrations of foraging swallows on 27 occasions, but I have never witnessed a successful attack. I have, however, seen bat falcons carrying four white-winged (*Tachycineta albiventer*), one rough-winged (*Stelgidopteryx ruficollis*), one blue-and-white (*Notiochelidon cyanoleuca*), and six unidentified swallows to nest sites. A bat falcon was observed carrying an adult red-capped cardinal (*Paroaria gularis*) and four unidentified small birds. Bat falcons have also been recorded catching 5 butterflies, 3 dragonflies, a cicada, and 10 unidentified large insects (SR, CC). Another bat falcon caught a *Brotogeris* parakeet as it flew into a fruiting tree along the edge of the river (GT). Bat falcons also regularly attended termite swarms, where I saw one individual catch over 50 termites. During three hours of observation, a pair of bat falcons fed a recent fledgling 26 large insects, including at least 5 butterflies, 2 cicadas, 3 dragonflies, and an orthopteran.

Elsewhere, the diet of the bat falcon has been thoroughly documented (Beebe 1950, Brown & Amadon 1968:824–825, Cade 1982:102–104). The Cocha Cashu data are biased in favor of aerial detecting detecting aerial captures of swallows, which forage over open water, and against detecting captures of forest birds and arthropods.

## DISCUSSION

RESOURCE DIVISION IN RAPTORS.—Based on the data presented here and a review of the literature, the raptors of this site can be divided into dietary generalists that eat prey from several taxa and specialists

TABLE 3. A preliminary guild classification of the forest-dwelling raptors of the Cocha Cashu area.

Hunting tactics	Prey	Species	
Aerial searching	Flying insects, prey on surfaces of trees	Swallow-tailed kite Plumbeous kite	
	Small vertebrates, and large insects	Bat falcon Short-tailed hawk	
	Carrion	King vulture Greater yellow-headed vulture	
Attacks from perches	Small vertebrates, large arthropods	Canopy Grey-headed kite Double-toothed kite (with monkeys) Tiny hawk Bat falcon (openings)	
		Understory Slate-colored hawk (flood plain) White-browed hawk (upland) Lined forest-falcon Barred forest-falcon	
		Snails Wasps	
		Birds, mammals	
		Snakes Aquatic animals	
		Hook-billed kite Red-throated caracara Ornate hawk-eagle Collared forest-falcon	
		Laughing falcon Black-collared hawk	
	Long (>50 m) attacks	Birds, occasionally mammals	Bicolored hawk Black-and-white hawk-eagle (?) Collared forest-falcon
		Mammals and lizards; occasionally birds	Black hawk-eagle Crested eagle Harpy eagle

that catch prey primarily from a single taxon. Specialists include the three snail-eating kites, the fish-eating osprey, the carrion-eating vultures, the two mostly insectivorous aerial kites (plumbeous and swallow-tailed), the bird-eating bicolored hawk, the snake-eating laughing falcon and, possibly, the mammal-eating harpy eagle. Dietary generalists include species that eat a mixture of arthropods and small vertebrates (*e.g.*, gray-headed and double-toothed kites, roadside and slate-colored hawks, barred and lined forest-falcons, black caracara, bat falcon), and those with extremely diverse diets (black-collared hawk, great black-hawk, crested eagle, ornate, hawk-eagle, collared forest-falcon). Zone-tailed, short-tailed, and tiny hawks and black-and-white hawk-eagles may specialize on birds, but there are too few data from the Manu to classify them.

Raptors can also be divided into species that primarily search on the wing, those that search from perches, and those that at least sometimes make long flights through the forest to attack prey. Species that hunt primarily on the wing include the four vultures, swallow-tailed and plumbeous kites, os-

prey, zone-tailed and short-tailed hawks, bat falcon and, occasionally, the black-and-white and black hawk-eagles. Species that search from perches include double-toothed, slender-billed, and gray-headed kites, roadside, slate-colored, and black-collared hawks, great black-hawks, collared, lined, and barred forest-falcons, bat falcons (occasionally) and ornate hawk-eagles. Harpy and crested eagles may both perch inconspicuously while searching for relatively immobile prey such as sloths and lizards and make long-range (> 50 m) attacks on trees where monkeys and birds aggregate (Eason 1989). Similarly, bicolored hawks may trapline fruiting and flowering trees and attack whatever is there at the time. Black-and-white and ornate hawk-eagles also were observed attacking prey from distances of at least 100 m. Attacks of forest-dwelling raptors, however, were rarely observed from start to finish. The foraging tactics used by the larger eagles remain largely a matter of speculation (Rettig 1978).

Combining information on hunting tactics and diet, several guilds of raptors can be distinguished (Table 3). The three guilds of aerial foragers consist

of six species that search for prey above the canopy. Bat falcons and short-tailed hawks appear to have overlapping diets with both species taking small birds. Bat falcons, however, are considerably smaller and forage extensively on insects and crepuscular bats and birds (*e.g.*, sand-colored nighthawk). Swallow-tailed and plumbeous kites both catch insects on the wing and eat large dragonflies, butterflies, and orthoptera. In general, swallow-tailed kites forage more over the forest than plumbeous kites, which prefer openings. The two carrion-eaters differ in the size of the carcasses they eat.

A few subgroups can be distinguished among the seven species that search for small vertebrates and insects from concealed perches (Table 3). Double-toothed kites follow primate troops almost exclusively, usually in the mid-canopy. Grey-headed kites forage more in the upper canopy and catch larger lizards and frogs and fewer insects. Slate-colored hawks forage lower than the double-toothed kites (T. A. Parker, pers. comm.) and take considerably larger prey and fewer insects. The white-browed hawk replaces the congeneric slate-colored hawk in upland forests, though little is known of its diet. The tiny hawk may be a specialist on small birds, but too little is known of its diet in the Manu to classify it. The two forest-falcons forage more in the forest understory than other guild members. In general, barred forest-falcons are restricted to younger flood plain forest, and lined forest-falcons are found in older flood plain and upland forests (*terra firma*) (Klein & Bierregaard 1988). Their territories, however, overlap broadly in mature flood plain forests (Terborgh *et al.* 1990).

Species that search for small vertebrates and insects from concealed perches (*e.g.*, forest-falcons) tend to be the most abundant diurnal raptors. These hawks exploit food at lower trophic levels where more food is likely to be available. Raptors (*e.g.*, eagles) that eat larger prey are correspondingly much less abundant.

The seven species that attack larger vertebrates from within the forest canopy have poorly known foraging ecologies. Crested eagles appear to forage more extensively on large reptiles (Bierregaard 1984), but the only prey observation at Cocha Cashu was a squirrel monkey. Harpy eagles forage on large mammals (up to the size of howler monkeys) (Eason 1989, Peres 1990, Sherman 1991), but also take iguanas and even bird nests (E. Alvarez, pers. comm.). Both collared forest-falcons and bicolored hawks attack birds, but differ somewhat in habitat selection and the size of prey attacked. Bicolored hawks prefer habitat edges and attack medium-

sized birds; whereas, collared forest-falcons forage more in the forest interior and have been observed attacking birds as large as the Spix's guan (1200–1300 g; S. Robinson, pers. obs.). Collared forest-falcons, however, occasionally forage along the edge of the forest and attack the same kinds of prey as the bicolored hawk. In Mexico, collared forest-falcons also ate many mammals (Rivera & Cordova 1992).

Too little is known of the diets and hunting tactics of black and black-and-white hawk-eagles for comparison with ornate hawk-eagles. All three species attack small mammals and large birds. Black hawk-eagles may take relatively more lizards and rodents (Sciuridae) (Funes *et al.* 1992); whereas, black-and-white hawk-eagles may concentrate more on attacking birds. Ornate hawk-eagles, however, are extremely generalized in their diet (Klein *et al.* 1988) and seem to overlap broadly with the other two hawk-eagles and the collared forest-falcon.

IMPACTS OF RAPTORS ON PREY POPULATIONS.—All raptors probably have major impacts on at least some of their prey, but only a few cases are well-documented. The tight clustering of nests in yellow-rumped cacique colonies appears to result at least in part because it improves defense against black caracaras (Robinson 1985). The cacique population of the Cocha Cashu area varies almost tenfold, largely in response to the success or failure of recent great black-hawk attacks on colonies (S. Robinson 1985, pers. obs.). During 1980–1985 when great black-hawk attacks were unsuccessful, caciques were the most abundant bird in the Cocha Cashu area (Robinson 1985, Terborgh *et al.* 1990). Since 1985, however, all large (> 40 nest) colonies have been destroyed by great black-hawks and the regional population has dropped by an average of 75 percent (S. Robinson, pers. obs.). Terborgh (1983, 1988) has hypothesized that the social organization and possibly the population dynamics of most primates are determined by raptor predation. Frequent predator attacks by hawk-eagles on parrots appear to dictate foraging patterns at a mineral lick (C. Munn, pers. comm.). Munn (1985, 1986) also hypothesized that raptor predation dictates the social organization of the multi-species flocks that dominate the forest canopy and understory bird communities. Social foraging in sand-colored nighthawks and swallows may largely function in defense against bat falcons. Several species, including caciques and oropendolas (S. Robinson, pers. obs.) and beach-nesting birds (Groom 1992), may benefit from mul-

ti-species nesting associations because they improve defense against raptors.

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