SPECIES DIVERSITY AND COMPARATIVE ECOLOGY OF RAINFOREST FALCONIFORMS ON THREE CONTINENTS

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ABSTRACT

When sample areas of some 100km^2 of primary rainforest are considered:

1. The Neotropical forests are 2.5 times richer in species than similar Indo-Malayan forests, and 2.7 times richer than their African counterparts.
2. On all three continents the number of raptor species increases by about 50 percent from the tropics to the equator.
3. Even when large and not very distant from the continent, Caribbean islands have 5–6 times fewer species than the adjacent mainland (5 species in Cuba *vs.* 22 to 33 in Central and South America) and the Old World islands have 2–5 times fewer species (Madagascar, 8 *vs.* 11–12; Sri Lanka, 9 *vs.* 11–13).

Four groups occur only in the New World, namely (1) the true forest vultures; (2) gregarious insectivorous kites which hunt in flight above the forest; (3) fast-flying, bird-hunting falcons and (4) snail-eating raptors. On the other hand, American forested rivers lack resident fishing raptors, widespread in the Old World forests. Other niches are occupied on every continent by one or several species: active predators of small or larger vertebrates, slow or stiff-hunting insectivores of the canopy, specialists in wasps' nests or snakes. Some striking convergent adaptations are found. Occasional fruit-eating and predation on birds' nests are a widespread habit among tropical forest raptors.

Morphological, vocal and behavioural adaptations of rainforest raptors are described. From their feeding habits, 8 to 18 percent of the species are generalists, 50 to 62 percent can be called semi-specialists and 25 to 41 percent are narrow specialists. Most of the species added to the communities from higher to lower latitudes belong to the last category.

INTRODUCTION

The rainforest belt can be divided into three main regions, the American, African and Indo-Malayan formations. Although their floristic composition varies greatly (e.g. the dominance of *Dipterocarpaceae* in Asia *vs. Leguminosae* and *Palmacae* in the New World) their climate, structure and regeneration stages are much alike. The tree species richness is least in Africa (100–150 species over 10cm in diameter per 10ha), intermediate in South America (150–200) and maximal in Southeast Asia (200–300). The total number of tree species reaches about 600 in the Ivory Coast, more than 800 in Gabon, 2500 in Amazonia, 3000 in the Malay Peninsula and even more in Borneo. Up to 122 tree species have been identified

in Gabon, 150 in New Guinea, 183 in Malaya and 186 in Brazil (Lebrun 1960; Richards 1952; UNESCO 1979). However, the number of bird species is not related to the floristic richness (Orians 1960).

METHODS AND STUDY SITES

I have surveyed on foot areas of 400 to 800km^2 of primary rainforest, during one to five months of intensive field work from 1967 to 1982 in southern Mexico, French Guiana and Surinam, southern Casamance (Senegal-Guinea border), southern Ivory Coast, northeastern Gabon, eastern and northeastern Madagascar, southern Nepal, central Malaya and northern Borneo. All raptor species were recorded and the completeness of the species list was checked with the relevant literature: Alvarez del Toro 1971; Barbour 1943; Haverschmidt 1968; Meyer de Schauensee 1966; Ridgely 1976 for America: Anon. 1980; Bannerman 1953; MacWorth Praed & Grant 1970; Morel 1972 for Africa: Milon *et al.* for Madagascar: Henry 1971 for Sri Lanka: Fleming *et al.* for Nepal: Lekagul & Cronin 1974 for Thailand: Medway & Wells 1976 for Malaya: Smythies 1981 for Borneo.

Most study sites were adjacent to larger expanses of nearly virgin forest and often in hilly country. Only the *shorea* forest of lowland Nepal is not a true rainforest but a semi-deciduous monsoon forest. Long watching periods just outside or above the forest, especially from rivers and rocky outcrops, helped to detect soaring birds.

The avifauna of other countries was assessed from the main regional guides (Barbour 1943; Blake 1977; Bond 1971; Butler 1979; Deignan 1963; Glenister 1971; Lekagul & Cronin 1974; Medway & Wells 1976; Meyer de Schauensee 1966; Ridgely 1976; Smythies 1968) and from world surveys (Brown & Amadon 1968; Mayr & Cottrell 1979; Wattel 1973). The large island of Borneo (736,000km^2) was included in the continental gradient because its avifauna is similar to that of the mainland. The taxonomy of Mayr & Cottrell (1979) was followed.

Only true forest or closed woodland species were listed following Brown & Amadon (1968) and personal experience. Species found only on edges or marginal habitats were omitted. Migrants breeding in the area (e.g. *Elanoides* and *Ictinia* in Mexico) were included, but not those only wintering (e.g. *Pernis apivorus* in Africa or *Aviceda leuphotes* in Asia).

Assessment of relative abundance is not attempted because of the variable conspicuousness of different species.

COMPOSITION OF COMMUNITIES

Tables 1 and *2* emphasize three main features:

- Tropical America has about 2.5 times as many species as have similar Indo-Malayan forests and 2.7 times as many as African rainforests.
- On all three continents the number of species increases by 45 percent–50 percent from below the tropic to the equator.
- Islands, even when large and not very distant from the continent, have many fewer species than similar mainland (5–6 times fewer species in the Caribbean; 2–5 times in the Old World).

The whole tropical American rainforest harbours 40 species of diurnal raptors, against 12 in Africa, where the forest area is half that of America, and 50 in Asia (from India to New Guinea), where the total forest area is hardly larger than in Africa but where many species have evolved on the numerous islands. Similar differences occur for whole avifaunas: nearly twice as many species are found in South America as in Africa (Keast 1972); 250 species of lowland rainforest are known from the Congo basin against 550 in Amazonia, with small patches holding hardly 200 species in Central Africa against more than 300 in Amazonia (Amadon 1973). All raptor species are different from one continent to the other, except for the Bat Hawk (*Macheirhamphus alcinus*), which is widespread throughout tropical Africa and Asia. By comparison, temperate forests have only 5–6 species, i.e. 2 to 2.6 times fewer than in the Old World tropical forests and 5–6 times fewer in the New World.

Several theories try to explain the increased diversity from temperate to tropical regions (Ricklefs 1980): habitat stability during geological times, higher speciation rates (sedentary populations easily isolated), greater productivity and selection, lower extinction rates and stronger interspecific competition (the latter resulting from abundant resources, spatial heterogeneity, high predation, stable environment). From the available data, neither vegetation structure, seasonal stability, resource abundance and diversity nor competition or predation pressure seem to differ significantly between the rainforests of different latitudes and different continents. There is also no evidence that speciation rates differ as a result of genetic processes (Mayr 1969).

Historical factors and colonization rates are now more favoured (Simberloff & Connor 1981) than species interactions (Diamond 1975) in explaining species numbers and community structure. The drastic splitting of the rainforests during the arid phases of the Quaternary is assumed to be an essential reason for the present species richness. For instance, during the dry periods of the Pleistocene there were probably up to eight forest refuges (speciation centres) around the Amazon basin, against two in the Congo (Haffer 1974; Vanzolini 1973). All these refuges were in the equatorial zone and, when the rainforest extended again, recolonization was centrifugal which may explain the decrease of species numbers away from the equator.

It is sometimes hypothesized that the richer African mammalian faunas compete with birds and partly replace them, so explaining the lower number of bird species. However, the mammals which are wholly or partly carnivorous (excluding Chiroptera, Insectivora, Edentata, rodents, otters and folivorous monkeys) are about as numerous on the two continents, from lists of rainforest species in Chiapas, Southern Mexico (Alvarez del Toro 1977), Surinam (Husson 1978), Taï National Park, Ivory Coast, (Thiollay unpubl.) and Gabon (Anon. 1980). From Mexico to Guiana, 14 to 24 such predators are recorded (5–7 *Didelphidae*, 3 *Procyonidae*, 2 *Mustelidae*, 3–5 *Felidae*, 1–7 Primates) against 18 to 24 from Ivory Coast to Gabon (7–8 *Viverridae*, *Mustelidae*, 2 *Felidae*, 7–14 Primates) and 11 in Casamance.

The increase in species numbers within a few degrees toward the equator is also found in other bird families. There is no evidence that an increase in abundance and stability of food resources, or a more complex vegetation structure allowing more niche specialization, is involved. From north to south, no turnover in the population composition occurs: the same species are found from the tropics to the equator (except two in Asia which are replaced by closely allied taxa). In the Old World almost all the new species added belong to new genera, whereas in America the number of genera increases only by 5 percent against 50 percent for the number of species.

Table 1: Species diversity of Falconiform populations in tropical rainforests on three continents, from the largest islands to the mainland and from the northern limit of the evergreen forest to the equator.

Note: * Species only found near small clearings, edges, rocky outcrops or along rivers.

A. Central and northern America

Localities surveyed: S. MEXICO: Palenque—Bonampak (Selva Lacandona)—Tikal (Guatemala)—GUIANA: Cayenne—Regina—Saül—St-Elie (French Guiana) + Voltzberg and Brownsberg reserves (Surinam—Others from literature.

Species	Cuba 20–21°N	S. Mexico 16–17°N	Panama 9°N	Guiana 4–5°N	E. Ecuador 1°S
Sarcorhamphus papa		+	+	+	+
Cathartes aura	+	+	+	(+)	(+)
Cathartes melambrotus				+	+
Leptodon cayanensis		+	+	+	+
Chondrohierax uncinatus	+	+	+	+	+
Elanoides forficatus		+	+	+	+
Harpagus bidentatus		+	+	+	+
Harpagus diodon				+	
Ictinia plumbea		+	+	+	+
Accipiter poliogaster					+
Accipiter striatus	+				
Accipiter superciliosus			+	+	+
Accipiter bicolor		+	+	+	+
Accipiter gundlachi	+				
*Geranospiza caerulescens**		+	+	+	+
Leucopternis schistacea					+
Leucopternis melanops				+	+
Leucopternis semiplumbea			+		+
Leucopternis albicollis		+	+	+	+
*Asturina nitida**		+	+	+	+
*Buteogallus urubitinga**		+	+	+	+
Harpyhaliaetus solitarius		+	+	+	+
Buteo platypterus	+				
Morphnus guianensis			+	+	+
Harpia harpyja		+	+	+	+
Spizastur melanoleucus		+	+	+	+
Spizaetus tyrannus		+	+	+	+
Spizaetus ornatus		+	+	+	+
Daptrius ater				+	+
Daptrius americanus		+	+	+	+
Micrastur ruficollis		+	+	+	+
Micrastur gilvicollis				+	+
Micrastur mirandollei			+	+	+
Micrastur semitorquatus		+	+	+	+
Micrastur buckleyi					+
*Falco rufigularis**		+	+	+	+
Falco deiroleucus		+	+	+	+
Species number	5	22	26	30	33

B. West Africa and Madagascar

Localities surveyed: MADAGASCAR: Périnet, Maroantsetra, Masoala peninsula. S. SENEGAL: Basse Casamance National Park. S. IVORY COAST: Taï National Park. NE. GABON: Makokou—Belinga.

Species	Madagascar 15°S	S. Senegal 12°30N	S. Ivory Coast 5°30N	NE. Gabon 0°30–1°N
Aviceda cuculoides		+	+	+
Aviceda madagascariensis	+			
*Machaerhamphus alcinus**	+	+	+	+
*Gypohierax angolensis**		+	+	+
Dryotriorchis spectabilis			+	+
Eutriorchis astur	+			
*Polyboroides typus**		+	+	+
*Polyboroides radiatus**	+			
Accipiter tachiro		+	+	+
Accipiter castanilius				+
Accipiter francesii	+			
Accipiter erythropus		+	+	+
Accipiter melanoleucus		+	+	+
Accipiter henstii	+			
Urotriorchis macrourus			+	+
Buteo brachypterus	+			
Spizaetus africanus			+	+
Stephanoaetus coronatus		+	+	+
Falco zoniventris	+			
Species number	8	8	11	12

C. South East Asia (Indo-Malayan forest)

Localities surveyed: S. Nepal = Chitwan National Park
Malaya = Taman Negara National Park
Borneo = Bako, Niah and Lambir Hills National Parks (Sarawak), Sepilok and Gomantong Forest Reserves (Sabah).

Species	Sri Lanka 7°N	S. Nepal 27°N	Thailand 15°N	Malaya 5°N	Borneo 2–4°N
Aviceda jerdoni	+		+		+
Pernis ptilorhynchus	+	+	+	+	+
*Machaerhamphus alcinus**				+	+
*Ichthyophaga humilis**		+	+	+	+
Spilornis cheela	+	+	+	+	+
Accipiter trivirgatus	+	+	+	+	+
Accipiter virgatus	+	+	+	(+)	(+)
Ictinaetus malayensis	+	+	+	+	+
Hieraaetus kienerii	+	(+)	+	+	+
Spizaetus cirrhatus	+	+	+	+	+
Spizaetus nipalensis	+	+	+		
Spizaetus alboniger				+	+
Spizaetus nanus				+	+
*Microhierax caerulescens**		+	+		
*Microhierax fringillarius** (or *latifrons*)				+	+
Species number	9	10	11	12	13

Table 2: Species numbers in rainforest continental study areas (including Borneo, see *Table 1*): active predators of birds and mammals (+small vertebrates and insects for the smallest specimens). Forest edge species, such as *Asturina nitida*, are not included.

	Asia	Africa	America
Small species (<400 g)	*Accipiter virgatus*	2–3 *Accipiter*	1–3 *Accipiter* 1–4 *Micrastur*
Medium size species (400–900 g)	*Accipiter trivirgatus*	*Accipiter melanoleucus* *Urotriorchus macrourus*	*Micrastur semitorquatus* *Spizastur melanoleucus*
Small eagles (900–1,800 g)	1–3 *Spizaetus* *Hieraaetus kienerii*	*Spizaetus africanus*	2 *Spizaetus* *Morphnus guianensis*
Large eagles (2,500–5,000 g)	*Spizaetus nipalensis*	*Stephanoetus coronatus*	*Harpyhaliaetus solitarius* *Harpia harpyja*
Total number per locality	4–6	4–7	8–14

The enrichment of the avifauna towards the equator involves not only species numbers but also individual abundance. Many species are rare in Mexico, Casamance or Nepal, on the northern limit of their range, but become increasingly common and widespread further south (e.g. *Ictinia, Elanoides, Daptrius* in America or *Accipiter erythropus* and *A. melanoleucus* in Africa). This changing status can be striking even within a few degrees of latitude, as for *Dryotriorchis*, which is more abundant in northern Gabon than in similar habitat in southern Ivory Coast. Only few species seem equally numerous from north to south, e.g. *Harpagus bidentatus* or *Accipiter tachiro*.

A small proportion of the northern migrants winter in the rainforest belt. They include *Buteo platypterus* and the subtropical populations of *Elanoides forficatus* and *Ictinia plumbea* in America; *Pernis apivorus*, some *Buteo buteo* and *Falco subbuteo* in Africa; and several *Accipiter, Aviceda* and *Buteo* in Asia. However most, if not all, stay on the edges, around clearings and natural openings or in secondary growth, and only exceptionally venture inside the dense primary forest, so their potential competition with resident species is much reduced. Only the migratory and sedentary populations of insectivorous aerial hunters (*Ictinia, Elanoides*) may come into close contact and compete.

Among the island avifaunas Cuba, like other Caribbean islands and although not too distant from the rich American mainland, is the poorest of the large tropical islands. Sri Lanka, owing to its proximity to the continent and to its quite recent isolation, has the same forest species as Southern India. Madagascar, isolated from Africa about 20 million years ago, has a comparatively rich forest avifauna with almost only endemic species.

ECOLOGICAL STRUCTURE OF COMMUNITIES

MacArthur (1969) has reviewed the properties of tropical communities and their interpretations. He emphasized the greater productivity and reduced seasonality making marginal ways of life profitable, the interspecific niche overlaps making coexistence of species more precarious and causing patchy distributions.

It is impossible to analyse the pattern of community organization in rainforest raptors unless more areas can be thoroughly studied, density of every species evaluated and their ecology made fairly well known. We are just able roughly to outline the niche of some species and compare these between latitudes and

continents. Even at this level, striking convergent adaptations are indicative of common evolutionary processes and environmental pressures.

From their feeding habits, forest diurnal raptors can be sorted into about a dozen well-defined types—some including several different adaptations—which allow comparisons between geographical populations.

1. True forest Vultures occur only in the New World (*Cathartidae*): the King Vulture (*Sarcorhamphus papa*) throughout the American rainforest and the Greater Yellow-headed Vulture (*Cathartes melambrotus*) only in South America. Where the latter is absent, the ubiquitous Turkey Vulture (*Cathartes aura*) and/or rarely the Lesser Yellow-headed Vulture (*C. burrovianus*) takes its place. Where *C. melambrotus* occurs, *C. aura* is usually restricted to edges and clearings, which suggests a competitive exclusion. These birds are able to locate dead animals on the forest floor despite competition from other carnivores, including ants. In Africa the Palm-Nut 'Vulture' (*Gypohierax angolensis*) occasionally eats carrion on the riversides. The Asiatic King Vulture (*Sarcogyps calvus*) can sometimes be seen above the rainforest but is much more a bird of dry open forest or grassland.

2. Hawks which actively hunt ground or arboreal vertebrates include the most numerous species (*Table 2*). They show a wide range of sizes (weights from 120 to 5000g), fairly divided between species and sexes as they show marked sexual size dimorphism. As a whole, twice as many species are found in America as in the Old World, mainly because of the added Forest Falcons (*Micrastur*) in the small size class. From north to south, the species richness in this group increases by 50–75 percent, mainly by the addition of medium-size species in the Old World and smaller species in America.

3. Slow hunting raptors of the canopy which eat mainly inactive and mimetic large insects, including caterpillars, or tree frogs and lizards: Cuckoo Falcons (*Aviceda*) in the Old World, Grey-headed Kite (*Leptodon cayanensis*) and possibly Yellow-throated Caracara (*Daptrius ater*) in America. Usually only one species is found in each locality.

4. Still hunting raptors, which watch mainly for large insects and lizards from dead trees above the canopy, whence they dive swiftly to catch their prey. The only representatives are the Falconets (*Microhierax*) in Asia and the Banded Kestrel (*Falco zoniventris*) in Madagascar. The Double-toothed Kite (*Harpagus bidentatus*) in America also uses a similar method but often stays below the canopy. No African bird has comparable hunting behaviour.

5. Predators of wasps' nests. The oriental Honey Buzzard (*Pernis ptilorhynchus*) is such a specialist in Asia, with both resident and wintering populations. In Africa, the Palearctic migrant Honey Buzzard (*Pernis apivorus*) takes its place from September to May. In America the Red-throated Caracara (*Daptrius americanus*) fills the same niche, along with *Leptodon cayanensis*.

6. The Swallow-tailed Kite (*Elanoides forficatus*) and the Plumbeous Kite (*Ictinia plumbea*), both widespread, are gregarious insectivorous raptors which hunt in flight above the forest in America, often occur together and share an unique niche, with no counterpart among Falconiforms in the Old World rainforests.

7. Fast-flying species which hunt outside the forest. In the Old World, the

widespread Bat Hawk (*Macheirhamphus alcinus*) hunts only at dusk and dawn, taking mostly bats and occasional birds or large insects. The American Bat Falcon (*Falcon rufigularis*) hunts at dusk, but also by day, and takes birds and insects as well as bats. The larger and rarer Orange-breasted Falcon (*Falco deiroleucus*) hunts mainly high-flying birds such as parrots, although I have also seen it catching bats and insects.

8. Every tropical forest has a specialized predator on snakes and other reptiles (taking occasionally other vertebrates): *Spilornis* in Asia, *Dryotriorchis* in Africa, *Eutriorchis* in Madagascar and one to four *Leucopternis* in the New World.

9. The only specialist of terrestrial and arboreal snails, the Hook-billed Kite (*Chondrohierax uncinatus*), is found in tropical America where *Leptodon cayanensis* may also take some snails.

10. The Harrier Hawks (*Polyboroides typus* and *P. radiatus*) in Africa and Madagascar, and the Crane Hawk (*Geranospiza caerulescens*) in America, actively search for small prey in trees, walking on branches and palms where they hang themselves with half-spread wings, exploring the epiphytes, thrusting and twisting their legs into cavities or crevices, poking their head in hollow trunks and probing with feet the rotten wood or bark. They are also efficient nest robbers, reaching young birds even in deep holes or hanging nests. On Hispaniola the Ridgway's Hawk (*Buteo ridgwayi*) has some of these habits but not to this extent (Wiley & Wiley 1981).

11. Fishing raptors are commonly found along the forested rivers of the Old World but not in America. In Asia the Lesser Fishing Eagle (*Ichthyophaga humilis*) eats only fish, whereas in Africa the Palm-nut Vulture (*Gypohierax angolensis*) includes many fruits and some crabs or carrion in its diet. The African Fish Eagle (*Haliaeetus vocifer*), a purely piscivorous species not listed in the table, also occurs along some rivers well within the forest. In America, the Great Black Hawk (*Buteogallus urubitinga*) is found along forest streams, feeding on a variety of vertebrates but rarely if ever on fish. In all the localities I have worked (except Madagascar) the Osprey (*Pandion haliaetus*) was a common wintering bird. Along with the herons it may fill on American rivers the otherwise vacant niche of a large fish predator.

Other specializations can be recognized, but they involve species already cited above. Occasional fruit-eating is widespread among tropical forest raptors, even among aerial hunters such as *Elanoides forficatus* (Busbirk & Lechner 1978). For some of them, palm fruits are a regular (*Daptrius ater, Polyboroides typus*) or even staple food (*Gypohierax angolensis*) (Brown & Amadon 1968, Thiollay 1978).

Taking eggs or young from birds' nests is also a common habit and most species do this occasionally, but particularly *Polyboroides, Elanoides* and *Daptrius*. The Indian Black Eagle (*Ictinaetus malayensis*) is the most specialized nest robber in spite of its large size.

From higher to lower latitudes, the new species added to the communities seem to be specialists rather than generalists, highly evolved species of the dense humid forest such as *Dryotriorchis, Urotriorchis, Accipiter, Micrastur* and *Leucopternis*. Probably because of a narrower ecological tolerance, they have not extended their distribution as far as other, more adaptable, species. Unfortunately our lack

of knowledge does not allow any measurement of niche widths or interspecific overlaps and a deeper analysis would be speculative.

The higher species diversity of Neotropical forests is due both to more species sharing a particular ecological function (see *Table 2* or the several reptile-eating *Leucopternis vs.* only one *Dryotriorchis* or *Spilornis* in the Old World) and to the adding of species with different feeding habits apparently not represented elsewhere, such as vultures, large aerial insectivores, or snail-eaters. The difference is also conspicuous at the family level: up to nine *Falconidae* inhabit the Amazonian forest, against one in equatorial Asia and none in Africa. Only the fishing raptors, widespread in the Old World, are strikingly lacking in Neotropical forests despite a richer fish fauna in the rivers and no more competitors from other groups (kingfishers, herons, otters, crocodilians or aquatic turtles).

SOME ADAPTATIONS OF RAINFOREST RAPTORS

In the dense moist forest, predatory birds have evolved morphological, behavioural and ecological adaptations different from their counterparts in open habitats or temperate forests. They show striking convergences between continents, indicative of similar environmental pressures.

Morphology

Long tails and short rounded wings are typical features of forest raptors, but the long tail can be so exaggerated in some rainforest species (e.g. *Dryotriorchis, Urotriorchis*) that they are apparently unable to soar above the canopy. The large eyes (*Dryotriorchis*) or ear openings (*Micrastur*) are adaptations to life in the dark understorey. Long bare legs are common and probably useful in reaching prey in dense vegetation. Combined with a short outer toe, an intertarsal joint ('heel') capable of moving in either direction and a bare face, they allow *Polyboroides* and *Geranospiza* to exploit epiphytes, hollows or crevices by foot-thrusting (Burton 1978; Cooper 1980). Very large wings and tail, with tips of long primaries widely separated, give *Ictinaetus* and *Polyboroides* a very low wing loading, allowing slow glides low around the trees in search of nests which are difficult to find. *Elanoides* is also capable of a slow, skilful glide, low above the canopy.

In Neotropical forests (but not in Old World ones), 16 species, whatever their size, are mainly white, especially on the underside, against 8 predominantly black or barred. The function of this conspicuous pattern is not understood. The similarity of plumage, diet, behaviour and habitat between some *Aviceda* (mainly *A. cuculoides*) and sympatric large cuckoos is perhaps another example of convergent adaptation to the forest life.

Voice

In such a dense habitat, vocal communication is of prime importance. Many species have loud and unusual voices, frequently used during the breeding season. Some sound like duets between members of a pair (*Micrastur*) or constant contact and alarm calls between members of social groups (*Daptrius*), or are given by the young up to several months after leaving the nest. They also seem to be territorial vocalizations, similar to true songs (e.g. *Dryotriorchis, Urotriorchis*). In some species (*Micrastur, Accipiter*) they are often uttered at dawn or dusk or even by night. Many are unlike the calls of temperate zone raptors and, unless the bird is seen, one cannot believe that they come from a hawk. In some species the calls vary greatly over the geographical range but may serve to separate species from

mere subspecies (*Accipiter tachiro-toussenelii* or *Micrastur ruficollis-gilvicollis*). In a more classical way, many eagles are very vocal during their courtship display above the forest and can thus be heard from afar, which probably helps them to maintain large territories with minimum energy costs or to find a mate in species with patchy distribution. One of the most extraordinary adaptations is that described by Smith (1969) for *Micrastur mirandollei* where the falcon, quietly sitting in dense vegetation, utters curious calls difficult to locate, attracting small birds which allow the raptor more successful attacks than otherwise.

Hunting behaviour

Most prey are difficult to see in the rainforest, where they have evolved an elaborate array of anti-predator adaptations. Still hunting is a necessary rule among tropical forest raptors, which spend long periods sitting motionless and inconspicuous. Individuals fly swiftly from one tree to another, soundless and unobtrusive. Once attacked, birds can be pursued tenaciously by *Accipiter* or *Spizaetus* for a long time and caught in difficult situations, which suggests that the hawks try to benefit from the very few opportunities given to them. Apart from the searching method of *Polyboroides*, few species pursue active hunting, such as *Micrastur semitorquatus* which runs along the branches, through dense thickets and even on the ground, more like a chachalaca than a falcon (Peeters 1963, pers. obs.). Some small eagles (*Hieraaetus kienerii, Spizaetus africanus*) catch birds by diving through the canopy. Several *Micrastur* and *Accipiter* have been seen following army ants, paying attention only to prey flushed by the ants, but some species may also catch the birds attracted by ants (e.g. *Leucopternis melanops*). Small hawks such as *Harpagus bidentatus* follow monkeys to take insects disturbed by branch-shaking. The social system and harsh loud calls of forest Caracaras (*Daptrius*) are unique among raptors and help to share the wasps' nests found between two or more individuals, thus enhancing hunting success of members of the group (pers. obs.).

Niche width

Ecological theories about the structure of bird communities state that in tropical avifaunas strong interspecific competition is avoided or reduced by most species being narrowly specialized whilst a few show broader niche overlap on super-abundant resources. An analysis of rainforest raptor species reveals a complex situation, but we know so little about their ecology that we can only outline some apparent trends.

The feeding of *Machaerhamphus alcinus* on bats, of *Chondrohierax uncinatus* on land snails, and of *Daptrius americanus* and *Pernis* on wasp grubs are examples of extreme specialization. Adaptive radiation in the *Accipiter* or *Micrastur* group illustrates a fine niche division between closely-related sympatric species (Black & Ross 1970; Brosset 1973). The regular spacing of sizes between both species and sexes is assumed to parallel similar differences in diet. Size displacements are indicative of interspecific competition for food, shaping each species according to others in the same community. For instance, *Accipiter tachiro* is smaller in West Africa (*A. t. macroscelides*), where it is the only medium-sized *Accipiter*, than in Gabon (*A. t. toussenelii*), where it occurs with *A. castanilius*, which is about the size of *macroscelides* (Louette 1974, and pers. data).

On the other hand, the difficulty of catching rare and patchily-distributed prey leads many species to more varied diets than formerly inferred from their anatomy (several kinds of both vertebrates and invertebrates or sometimes birds' eggs and fruits). I have also seen many species hunting high in the canopy, as well as near

the ground (e.g. *Urotriorchis macrourus, Accipiter tachiro, A. virgatus, Micrastur semitorquatus*). It is surprising to see a fast and powerful predator such as *Accipiter tachiro*, able when trained in captivity to kill birds even bigger than itself (Brosset 1969), eating in the wild mainly frogs, lizards, small rodents and insects taken on the ground by still hunting methods (Thiollay 1978). Many other forest raptors freely include in their food much smaller and weaker prey than their size and strong feet or bill would suggest. Possibly higher vertebrates are rare or difficult to catch. Nevertheless, some species do indeed specialize on apparently difficult prey, such as *Accipiter superciliosus* on hummingbirds (Stiles 1978).

Population dynamics

The few data available imply that rainforest raptors have more of a K strategy than other populations. They seem to have late sexual maturity, small clutches (often one or two eggs), low productivity (no more than one young per pair every two years for large eagles), long fledging period, 'life-long' pair bond and great longevity. They are strictly sedentary, except some insectivorous species in the northern part of their range (*Elanoides, Ictinia*). However, we know nothing about the dispersion pattern of the immature birds, which could be a key factor explaining how various species survive with apparently such low and irregular densities.

More detailed recent studies suggest that rainforests may be more seasonal habitats than previously believed, and many species, including some raptors, have clearly defined breeding seasons, although possibly different from one area or year to another.

Ecological structure

Among the eleven well-defined feeding types, seven have representatives in both the Old and the New World, three are found only in America (diets based on carrion, flying insects and snails respectively) and one (fish-eaters) is found only in Africa and Asia. According to MacArthur (1972), there are more diet specialists where food resources are abundant and more generalists where the habitat is less productive.

We can divide the species of *Table 1* according to the number and relative importance of food classes in the average diet: mammals, birds' nest contents, carrion, amphibians, reptiles, fishes, insects, other arthropods, snails, fruits (from Ali & Ripley 1978; Brown & Amadon 1968; Thiollay 1978). Three main categories may be distinguished: narrow specialists (one food class accounting for more than 75 percent of the diet), semi-specialists (one food class accounting for 50–75 percent of the diet) and generalists (at least three classes, each making up to 20 percent or more of the food). From the northernmost to the southernmost study area, the number of generalists remains stable on the three continents (four in the Neotropics, one in the Old World) accounting for 8 to 18 percent of the species. The most numerous species are semi-specialists (11–17 in the neotropics; 5–7 in the Old World). They account for 50 to 62 percent of the species and show similar increases (20–55 percent) from north to south. About one-third of the species are narrow specialists (25–41 percent, i.e. 7–12 species in America and 2–5 elsewhere), and they increase much more than the previous group (67–150 percent) from higher to lower latitudes.

The general trend between tropics and equator seems to favour more the specialists than the generalists, but unless some foraging adaptations and food sources allow narrow diets, more opportunistic feeding habits are necessary for most species to persist in space and time in the tropical forests.

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