COMPOSITION OF FALCONIFORM COMMUNITIES ALONG SUCCESSIONAL GRADIENTS FROM PRIMARY RAINFOREST TO SECONDARY HABITATS

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ABSTRACT

The raptor populations of a succession of seven habitats, from the primary undisturbed forest to the derived pastures or plantations in southern Ivory Coast, is described. A comparative survey, considering only four main habitats, was made in Guiana and southern Mexico.

Similar patterns of species distribution are found on the two continents:

1. Between 36 and 42 percent of the species reach their greatest densities in the primary forest and decrease rapidly as soon as the forest begins to be cleared.
2. Some primary forest species (18–21%) are more tolerant and rarely decrease, so long as areas of secondary forest remain.
3. Two or three species (8–14%) are more abundant in the intermediate stages of the succession than in either extremity.
4. An equal number of species, appearing early in the succession but absent from the primary forest, survive as long as large trees are available.
5. Between 14 and 25 percent of the whole set of species are savannah birds, occurring only in large clearings and now spreading into the forest belt.

To preserve the true forest species, undisturbed areas of primary forest have to be spared during lumbering operations, clearings have to be small, separated by patches of forest and dotted with large trees. Human hunting of medium-sized animals must be limited if eagles are to be saved.

INTRODUCTION

Most of the world's tropical rainforests are now heavily exploited and are rapidly being turned into a variety of secondary habitats and, in extreme cases, into treeless farmlands, pastures or bare eroded slopes. Many forest birds disappear when the pristine forest structure is disturbed. Others survive greater habitat changes, but soon begin to compete with species originally occurring in small and transient natural gaps of the forest or along forest edges. As clearing spreads, the latter are themselves replaced by grassland species.

It is important for management and conservation to know the tolerance of each

species to habitat change and the limits of its distribution along the succession. It is also important to know the bird population structure in the main destruction stages into which tropical forests are now ultimately converted. Assessing the sensitivity of species to different treatments of the forest will allow us to recommend measures which take into account the conservation of forest bird species diversity. I shall be concerned here only with raptors, but the problems threatening their survival are similar for many other forest animals.

STUDY SITES AND METHODS

Surveys were made from 1967 to 1980 in southwestern Ivory Coast from 5° to 7°N and 5° to 8°W, between Toumodi–Gagnoa–Daloa–Duéké in the north and Grand Lahou–Sassandra–San Pedro–Grabo in the south, especially in and around the largest area of primary rainforest (Taï National Park) remaining in West Africa (Thiollay 1975a, 1975b and unpubl. data). Eight species were not taken into account because they were rare; at their southern limit; not usually recorded by day (*Machaerhamphus alcinus*); or only around human settlements (*Necrosyrtes monachus*), on rivers (*Pandion haliaetus*), in patches of savannah (*Falco cuvieri, F. biarmicus, Aquila wahlbergi*) or in gallery forest (*Hieraaetus dubius, Circaetus cinerascens*). Comparable data were obtained in Ghana, Cameroun and Gabon, with results identical to those of the Ivory Coast.

Similar surveys were conducted in the northern half of French Guiana and Surinam (4° to 6°N) in December–January 1981/2, after comparable studies in similar habitats of southeastern Mexico, between 16° to 20°N and 91° to 97°W (Veracruz, Tabasco, and Chiapas states), from March to September 1975 to 1979, especially in the Selva Lacandona area (Thiollay 1978 and unpubl. data). The latter more extensive counts were used to check and complete results obtained in the Guianas, where all the Mexican raptors were found, along with additional species, but where some of them were rare (*Elanus, Polyborus, Falco femoralis*).

In order to detect as many species as possible, two methods were combined:

a) Walking on small paths or larger tracks in the forest, stopping where wide openings allowed birds soaring over the forest to be seen.
b) Slowly driving on small roads through cleared and cultivated areas, sometimes crossing remaining patches of secondary forest. Again frequent stops allowed careful searches for flying or sitting birds.

All the raptors seen were counted, whatever their age, sex, or activity. It was difficult to obtain accurate figures of relative abundance for so many elusive species, whose conspicuousness varied widely between habitats and seasons. The most secretive species were underestimated and the abundance of forest species was overestimated in the more open habitats. The results were converted into coefficients giving a rough figure of each species' relative abundance along the succession (*Table 1* and *Figure 1*): 1 = Rare, patchy distribution; 2 = Regular in small numbers; 3 = Common and widespread. Exceptional sightings were excluded. These coefficients were thus based on frequencies of records and not on actual densities, which were too difficult to assess. They indicated the value of each habitat for each species involved (respectively marginal, suboptimal and optimal). Their sum was taken as a general index of species abundance (*Figures 2* and *3*).

Table 1: Falconiform populations along a man-disturbed rainforest succession in southern Ivory Coast.
For the description of stages I to VII, see text.
n = total number of birds seen during counts in the habitat, irespective of the time spent.
Abundance indices = proportions of n:
+ =<1%; 1 = 1 to 5%; 2 = 6 to 10%; 3 = 11 to 20%; 4 = 21 to 40%; 5 = >40%.
PF = Virgin primary rainforest species.
SF = Mainly secondary forest species (and primary forest edges).
OG = Open grassland species.
SG = Low secondary growth or woodland savannah species.
EM = Dry season Ethiopian migrant.
PM = Dry season Palearctic migrant.

Species	Species status	Forest types I (n = 108)	II (n = 106)	III (n = 111)	IV (n = 148)	V (n = 432)	VI (n = 431)	VII (n = 114)
Aviceda cuculoides	PF	2	1	1	1	1	+	
Pernis apivorus	PM		+	1	1	1	+	
Elanus caeruleus	OG						+	1
Milvus migrans	EM			1	3	4	5	5
Gypohierax angolensis	SF	3	4	4	4	3	2	1
Dryotriorchis spectabilis	PF	1	1	+				
Polyboroides typus	SF	3	3	4	4	4	3	1
Accipiter tachiro	PF	3	2	2	1	1	1	
Accipiter erythropus	PF	2	1	1	1	1	+	
Accipiter melanoleucus	PF	1	1	1	1	+		
Urotriorchis macrourus	PF	3	2	1	+	+		
Kaupifalco monogrammicus	SG				1	1	1	1
Buteo auguralis	EM		+	2	2	2	1	1
Lophaetus occipitalis	SG					1	+	+
Spizaetus africanus	PF	2	2	1	1	+		
Stephanoetus coronatus	PF	2	2	1	+			
Falco ardosiaceus	OG						1	2
Falco tinnunculus	PM							+

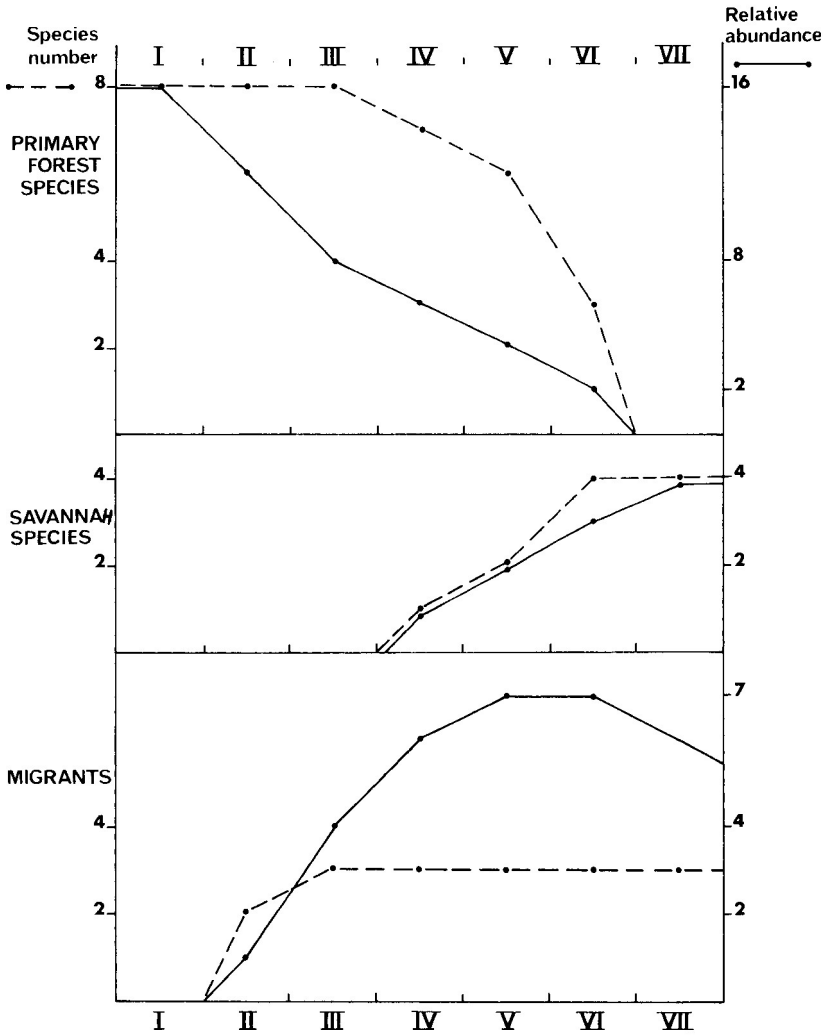


Figure 1: Species diversity and relative abundance of three groups of Falconiforms (involving all the species except the widespread *Gypohierax* and *Polyboroides*) along the succession of rainforest habitats in southern Ivory Coast (see *Table 1*).

Relative abundance (plain line) = sum of abundance indices in a given habitat.

Dotted line = number of species seen in the habitat.

SUCCESSION OF SECONDARY HABITATS

The microclimatic features of the low layer of the primary forest, much less marked in the secondary forest, are among others:

- Extreme stillness of the air (only exceptional squalls produce wind at ground level).
- Smaller daily range of temperatures than outside the forest (lower maximum and higher minimum).
- Humidity saturation at night and higher minimum during the day.
- Very dim light (away from the sunflecks), approximately 0.5 to 1.0 percent of full daylight.

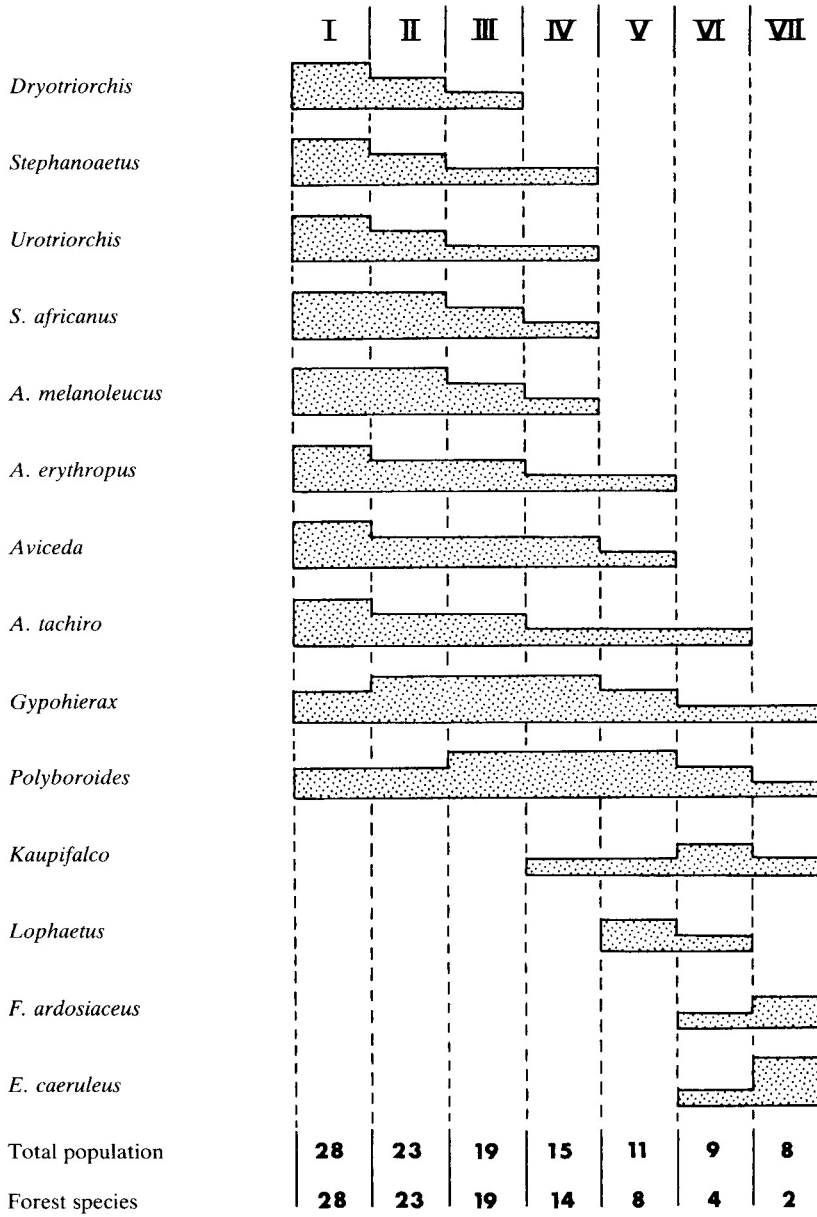
A typical secondary forest consists of lower trees, of smaller average dimensions and of many fewer species than a primary forest. Abundance of climbers and saplings gives it a denser and more tangled appearance which makes it difficult to penetrate, contrary to most primary forest. In the earliest stages of the succession, it is often an even-aged stand of one or a few woody species. The structure becomes very irregular at later stages. The secondary vegetation is dense, highly productive and rapidly growing. The composition and structure of the successive communities which develop vary widely according to how long and in what way the area has been cleared, the slope, rainfall, soil, etc. The first stage (one or a few years) is a dense growth of ephemeral weeds and sedges, followed by trees (*Musanga, Cecropia, Macaranga, Trema*) which develop completely in about 20 years. The following progressive growth of primary forest species may last up to more than 100 years. If secondary communities are subjected to fire, grazing or frequent periods of cultivation, deflected successions are initiated in which grasses such as *Imperata cylindrica* replace the forest by a grassland which can maintain itself indefinitely if periodically burnt or grazed. Excessive deterioration of soil fertility may lead to bare eroded land.

In the Ivory Coast, where a longer and more detailed study was made, I distinguished seven habitats (see *Figures 2* and *3*):

I = Primary (virgin) forest.
II = Forest partly opened by local selective logging and in the process of regeneration.
III = More depleted forest than above with less than 25 percent of its area occupied by small clearings and plantations.
IV = Forest subjected to more intensive logging (two or three times), followed by scattered shifting cultivations giving an irregular mosaic of clearings, secondary growths and at least 25 percent of the area of moderately depleted forest.
V = All the area covered with heavily modified secondary forest and varied cultivations and regrowths.
VI = Some large trees edging or shading plantations as the only remnants of forest.
VII = Secondary pastures or commercial plantations (Heveas, Palm trees, Pineapples), with only very few isolated wild trees.

In the Guianas, only four main habitats have been considered:

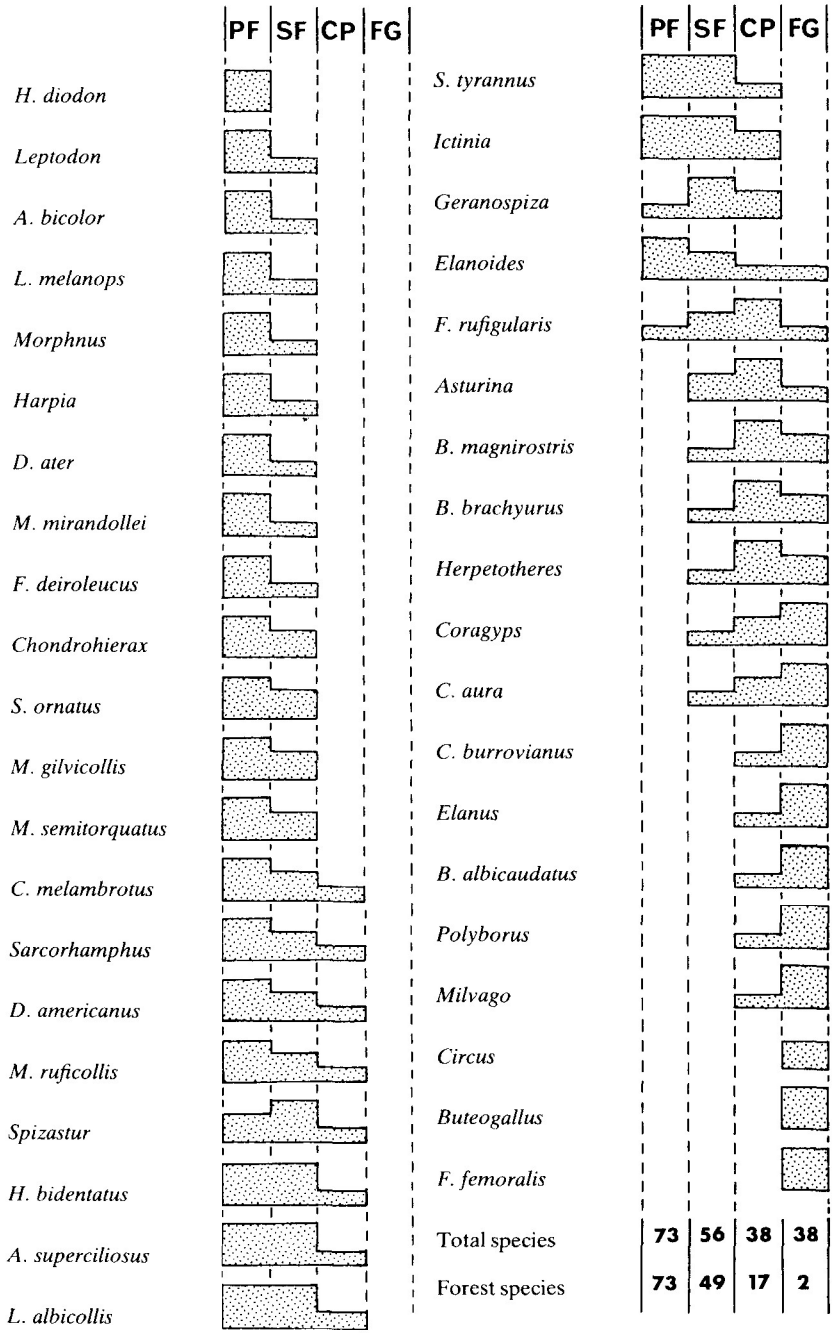
PF = Primary undisturbed forest, including edges.
SF = Secondary forest with small clearings.
CP = Large clearings, plantations and areas of secondary growth with patches of secondary forest.
FG = Farmland and grassland with scattered trees, i.e. fields, pastures or derived savannah.



Figures 2 and 3: Distribution and relative abundance of sedentary species along the gradient from primary forest to cleared and cultivated areas in (*Figure 2*) southern Ivory Coast (seven habitats) and (*Figure 3*) the Guianas (four main habitats).

The frequency of a species (height of the dotted figures) is ranked from 1 to 3 (see text) in habitats where it is of regular occurrence. These ratings, drawn from actual counts, are summed for each habitat giving coefficients for the total raptor population or only for primary forest species.

Generic name is given alone when only one species occurs (see text). Otherwise the following genus abbreviations are used:
A = *Accipiter*; B = *Buteo*; C = *Cathartes*; D = *Daptrius*; E = *Elanus*; F = *Falco*; H = *Harpagus*; L = *Leucopternis*; M = *Micrastur*; S = *Spizaetus*.


PF
SF
CP
FG
H. diodon
Leptodon
A. bicolor
L. melanops
Morphnus
Harpia
D. ater
M. mirandollei
F. deiroleucus
Chondrohierax
S. ornatus
M. gilvicollis
M. semitorquatus
C. melambrotus
Sarcorhamphus
D. americanus
M. ruficollis
Spizastur
H. bidentatus
A. superciliosus
L. albicollis
S. tyrannus
Ictinia
Geranospiza
Elanoides
F. rufigularis
Asturina
B. magnirostris
B. brachyurus
Herpetotheres
Coragyps
C. aura
C. burrovianus
Elanus
B. albicaudatus
Polyborus
Milvago
Circus
Buteogallus
F. femoralis
Total species 73 56 38 38
Forest species 73 49 17 2

The population of a given habitat is taken on a regional basis to include all the species occurring in what can in fact be divided into several microhabitats, each with a particular set of species.

RESULTS

From *Table 1* and *Figure 2*, we see that everywhere the primary forest is richer than derived habitats, as far as residents are concerned. The species richness decreases by 40 to 50 percent from the first to the last stage, with a nearly complete turnover of the population and different species involved.

Although the avifauna is about three times richer in Guiana than in Ivory Coast, the species pattern of distribution along the gradient is similar in the two countries. Of the whole set of species considered, 57 percent have their optimal density in the primary forest (23 and 8 from a total of 40 and 14 respectively), 38 percent reach the third stage in Guiana (excluding the 2 aerial Kites) and the similar fifth stage in Africa, none occurring in the last stage.

A decline in the number of species occurs with only moderate logging, although we have no data on the effect of disturbance on their densities and breeding success. In areas where farmers have cleared small patches, the numbers of forest species may decline by seven to ten percent, but new species begin to appear, either residents or wintering migrants. When the clearings spread at the expense of the forest, species of open habitat settle and replace the original forest species.

In fact, there are five species categories among the residents:

1. The primary forest species quickly decrease along the succession: the first five of *Figure 2* in Africa (36% of all the species occurring in the succession) and the first 17 of *Figure 3* in America (42%). They are the most sensitive to any disturbance and the first to go.
2. Some primary forest species are more tolerant to clearing and modification of their original habitat, such as *Aviceda*, most *Accipiter*, *H. bidentatus*, *L. albicollis*, *S. tyrannus*, *Spizastur*, *Ictinia* and *Elanoides*, i.e. three (21%) in Africa and seven (17.5%) in America. They rarely decrease as long as large areas of secondary forest remain.
3. Species very local in the primary forest, abundant in the intermediate stages of the succession and decreasing in the last stages, include *Gypohierax* and *Polyboroides* in Africa (14%), *Geranospiza*, *F. rufigularis* and *Asturina* in America (7.5%). They are now all expanding their range with the advancing destruction of virgin forests.
4. Species absent from primary forest, appearing early in the succession and surviving as long as large trees or patches of secondary forest are available, include *Kaupifalco* and *Lophaetus* in Africa (14%), *B. magnirostris*, *B. brachyurus* and *Herpetotheres* in America (8%). Most of them are widespread and locally common.
5. Open grassland species occurring only in large clearings with very few trees, i.e. *F. ardosiaceus* and *Elanus* in Africa (14%) and the last ten species of *Figure 3* in America (25%). They were originally savannah species, now spreading into the forest belt.

The habitat changes and consecutive disappearance of species are not only a matter of vegetation structure but also depend upon the remaining prey availability. In particular, large eagles such as *Stephanoaetus* or even *Harpia* can be found well outside the true forest if prey are common, whereas they are lacking from

structurally well-preserved rainforest where excessive hunting has reduced their mammalian food.

The species diversity comes from the heterogeneous structure of the primary forest, where rivers, rocky outcrops, storms, landslides, dead tree falls, lowland marshes or soil conditions provide a large variety of secondary-like habitats and ecotones. Species of such habitats quickly invade man-made clearings and become much more abundant and widespread than they formerly were in the extensive unbroken forest. So a local and moderate exploitation of the primary forest increases the species diversity on a regional scale, but if all the forest is changed into agricultural land, the resulting avifauna is much poorer than the original.

Few holarctic migrants winter mainly or only in the forest belt and they are always encountered in secondary habitats or forest edges. The most typical are the Honey Buzzard (*Pernis apivorus*) in Africa and the Broad-winged Hawk (*Buteo platypterus*) in tropical America.

CONCLUSION

The sequence of raptor communities along gradients from primary forest to secondary man-made habitats is rather similar to the succession found from the equator towards the tropics, i.e. from the rainforest through the semi-deciduous forest, the gallery-savannah mosaic, the woodland savannah, the scrub savannah and the treeless grasslands. In both cases forest species are progressively replaced by gallery or edge species, then by open woodland, savannah or grassy marshland species, with a steadily decreasing overall diversity.

For management of raptors, several principles have to be kept in mind to preserve as much as possible of the true forest species—and the overall community diversity during human exploitation of the rainforest.

- Since modern lumbering techniques are always destructive in tropical forests, logging has to be made along few roads, leaving large undisturbed areas between. Only selective logging throughout the forest is proportionately more destructive than intensive logging on a smaller part of the area.
- Several small cultivated clearings, separated by well-preserved patches of forest, are better than fewer but larger clearings.
- Sparing large trees throughout the clearings allows many species from the nearby forest to hunt in the open (probably often on species harmful to the plantations, which may benefit the farmer). In this respect, cultivations shaded by large trees (coffee, cacao, etc.) are richer than treeless plantations.
- Stable habitats and permanent cultivations are preferable to shifting cultivation, which leads to large, poorly-exploited areas of young dense secondary growth where few raptors are able to hunt, except those feeding in the canopy of large trees (if still present).
- Whatever the structure of the remaining forest, it is essential that all bird species and at least medium-sized animals are maintained in good densities, a requirement rarely encountered in tropical countries where all animals are freely hunted.
- When forest has disappeared, resulting grasslands (extensive pastures) are much richer in raptors than any plantations, but true forest species rarely occur in such grazing lands.

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