

Part 1

Current Studies of African Raptors

Bateleur *Terathopius ecaudatus*



Conveners:

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Stability and long-term changes in a West African raptor community

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ABSTRACT

Breeding and non-breeding diurnal raptors were censused in 1972 and 1996 over the same 2,700 ha palm savanna and gallery forest mosaic at Lamto Reserve, central Côte d'Ivoire. This protected area, once part of the Guinean savanna belt of West Africa, became increasingly isolated within highly degraded, deforested, cultivated and overhunted habitats. All seven large forest raptors and resident savanna eagles disappeared before the mid 1980's. Among the 12 remaining breeding raptors, four species increased (including two seasonal migrants), four species remained stable (including two forest accipiters) and four species decreased, but not significantly (including the 2 largest species). All 14 non-breeding raptors (Palearctic and African migrants), remained stable or increased. With an average of 63 breeding pairs/1000 ha, this area supports one of the highest densities of diurnal raptors ever recorded. Some savanna species, here at their southernmost extension, may have shifted their distribution southward or increased in the southern portion of their range (Gabar Goshawk *Micronisus gabar*, Black Kite *Milvus migrans*, Wahlberg's Eagle *Aquila wahlbergi*) after droughts and habitat losses that occurred between the two censuses. Deforestation and large scale cultivation around the reserve may have favoured European Marsh Harrier *Circus aeruginosus* and Lanner Falcon *Falco biarmicus*, while resulting fragmentation of natural habitats probably drove larger eagles to extinction. Within the reserve, decreasing oil palm fruits as food may have affected specialized consumers (Palm-nut Vulture *Gypohierax angolensis*, African Harrier-hawk *Polyboroides typus*).

INTRODUCTION

There are still few studies of the long-term dynamics of a complete raptor community, least of all in the tropics. In Africa, the pioneering population monitoring of eagles in Kenya by Brown (1952-1955) and in Zimbabwe by Gargett (1990) are noteworthy. Furthermore, the consequences of habitat fragmentation and isolation on bird communities, currently a deep concern, have been thoroughly analyzed in temperate forests (Wilcove & Robinson 1990; Saunders *et al.* 1991; Villard *et al.* 1995) and open habitats (Soulé *et al.* 1992; Herkert 1994; Knick & Rotenberry 1995), as well as in tropical forests (Laurance & Bierregaard 1997) but rarely in Africa (Newmark 1991) and never specifically on a raptor community.

Reserves that protect natural habitat patches are often bound to become isolated within a matrix of initially similar but soon degraded habitat increasingly unsuitable for at least some species that eventually survive only in the reserve. Moreover, edge effects add their negative consequences to those of isolation and further imperil the survival of small populations (Burkey 1989; Andren 1994). This process, well known in forest fragments, may also occur in grasslands (Saunders 1989). Raptors are highly sensitive to prey availability, vegetation structure, pollution and human disturbance and thus are good indicators of environmental changes (Newton 1979).

The Lamto Reserve, Côte d'Ivoire, offered an opportunity to monitor long-term changes in an undisturbed patch of natural savanna, more and more isolated in an increasingly modified and impoverished landscape. The protected area was studied continuously since 1962, against which the dynamics of the raptor population over the last thirty years could be interpreted, owing to the data accumulated on the distribution and habitat of the species involved (Thiollay 1972, 1975a, 1975b, 1975c, 1977b, 1985, 1988). It was exposed to three major threats of outside origin:

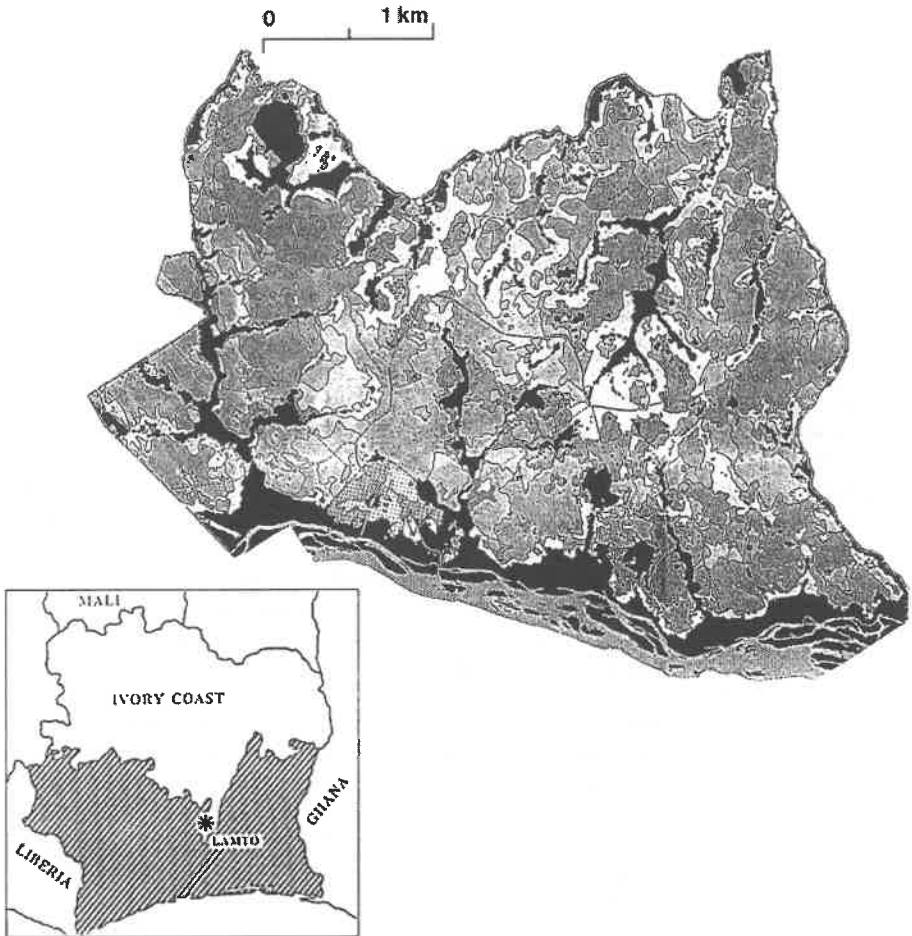
- 1) Climate changes that occurred in sub Saharan Africa in recent decades, especially dry spells and a general deficit of rainfall before 1990, from the Sahel to humid coastal Côte d'Ivoire (Paturel *et al.* 1995; Servat *et al.* 1996). This will be referred to as global changes.
- 2) Increasing human pressure on the regional landscape, particularly around the Lamto Reserve, leading to fragmentation and degradation of natural habitats and probable extinction of some raptor populations. This will be distinguished as regional changes.
- 3) Vegetation changes inside the reserve (increasing tree cover, invasion of exotic shrubs, exploitation of palms). These will be called local changes.

STUDY AREA

The 2,700 ha Lamto Reserve is a gallery forest-palm savanna mosaic in south central Côte d'Ivoire, West Africa (6°13'N; 5°02'W). On the north-south gradient from the Sahara desert to the rain forest along the Gulf of Guinea coast, it is at the southernmost tip of the savanna belt, and one of the very last natural remnants of the humid South Guinean Savanna that typically fringed the northern edge of the dense forest zone between 6° and 8° N. During the last 35 years (J.L. Tirefort, comm. pers.), the mean annual rainfall, by 5-year periods, averaged 1,240-1,383 mm in 1962-1966 and 1987-1996, but between 1967 and 1986, it was consistently lower (1,120-1,186 mm) in connection with the generally drier climate over most of West Africa, culminating in drought years in the early 1970s and 1980s (Servat *et al.* 1996). The rains increase from late February to May, peak in June and September-October and quickly decrease in November. Each year, all the savanna is burnt in January (height of the dry season) to maintain the vegetation in a steady state and avoid more damaging late fires.

The network of gallery forests stems from a wide riverine forest along the Bandama River, becoming narrower away from it along small watercourses, and ultimately giving way to isolated woodlots on gentle upper slopes (Fig. 1). From 1963 to 1988, the total forest coverage of the reserve increased from 15.6% to 17.9% (Gautier 1989). There has been also a significant increase of the mean tree density of savanna woodlands (Gautier 1990). The savanna can be divided into three broad habitat categories (Table 1), all of them dominated by 20-m tall *Borassus* palms (*Borassus aethiopicum*), 3-15-m tall deciduous trees (mostly *Crossopteryx*, *Piliostigma*, *Cussonia*, *Terminalia* and *Vitex*) and a thick continuous grass cover (1.0-1.5 m) in the rainy season. In the early 1980s, an introduced shrub, *Chromolaena odorata*, began to invade the reserve and now forms dense thickets, 2-3 m high, along most gallery forests, in woodlots and little-burnt woodlands. This is the major habitat change since the early studies. The Oil Palm *Elaeis guineensis*, once a common tree in gallery forests and an important fruit source for several large birds, decreased through overexploitation by poachers for wine. Most large mammals have been extirpated and only a few Kob *Kobus kob*, Busbuck *Tragelaphus scriptus*, Buffalo *Syncerus cafer*, Hippopotamus *Hippotamus amphibius* and monkeys *Cercopithecus* spp. survive.

Figure 1. Vegetation map of the study area, Lamto Reserve. The lower edge is the Bandama River with forested islands. Gallery forests and woodlots are in black, and increasingly lighter shades sketch the three progressively less wooded savanna types (Table 1).



In the 1960s, the surrounding region was still covered with natural savannas and extensive forest tracts. Signs of increasing human pressure were already apparent, i.e. a general decrease of *Borassus* and Oil Palms, overhunting, and clearing of forest patches for logging and agriculture. This large scale process of habitat degradation continued unabated and is still going on. Additionally, agricultural development schemes have turned large areas of savanna and forest into rice fields, oil palm plantations, cattle pastures and extensive coffee or cocoa plantations. Logged forests and plantations, which burnt during the drought years, are now dense thickets of *Chromolaena* dominated by isolated trees (*Ceiba*, *Bombax*, *Sterculia*) and dead trunks. A dam on the river, just upstream from the reserve, prevented the seasonal flooding of the riverine forest and turned its formerly open understorey into an impenetrable thicket. Thus, the Lamto savanna progressively became an island of little- disturbed natural habitat, within an increasingly modified region this is covered by a variety of secondary vegetation types which are often unsuitable for some of the original raptor species.

Table 1. Structure, composition and relative area of the three main types of savanna on the Lamto Reserve. Gallery forests, woodlots, a few tracks and buildings account for the remaining 18 % of the study area (see Thiollay 1970a).

<i>Main types of savanna</i>	<i>Mean palm + broadleaf tree cover</i>	<i>Dominant graminean species</i>	<i>Proportion of the total reserve area</i>
Open grassland	<=7%	<i>Loudetia simplex</i>	19.2%
Thin woodland	8-36%	<i>Hyparrhenia</i> sp.	37.7%
Dense woodland	37-80%	<i>Imperata cylindrica</i>	25.1%

METHODS

The raptor community was intensively surveyed from 1967 to 1973, both within the reserve and in a surrounding radius of about 50 km (Thiollay 1975a, 1975b, 1976, 1977a, 1978a). After one-month visits in 1983 and 1984, the whole 2,700 ha study area was searched again in February-March 1996, but not the surrounding region. The most complete census was carried out from November 1971 to May 1972, thus covering the entire breeding season of every species. This was the year of reference, compared to the shorter survey of February-March 1996 that concentrated on the peak of the reproduction of most species (Thiollay 1976). The 1972 census was fairly representative of a stable population from 1967 to 1973, as suggested by the 75 active breeding sites found in early 1968 that were all still occupied by a pair of the same species in 1972 (some of them using alternative nests).

I censused all territorial pairs, whether successfully breeding or not, and whether resident or seasonal migrants. Additionally, I tried to make conservative estimates of the number of unmated individuals of each breeding species and of non-breeding migrants. Only the latter birds were counted separately in February and March, because they steadily decreased after their maximum numbers of early February (Thiollay 1975a, 1975b).

During day-long walks, I searched the entire area carefully, crossing at least twice every 100 x 100 m square (grid-cell superimposed on Fig. 1) and passing within less than 50 m of every spot at least once. Absolutely all individual *Borassus* palms and large trees in savanna and gallery forests were checked for nests and each nest structure was controlled repeatedly for signs of occupation. All nests were actually visited throughout the breeding season in 1972, but not in 1996 where the only goal was to assess the number of breeding pairs. All nests and observed individuals with their behaviour were located on enlarged vegetation maps.

All pairs of Black Kite *Milvus migrans*, Long-crested Eagle *Lophaetus occipitalis* and Grey Kestrel *Falco ardosiaceus* and most pairs of other species were identified when their nest was found, at any stage. Alternatively, the following criteria, recorded on at least two different days over the same area, were used to record breeding presence: African Cuckoo Hawk *Aviceda cuculoides* = display flight of an adult; Bat Hawk *Macheirhamphus alcinus* = 2 adults hunting at dusk; Palm-nut Vulture *Gypohierax angolensis* = a pair of adults calling or chasing other raptors; African Goshawk *Accipiter tachiro* = adult displaying at dawn; Western Little Sparrowhawk *A. erythropus* = adult calling or carrying prey; Shikra *A. badius* = a pair calling or mobbing other raptors; Lizard Hawk *Kaupifalco monogrammicus* = one or two adults singing simultaneously with a neighbouring pair; African Hobby *F. cuvieri* = pair repeatedly calling and mobbing raptors. Non-soaring forest species (Congo Serpent Eagle *Dryotriorchis spectabilis*, Long-tailed Hawk *Urotriorchis macrourus*) were located by searching throughout the undergrowth of the wide gallery forests, mainly along the Bandama River, and especially by listening for calls early and late in the day. Eagles were mostly observed from outside the forest when they were hunting along edges or soaring and displaying over the canopy.

The monthly number of non-breeding migrants and additional unmated individuals of resident species was probably underestimated, because no bird was marked and individuals moved often, sometimes over long distances. The study area was divided into savanna patches, bounded by the network of galleries and woodlots. Along transects allowing a thorough visual coverage of the study area, I recorded the number and position of all individuals not referable to a known pair in as many contiguous patches as possible (≥ 3) during the same half-day, and only when they stayed within the same patch all the time that they were in view. For each month, I summed over the whole reserve the minimum number of birds that were seen in each patch at every passage. For resident species whose immature plumage was easily recognized (Palm-nut Vulture, African Harrier Hawk *Polyboroides typus*), I counted as extra birds only non-adult birds. For other breeding species, only individuals seen together with a territorial pair were considered as extra birds. Black Kites were counted at roosts and other large gatherings, assuming that breeders may have also joined such groups.

Numbers of raptors were full counts over the total reserve area. The between-year differences in population size were tested by a chi-square test with Yates correction and one degree of freedom, in a 2×2 Goodness-of-fit test based on the null hypothesis of equal numbers from the two sample periods. However, only considerable changes were statistically significant, whereas smaller differences may also have been real, since counts were accurate and exhaustive.

RESULTS

Breeding diurnal raptors

This raptor community exhibited a remarkable long-term stability (Table 2). Among the 13 breeding species (excluding extinct forest species), only the status of the two rarest species changed. A single pair of Long-crested Eagle bred on the reserve at least until 1973. It was last seen on the study area in 1983 and none was recorded in 1996. The Lanner Falcon *F. biarmicus* was a scarce resident in open areas, including towns, in the Lamto region and it was sighted only twice on the reserve before 1973. By 1983, one pair had already settled in the study area. In 1996, a breeding pair was still found but it was defending its territory against 1-2 additional individuals and observations throughout the reserve also suggested that the actual population size may have been more than one pair. Both the eagle's demise and the falcon's increase may be related to the large scale anthropogenic changes in the region around the reserve, namely deforestation and woodland clearing that mean habitat losses for the former and benefits for the latter.

Among the eleven other species, different trends were detectable in 1996 (Table 2):

- i) The Grey Kestrel, a sedentary and solitary species of the most open grasslands, had a stable population from 1967 to 1973 and increased to 5 pairs in 1996. Its habitat requirements are quite similar to those of the Lanner Falcon and the growth of its population may also come from regional habitat changes, since the trend towards increasing woodland cover in the reserve should not have favoured this species.
- ii) The two African migrants increased. The rise of the Shikra population, from 12 to 15 pairs, though not significant ($\text{Chi}^2 = 0.148$, $P > 0.7$), was probably real because the 1972 survey was more complete than the shorter 1996 survey where early or late nesting attempts may have been missed. The four-fold increase of the Black Kite breeding population (10 to 43 pairs) was striking ($\text{Chi}^2 = 19.32$, $P < 0.001$), while the non-breeding individuals were still at least as numerous as in 1972. Only isolated pairs of Black Kites were formerly breeding in the reserve. In 1996, there were also two colonies, of 8 and 10 active nests respectively and 30-50 m from each other.
- iii) The two small forest raptors, the African Goshawk and the Western Little Sparrowhawk, had stable populations: the same number of pairs were found in the same portions of the large riverine forest of the Bandama River over the 25 years interval. This was in strong contrast with the disappearance of all larger forest raptors. Even the more widespread Bat Hawk showed at least a 50% decrease and no nest was found in 1996. However, it is often an unpredictable nester and it is unclear whether this was a real population decline.

Table 2. Raptor population size on the 2,700 ha savanna-forest mosaic of Lamto Reserve. Pairs included all settled pairs identified, even when breeding was not proved or was unsuccessful. Individuals = minimum number of unpaired residents and migrants in February and March separately in 1972 and in late February - early March together in 1996. Res = resident (breeding) species: Afr = African migrant (locally breeding or not); Pal = Palearctic wintering migrant. Names from Dowsett & Forbes-Watson (1993).

<i>Species</i>	<i>Status</i>	<i>Breeding pairs</i>		<i>Non-breeding individuals</i>	
		1972	1996	1972	1996
African Cuckoo Hawk	Res	10	6	4-3	2
European Honey Buzzard	Pal		1-3	1	
Bat Hawk	Res	4	2	?	?
Black-shouldered Kite	Res			1-0	0
Black Kite	Afr	10	43	152-58	125
Palm-nut Vulture	Res	13	11	20-18	15
Brown Snake Eagle	Afr			0	1
W. Banded Snake Eagle	Afr			0-1	2
African Harrier-hawk	Res	34	29	13-12	9
Montagu's Harrier	Pal			1-0	0
Eurasian Marsh Harrier	Pal			0	3
Gabar Goshawk	Afr			0	1
African Goshawk	Res	4	4	?	?
Shikra	Afr	12	15	4-7	6
W. Little Sparrowhawk	Res	3	3	?	?
Grasshopper Buzzard	Afr			88-45	69
Lizard Hawk	Res	38	36	12	11
Common Buzzard	Pal			2-1	2
Red-necked Buzzard	Afr			2-1	1
Tawny Eagle	Afr			1-0	0
Wahlberg's Eagle	Afr			3-1	6
Long-crested Eagle	Res	1	0	1	0
Common Kestrel	Pal			1-0	0
Grey Kestrel	Res	3	5	1	1
European Hobby	Pal			1-1	1
African Hobby	Res	17	15	9	7
Lanner Falcon	Res	0	1	0	1
TOTAL		149	170	317-174	264

- iv) The 5-10% drop of the two most abundant small resident raptors, the Lizard Buzzard and the African Hobby (Table 2) was not significant ($\text{Chi}^2 = 0.014$ and 0.031 , $P > 0.8$) and unlikely to be real because both species were beginning to breed during the 1996 survey and some late-settling pairs may have been overlooked.
- v) The two large common raptors, so characteristic of the palm savanna-forest mosaic, Palmnut Vulture and African Harrier-hawk, both decreased by 15% (Table 2). This limited decline was not significant ($\text{Chi}^2 = 0.042$, $P > 0.8$ and 0.254 , $P > 0.6$ respectively), but may have been real, because adult pairs and their nests were very conspicuous and unlikely to be missed. The number of birds in immature plumage also decreased consistently by about 20%. The two species shared the same staple diet of oil palm fruits in this area (Thiollay 1978a). Many of these palms have been felled on the reserve during the last two decades. This may have reduced a major food source and may explain a decline of these two specialized raptors.
- vi) The African Cuckoo Hawk also decreased from 10 to 6 pairs, though not significantly ($\text{Chi}^2 = 0.563$, $P > 0.4$). Mostly a foliage gleaner of large insects from open woodlands to dense

forest (Thiollay 1977a, 1978a), it was a secretive and late breeder and the 1996 census may have been incomplete. Nevertheless it was a sensitive indicator of habitat impoverishment (Thiollay 1988) and its apparent decrease may have been real.

Overall, the breeding raptor population decreased from 1972 to 1996 by a mere 8.6%, excluding Black Kites, and it actually increased if Black Kites were included. The total density was still 47 breeding pairs of raptors per 1000 ha and even 63 pairs/1000 ha with Black Kites. This density may be overestimated because some peripheral pairs had home ranges extending outside the reserve although their nest was within the boundaries.

Non-breeding raptors

The fourteen non-breeding species recorded in February-March in the Lamto savanna (Table 2) could be divided into three categories (see Thiollay 1977b and 1985b for their regional status):

- i) The resident Black-shouldered Kite *Elanus caeruleus* was common around the reserve in the most open cultivated areas but only occasional individuals came to forage in the dense natural savanna woodland of the protected area.
- ii) Among the six Palearctic wintering migrants, three species were regular (1-2 individuals) in both February and March surveys in 1972 and 1996: European Honey-Buzzard *Pernis apivorus*, Common Buzzard *Buteo buteo* and Eurasian Hobby *F. subbuteo*. Montagu's Harrier *Circus pygargus* and Common Kestrel *F. tinnunculus*, widespread in West Africa but uncommon in southern savannas, were not resighted in 1996. The Eurasian Marsh Harrier *C. aeruginosus*, a rare vagrant in the Lamto savanna before 1973, was seen hunting daily in 1996. It may have actually increased in the surrounding areas, attracted by new large ricefields and dams, becoming as a result more frequent on the reserve.
- iii) Of seven Ethiopian seasonal migrants, only the occasional Tawny Eagle *Aquila rapax* was not resighted in 1996. The Brown Snake Eagle *Circaetus cinereus* and Gabar Goshawk *Micronisus gabar* were previously rare in the Lamto region and exceptional on the reserve. Conversely, they were observed several times in 1996 within the reserve alone. This suggests a southward shift of their southern limit. Two regular migrants on the reserve (1-2 individuals) Western Banded Snake Eagle *C. cinerascens* and Red-necked Buzzard *B. auguralis*, were at least as frequent in 1996 as in 1972. The Wahlberg's Eagle *A. wahlbergi* had increased 2-3 fold by 1996. The number of individuals was too small to detect a statistical difference ($\chi^2 = 1.125$, $P < 0.3$), but they were seen consistently more often in 1996 than in 1972. The abundant Grasshopper Buzzard *Butastur rufipennis* had a population size not significantly different in 1996 ($\chi^2 = 0.017$, $P > 0.9$), compared to 25 years ago. Since foraging birds tended to be regularly spaced and aggressively maintained a minimum inter-individual distance, the Lamto area was probably saturated. In the early years, the density of Grasshopper Buzzards was much lower outside the reserve. This suggests that undisturbed savanna was preferred over degraded grasslands. Because of this concentration effect, any overall increase of the population would not show up within the reserve and evidence of any decrease would be delayed.

Vanished forest raptors

Six medium-sized to large species were associated with the wide gallery forest along the Bandama River and disappeared in the 1970's. Their demise was coincidental with the clearing of contiguous and extensive forests and savanna woodlands on the opposite side of the river, whose former breeders may have sustained their marginal populations of the Lamto area. Congo Serpent Eagle was recorded three times and Black Sparrowhawk twice in 1967-1970 on the reserve. Two pairs of Long-tailed Hawk were established in 1967-73. I located the species in 1983-84 in a single area but in 1996 none could be found. One pair of Ayres' Hawk Eagle *Hieraaetus dubius* was resident until 1972 and was not seen subsequently. One pair each of Cassin's Hawk Eagle *Spizaetus africanus* and Crowned Eagle *Stephanoaetus coronatus* were observed from 1967 until they disappeared after 1970, apparently without having bred successfully during this period (nest of Crowned Eagle found).

DISCUSSION

In spite of serious environmental degradation in the region, the overall stability of local raptor populations on the Lamto Reserve is remarkable. It may be questionable to infer a long-term trend and the influence of environmental changes from only two brief surveys, for a locally dynamic bird population in which stochastic between-year fluctuations may occur. Moreover, any detectable response of a population inside a protected area may be delayed and buffered by locally suitable conditions with resultant saturated population density, by a high longevity of many tropical species and by the concentration of birds attracted by better conditions and security inside the reserve. Therefore the following interpretations of the results remain tentative, even though they are supported by extensive surveys over most of West Africa and by a comprehensive experience of Côte d'Ivoire (Thiollay 1977b, 1978b, 1985). The long-term changes in this raptor community may have three different origins, that can be called global, regional and local.

Global changes in West Africa come mainly from decreasing rainfall and are more spectacular in the Sahel than at humid southern latitudes. Rainfall may affect vegetation, food supply and breeding success and this may influence bird population size, timing and extent of seasonal migrations and/or a shift of geographical range. The Lamto area being one of the wettest and southernmost extensions of natural savanna in West Africa, a decrease of rainfall may result in the appearance of new species from northern zones or in an increase of migrants formerly staying further north. In fact, the few cases found of increases were of migrants (Black Kite, Gabar Goshawk, Wahlberg's Eagle) and no significant decrease that could have suggested worsening conditions somewhere along their seasonal distribution.

Regional changes are driven mainly by the effects of human population growth and conversion of natural habitats. Large scale deforestation, clearing of savanna woodlands for plantations, heavy exploitation of *Borassus* and oil palms, large ricefields, dams and persistent hunting pressure, all occur throughout Central Côte d'Ivoire and in the immediate vicinity of Lamto Reserve. As a result of this habitat degradation or destruction, as well as direct killing, some species should decrease or disappear outside the reserve. Small remaining populations inside the protected area are thus increasingly isolated. This was probably how the eagles became extinct. The expected consequences are also an increasing occurrence, inside the reserve, of species that have successfully adapted to the new man-made habitats in the surrounding region. Such a spill-over may be illustrated by the Marsh Harrier and Lanner Falcon. Even without a population increase, a species sensitive to habitat loss outside the reserve may use the natural savanna as a refuge and cause a local increase.

Local changes are those affecting the vegetation inside the reserve and, as a result, the bird community. Three main factors emerged that could be related to observed changes in species abundance: developing tree cover, illegal felling of palms and invasion of *Chromolaena* thickets. The long-term trend towards an increasing density of savanna woodland (Gautier 1989, 1990) has had no obvious consequences on raptors up to 1996. The reduction of oil palm fruits may explain the moderate decrease of the Palm-nut Vulture and African Harrier Hawk, major consumers of this food resource (Thiollay 1978a). The more adaptable and successful Black Kite, another important consumer of palm fruits in the Lamto area, may have turned to alternative food sources or may exercise stronger competition, including outside the reserve, with the above raptors on this critical resource during the dry (breeding) season. The dramatic invasion of *Chromolaena* thickets, in and along gallery forests and woodlands, has changed the structure of what was a specific foraging habitat of African Cuckoo Hawk and African Goshawk. Most of the savanna species did not seem to have experienced extinctions predicted as a consequence of fragmentation (Robinson & Quinn 1992). This may be because the grassland area on the reserve was sufficient to hold viable populations and/or they were still connected with healthy populations outside.

Forest species, conversely, have suffered significantly from habitat fragmentation. Forest patches around the reserves were more reduced or degraded than savanna stands. As a result, their populations could not rescue those of the reserve. The protected forest area was also six times smaller than that of savanna, and was highly fragmented into narrow galleries. Extinction is known to increase exponentially with the degree of fragmentation (Burkey 1989), whereas small patch size and isolation

worsen the effects of habitat loss on declining populations (Andren 1994). Finally, forest birds are less mobile than many savanna birds, and this greatly increases their extinction probability in isolated fragments (Burkey 1989). Local extinctions involved large forest species, but not migrant savanna eagles (*Aquila*, *Circus*).

The overall density of breeding raptors in the Lamto Reserve is still one of the highest ever documented for a community of non-colonial Falconiformes (Thiollay 1975b). Among possible reasons is the dominance of small to medium-sized species, with very few large eagles or vultures which are prominent in other African savannas (e.g., MacDonald & Gargett 1984). The lush vegetation, the short dry season and the high habitat heterogeneity, combining forests, open grasslands and woodlands, are also likely to promote both species diversity and high densities through abundant and varied food sources. The high raptor species-richness, however, is outmatched in some (much larger) national parks of Côte d'Ivoire (Table 3) or elsewhere in Africa (e.g., Thiollay 1970b, 1978c; Hartley 1993) and in comparable grassland-forest mosaic in the Neotropics (38 species in an area of similar size in Venezuela, Thiollay 1996).

Table 3. Species richness of breeding raptors in the (small) Lamto Reserve compared to three (large) national parks surveyed in Côte d'Ivoire (Taï, in the southwestern rain forest area; Maraoué, in the central forest-savanna contact-zone; Comoé in the northern Guinea savanna: Thiollay 1975c).

	<i>Vultures</i>	<i>Savanna eagles</i>	<i>Other savanna species</i>	<i>Forest raptors</i>	<i>TOTAL</i>
Taï	1	0	3	8	12
Lamto	1	3	9	8	21
Maraoué	2	5	11	6	24
Comoé	4	7	12	3	26

Implications for conservation

Three consequences of human population growth and of unsustainable exploitation were found to be especially damaging:

- 1) clearings and unburned patches of savanna are quickly invaded by *Chromolaena* thickets which prevent natural regeneration,
- 2) the hunting pressure eliminated almost all game (including large birds) outside the reserve and may threaten raptors ranging across the boundaries, and
- 3) palms which provide important nesting, roosting and perching sites (*Borassus*) or food supplies (*Elaeis*, *Raphia*) are drastically reduced.

Therefore, it is crucial to prevent such encroachment if this last refuge is still to play its conservation role. The area of protected savanna, albeit small (about 2200 ha), maintained a stable population of most raptors over three decades in spite of important habitat changes all around. Conversely, the less than 500-ha forested area, fragmented into narrow galleries, then isolated by regional deforestation and degraded by invasion of *Chromolaena*, lost its larger species, which already had small populations. Such a protected area may act as a refuge and contribute significantly to the conservation of the regional biodiversity. The *Borassus* palm savanna-forest mosaic occurred within a narrow belt along the northern edge of the rain forest zone. African Harrier Hawk, Lizard Hawk and African Hobby, at least, reached a higher density here than in any degraded area and in any other vegetation zone (Thiollay 1988). There is no other protected area in Côte d'Ivoire that includes a sizeable patch of this palm savanna and it is barely possible to increase the size of the Lamto Reserve owing to the unavailability of pristine habitat around. The annual burning management maintains this palm savanna and limits the increase of both natural woodland and *Chromolaena* thickets, as proved by the comparative evolution of the surrounding region. Burning remains a critical tool for the conservation of this original habitat and its associated avifauna.

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