Raptors in changing West African savannas : the impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon

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Chapter 8

Effects of land transformation on raptors in West African savannas: the role of breeding range, migratory behaviour and body size

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Abstract

Overexploitation of the land is a major cause of biodiversity loss in West Africa, reflected by strong raptor population declines. To provide insight into the region's dramatic raptor population declines, we investigated associations between raptor richness, species' distribution and elements of land use in the Sudano-Sahelian Inundation zone, Sudan and Guinea savanna zone of Cameroon. We specifically examined the role of breeding distribution, migratory behaviour, and body size, on patterns of raptor richness. A total of 55 species among 15,661 individuals were recorded during road surveys, which covered four years and dry and wet seasons. Results revealed strong evidence for the importance of original habitat, protection at National Park level, cultivation, and human population size in shaping patterns of raptor richness, but the importance and direction of responses differed between species groups and biogeographical zones. Whereas Palearctic raptor richness was indifferent to land use, Afrotropical raptor richness was negatively related to habitat modification and human populations in the Inundation zone and Sudan zone, but peaked at moderate levels of woodland clearance in Guinea savanna. We found evidence for greater sensitivity to habitat modification among large raptors compared to small raptors, and Afrotropical sedentary compared to Afrotropical migratory raptors. Our results suggest that the majority of Palearctic raptors seem to cope with current trends in land transformation, but strict regulations pertaining to the management of protected areas and their buffer zones are necessary to sustain their rich raptor assemblages and prevent local extinction of large raptors.

Left: Juvenile African Hawk Eagle circling over bushland in northern Cameroon.

8.1 Introduction

Clearing and modification of indigenous vegetation for agriculture have caused strong declines in global biodiversity (Foley *et al.* 2005). In Africa, rapid human population growth drives overexploitation of the land and is a major cause of past, present and future biodiversity loss (Biggs *et al.* 2008), reflected by a decrease in richness with increasingly intensified land use of a range of species (Homewood *et al.* 2001, Serneels & Lambin, 2001, Sinclair *et al.* 2002, Fabricius *et al.* 2003, Söderström *et al.* 2003, Blaum *et al.* 2007). Compared to the rest of the continent, West Africa's biodiversity stands out for being most severely threatened (Newmark 2008, Craigie *et al.* 2010). This was attributed to human population densities and rates of habitat conversion, which were higher in West Africa's sub-Sahelian savannas than elsewhere on the continent (Brink & Eva 2009). Although they constitute the last refuges for wildlife, West Africa's protected areas are highly fragmented and frequently too small and/or inadequately protected to prevent extinction from poaching or other deleterious human influences (Brashares *et al.* 2001, Newmark 2008). Therefore, the long-term persistence of many species of indigenous plants and animals is highly dependent on land use in the human-dominated landscapes and on their capacity to survive within these (Benton *et al.* 2003, Martin *et al.* 2007).

One of the most dramatic illustrations of the loss of diversity in West African savannas is the widespread, strong impoverishment of its raptor populations during the past 40 years (Thiollay 2006a,c, 2007b). However, not all species declined as strongly, and few apparently remained stable, at least locally (Thiollay 2001, 2006a), pointing to variation in species-specific response to environmental alteration and degree of development. Differences in sensitivity to habitat transformation depends on life-history traits such as niche breadth (Swihart *et al.* 2006), behavioral flexibility (Sol *et al.* 2005, 2010), and body mass (Owens & Bennett 2000, Gehring & Swihart 2003), and may vary between migrant and sedentary species (Herremans & Herremans-Tonnoeyr 2000). Because large raptors have greater body mass, energy needs, and corresponding area requirements (Jaksic & Braker 1983, Marti *et al.* 1993), they are likely to be more vulnerable to habitat disturbance and loss of prey populations than smaller raptors. This is supported by reports of more severe declines of large compared to small raptors in West Africa (Thiollay 2006b, 2007a). Afrotropical raptors, defined here as the array of (partially) nomadic, sedentary, and migratory raptors breeding in sub-Saharan Africa (Thiollay 1977a, 1989), depend on the region for secure nest sites and to sustain their breeding efforts. Consequently, their vulnerability to land use change is likely to be greater than that of Palearctic migrants, whose adaptive foraging strategies to face changing conditions at winter grounds (Cortés-Avizanda *et al.* 2011) appear to reflect those at breeding grounds, where some have adapted to human-transformed habitat for the improved feeding or nesting conditions (Sergio & Bogliani 2000, Suárez *et al.* 2000, Cardador *et al.* 2011). Like Palearctic migrants, Afrotropical migratory raptors are typically adapted to opportunistic exploitation of seasonally abundant food resources (Thiollay 1978a, Thiollay & Clobert 1990), which may similarly enhance their flexibility in response to changing conditions caused by anthropogenic land use. In contrast, sedentary raptors depend on productive year-round territories to support them and their reproductive efforts, which make them especially vulnerable to a decrease of habitat quality with anthropogenic transformation, despite a potentially high degree of behavioral flexibility of their responses to seasonal changes in the environment (Sol *et al.* 2005, 2010).

Despite strong evidence for general population declines, the influence of breeding distribution (Afrotropical/Palearctic), body size and migratory behaviour in influencing sensitivity to land use change remain little studied. Also, few studies address differences in sensitivity to habitat modification across multiple landscapes, although landscape composition and location in relation to range boundaries may explain divergent species responses (Radford & Bennett 2004, Swihart *et al.* 2006). To address this caveat, we investigated environmental factors underlying patterns of Palearctic and Afrotropical raptor community richness in three broad biogeographical zones of northern Cameroon, characterized by different productivity, vegetation composition and degree of exploitation: the Sudano-Sahelian Inundation zone, the Sudan savannas and the Guinea savannas. Our main prediction is that the richness of raptors varies along gradients of increased habitat transformation, characterized by components that quantify the intensity of land use. Specifically, we expect that Afrotropical raptors respond negatively to elements of anthropogenic pressure, whereas Palearctic raptors do not. Further, Afrotropical sedentary raptors are expected to show stronger, negative responses to anthropogenic land use change than Afrotropical migratory raptors, and large Afrotropical raptors are expected to show stronger responses than smaller Afrotropical raptors. Finally, we evaluate species-specific responses to land use across communities, to gain further insight into interspecific variation in sensitivity to land use change.

8.2 Materials and methods

Study area

Surveys of diurnal raptors (Falconiformes) along roads were conducted in the Far North, North and Adamawa Provinces of Cameroon (7º6’N-12º2’N and 13º’E-15º3’E, Figure 1). The climate is semi-arid, with rains occurring between April into October, peaking between June-September in the north and between May-October in the south. A cold dry season (Nov-Jan) precedes a hot season (Feb-May) during which the first rains occur (several weeks earlier and ending later in the southern part of the study area). Mean annual temperature is 24 ºC-28 ºC and peaks in March-May when temperatures of 47 ºC are reached in the north.

Road surveys covered three biogeographical zones differing in productivity and vegetation composition (Figure 1). Zone 1. Sudano-Sahelian Inundation zone. Located at the transition of the Sahel and the Sudan climatic zones (rainfall: 450-700 mm/annum), it incorporates the Waza-Logone floodplains, which are part of the more extensive Lake Chad Basin. The vegetation consists of edaphic grassland mosaics with communities of *Acacia* and broad-leaved trees (White 1983), notably *Sclerocarya birrea* woodland with *Anogeissus leiocarpus*, *Balanites aegyptiaca,* and *Acacia seyal*. The duration, depth and extent of Inundation of the grasslands vary in extent between years (Scholte 2005). Since 1979, the natural hydrological regime of *c*. 1500 km^2 of the floodplains has been affected by the construction of an embankment along the Logone River to develop irrigated rice scheme, which was partly rectified in 1994 by the opening of a containment dike. The floodplains are used intensively for fishing and dry-season grazing, while expanding agriculture includes mainly dry-season sorghum, millet, and rice. The 1700-km^2 Waza N.P. but especially the 45-km^2 Kalamaloué N.P. have been plagued by poaching, which has nearly wiped out large herbivores in Kalamaloué (Scholte 2003).

Zone 2. Sudan savanna zone. The most extensively cultivated zone with intermediate rainfall (700-1100 mm/annum) and few remaining patches of original undifferentiated Sudanian woodlands (White 1983), in scattered, small (< 40 km^2) and inadequately protected forest reserves with *Isoberlinia doka, Balanites aegyptiaca, Piliostigma reticulatum* and *Combretum erythrophyllum*. The zone is characterized by densely populated hilly terrain which rises to 1000 m a.s.l. on the Mandara Plateau, where isolated peaks reach 1442 m. Deforestation in this region has been significant during the past 20 years, locally up to 30% of the former woodland cover (Fotsing 2009). Sorghum, millet, maize, beans, and groundnut are the most important food crops and cotton is cultivated throughout the region as the main cash crop.

Zone 3. Guinea savanna zone. Located in the North Province, with three National Parks (Bénoué, Boubandjidda, Faro) covering an area of approximately 7600 km^2. Twenty-eight sport-hunting concessions cover an additional 16,000 km^2 of natural savanna habitat and are effectively managed as protected areas but with hunting quota for larger mammals and gamefowl (Mayaka 2002). The entire area supports regionally important herbivore and carnivore populations. The vegetation type is a transition between Sudanian woodland with abundant *Isoberlinia* and the Guineo-Congolian forest transition (White 1983), with high rainfall (1100-1600 mm/annum) and tree species composition (*Borassus*, *Diospyros*, *Isoberlinia*, *Ficus*) typical of (northern) Guinea savannas (Thiollay 1978a). The terrain is undulating with some scattered rocky outcrops intersected by the perennial Bénoué and Faro Rivers and their tributaries. Human settlements are small, concentrated near major roads and surrounded by agricultural fields, particularly traditional food crops such as millet but increasingly also cotton. The local cotton producer works together with local authorities to encourage immigration into the region, leading to high human population growth rates (*c*. 5%; Mayaka 2002).

Road surveys

Raptors were surveyed along the network of roads known to be navigable at least 10 months of the year with sufficient spatial spread to provide representative coverage of the survey area (Figure 1), between April 2007 and December 2010. Eight transects were surveyed in each zone, varying in length from 35 to 115 km. The total length of the road transects used was 395 km in the Inundation zone, 885 km in Sudan savanna, and 515 km in Guinea savanna. Given inter-specific variation in the timing and extent of seasonal movement by West African raptors (Thiollay 1978a), and the timing of breeding seasons which may influence vulnerability to land use, we repeated surveys in the dry (15 October-

15 April) and wet seasons (15 April-15 October). Each transect was surveyed twice in each three-month period (e.g. 15 October-15 January) for a total of four repeats per season (i.e., total distance covered: 14,360 km). Repetitions for each transect were spread evenly throughout the study period, i.e. one survey for every 6-month period. Repeat transect surveys were initiated from opposite directions to reduce a time bias in raptor detectability resulting from activity patterns in response to the increase of air temperature.

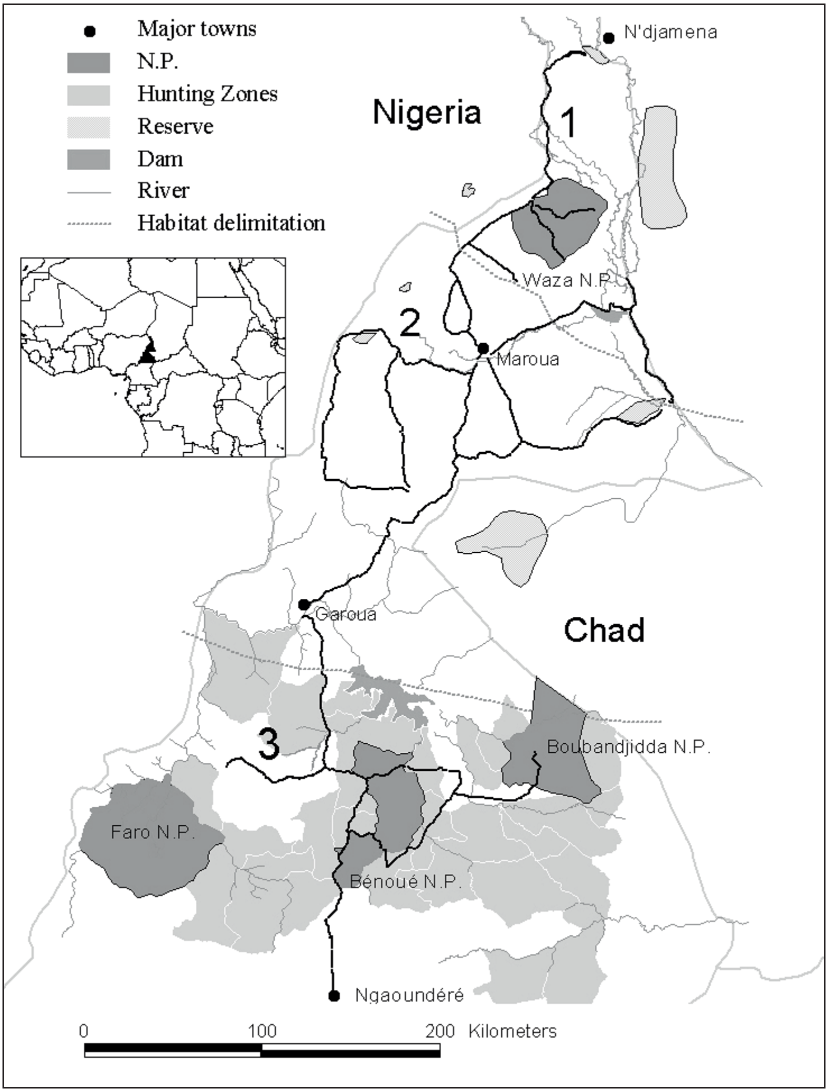

Figure 1. The study area in northern Cameroon with the delimitation of the three main biogeographical zones (1: Inundation zone, 2: Sudan savanna, 3: Guinea savanna) and the location of National Parks, hunting concessions, and forest and faunal reserves (“Reserve”). Road transects are indicated as black lines.

Raptor counts were conducted along road transects following widely-use methods (Fuller & Mosher 1981, Bibby *et al.* 1992) by two experienced observers (one driving) from a slow-driving vehicle (20-25 km/hour). Despite shortcomings related to the non-random distribution of raptors to roads (Meunier *et al.* 2000), examinations of raptor-habitat associations can successfully be made using road surveys (Sánchez-Zapata *et al.* 2003, Carrete *et al.* 2009), provided that potential differences in raptor detectability between habitats are addressed (Millsap & LeFranc 1988). All raptors perched or flying on either side of the road within eyesight range were recorded and identified with 10x42 binoculars. Short stops (*c.* 20-30 s) were made at 1-km intervals to record habitat characteristics (see below) and to enhance detectability of small and/or inconspicuous species. The transect length and position of each raptor along the transect was recorded with a geographical positioning system and the perpendicular distance from the road to the raptors measured with a calibrated rangefinder to allow estimation of effective strip width (Buckland *et al.* 1993). Surveys were conducted only with fine weather, i.e. under clear or slightly clouded skies with low to moderate winds, starting at 06:30 to 7:30 depending on the season and finalized before *c.* 11:30-12:30 (depending on latitude and season) to avoid counting when a rise in air temperature lowered detectability of the majority of raptors compared to the morning hours.

Habitat variables

The habitat along transects was characterized during road transects by the same observer, using habitat variables measured at 1-km intervals and at the scale of a 1-km^2 block or a 2-ha plot centred on the road: (1) grass cover (GRASS): the percentage cover of the rooted herbaceous vegetation (grasses and forbs; 2 ha), (2) tree density (TREE): the number of trees > 5 m (2 ha), (3) agriculture (AGRI): the percentage cover of food crops: sorghum, millet, or other food crops (1-km^2), (4) cotton cultivation (COT): the total number of ha covered by cotton fields (1-km^2), (5) human habitation (VIL): the surface area covered by towns, villages, or other settlements characterized by houses (i.e., temporary settlements of nomadic shepherds were excluded) as a proxy measure of sedentary human population size (1-km^2), (6) natural habitat (NAT): the percentage cover contiguous habitat which retained a vegetation composition and structure similar to the original habitat (1-km^2). We distinguished cotton cultivation from food crops, since pesticide use in heavy in cotton fields, with potentially negative effects on raptors and their food supply, whereas food crops (e.g. sorghum, millet, rice) may support high rodent numbers and pesticide input is generally negligible (Chapter 2). In addition, we measured the (7) distance (in km) to the nearest National Park (PARK), and (8) the distance to the nearest conservation area (i.e. National Park, Hunting Consession, forest reserve, faunal reserve; RES) using ArcView GIS 3.2 software (Esri 1999). The distinction between National Park and all conservation areas as potential sources of raptor populations was made because protection levels frequently differ considerably between National Parks and other reserves with important consequences for conservation of raptor populations (Thiollay 2007a). Kalamaloué N.P. was categorized as conservation area, since its management since the 1990s is comparable to a forest reserve rather than a National Park (Scholte 2003). Field estimates of the cover of natural habitat were compared to cover estimates generated using satellite images of the study area (Cnes/Spot Image 2010) in ArcView 3.2 and these were highly correlated (r = 0.90-0.96), supporting the validity of our field estimates. Estimates of grass cover were made at every road survey and averaged for the late dry season (Inundation and Sudan zone: March-April; Guinea zone: Feb-March), when grass cover is at its minimum (Thiollay 1978a) and when differences between sites are greatest depending on the degree of utilization (grazing, trampling, fires). For all other variables, estimates were made at the beginning, middle and end of the study period and mean values were used for analyses.

Statistical analyses

Richness and presence or absence of raptors was examined for 5-km road stretches, which were the sampling units for statistical analyses. We examined patterns of richness separately for (1) Afrotropical raptors, (2) Palearctic raptors, (3) Afrotropical eagles and vultures, including Secretary Bird *Sagittarius serpentarius*, (4) Afrotropical small to medium-sized Afrotropical raptors, (5) Afrotropical sedentary raptors, and (6) Afrotropical migrants (cf. Table 1). Raptors were assigned to groups based on their taxonomic position and status between 8ºN and 12ºN (Thiollay 1977a). Palearctic migrants breed in Eurasia and/or Northern Africa and winter in sub-Saharan Africa. Populations of Afrotropical migrants are characterized by regular latitudinal displacements over relatively short distances (500-1500 km), e.g. Grasshopper Buzzard *Butastur rufipennis*, African Swallow-tailed Kite *Chelictinia riocourrii* (Thiollay, 1978a), or longer distances (*c*. 3500 km), e.g. Wahlberg's Eagle *Aquila wahlbergi* (Meyburg *et al.* 1995). Sedentary raptors do not display regular latitudinal population displacements, despite limited wet season movements by some, e.g. Lizard Buzzard *Kaupifalco monogrammicus* (Thiollay 1977a). Black Kite *Milvus migrans*, Common Kestrel *Falco tinnunculus*, and Egyptian Vulture *Neophron percnopterus* populations were composed of both Afrotropical and Palearctic individuals, which were distinguishable for Common Kestrel (based on plumage differences between races) and Egyptian Vulture (based on behaviour). Separation between local and Palearctic populations was omitted for Black Kite as the two races could not be safely distinguished at all times, but the vast majority of Black Kites referred to the Afrotropical race. Hooded Vulture was excluded from the community richness analyses because it is the only raptor in the region which is strongly associated with human habitation throughout the year (Thiollay 1977a). Richness was obtained as the total number of species recorded after eight repeat surveys of a transect segment, which was sufficient to obtain an asymptotic value for richness in the three biogeographical zones (data not shown).

Apart from richness, we modelled the presence/absence of raptors separately for each of the repeated surveys (n = 8), for species with sufficient observations (> 100 individuals on all transects combined) to allow analysis of habitat preference in at least two zones. For these models, potential detectability differences of raptor between segments were examined to assess their potentially confounding influence on habitat models. Since differences in volume and distribution of foliage are the most important elements affecting raptor detectability during road surveys (Millsap & Lefranc 1988) and the density of the vegetation structure varied with the extent of natural habitat, we estimated detection probabilities for segments with > 60% natural habitat cover ("dense habitat") and those with < 40% natural habitat (“open habitat”). Raptors were grouped to three size categories (small, medium-sized, large) assumed to have approximately comparable detectability. For each raptor size category an effective strip width was estimated separately for segments in the two habitat categories (dense/open) in each zone. Hereto, we tested six detection functions (half-normal + cosine and hermite polynomial adjustments, hazard rate + cosine and simple polynomial, uniform + cosine and simple polynomial) fitted to the perpendicular distances estimated for flying and perching raptors, in Distance 6.0 software (Thomas *et al.* 2006). We also examined detection probabilities separately for small to medium-sized Dark Chanting Goshawk *Melierax metabates*, Shikra *Accipiter badius*, Grasshopper Buzzard, Fox Kestrel *Falco alopex* in the relatively dense Guinea zone, because we expected vegetation thickness to potentially have the largest influence on detectability of these raptors. Following Buckland *et al.* (1993), models with the lowest Akaike Information Criterion (AIC) value were selected for estimation of the strip width and significant differences were based on overlap of 95% confidence intervals.

We used Generalized Linear Mixed Models (GLMMs) to describe the effect of multiple explanatory variables on raptor richness and presence using SPSS 19.0 (SPSS Inc, Chicago, IL, USA). The GLMMs allowed us to control for autocorrelation between 5-km segments within transects. Associations were examined by fitting the six habitat variables and distance to the nearest National Park and conservation area as fixed effects and richness and presence/absence as dependent variables. The linear and quadratic forms of all explanatory variables were tested. Before modelling, we verified collinearity between predictor variables for each biogeographical zone using Spearman Rank Correlation tests. Pairs of strongly intercorrelated, explanatory variables ($r > 0.60$) were considered to be estimates of one underlying factor and we retained those with the lowest corrected Akaike Information Criterion (AICc) value from univariate models of the two predictors (Burnham & Anderson 2002). Since transects were widely spaced (Figure 1) and surveyed at the same time (i.e. day), we assumed transects to be independent subjects. For the richness models, transects were included as subjects and segments as repeated effect variables since the transect survey methodology resulted in segments being repeat measures in space. We specified a first-order autoregressive (AR-1) covariance type to account for significant spatial autocorrelation between segments. Richness was modeled with Poisson, Negative Binomial, or Gamma errors and logarithmic link functions. For the species-specific presence/absence data, binomial models were used with transects as random blocks to account for correlation among segments within the same transect and segments as subjects and survey periods ($n = 8$ for each segment) as repeated effect variables. An AR-1 variance type was used to account for temporal autocorrelation between repeat surveys. All models were built following a backward stepwise procedure and the model with the lowest AICc value and only significant terms was considered the final model.

8.3 Results

We recorded 55 species among 15,661 individuals on surveys in the three biogeographical zones combined, dominated by Black Kite (24%), Hooded Vulture (21%), and Grasshopper Buzzard (10%; Table 1). Habitat characteristics differed between the Inundation zone, Sudan and Guinea savannas, with a greater degree of transformation in the Sudan zone compared to the two other zones (Figure 2). The detection probabilities of the most common (i.e. > 100 individuals seen) small, medium-sized and large raptors in the three zones did not differ significantly ($P > 0.05$) between segments covered by different degrees of natural habitat (Appendix 8.1). Similarly, examination of strip widths on segments with different natural vegetation cover in the Guinea zone, for Dark Chanting Goshawk, Grasshopper Buzzard, Shikra, and Fox Kestrel, did not reveal significant differences (Appendix 8.1). Based on these results, we concluded that detectability would not confound our models of species presence in the three biogeographical zones.

Table 1. Raptors observed and number of individuals and taxonomic position. Categories refer to those used for models; (1) Afrotropical raptors, (2) Palearctic migrants, (3) Afrotropical eagles and vultures, (4) small to medium-sized Afrotropical raptors, (5) Afrotropical sedentary raptors, (6) Afrotropical migrants.

ACCIPITRIFORMES		
PANDIONIDAE	***n***	**Category**
Osprey *Pandion haliaetus*	13	2
ACCIPITRIDAE		
Eagles		
African Fish Eagle *Haliaeetus vocifer*	27	1, 3, 5
Bateleur *Terathopius ecaudatus*	154	1, 3, 5
Short-toed Eagle *Circaetus gallicus*	98	2
Beaudouin's Snake Eagle *Circaetus beaudouini*	48	1, 3, 6
Brown Snake Eagle *Circaetus cinereus*	88	1, 3, 5
Western Banded Snake Eagle *Circaetus cinerascens*	31	1, 3, 5
Wahlberg's Eagle *Aquila wahlbergi*	475	1, 3, 6
Tawny Eagle *Aquila rapax*	188	1, 3
Steppe Eagle *Aquila nipalensis*	52	2
Lesser Spotted Eagle *Aquila pomarina*	1	2
Eastern Imperial Eagle *Aquila heliaca*	3	2
Martial Eagle *Polemaetus bellicosus*	26	1, 3, 5
Long-crested Eagle *Lophaetus occipitalis*	147	1, 3, 5
Booted Eagle *Hieraaetus pennatus*	262	2
Ayres's Hawk Eagle *Hieraaetus ayresii*	37	1, 3
African Hawk Eagle *Hieraaetus spilogaster*	37	1, 3, 5
Vultures		
Hooded Vulture *Necrosyrtes monachus*	3345	-
Egyptian Vulture *Neophron percnopterus*[a]	28	2
White-headed Vulture *Trigonoceps occipitalis*	20	1, 3, 5
African White-backed Vulture *Gyps africanus*	195	1, 3
Rüppell's Vulture *Gyps rueppellii*	520	1, 3
Lapped-faced vulture *Torgos tracheliotus*	40	1, 3
Small and medium-sized Accipiters		
African Harrier Hawk *Polyboroides typus*	65	1, 4
Black Kite *Milvus migrans*[a]	3730	1, 4, 6
Eurasian Marsh Harrier *Circus aeruginosus*	491	2
Pallid Harrier *Circus macrourus*	47	2
Montagu's Harrier *Circus pygargus*	73	2
Black-winged Kite *Elanus caeruleus*	526	1, 4
African Swallow-tailed Kite *Chelictinia riocourii*	279	1, 4, 6
African Cuckoo Hawk *Aviceda cuculoides*	20	1, 4, 5
Bat Hawk *Macheiramphus alcinus*	3	1, 4, 5
Shikra *Accipiter badius*	153	1, 4, 6
Gabar Goshawk *Micronisus gabar*	270	1, 4

Table 1. (Continued).

Ovambo Sparrowhawk *Accipiter ovampensis*	4	1, 4
Lizard Buzzard *Kaupifalco monogrammicus*	31	1, 4, 5
Levant Sparrowhawk *Accipiter brevipes*	1	2
Dark Chanting Goshawk *Melierax metabates*	724	1, 4, 5
European Honey Buzzard *Pernis apivorus*	16	2
Grasshopper Buzzard *Butastur rufipennis*	1517	1, 4, 6
Red-necked Buzzard *Buteo auguralis*	259	1, 4, 6
Common Buzzard *Buteo buteo*	1	2
Long-legged Buzzard *Buteo rufinus*	12	2
SAGITTARIIFORMES		
SAGITTARIIDAE		
Secretary bird *Sagittarius serpentarius*	1	1, 3
FALCONIFORMES		
FALCONIDAE		
Common Kestrel *Falco tinnunculus*[a]	150	2
Lesser Kestrel *Falco naumanni*	16	2
Fox Kestrel *Falco alopex*	794	1, 4, 5
Barbary Falcon *Falco pelegrinoides*	6	2
Peregrine Falcon *Falco peregrinus*	1	2
Lanner Falcon *Falco biarmicus*	351	1, 4
Grey Kestrel *Falco ardosiaceus*	178	1, 4, 5
Red-necked Falcon *Falco chicquera*	98	1, 4, 5
African Hobby *Falco cuvierii*	6	1, 4, 5
Eurasian Hobby *Falco subbuteo*	1	2
Red-footed Falcon *Falco vespertinus*	2	2
Unidentified raptors[b]	102	-

[a] Of Afrotropical and Palearctic origin

[b] Not included in models

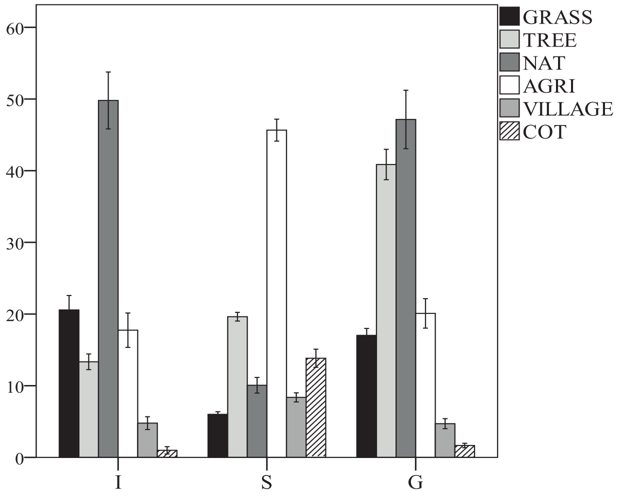

Figure 2. Habitat variables in the three biogeographical zones in Cameroon (I: Inundation zone; S: Sudan savanna; G: Guinea savanna). Value refer to percentage dry-season grass cover (GRASS), percentage cover natural habitat (NAT), percentage cover food crop cultivation (AGRI), human habitation (VIL), the number of trees (TREE) and ha cotton (COT) on 5-km transect segments. Grass and tree cover based on mean values at five 2 ha-plots for each segment; for other variables, assessment based on five 1-km^2 plots for each segment. Median values for all habitat variables differed across biogeographical zones (Kruskal-Wallis tests; $P < 0.001$).

Response to land use

Afrotropical and Palearctic raptors

Afrotropical raptor richness decreased with increasing distance to protected areas in the Inundation zone (Table 2). Food crop cultivation, cotton cultivation, and human population size negatively shaped Afrotropical raptor richness in the Sudan zone. Afrotropical raptor richness was negatively related to the extent of natural habitat in the Guinea zone, albeit in a nonlinear fashion (Table 2), suggesting that the small to moderate loss of original habitat positively influenced Afrotropical raptor richness. In contrast to Afrotropical raptors, the richness of the Palearctic migrant assemblage was indifferent to land use, but species-specific models included both a positive association with food crop cultivation and a negative association with cotton (Table 3).

Afrotropical migratory and sedentary raptors

Patterns of community richness were shaped by different environmental factors in sedentary and Afrotropical migratory raptors. Community-specific models (Table 2) indicated that Afrotropical migrant richness was positively associated with National Park protection and natural habitat, and negatively with food crop cultivation, in the Inundation and Sudan zone, suggesting the Afrotropical migrant assemblage was vulnerable to anthropogenic land use change. Species-specific model did reveal positive associations between Wahlberg’s Eagle and African Swallow-tailed Kite presence and food crops. In contrast, richness of the Afrotropical migrant assemblage was positively associated with food crops in the Guinea savanna zone (Table 2). Sedentary raptor richness was positively associated with natural habitat, and negatively with human populations, food crops and cotton (Table 2), suggesting sedentary raptors were generally sensitive to anthropogenic disturbance and land transformation. Similar to the migrants, responses to land use varied between sedentary species: Rüppell’s Vulture *Gyps rueppellii* and African White-backed Vulture *Gyps africanus* were positively associated with natural habitat, Grey Kestrel *Falco ardosiaceus* negatively with food crops, while Fox Kestrel, Dark Chanting Goshawk, and Long-crested Eagle *Lophaetus occipitalis* were negatively associated with natural habitat, suggested they profited from clearance of woodlands (Table 3). Finally, representatives of both Afrotropical migratory and sedentary raptor assemblages displayed contrasting responses to the area under cultivation (Wahlberg’s Eagle, Grey Kestrel) or natural habitat (Long-crested Eagle) in different biogeographical zones.

Large and small to medium-sized raptors

Large and small to medium-sized raptors were positively associated with measures of habitat preservation, or negatively to human populations, food crops, and cotton cultivation in the Sudan and Inundation zones (Table 2). A difference in sensitivity to habitat disturbance between Afrotropical raptors categorized to size was apparent in the Guinea zone. Here, richness of small to medium-sized Afrotropical raptors was negatively related to natural habitat, suggesting a majority of species responded favorably to habitat clearance, whereas large raptor richness was negatively associated with the distance to the nearest National Park. Exceptions to the general pattern were recorded, e.g. Tawny Eagle *Aquila* *rapax*, a large sedentary eagle, was positively influenced by anthropogenic land transformation in the Guinea savanna (Table 3).

Table 2. GLMM examining the relationship between raptor richness on 5-km transect segments in the Inundation zone (n = 79 segments), the Sudan savanna (n = 177), and the Guinea savanna (n = 103). Richness refers to combined species number for eight repeat surveys of each transect segment. Explanatory variables represent those that entered the minimal adequate model after backward stepwise regression, eliminating nonsignificant terms until only significant terms remained. Explanatory variables fitted to the models: (1) dry-season grass cover (GRASS), (2) tree density (TREE), (3) food crops (AGRI), (4) cotton cultivation (COT), (5) human habitation (VIL), (6) the percentage cover contiguous natural habitat (NAT), (7) distance to the nearest National Park (PARK), and (8) the distance to the nearest protected area (RES).

Explanatory variable	***B* ±SE**	***t***	***P***
Inundation zone			
Afrotropical raptors[1]			
$F_{1,77} = 10.31$, $P < 0.01$	AICc = 43.5		
(Intercept)	2.35±0.10	23.63	< 0.001
PARK	-0.007±0.002	-3.20	< 0.01
Palearctic raptors[1]	- *		
Eagles and vultures[1]			
$F_{1,77} = 14.33$, $P < 0.001$	AICc = 184.5		
(Intercept)	1.04±0.18	5.91	< 0.001
PARK	-0.019±0.005	-3.79	< 0.001
Small to medium-sized Afrotropical raptors[2]			
$F_{1,76} = 8.68$, $P < 0.001$	AICc = 32.6		
(Intercept)	1.72±0.09	19.70	< 0.001
NAT	0.003±0.001	2.43	< 0.05
PARK	-0.003±0.001	-2.25	< 0.05
Sedentary raptors[1]			
$F_{1,77} = 4.60$, $P < 0.05$	AICc = 144.1		
(Intercept)	0.38±0.20	1.95	0.06
NAT	0.006±0.003	2.14	< 0.05
Afrotropical migrants[3]			
$F_{1,76} = 15.73$, $P < 0.001$	AICc = 64.9		
(Intercept)	1.36±0.09	16.03	< 0.001
PARK	-0.01±0.002	-4.60	< 0.001
TREE	0.008±0.003	2.41	< 0.05
Sudan savanna			
Afrotropical raptors[1]			
$F_{1,173} = 8.73$, $P < 0.001$	AICc = 189		
(Intercept)	2.18±0.13	17.3	< 0.001
VIL	-0.012±0.004	-3.46	< 0.01
AGRI	-0.005±0.002	-3.06	< 0.01
COT	-0.004±0.002	-2.23	< 0.05
Palearctic raptors[1]	-		
Eagles and vultures[4]			
$F_{1,175} = 9.67$, $P < 0.01$	AICc = 474.2		
(Intercept)	-0.15±0.14	-1.05	0.30
NAT	0.012±0.004	3.11	< 0.01
Small to medium-sized Afrotropical raptors[1]			
$F_{1,172} = 5.52$, $P < 0.001$	AICc = 210.3		
(Intercept)	1.79±0.10	17.2	< 0.001
VIL	-0.013±0.004	-3.47	< 0.01
AGRI	-0.003±0.002	-2.09	< 0.05
AGRI^2	-0.000±0.000	-1.75	< 0.05
COT	-0.004±0.002	-2.03	< 0.05

Table 2. (Continued).

Sedentary raptors[1]			
$F_{1,174} = 4.26$, $P < 0.05$	AICc = 385.8		
(Intercept)	0.86±0.19	4.56	< 0.001
COT	-0.007±0.003	-2.03	< 0.05
AGRI	-0.005±0.003	-1.87	< 0.05
Afrotropical migrants[1]			
$F_{1,175} = 4.89$, $P < 0.05$	AICc = 305.5		
(Intercept)	1.13±0.14	7.88	< 0.001
AGRI	-0.005±0.002	-2.21	< 0.05
Guinea savanna			
Afrotropical raptors[1]			
$F_{2,100} = 10.72$, $P < 0.001$	AICc = 96.7		
(Intercept)	2.16±0.11	20.5	< 0.001
NAT	-0.004±0.001	-3.57	< 0.01
NAT^2	-0.000±0.000	-2.02	< 0.05
Palearctic raptors[1]	-		
Eagles and vultures[1]			
$F_{1,101} = 3.58$, $P < 0.05$	AICc = 187.1		
(Intercept)	1.10±0.14	8.18	< 0.001
PARK	-0.023±0.012	-1.89	< 0.05
Small to medium-sized Afrotropical raptors [1]			
F = 41.32, df1 = 1, df2 = 101, $P < 0.001$	AICc = 134.1		
(Intercept)	1.89±0.11	17.60	< 0.001
NAT	-0.010±0.002	-6.43	< 0.001
Sedentary raptors[1]			
$F_{2,100} = 8.52$, $P < 0.001$	AICc = 122.6		
(Intercept)	2.07±0.13	16.41	< 0.001
TREE	-0.009±0.002	-4.07	< 0.001
VIL	-0.013±0.007	-1.89	< 0.05
Afrotropical migrants[1]			
$F_{1,101} = 4.76$, $P < 0.05$	AICc = 177.3		
(Intercept)	0.64±0.12	5.32	< 0.001
AGRI	0.008±0.004	2.18	< 0.05

[1] GLMM with poisson errors and a logarithmic link function.
[2] GLMM with gamma errors and a logarithmic link function.
[3] GLMM with normal errors and a logarithmic link function.
[4] GLMM with negative binomial errors and a logarithmic link function.
* No significant terms after stepwise regression.

8.4 Discussion

Our results revealed strong evidence for the importance of habitat preservation and human disturbance on shaping raptor communities in Cameroon, corroborating previous results from the region (Thiollay 2006a,b, 2007a, Anadón *et al.* 2010) and elsewhere in Africa (Brandl *et al.* 1985, Sorley & Anderson 1994, Herremans & Herremans-Tonnoeyr 2000, Virani *et al.* 2011). Sensitivity to land use varied, however, between small to medium-sized and large raptors, Afrotropical and Palearctic raptors, and Afrotropical sedentary and migratory raptors. Afrotropical large eagles and vultures seemed more sensitive to habitat transformation than Afrotropical medium-sized to small raptors, at least in moderately transformed Guinea savannas. In the dense Guinea savannas, richness of the entire Afrotropical raptor community peaked at moderate levels of habitat modification, which might have made available prey resources normally unavailable to open-country generalists

Table 3. GLMM with binomial errors and logit link function examining the relationship between raptor presence (0: reference category) on 5-km transect segments in the Inundation zone ($n = 79$ segments), the Sudan savanna ($n = 177$), and the Guinea savanna ($n = 103$), for raptors for which > 100 individuals were recorded. Odds ratios and model accuracy (Acc) are presented. Explanatory variables represent those that entered the minimal adequate model after backward stepwise regression. Explanatory variables fitted to the models: (1) dry-season grass cover (GRASS), (2) tree density (TREE), (3) food crops (AGRI), (4) cotton cultivation (COT), (5) human habitation (VIL), (6) the percentage cover contiguous natural habitat (NAT), (7) distance to the nearest National Park (PARK), and (8) the distance to the nearest protected area (RES), and year (random term). The significance of the model terms is indicated using asterisks: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$. Size categories of raptors for estimation of detectability are indicated (1 = large, 2 = medium-sized, 3 = small).

		Inundation zone			**Sudan savanna**			**Guinea savanna**		
Species	**Size**	**variable**	**Exp(*B*)**	**Acc (%)**	**variable**	**Exp(*B*)**	**Acc (%)**	**variable**	**Exp(*B*)**	**Acc (%)**
Afrotropical raptors										
Black-winged Kite	3	-[1]			VIL	0.927***	90.0	AGRI	1.051***	86.7
Lanner Falcon	2	-			COT	0.986*	92.9	AGRI	1.025**	93.6
					AGRI	1.014*				
Gabar Goshawk	3	NAT	1.017***	88.4	NAT	1.011**	93.3	-		
		TREE	0.969*							
Tawny Eagle	1	TREE	1.036*	89.9	-			AGRI	1.035**	98.1
Afrotropical migrants										
Black Kite	2	VIL	0.971*	61.4	COT	0.984**	84.7	-		
Grasshopper Buzzard	2	NAT	1.010*		-			AGRI	1.036***	85.1
		GRASS^2	1.000*(-)[2]							
		PARK	0.960***							
Wahlberg's Eagle	1	AGRI	1.021**	87.5	AGRI	0.993**	89.2	RES	0.988*	88.1
		TREE	1.025*							
		PARK	0.981*							
African Swallow-tailed Kite	3	PARK	0.963**	89.2	AGRI	1.022**	95.7	-		
					GRASS	0.834**				
Red-necked Buzzard	2	NAT	1.019*	96.5	AGRI	0.990*	91.7	-		
Shikra	3	TREE	1.060**	97.8	TREE	1.038*	97.0	NAT^2	0.999**	91.7
					AGRI	0.985*		COT	0.859*	
Afrotropical sedentary raptors										
Hooded Vulture	1	VIL	1.029*	87.7	VIL	1.064***	67.3	VIL	1.076***	98.5
Fox Kestrel	3	-[2]			COT	0.967***	84.2	NAT	0.958***	91.1
					TREE	0.975*				
Dark Chanting Goshawk	2	AGRI	0.982*	70.2	AGRI^2	1.000*** (-)	85.7	NAT	0.972***	90.8
		NAT	1.013*		VIL	0.969*		GRASS	1.049**	
Rüppell's Vulture	1	-			-			NAT	1.031*	97.5
Bateleur	1	PARK	0.936*	92.6	NAT	1.060**	99.6	PARK	0.863***	93.1
African White-backed Vulture	1	PARK	0.960***	93.5	-			NAT	1.017*	97.7

Table 3. (Continued).

		Inundation zone			**Sudan savanna**			**Guinea savanna**		
Species	**Size**	**variable**	**Exp(*B*)**	**Acc (%)**	**variable**	**Exp(*B*)**	**Acc (%)**	**variable**	**Exp(*B*)**	**Acc (%)**
Grey Kestrel	3	AGRI	1.041***	98.6	TREE^2	0.999*	95.0	AGRI	0.978*	91.4
		TREE^2	0.994***		GRASS^2	1.002*		GRASS^2	0.999*	
Long-crested Eagle	1	-			GRASS	1.153***	99.5	NAT	0.988**	
					NAT	1.042**		COT	1.100**	
					COT	0.938*				
Palearctic raptors										
Booted Eagle	1	AGRI	1.016**	87.8	NAT	0.976**	94.7	-		
					VIL	0.972*				
					TREE	1.029*				
					GRASS^2	0.996*				
Eurasian Marsh Harrier	2	-			-			-		
Common Kestrel	3	-			COT	0.965**		-		
					TREE	0.963*				

[1] No significant terms in model after stepwise regression.

[2] Represents a nonlinear, predominantly negative relationship.

(Thiollay & Clobert 1990). This would have allowed raptors with different habitat preferences, diets, and foraging strategies to coexist (Rodríguez-Estrella *et al.* 1998, Anderson 2001). In contrast, richness of Afrotropical raptor was positively associated with elements of habitat preservation, and negatively with food crop and cotton cultivation, in the Inundation and Sudan savanna zones. These results indicate that sensitivity to land use may be greater in fragile, less productive or overexploited systems, compared to more productive and moderately affected systems, adding to existing evidence for differential responses across multiple landscapes in other taxa (Radford & Bennett 2004, Swihart *et al.* 2006).

In contrast to the Afrotropical raptor community, we did not detect a general pattern of Palearctic species richness in response to land use, suggesting that the relationships of Palearctic migrants with land use are more complex compared to Afrotropical raptors. Possibly, divergent diets and opportunistic foraging strategies by Palearctic raptors, some of which have been shown to converge on transient food sources (Cortés-Avizanda *et al.* 2011, Limiñana *et al.* 2012), in addition to intraspecific variation of habitat selection (Chapter 2), might have obscured general habitat patterns of the Palearctic raptor assemblage. Our results suggest that some Palearctic raptors will suffer under certain land use transformations, and others will benefit. A negative effect of agricultural intensification (i.e. cotton fields) on Common Kestrels in the Sudan zone was possibly related to heavy pesticide use in cotton, which depressed insect prey (Stechert *et al.* 2011). In contrast, the presence of Eurasian Marsh Harrier *Circus aeruginosus* was not associated with land use and Booted Eagle *Hieraaetus pennatus* responded positively to food crop cultivation in the Lake Chad Basin. Interestingly, numbers of both species have remained exceptionally stable, possibly even increasing in some areas of West Africa (Thiollay 2001, 2006a), perhaps partly due to a high level of behavioral and ecological flexibility in response to changing conditions as also exhibited on their European breeding grounds (Suárez *et al.* 2000, Cardador *et al.* 2011). Wintering conditions for these and other Palearctic raptors exploiting rodent populations may have locally improved due to agricultural expansion (Chapters 2, 9), whereas insectivorous raptors are more vulnerable to the widespread depletion of their largely insectivorous prey base, from droughts, pesticide spraying in agriculture, and locust control operations (Sánchez-Zapata *et al.* 2007; Mihoub *et al.* 2010).

Sedentary birds, i.e. those that depend on year-round territories, have been shown to possess morphological traits that allow them to cope relatively well with changing environments (Lefebvre *et al.* 1997, Sol *et al.* 2005, 2010), whereas migratory species were said to have rather limited capacity to produce flexible responses to changing conditions. Although such adaptability to habitat change held for few sedentary raptors, overall community responses suggested otherwise. Instead, we recorded evidence for greater sensitivity to land use by Afrotropical sedentary raptors compared to Afrotropical migratory raptors; Afrotropical migrant richness increased with agriculture in the Guinea savannas, whereas sedentary raptors in our study area responded negatively to elements of anthropogenic pressure in all biogeographical zones. These results indicate that Afrotropical migrants profited locally from moderate anthropogenic disturbance, which may favor their hunting strategies (Thiollay & Clobert 1990), whereas the sedentary raptor assemblage was generally vulnerable to changing conditions. Still, Afrotropical migrants responded positively to National Park protection, and negatively to food crop cultivation, in the Inundation and Sudan zones, where the majority of Afrotropical migrants breed (Thiollay 1978a), suggesting that their vulnerability to modification varied with breeding status or landscape context, or a combination of both.

Management implications

The results of our surveys indicate that large, sedentary raptors are most vulnerable to habitat destruction, which corresponds with the reported strong declines in this group (Thiollay 2006a, 2007a). The decreasing richness of large raptors with increasing distance from National Parks points to a risk of reduced connectivity between fragmented populations within otherwise heavily disturbed and rapidly transforming landscapes, which may significantly affect population viability (Clerici *et al.* 2006, Newmark 2008). Furthermore, their wide-ranging habits make large raptors extremely vulnerable to factors operating in buffer zones of protected areas, such as persecution and pesticide poisoning (Herholdt & Kemp 1997, Ogada & Keesing 2010), particularly when they affect survival of reproductive individuals (Brown 1991, Whitfield *et al.* 2004). High mortality in buffer zones might explain massive edge effects as reported from Botswana’s protected areas, where large raptor populations were already > 40% lower in the peripheral 30 km than in the core (Herremans & Herremans-Tonnoeyr 2000). Using these criteria, all National Parks in northern Cameroon and many protected areas in the region qualify only as peripheral areas, inadequate for preserving the largest species, which may be why some are declining even inside protected areas (Thiollay 2006a). To minimize human pressure which greatly threatens wildlife (Brashares *et al.* 2001), including raptors and their prey populations, in the region’s National Parks, we reiterate the need for re-evaluation of the current system of buffer zone management for the benefit of local communities, including shared benefits from National Park income (Mayaka *et al.* 2005). Such efforts should then coincide with measures to limit natural resource use by human populations within buffer zones, for example through active discouragement of rural development activities (Scholte 2003).

Away from protected areas, where land use planning is effectively in the hands of traditional authorities (Olson 1999), further loss of natural habitat in exploited landscapes, such as the Sudan savannas of Cameroon and elsewhere in the region, could theoretically be avoided with substantial investments in agricultural practices (Fotsing 2009), which would lower the necessity to expand into remaining bushlands. Such actions would safeguard important habitat for breeding and cover for raptors. However, steep human population growth rates and little improving yields (Njomaha 2004) suggest that continuous expansion of agriculture for food production and, more recently, biofuels, are likely to continue unabated. Moreover, extractive exploitation of bushlands is not likely to cease even if agricultural practices would improve due to the growing need for and widespread commercialization of increasingly scarce firewood, thatch, and bushmeat. Heavy grazing pressure in bushlands further impacts prey populations (Meik *et al.* 2002, Blaum *et al.* 2007) and our data suggest that some raptors (Long-crested Eagle, Dark Chanting Goshawk) may be more vulnerable to grassland deterioration than others.

Finally, the significantly negative relationship of cotton cultivation with raptor richness and species-specific distribution patterns suggests that cotton production is a serious concern to raptor conservation in the region. Cotton is the region's major cash crop and production increased fivefold between 1970 and 2009 in Cameroon and three to tenfold in five other countries of West Africa (FAOSTAT 2012). Despite a recent ban on endosulfan in various West African countries, cotton production in West Africa continues to use it and other pesticides such as DDT (Matthews *et al.* 2003, Stechert 2011). Given the proven sensitivity of raptor populations to organochlorines (Newton 1979), carry-over effects of endosulfan and DDT with corresponding metabolites for wide-ranging taxa at higher trophic levels (Stechert 2011), and close correlations between their use in agriculture and raptor blood concentration levels (Martínez-López *et al.* 2009), it is not surprising that raptor populations are negatively affected in areas where cotton is produced. Future studies need to further evaluate the relative importance of cotton production on the viability of the region's raptor populations. In the meantime, we stress the importance of a precautionairy and effective ban on the use of endosulfan and DDT, at least around West Africa's major protected areas, together with the introduction of environmentally sustainable cotton production (e.g. adopting integrated pest management, biopesticides, biological control) to replace current production practices.

Appendix to Chapter 8

Appendix 8.1. Estimated strip width (ESW) for large, medium-sized and small raptors (cf. Table 4), and separate for four common raptors in the three biogeographical zones of northern Cameroon, separated by habitat category. The number of individuals (*n* indicated) on 5-km segments, detection functions fitted to perpendicular distances, and cut-off values are presented. Segments were categorized based on the extent of natural habitat; 1: > 60% natural habitat on segment ("dense habitat"); 2: < 40% natural habitat ("open habitat").

Raptor group	**Biogeo-graphical zone**	**ESW (m)**	**95% CI**	**95% CI**	**Detection function**	***n***	**Cut-off (m)**
Inundation zone							
Large	1	227.95	203.06	255.89	uniform cosine	446	680
Large	2	269.96	233.34	312.34	half-normal cosine	237	680
Medium-sized	1	159.24	147.62	171.79	half-normal cosine	1614	500
Medium-sized	2	208.78	171.24	254.55	hazard rate polynomial	282	500
Small	1	167.83	148.86	189.23	hazard rate polynomial	286	500
Small	2	202.13	170.63	239.45	half-normal cosine	74	500
Sudan savanna							
Large	1	239.79	211.92	270.51	half-normal cosine	593	680
Large	2	198.32	174.99	224.77	hazard rate polynomial	861	680
Medium-sized	1	209.77	190.74	230.7	hazard rate polynomial	793	500
Medium-sized	2	177.88	161.97	195.35	half-normal cosine	478	500
Small	1	200.78	181.6	221.99	hazard rate polynomial	648	500
Small	2	200.96	181.33	222.72	hazard rate polynomial	457	500
Guinea savanna							
Large	1	265.44	247.38	284.81	half-normal cosine	343	680
Large	2	237.01	187.13	300.2	half-normal cosine	75	680
Medium-sized	1	189.12	172.4	207.46	half-normal cosine	435	500
Medium-sized	2	203.22	184.09	224.34	half-normal cosine	244	500
Small	1	193.62	169.4	221.31	hazard rate polynomial	310	500
Small	2	190.59	167.78	216.5	half-normal cosine	130	500
Dark Chanting Goshawk	1	199.46	159.66	249.18	half-normal cosine	43	500
Dark Chanting Goshawk	2	227.04	177.24	290.83	half-normal cosine	36	500
Grasshopper Buzzard	1	163.88	137.96	194.66	hazard rate polynomial	132	500
Grasshopper Buzzard	2	170.95	149.39	195.62	half-normal cosine	168	500
Fox Kestrel	1	176.9	136.77	228.8	half-normal cosine	33	500
Fox Kestrel	2	232.44	193.57	279.11	half-normal cosine	71	500
Shikra	1	110.56	86.549	141.23	half-normal cosine	36	500
Shikra	2	82.843	63.329	108.37	half-normal cosine	47	500