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Raptor habitat use in the Lake Chad Basin: insights into the effect of flood-plain transformation on Afrotropical and Palearctic raptors

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Summary

West African flood-plains have undergone major land-use transformations in the second half of the 20th century. To obtain insight in the effect of flood-plain development for irrigated rice cultivation on the abundance, richness, and diversity of Palearctic and Afrotropical raptors, we conducted monthly transect surveys covering dry and wet seasons in four major habitats on the Waza-Logone flood-plain of Cameroon: dry grasslands, cultivated grasslands, rice fields, and seasonally flooded grasslands resembling natural flood-plain vegetation. We recorded 36 raptor species among 2,533 individuals, dominated by Black Kite *Milvus migrans*, which comprised 42% of counts. Although richness and diversity were not related to land-use for Palearctic raptors, Afrotropical raptor diversity was higher on the flooded grasslands compared to the newly created cultivated habitats and dry grasslands. The abundance of Afrotropical raptors did not significantly differ across habitats but was lower in rice-fields when Black Kite and Hooded Vulture *Necrosyrtes monachus* were excluded. Conversely, Palearctic raptor abundance was highest in post-harvest rice fields, demonstrating the importance of the rice fields as foraging habitat for Palearctic raptors. Further transformation of West Africa's flood-plains is expected, reducing their capacity for Afrotropical raptors, while Palearctic raptors may benefit from expansion of rice-fields, but more research is needed on their vulnerability to pesticide use.

Résumé

Les plaines d'inondation de l'Afrique de l'Ouest ont subi d'importantes transformations dans la deuxième moitié du xxe siècle, notamment pour le développement de la culture du riz irrigué. Pour évaluer l'effet de ces transformations sur l'abondance, la richesse et la diversité des rapaces paléarctiques et africains, nous avons effectué des comptages mensuellement, couvrant les saisons sèches et humides dans quatre types d'habitats de la plaine du bas Logone, au nord Cameroun: les plaines sèches, les plaines cultivées, les rizières, et les plaines saisonnièrement inondées, ressemblant à la végétation originale. Nous avons enregistré 36 espèces de rapaces parmi 2,533 individus, dominés par *Milvus migrans*, qui représente 42% des effectifs. Bien que la richesse et la diversité n'étaient pas liée au type d'habitat pour les rapaces paléarctiques, la diversité des espèces africaines était plus élevée sur les plaines inondées par rapport aux habitats cultivés et aux plaines sèches. En plus, l'abondance des rapaces africains était plus faible dans les rizières quand *Milvus migrans* et *Necrosyrtes monachus* ont été exclus. Au contraire, l'abondance des rapaces paléarctiques était la plus élevée dans les rizières, montrant l'importance des champs de riz pour ce groupe en saison sèche et post-récolte. De nouvelles transformations des plaines inondées sont prévues, qui peuvent mener à la réduction de leur capacité d'acceuil pour les rapaces africains,

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tandis que les rapaces paléarctiques pourraient en bénéficier grâce à l'extension des rizières, mais plus de recherche est nécessaire sur leur vulnérabilité face à l'utilisation des pesticides.

Introduction

Raptors are generally recognised as being sensitive to environmental change triggered by anthropogenic causes (Sergio *et al.* 2006, 2008), but moderate habitat alteration may positively influence raptor diversity and abundance if it coincides with increased foraging and nesting availability (Rodríguez-Estrella *et al.* 1998, Sánchez-Zapata and Calvo 1999). However, increasingly rapid processes of urbanisation and agricultural intensification in developing countries may negate the adaptive response of raptors to semi-natural habitats created over longer periods by humans (Carrete and Donázar 2005). In West Africa, the seasonally flooded grasslands of the Senegal River Delta, the Inner Niger Delta, the Lake Chad Basin, and their associated river systems are prime examples of habitats which have been rapidly and dramatically altered by developments aimed at fulfilling the needs of growing human populations (Zwarts *et al.* 2009). Embanking many West African flood-plains in the second half of the 20th century for the development of rice irrigation schemes preceded the conversion of highly productive, seasonally inundated grasslands into semi-natural habitats dominated by desiccated grasslands, cultivated fields, and human habitation. Such developments severely impacted flood-plain dynamics, significantly depressing their productivity and associated wildlife populations (Loth 2004, Zwarts *et al.* 2009). Raptors were correspondingly affected, their declines in the West African inundation zones being among the most severe in a vast region of central West Africa between 1973 and 2004 (Thiollay 2001, 2006).

Despite the great importance of West Africa's flood-plains and their associated cultivated habitats to raptor populations, particularly Palearctic raptors (Thiollay 1989), their utilisation by raptors has been relatively little studied (Thiollay 1978, Zwarts *et al.* 2009). In the absence of studies on habitat use, it is unclear how habitat transformation of flood-plains may have impacted Afrotropical and Palearctic raptors. Our aim here was to examine habitat use by raptors on the Waza-Logone flood-plain in northern Cameroon, in order to evaluate the effect of flood-plain habitat modification on the abundance, diversity and richness of Afrotropical and Palearctic raptor assemblages. Since distribution patterns of raptor populations in West Africa are highly dynamic due to almost continuous displacement in response to seasonal rains and changes in prey availability (Thiollay 1989), our assessment included monthly counts incorporating dry and wet seasons. Based on previous findings (Thiollay 2001, 2006, Anadón *et al.* 2010), we predicted that the habitats least affected by development and human exploitation, i.e. seasonally flooded grasslands and dry, protected grasslands, are preferred over cultivated habitats by Afrotropical raptors, indicated by their greater abundance, diversity and richness. Conversely, Palearctic raptors have been shown to be generally less sensitive to human exploitation, readily foraging over disturbed and cultivated habitats (Herremans and Herremans-Tonnoeyr 2000, Buij *et al.* 2012, Limiñana *et al.* 2012). For this reason, the abundance, diversity and richness of Palearctic raptors was expected to be greater in transformed grasslands with sorghum- and rice-fields, which harbour abundant and easily accessible rodent prey (Poulet 1985, Buij *et al.* 2012), compared to flooded or dry grasslands.

Methods

Study area

The study area was situated in the Waza-Logone flood-plain of the Far North of Cameroon, in the inundation zone of the Logone River, which is part of the more extensive Lake Chad Basin (10°15′N-11°55′N and 14°24′E-15°15′E; Figure 1). The Waza-Logone flood-plain is located in the transition zone between the Sudan and Sahel climatic zones in Cameroon and encompasses desiccated and flooded grasslands, open savanna woodland, and cultivation, notably rice and dry-season sorghum. The area was designated a Wetland of International Importance by the Ramsar Convention in 2006, for its important wildlife concentrations including migratory and African wetland birds.

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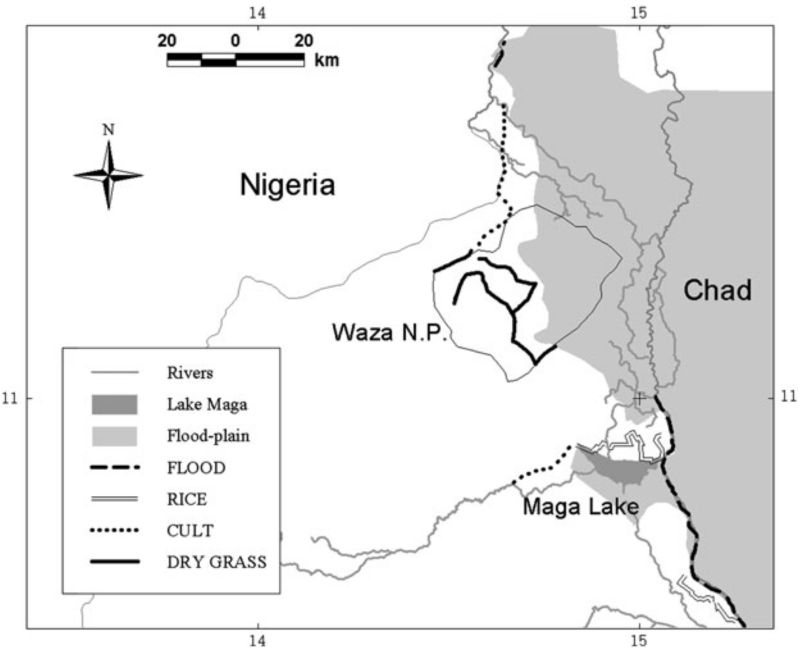

Figure 1. Location of roads used for transect surveys in the Lake Chad Basin of northern Cameroon.

Part of the flood-plain is protected in the Waza National Park, proclaimed as Biosphere Reserve in 1979 (WCMC 1983). Lake Maga, an artificial wetland resulting from the construction of the Maga dam, the Logone flood-plains and Waza National Park are Important Bird Areas (BirdLife International 2012a,b,c). The climate is semi-arid, with rains peaking between June and September (c.500-600 mm *per annum*).

The flood-plains are situated along the Logone River, largely east and north of Waza National Park, with a surface area of 8,000 km^2 in Cameroon. The inundation in the Waza-Logone flood-plain extends from August to November in average years, and duration, depth and extent of flooding is much lower during dry years (Scholte *et al.* 2000). An earthen dam was constructed along the Logone River in 1979 to allow the development of a rice irrigation scheme with 70 km^2 of rice-fields, reducing flooding on 1,500 km^2 of the flood-plain. The negative impact on the ecology of the plains, its grass species composition and biomass, herbivore and bird populations was partly rectified in 1994 through the breaching of the dam just north of the rice-fields (Loth 2004). The ecological success from the partial re-flooding of the desiccated plains triggered human immigration into the area, leading among other things to a threefold increase in livestock numbers (Scholte 2003). The dry plains are used for sorghum cultivation in the dry season (October–March), when rice-fields are mostly inactive, partly burnt, and grazed by livestock. The flood-plains are home to antelope populations, such as kob *Kobus kob* and topi *Damaliscus korrigum*, mostly inside the national park. Since the mid-1960s their numbers have declined by 94% and 96%, respectively, following droughts, the damming of the Logone River, and, more recently, poaching inside the park.

Habitat types

To obtain insight into the effect of flood-plain transformation on the abundance, richness, and diversity of Palearctic and Afrotropical raptors, we conducted surveys along transects in four major flood-plain

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habitat types. Landsat MSS satellite images in combination with field observations were used to distinguish between major habitat types differing in degree of transformation and productivity:

1) Dry grasslands (DRY GRASS). Largely desiccated flood-plain with woodlands on higher ground, located entirely inside Waza National Park. The habitat is dominated (95%) by *Sclerocarya birrea* on higher ground and *Acacia seyal* on black clay soils which become saturated with water during the rainy season and which are covered in annual herbs and grasses such as *Sorghum arundinaceum*. Sections of the habitat (2–25%) are still inundated from August to November but the area affected by inundation and the depth of floodwaters declined considerably with the construction of the Lake Maga dam. Numerous artificial and natural waterholes surrounded by *Tamarindus indica* and *Balanites aegyptiaca* trees hold water until the second half of the dry season;
2) Cultivated grasslands (CULT). Located outside the park. Similar habitat as above, a desiccated flood-plain dominated by *Acacia seyal* trees and numerous pools surrounded by stands of *Tamarindus indica* and *Balanites aegyptiaca*, and some flooded areas during the wet season. Wood cutting has reduced woody plant cover, notably *Acacia seyal*. This area is interspersed by traditionally cultivated dry-season sorghum in so-called "*karal* fields" (c.30% of total land cover), and few villages;
3) Irrigated rice-fields (RICE). Located north of the Lake Maga dam and along the Logone River, rice fields make up >85% of the surveyed habitat. The area is no longer subject to seasonal flooding. Reedbeds (*Typha*), small shrubs (*Mitragyna*, *Acacia*, *Ziziphus*) and annual grasses and herbs fringe the lake and the network of canals that border the irrigated rice-fields. Scattered *karal* fields remain in between the rice-fields (< 0.05% of the surface area). Rice is cultivated biannually, in April–June and August–October, and harvested in June and October. Rice-fields are largely dry between October and March, when fires and grazing further reduce the remaining rice stubble and sparse herbaceous cover. Most trees have been removed to prevent breeding of Red-billed Queleas *Quelea quelea* apart from stands of *Azadirachta indica* and *Eucalyptus* around numerous villages and a few palms (*Hyphaene thebaica*, *Borassus aethiopum*), larger *Acacia* and *Faedherbia albida* trees;
4) Seasonally flooded grasslands (FLOOD). The habitat is dominated (65%) by grassy plains, which are partly flooded from August to November and covered with perennial grasses such as *Echinochloa pyramidalis*, *Oryza longistaminata*, *Hyparrhenia rufa* and *Vetiveria nigritana* (Scholte *et al.* 2000). Part of the habitat (c.35%) consists of raised and non-flooded areas with mature *Faedherbia albida*, *Hyphaene thebaica* and *Borassus aethiopum* among small-scale cultivation and scattered human settlements (permanent and temporary).

Survey methods

Raptor surveys were performed along ten transects of 2 km each, totalling 20 km in each of the four major habitat categories (Figure 1). First, the entire road network in the study area was mapped, after which dirt and tar roads which were known to be navigable for at least 10 months of the year were selected. In all habitats 70–90 km of navigable roads were identified. To reduce auto-correlation between them, transects were allocated in each habitat type using randomly generated GPS locations on the navigable road network in ArcView GIS 3.2 software (ESRI 1999) and the linear distance from the end of one transect to the start of the next was held at min 2 km and max 4 km. As raptor habitat utilisation is likely to vary seasonally due to effects of cultivation, grazing, floods, fires, and rains, surveys were repeated at monthly intervals, and each transect was surveyed once per month between October 2007 to July 2008 for a total of 10 surveys for each transect (i.e. 800 km driven in total). Surveys were conducted during the first ten days of each month and consisted of a combination of road surveys from a driving vehicle, and spot counts to assess raptor presence along transects, with the two observers each scanning one side of the transect.

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While road surveys have proven useful for comparisons of raptor community composition between habitats (Fuller and Mosher 1981, Bibby *et al.* 1992), they were combined with spot counts because these enhance detectability of raptors hunting on the wing (Herremans and Herremans-Tonnoeyr 2000). We incorporated a 3-min spot count halfway along each 2-km transect, during which both observers scanned for raptors. To standardise count efforts, the total time spent surveying a 2-km transect was held at c.15 min. Surveys were conducted only in fine weather, i.e. clear or slightly cloudy skies with low to moderate winds, starting at 06h30 to 07h30 depending on the season (and the increase in air temperature). Transect surveys for a single habitat type were always conducted within three hours including time to traverse distances between transects, thus covering peak activity hours of all recorded species. All diurnal raptors perched or flying within eyesight range, on either side of the road and during spot counts were recorded with a GPS and identified with 10 x 42 binoculars. GPS positions were taken of birds perpendicular to the transect line, thus raptors detected beyond either end of the transect were not included. The perpendicular distance from the road to each perched or flying raptor at the location of initial detection was measured with a calibrated rangefinder, which enabled estimation of the effective strip width (ESW; Buckland *et al.* 1993) to evaluate potential differences in raptor detectability between habitat categories which would confound comparisons of relative abundance between habitats. To examine changes in herbaceous cover which affects foraging site selection in raptors by influencing prey accessibility (Preston 1990), the percentage cover of the rooted herbaceous vegetation along transects was characterised at 1-km intervals using a nested 2-ha plot centred on the road.

Palearctic and Afrotropical raptors

Data were pooled for Palearctic migrants and Afrotropical species according to the breeding range of the majority of individuals making up the populations in the region (Thiollay 1977). Palearctic migrants are species which breed in Eurasia or Northern Africa and spend the Palearctic non-breeding season in sub-Saharan Africa (juveniles of various species also spend the northern breeding season in the Sahel; Thiollay 1977). Afrotropical species were recorded in the area during a large part of the year (timing different per species) and many were recorded breeding, including those species with long- (e.g. Wahlberg's Eagle *Aquila wahlbergi*; Meyburg *et al.* 1995) and short-distance seasonal displacements (Grasshopper Buzzard *Butastur rufipennis*), and/or nomadic movements (e.g. Black-winged Kite *Elanus caeruleus*; Thiollay 1977). Black Kite *Milvus migrans* populations were composed of Afrotropical Yellow-billed Kites (*M. m. parasitus/aegyptius*; Johnson *et al.* 2005) and Palearctic Black Kites (*M. m. migrans*) and the two races could not be safely distinguished most of the time. However, the majority of individuals identified ($> 98\%$) referred to *M. m. parasitus/aegyptius* and Black Kite was therefore treated as an Afrotropical raptor.

Data analysis

To determine whether detectability of raptors differed between habitat categories, we calculated ESW for raptors in each habitat category using Distance 6.0 software (Thomas *et al.* 2006). Raptors were grouped into three size categories based on mean adult body mass (small: < 300 g, medium: 300–800 g, large: > 800 g; Ferguson-Lees and Christie 2001) assumed to have approximately comparable detectability. To determine ESW separately for each raptor size category, six combinations of key functions with expansion series were used to model the detection functions: the half-normal key function with cosine and hermite polynomial adjustment terms, the hazard-rate key function with cosine and simple polynomial, and the uniform key function with cosine and simple polynomial. Following Buckland *et al.* (1993), models with the lowest Akaike Information Criterion (AIC) value were selected for estimation of ESW and significant differences of ESW between habitats for each size category were based on overlap of 95% confidence intervals.

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For comparing richness and diversity of the raptor assemblage between habitat categories, we used sample-based rarefaction, which allowed for the statistically robust comparisons based on equivalent numbers of individuals and samples (Colwell *et al.* 2004). Sample-based rarefaction computes the expected number of species when samples are drawn at random (without replacement) from a set of samples that are collectively representative of an assemblage (Gotelli and Colwell 2001). We used the cumulative species number on the 2-km transects (n = 10 in each category) as our units of replication. The Mao Tau estimator of rarefied species richness (Mao *et al.* 2005) was used to compute rarefaction curves in EstimateS Version 8.0 software (Colwell 2006). Samples were randomised 50 times for each dataset. We standardised comparisons by comparing expected species numbers at equal effort (i.e. similar number of individuals observed; Gotelli and Colwell 2001). Differences in species diversity were compared in EstimateS using Shannon diversity estimates, which weighs species proportionately to their frequencies in the sample rather than favouring common or rare species such as species richness or other diversity indices (e.g. Simpson's index; Jost 2006). We used sampling with replacement which allowed estimation of confidence intervals and comparisons of diversity between habitats sampled at equal effort. The criterion used to determine whether the richness and diversity estimations were significantly different ($P < 0.05$) was the absence of overlap among the 95% confidence intervals for richness estimates (Colwell *et al.* 2004).

Generalized Estimated Equations (GEEs) with binomial errors were used to analyse the distribution of the most common species among the four main habitat types in SPSS 19.0 (SPSS Inc, Chicago, IL). GEEs are an extension of Generalized Linear Models that allow the analysis of correlated data arising from repeated measures (in the binomial model: monthly species presence on 2-km transect segments; Hardin and Hilbe 2003). Thus, habitat (four categories: DRY GRASS, CULT, RICE, FLOOD) was fitted as the predictor variable and binomial presence data for each species as dependent variables. The 2-km segments in each habitat category were taken as subject variables with months (n = 10) as within-subject variables. We specified independent or first-order autoregressive (AR-1) covariance types to account for potential temporal autocorrelation between subsequent transect surveys. Apart from binomial models to test species presence, we investigated associations between habitat and the abundance of all raptors, Afrotropical raptors, and Palearctic raptors on 2-km transects using GEEs with Poisson and Negative Binomial errors and log link functions. Final model selection was based on quasi-likelihood under the independence model criterion (QIC; Hardin and Hilbe 2003). Differences between habitats for all models were tested using pair-wise comparisons in GEE and considered significant at $P < 0.05$ but adjustments were made for Type I error using Bonferroni correction. Kruskal-Wallis tests were used to explore differences in mean monthly grass cover values between the four main habitat types. For all analyses, tests are two-tailed and statistical significance was set at $\alpha < 0.05$.

Results

In total 36 species were recorded during surveys (Table 1). Thirty-six percent of those (13 species) were Palearctic migrants, which constituted 19% of the total number of raptors observed (n = 2,533). Black Kites, which included only a small percentage of Palearctic origin (Table 1), comprised 42% of all raptors and 51% of Afrotropical raptors detected. Other common raptors were Hooded Vulture *Necrosyrtes monachus* (11% of total numbers), Grasshopper Buzzard (9%), and Western Marsh-harrier *Circus aeruginosus* (8%). Species diversity had clear patterns related to habitat categories only for Afrotropical raptors (Figure 2a), with a significantly higher diversity on seasonally flooded grasslands compared to other habitats. Grass cover also differed between habitat categories (χ^2_3 = 8.48, $P < 0.05$), and was significantly higher in the floodplain than in the other habitats. Conversely, Palearctic raptor diversity and diversity of the entire raptor assemblage did not differ significantly across habitats. Further, no significant differences in species richness were recorded between habitat categories for overall, Afrotropical, and Palearctic raptor richness (Figure 2b).

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Table 1. Total number of raptors detected on 10 2-km transects surveyed at monthly intervals between October 2007 and July 2008 in the partly cultivated grasslands (CULT), dry grasslands (DRY GRASS), rice-fields (RICE), and seasonally flooded grasslands (FLOOD). Numbers are presented separately for the wet (four counts; May-Oct) and dry season (six counts; Nov-April).

	CULT		DRY GRASS		RICE		FLOOD		
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Total
Palearctic raptors									
Western Marsh-harrier *Circus aeruginosus*	13	13	18	8	94	3	49	0	198
Booted Eagle *Hieraaetus pennatus*	7	0	11	0	62	0	11	0	91
Common Kestrel *Falco tinnunculus*	16	0	11	0	13	0	5	0	45
Steppe Eagle *Aquila nipalensis*	1	0	3	0	33	0	3	0	40
Long-legged Buzzard *Buteo rufinus*	2	0	1	0	20	0	3	0	26
Montagu's Harrier *Circus pygargus*	6	0	3	0	12	0	5	0	26
Pallid Harrier *Circus macrourus*	2	0	2	1	16	0	1	0	22
Short-toed Snake-eagle *Circaetus gallicus*	3	1	6	0	5	0	2	0	17
Lesser Kestrel *Falco naumanni*	2	0	2	0	0	0	0	0	4
Osprey *Pandion haliaetus*	0	0	0	0	1	0	3	0	4
Barbary Falcon *Falco pelegrinoides*	2	0	0	0	0	0	0	0	2
Red-footed Falcon *Falco vespertinus*	0	1	0	0	0	0	0	0	1
Egyptian Vulture *Neophron percnopterus*	0	0	1	0	0	0	0	0	1
Afrotropical raptors									
Black Kite *Milvus migrans*[1]	191	22	299	45	388	3	78	27	1053
Hooded Vulture *Necrosyrtes monachus*	1	0	0	1	15	3	170	91	281
Grasshopper Buzzard *Butastur rufipennis*	97	66	43	28	1	0	4	0	239
Dark Chanting-goshawk *Melierax metabates*	9	2	16	3	10	12	35	25	112
White-backed Vulture *Gyps africanus*	1	0	3	0	1	0	37	18	60
African Swallow-tailed Kite *Chelictinia riocourii*	13	1	39	0	1	0	3	0	57
Black-winged Kite *Elanus caeruleus*	2	1	7	1	22	8	5	10	56
Tawny Eagle *Aquila rapax*	4	3	12	5	2	1	4	3	34
Gabar Goshawk *Micronisus gabar*	3	2	5	2	0	4	10	8	34
Lanner Falcon *Falco biarmicus*	13	4	6	3	1	0	0	2	29
Wahlberg's Eagle *Aquila wahlbergi*	0	1	3	5	5	3	10	0	27
Red-necked Falcon *Falco chicquera*	1	0	1	0	4	1	11	9	27
Rueppell's Vulture *Gyps rueppellii*	0	0	0	2	2	0	7	1	12
African Fish-eagle *Haliaeetus vocifer*	0	0	6	2	0	0	1	1	10
Bateleur *Terathopius ecaudatus*	0	0	2	6	0	0	2	0	10
Long-crested Eagle *Lophaetus occipitalis*	0	1	1	0	0	1	3	0	6
Shikra *Accipiter badius*	0	0	1	1	0	0	1	0	3
Beaudouin's Snake-eagle *Circaetus beaudouini*	1	0	0	0	0	0	0	0	1
Brown Snake-eagle *Circaetus cinereus*	0	0	0	1	0	0	0	0	1
Grey Kestrel *Falco ardosiaceus*	0	0	0	0	0	0	0	1	1
African Harrier-hawk *Polyboroides typus*	1	0	0	0	0	0	0	0	1
Secretarybird *Sagittarius serpentarius*	0	0	0	0	0	0	0	1	1
Lappet-faced Vulture *Torgos tracheliotus*	0	0	1	0	0	0	0	0	1
Total individuals	391	118	503	114	708	39	463	197	2,533
Species number	23	13	26	16	21	10	25	13	36

[1]A proportion of Black Kites *Milvus migrans* (c.1–2% of numbers between October-March) was identified as the Palearctic subspecies *migrans*, the bulk constituted by the Afrotropical subspecies *M. m. parasitus/ aegyptius* (Yellow-billed Kite).

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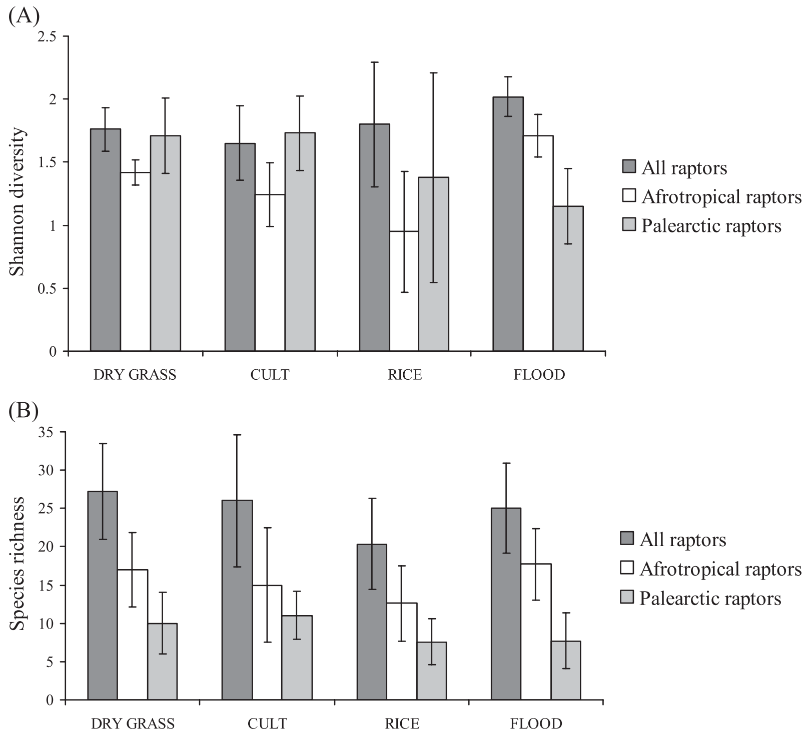

Figure 2. Raptor diversity and richness in four habitat types on the Waza-Logone flood-plain. Shannon diversity indices (A) and species richness (B) are presented for all raptors, Afrotropical raptors, and Palearctic raptors. Indices were estimated at equal sampling effort. Values are presented with 95% CIs.

Prior to examinations of species-habitat associations, estimation of ESW using Distance 6.0 showed these did not significantly differ ($P < 0.05$) between the four habitat categories for the three raptor size categories, dismissing the need for corrections of relative abundance estimates due to differences in detectability between habitats. GEE model results indicated that raptor abundance did not differ among habitats for the 10-month survey period ($\chi^2_3 = 1.81$, $P = 0.61$), which remained the case when the most abundant species, Black Kite and Hooded Vulture, to a different degree commensal with humans, were excluded from the analysis. Also, the abundance of Afrotropical species did not differ among habitats ($\chi^2_3 = 1.16$, $P = 0.76$). However, Afrotropical raptors were significantly less abundant in rice-fields compared to other habitats when Black Kite and Hooded Vulture were excluded ($\chi^2_3 = 32.7$, $P < 0.001$). Conversely, Palearctic migrants were significantly more abundant in rice-fields compared to other habitats ($\chi^2_3 = 51.8$, $P < 0.001$). This was mirrored by species-specific binomial models for most common Palearctic migrants (Table 2), although no significant habitat effect on presence was detected for Montagu's Harrier *Circus pygargus* ($\chi^2_3 = 3.87$, $P = 0.27$), Common Kestrel *Falco tinnunculus* ($\chi^2_3 = 4.30$, $P = 0.23$), and Short-toed Snake-eagle *Circaetus gallicus* ($\chi^2_3 = 3.19$, $P = 0.36$). Raptors significantly associated with rice-fields over other habitats (Table 2) were regularly observed capturing rodents (*Arvicanthis* spp. and *Mastomys* spp.). Inspection of the combined monthly counts for these five Palearctic migrants showed that rice-fields were favoured from November (Figure 3), corresponding with a decrease in herbaceous cover. Monthly counts appeared to follow a similar

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Table 2. Relationship between raptor presence and habitat, for (A) Afrotropical and (B) Palearctic raptors. Generalized Estimating Equations with binomial errors and a logit link function were used with habitat (four categories: CULT: cultivated grasslands; DRY GRASS: dry grasslands; RICE: rice fields; FLOOD: flood-plain) fitted as predictor variable and binomial presence data for each species as dependent variables. Model fit and mean differences between habitat categories are presented after pairwise comparisons and Bonferroni correction for Type I errors. Only species for which habitat was significantly associated ($P < 0.05$) with presence are reported.

(A)

(I) habitat	(J) habitat	Black Kite		Grasshopper Buzzard		Dark Chanting-goshawk		White-backed Vulture		Black-winged Kite	
		(I-J)	SE	(I-J)	SE	(I-J)	SE	(I-J)	SE	(I-J)	SE
CULT	DRY GRASS	-0.22**	0.06	0.08	0.07	-0.09	0.05	-0.01	0.02	-0.03	0.03
	RICE	0.02	0.06	0.40***	0.05	-0.08	0.04	0.00	0.01	-0.17***	0.04
	FLOOD	0.04	0.06	0.37***	0.05	-0.32***	0.06	-0.15**	0.04	-0.05	0.02
DRY GRASS	RICE	0.24***	0.06	0.32***	0.06	0.01	0.05	0.01	0.02	-0.14**	0.04
	FLOOD	0.26***	0.06	0.29***	0.06	-0.23*	0.08	-0.14*	0.04	-0.02	0.03
RICE	FLOOD	0.02	0.06	-0.03	0.02	-0.24**	0.06	-0.15**	0.04	0.12*	0.04
	Model fit	$\chi^2_3 = 26.2$, $P < 0.001$		$\chi^2_3 = 54.6$, $P < 0.001$		$\chi^2_3 = 27.4$, $P < 0.001$		$\chi^2_3 = 21.2$, $P < 0.001$		$\chi^2_3 = 21.7$, $P < 0.001$	

(I) habitat	(J) habitat	Gabar Goshawk		Lanner Falcon		Red-necked Falcon		Hooded Vulture	
		(I-J)	SE	(I-J)	SE	(I-J)	SE	(I-J)	SE
CULT	DRY GRASS	0.00	0.02	0.03	0.04	0.00	0.01	0.00	0.01
	RICE	0.03	0.02	0.11**	0.03	-0.03	0.02	-0.08***	0.02
	FLOOD	-0.06	0.03	0.11**	0.03	-0.13***	0.02	-0.49***	0.06
DRY GRASS	RICE	0.03	0.02	0.08**	0.02	-0.03	0.02	-0.08***	0.02
	FLOOD	-0.06	0.03	0.08**	0.02	-0.13***	0.02	-0.49***	0.06
RICE	FLOOD	-0.09*	0.03	0.00	0.01	-0.10**	0.03	-0.41***	0.06
	Model fit	$\chi^2_3 = 8.47$, $P < 0.05$		$\chi^2_3 = 12.8$, $P < 0.01$		$\chi^2_3 = 23.2$, $P < 0.001$		$\chi^2_3 = 79.8$, $P < 0.001$	

(B)

(I) habitat	(J) habitat	Pallid Harrier		Booted Eagle		Western Marsh-harrier		Long-legged Buzzard		Steppe Eagle	
		(I-J)	SE	(I-J)	SE	(I-J)	SE	(I-J)	SE	(I-J)	SE
CULT	DRY GRASS	0.00	0.02	-0.04	0.03	0.00	0.04	0.01	0.02	-0.02	0.02
	RICE	-0.07*	0.03	-0.24***	0.04	-0.22***	0.04	-0.12***	0.03	-0.15**	0.04
	FLOOD	0.01	0.02	-0.04	0.02	-0.05	0.05	0.00	0.02	-0.01	0.02
DRY GRASS	RICE	-0.07*	0.03	-0.20***	0.04	-0.22***	0.04	-0.13***	0.03	-0.13**	0.04
	FLOOD	0.01	0.02	0.00	0.03	-0.05	0.05	-0.01	0.02	0.01	0.02
RICE	FLOOD	0.08**	0.02	0.20***	0.04	0.17***	0.05	0.12***	0.03	0.14**	0.04
	Model fit	$\chi^2_3 = 12.5$, $P < 0.01$		$\chi^2_3 = 51.5$, $P < 0.001$		$\chi^2_3 = 34.4$, $P < 0.001$		$\chi^2_3 = 23.2$, $P < 0.001$		$\chi^2_3 = 19.1$, $P < 0.001$	

***$P < 0.001$.
**$P < 0.01$.
*$P < 0.05$.

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pattern on flooded grasslands, although numbers were lower here compared to rice-fields. In comparison, numbers of these Palearctic migrants peaked earlier in the dry season in cultivated and dry grasslands, which experienced a strong decline in herbaceous cover early in the dry season (Oct–Dec), compared to rice-fields and flooded grasslands (Figure 3).

Habitat associations for common Afrotropical raptors were more variable compared to Palearctic raptors (Table 2). Seasonally flooded grassland was favoured by generalists (Dark Chanting-goshawk *Melierax metabates*), bird specialists (Gabar Goshawk *Micronisus gabar*, Red-necked Falcon *Falco chicquera*), and vultures (White-backed *Gyps africanus* and Hooded Vulture). Conversely, dry and cultivated grasslands were more attractive than flooded grasslands and rice-fields to Lanner Falcon and Grasshopper Buzzard (Table 2), whereas Black Kite was more strongly associated with dry grasslands than other habitats. Distribution patterns for Tawny Eagle *Aquila rapax* (χ^2_3 = 5.92, P = 0.12), Wahlberg's Eagle (χ^2_3 = 3.45, P = 0.33), and African Swallow-tailed Kite *Chelictinia riocourii* (χ^2_3 = 2.56, P = 0.46) were indifferent to land-use. The Black-winged Kite, a rodent specialist, was the only Afrotropical species with a preference for rice-fields (Table 2), and at least three pairs were recorded breeding in *Faedherbia albida* trees in rice-fields.

Discussion

Our data revealed a strikingly different distribution pattern in terms of abundance of Afrotropical and Palearctic raptors with regard to rice-fields, which were generally avoided by Afrotropical raptors but preferred by Palearctic raptors. The attractiveness of rice-fields to Palearctic raptors augments reports of raptors converging on post-harvest rice-fields in Europe (Boano and Toffoli 2002, Lourenço 2009), Asia (Fujioka *et al.* 2010), and the Americas (Remsen *et al.* 1991, Petit *et al.* 1999, Elphick 2004, Pandolfino *et al.* 2011). Evidently, the attractiveness of different habitat types may shift over the course of the winter season (cf. Figure 3), and the accessibility of rodents in rice-fields increased from November with decreasing herbaceous cover. Rodents are similarly common in sorghum fields (Buij *et al.* 2012), but these were localised in dry, unproductive grasslands, probably lowering their attractiveness to Palearctic raptors compared to rice-dominated

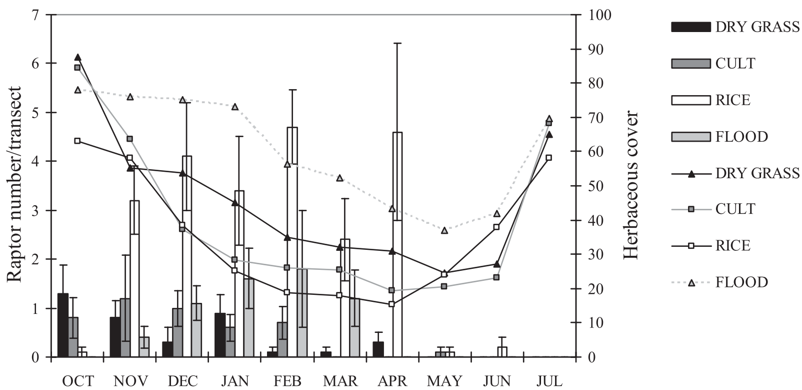

Figure 3. Mean raptor numbers ± SE on 2-km transects of five Palearctic raptors (Booted Eagle, Western Marsh-harrier, Steppe Eagle, Long-legged Buzzard, Pallid Harrier) favoring rice cultivation (RICE) over cultivated grassland (CULT), dry grassland (DRY GRASS), and seasonal flood-plains (FLOOD), from October 2007 to July 2008 in the Waza-Logone flood-plain of northern Cameroon. Lines represent the mean herbaceous layer cover on 2-km transects in each of four habitat categories during the same period.

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habitats. Intensive tree-pruning, logging, and human exploitation of tree-lined canals for fishing and bushmeat (rats, frogs) leading to high levels of human disturbance detrimental to breeding raptors (Newton 1979), explained the lack of suitability of rice-fields to Afrotropical raptors. Furthermore, rice-fields were flooded and cultivated from April, well before the arrival of the seasonal floods (August–September), limiting prey accessibility for sedentary raptors during an eight month period. Interestingly, Black-winged Kites, which are known to profit from rodent outbreaks with prolonged or variable breeding seasons (Ferguson-Lees and Christie 2001) and prefer cultivated landscapes with few trees for breeding (Balbontin *et al.* 2008), were the only raptors breeding among rice-fields and the only Afrotropical raptor species which increased in the area following irrigation rice scheme development (Thiollay 2001).

The situation on the original flood-plain, with its abundant wildlife and prey resources, may not be duplicated today, since the diminished productivity of the former grasslands were only partially compensated by flood-plain rehabilitation (Scholte 2005). At the same time, growing human populations, increased livestock numbers, and agricultural expansion have greatly intensified pressure on natural resources in the area (Scholte 2003), with potentially important consequences for raptor prey resources. In the absence of the original habitat, we focused our comparison on existing habitats, including the habitat most resembling the original flood-plain. This habitat differed from the newly created cultivated habitats and dry grasslands by a significantly higher grass cover, which is among the most important determinants of prey availability and foraging distribution of many raptors (Thiollay 1978), and characterised the original flood-plain (Scholte *et al.* 2000). The surveyed flood-plain habitat thus retained an essential component of the original grasslands, at least to foraging raptors, justifying our comparisons.

Our results revealed a greater diversity of Afrotropical raptors on the flood-plain compared to the newly created cultivated habitats and dry, protected grasslands, underlining the importance of the flood-plain to raptors. We found a preference for flood-plain habitat by five Afrotropical raptors, three of which (Dark Chanting-goshawk, White-backed Vulture, Hooded Vulture) declined significantly in the area between 1973 and 2000 (Thiollay 2001), while two others (Gabar Goshawk, Red-necked Falcon) were either too infrequently recorded to evaluate population trends, or remained stable. Although wide-ranging vultures (Kendall and Virani 2012) are likely to have been affected by practices that affected the wider region (e.g. traditional medicine trade; R. Buij, unpubl. data), these results suggest that the observed raptor declines might have at least partly been related to flood-plain embankment, which greatly reduced the extent of flood-plain habitat.

Contrary to expectations, Afrotropical raptor abundance, richness and diversity on the dry, protected grasslands was comparable to the cultivated grasslands, suggesting that the moderately affected cultivated grasslands still supported suitable habitat for many raptors. However, species-specific models did show variable responses, e.g. Black Kite preferred protected, dry grasslands over cultivated grasslands, whereas Lanner Falcon and Grasshopper Buzzard equally preferred dry and cultivated grasslands. These discrepancies corresponded to differences in long-term population trends between Black Kite populations (strong decrease; Thiollay 2001), and Lanner Falcon and Grasshopper Buzzard (stable), perhaps pointing to differences in species-specific sensitivity to anthropogenic impact. The observed preference for dry grasslands over flood-plain by Black Kite, Grasshopper Buzzard, and Lanner Falcon may be related to limitations on the number of breeding sites and prey availability on the flood-plain. Grasshopper Buzzard and Black Kite breed during the transition from the dry to wet seasons (March–July; R. Buij, unpubl. data) and require adequate tree cover for nesting, thus favouring well-wooded dry grasslands over the partly treeless flood-plain. In addition, prey accessibility is compromised when grass cover is high (Thiollay and Clobert 1990), as is the case during much of the year on the flood-plain.

Implications for flood-plain management

Despite their importance to Palearctic and Afrotropical birds and wildlife in general (Zwarts *et al.* 2009), only a small proportion of the West African flood-plains have received protected status.

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Waza National Park protects < 10% (700 km^2) of the Waza-Logone flood-plain, while regional protection of other flood-plain systems is limited to Djoudj and Diawling National Parks in the Senegal River Delta and various small reserves in Nigeria, Chad, and Mali. As a result, flood-plains have been vulnerable to development initiatives, and rice irrigation schemes have become a common feature of flood-plains over the past 50 years (Zwarts *et al.* 2009). During this period, the area planted with rice increased from 4,000 to 31,000 km^2 in six Sahelian countries with large flood-plain systems (FAOSTAT 2012) and such growth is not likely to stop any time soon (Zwarts *et al.* 2009). Their convergence on rice-fields implies that Palearctic migrants are vulnerable to aspects pertaining to the management of the rice-fields. Firstly, any positive effect of increased prey availability can be drastically altered by changes to the flooding regime, which may negatively affect the abundance and richness of raptors (Elphick 2004). Secondly, application of harmful pesticides in rice is hardly supervised and likely to affect raptors through secondary poisoning (Mullié *et al.* 1991), as reported from neighbouring Chad (Keith and Bruggers 1998), but little is known about pesticide impact on raptors in the region. Deliberate, large-scale poisoning of birds for food, as reported in some East African rice schemes (Odino 2010), has not been observed in Cameroon. However, poisoning of small waterholes, already reported from the region in the 1970s (Green and Sayer 1979), is a frequently used method to harvest birds (particularly passerines) for consumption, and also kills raptors (R. Buij pers. obs.). An important recommendation emanating from this study would be a strict ban on the use of pesticides highly toxic to birds from rice fields. Instead, raptors could be promoted as valuable predators of crop-pests and assisted through supplementation of perches (Sheffield *et al.* 2001).

Habitat quality for Afrotropical raptors is further affected by the intensive exploitation of the Waza-Logone flood-plains and surrounding woodlands, where human disturbance, wood extraction and tree pruning progressively limit nest site availability. Poaching in Waza National Park has been on the increase since the late 1990s and has decimated large wildlife populations (De Iongh *et al.* 2009), to the detriment of shy scavengers (e.g. Tawny Eagle, Bateleur *Terathopius ecaudatus*). Raptors are poached for meat and persecuted for trade (R. Buij, unpubl. data), which has contributed to declining vulture and possibly Secretarybird *Sagittarius serpentarius* populations. Flood-plain rehabilitation triggered a 34% increase in sedentary fishermen in two years who intensively utilise the fish resources in the park (Scholte 2003), which together with the reduced flooding extent led to declining fish stocks, weakening the prey base for the few remaining African Fish-eagle *Haliaeetus vocifer* pairs in the far north. Limitations to any of these exploitative utilisations will benefit raptor populations and other wildlife using the flood-plains, underlining the importance for improved protection of Waza National Park and restrictions on developments that stimulate further human immigration into the area.

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