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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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Citation

Buij, R. (2013, January 24). *Raptors in changing West African savannas : the impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon*. Retrieved from https://hdl.handle.net/1887/20446

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Author: Buij, Ralph
Title: Raptors in changing West African savannas : the impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon
Issue Date: 2013-01-24

Raptors in changing West African savannas

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Cover photos (front: Grasshopper Buzzard, back: Pallid Harrier): Ralph Buij
Photos: Ralph Buij
ISBN: 978-90-6464-626-3

Raptors in changing West African savannas

The impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon

PROEFSCHRIFT

ter verkrijging van de graad van Doctor aan de Universiteit Leiden,
op gezag van de Rector Magnificus Prof. mr. P.F. van der Heijden,
volgens het besluit van het College voor Promoties
te verdedigen op donderdag 24 januari 2013
klokke 16.15 uur

Ralph Buij

geboren te Eindhoven
in 1976

Promotiecommissie:

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Table of Contents

Chapter 1	Introduction	7
Chapter 2	Inter- and intraspecific differences in habitat use and conservation implications for Palearctic harriers on the core Sahelian wintering grounds	19
Box A	Pallid Harrier bird hunting behaviour and capture success in northern Cameroon	41
Chapter 3	Breeding biology and nestling development of the Grasshopper Buzzard	53
Chapter 4	Effects of land use change in Sudano-Sahelian West Africa on the diet and growth of an avian predator	71
Chapter 5	Breeding performance of Grasshopper Buzzards in a natural and human-modified West African savanna	89
Chapter 6	Breeding biology and diet of the African Swallow-tailed Kite in Senegal and Cameroon	109
Chapter 7	Response to habitat modification by foraging Dark Chanting Goshawks in a West African savanna	125
Chapter 8	Effects of land transformation on raptors in West African savannas: the role of breeding range, migratory behaviour, and body size	143
Chapter 9	Raptor habitat use in the Lake Chad Basin: insights into the effect of floodplain transformation on Afrotropical and Palearctic raptors	165
Chapter 10	Biogeographical and anthropogenic determinants of landscape-scale patterns in a raptor assemblage in Cameroon	183
Box B	Sightings of Sooty Falcon in the far north of Cameroon	207
Chapter 11	Synthesis	213
	References	223
	Summary	245
	Samenvatting	251
	Acknowledgements	257
	Curriculum vitae	260

Chapter 1

General introduction

Ralph Buij

1.1 Introduction

Over the past 40 years unprecedented land cover and land use changes have occurred in sub-Saharan Africa, which is mainly driven by overexploitation of the land, notably for the expansion of croplands (Brink & Eva 2009). Agricultural expansion has increased sharply with human populations, which were reported to have tripled between 1970 and 2010 from just under 250 million to over 850 million (World Bank 2012). The resulting loss of native habitats has contributed to significant wildlife declines in Africa's savannas, which are widely represented outside protected area network but under immense pressure from human populations (e.g. Ottichilo *et al.* 2000, Homewood *et al.* 2001, Serneels & Lambin 2001, Sinclair *et al.* 2002, Darkoh 2003, Blaum *et al.* 2007, Biggs *et al.* 2008, Craigie *et al.* 2010). Compared to the rest of the continent, West Africa's biodiversity stands out for being most severely threatened (Clerici *et al.* 2006, Newmark 2008, Fa & Brown 2009, 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), because dry forests are easy to clear for agriculture and have often fertile soils with suitable climate for livestock husbandry (Murphy & Lugo 1986). Protected areas in West Africa are widely scattered and few cover the range of habitats necessary to maintain the diverse assemblage of species adapted to different vegetation types and structure (Thiollay & Clobert 1990), or support migratory populations with almost constantly shifting populations along latitudinal gradients (Thiollay 1978a). West Africa's protected areas do have a crucial role in safeguarding fragmented wildlife populations in the face of growing human pressure, but their limited size, coverage and increased isolation are likely to severely compromise their effectiveness in doing so (Chape *et al.* 2005, Clerici *et al.* 2006, Brashares *et al.* 2001). As human populations, markets, and infrastructure continue to drive conversion of forested and pastoral lands to other land uses around protected areas (Clerici *et al.* 2006, Newmark 2008), predominantly agriculture (Odihi 2003, Tappan *et al.* 2004, Paré *et al.* 2008, Ouedraogo *et al.* 2010), little is known about the processes that sustain wildlife populations within increasingly human-transformed savanna landscapes.

1.2 West African raptor decline

Birds of prey, or raptors (in this thesis treated as diurnal raptors belonging to the order Falconiformes, i.e. excluding owls), like other top predators, are among the most vulnerable taxa to environmental disturbance (Newton 1979). Consequently, their presence has been often cited as indicative for the biological diversity of the ecosystems on which they depend, since top predators select such sites, promote ecosystem diversity by top-down predation, or provide essential resources, such as carrion for scavengers (reviewed in Sergio *et al.* 2006, 2008). As raptors are relatively easily observed top predators, they are among the most useful higher taxa to evaluate the state of the environment over wide areas in open to semi-open areas, including savannas. To date, a range of studies have inferred from spatial variation in raptor populations, that habitat transformation through human interference is having an huge impact on ecosystem functioning and species diversity (e.g.

Herremans & Herremans-Tonnoeyr 2000, Sánchez-Zapata *et al.* 2003, Machange *et al.* 2005, Carrete *et al.* 2009). The largest among the raptors, which require the largest areas to support breeding efforts, are ideal "umbrella species", meaning that areas large enough to support these species automatically provide adequate resources for populations of smaller, less demanding species. Also, raptors may be "flagship species", driving public interest and support for conservation programs through their charismatic appearance and behavior, which may have aided the recovery of several species in temperate regions after decades of persecution and environmental contamination (Newton 1979, 1998, Zuberogoitia & Martínez 2011).

In Africa, raptors population declines have been documented since the 1970s, throughout the continent (e.g. Brandl *et al.* 1985, Sorley & Anderson 1994, Herremans & Herremans-Tonnoeyr 2000, Thiollay 2000, 2001, 2006a, 2007a, Anadón *et al.* 2010, Ogada & Keesing 2010, Ogada & Buij 2011, Virani *et al.* 2011). The particularly dire state of raptors in the West Africa's Sudan and Sahel savannas was illustrated by repeated counts of raptors along road transects in four West African countries (Cameroon, Niger, Burkina Faso, Mali) by Jean-Marc Thiollay, between 1969-1973 and again between 2000-2004. Despite regional variation in the severity of the declines, the overriding population trend was negative, especially outside protected reserves (Thiollay 2001, 2006a,b,c, 2007a,b). Given their indicator role, the raptor decline implied a general "ecological collapse" according to Thiollay (2006a), reflecting similar trends for medium-sized to large vertebrates and gamebirds in the region (Thiollay 2006b). Large Afrotropical raptors, which sit at the apex of food pyramids, were disproportionably hard hit, illustrated among others by the 98% decline of large vulture populations outside protected areas, and 86-93% decrease of populations of four large eagles (Thiollay 2006a). Many formerly widespread large raptors now survive only in a few pockets of intact habitat, mostly inside protected areas, while populations of some are on the brink of regional extinction, or have already disappeared (Thiollay 2006a).

The widespread, dramatic impoverishment of almost the entire West African raptor assemblage in less than four decades is unprecedented in Africa. It is, in fact, the most devastating decline reported for avian taxa at this scale in Africa, and it affects an area of global importance to raptor conservation, with 69 regularly occurring raptor species (excluding vagrants; Borrow & Demey 2004), representing 22% of the world's raptors. Of these, 13 are considered threatened ("Near Threatened", "Vulnerable", or "Endangered"; IUCN Red List 2012), including three out of 23 regularly recorded Palearctic raptors, which breed in the Palearctic and winter in sub-Saharan Africa. This suggests that factors which affect raptors here might also have repercussions for endangered populations in Eurasia. Overall, the reported raptor declines coincide with and reflect the relatively high anthropogenic pressure on dwindling resources in this part of Africa, and as such, they offer a glimpse into the future for most of the continent, and how raptors cope with the changing conditions.

1.3 Palearctic and Afrotropical raptors

The raptor population trends in West African savannas were alarming for their scope, both in terms of numbers and the scale at which they were detected. However, not all species declined as strongly, and few apparently remained stable locally (Thiollay 2001, 2006a), pointing to variation in species-specific response to environmental alteration and degree of development (e.g. Rodríguez-Estrella *et al.* 1998, Sergio & Bogliani 2000, Anderson 2001, Thiollay 2007a, Carrete *et al.* 2009, Cardador *et al.* 2011). Such differences in sensitivity to habitat transformation depends on life-history traits such as body mass (Owens & Bennett 2000, Gehring & Swihart 2003), relative brain size (Sol *et al.* 2005, 2010), dispersal (Pereira *et al.* 2004) and niche breadth (Swihart *et al.* 2006). Interspecific differences in body mass, energy needs, and diet (Schipper 1973, Jaksic & Braker 1983, Marti *et al.* 1993, Garcia & Arroyo 2005), may render large birds more vulnerable to change (Gaston & Blackburn 1996, Gillespie 2001), and this also seems to hold for raptors (e.g. Thiollay 2006a,b, 2007a). Similarly, sexually dimorphic raptors may exhibit distinct sex-related spacing patterns based on differences in diets and energy requirements (Marquis & Newton 1982, Smallwood 1988), allowing the possibility of intraspecific variation in vulnerability to land use change.

Recent studies further suggest that sedentary birds, i.e. those that depend on year-round territories, have morphological and behavioral traits that allow them to cope relatively well with changing environments (Sol *et al.* 2005, 2010), whereas migratory species tend to be less flexible. This was related to differences in brain size, relative to the size of the body; the relatively smaller brains of migrants may limit their capacity to produce flexible responses to challenging feeding conditions (Lefebvre *et al.* 1997), for example as a result of habitat destruction. On the other hand, Palearctic birds have been attributed with strong flexibility in habitat use on their winter grounds, occupying a wider range of habitat types and employing a higher diversity of foraging techniques, even profiting from anthropogenic habitat alteration (Moreau 1972, Morel & Morel 1992, Jones *et al.* 1996, Wilson & Cresswell 2002). Evidence suggests that, like other migrants, Palearctic raptors wintering in Africa also readily occupy man-modified habitats (Herremans & Herremans-Tonnoeyr 2000, Anadón *et al.* 2010, Limiñana *et al.* 2012), which might imply that they are rather flexible in adjusting to changing conditions on their winter grounds. Still, populations of Palearctic migratory birds wintering in Africa have suffered sustained and often severe declines over the past few decades, which were not apparent for non-migratory species (residents and short-distance migrants) breeding in the same habitats in Europe (Sanderson *et al.* 2006). Although declines may have been due partly to effects outside the African winter grounds, e.g. hunting at migration points (Zalles & Bildstein 2000), or deterioration of staging areas and increased flight distances over the Sahara (Doswald *et al.* 2009), ample evidence suggests that deteriorating conditions on West African wintering grounds influence survival and population numbers of Palearctic birds (e.g. Peach *et al.* 1991, Szép 1995, Eraud *et al.* 2009), including raptors (Clarke 2002, Grande *et al.* 2009, Zwarts *et al.* 2009, Mihoub *et al.* 2010).

Sensitivity to habitat change may increase, or have more significant consequences at population level during the reproductive season (Newton 1979). 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 (seasonally) productive territories, and consequently, are likely to be more vulnerable to land use change than Palearctic migrants (Herremans & Herremans-Tonnoeyr 2000, Anadón *et al.* 2010). Similar to Palearctic migrants, some Afrotropical raptors respond to marked seasonal fluctuations in food supply by adopting a migratory lifestyle, displaying regular north-south population movements along a latitudinal gradient of declining rainfall (Thiollay 1978a). The timing and extent of seasonal movements varies between species, some are only partially migratory or nomadic, while population displacements for Afrotropical migrants, or intra-African migrants, occur between West Africa's forests and wet Guinea savannas and the arid Sahel (Thiollay 1977a, 1978a), while at least one species visits from southern Africa (Wahlberg's Eagle *A. wahlbergi*; Meyburg *et al.* 1995). Several Afrotropical migrants are among the most common raptors in West Africa, suggesting that they are coping fairly well with changing conditions, similar to some migratory raptors on European breeding grounds (Sergio & Bogliani 2000, Suárez *et al.* 2000, Cardador *et al.* 2011). On the other hand, persecution and disturbance by humans might depress reproductive output in West African agro-ecosystems and have been shown to limit the potential nest distribution of raptors (Bisson *et al.* 2002, Bamford *et al.* 2009). Furthermore, breeding densities are limited by saturation effects even in patches of optimal habitat, while effects of suboptimal food conditions, which are more likely in degraded habitats, may constrain nestling development and reproductive output of raptors breeding in rural landscapes.

Their high site fidelity suggests that Afrotropical sedentary raptors might be more vulnerable to habitat deterioration than Afrotropical migrants, since sedentary raptors depend on productive ranges to sustain them year-round. Despite a potentially greater foraging flexibility which may allow them to cope with seasonal environments (Schultz *et al.* 2005, Sol *et al.* 2005), increasingly rapid processes of urbanization and agricultural intensification in developing countries may negate the adaptive response of raptors to changing habitats (Carrete & Donázar 2005). For populations of sedentary raptors in agro-ecosystems, declining food resources (Herremans & Herremans-Tonnoeyr 2000) or shifts in prey abundance and selection (Ogada & Kibuthu 2009) may particularly worsen foraging conditions, potentially hampering long-term population persistence.

1.4 Research aims

As described in the preceding sections, land use can have various effects on the life cycle of raptors and depend upon species-specific adaptability to changing conditions. Studies of raptors in Africa have merely begun to scratch the surface of the myriad of effects that may influence population persistence, and clues to the mechanisms and causal drivers behind population declines remain little studied. Moreover, it is unclear how changing conditions differently affect the diverse assemblage of Afrotropical and Palearctic raptors, and how vulnerability, or adaptability to changing environments, relates to life-history traits such as

sex, age, body mass, and diet. This thesis aims to shed light on such mechanisms by quantifying the effects of land transformation on foraging, diet, and reproductive output. More specifically, it addresses the following questions:

I How do intraspecific traits, i.e. sex and age, and interspecific body mass and diet differentiation influence foraging habitat selection by Palearctic raptors on African wintering grounds?
II What is the effect of habitat transformation on nestling diet and growth, and on nest density and reproductive output, in Afrotropical migratory raptors?
III What is the impact of habitat transformation on diet and foraging, in terms of effort and energy intake, in a sedentary Afrotropical raptor?
IV How does sensitivity to habitat modification differ between Palearctic and Afrotropical raptors, Afrotropical migratory and sedentary raptors, and between Afrotropical raptors of different size?
V How do protected area coverage and land use influence biogeographical patterns of abundance, richness, and diversity of raptors in West African savannas?

1.5 Study area

In order to answer these question, a field study was carried out in northern Cameroon from 2007-2010. Research was mostly conducted in the Far North and North Regions of Cameroon, but extended into the Adamawa Region, thus incorporating the three northernmost provinces of the country (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 Lake Chad Inundation zone.

Species-specific examinations were performed in the Lake Chad Inundation zone and its fringing woodlands, located in the transition zone of the Sudan and Sahelian savanna belts (rainfall: 450-700 mm/annum). The region supports edaphic grassland mosaics with communities of *Acacia* and broad-leaved trees (White 1983). The 8000 km^2 Waza-Logone floodplains are part of a much larger floodplain area shared with Chad. These flooded grasslands are fringed by open *Sclerocarya birrea* woodland with *Anogeissus leiocarpus*, *Balanites aegyptiaca*, and *Acacia seyal*. Agriculture in the area includes mainly dry-season sorghum, millet, and rice. Human population density is low (10-25 people/km^2) but has increased following partial floodplain rehabilitation (Scholte 2003). Although West Africa's floodplains are of regional importance to migratory raptors (Zwarts *et al.* 2009), the Waza-Logone floodplains and other floodplains associated with the greater Lake Chad Basin were labelled as the "centre of overwintering" for Palearctic migratory raptors, in reference to various Palearctic raptors which are rare further west (Thiollay 1978b). Thiollay (2001) suggested that a major reason for the recent raptor decline in the region was

the construction of a dam which caused the desiccation of 1,500 km^2 of the floodplains to create agricultural schemes. Re-flooding of part of the desiccated floodplains by the breaching of the Logone river embankment in 1994 raised flooding levels in an area of 600 km^2 and rehabilitated 180 km^2, with positive effects on vegetation dynamics, waterbird and antelope population recovery (Scholte 2005). The 1700-km^2 Waza National Park protects part of the floodplains and small populations of herbivores, notably Elephants *Loxodonta africana*, Buffon's Kob *Kobus kob* and Topi *Damaliscus korrigum*, but large wildlife has been virtually exterminated in the 45-km^2 Kalamaloué N.P. (Scholte 2003) and also threatens Waza N.P. (De Iongh *et al.* 2009).

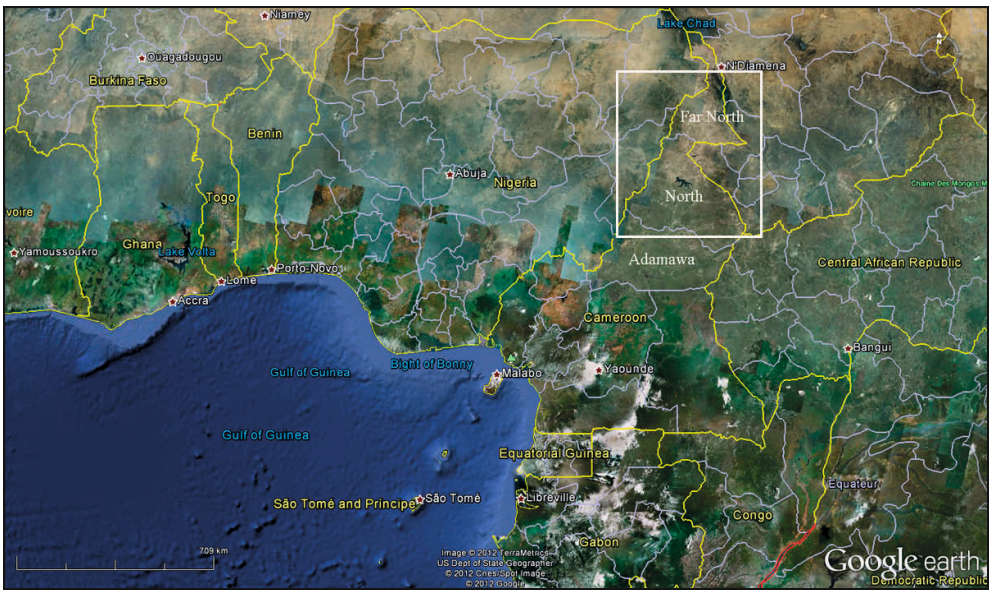

Figure 1. Location of the study area in the north of Cameroon. Country borders are yellow and provincial or state borders are blue. Satellite image © Google Earth.

To the south, the Sudan savanna belt (rainfall: 700-1100 mm/annum) with undifferentiated Sudanian woodlands (White 1983) is characterized by hilly terrain which rises to the Mandara Mountains in the west at 500-1000 m a.s.l. with isolated peaks up to 1442 m. The entire area is densely populated (averagely *c.* 50 people/km^2, but > 100-150 people/km^2 in many areas, locally up to 350 people/km^2) and deforestation has been significant during the past 20 years (Fotsing 2009). Sorghum, millet, maize, beans, and groundnut are the most important food crops and cotton is cultivated throughout the zone as the main cash crop. Few patches of natural habitat remain in scattered, small (< 40 km^2) and heavily exploited forest reserves with *Isoberlinia doka*, *Balanites aegyptiaca, Piliostigma reticulatum* and *Combretum erythrophyllum*.

The Guinea savanna belt south of the Sudan savanna (rainfall: 1100-1600 mm/annum) is on undulating terrain with some scattered rocky outcrops. The Bénoué Valley encompasses a

large river system and three National Parks (Bénoué, Boubandjidda, Faro) covering an area of approximately 7600 km^2. Twenty-eight sport-hunting zones cover an additional 16,000 km^2 and are managed as protected areas but with hunting quota for larger mammals and gamefowl (Mayaka 2002). The region has a low human population density (on average 13 people/km^2), which is rapidly increasing (growth rate is *c*. 5%; Mayaka 2002). Cultivation covers *c*. 20% of the zone, particularly traditional crops such as millet but increasingly cotton. Herbaceous layer cover during the study period varied between 17% (mean minimum) to 81% (mean maximum).

1.6 Thesis outline

The thesis is organized into sections dealing with the effect of land use on selected species groups or species within the Palearctic migratory, Afrotropical migratory, and sedentary raptor assemblages, and a section dealing with habitat associations of the entire assemblage, at different spatial scales. This section introduces the West African raptor assemblage, the research questions, and the study area, quantifying aspects of land transformation during the past 40 years, which corresponds with a period of extensive land transformation and impoverishment of the raptor assemblage in Cameroon (Thiollay 2001).[1] The second section is divided into seven chapters, and discusses the impact of land transformation on Palearctic, sedentary and Afrotropical migratory raptors. The third section encompasses three chapters and combines lessons learnt from species-specific investigations to evaluate habitat associations of Palearctic migrants, African migrants and sedentary raptors. The fourth section concludes with a synthesis of the thesis results. Specifically, the chapters address the following:

Chapter 1 includes a description of the raptor assemblage and the study area in northern Cameroon, with delineation of the research themes and outline of the study. Chapter 2 assesses the foraging distribution of sex and age groups within three sexually dimorphic Palearctic harriers, to examine the role of body mass, sex and age groups, on habitat use and vulnerability to land transformation. The foraging patterns of the harriers are investigated in northern Cameroon, using point counts in five habitat types along a gradient of transformation on the Waza-Logone floodplain. Pellet analyses provide details of harrier diet, which are used to explain the observed foraging patterns. Box A analyzes in more detail the bird hunting success by Pallid Harriers *Circus macrourus*, with a discussion of habitat elements that facilitate hunting.

Chapters 3-5 examine the relationship between land use, food availability, nest success, productivity, and growth in an Afrotropical migrant, the Grasshopper Buzzard *Butastur rufipennis*, a species threatened by extensive land transformation in its Sudano-Sahelian breeding range. Chapter 3 provides the first detailed information of the breeding biology

[1] The study area in northern Cameroon is situated on the transition boundary between West and Central Africa, which is commonly placed on a line running from Mt. Cameroon in the south to Lake Chad in the north of Cameroon. Because of the greater ecological similarity with the West African savannas compared to the wet savannas and forests that dominate Central Africa, northern Cameroon is often included as part of the West African savanna region (cf. Tchamba 1996, Thiollay 2001) and this classification is adopted here.

and nestling development of the Grasshopper Buzzard. Using the information from Chapter 3, Chapter 4 examines the importance of land use and rainfall on Grasshopper Buzzard nesting growth parameters, to understand how changing environmental conditions within its breeding range impact nestling growth and condition at fledging. This includes an investigation of diet composition and energetic content of food brought to the nests, and how these may explain the observed growth patterns. Chapter 5 examines the relationship between environmental conditions, nest density and reproductive parameters in the Grasshopper Buzzard, based on an assessment of reproductive output at nests in transformed and natural habitat. Chapter 6 reports on the breeding biology of another Afrotropical migrant, the African Swallow-tailed Kite *Chelictinia riocourii*, in Cameroon and Senegal, including a diet comparison of kites during breeding and non-breeding seasons, to evaluate how diet shifts between seasons may influence vulnerability to land transformation. The chapter also discusses how nest dispersion related to land use may influence breeding performance.

Chapter 7 attempts to evaluate the impact of habitat transformation on foraging in sedentary Dark Chanting Goshawks *Melierax metabates*, by examining differences of microhabitat selection, foraging effort and energy intake in natural and transformed habitats. To determine microhabitat selection by hunting goshawks, six male goshawks are radio-tracked in both habitat types and vegetation structure at patches used by hunting goshawks compared with nearby unused patches. This method also permits for an assessment of hunting effort and energy intake through estimation of prey energy content.

Chapter 8 investigates environmental factors underlying habitat-scale patterns of raptor community richness in northern Cameroon, to provide insights into the raptor decline and identify elements of habitat transformation that most threaten raptors in the region. Year-round patterns of raptor richness and abundance were documented along road transects in the Lake Chad Inundation zone, Sudan savanna and Guinea savanna of Cameroon, covering four years and dry and wet seasons, and related to vegetation structure, human population size, and land use along the transects. To assess their presumed differences in sensitivity, I separately analyzed habitat associations of Afrotropical raptors to Palearctic raptors, sedentary raptors to Afrotropical migratory raptors, and large raptors (eagles and vultures) to smaller raptors. Chapter 9 documents habitat associations of raptors on the Waza-Logone floodplains, which represent a highly localized but threatened habitat of great importance to raptors, to provide insight into the effect of Sahelian floodplain transformation on Palearctic and Afrotropical raptors. Chapter 10 assesses the role of biogeographical zonation, protected area coverage, and land use at broad, landscape-scale patterns of abundance, richness, and diversity of raptors in northern Cameroon. Further, the conservation value for raptors of Cameroon's northern savannas, and those elsewhere in West Africa, is examined on a continental and global scale, to ascertain their value to global raptor conservation. Box B finally describes the first observation in Cameroon of globally endangered Sooty Falcon *Falco concolor*, indicative for the scarcely documented raptor richness of the region and a potential migration route through this part of Africa.

Chapter 11 represents the concluding section, which discusses the main findings and puts them into the wider perspective of raptor conservation. The chapter includes recommendations for conservation projects.

Chapter 2

Inter- and intraspecific differences in habitat use and conservation implications for Palearctic harriers on the core Sahelian wintering grounds

Ralph Buij, Dirk van der Goes, Hans H. de Iongh, Sama Gagare, Patsy Haccou, Jan Komdeur & Geert R. de Snoo

Published in:

Ibis (2012), 154: 96-110

Abstract

The floodplains of the West-African Sahel region experienced extensive habitat transformation during the past four decades, coinciding with an impoverishment of raptor populations. We investigated foraging patterns of Palearctic migratory Eurasian Marsh Harriers *Circus aeruginosus*, Pallid Harriers *C. macrourus*, and Montagu's Harriers *C. pygargus* on a floodplain system in northern Cameroon to determine species, sex and age-related habitat preferences. Sex and age-class have rarely been incorporated into general studies of raptor habitat associations, despite clear evidence for sex- and age-related differences in foraging strategies and diet composition, potentially carrying strong conservation implications. I found evidence of intersexual differences in foraging preference related to land use, notably in the most weight dimorphic Pallid Harriers, but also in Marsh and Montagu's Harriers, and some evidence that juveniles exploited different habitats from adults. These constitute the first quantitatively documented foraging differentiation in Palearctic raptors on African winter grounds, indicating that general patterns of habitat use in wintering raptors may be obscured by sex and age-specific preferences. Contrary to expectations, we recorded limited evidence for interspecific foraging segregation, i.e. avoidance of desiccated grasslands by Marsh and Montagu's Harriers not evident in Pallid Harriers. Food partitioning by prey mass was related to harrier body mass and facilitated by a diverse supply of prey on human-transformed floodplains. Anticipated further large-scale conversion of floodplain habitat into desiccated grasslands raises concerns about the impact of future Sahelian floodplain development on the survival of wintering harriers.

Left: Marsh (top) and Pallid Harrier foraging over sorghum fields in northern Cameroon.

2.1 Introduction

Eurasian raptors are relatively little studied on their wintering grounds in the Sahel region of West Africa, despite the critical importance of this region as a wintering area for many Palearctic raptors, including several endangered species (Thiollay 1989, Tucker & Heath 1994). Dramatic raptor population declines throughout the Sahel between the 1960s and 2004 (e.g. Thiollay 2006a,b, 2007a) were associated with extensive changes in land use, including severe overgrazing of grasslands, loss of soil, and deforestation for agricultural expansion, which have characterized the region during the past four decades (Chomitz & Griffiths 1997, Wardell *et al.* 2003, Wood *et al.* 2004, Mortimore & Turner 2005, Reij *et al.* 2005), suggesting that the winter range of Eurasian raptors has greatly impoverished. Counts along road transects indicate, however, that migratory raptors may have been less affected by expanding cultivation in the Sahel than Afrotropical species (Thiollay 2000, Anadón *et al.* 2010), but trends vary regionally and between species (Thiollay 2001, 2006a, 2007a), while long-term comparisons are complicated by differences in rainfall patterns, which influence prey populations.

The inundation or floodplain zones of the Senegal and Niger Rivers and the Lake Chad Basin support relatively high migratory raptor densities, and were labeled essential for the conservation of Eurasian raptors wintering in West Africa (Thiollay 1989). This is particularly true for the Palearctic harriers, Eurasian Marsh Harriers *Circus aeruginosus* (hereafter: Marsh Harrier), Montagu's Harriers *C. pygargus*, and Pallid Harriers *C. macrourus*, which occur in often much higher densities on floodplains compared to surrounding dryland savannas (Thiollay 1977a, 1978b, 1989, 2006a, Zwarts *et al.* 2009). Their high densities and *c.* 6-month stay on the wintering grounds make Eurasian harrier populations especially vulnerable to changing conditions on the floodplains. Between the 1960s and 2000, when Sahelian floodplains and lakes lost over half of their surface area resulting from decreased rainfall and the development of rice irrigation schemes (Zwarts *et al.* 2009), numbers of Pallid and Montagu's Harriers wintering in the Sahel significantly declined over vast areas, while Marsh Harrier numbers remained stable or perhaps increased (Thiollay 2006a). These trends largely reflected the situation on Eurasian breeding grounds (BirdLife International 2010a, 2010b, 2010c), and were related to circumstances there rather than climatic conditions in the Sahel (Trierweiler & Koks 2009), but accumulating evidence suggests that ecological conditions in the Sahel influence survival, breeding output and population numbers of Afro-Palearctic migrants (e.g. Peach *et al.* 1991, Szép 1995, Cowley & Siriwardena 2005, Schaub *et al.* 2005, Eraud 2009), including raptors (Grande *et al.* 2009, Zwarts *et al.* 2009, Mihoub *et al.* 2010).

Raptors frequently exhibit sexually distinct spacing patterns on their winter grounds, which have been attributed to sex-specific habitat preferences with regard to foraging efficiency and preferred prey type and size (e.g. Koplin 1973, Opdam 1975, Stinson *et al.* 1981, Marquis & Newton 1982, Thirgood *et al.* 2003), or female dominance over males for superior foraging sites (e.g. Mills 1976, Bilstein & Collopy 1985, Temeles 1986, 1987, Smallwood 1987, 1988, Ardia & Bildstein 1997). Such differential habitat use is often associated with reversed sexual size dimorphism, leading to higher energy demands (Nagy

1987, 2005, Marti *et al.* 1993) and higher mean prey mass in larger females compared to males (Storer 1966, Schipper 1973, Opdam 1975, Schipper *et al.* 1975, Kenward *et al.* 1981, Martínez & Calvo 2005, but see Kennedy & Johnson 1986, Boal & Mannan 1996). Age may also influence habitat selection, as a consequence of differences in foraging ability and tactics related to differences in experience and morphology between age groups (Bennets & McClelland 1991, 1997, Bustamente *et al.* 1997, Simmons 2000, Kitowski 2003). In spite of the clear intraspecific discrepancies and the important consequences that sex and age-related differences in habitat use can have on life-history and population regulation (e.g. Morton *et al.* 1987, Marra & Holberton 1998), relatively little attention has been given to sex and age in studies of raptor habitat associations. In fact, habitat models, which are of critical importance to designing conservation policies, rarely incorporate sex and age as a variable, potentially biasing estimation towards the more frequently encountered sex or age-class. For species that exhibit strong intersexual differences in foraging behaviour, such lack of discrimination between sex categories could overestimate the importance of habitat features for one sex, while underestimating them for the other (e.g. Conde *et al.* 2010).

In order to elucidate the impact of habitat transformation on Palearctic harriers, we investigate habitat occupancy by sex and age categories along a gradient of habitat transformation on the floodplains of the Lake Chad Basin. Habitat mosaics in human-impacted landscapes in the Sahel offer a variety of abundant food sources related to land use, such as diurnal rodents in cultivated fields (e.g. Poulet 1985, Adeyemo *et al.* 2005) and grasshoppers in grasslands in succession (Mullié & Guèye 2010). Intersexual differentiation of habitat use is likely under such conditions, as reversed size dimorphism and accompanying morphological differences are well developed in harriers (Nieboer 1973, Schipper *et al.* 1975, Bildstein & Hamerstrom 1980, Davygora & Belik 1994, Clarke 1996, Simmons 2000, Bavoux *et al.* 2006), determining differences in energetic requirements (Riedstra *et al.* 1998), hunting strategies, and diets (Nieboer 1973, Schipper *et al.* 1975, Clarke 1996, Fritz *et al.* 2000). Based on previous studies (Lack 1946, Schipper 1973, 1977, Jaksic & Braker 1983, Bozinovic & Medel 1988, Clarke *et al.* 1993, Marti *et al.* 1993, Garcia & Arroyo 2002, 2005, Gliwicz 2008), we further hypothesize that differences in body mass result in interspecific differentiation of habitat use, while differences in morphology (Bildstein & Hamerstrom 1980) and foraging tactics (Kitowski 2003) between age groups are expected to influence their habitat use. We predict that: (1) adult male and female harriers forage in different habitats which offer differently-sized prey, and this difference is greatest for the strongly sexually dimorphic Pallid Harrier and less evident for the least sexually dimorphic Montagu's Harrier (cf. Simmons 2000); (2) large-bodied Marsh Harriers (530-720 g) consume averagely larger prey items than Pallid (310-440 g) and Montagu's Harriers (265-345 g); (3) diet overlap is small between Marsh and Montagu's Harrier (body mass ratio: 2.0), large for Pallid and Montagu's Harrier (1.2), and intermediate for Marsh and Pallid Harrier (1.7), resulting in interspecific differences in habitat use depending on body mass ratios and preferred prey distribution; (4) juveniles prefer different habitats from adults due to differences in foraging tactics. Based on our findings, we evaluate the impact of changes in land-use in the core winter areas, and

consider the implications of future land transformation for population persistence of migratory harriers.

2.2 Materials and methods

Study area

Habitat use was investigated in a *c*. 800-km^2 area of the Logone floodplain in the Far North of Cameroon (mean rainfall *c*. 500 mm), from January-March in 2009 and 2010. Weather conditions between January and March are fairly constant with temperatures rising as high as 40 ºC in March and no precipitation. Since the construction in 1979 of an earthen dam along the Logone River for a rice irrigation scheme, flooding of the area downstream of the irrigated rice fields was prevented, resulting in significant changes in vegetation composition and production (Scholte *et al.* 2000), partly rectified by re-opening of the dam in the mid 1990s (Loth 2004). Five habitat types were distinguished (Figure 1): (1) floodplain, seasonally flooded grasslands (Aug-Nov) largely devoid of woody plants and dominated by low-creeping and perennial grasses, with inundated depressions (surface area: 92 km^2); (2) rehabilitated floodplain, mostly comparable vegetation composition to the pre-dam situation, despite limited recovery of tussock grasses (Scholte *et al.* 2000; 87 km^2); (3) dry grassland, desiccated former floodplain with strongly reduced grass cover dominated by *Sorghum arundinaceum*, forbs and stands of *Acacia seyal*, frequently encroached by woody shrubs (*Piliostigma reticulatum*, *Ziziphus* spp.; 189 km^2); (4) sorghum fields, with crops at harvest time, and comparable vegetation composition and structure to dry grassland outside the cultivated fields (56 km^2); (5) rice fields, naturally flooded or irrigated between April-November, with rice stubs remaining after harvest between December-March, surrounded by canals with grassy margins and isolated woody plants (79 km^2).

Quantifying habitat use by foraging harriers through observation plots

Observations on harrier foraging were conducted from the centre of an observation plot (hereafter: plot) with a 350-m radius, which was the maximum area that allowed identification of sex and age categories of foraging harriers. Each year 10 plot counts were conducted in each of the five major habitat types, amounting to 20 plots per habitat type for 2009 and 2010 combined and 100 plots for the entire study. We used Landsat MSS satellite images and ArcView GIS 3.2 software to discern and delineate the major habitat types, which was further verified in the field. Plots were randomly allocated within the delineated habitats using a grit, taking accessibility into account (plots > 5 km from the existing dirt road network were excluded). When visibility from the centre of the plot was less than 350 m at 360º, plots were re-orientated in a northerly direction in the field to the nearest suitable area with full visibility of the plot. To minimize pseudoreplication, plots were at least 2 km apart in the same year, while plots in 2010 were always at least 800 m from plots surveyed in 2009. Observations in the plots were conducted between 21 January and 14 March in 2009, and between 26 January and 17 March in 2010. This period coincides with the known winter period of Montagu's (Trierweiler *et al.* 2007, Trierweiler 2010), Marsh (Strandberg *et al.* 2008), and Pallid Harriers (Terraube *et al.* 2012) in the Sahel. Plot watches were

alternated between habitats to avoid timing-related biases in habitat preference. Observations took place during harrier activity peaks (R. Buij unpubl. data), in the morning (06:30-09:45) and in the late afternoon (15:00-18:15). Repeated plot watches were alternated between early morning and late afternoon or vice versa, to avoid a bias due to survey timing in relation to harrier activity peaks and the proximity of roosts. The distance of landmarks (e.g. shrubs, dikes) to the centre of the plot was measured using a calibrated parallax-type rangefinder to define the limits of the plot and exclude harriers foraging outside the plot. Plot watches were cancelled on two occasions when harmattan sandstorms reduced visibility to below 400 m. No plot was sampled while fires were burning or still smoldering. Watches were performed simultaneously by two experienced observers, always including the main author, using 10 x 42 binoculars. To avoid missing harriers flying behind vegetation or at very low altitudes (even in ditches), observations were consistently performed from a raised object (termite mound, roof of the car) in the centre of the plot so that observer eyelevel was at approximately 3 m. During watches, continuous scans for harriers were made by both observers and as harriers entered the plot, the following was recorded: species, sex, age (juvenile: 2nd cy, or adult: 3rd cy or older; Forsman 1999), entry time and time spent in the plot. Harriers were photographed to later confirm species identification, sex and age. Harriers in quartering flight or circling (< 100 m altitude) within the limits of the plot were included in the analyses.

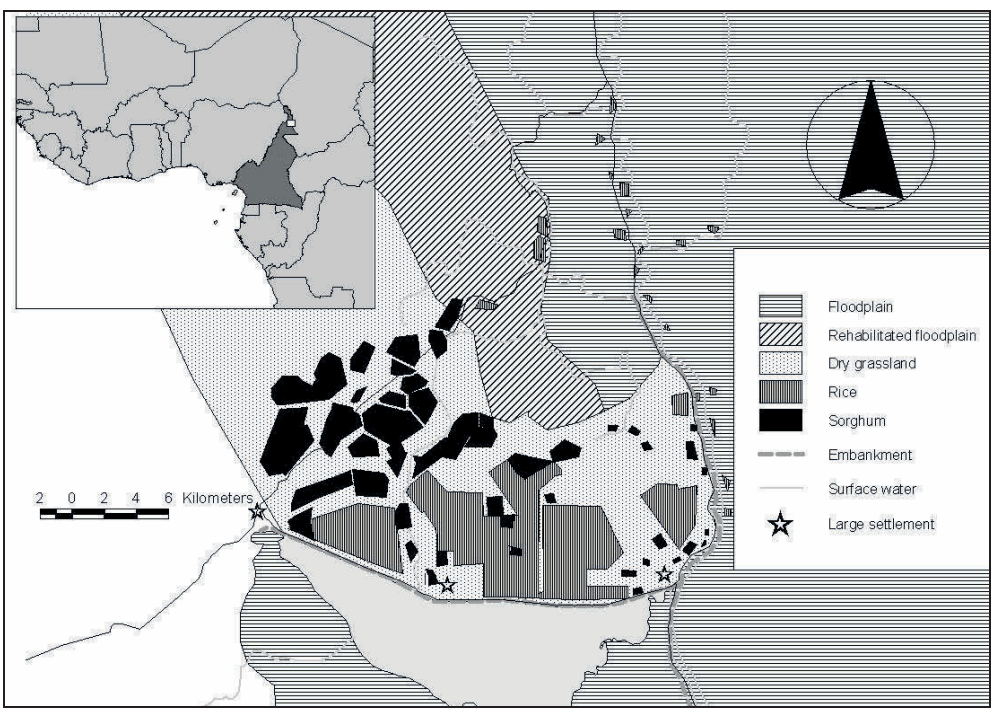

Figure 1. Location of the study area in northern Cameroon, illustrating the main habitat types and the location of the embankment and reservoir created to accommodate irrigated rice cultivation on the Logone floodplain.

Prey abundance

Prey abundance measures for small mammals, birds, and grasshoppers were recorded for each plot between the same dates that plot surveys were conducted. The relative abundance of small mammals was determined using a custom-made trap design, in which cement is flattened in a 30-cm circle centered on *c.* 20 g of peanut butter to allow identification of small mammal tracks. Cement traps were laid out on a rectangular grid (200 x 200 m) and at 50-m intervals in the centre of the plot. Small mammal abundance was indexed using the presence or absence of their tracks on 16 cement traps for each plot. Cement traps were set up in the late afternoon and were revisited after 17 hours. Tracks were categorized into diurnal rodents (dominated by Unstriped Grass Rats *Arvicanthis* spp.) and other small, predominantly nocturnal mammals, for their different mean body mass (> 100 g in diurnal rodents vs. < 40 g in nocturnal small mammals) and activity patterns (Duplantier & Granjon 1990, McElhinny *et al.* 1997), which influences their availability to harriers. The reliability of the technique in providing an index of relative small mammal abundance was tested through simultaneous conventional trapping with standard design Sherman traps (Kisiel 1972) placed adjacent (30 m) to cement traps, both baited with peanut butter (100 trap nights in 10 trap sites equally divided between the five habitats). The proportion of cement traps on which tracks were detected (traps with sign/total traps) was strongly correlated with the capture success rate using Sherman traps (traps with small mammal/total traps) at the trap sites for diurnal rodents ($r_s = 0.86$, $n = 10$, $P < 0.001$) and nocturnal small mammals ($r_s = 0.55$, $n = 10$, $P < 0.001$), confirming the reliability of this method. Grasshopper abundance was determined within each plot by counts of individuals < 3 m from four parallel 250-m transect lines at 50-m intervals, starting from a predetermined fixed compass direction from the centre of the plot. Two size-classes (medium: 30-60 mm; large: > 60 mm) were distinguished as foraging harriers may select for larger size-classes (Trierweiler & Koks 2009, Mullié & Guèye 2010). Cumulative grasshopper counts on the four sub-transects (1000 m per plot) were used as a measure of grasshopper abundance for each plot. Bird species abundance was assessed simultaneously with harrier watches, as one observer counted all passerines and non-passerine birds flying and sitting within the boundaries of the plot. The number of passerines and non-passerines observed during two 1-hour observation sessions was averaged for each plot, for a total of 20 averaged counts per habitat type. As Red-billed Queleas *Quelea quelea* often occurred in large groups, estimates of the total number of birds in a single group were rounded to the nearest 1000 for groups numbering > 10,000 individuals.

Vegetation measurements

Vegetation measurements for each plot were recorded along the same transect lines (4x250 m) used for grasshopper abundance estimates. On each 250-m transect line, 25 squares measuring 100 m^2 were sampled at regular intervals for percentage surface cover of the rooted herbaceous layer (grasses, rice included, and forbs). The height of the herbaceous layer was measured in a 0.30 m^2 circle in the middle of each square using a two-meter stick (cm-scale). The mean herbaceous layer height and cover estimates derived from the 100 measurements per plot were used in subsequent regression analyses. The number of trees

and woody shrubs (i.e. all woody plants) were counted for the entire plot from the centre of the plot and their cumulative number used in analyses.

Pellet analyses

Harrier diet was investigated using intact (i.e. fresh) pellets gathered from night roost sites (Clarke 1996) in the study area between January and April, in 2009 and 2010. Fourteen roost sites were discovered with one to > 80 harriers per roost. Repeated counts (n = 3-6) at single roosts coinciding with pre-roost circling after sunset were conducted before and at collection dates to determine the maximum number of individuals visiting the roost, including their age and sex composition (Appendix 2.1). Although two to three species were present at most roosts, those comprising one species only were used for pellet analyses; except for the likely inclusion of a small percentage of Montagu's Harrier pellets in the Pallid Harrier sample despite attempts to distinguish between the species using moulted feathers near the pellet. A random sub-sample of pellets from the start (January) and end (March-April) of the study period and equally divided among years was used for diet analysis. Items (e.g. mandibles, legs, jaw bones) were identified to class or order, or if possible to family, genus, or species level using a regional reference collection (AGRHYMET, Niger). The frequency by number of prey in each of five main prey categories (small mammals, grasshoppers (including crickets), other insects, birds, reptiles) was calculated by dividing the number of prey in the prey category by the total number of prey items identified from the pellet sample. Prey numbers per taxon in each of the five prey categories were multiplied by the average mass of the taxon (at species, genus, or family level) to calculate the proportion of total biomass for each prey category; the mean biomass of prey in the pellet sample was estimated by multiplying the frequency of occurrence of the different prey types in diet by their estimated mean biomass. Average adult mass was available for grasshoppers and crickets (Mullié & Guèye 2010; W.C. Mullié in litt.) and calculated based on a locally obtained random sample of specimens for small mammals (*Arvicanthis* spp., n = 24; *Mastomys* spp., n = 5; *Crocidura* spp., n = 7; *Lemniscomys* spp., n = 5), beetles (n = 7), mantids and termites (Mantidae, n = 12; Termitidae, n = 22), and reptiles (Colubridae, n = 3; Viperidae, n = 2). For small mammal, reptile and insect prey items identified to order (66%, n = 843), the average mass of the identified genera in the order was used. Since the majority of birds (93%; n = 15) were only identified to class (a Red-billed Quelea was identified in a Pallid Harrier pellet), the mean adult mass of birds (from Del Hoyo *et al.* 1992, 1996, 1997, 2004, 2010) captured by Pallid (n = 21 birds captured) and Marsh Harriers (n = 9) in the study area from 2006-2010 was used to calculate bird prey mass (Appendix 2.1, R. Buij unpubl. data). For Montagu's Harrier, the average estimated biomass for bird prey in the breeding range was used (Arroyo 1997). The dominant habitat types around the roost sites differed which may introduce a bias in the pellet analyses due to habitat-specific prey preferences. However, recent satellite track data of Montagu's and Marsh Harriers show that harriers forage over extensive areas on their wintering grounds (Strandberg *et al.* 2008, Trierweiler 2010). One satellite tracked Montagu's Harrier utilized a 3500-km^2 area of the Waza-Logone floodplain in a period of several weeks in the winter of 2007/08 and 2008/09, incorporating the entire study area and all major habitat types (Dutch Montagu's Harrier Foundation

unpubl. data). We therefore assume that the pellet analysis provides a representative sample of the local diet of the harriers, governed mostly by local prey preferences rather than habitat directly surrounding the roost.

Statistical analyses

Analyses were performed using R (package car) and SPSS version 16.0 (SPSS Inc. 2007). We investigated foraging time and presence of harriers in relation to the five main habitat types: rice, sorghum, dry grassland, rehabilitated floodplain, and floodplain. Foraging time by males, females, and juveniles were analyzed separately for each species and summed for the two-hour observation periods per plot. Given the risk of incorrect inference associated with zero-inflated datasets due to a combination of true and false zero estimates (Martin *et al.* 2005), we followed recommendations by Fletcher *et al.* (2005) and analyzed harrier foraging data in plots using a two-steps process: first, by creating two datasets from the original using (1) binomial presence data (present/absent) and (2) the total foraging time in plots given presence; secondly, by modeling the presence data using Logistic Regression Models, and the foraging time data using a Generalized Linear Model (GLM). A negative binomial distribution with a log link function was used to model the positive foraging time data (cf. Welsh *et al.* 1996) and model adequacy was verified by examination of residuals (McCullagh & Nelder 1989). Shapiro-Wilk or Kolmogorov-Smirnov tests were used to test for normality depending on sample size; data were log-transformed before analyses to adhere to normality. Mann-Whitney *U*-tests were used to test for interannual differences in prey abundance and habitat variables, and foraging time for the nine sex and age categories (n = 50 plots per year). Associations were investigated using Spearman and Pearson correlations. Kruskal-Wallis tests were used to explore differences between the five main habitat types regarding the abundance of prey categories; Mann-Whitney *U*-tests were used to evaluate pairwise differences between the habitat types for the different prey categories. Chi-square goodness-of-fit tests were used to examine differences between years and seasons in the contribution of the main prey categories to the pellet sample, and of their differential occurrence in the diet of the three species. Mann-Whitney *U*-tests were used to test for differences in the prey biomass between the three species. Pianka's (1973) Index was used to calculate diet overlap between the harrier species using the percentage frequency of the five main prey categories in the diet. For all analyses, tests are two-tailed and statistical significance was set at $\alpha < 0.05$. The sequential Bonferroni correction was used to adjust the significance level when multiple tests were performed on the same data set (Rice 1989).

2.3 Results

Habitat use by harriers

The cumulative harrier foraging time in 100 plots was 49.2 hours for both years combined, and foraging time was similar between the years for the nine sex and age categories ($P > 0.05$). A total of 1446 foraging bouts was recorded, 333 for Montagu's Harrier, 309 for Pallid Harrier, and 804 for Marsh Harrier (Appendix 2.2). Harrier foraging presence

differed between habitat types for Pallid Harrier (χ^2_4 = 14.6, *n* = 100, *P* < 0.01) and Marsh Harrier (χ^2_4 = 10.9, *n* = 100, *P* < 0.05), but none of the habitat types contributed significantly to the models (*P* > 0.05). Presence was unaffected by habitat type for Montagu's Harrier (χ^2_4 = 5.03, *n* = 100, *P* = 0.28). Harrier foraging time given presence (Figure 2) differed between habitat types for Marsh (χ^2_4 = 25.3, *n* = 92, P < 0.001) and Montagu's Harrier (χ^2_4 = 9.87, *n* = 76, P < 0.05), which foraged significantly less over dry grasslands than other habitat types, but not for Pallid Harrier (χ^2_4 = 4.97, *n* = 78, *P* = 0.29). Male Montagu's and Pallid Harriers foraged significantly less often over rice fields than floodplain habitat (Table 1), or spent averagely less time foraging over rice than over other habitats (Figure 3). Conversely, females of both species significantly preferred rice fields over flooded grassland in terms of their foraging presence (Table 1), and, for female Pallid Harrier, time spent foraging (Table 2). Sex differences in habitat use were also evident in Marsh Harriers, as females were significantly more often encountered over rice fields and floodplain than other habitats, whereas males merely avoided dry grasslands (Table 1). Habitat models further suggested that juvenile Pallid Harriers preferred rice fields, reflecting habitat models for adult females, but different from the avoidance of rice by males (Tables 1). Juvenile Marsh Harriers preferred sorghum fields over original floodplain habitat (Table 2), which was not evident in either adult sex.

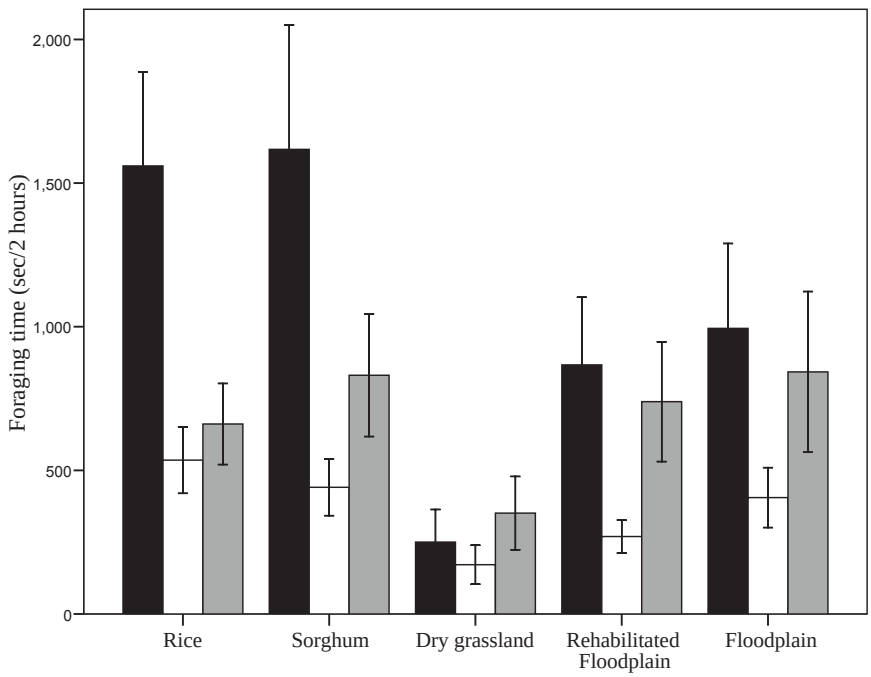

Figure 2. Harrier foraging time by habitat type on observation plots in 2009 and 2010. Foraging time given presence is indicated, for Marsh (black bars; *n* = 92 plots), Pallid (clear bars; *n* = 78), and Montagu's Harrier (grey bars; *n* = 76). Data are mean estimates ±S.E.

Table 1. Logistic regression of harrier presence for each of nine sex and age categories as recorded inside 50 observation plots in 2009 and 50 observation plots in 2010 on the Logone floodplains (n = 20 plots per habitat type). Overall model fit is indicated. Significant values in bold. The reference habitat type is floodplain.

Explanatory variable	***B*** **±S.E.**	**Wald** χ^2	***P***
Montagu's Harrier: female			
Rice	**2.23±0.74**	**9.06**	**<0.001**
Sorghum	1.19±0.72	2.73	0.10
Dry grassland	-0.81±0.93	0.76	0.38
Rehabilitated floodplain	-0.35±0.84	0.17	0.68
Constant	-1.39±0.56	6.15	0.01
Model fit: χ^2_4 = 23.5, n = 100, P < 0.001			
Montagu's Harrier: male			
Rice	-1.24±0.66	3.49	0.06
Sorghum	-0.62±0.65	0.91	0.34
Dry grassland	-1.24±0.66	3.49	0.06
Rehabilitated floodplain	0.23±0.68	0.11	0.74
Constant	0.62±0.47	1.74	0.19
Model fit: χ^2_4 = 8.74, n = 100, P = 0.07			
Montagu's Harrier: juvenile			
Rice	0.81±0.65	1.58	0.21
Sorghum	**1.50±0.69**	**4.76**	**0.03**
Dry grassland	0.61±0.64	0.90	0.34
Rehabilitated floodplain	0.00±0.65	0.00	1.00
Constant	-0.41±0.46	0.79	0.37
Model fit: χ^2_4 = 7.21, n = 100, P = 0.13			
Pallid Harrier: female			
Rice	**2.83±0.81**	**12.18**	**<0.001**
Sorghum	0.48±0.70	0.47	0.49
Dry grassland	0.48±0.70	0.47	0.49
Rehabilitated floodplain	-0.29±0.76	0.14	0.71
Constant	-1.10±0.52	4.53	0.03
Model fit: χ^2_4 = 23.4, n = 100, P < 0.001			
Pallid Harrier: male			
Rice	**-2.01±0.73**	**7.56**	**0.01**
Sorghum	-0.62±0.65	0.91	0.34
Dry grassland	**-1.72±0.70**	**6.07**	**0.01**
Rehabilitated floodplain	-0.62±0.65	0.91	0.34
Constant	0.62±0.47	1.74	0.19
Model fit: χ^2_4 = 12.2, n = 100, P < 0.05			
Pallid Harrier: juvenile			
Rice	**2.01±0.73**	**7.56**	**0.01**
Sorghum	1.03±0.65	2.45	0.12
Dry grassland	0.62±0.65	0.91	0.34
Rehabilitated floodplain	0.42±0.65	0.42	0.52
Constant	-0.62±0.47	1.74	0.19
Model fit: χ^2_4 = 9.90, n = 100, P < 0.05			
Marsh Harrier: female			
Rice	0.00±1.05	0.00	1.00
Sorghum	**-1.79±0.87**	**4.20**	**0.04**
Dry grassland	**-3.58±0.93**	**14.79**	**<0.001**
Rehabilitated floodplain	**-2.40±0.87**	**7.59**	**0.01**
Constant	2.20±0.75	8.69	<0.001
Model fit: χ^2_4 = 33.3, n = 100, P < 0.001			

Table 1. (Continued).			
Marsh Harrier: male			
Rice	-1.10±0.91	1.47	0.23
Sorghum	-1.10±0.91	1.47	0.23
Dry grassland	**-2.82±0.88**	**10.23**	**<0.001**
Rehabilitated floodplain	-0.81±0.93	0.76	0.38
Constant	2.20±0.75	8.69	<0.001
Model fit: $\chi^2_4 = 16.5$, $n = 100$, $P < 0.01$			
Marsh Harrier: juvenile			
Rice	0.46±0.97	0.23	0.64
Sorghum	-0.64±0.81	0.61	0.43
Dry grassland	**-1.53±0.77**	**3.96**	**0.05**
Rehabilitated floodplain	0.00±0.89	0.00	1.00
Constant	1.74±0.63	7.67	0.01
Model fit: $\chi^2_4 = 8.54$, $n = 100$, $P = 0.07$			

Table 2. GLM of foraging time for sex and age categories given presence on plots on the Logone floodplains in 2009 and 2010. Overall model fit is indicated. Significant values in bold. The reference habitat type is floodplain.

Explanatory variable	***B* ±S.E.**	**Wald χ^2**	***P***
Montagu's Harrier: female			
Intercept	6.56±0.50	5.58	<0.001
Rice	-0.35±0.57	-1.47	0.53
Sorghum	-0.46±0.60	-1.64	0.45
Dry grassland	-0.98±0.87	-2.68	0.26
Rehabilitated floodplain	-0.16±0.76	-1.66	0.84
Model fit: $\chi^2_4 = 1.41$, $n = 32$, $P = 0.85$			
Montagu's Harrier: male			
Intercept	6.12±0.28	5.57	<0.001
Rice	**-0.95±0.47**	**-1.87**	**0.04**
Sorghum	0.44±0.42	-0.39	0.30
Dry grassland	-0.90±0.47	-1.82	0.06
Rehabilitated floodplain	-0.21±0.39	-0.97	0.58
Model fit: $\chi^2_4 = 11.1$, $n = 51$, $P < 0.05$			
Montagu's Harrier: juvenile			
Intercept	5.49±0.35	4.80	<0.001
Rice	0.06±0.46	-0.84	0.89
Sorghum	0.58±0.44	-0.28	0.18
Dry grassland	-0.41±0.47	-1.32	0.38
Rehabilitated floodplain	0.76±0.50	-0.22	0.13
Model fit: $\chi^2_4 = 9.02$, $n = 54$, $P = 0.06$			
Pallid Harrier: female			
Intercept	4.85±0.45	3.97	<0.001
Rice	**1.15±0.51**	**0.15**	**0.02**
Sorghum	1.05±0.59	-0.10	0.07
Dry grassland	-0.09±0.59	-1.25	0.88
Rehabilitated floodplain	-0.29±0.67	-1.61	0.67
Model fit: $\chi^2_4 = 12.9$, $n = 40$, $P < 0.05$			
Pallid Harrier: male			
Intercept	5.50±0.27	4.98	<0.001
Rice	-0.94±0.57	-2.06	0.10
Sorghum	-0.03±0.41	-0.85	0.94
Dry grassland	-0.03±0.52	-1.05	0.96
Rehabilitated floodplain	-0.49±0.42	-1.31	0.23
Model fit: $\chi^2_4 = 3.53$, $n = 43$, $P = 0.47$			

Table 2. (Continued).			
Pallid Harrier: juvenile			
Intercept	5.47±0.41	4.67	<0.001
Rice	-0.02±0.48	-0.96	0.97
Sorghum	0.13±0.50	-0.85	0.80
Dry grassland	0.01±0.52	-1.01	0.99
Rehabilitated floodplain	-0.38±0.53	-1.41	0.47
Model fit: $\chi^2_4 = 1.32$ $n = 53$, $P = 0.86$			
Marsh Harrier: female			
Intercept	5.97±0.24	5.51	<0.001
Rice	0.49±0.33	-0.17	0.14
Sorghum	0.18±0.37	-0.56	0.64
Dry grassland	-0.34±0.55	-1.42	0.54
Rehabilitated floodplain	0.15±0.41	-0.66	0.72
Model fit: $\chi^2_4 = 3.31$ $n = 61$, $P = 0.51$			
Marsh Harrier: male			
Intercept	5.77±0.24	5.31	<0.001
Rice	-0.51±0.35	-1.19	0.15
Sorghum	0.15±0.35	-0.54	0.67
Dry grassland	**-1.58±0.45**	**-2.46**	**<0.001**
Rehabilitated floodplain	-0.42±0.34	-1.09	0.23
Model fit: $\chi^2_4 = 13.5$, $n = 71$, $P < 0.01$			
Marsh Harrier: juvenile			
Intercept	6.04±0.24	5.57	<0.001
Rice	0.65±0.34	-0.02	0.06
Sorghum	**0.72±0.35**	**0.02**	**0.04**
Dry grassland	-0.48±0.39	-1.24	0.22
Rehabilitated floodplain	-0.18±0.34	-0.85	0.60
Model fit: $\chi^2_4 = 15.4$, $n = 78$, $P < 0.01$			

Habitat and prey abundance relationship

Strong relationships were recorded between the main prey categories and habitat types (Table 3). Inter-annual differences were absent for prey and habitat variables ($P > 0.05$) except for mean grass cover, which was lower on plots in 2010 compared to 2009 ($U_{50,50} = 805$, $Z = -2.94$, $P < 0.01$). The abundance of medium-sized and large grasshoppers in the plots was strongly associated with the mean height of the grass layer ($r_s = 0.52$, $n = 100$, $P < 0.001$), and moderately so with the number of woody plants ($r_s = 0.37$, $n = 100$, $P < 0.001$), while nocturnal small mammal abundance was moderately associated with the number of woody plants inside plots ($r_s = 0.36$, $n = 100$, $P < 0.001$).

Harrier diet

The most important harrier prey types in terms of frequency and proportion biomass to the diet were small mammals, grasshoppers, and birds (Figure 4). Grasshopper species in size-classes medium (e.g. *Acorypha clara*) and large (e.g. *Ornithacris cavroisi*) were recorded in pellets of all three species, large species (*Ornithacris cavroisi*, *Acanthacris ruficornis*) constituting the bulk of the grasshoppers identified (75.7%; $n = 214$).

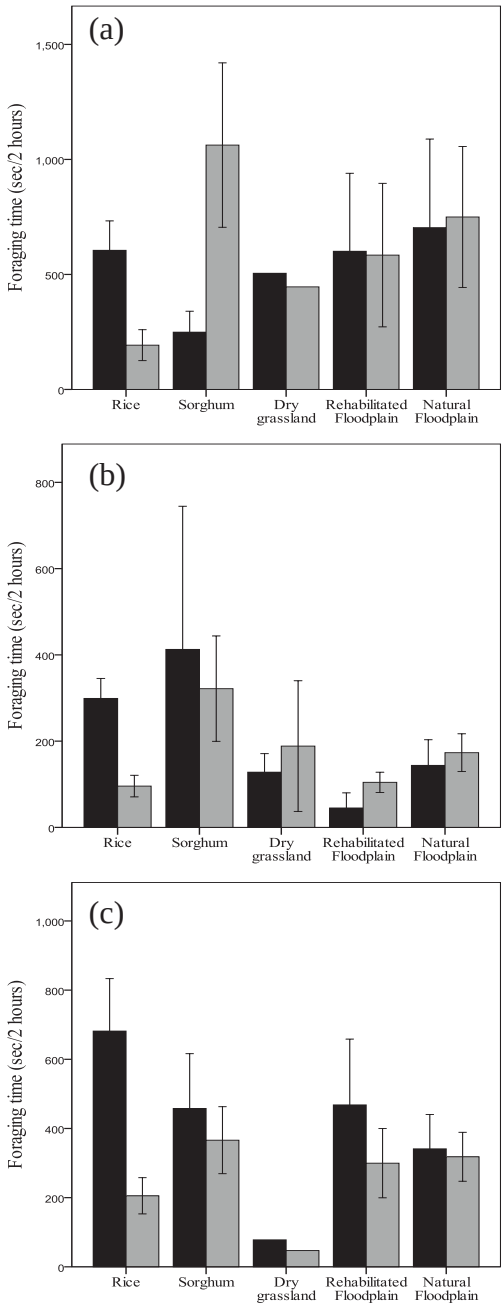

Figure 3. Harrier foraging time by habitat type on observation plots in 2009 and 2010. Foraging time given presence is indicated for female (black bars) and male (grey bars) (a) Montagu's, (b) Pallid, and (c) Marsh Harrier. Data are mean estimates ±S.E.

Table 3. Prey abundance in harrier observation plots within the five major habitat types. Diurnal rodents and nocturnal small mammal abundance estimates are the proportion of traps with positive signs out of 16 traps per observation plot. Passerines and non-passerines represent the number of birds counted in each category within two observation hours in a plot. Grasshoppers refers to the number of medium-sized (m; 30-60 mm) and large (l; > 60 mm) grasshoppers on 1-km transects in the observation plots. Kruskal-Wallis tests were used to explore differences between the five main habitat types. Letters (a, b, c) indicate significant differences ($P < 0.05$) between the groups after pairwise comparisons using Mann-Whitney *U*-tests adjusted by sequential Bonferroni correction. Data are presented as means ±S.E.

Prey type	**Rice (n = 20)**	**Sorghum (n = 20)**	**Dry grassland (n = 20)**	**Rehabilitated floodplain (n = 20)**	**Floodplain (n = 20)**	χ^2_4	***P***
Diurnal rodents	0.66 ± 0.05^{a}	0.63 ± 0.06^{a}	0.27 ± 0.06^{b}	0.18 ± 0.04^{b}	0.05 ± 0.02^{b}	56.8	<0.001
Nocturnal small mammals	0.05 ± 0.02^{a}	0.25 ± 0.05^{bc}	0.35 ± 0.06^{b}	0.10 ± 0.03^{ac}	0.20 ± 0.03^{b}	29.9	<0.001
Passerines	18.25 ± 4.20^{a}	211.4 ± 100.3^{ab}	299.9 ± 191.2^{b}	248.0 ± 121.2^{ab}	1026.9 ± 388.7^{b}	19.9	<0.01
Non-passerines	117.3 ± 49.9^{ab}	4.15 ± 0.79^{a}	18.95 ± 3.88^{b}	80.15 ± 43.43^{b}	37.15 ± 13.18^{ab}	15.7	<0.01
Grasshoppers (m)	3.80±1.07	8.55±2.32	10.7±4.64	6.15±1.68	2.15±0.55	7.64	0.11
Grasshoppers (l)	0.90 ± 0.35^{a}	7.85 ± 2.71^{b}	4.53 ± 1.79^{ab}	9.47 ± 3.54^{b}	2.95 ± 1.03^{ab}	14.2	<0.01

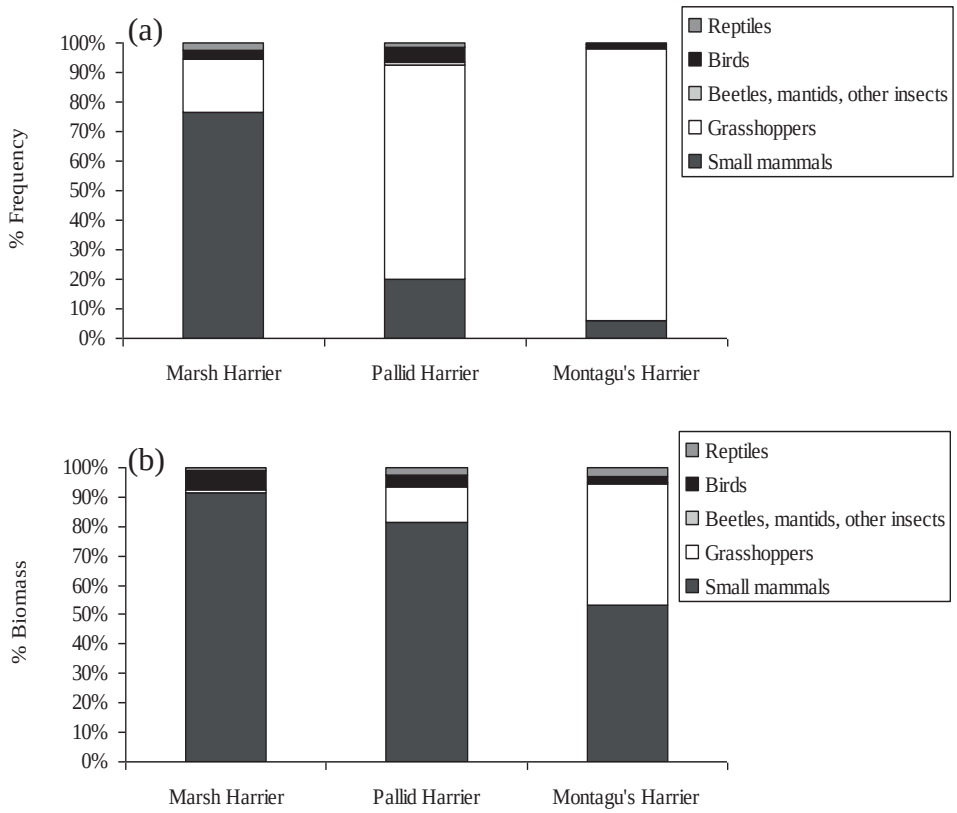

Figure 4. Pellet contents of Marsh Harriers (*n* = 60), Pallid Harrier (*n* = 51), and Montagu's Harrier (*n* = 90) in 2009-2010 in the Logone floodplain of northern Cameroon: (a) prey categories in pellets as percentage of total prey number and (b) as percentage of total prey biomass. Grasshoppers (includes crickets) identified to species: *Acanthacris citrine*, *Ornithacris cavroisi*, *Diabolocantops axillaris*, *Acorypha clara*, *Acorypha glaucopsis*, *Gryllotalpa Africana*.

Small mammals included diurnal rodents, such as Unstriped Grass Rats, which comprised the majority of identified small mammals in pellets of Marsh Harriers (100%; *n* = 35), Pallid Harriers (80.0%; *n* = 15), and Montagu's Harriers (78.6%; *n* = 14), and nocturnal small mammals, such as White-toothed Shrews *Crocidura* spp. and Zebra Mice *Lemniscomys* spp. No significant differences in the percentage frequency of the main prey categories (small mammals, birds, reptiles, grasshoppers, and other insects) were noted between years for Marsh Harrier ($\chi^2_4 = 9.81$, $P = 0.26$), Pallid Harrier ($\chi^2_4 = 7.42$, $P = 0.13$), and Montagu's Harrier ($\chi^2_4 = 9.01$, $P = 0.27$); the same was true for pellets collected in January and March-April (Marsh: $\chi^2_4 = 5.82$, $P = 0.35$; Pallid: $\chi^2_4 = 5.41$, $P = 0.25$; Montagu's: $\chi^2_4 = 3.03$, $P = 0.58$). Mean biomass of prey consumed by Montagu's Harrier (4.97±0.56 g, *n* = 610) was lower compared to mean prey biomass of Pallid (13.4±2.38 g, *n* = 139; $U_{610,139} = 21996$, $Z = -9.94$, $P < 0.001$) and Marsh Harrier (68.8±5.80 g, *n* = 61; $U_{61,610} = 1472$, $Z = -13.8$, $P < 0.001$); mean prey biomass of the latter two also differed

significantly ($U_{61,139}$ = 1278, Z = -8.10, P < 0.001). Dietary overlap between diets according to Pianka's (1973) Index taking into account the percentage frequency of the total prey numbers to the diet for the five main prey categories was 0.34 between Marsh and Montagu's Harriers, 0.48 between Marsh and Pallid Harriers, and 0.98 between Montagu's and Pallid Harriers, indicating an almost complete diet overlap for the smaller species. The percentage contribution of the different prey categories to the diet differed, however, between Montagu's and Pallid Harrier (χ^2_4 = 107.1, P < 0.001), Montagu's and Marsh Harrier (χ^2_4 = 2074.1, P < 0.001), and Pallid and Marsh Harrier (χ^2_4 = 323.6, P < 0.001).

2.4 Discussion

Our results illustrate significant differences in the habitat preferences of male and female harriers, notably in the most weight dimorphic Pallid Harriers, but also in Marsh and Montagu's Harriers. This confirms our predictions and earlier findings in temperate regions (Nieboer 1973, Schipper *et al.* 1975, Clarke 1996, Fritz *et al.* 2000) but constitutes the first such quantitatively documented differentiation in Palearctic raptors on African winter grounds. Differences in foraging distribution was particularly evident in relationship to rice fields for Montagu's and Pallid Harriers, as females selected rice fields over the original floodplain habitat, whereas the opposite was true for males. Possibly, subtle differences in activity patterns of diurnal rodents in relation to particular habitat elements (e.g. presence of water; Sicard *et al.* 1993) governed the preference by female harriers for rice fields compared to sorghum, which had a comparable abundance of diurnal rodents, exceeding diurnal rodent density in non-cultivated habitats. Conversely, male foraging in Montagu's and Pallid Harriers appeared to be geared toward smaller prey items (< 40 g; small mammals, large grasshoppers), which were relatively uncommon in rice fields, which may explain their avoidance of rice fields while foraging.

Although we recorded no agonistic interactions or signs of territoriality (described in Bildstein & Collopy 1985, Temeles 1986, 1987), competitive exclusion from jointly preferred habitats may be too subtle to discern and might have played a role in differential habitat use. Frequent observations of loosely associated foraging parties of different species, sex and age-classes (R. Buij pers. obs.) suggest, however, that opportunistic cuing on the presence of other harriers might be more common rather than avoidance or exclusion behaviour. We tentatively conclude, therefore, that sex differences in preference for food type and size correlated with energy needs (Nagy 1987, 2005), possibly in addition to differences in foraging abilities (Schipper *et al.* 1975, Davygora & Belik 1994, Clarke 1996), underlies the observed patterns of habitat use.

The observed preference for rice and sorghum fields by juvenile Pallid and Marsh Harriers, respectively, lent some support to our prediction that juveniles selected different foraging habitat from adults, assuming juvenile populations were approximately equally sex-balanced. Juveniles might have been particularly attracted to cultivated fields for their high densities of profitable prey (i.e. diurnal rodents), while easy prey detection due to scarce vegetation cover may be an important driver of habitat selection by juvenile raptors (Bustamente *et al.* 1997). Additionally, preference for cultivated fields might have been

stimulated by the foraging success of conspecifics or numerous other raptors using this habitat (Chapter 9), as such clues may also guide foraging in juveniles (Ellis *et al.* 1993, Kitowski 2009, Biondi *et al.* 2010).

Contrary to expectations, we recorded limited evidence for interspecific foraging segregation, apart from the significant avoidance of dry grasslands by Marsh and Montagu's Harriers not evident in Pallid Harriers. Irrespective of the generally comparable patterns of habitat use, the mean prey mass differed significantly between harriers, mainly because heavier species took heavier prey items with greater frequencies, and were related to interspecific differences in body mass which determine food requirements (Nagi 1987, 2005). As expected, partitioning of prey type was most evident in the relatively limited diet overlap between the species which differ most in size (i.e. Marsh and Montagu's Harrier), with almost complete overlap between the similarly-sized species (Pallid and Montagu's Harrier). The pellet sample from the Pallid Harrier roosts probably included Montagu's Harrier pellets at one site, potentially inflating the proportion of grasshoppers to the Pallid Harrier diet (Appendix 2.1). We suspect this did not significantly affect diet analyses, however, since Pallid Harriers greatly outnumbered Montagu's Harriers at the roosts (85% vs. 15% of individuals), while sample quality was further enhanced by our efforts to exclude Montagu's Harrier pellets. Although a sex bias at roosts, most likely females and males for respectively Marsh and Montagu's Harriers (Appendix 2.1), might have biased mean prey mass towards either the higher or lower end of the prey spectrum, it is unlikely that these would have rendered the differences insignificant given the strong degree of prey mass differentiation. We conclude, therefore, that food partitioning by prey mass occurs between wintering harriers and that it is facilitated by a diverse supply of prey related to a mosaic of habitat types on the human-transformed floodplains. Because raptor diet composition and mean prey weight are largely influenced by the available food (Jaksic & Braker 1983), and high food overlap is more likely with abundant prey (Lack 1946, 1971), interspecific dietary differentiation might be less evident early in the winter season (Sep-Dec) when prey is less patchily distributed and prey numbers are higher (e.g. grasshoppers; Mullié & Guèye 2010). Future studies might reveal whether intersexual foraging segregation and interspecific food differentiation occur in sites with more abundant and more homogeneously distributed food resources.

Conservation implications

Our observations suggest that patterns of habitat use in wintering raptors may be obscured by sex and age-specific preferences if sex and age are not integrated into habitat models, potentially leading to erroneous conclusions about the effects of land use change. This is particularly relevant given the often sex or age-biased composition of nonbreeding harrier populations (Thiollay 1977b, Stronach 1991, Arroyo *et al.* 1995, Clarke 1996, Strandberg *et al.* 2008), and might partly underlie some of the equivocal results of habitat associations in wintering harriers (e.g. Morel & Roux 1966, Cormier & Baillon 1991, Clarke 1996, Arroyo *et al.* 2005, Trierweiler & Koks 2009, this study). The comparable use of natural floodplain and cultivated habitats suggests that floodplain conversion for cultivation is not necessarily disadvantageous to harriers. Rather, population explosions of diurnal rodents following

cultivation appear to be a positive development, especially given the generally low availability of diurnal small mammals in the Sahel (Thiollay 1989, Simmons 2000). Furthermore, the interspecific food niche segregation associated with increased landscape and food resource heterogeneity suggests that floodplain development may facilitate co-existence of large numbers of harriers. However, the avoidance of the newly created rice fields and dry grasslands by male Pallid and Montagu's Harriers, and dry grasslands by both sexes of the Marsh Harriers, indicates that floodplain development also has important negative consequences. This is particularly relevant given that a much larger surface area of productive floodplain habitat is generally lost compared to rodent-rich agricultural land gained following embankments to develop rice schemes. The creation of 8000 ha of irrigated rice fields in North Cameroon, for example, resulted in the partial or complete suppression of flooding on 150,000 ha of floodplain habitat, greatly reducing vegetation productivity (Loth 2004, Scholte 2005). Despite largely comparable prey populations to the flooded grasslands, the desiccated grasslands are utilized less often by harriers, possibly caused by the low prey catchability in overgrazed, bush encroached grasslands, where rodent and grasshopper prey may remain concealed from the heat and predators (Chappell & Whitman 1990, Harrison & Fewell 1995, Manson & Stiles 1998, Gray *et al.* 2000), while limited vegetation cover constrains harrier hunting options (Schipper 1977, Preston 1990). We recorded positive relationships between both woody plants and grass height with grasshopper numbers, and woody plants and small mammals, indicating that overgrazing and vegetation clearance negatively affects these harrier food sources. To a certain degree, flooded grasslands are able to cope with the substantial grazing pressure after the floods recede (Scholte & Brouwer 2008), when the extent and depth of the flooding is not severely impacted as well. Limited access of livestock protects the often marginal vegetation cover in cultivated fields, at least until harvest time. Conversely, the high grazing pressure on dry grasslands is intensified by accessibility early in the dry season and a growing shortage of pastures in the Sahel (Turner & Hiernaux 2008), and exacerbated by drought conditions, which are predicted to increase in the future (e.g. Hulme *et al.* 2001, Held *et al.* 2005). Such conditions are likely to lead to irreversible vegetation degradation (e.g. Van de Koppel & Rietkerk 2000), exhausting prey populations (e.g. Fielding & Brusven 1995, Dennis *et al.* 1998, Fabricius *et al.* 2003, Blaum *et al.* 2007) to the detriment of raptors (Herremans & Herremans-Tonnoeyr 2000).

Our results show that harrier foraging on rehabilitated floodplains is similar to the pre-dam situation, with comparable prey populations 16 years after reflooding. Whereas floodplain rehabilitation is desirable from various other ecological and socio-economical perspectives (Scholte 2005), further loss of floodplain habitat in the Sahel seems inevitable to satisfy the increased demand for rice and heavy subsidies associate with its large-scale production. Between 1961 and 2008, the area cultivated with sorghum increased from 6.6 to 13.3 million ha, while that of rice increased from 0.4 to 3.2 million ha in six Sahelian countries with large floodplain systems (FAOSTAT 2011). The high human population growth rate for the Sahel (*c.* 3% per year) is projected to further boost particularly urban populations (3.8 fold increase between 2010 and 2050 for six Sahelian countries with floodplains, 1.4 fold for rural populations; FAOSTAT 2011), leading to an increased demand for rice over more traditional foods such as sorghum (Zwarts *et al.* 2009). In addition to the detrimental

effect of lost floodplain productivity, the often unregulated utilization of highly hazardous pesticides in rice fields constitutes a threat to wintering harrier populations (Mullié *et al.* 1991, Keith & Bruggers 1998). The anticipated further large-scale loss of floodplain habitat coupled with intensification of the existing cultivated habitats raise concerns about the impact of future Sahelian floodplain development on the survival of wintering harriers. The high conservation value of the remaining floodplain habitat and associated agricultural fields for harriers calls for close monitoring of future developments affecting these habitats.

Appendix to Chapter 2

Appendix 2.1. Harrier pellet samples. Information on pellets collected at roost sites of Montagu's (Mo), Pallid (P) and Marsh Harriers (M) from January-April in 2009 and 2010. The number of different roost sites where pellets were collected is given, the mean maximum number of individuals at each roost site, the number of pellets collected, the number of pellets used for analyses, the dominant habitat surrounding the roost, and the mean percentage contribution of each sex and age category to the individuals visiting the roosts.

Sp.	**Roost sites (*n*)**	**Mean max. number/ roost**	**Pellets collected (*n*)**	**Pellets analyzed (*n*)**	**% adult male (range)**	**% adult female (range)**	**% unsexed juvenile (range)**
Mo	3	22 (9-42)	> 500	90	59 (45-73)	20 (15-22)	21 (19-33)
P[1]	4	7 (1-15)	51	51	17 (7-25)	10 (5-15)	73 (65-88)
M[2]	2	43 (25-60)	255	60	19 (14-23)	unknown	unknown

[1] The large roost was also visited by five male (two adults/three juveniles) Montagu's Harriers.
[2] No distinction could be made between females and juveniles at the roosts due to low light conditions during arrival of most birds at the roosts.

Appendix 2.2. Harrier foraging bouts on observation plots for species, habitat, and year. The total number of harrier entries into observation plots in 2009 (*n* = 50 plots) and 2010 (*n* = 50 plots) is indicated. Ri = rice, So = sorghum, Dr = dry grassland, Rf = rehabilitated floodplain, Fl = floodplain.

	2009						**2010**					
Species	**Ri**	**So**	**Dr**	**Rf**	**Fl**	**Total**	**Ri**	**So**	**Dr**	**Rf**	**Fl**	**Total**
Montagu's Harrier	37	48	16	33	24	**158**	34	53	15	28	45	**175**
Pallid Harrier	50	36	27	23	26	**162**	53	24	17	9	44	**147**
Marsh Harrier	120	113	34	85	105	**457**	127	67	15	50	88	**347**

Box A

Pallid Harrier bird hunting behaviour and capture success in northern Cameroon

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Published in:

Ostrich (2012), 83: 27-32

Abstract

Little is known about foraging by Palearctic harriers on their wintering grounds, while such information may aid conservation efforts. I present detailed observations of Pallid Harrier *Circus macrourus* behaviour when hunting birds, the bird prey species and bird capture success in northern Cameroon. Four hunting strategies are described to capture birds: fast contour flight, overt approach with rapid acceleration, covert ambush, and stoop from flight. Capture success of 149 bird capture attempts by 47 Pallid Harriers was 18.8%, but it differed with hunting strategy used. Covert ambush and overt approach strategies were more successful compared to fast contour flight. Red-billed Quelea was the most commonly targeted and captured bird prey.

Left: Male Pallid Harrier at the edge of a waterhole in Waza National Park.

Introduction

The foraging strategies and predatory success of Palearctic harriers in their wintering quarters are insufficiently known, while such information may aid conservation efforts. This is particularly true for Pallid Harriers *Circus macrourus* wintering in sub-Saharan Africa and India (Brown *et al.* 1982, Galushin *et al.* 2003). In the breeding areas in Kazakhstan, Pallid Harriers target mainly small mammals (72% of total prey biomass) during high vole abundance years, and capture success decreases as vole abundance decreases; during periods of low vole abundance, the proportion of reptiles and particularly birds (up to 59% of total biomass) in the diet increases (Terraube *et al.* 2011). Despite the specialization on small rodents on the breeding grounds, as well as morphological features that suggest a superior capacity to detect rodents compared to other harriers (i.e. a well-developed facial disc; Terraube *et al.* 2011), other morphological features enable fast flight and agility needed in pursuit of bird prey (Davygora & Belik 1994, Clarke 1996). These include relatively short and pointed wings, comparable to other bird-eating raptors such as falcons. The similarity of Pallid Harriers to bird-eating raptors is further justified by a comparatively high index of sexual dimorphism (0.7; Del Hoyo *et al.* 1994). Apart from orthopterans, birds are supposed to be important prey on wintering grounds, supplemented by small rodents and reptiles (Clarke 1996, Ferguson-Lees & Christie 2001, Naoroji 2006). Birds known to be caught include passerines (larks and pipits), lapwings, doves, and crows (Davygora & Belik 1994, Clarke 1996, Naoroji 2006). On the breeding grounds, Pallid Harriers have been observed catching birds by forcing them high enough to be caught in the air (Davygora 1985), sometimes executing complicated aerial pirouettes in pursuit of passerine birds (Davygora & Belik 1994). Observations of wintering male Pallid Harriers in India have shown that the hunting flight to capture larks is fast, low and direct, using the stands of taller grass to conceal the attack (Clarke 1996). Stoops at passerines on or close to the ground have also been observed in India. Apart from these observations, quantitative and qualitative detailed information about foraging techniques and hunting success by Pallid Harriers in the wintering areas is scarce, particularly in Africa. A frequently observed hunting strategy by Pallid Harriers in the Lake Chad region of northern Cameroon is a low quartering flight (R. Buij pers. obs.), involving characteristic flaps-with-glides on outstretched wings. The harrier typically moves with wings raised and at relatively low speed at 1-6 m altitude or occasionally higher above the ground, scanning for ground-dwelling prey, notably orthopterans and rodents. Once prey is detected, the harrier rapidly turns to the ground, frequently twisting at a 90˚ angle to catch prey on the ground. Predatory success is difficult to assess under these conditions, as harriers often fly off with the quarry to feed on it elsewhere, or consume it on the spot and often out of sight in dense grass. Compared to ground-dwelling prey, capture success is more easily assessed when birds are targeted, as these are most often caught in the air. Whereas rodents and orthopterans constituted resp. 14% and 78% of total prey items in pellets collected on the Waza-Logone floodplains south of Lake Chad (Chapter 2), birds are less frequently captured, as suggested by a 6% frequency among remains in pellets. Contrary to the highly productive and prey-rich floodplains of the Lake Chad region, however, birds may be more frequently hunted in poorer habitats where other prey is scarce, as was observed in the Velavadar grasslands in India (Clarke 1996). Here, we present a detailed description of

foraging behaviour and capture success for each of the hunting strategies used by Pallid Harriers in northern Cameroon where bird prey is involved.

Materials and methods

The Waza-Logone region in the Far North of Cameroon (10-12˚N, 14-15˚E) is characterized by open woodland savanna with scattered waterholes inside and surrounding the Waza National Park, marshes, cultivated (sorghum, rice, millet, onions) fields with scattered trees and shrubs, and seasonally inundated grassy floodplains bordering the Logone River. It has the highest density of Pallid Harriers in northern Cameroon (cf. Chapter 10). Opportunistic observations of hunting Pallid Harriers were made in a *c.* 6,500-km^2 study area (Figure 1) from inside a car (at water sources), a high vantage point (rooftop of a car or a termite mound), or on foot, using 10x42 binoculars, between October 2006 and April 2010.

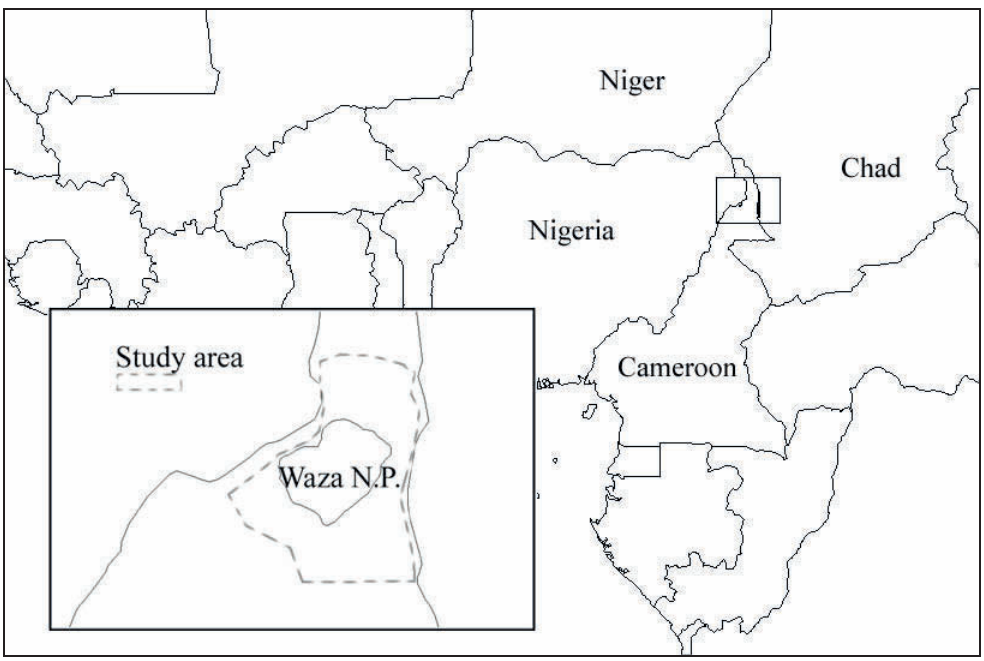

Figure 1. Map of the study area in northern Cameroon.

Most observations were made between January and March and from 06:00-09:00 and 16:30-18:00. To arrive at an unbiased sample of bird hunting behaviour which prevented overrepresentation of certain sex and age groups, all Pallid Harriers observed < 200 m of the author and attempting to capture bird prey were included in the analysis. Hunting behaviour was classified into four strategies:

1) fast contour flight. The harrier uses edges of farmland, bushland, dikes, and stands of tall grass as cover to ambush bird prey. The harrier flies rapidly, alternating series of strong wingbeats with gliding on flat or slightly raised wings, often very low (5-50 cm) but also higher (1-7 m) above the ground. The wings are held back at the carpal point, quite unlike the outstretched wings of most foraging harriers. When ditches are used, harriers fly fast with their body almost touching the ground in the ditch to suddenly sweep over the edge of the ditch. The harrier thus makes a concealed approach even when herbaceous vegetation is absent (e.g. in recently ploughed rice fields). Although large areas are frequently traversed in a rapid straight line using this strategy, harriers also repeatedly return to smaller foraging areas (1-2 ha) and fly rapidly between bushes and trees, frequently changing direction and speed when pursuing birds;

2) overt approach with rapid acceleration. Different from the previous in that the harrier does not make an effort to conceal itself as it approaches. Attacks are usually directed at flocks of birds, and harriers fly at them at medium to high speed, 1-25 m above the ground. Harriers often accompany the flocks by flying parallel with them (Figure 2), frequently accelerating to attain greater speed during capture attempts. Birds are isolated from the group and caught in the air;

Figure 2. Adult male Pallid Harrier *Circus macrourus* flies parallel to a flock of Red-billed Queleas *Quelea quelea*

3) covert ambush. The harrier hides on the ground, usually in the shade underneath or behind dense low shrubs and bushes (e.g. *Piliostigma reticulatum*), on a branch of a low tree at the water's edge, or behind tufts of tall grass inside or at the edge of the waterhole. Hunts are occasionally initiated from a more exposed position on the ground (Figures 3a,b). As soon as birds start descending to the water's edge to drink, attacks are mounted from the covert position Birds are either caught after short pursuits, often with rapid turns and twists, or the attempt is terminated after 2-7 sec. The harrier subsequently returns to an ambush position (individuals were observed to regularly return to the same ambush positions), waiting for other birds to arrive at the water, or departs from the site;

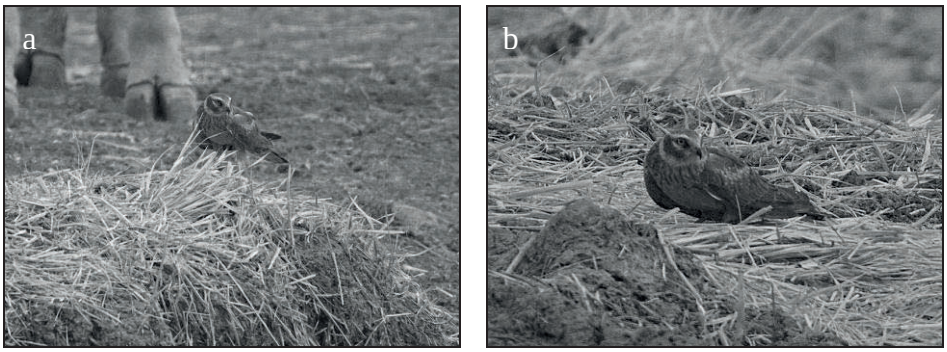

Figure 3. (a) Juvenile male Pallid Harrier waiting for Red-billed Queleas to arrive at a waterhole and (b) crouching at the arrival of a flock of birds at the waterhole

4) stoop from flight. The harrier circles to a height of 50-150 m and dives down in a rapid descent with arched wings raised above the body and closed tail held upwards, to stoop at birds foraging on the ground.

Capture attempts were defined as an attempt to catch a bird involving a directed flight towards a potential bird prey which is approached to within 5 m. Whether strikes were successful or not was always obvious: birds were almost always caught in the air and carried off to be plucked elsewhere. Photographs were taken of all harriers and examined later to determine sex and age and in some cases to identify the prey species. Harriers were classified to age (1-2nd, 3rd and > 3rd cy) and sex following Forsman (1999). All harrier hunting attempts were GPS referenced using a Garmin GPS device. The habitat at the location (circle with a 100-m radius centred on the harrier) where the hunting attempt was made was classified into four categories: (1) water source: artificial or natural depression which holds water throughout the dry season, usually in woodland savanna but also in more open grassland savanna, (2) dry open woodland: wooded grassland dominated by *Sclerocarya birrea*, *Acacia seyal*, *Tamarindus indica* and *Balanites aegyptiaca* trees, largely inside and south of Waza N.P.; (3) floodplain: largely treeless grasslands bordering the Logone River east and north of Waza N.P., which are partly flooded from August to November, and (4) rice fields: located north of the Lake Maga dam and along the Logone River and cultivated biannually between April-October. Theoretically, harriers may have been repeatedly sampled as they were not marked. Repeated sampling of the same

individuals on different days was probably negligible, however, given the high harrier density, their mobility as well as coverage and size of the study area and duration of the study. To further reduce the likelihood of repeated sampling of individuals we excluded from the sample those capture attempts by harriers of similar sex and age observed in the same month and in the same general area (defined as a circle with a 5-km radius around the harrier). At waterholes, distinct barring on the underside of the primaries of females and juveniles and various plumage features in adult birds, visible on photographs, always allowed distinction between individual harriers at least during the same winter period. In total, hunting attempts by 47 individuals were recorded. Thirty-five individuals were observed to perform multiple attempts and their hunting success was determined as the mean capture success for their capture attempts combined. Chi-square and Mann-Whitney *U*-tests were used to investigate differences in hunting success between sex and age categories and for different hunting strategies. Hunting attempts in which a combination of tactics was used were excluded.

Results

Table 1 presents data on the different hunting strategies, including the capture attempts observed for males and females.

Fast contour flight

A regular hunting technique used by Pallid Harriers in the Lake Chad area, in all habitats. Both male and female Pallids were seen following edges of bushland or agricultural fields ("contour-hugging") and suddenly "hopping" over bushes, grass tufts and reeds to surprise prey on the other side. This strategy was used to surprise attack a variety of birds from small passerines (Red-billed Quelea *Quelea quelea*, Yellow Wagtail *Motacilla flava*, *Ploceus* species) to waders (*Tringa* sp., Spur-winged Lapwing *Vanellus spinosus*), Clapperton's Francolins *Francolinus clappertoni* and young Helmeted Guineafowl *Numida meleagris*. Red-billed Queleas were often chased as the harrier weaved through clumps of bushes and trees; they were caught in three instances following a fast contour flight strategy.

Overt approach with rapid acceleration

This hunting strategy was observed on the floodplains where Pallid Harriers hunted Red-billed Queleas and other seedeaters as these congregated in large numbers (several 100,000s in a 1 km^2 area) at the end of the dry season, between February-April. Two to five Pallid Harriers were observed accompanying a quelea flock simultaneously. All successful attempts (n = 4) were directed at queleas. The advantage of simultaneous attacks by several harriers may be to create confusion among Red-billed Queleas, making them easier to isolate from the flock. It may also have a downside, however, as successful attempts are easily observed by other harriers. Kleptoparasitism was recorded in one instance where a male Pallid Harrier was robbed of its food by a female Pallid.

Covert ambush

Observed at three waterholes out of a total of 10-15 waterholes (natural and artificial) in the study area depending on time of the year, inside and around the Waza National Park and mostly during the second half of the dry season (Feb-April). On six occasions, capture attempts were opportunistically mounted when a drinking harrier observed a flock of drinking birds at the waters' edge (Figures 4a,b). Three harriers (out of a total of 10 individuals observed) crouched very low to the ground before mounting an attack (Figures 3 and 4). A 2nd cy male Pallid Harrier kept its body flat on the ground for 5-10 sec while waiting in ambush in at least six out of 11 attacks observed, adopting a posture reminiscent of incubation. Attacks were mounted 10-30 m from the intended prey which was approached in rapid flight at 10-150 cm above ground level (Figure 5a). The behaviour was observed in the morning hours on clear, hot days (09:00-11:00) and in the afternoon (15:30-17:00), during peak hours for drinking birds. One particularly successful 2nd cy male Pallid Harrier caught an Ethiopian Swallow *Hirundo aethiopica* on two occasions after an ambush attack, in a period of 25 min. Prey was transported and consumed at 45 m or more from the waterhole, usually in the shade underneath a bush, probably to avoid losing the prey to other raptors at the waterhole (Figure 5b). Once, a Red-billed Quelea fell into the water after being pursued by a 3rd cy female Pallid Harrier, after which the harrier caught the bird in the water and dragged it on land. Red-billed Queleas were caught in 13 out a total of 67 covert ambush attacks observed. Other prey caught using this strategy included a Cut-throat *Amadina fasciata* (1), Yellow Wagtail (1), *Ploceus* species (2), and Namaqua Dove *Oena capensis* (1).

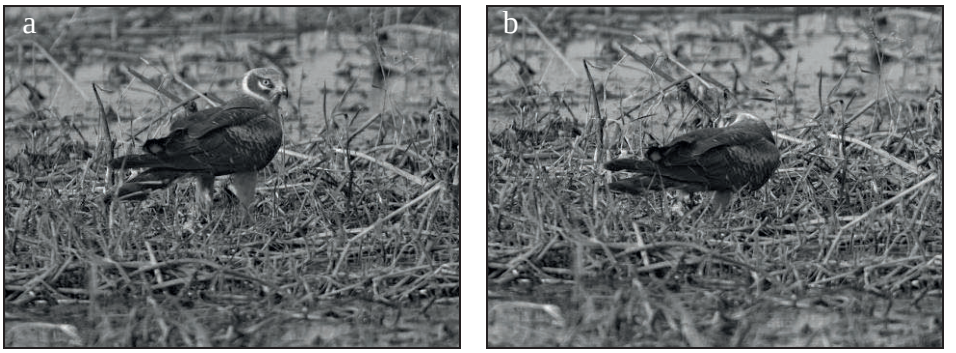

Figure 4. (a) Juvenile male Pallid Harrier scanning for birds while occasionally drinking and (b) crouching as potential prey arrives

Stoop from flight

This strategy was observed only twice on the floodplains. Two male (ad/2nd cy) Pallid Harriers were observed stooping on a Yellow Wagtail (successful) and a Red-billed Quelea (unsuccessful).

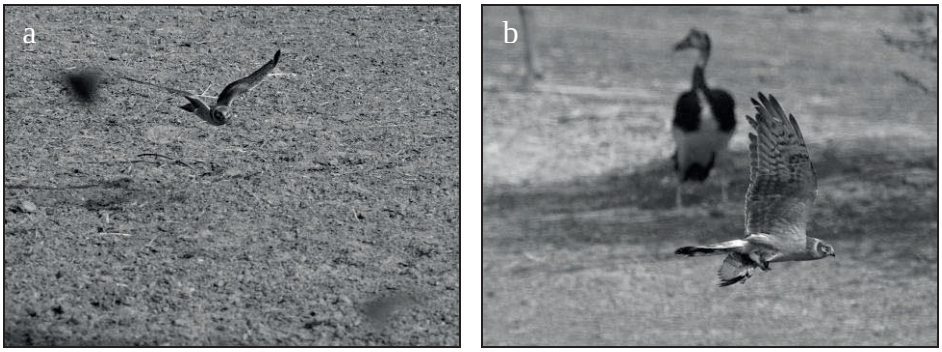

Figure 5. (a) Juvenile male Pallid Harrier in low, fast flight at Red-billed Queleas after covert ambush at a waterhole and (b) departing for cover after having caught a Namaqua Dove at a waterhole

Prey capture success with age and sex

Overall, bird prey capture success of Pallid Harriers in the Lake Chad Basin was 18.8% (n = 149), but it differed with hunting strategy used (Table 1). Covert ambush was significantly more successful than the other commonly observed hunting technique, fast contour flight, when all capture attempts are considered ($\chi^2_1 = 12.3$, $P < 0.001$) and when individual capture success is compared ($U_{10,25} = 66.5$, $Z = -2.78$, $P < 0.01$). Overt approach attempts were marginally more successful than fast contour flight overall ($\chi^2_1 = 3.02$, $P = 0.08$), and per individual ($U_{10,25} = 90.0$, $Z = -1.83$, $P = 0.07$). No significant difference was recorded between the overall capture success of overt approach and covert ambush attempts ($\chi^2_1 = 1.36$, $P = 0.24$), or between individuals using these strategies ($U_{10,10} = 42.0$, $Z = -0.65$, $P = 0.52$). Capture success was similar between the sexes for all capture attempts combined ($\chi^2_1 = 0.001$, $P = 0.97$) and for individuals separate ($U_{11,36} = 165.0$, $Z = -1.03$, $P = 0.31$). More bird capture attempts were recorded for males than females: 71.1% of capture attempts (n = 149) and 76.6% of individuals involved in capture attempts (n = 47) were males. No effect of age was found on capture success for all capture attempts combined ($\chi^2_1 = 0.82$, $P = 0.37$) and for individuals separate ($U_{27,20} = 223.0$, $Z = -1.25$, $P = 0.21$): 15.7% of strikes was successful in immature (1st and 2nd cy; n = 70) harriers and 21.5% in adults (3rd cy and older; n = 79). Most successful attempts were observed near a water source (78.6%), 21.4% of captures occurred on the floodplain. Red-billed Queleas were targeted (58.6% of bird capture attempts) and captured (71.4% of successful attempts) most often.

Discussion

These are the first detailed observations of bird hunting by Pallid Harriers on the African winter grounds. Although observations were conducted in a tiny portion (< 0.1%) of the *c.* 11 million km^2 winter range of the Pallid Harrier in Africa, they cover a wide range of winter habitats from more localized rice fields and floodplains to more typical winter habitat such as open grassland and dry savanna (Ferguson-Lees & Christie, 2001), and are

likely to be representative for bird hunting behaviour in other parts of the African winter range. Pallid Harriers frequently hunt birds in northern Cameroon using a fast contour flight. A similar strategy was employed to catch larks in winter in India (Clarke 1996, Naoroji 2006) and passerines on the central Asian breeding grounds (Terraube *et al.* 2011).

Table 1. Hunting strategy, number of males (M) and females (F) observed, number of attempts, and hunting success for the three common hunting strategies in northern Cameroon. FCF = fast contour flight; OARA = overt approach with rapid acceleration; CA = covert ambush. Dominant habitat is indicated by WS = water source, WD = dry open woodland, FL = floodplain, and RF = rice fields. Mean capture success per individual represents the mean percentage successful attempts of the total number of attempts observed for each individual. Overall capture success is the percentage of successful attempts for all attempts observed.

Hunting strategy	**M**		**F**		**Attempts per ind. ±S.E.**	**Capture success per ind. ±S.E.**	**Overall capture success**	**WS**	**WD**	**FL**	**RF**
	Ind.	**At.**	**Ind.**	**At.**							
FCF	17	41	8	16	2.28±0.26	6.67±4.30	5.26	39	5	9	4
OARA	10	23	-	-	2.30±0.34	17.5±7.50	17.4	-	-	23	-
CA	7	40	3	27	6.70±1.48	25.6±10.4	29.9	67	-	-	-

Similar to the situation in India, most attempts to catch birds in Cameroon were conducted by males. As the proportion of males to females wintering in the region is approximately equal (Chapter 2) and the analyses include a representative sample of bird-hunting Pallid Harriers in the area, the results suggest that males target birds more frequently than females. These observations are consistent with subtle differences between the sexes in structural characteristics, such as wing shape, related to higher agility in males (Davygora & Belik 1994, Clarke 1996). Additionally, differences in habitat utilization between the sexes in the region suggest that females preferably target rodents in rice fields, whereas males prefer floodplain habitat over rice, possibly due to the greater abundance of passerines on floodplains (Chapter 2).

The bird capture success using fast contour flight on the Waza-Logone floodplain is relatively low at least compared to the two other common strategies. Considering the frequent use of this hunting strategy in rice fields (with abundant rodents but relatively few passerine birds), particularly by female Pallid Harriers, it may also be effective to capture rodents by surprise, although we have no data to support this. In contrast to fast contour flights, covert ambush behaviour was not previously described for Pallid Harriers, although other open grassland raptors are known to ambush rodent prey; Ferruginous hawks *Buteo regalis* often crouch waiting at a burrow (Wakeley 1978), and a Steppe Eagle *Aquila nipalensis* was observed ambushing a ground squirrel (Tingay 2008). Pallid Harriers use an ambush technique to capture birds, notably Red-billed Quelea, which was the most commonly captured bird in the study area. At the time when flood waters have receded almost completely from the Waza-Logone floodplains by Feb-Mar, Red-billed Queleas gather in large flocks at water sources and to feed on ripened grass seeds, making them a conspicuous and superabundant food source. Bird prey capture success of Pallid Harriers in the Lake Chad Basin is comparable to bird capture success of Northern Harriers *Circus hudsonius* (Toland 1986), African Marsh Harriers *Circus ranivorus* (Simmons 2000), and

Pallid Harriers in Kazakhstan in low vole years, when they are feeding mainly on birds (Terraube *et al.* 2011). Given the greater frequency of other, less agile prey (rodents and orthopterans) in the Pallid Harrier diet compared to bird prey, overall prey capture success is probably higher. On the other hand, bird capture success differs with hunting strategy used and one successful strategy, covert ambush, is likely to be overrepresented in our sample, accounting for 45% of the observed capture attempts but observed only at water sources. Another fairly successful strategy, overt approach with rapid acceleration, was observed exclusively where Red-billed Queleas congregated in flocks numbering several 1000s. Since such congregations of queleas are temporally and spatially restricted to specific areas and the majority of Pallid Harriers hunt away from relatively scarce water sources most of the time, mean bird capture success by wintering Pallid Harriers in the Lake Chad Basin is likely to be lower than 18.8%.

Habitat structure is an important factor influencing hunting behavior, and certain habitat elements are a prerequisite especially for covert ambush and fast contour flight. Pallid Harriers were seen to use stands of tall grass and shrubs to surprise attack queleas and other prey. Covert ambush attacks were exclusively seen near waterholes surrounded by green shrubs and tall grass within 40 m of the water, used by queleas and other birds for perching and cover and by harriers to hide before an attack. Overgrazing, bush fires, and extensive bush clearance in particular near water are therefore likely to negatively impact Pallid Harrier hunting options. In addition, the widespread misuse of pesticides to kill birds for consumption at water sources represents a threat to Pallid Harriers, as well as secondary poisoning during quelea control operations (Keith & Bruggers 1998). Intersexual differences in prey preferences and habitat utilization may result in differences in vulnerability to land use change and pesticide use. Further investigations on the diet and prey capture success, including rodents and orthopterans, by both sexes under different land use regimes are needed to fully understand the impact of habitat transformation on Pallid Harrier foraging in the winter range.

Chapter 3

Breeding biology and nestling development of the Grasshopper Buzzard

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Published in:

Ostrich (2012), 83: 137-146

Abstract

Research into the effect of environmental variables on reproductive success of tropical raptors is often constrained by the lack of information on breeding biology. We provide the first detailed information of the breeding biology and nestling development of the Grasshopper Buzzard *Butastur rufipennis*, an Afrotropical migratory raptor threatened by extensive land transformation in its breeding range. Breeding coincided with the transition from the dry to the wet season. The mean incubation period was 30 days and mean fledging period 36 days. The breeding period was characterized by rapid establishment of territories and short post-fledging dependency periods related to the onset of migration shortly after breeding. Growth rate of body mass, tarsus, wing and primary feathers were similar between sexes, which showed significant but moderate body mass dimorphism at fledging (♂85-90% of ♀). Second hatchlings were smaller in body mass and structural dimensions compared to similarly-aged first hatchlings and singles of the same sex. Survival of second hatchlings was related to body mass ratio with first hatchlings, while brood reduction occurred through food competition and siblicide. We provide ageing formulae and photographic records to facilitate further studies of Grasshopper Buzzard nestling development and reproductive success in the region.

Left: Grasshopper Buzzard at perch in Waza National Park.

3.1 Introduction

Little quantitative information exists on the breeding biology, nestling growth and development of the majority of raptors in tropical Africa (Virani & Watson 1998), despite the importance of such information for conservation management of threatened species (Steenhof & Newton 2007). The breeding biology and nestling development of the Grasshopper Buzzard *Butastur rufipennis* are largely undescribed, apart from anecdotal accounts of nests in Niger and Mali (Cheke 1995, Brouwer *et al.* 2000), and despite its status as the second most common Afrotropical raptor in western Africa (Ferguson-Lees & Christie 2001). Grasshopper Buzzard populations migrate roughly between 7-18ºN in West Africa, exploiting abundant and easily accessible prey following rains northwards and increasing prey availability, notably grasshoppers, as dry season fires and grazing reduce grass cover southwards (Thiollay 1978a). During the breeding season, insects and reptiles are the most commonly taken prey, but reptiles, mammals, and amphibians dominate the prey biomass (Chapter 4). The species' main breeding area ranges between 9-15ºN (Ferguson-Lees & Christie 2001) and coincides almost entirely with the Sudano-Sahelian and Sahelian climate zones, exposing it to the rapidly changing and increasingly deteriorating breeding conditions for raptors in this region (Thiollay 2006a, 2007a). The widespread over-exploitation of the habitat following explosive human population growth in this region contributed to significant Grasshopper Buzzard population declines such as those reported in protected (-33%) and cultivated areas (-57%) in a large region of Sudano-Sahelian West Africa between 1969 and 2004 (Thiollay 2006a). In light of these declines, detailed information on the breeding biology of the species is urgently required to assist studies that attempt to evaluate reproductive output in the increasingly transformed breeding habitats.

In this chapter, we describe for the first time aspects of the breeding biology of the Grasshopper Buzzard based on 2 years of observations (2009 and 2010) in northern Cameroon. We quantify growth and development of nestlings, including the timing of plumage development and growth rate of different body parts. We investigate the influence of sex on body and feather growth, and how nestlings order in the hatching sequence influences growth, development, and survival. Lastly, we present a morphological guide and develop ageing formulae that will aid further studies into reproductive success in this species.

3.2 Materials and methods

The study was conducted between 2 May and 22 July 2009 and 3 May and 25 July 2010, in and southwest of the Waza National Park in the Far North of Cameroon (11°00'N-11°40'N and 14°20'E-15°00'E), covering *c*. 14 km^2 (2009) and 20 km^2 (2010) inside the National Park and 32 km^2 (2009) and 20 km^2 (2010) in the cultivated habitat. The topography of the area is generally flat with some gentle slopes and rocky outcrops. The vegetation is characterized by open woodland dominated by *Sclerocarya birrea*, *Anogeissus leiocarpus*, and *Balanites aegyptiaca*. The habitat inside Waza National Park consists of mature and

largely intact woodland savanna, whereas the human-dominated, disturbed habitat outside Waza National Park is characterized by a mosaic of cultivated fields (notably sorghum and millet), settlements, and fragments of heavily exploited woodland. The climate is semi-arid with a dry season from November to April, when the first rains occur, followed by a wet season from May into October, with a mean annual precipitation of *c*. 500 mm. Mean annual temperature is 28 ºC and peaks before the rainy season from March-May when temperatures of 47 ºC are reached, with a mean daily minimum of 21 ºC and mean daily maximum of 41 ºC.

Nestling measurements and growth patterns

The study area was intensively searched for Grasshopper Buzzard nests between 2 and 18 May in 2009 and between 3 and 16 May in 2010, which coincided with the first half of the incubation period for three nests at this latitude in 2008 (R. Buij pers. obs.). All occupied Grasshopper Buzzard nests, defined as those nests lined with green leaves and/or containing one or more eggs or nestlings, were GPS marked and their status (e.g. green lining, number of eggs) recorded. Additional nest searches in the second half of May and June were combined with visits to occupied nests. Nests without eggs were revisited at 1-week intervals to determine their status until 4 weeks after discovery and were declared abandoned in the absence of adults attending. Nests which had failed early in the breeding season (first two weeks of May) were revisited 2-3 times at later stages (20 May-15 June) to investigate whether renesting had occurred. We used a mirror on a pole to record the clutch size in order to reduce time spent at the nest and subsequent disturbance to a minimum. At later stages, nests were accessed by climbing the trees.

Occupied nests were revisited at approximately two-weekly intervals during incubation, at averagely 7-day intervals following hatching in 2009, and at averagely 5-day intervals (due to increased human resources) following hatching in 2010. The morphological and morphometric development of nestlings was studied from hatching to nestling death or fledging, or later until it became impossible to capture the young. In case nestlings fledged prematurely as a result of our actions, they were returned to the nest. Nests were not visited at higher intensity during hatching to avoid unnecessary disturbance. Nestlings still damp when first measured were classified as hatching on the day of the visit, while dry nestlings were classified as having hatched either the day before or two days previous to the visit depending on features of nestlings of known age, such as opening of the eyes, posture and coordination. Eggs that were opened on the day of the visit were noted as hatching the same day or the day after the visit depending on the size of the opening (crack or larger opening). Hatch date was taken as day 0. When additional nestlings or eggs were present on the nests, nestlings were marked on the right or left tarsus using a waterproof marker pen, which was repeated on subsequent visits. Photographic records (dorsolateral view) were made of the body plumage development of all nestlings in 2010 at each measurement, allowing estimation of the timing of the emergence of second down and appearance of body feathers. As nestlings were not inspected at daily intervals, feather development data for each feature were estimated from a proportion of nestlings (25-30%; n = 224).

We measured body mass, tarsus, wing length, and length 8th primary for each nestling at each visit. The terminology for body parts follows Boal (1994). Wing length was measured to the nearest mm as the chord between the carpal joint and the tip of the 8th or longest primary when flattened against a stopped ruler. Prior to the emergence of flight feathers the distance between the tip of the radius ulna and the carpal joint was measured. Length of the 8th primary was measured as the distance between the tip and base of the 8th primary. Tarsus length was measured to the nearest mm with a caliper. Body mass was measured using digital scales accurate to 0.1 g. The wing and 8th primary length were thought to potentially aid in aging nestlings. Wing measurement used to generate age formulae were restricted to those nestlings for which hatch dates were known to the nearest day and which fledged. Incubation periods were calculated for nine breeding pairs with known laying and hatching dates. Hatch dates of nestlings of unknown age were calculated from wing measurements and were used to calculate mean laying date (cf. Olsen & Olsen 1987). Fledging periods were assessed from nests which were visited until all nestlings had fledged.

To sex nestlings, a small blood sample (0.01 ml) from the alar vein was obtained from the nestling when it was older than *c.* 15 days. All nestlings surviving to that age were molecularly sexed in 2009 and 2010 using the primers described in Fridolfsson & Ellegren (1999) and an adjusted version of their PCR methods. PCR products were separated by electrophoresis on a 2% agarose gel, and visualized by ethidiumbromide staining. Females could be identified by two bands on the agarose gel, while males showed only one, which concurred with results in the majority of species (Kahn *et al.* 1998, Fridolfsson & Ellegren 1999).

Individual growth curves were graphically fitted (Ricklefs 1967) to body mass, tarsus, and wing measurements for 50 male and 36 female nestlings at 73 nests measured in 2009 and 2010. Curves were not fitted to data for nestlings when early measurements were missing or asymptotes were difficult to estimate due to premature death of the nestling, as this reduces the reliability of estimating growth parameters. The growth pattern of nestlings was defined by asymptote values for body mass, tarsus, and wing length estimated by fitting Gompertz and logistic equations to the growth data following the method proposed by Ricklefs (1967). These models fitted the data better than von Bertalanffy models, which were also tried. Similarly, we estimated the time interval for growth from 10 to 90% of the body mass asymptote ($W_{10\text{-}90}$), tarsus ($T_{10\text{-}90}$), and wing ($Wi_{10\text{-}90}$) asymptote; and the body mass, tarsus, and wing growth rate between 0-10, 11-20, 21-30 days. These were estimated considering 18.5 g (18/19 g) as the average body mass at hatching (age = 0 days) for first-hatch nestlings, and 18 g (17.5/18.5 g) for second-hatched nestlings, based on two nests containing two hatchlings each which were weighed when still wet. The wing length at hatching was 16 mm for first hatchlings/singles and 15 mm for second hatchlings, and tarsus length was 18 mm for first hatchlings/singles and 17 mm for second hatchlings. Fledging body mass was the body mass at the last check prior to fledging, and body mass recession rate was calculated as the slope of the line fitted to the body mass values from the date that maximum body mass was reached. For the growth rate of the 8th primary, we fitted the primary length measurements to a line, allowing estimation of primary emergence (i.e.

when the line intersects the X-axis), and the age at which the 8th primary reaches the length necessary for fledging (i.e. the known age of first flight with this feather length).

Breeding behaviour

Observations of display, nest construction, and incubation behaviour were made from end March in 2009 and 2010, from a vehicle at 14 territories in April 2009 and 2010 and in combination with nest searches in May. The behavioral data during the nestling phase were based on 105 h of observation at 29 nests, 20 in 2009 and 9 in 2010, 17 in cultivated areas and 12 in Waza National Park. Observations were conducted at nests with a full view of the nest and the immediate surroundings (< 200 m), by two observers using binoculars and a telescope from a concealed position or using a car as a hide at 75-150 m from the nest tree. Observations were made between 06:00 and 11:00, which incorporated daily peak activity hours (*c*. 07:00-10:00). Day-long observations at five nests had indicated a sharp decline in activity from *c*. 10:00-10:30 and significantly fewer displacements and food deliveries during the afternoon activity peak (from 16:00-17:00) compared to morning hours. Records were made at 5-min intervals of the position of the male and the female in relation to the nest tree (distance to nest tree in m), attendance at the nest, display flights, courtship, response to conspecifics, other raptors and potential mammalian predators.

Statistical analyses

Analyses were conducted in SPSS 19.0 (SPSS Inc., Chicago, IL, USA). Mann-Whitney *U*-tests were used for investigating differences in laying dates, nestling development, growth parameters. Kruskal-Wallis tests were used to examine whether median laying or hatch dates of respectively the first egg or hatchling were different for nests with different clutch size (n = 1, 2, or 3), hatchling number (n = 1, 2, or 3), and fledgling number (n = 0, 1, or 2); laying or hatch dates were calculated as the number of days from the first recorded laying or hatch date in the study area for 2009 and 2010 separately. The sequential Bonferroni correction was used to adjust the significance level when multiple tests were performed on the same data set (Rice 1989). Spearman Rank Order and Pearson correlation were used to explore associations. Chi-square goodness-of-fit tests were used to test for difference in sex ratios between nestlings. We used χ^2 contingency tables to test for an interaction between nestling mortality and hatch order; and for an interaction between male and female nestlings that survived to fledging and hatch order. For nests with two nestlings, the effect of the independent variables sex of the first and second hatchling on dependent variable nestling mortality was examined using logistic regression. The relationship between age and growth parameters was investigated using linear regression. Kolmogorov-Smirnov and Shapiro-Wilk tests were used to test for normality. All data are expressed as means ±S.D. unless indicated otherwise and all tests are two-tailed.

3.3 Results

Egg laying, incubation and fledging periods

In total, 268 occupied Grasshopper Buzzard nests were discovered, 138 in 2009 and 130 in 2010. Laying was surprisingly synchronous between and within years: laying date for the first egg was estimated at 5 May for 2009 (± 3.6 days; range: 21 April-15 May; n = 86) and 9 May for 2010 (± 7.1 days; range: 25 April-28 May; n = 66; U = 1799, Z = -3.88, P < 0.001). Laying succeeded the first seasonal rains in the study area in both years (2009: 8 April, 2010: 22 April). No significant relationship existed between clutch size and laying date (χ^2_2 = 4.13, n = 152, P = 0.13). The incubation period from laying to hatching of the last egg could be assessed at 30.1 days (± 0.87 days; range: 29-32 days; n = 9). We recorded no incidents of renesting at nests which had failed. First and second nestlings hatched 1.9 days apart (± 0.85 days, n = 50; range: 1-4 days). The fledging period, i.e. the period from hatching to the first flights and roosting away from the nest tree, was 35.9 days (± 4.3 days; range: 30-57 days; n = 64) and did not differ between first and second hatchlings ($U_{51,13}$ = 219, Z = -0.58, P = 0.34). Fledging period and hatch date were unrelated for first hatchlings (r_s = -0.03, n = 51, P = 0.79). Observations of juvenile Grasshopper Buzzards (n = 6) capturing termites in the absence of adults and at least 400 m from the nearest nest site on 15 July 2009 suggests that foraging independence was achieved within at most 16-18 days after dispersal from the nest territory (i.e. at an age of *c*. 58 days), assuming that these juveniles were among the earliest recorded hatchlings in 2009.

Nestling sex ratio

Of the nestlings sexed (n = 153), 42% (2009: 38%; 2010: 45%) were females and 58% (2009: 62%; 2010: 55%) were males. Sex ratios did not differ significantly from parity during the first half of the nestling phase for both years combined (nestling age ≤ 18 days, 57% ♂ vs. 43% ♀; χ^2_1 = 1.85, n = 106, P = 0.17), but sex ratios were significantly male-biased (61% ♂ vs. 39% ♀) at fledging (nestling age ≥ 29 days; χ^2_1 = 6.14, n = 137, P < 0.05). No relationship was recorded between sex and hatch order for first and second hatchlings that fledged (χ^2_1 = 0.35, n = 136, P = 0.56).

Breeding behaviour

Courtship and territorial display flights were recorded from the last week of March and characterized by slow flapping and soaring flights, by both partners above the nesting territory. The earliest nest building was recorded on 5 April (n = 2). Of 93 nests occupied in 2009, 6.5% were reused in 2010. The nests were shallow structures *c*. 30-40 cm across and lined with green leaves (usually of *Sclerocarya birrea*) in the majority of nests (> 96%; n = 244). Nests were placed in the fork of small side branches or on top of larger side branches (98%; n = 244), rarely in the tree top (2%). Males were seen to provide food to the incubating female. Female time spent at the nest declined with age of the first nestlings (r_s = -0.52, n = 29, P < 0.01), as did time spent at < 50 m from the nest tree (r_s = -0.57, n = 29, P

< 0.01). Males were observed up to 1 km from the nest; their time spent < 50 m from the nest was not related to age of the nestlings (r_s = -0.17, n = 29, P = 0.22). Throughout the nesting cycle, females spent 75.2% (± 24.4, n = 29) and males spent 25.6% (± 21.9, n = 29) of the peak morning activity hours < 200 m from the nest tree. Females participated in hunting for the nestlings from age 4-5 days but possibly earlier. The majority of prey captured by females was in the immediate vicinity (< 100 m) of the nest tree (87%; n = 22 captures), while males captured 66% (n = 29 captures) of prey items < 200 m from the nest. Both parents defended the nest territory against conspecifics up to *c*. 50-200 m from the nest, by flying straight at them followed by parallel gliding or tail chasing. Larger raptors, corvids, and potential mammalian predators (Patas Monkey *Erythrocebus patas*, Serval *Felis serval*) were harassed up to *c*. 400 m from the nest; an African Hawk Eagle *Hieraaetus spilogaster* was simultaneously chased by three pairs on one occasion. The majority of food items (mostly insects, grasshoppers, skinks) were swallowed whole by the nestlings from *c*. 10 days, while larger items (rodents, frogs, snakes, agamas) were (partly) dismembered and occasionally fed to the nestlings up to age 20-25 days. Older nestlings often claimed small prey and larger food items dropped at the nest by both parents, as well as smaller portions presented during feeding sessions. Females dismembered prey for the nestlings, but on two occasions, males were observed feeding the nestlings, once simultaneously with the female. Nestlings frequently roosted on branches near the nest before fledging (30-34 days), which commenced with short flights to neighboring trees. In four instances the nest area (< 100 m from the nest tree) was found vacated 3-5 days after all nestlings had fledged.

Nestling development: plumage and bare parts

Measurements were conducted on a total of 121 nestlings at 74 nests in 2009 and 103 nestlings at 65 nests in 2010. Figure 1 shows the general appearance of the nestlings at different ages. The first week after hatching, nestlings were covered in buffish-white prepennae down, variable in the intensity of the buff coloration (pale buff to tawny buff), which was most intense on the crown and wings. The iris is dark grayish brown throughout the nestling phase. By day 5 (5-7) a light greyish-white second (preplumulae) down gradually replaced the first down, reducing buffish coloration which was to a variable degree retained until day 14-18 on the majority of nestlings (80%; n = 46), particularly on the head, neck, back and wings, until the second down was fully developed. The pink skin was clearly visible through the second down. The remiges emerged at day 8-10 in most nestlings, later in three second hatchlings (13-15 days). The retrices emerged a day later. The timing of the emergence of body feathers was highly variable and related to hatching order; first body feathers emerged later in second than in first hatchlings ($U_{34,18}$ = 70, Z = -4.60, P < 0.001). No relationship was found between the emergence of body feathers and sex ($U_{25,27}$ = 264, Z = -1.37, P = 0.17). Body feathers first emerged on the scapulars at day 11-15 (as late as 19-21 days in six second hatchlings). Pins on the breast normally emerged at day 15-18 (but as late as day 22 and 24 for two second hatchlings), those on the cheeks at days 15-22 (but as late as day 25 and 26 in two second hatchlings), and those on the crown at day 16-23. Pins appeared last on the tarsi, at the earliest on day 18 and at the latest on day 26. The majority of nestlings (71%; n = 41) fledged while down was still visible on the

crown and breast. The egg tooth was lost at day 10-12 (n = 8), although four nestlings retained a clearly visible egg tooth until day 14-16. At hatching, the legs were a pinkish color, the cere light yellow and the talons whitish. The legs gradually lost their pinkish tinge and turned light yellow at 3-6 days, while the talons turned grey at 10-12 days (n = 8) and gradually uniform dark grey thereafter. The cere and legs turned darker yellow with age although the intensity of the coloration of both differed between nestlings. The bill was grey upon hatching and darker at the tip of the upper mandible, turning into a more uniform dark grey at 12-16 days (n = 13).

Figure 1. Grasshopper Buzzard nestlings at different ages (number of days indicated) in northern Cameroon, May-July 2010.

Nestling growth parameters

Table 1 presents the data for the growth equation parameters *t*, *a*, and growth rates for body mass, wing, and tarsus from day 0-10, 11-20, 21-30 for 86 nestlings that survived to fledge, by sex and hatching order. As brood size had no significant effect on their growth parameters ($P > 0.05$), data for first and single hatchlings were grouped. The body mass asymptote was strongly correlated for females with the values of *t* ($r = 0.50$, $n = 36$, $P < 0.01$) but not for males ($r = 0.23$, $n = 50$, $P = 0.06$). $W_{10\text{-}90}$ and *t* were highly significantly correlated for males ($r_s = 0.94$, $n = 50$, $P < 0.001$) and females ($r_s = 0.91$, $n = 36$, $P < 0.001$). $W_{10\text{-}90}$ was strongly correlated with $Wi_{10\text{-}90}$ ($r_s = 0.63$, $n = 86$, $P < 0.001$), $T_{10\text{-}90}$ ($r_s = 0.59$, $n = 86$, $P < 0.001$), and the intercepts of the 8th primary regressions ($r_s = 0.65$, $n = 60$, $P < 0.001$). The slopes of the 8th primary regression were not correlated to $W_{10\text{-}90}$ ($r_s = -0.07$, $n = 60$, $P = 0.25$). Figure 2 presents body mass, tarsus and wing growth curves for all measured nestlings (i.e. including those that died prematurely). As differences between the growth rates of the wings were absent between the sexes for first and second hatchlings (Table 1, Figure 2f), these measures can be used to assess the age of unsexed nestlings. After the emergence of the 8th primary at day 8 for first hatchlings and day 10 for second hatchlings the wing length is linear up to approximately day 30. The age of hatchlings can then be determined by the following formulae: age first hatchling (days) = 0.119 x wing length (mm) + 4.519 ($F_{1,350} = 6555$, $r^2 = 0.95$, $P < 0.0001$); age second hatchling (days) = 0.116 x wing length (mm) + 7.844 ($F_{1,100} = 508$, $r^2 = 0.84$, $P < 0.0001$). For both sexes, the growth of the wing at nest departure was not yet fully completed. Comparison of wing length with asymptotic length reveals that wing length was at 84% (80-86%) of mature length, and further advanced in first hatchlings compared to second hatchlings.

In nests with more than one nestling, a greater proportion of second hatchlings died (62.5%, $n = 56$) compared to first hatchlings (23.2%, $n = 56$; $\chi^2_1 = 17.6$, $P < 0.001$). Of 16 nests with third-hatched nestlings, only two survived to fledge (i.e. 87.5% died). Second and third nestlings died at a mean age of 9 days (± 5.7; range 1-24; $n = 22$). A logistic regression analysis for nests with two nestlings of known sex ($n = 27$) showed no significant effect of sex of the first and second hatchling on nestling mortality from the age of 15 days ($\chi^2_2 = 1.42$, $n = 54$, $P = 0.42$). For second nestlings for which circumstantial evidence suggested starvation and/or siblicide (weak, hardly responsive, large wounds to neck and head from attacks by the one to two day older sibling), death was related to the ratio of their body mass to the older nestling: the body mass ratio of first to second nestlings that survived was significantly lower compared to the body mass ratio of similarly-aged first to second nestlings that died (Figure 3; $U_{22,22} = 83.5$, $Z = -3.72$, $P < 0.001$). In one nest with a day-old and two-day old nestling, the latter was observed attacking the younger bird by pecking at its back and head, which bore large wounds (cf. Figure 3c,d to Chapter 5). The second nestling died after 1-3 days. The surviving first hatchling on this nest was atypical for its extremely long fledging period (57 days; the longest reported), suggesting growth was severely retarded and siblicide was related to suboptimal food supply.

Table 1. Growth equation parameters *a* (the asymptote of growth curves), *t* (the inflection point), and growth rates for body mass, wing, and tarsus during 0-10, 11-20, and 21-30 days after hatching for 86 nestlings in 2009 and 2010. Data were fitted separately for first hatchlings/singles (38 males, 30 females) and second hatchlings (12 males, 6 females). As brood size had no significant effect on their growth parameters ($P > 0.05$), data for first and single hatchlings were grouped. Letters (a, b, c) indicate significant differences ($P < 0.05$) between hatchling groups after Mann-Whitney *U*-tests with sequential Bonferroni correction.

Growth parameters	Males 1st	Females 1st	Males 2nd	Females 2nd
Body mass[1]				
a (g)	314.8±42.9[a]	360.1±45.9[b]	276.7±54.4[a]	269.7±51.9[a]
t (d)	12.6±2.3	12.7±2.0	14.5±3.8	13.3±3.7
$W_{10\text{-}90}$ (d)	21.0±3.7	20.3±3.3	25.7±7.4	24.2±8.2
body mass gain 0-10 (g/d)	10.8±2.7[ac]	12.0±2.1[a]	7.9±2.6[b]	8.6±2.6[bc]
body mass gain 11-20 (g/d)	13.6±2.4[a]	16.1±2.3[b]	10.9±2.2[c]	11.1±3.5[ac]
body mass gain 21-30 (g/d)	4.3±2.3	5.1±2.7	5.0±3.5	4.4±3.3
body mass max (g)	310.4±39.2[a]	357.6±34.0[b]	263.0±41.0[c]	294.4±62.5[ac]
fledge body mass (g)	301.0±44.6[a]	353.1±44.5[b]	255.6±46.5[c]	284.3±64.1[abc]
body mass recess (g/d)	1.7±2.4	1.5±2.9	2.3±4.0	0.8±1.8
Tarsus length[2]				
a (mm)	58.2±2.6[a]	58.5±2.4[a]	55.0±2.6[b]	55.6±3.5[ab]
t (d)	6.0±1.1	6.1±1.1	6.7±1.4	6.3±2.0
$T_{10\text{-}90}$ (d)	29.3±4.9[ab]	28.8±3.6[a]	34.6±6.8[b]	35.7±6.4[b]
tarsus gain 0-10 (mm/d)	1.9±0.3[a]	2.0±0.2[a]	1.5±0.3[b]	1.6±0.2[b]
tarsus gain 11-20 (mm/d)	1.4±0.1[a]	1.4±0.1[a]	1.3±0.1[b]	1.3±0.1[ab]
tarsus gain 21-30 (mm/d)	0.5±0.2	0.5±0.1	0.6±0.2	0.6±0.2
tarsus max (mm)	55.9±2.2[ac]	56.3±1.6[a]	52.5±2.4[b]	53.3±2.2[bc]
Wing length[2]				
a (mm)	251.2±15.1	253.5±17.2	244.5±22.8	232.2±29.0
t (d)	19.5±2.3[a]	19.2±1.6[a]	23.0±4.0[b]	20.6±4.0[ab]
$Wi_{10\text{-}90}$ (d)	30.7±3.5[ab]	30.1±2.0[a]	35.3±5.7[b]	32.6±5.9[ab]
wing gain 0-10 (mm/d)	3.6±0.8[a]	3.6±0.6[a]	2.4±0.8[b]	2.7±0.9[ab]
wing gain 11-20 (mm/d)	8.0±1.1[ac]	8.1±0.6[a]	6.2±1.5[b]	6.6±1.4[bc]
wing gain 21-30 (mm/d)	7.3±0.7	7.5±0.7	7.1±0.9	6.8±1.6
wing max (mm)	216.2±14.4[a]	216.1±21.0[a]	196.6±17.2[b]	192.0±30.8[ab]
Primary length[3]				
primary growth rate (mm/d)	6.3±0.8	6.4±0.4	5.7±0.8	6.0±0.8
primary emergence (d)	8.3±1.3	8.3±1.0	10.2±2.6	9.1±3.0
primary flight (d)*	34.3±4.3[a]	33.4±1.7[a]	38.9±4.8[b]	36.1±2.3[ab]

[1] Data were fitted to Gompertz and logistic models.
[2] Data were fitted to logistic models.
[3] Linear regression equations were fitted for the relationship between age and length of the 8th primary for day 11-30 when wing growth is approximately linear (cf. Figure 2f,g), for 40 first hatchlings/singles and 11 second hatchlings of known age measured in 6 age periods at 4-day intervals in 2010.
* The age at which primaries achieved length for first flight was determined at 160 mm ($n = 9$ nestlings).

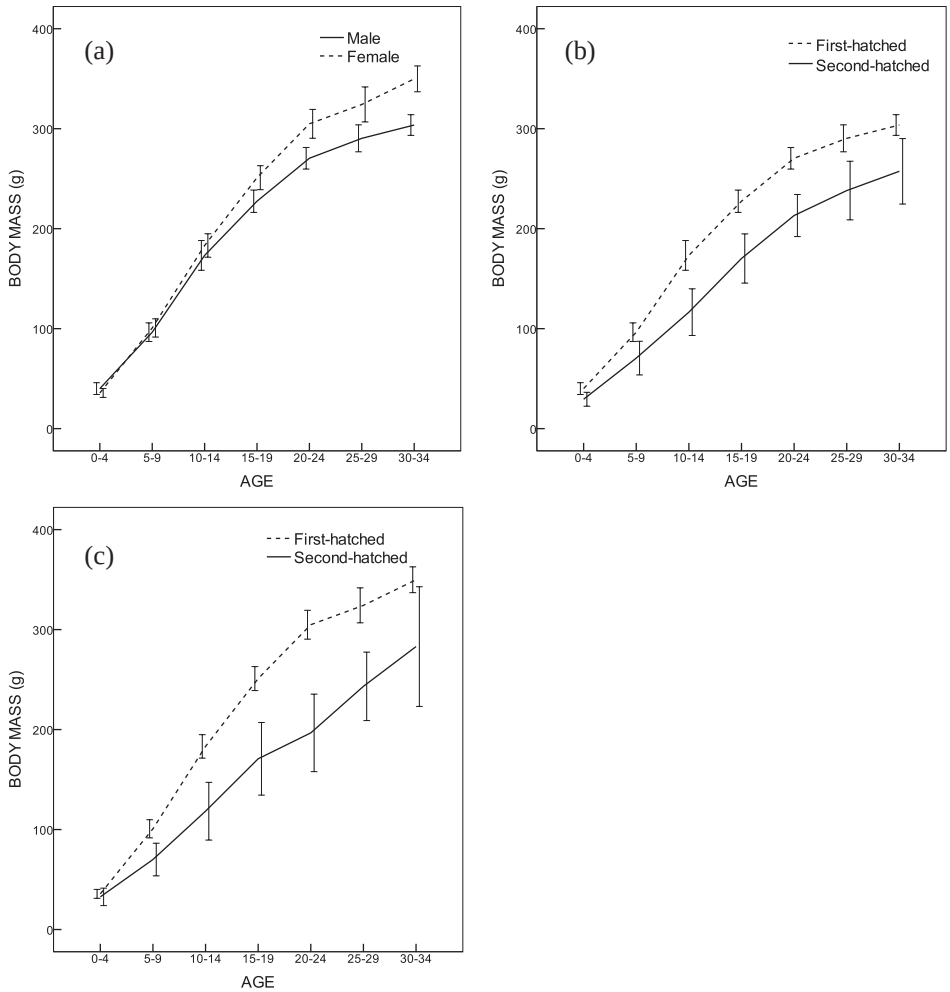

Figure 2. (a) Mean body mass for first hatchlings/singles of known age (n = 68 males, n = 50 females); (b) for first hatchling/single (n = 64) and second hatched (n = 20) male nestlings; and (c) for first hatchling/single (n = 48) and second hatched (n = 13) female nestlings. Error bars indicate 95% confidence intervals of the means.

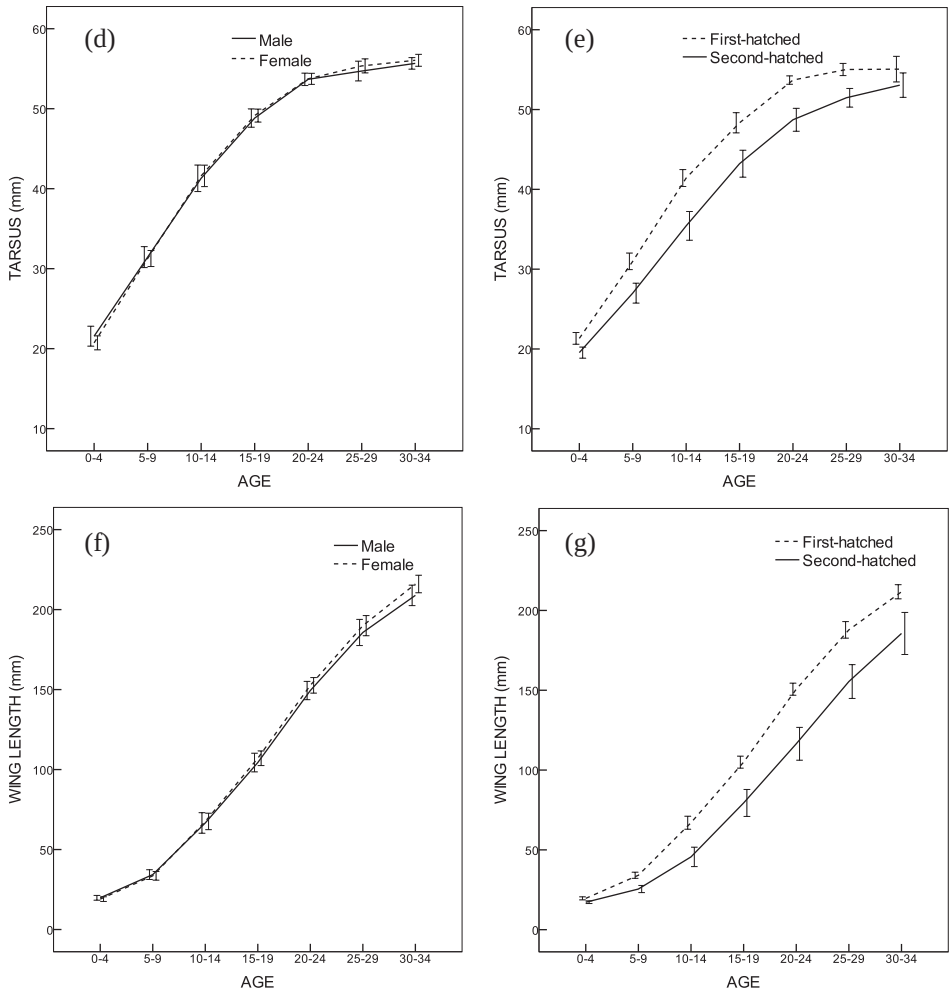

Figure 2. (d) Mean tarsus length for first hatchlings/singles (n = 68 males, n = 50 females); and (e) for first hatchlings/singles (n = 139) and second hatchlings (n = 68) of known age; (f) mean wing length for first hatchlings and singles (n = 68 males, n = 50 females); and (g) for the first hatchlings/singles (n = 139) and second hatchlings (n = 68) of known age. Data for first and single hatchlings were grouped since brood size had no significant effect on these parameters. Error bars indicate 95% confidence intervals of the means.

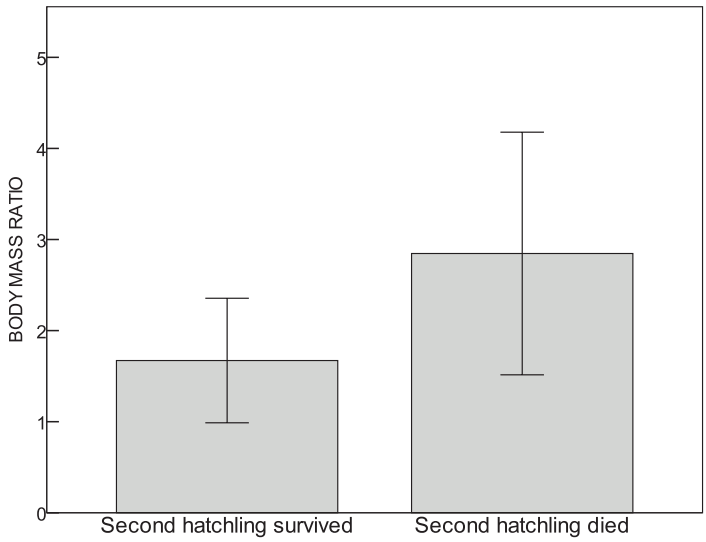

Figure 3. Mean body mass ratio for similarly-aged Grasshopper Buzzard nestlings (body mass first hatchling /body mass second hatchling), for second hatchlings surviving to fledging (n = 22) or dying prematurely (n = 22), at 44 nests in 2009 and 2010 where circumstantial evidence suggested starvation and/or siblicide caused the death of the second hatchling.

3.4 Discussion

Timing of breeding and rainfall

The period from the start of incubation to fledging was shorter in Grasshopper Buzzards (66 days) than in the *c*. 28% heavier Grey-faced Buzzard *B. indicus* breeding in China (71 days; Deng *et al.* 2004), as were values for the time interval for growth from 10 to 90% of the body mass asymptote (22 vs. 25-27 days). Whereas predation rates were rather low at Grey-faced Buzzard nests (Deng *et al.* 2004), high predation risk for small and medium-sized raptors in savannas (Thiollay 1976) is likely to be a strong selective pressure favoring short incubation and nestling periods. The pronounced seasonal variability in vegetation cover further constrains the length of the breeding season for Grasshopper Buzzards, whose hunting success decreases with increasing grass cover and height (Thiollay & Clobert 1990). The importance of low herbaceous cover for optimal prey accessibility, and rainfall as an apparent timing mechanism for laying, is underlined by the synchronous breeding periods between and within years, and the fact that breeding is initiated progressively later with increasing latitude (Brouwer *et al.* 2000), corresponding with a latitudinal shift in the start of the rainy season.

Our observations suggested a postfledging dependence period of approximately three weeks, which is comparable to migratory Palearctic harriers and kites (Newton 1979), but rather short compared to smaller and similarly-sized tropical raptors (Delannoy & Cruz

1988, Thorstrom & Quixchán 2000). Rapid postfledging independence appears to be driven by the northward migration soon after fledging, which generally shortens post-fledging dependence in raptors (Newton 1979, Bustamante & Hiraldo 1989), and facilitated by the dependence on easily caught insect prey, rather than more agile prey (e.g. birds; Delannoy & Cruz 1988, Griffin *et al.* 1998). Insects reach peak abundance in the study area in July (Njiforti 1997), when juveniles disperse from the nest territories, and decreases again from August when the majority of the population has moved into the Sahel where they feed on grasshoppers (Jensen *et al.* 2007).

Nestling growth and sex

Early development in both sexes was characterized by rapid body growth, wing growth, tarsus growth, early inflection points, and early emergence of primaries, which is the general growth pattern of raptors (Ricklefs 1968). Whereas growth rate is inversely related to body size at species level (Ricklefs 1968), we did not find a relationship between growth rate and asymptotic body mass of nestlings, although later inflection points in females were associated with greater asymptotic body mass. The moderate sexual size dimorphism (fledged females averaged 10-15% heavier than males depending on hatch order) is expected for raptors feeding predominantly on reptiles and insects (Newton 1979) and offering generally small, monopolizeable food items to nestlings, which would otherwise lead to excessive mortality in the smaller males (Anderson *et al.* 1993). Growth rate of body mass, tarsus, wing and primary feathers were similar between sexes, contrasting growth patterns in more strongly sexually dimorphic raptors, which are characterized by earlier development of feathers and younger fledging age by males than females (e.g. Richter 1983, Bortolotti 1984).

The significantly male-biased sex ratio (61%) at fledging was in accordance with Fisher's (1930) hypothesis, which predicts biased population sex ratios at the end of parental care in favor of the smaller, less costly males (in terms of energy requirements; Riedstra *et al.* 1998), assuming that the benefits associated with raising either sex are equal (Frank 1990). However, male-biased sex ratios have only rarely been observed in raptors (Rosenfield *et al.* 1996, Brommer *et al.* 2003), possibly because body size is generally a poor indicator of potential parental costs (Boulet *et al.* 2001). Although sex ratio did not differ significantly from parity for nestlings ≤ 18 days, it was already male-biased (57%), and greater female mortality compared to males before the age at which nestlings were sexed (*c.* 15 days) might have caused a sex ratio shift. Alternatively, clutches might have already been sex-biased, although the unpredictable food conditions during the nestling phase limit options for adaptive modification of clutch sex ratio (Appleby *et al.* 1997, Komdeur *et al.* 1997). We also did not record a male bias among second hatchlings, which would suggest parents favoring second-hatched males over second-hatched females for greater returns in the former (McDonald *et al.* 2005), nor did we find evidence that sex influenced the mortality odds of second hatchlings at nests with two nestlings. We suspect, therefore, that other factors leading to increased starvation risk of female nestlings compared to males, such as averagely poor food conditions and/or poor condition of the parents prior to egg laying

(Wiebe & Bortolotti 1992, Aparicio & Cordero 2001; but see Hipkiss *et al.* 2002), might have contributed to the male-biased sex ratio at fledging.

Nestling growth and hatch order

Irrespective of gender differences, second-hatched Grasshopper Buzzards were consistently smaller in body mass and structural dimensions compared to first hatchlings and singles, suggesting an age difference far in excess of the actual difference (cf. Figure 1). The same was true for third hatchlings, although death of the majority of third hatchlings at a young age precluded examination of their growth parameters. In contrast to other raptors (McDonald 2003, Mougeut & Bretagnolle 2006), wing length was dependent on hatch order, necessitating different ageing formulae for broods with multiple nestlings. Second-hatched Grasshopper Buzzards were also characterized by retarded development of body plumage, contrary to other birds (Boag 1987, Donazar & Ceballos 1989), and primary development. However, primaries showed little variance in growth rates, confirming a frequently observed pattern in raptors that primaries are less likely to be influenced by food shortages than body mass (Picozzi 1980, Bortolotti 1984; but see Negro *et al.* 1994).

The significantly greater body mass (males), wing, and tarsus length of first hatchlings compared to second hatchlings shortly after hatching suggested that the inferiority of the latter already existed at hatching, as reported for other raptors (Dijkstra *et al.* 1990). Such a developmental deficit may be reinforced when smaller siblings are outcompeted by larger siblings (Edwards & Collopy 1983, Bortolotti 1986), and aggravated by hypothermia experienced by smaller siblings (Ricklefs 1983). According to Lack's (1947, 1954) brood reduction hypothesis, the feeding hierarchy resulting from asynchronous hatching allows the youngest nestling to be rapidly eliminated if food supply is short, which might be adaptive when food supply during brood-rearing is unpredictable. Indeed, we found that death of second hatchlings depended on their body mass ratio with first siblings, irrespective of differences in sex and age of nestlings, indicating that brood reduction was facilitated by a more pronounced intrabrood mass hierarchy and a difference in competitive ability between nestlings (Wiebe & Bortolotti 1995). The young age at which second-hatched nestlings died (9 days) might be especially beneficial for survivors, because fewer resources are wasted (Husby 1986). We observed several cases where the elder sibling frequently attacked the smaller sibling, suggesting that brood reduction in Grasshopper Buzzards was also achieved through siblicide, as commonly reported in large raptors (e.g. Meyburg 1974, Brown 1976, Edwards & Collopy 1983), but less often in smaller species (Bortolotti *et al.* 1991, Gerhardt *et al.* 1997, Viñuela 1999). Often, siblicide goes hand in hand with monopolizeable food items delivered at nests (Mock 1985, Mock *et al.* 1987), which favors aggressive dominance of the larger nestling to guarantee their access to food at the expense of smaller siblings. Indeed, the majority of prey items fed to nestling Grasshopper Buzzards was small and swallowed whole, and prey was often claimed by larger nestlings which generally appeared to be in the most favorable position, also during parental feeding sessions. Although we found some evidence that siblicide was driven by suboptimal food supply, follow-up studies should clarify what role it has in regulating brood reduction under different food conditions.

Chapter 4

Effects of land use change in Sudano-Sahelian West Africa on the diet and growth of an avian predator

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In press: *Ibis*

Abstract

Raptor populations in Sudano-Sahelian West Africa are severely affected by widespread habitat alteration which depletes prey populations, potentially aggravated by changing rainfall patterns. We studied Grasshopper Buzzards *Butastur rufipennis* at nests in natural and transformed habitats in the Sudano-Sahelian region of northern Cameroon to investigate the effect of habitat transformation and rainfall on nestling diet and growth. Grasshoppers and small mammals were more frequently taken in natural habitat, whereas lizards were most frequently taken in transformed habitat. These dietary differences reflected differences in prey availability around nests in natural and transformed habitats. Land use was a significant predictor of asymptotic weight: nestlings in natural habitat attained a larger mass compared to nestlings in transformed habitat, when potentially confounding variables such as hatch order, gender, hatch date, rainfall, or the presence of siblings were taken into consideration. These results suggest that body condition at fledging was habitat-dependent, with potential consequences for subsequent survival. However, we recorded no differences in caloric content of food delivered to nests in natural and transformed habitat, which was possibly related to prey caught during twilight hours. Higher precipitation levels during the nestling phase were associated with higher nestling growth rate. Based on our results, we predict unfavourable future conditions for nestling growth of raptors in Sudano-Sahelian savannas, as a consequence of widespread habitat transformation and diminished rainfall.

Left: recently fledged Grasshopper Buzzard in northern Cameroon.

4.1 Introduction

Since the 1950s, rates of land transformation have peaked in the tropical and sub-tropical dry forests, grasslands and savanna ecosystems (UN Millenium Ecosystem Assessment 2005), which support some of the richest raptor communities in the world (Zalles & Bildstein 2000). In comparison to northern latitudes, tropical raptors may have evolved different breeding strategies in response to greater diversities of prey and predators, and different climatic conditions, illustrated among others by the longer breeding seasons and lower reproductive rates compared to raptors of northern latitudes (e.g. Newton 1979, Mader 1982, Delannoy & Cruz 1988). Nevertheless, breeding in tropical regions is almost certainly governed as much by food supply as in temperate regions (Newton 1979) and timed to coincide with peaks in food availability influenced by seasonal rains (Thiollay 1976). Similar to temperate regions, anthropogenic changes in land use can influence raptor food supply, resulting in raptor population declines along gradients of intensified land use (Thiollay 2007a, Carrete *et al.* 2009). A reduction in vegetation cover has the potential to lower invertebrate and vertebrate populations in savanna regions (Caro 2001, Fabricius *et al*. 2003, Blaum *et al.* 2007) to the detriment of raptors (Herremans & Herremans-Tonnoeyr 2000), while agricultural expansion may drive diet shifts (Ogada & Kibuthu 2009), which have the potential to impair long-term productivity and population persistence.

Apart from the more obvious impact on productivity, changes in food supply with habitat alteration might also have rather subtle effects. Food availability around nests may determine intraspecific variation in nestling growth rates, in addition to a variety of factors that influence offspring provisioning (Collopy 1986, Negro *et al.* 1994), such as nestling sex, hatching order, hatching date, brood size, experience of the parents and weather (Richter 1983, Ricklefs 1983, O'Connor 1984, Bortolotti 1986, Donazar & Ceballos 1989, Viñuela 1996). Given their potential sensitivity to food supply, nestling growth rates may be influenced by environmental factors that govern prey populations around nests, such as land use and productivity (Newton *et al*. 1979), through their impact on prey abundance (Moss 1979) and quality (e.g. total prey mass; Bortolotti 1989). Under conditions of food deprivation, nestling growth rate and development may be impaired, dependent upon the position of the nestling in the intrabrood size hierarchy (Newton 1979, 1986). In general, mass gain is more heavily affected than feather growth, thus avoiding major delays in the date of fledging (Moss 1976). As a result, changes in diet composition and prey quality induced by habitat alteration might negatively influence nestling condition at fledging, an aspect that has received scarce attention, despite the potentially important consequences for population persistence (Rodríguez *et al*. 2006).

In an effort to address this topic, we studied the diet and growth of Grasshopper Buzzard *Butastur rufipennis* nestlings in natural and transformed habitats of the Sudano-Sahel region of northern Cameroon. After having spent the dry season in West Africa's Sudano-Guinea savannas, the whole population migrates 500-1200 km north to breed in the Sudano-Sahelian savannas at the transition period from the dry to the wet season, when reduced vegetation cover and seasonal rains enhance prey availability (Thiollay 1978a, Thiollay & Clobert 1990). Land conversion for cultivation, woodcutting and heavy grazing

pressure affect large parts of its breeding range (Thiollay 2006a), depressing prey populations, a threat aggravated by the effect of changing rainfall patterns (Zwarts *et al.* 2009). However, productivity and nest success were found to be unaffected by land use in Cameroon (cf. Chapter 5), suggesting that Grasshopper Buzzards cope fairly well with habitat changes. Here, we examined the influence of land use and rainfall on nestling growth parameters to understand the importance of changing environmental conditions in the Sudano-Sahel region on nestling growth and condition at fledging. In particular, we studied diet composition, analyzing the variations in diet between natural and transformed habitat and the energy content of prey species delivered to nestlings, and how these may explain the observed growth patterns. We predicted that (1) nestling diets would differ between transformed and natural habitat as a result of a difference in prey availability between habitats; (2) the total caloric content of prey delivered at Grasshopper Buzzard nests would be lower in transformed compared to natural habitat; (3) these differences would affect nestling growth in the two habitats, leading to improved growth and mass at fledging in natural habitats.

4.2 Materials and methods

Study area

The study was conducted between 2 May - 22 July 2009 and 3 May - 25 July 2010, in natural habitats in the southwestern part of the Waza National Park and in transformed habitats to the South of Waza National Park, in the Far North of Cameroon (11°00'N-11°40'N and 14°20'E-15°00'E). The topography of the area is generally flat with some gentle slopes and rocky outcrops. The vegetation is characterized by open woodland on sandy soils, dominated by *Sclerocarya birrea*, *Anogeissus leiocarpus*, and *Balanites aegyptiaca*. The habitat inside Waza National Park consists of intact woodland savanna, whereas the transformed habitat outside Waza National Park is characterized by a mosaic of farmland (notably sorghum and millet), under cultivation at the start of the growing season in April-July, by settlements, and by fragments of heavily exploited woodland. Bush fires reduce the grass biomass in most areas between October and December. Grazing pressure is limited inside the National Park where much of the grass layer is retained into the next wet season, whereas grasslands outside the park are under heavy grazing pressure by livestock (Scholte 2005). The region is at the transition of the Sudano-Sahelian and Sahelian climatic zones (493 mm mean annual rainfall in 1984-2009; Cameroon Ministry of Agriculture and Rural Development 2011), with a dry season from November to April, when the first rains occur, followed by a wet season that lasts until October.

Nestling growth

Six (2009) and ten (2010) sample areas were allocated for nest searches equally distributed inside Waza National Park (natural habitat) and in the human-transformed areas outside the Waza National Park (transformed habitat), but within the limits of the lowland woodland zone (i.e. not extending onto the surrounding Mandara Mountains or seasonally inundated floodplains, where breeding records of Grasshopper Buzzards are rare; R. Buij unpubl.

data). Nest sample areas covered respectively *c*. 14 km^2 (2009) and 20 km^2 (2010) inside the National Park and 32 km^2 (2009) and 20 km^2 (2010) in the cultivated habitat, and were systematically inspected for nests by searching all potentially suitable nest trees. Additional occupied nests discovered over the course of the study outside these census areas were also included in the analysed sample. All occupied raptor nests, defined as those nests lined with green leaves and/or containing one or more eggs or nestlings, were GPS marked and their status (e.g. green lining, number of eggs) noted. In total, 268 occupied Grasshopper Buzzard nests were discovered and 175 of those produced nestlings. Of these, 139 nests were revisited for nestling measurements at 7-day intervals following hatching in 2009 and at 5-day intervals following hatching in 2010. We used digital scales accurate to 0.1 g to record the weight of the nestlings. In total, sequential weight measurements were available for 86 nestlings (50 males, 36 females) at 73 nests, covering for each nestling the period from the first day after hatching to fledging, or later until it became impossible to capture the young. One or more nestlings were lost in 29 nests (40%). Brood reduction, i.e. when circumstantial evidence suggested death of younger siblings through starvation (*sensu* Ricklefs 1965), occasionally in combination with siblicide, resulted in the loss of a nestling at 15% of nests in transformed habitat (n = 39 nests) and at 29% of nests in natural habitat (n = 34) and may have accounted for unexplained disappearances of nestlings at other nests. The nestlings were molecularly sexed using the primers described in Fridolfsson & Ellegren (1999), and an adjusted version of their PCR methods.

Individual growth curves were graphically fitted (Ricklefs 1967) to weight measurements for nestlings. Curves were not fitted to data for nestlings in two cases: (1) when early measurements were missing, or (2) when asymptotes were difficult to estimate due to death of the nestling before the 'growth plateau age' of 26 days. The growth curve was defined by the asymptotic values for weight estimated by fitting Gompertz and logistic equations to our growth data following the method proposed by Ricklefs (1967). Similarly, we estimated the time interval (in days) for growth from 10 to 90% of the weight asymptote, and the growth rate between 0-10, 11-20, and 21-30 days. Measures of weight gain were considered for these three periods because: (1) relationships were expected to differ among these stages and (2) certain covariates (e.g. brood size) varied along the breeding season. Growth curves were fitted considering 18.5 g as the weight at hatching (age = 0 days) for first hatchlings/singles, and 18.0 g for second-hatched nestlings, based on two hatchlings weighed when still wet at two nests. Hatching dates of nestlings of unknown age were calculated from wing measurements of known-age nestlings (Olsen & Olsen 1988). The duration of the fledging period was assessed from nests which were visited until all nestlings had fledged.

Environmental and prey variables

In order to examine differences between habitats and investigate their influence on nestling growth, we determined environmental and prey parameters for 62 nests with nestlings in natural habitat and for 63 nests in transformed habitat. We determined tree density and grass height and cover because we hypothesized that they could influence prey availability and accessibility. These parameters were measured within a 200-m radius of the nest tree,

which represented *c*. half the mean local nearest neighbour distance and the core foraging area for Grasshopper Buzzards (Chapter 3). Grass height and percentage cover were visually estimated during the incubation period (May) on four 25 m^2 squares at 25 m distance from the nest in the four cardinal directions, and were averaged for a mean score per nest tree. The number of live trees ≥ 8 m within 200 m of the nest was counted. Rainfall data were obtained from three meteorological stations located in the north, northwest and south of the study area (villages of Waza, Mbreché, Boundéri). The cumulative precipitation (mm) was considered for the months (April and May) preceding, and the months (June and July) following, the local mean hatching date (2009 = 2 June; 2010 = 6 June).

Prey abundance was assessed between 1-15 July in 2009 and 2010, on two pairs of parallel transect lines of 200 m (i.e. 800 m per nest) running in a northerly and southerly direction and 25 m apart, centred on the nest tree. In both years, prey surveys coincided with the second half of the nestling phase, i.e. with a decrease in maximum daily temperature and longer prey activity peaks. Prey transects were walked during peak prey activity hours from 07:00–12:00, the exact timing depending on weather conditions. Overcast or rainy conditions were avoided. The number of individual lizards (Agamidae and Scincidae), snakes, toads, frogs and grasshoppers were recorded within 3 m on either side of the transect line, which was the maximum distance at which these could be recorded irrespective of the degree of grass cover, which often limited detectability at greater distances. We only included grasshoppers > 40 mm as we did not record grasshoppers < 40 mm among prey items and these are rarely taken by Grasshopper Buzzards (Thiollay & Clobert 1990). Rodent burrows were counted on 100-m sections of the transect lines within 3 m on either side of the transect line, which is an effective method to estimate the relative abundance of small mammals in arid ecosystems (Vanak & Gompper 2010). Prey availability for raptors feeding on terrestrial prey is influenced by prey abundance and the height and density of the herbaceous layer (Preston 1990, Thiollay & Clobert 1990). We thus converted prey abundance estimates to prey availability (adapted from Thirgood *et al*. 2003) for all prey except grasshoppers (see below), estimated as: relative prey abundance/(grass height x grass cover). The grass layer here refers to the herbaceous layer, including rooted grass plants and forbs. The lowest score for the product of grass height (in cm) and grass cover (0-100%) was set at 1; at this score, relative prey abundance equals relative availability. We assumed that availability of grasshoppers was not affected by grass height and cover as much as more terrestrial prey, which was supported by frequent observations of Grasshopper Buzzards capturing grasshoppers at the top of grass stalks or in the air, whereas for example reptiles were most often captured at ground level (occasionally in trees). We therefore used the grasshopper availability index proposed by Thiollay & Clobert (1990), which has proved sensitive to the density, activity level and conspicuousness of grasshoppers (Thiollay 1978a), recorded by counts of fleeing grasshoppers along a slowly walked linear transect.

Diet

The percentage contribution of prey items to the diet of Grasshopper Buzzards in transformed and natural habitats was investigated using direct observations, prey remains, and pellets collected throughout the nestling phase in 2009 and 2010. If present, prey remains and pellets were collected at each nest with nestlings during each nest visit and either discarded (e.g. pellets, insect wings, legs, feathers) or returned to the nest (fresh remains). Fresh remains were photographed and/or identified to species level to avoid double counting on subsequent visits. Direct observations to register prey items carried to the nests were conducted during 194 h of observation (mean time per nest = 6.7 h) in natural habitat (8 nests in 2009 and 21 nests in 2010) and 188 h (mean time per nest = 5.7 h) in transformed habitat (11 nests in 2009 and 22 nests in 2010). Nests used for observations were randomly selected from the pool of nests with nestlings at different age stages, in equal proportions of nestling age and number in natural and transformed habitat. Observations were conducted between 06:00–11:00 by two observers using binoculars and a telescope from a concealed position. Prey items delivered to nests were classified by type (family or species) and size (small, medium, or large) by comparison with the bill and tarsus length of the adults, for estimation of caloric content of prey items delivered at nests. For all methods of analysis (pellets, direct observation, prey remains), we determined prey frequency, expressed as number of individual prey items in each prey category (family, order, or class) divided by total items in the sample. Pellets were analyzed using a regional reference collection (Aghrymet, Niger). Prey numbers per taxon were multiplied by the average mass of the taxon to calculate the proportion by mass for each prey category. Average adult mass was available for grasshoppers (Mullié & Guèye 2010) and, based on a locally obtained random sample of specimens, for small mammals (Rodentia, n = 26), beetles (Coleoptera, n = 7), frogs and toads (Anura, n = 4), scorpions (Scorpionida, n = 2), sunspiders (Solifugae, n = 2), and reptiles (Squamata, n = 12; Serpentes, n = 5). Mean mass for small invertebrates (Blattodea, Diplopoda, Hymenoptera, Heteroptera, Neuroptera) was estimated using the cumulative mass of 8-50 individuals of each order collected in the field divided by the number of individuals. The mean adult mass of birds recorded as prey during nest observations was taken from Del Hoyo *et al.* (1994, 1997, 2001, 2005, 2010) and the mass of juvenile birds was assumed to be 25-50% of the adult mass.

Energy content delivered to nests

Prey items delivered to nests were used to examine differences in gross energy content supplied to nestlings in different age groups in both habitats. In an effort to standardize comparisons between nest observations, we estimated energy content of prey items delivered between 07:00–10:30 for all nests, coinciding with peak activity hours for important prey (grasshoppers and reptiles) and foraging Grasshopper Buzzards (R. Buij unpubl. data). The gross energy content of prey delivered to nests was derived from mean energy values of the different prey items, their number and estimated mean dry weight. Prey energy content, categorized to taxon and size, was determined for lizards, grasshoppers, birds, and small mammals using bomb calorimetry (kJ/g; Gessaman 1987). Prey specimens were oven dried to a constant mass (± 0.0001 g) before homogenization.

From each prey specimen, pellets (n = 1-4) were prepared (*c.* 1 g) using a pellet press. The pellets were dried before weighing (± 0.0001 g), and combusted in an IKA C5000 adiabatic calorimeter, which was calibrated using a benzoic acid standard (Gessaman 1987). For reptiles collected in the study area, energy content was determined for one specimen among three different size classes: small (Scincidae, body length excluding tail < 6 cm); medium (Scincidae > 6 cm); and large (Agamidae). For small mammal (Muridae and Gerbillinae, n = 2 specimens), bird (Ploceidae, n = 1) and grasshopper prey (Acrididae, n = 1), energy content was determined for the most commonly captured taxa.

For prey items differing in size from those for which energy content was assessed, we used fresh weight values of specimens collected in the study area (lizards, n = 6; grasshoppers, n = 5) and estimated their dry weight based on prey-specific conversion factors (0.28 and 0.29 for Scincidae > 6 cm and Agamidae, respectively; 0.33 for lizards < 6 cm; 0.39 for grasshoppers). The energy content of snakes of different length was calculated based on weight-length relationships of whip and grass snakes (Colubridae; Kaufman & Whitfield Gibbons 1975), which were the most commonly captured snakes, and published energy content (Secor & Nagy 1994). Caloric values for termites (Nagy *et al*. 1984, Williams *et al*. 1997), frogs (Koplin *et al*. 1980), scorpions (Green *et al*. 1991) and beetles (Allen 1989, Oba *et al*. 2008) were similarly drawn from the literature.

Statistical analyses

Analyses were conducted in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). We used a backward stepwise Generalized Linear Model (GLM) to assess the determinants of the nestling weight parameters. Parameters considered for inclusion in the initial models and biologically meaningful two-way interactions were hatch order, hatch date, year, sex, land use (natural/transformed habitat), the occurrence of brood reduction (present/absent), cumulative rainfall in April, May (pre-hatching), June and July (post-hatching), and reptile and grasshopper availability around the nest. Brood reduction was defined here as the loss of a second-born or third-born nestling over the course of the nestling phase or a specific time period therein (between 0-10, 11-20, and 21-30 days), through starvation, siblicide, or an unknown cause. In addition, we included the time the hatchling spent at the nest with at least one sibling (in days) since such time was assumed to influence hatchling growth. This time was calculated based on the midpoint between the last visit in which a sibling was recorded at the nest and the next visit when the sibling had vanished. For models of the growth rate between 0-10, 11-20, and 21-30 days, we used the time spent with at least one sibling during this specific period.

In order to reduce collinearity and the number of variables in the models, pairs of strongly intercorrelated, explanatory variables (r > 0.60) were considered to be estimates of one underlying factor and the one considered to be most important was retained for analysis (Green 1979). We eliminated terms and interactions from the initial model until only significant terms remained. An identity link function and normal error distribution were used to model values for the weight asymptote (a), the time interval for growth from 10-90% of the weight asymptote, and weight gain between 0-10, 11-20, and 21-30 days, which

was calculated as the weight on the last day minus the weight on the first day, divided by the number of days. Mann-Whitney *U*-tests and independent samples *t*-tests were used for investigating differences in vegetation and nestling growth parameters, energy content, and fledging periods between transformed and natural habitats. Spearman's and Pearson's coefficients were used to explore associations. Relationships between age and growth parameters were investigated using standard linear regression. Differences in diets were examined using Chi-square tests. Diet Breadth (DB) was measured using Levins' index DB $= 1/\sum p_i^{\,2}$, where p_i = proportion of the diet contributed by the *i*th taxon (Levins 1968). Values from this index range from 1 to *n*, where *n* is the number of prey taxa in the diet. Kolmogorov-Smirnov and Shapiro-Wilk tests were used to test for normality, and data were log-transformed to adhere to normality. All tests were two-tailed. Mean values are presented ±S.E.

4.3 Results

Habitat

In transformed habitats, the nests sampled for offspring growth had significantly lower grass cover and height in their surroundings than those in natural habitats (Figure 1), while tree density was similar between habitats.

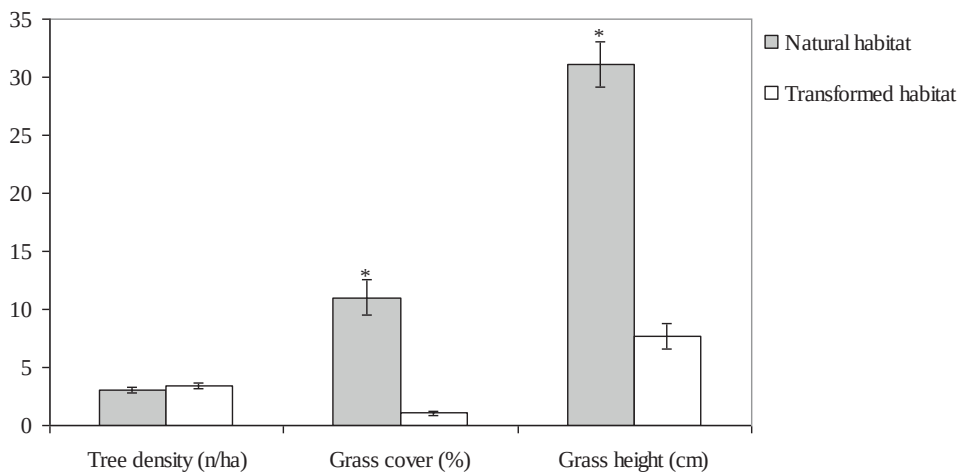

Figure 1. Mean (± S.E.) tree density, grass cover and grass height surrounding Grasshopper Buzzard nests with nestlings in natural (*n* = 62 nests) and transformed habitats (*n* = 63 nests). Asterisks indicate significant differences between habitats (Mann-Whitney *U*-tests; * $P < 0.001$).

Nestling growth

GLMs examining nestling weight parameters indicated a significant association of growth rate and asymptotic weight with hatch order, and the interaction of sex and hatch order,

indicating faster weight gain and greater body mass in first-born hatchlings compared to second-born hatchlings, and greater body mass in first-hatched females compared to first-hatched males (Table 1). In addition, estimated asymptotic weight, growth rate, and weight gain from day 10 were higher in natural than in transformed habitats (Table 1). Land use was the only parameter significantly associated with growth rate for nestlings older than 20 days (Table 1). Rainfall in June was positively associated with growth rate during the first 10 days (Table 1).

Table 1. Generalized Linear Models examining the effect of environmental variables, sex and hatching order on nestling growth parameters. Growth parameters were obtained for 50 male and 36 female nestlings (68 first-born or single nestlings, 18 second-born hatchlings) measured from hatching to fledging. Final models were obtained after stepwise elimination of non-significant terms. ***B*** is the parameter estimate, relative to the reference category (***B*** = 0) for class variables. See text for abbreviations.

Explanatory variable	***B*** **±S.E.**	**Wald** χ^2	***P***
a **(g)**			
Intercept	258.5±16.8	235.7	< 0.001
[order=1]	77.3±18.4	17.6	< 0.001
[order=2]	0	.	.
[sex=male] * [order=1]	-39.2±10.4	14.3	< 0.001
[sex=female] * [order=1]	0	.	.
[sex=male] * [order=2]	9.80±20.3	0.23	0.63
[sex=female] * [order=2]	0	.	.
[land use=natural]	33.5±9.24	13.1	< 0.001
[land use=transformed]	0	.	.
Model fit: $\chi^2_4 = 42.0$, $P < 0.001$			
weight 10%-90% (d)			
Intercept	3.60±0.16	484.1	< 0.001
[order=1]	-0.22±0.06	16.4	< 0.001
[order=2]	0	.	.
Rain June	-0.005±0.002	5.53	0.019
Model fit: $\chi^2_2 = 18.4$, $P < 0.001$			
weight gain 0-10 (g/d)			
Intercept	4.29±1.88	5.19	0.23
[order=1]	3.37±0.63	28.8	< 0.001
[order=2]	0	.	.
Rain June	0.06±0.02	6.84	0.009
[sex=male]	-1.02±0.51	3.94	0.047
[sex=female]	0	.	.
Model fit: $\chi^2_3 = 32.2$, $P < 0.001$			
weight gain 11-20 (g/d)			
Intercept	12.0±0.68	309.5	< 0.001
[order=1]	3.19±0.65	23.9	< 0.001
[order=2]	0	.	.
[sex=male]	-2.09±0.54	14.8	< 0.001
[sex=female]	0	.	.
[land use=natural]	1.35±0.54	6.17	0.013
[land use=transformed]	0	.	.
Model fit: $\chi^2_3 = 45.0$, $P < 0.001$			
weight gain 21-30 (g/d)			
Intercept	0.48±0.04	124.6	< 0.001
[land use=natural]	0.19±0.06	9.34	0.002
[land use=transformed]	0	.	.
Model fit: $\chi^2_1 = 7.10$, $P < 0.01$			

The length of the fledging period for first-born hatchlings did not differ between transformed (35.9±1.21 days, n = 20) and natural habitat (36.2±0.50 days, n = 21; $U_{20,21}$ = 168.5, Z = - 1.10, P = 0.27).

Food availability and diet

Table 2 presents the percentage contribution of prey items to the diet in transformed and natural habitats. Based on nest observations, there were no differences in diet composition between nestling age groups (< 15 days, n = 18 nests; ≥ 15 days, n = 19 nests; χ^2_5 = 8.71, P = 0.17); hence, prey data were pooled for all age groups. The majority of pellets collected was produced by nestlings aged 21 days or older: 73% (n = 67) of pellets in natural habitat and 70% (n = 51) in transformed habitat, whereas nestlings aged 0-10 days produced only 6% of the pellet sample in the natural habitat and 4% in the transformed habitat. Diet composition did not vary between years for nest observations (χ^2_3 = 2.79, P = 0.22) and pellets (χ^2_3 = 4.29, P = 0.26), but a greater incidence of amphibians was present in prey remains in 2010 than in 2009 (χ^2_3 = 99.3, P < 0.001). Levin's Index of diet breadth based on all pooled prey items was 4.47 in natural habitat (n = 750 items) and 4.35 in transformed habitat (n = 652). In all methods of analysis (observations, pellets and remains), reptiles were more frequent in the diet in transformed compared to natural habitat (all $\chi^2_1 \geq 14.5$, P < 0.001). Conversely, the proportion of grasshoppers was consistently higher in the natural habitat (all $\chi^2_1 \geq 5.73$, P < 0.05). Similarly, small mammals were more frequent prey in natural habitat according to nest observations (χ^2_1 = 8.78, P < 0.01), but only marginally so according to prey remains (χ^2_1 = 3.06, P = 0.08) and pellets (χ^2_1 = 2.71, P = 0.10). The pattern of occurrence of reptiles, grasshoppers and small mammals in the diet paralleled the availability of these prey across habitats (Table 3).

Table 3. Prey abundance and availability surrounding nests with nestlings in natural (n = 62 nests) and transformed habitat (n = 63). Prey was classified to order and family for reptiles (Squamata). Grasshoppers (Orthoptera), reptiles, and amphibians (toads and frogs; Anura) were counted along 800-m transects. Small mammal abundance (Rodentia) refers to counts of small mammal burrows along 400-m transects (see text for details). The availability of terrestrial prey was estimated as prey abundance/(grass height x grass cover), except for grasshoppers, for which counts along transect lines were assumed to represent their availability. Asterisks indicate significant differences between habitats (Mann-Whitney U-tests; *P < 0.05; **P < 0.01; ***P < 0.001).

Prey abundance	**Natural**	**Transformed**
Orthoptera**	7.40±0.64	5.06±0.53
Squamata***	3.52±0.34	1.92±0.22
Scincidae***	2.45±0.27	1.14±0.16
Agamidae	0.87±0.15	0.52±0.10
Serpentes	0.02±0.02	0.03±0.02
Anura	0.08±0.04	0.10±0.10
Rodentia***	27.5±3.54	5.54±0.63
Prey availability		
Orthoptera**	7.40±0.64	5.06±0.53
Squamata*	1.26±0.18	1.82±0.22
Scincidae	0.84±0.12	1.06±0.16
Agamidae	0.38±0.09	0.49±0.09
Serpentes	0.00±0.00	0.03±0.02
Anura	0.01±0.01	0.09±0.09
Rodentia*	9.57±1.48	5.06±0.57

Table 2. Percentage contribution of prey items to the diet of Grasshopper Buzzards, from direct observations at nests in natural (n = 29 nests) and transformed (n = 33) habitat, prey remains found at nests in natural (n = 61) and transformed habitat (n = 75), and pellets collected at nests in natural (n = 41) and transformed habitat (n = 40). F = number of prey items in pellets as percentage of the total prey number; B = cumulative mass of each prey category as percentage of total prey mass. Figures referring to classes are presented in bold. Within the table, n refers to the number of prey items.

		Direct observations				**Remains**				**Pellets**			
Prey item		natural (n = 145)[a]		transformed (n = 133)[a]		natural (n = 182)[a]		transformed (n = 221)[a]		natural (n = 441)[ab]		transformed (n = 310)[ac]	
Class	(Sub)order/ *family*	**F**	**B**	**F**	**B**	**F**	**B**	**F**	**B**	**F**	**B**	**F**	**B**
Mammalia[1]		**2.76**	**8.28**	**1.50**	**3.00**	**9.34**	**17.37**	**5.88**	**9.71**	**8.39**	**46.71**	**5.81**	**29.97**
	Rodentia	2.76	8.28	1.50	3.00	9.34	17.37	5.88	9.71	8.39	46.71	5.81	29.97
Aves[2]		**0.00**	**0.00**	**0.75**	**0.50**	**2.20**	**9.78**	**3.17**	**5.28**	**6.58**	**12.20**	**6.13**	**10.55**
	Passeriformes	0.00	0.00	0.75	0.50	0.55	0.34	1.36	1.40	6.58	12.20	6.13	10.55
	Coraciiformes	0.00	0.00	0.00	0.00	0.55	1.77	1.36	3.89	0.00	0.00	0.00	0.00
	Galliformes	0.00	0.00	0.00	0.00	0.55	3.41	0.00	0.00	0.00	0.00	0.00	0.00
	Columbiformes	0.00	0.00	0.00	0.00	0.55	4.26	0.00	0.00	0.00	0.00	0.00	0.00
Reptilia[3]		**26.90**	**59.87**	**57.14**	**86.69**	**46.15**	**60.87**	**59.73**	**73.18**	**5.22**	**17.63**	**10.97**	**37.19**
	Squamata	26.90	59.87	57.14	86.69	46.15	60.87	59.73	73.18	5.22	17.63	10.97	37.19
	Serpentes	2.07	3.10	7.52	7.49	8.79	8.17	8.14	6.72	3.17	8.84	5.81	14.99
	Scincidae	15.86	38.07	24.81	39.57	10.99	16.35	16.74	22.12	1.81	8.08	3.87	15.99
	Agamidae	2.76	7.72	15.04	27.98	10.44	18.12	15.38	23.71	0.00	0.00	1.29	6.22
Amphibia		**18.62**	**22.35**	**6.77**	**5.40**	**10.44**	**7.77**	**15.38**	**10.16**	**0.68**	**1.51**	**1.61**	**3.33**
	Anura	18.62	22.35	6.77	5.40	10.44	7.77	15.38	10.16	0.68	1.51	1.61	3.33
Hexapoda		**48.97**	**8.67**	**31.58**	**3.97**	**28.02**	**3.46**	**14.93**	**1.51**	**74.83**	**19.82**	**70.65**	**16.85**
	Orthoptera	42.07	8.42	26.32	3.50	27.47	3.41	9.95	1.10	42.18	15.65	35.48	12.21
	Coleoptera	2.07	0.10	4.51	0.45	0.55	0.05	4.98	0.41	14.06	3.91	17.10	4.41
	Blattodea	2.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00
	Hymenoptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.10	0.21	15.48	0.19
	Heteroptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.01
	Neuroptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.49	0.05	1.94	0.03
Diplopoda		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.23**	**0.05**	**0.65**	**0.13**
Arachnida		**2.76**	**0.83**	**2.26**	**0.44**	**3.85**	**0.76**	**0.90**	**0.16**	**4.08**	**2.06**	**4.19**	**1.97**
	Solifugae	0.69	0.17	0.75	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Scorpionida	2.07	0.66	1.50	0.32	3.85	0.76	0.90	0.16	0.91	0.59	0.97	0.58

[a] Total number of prey items recorded.
[b] 67 pellets analyzed.
[c] 51 pellets analyzed.
[1]Includes Muridae, Gerbilidae, Soricidae.
[2]Includes Red-billed Quelea *Quelea quelea*, African Grey Hornbill *Tockus nasutus* (juv), Lilac-breasted Roller *Coracias caudatus* (juv), Heuglin's Wheatear *Oenanthe heuglini* (juv), Chestnut-bellied Starling *Lamprotornis pulcher* (juv), Clapperton's Francolin *Francolinus clappertoni* (juv), and a dove *Streptopelia* sp.
[3]The most frequently captured reptiles were Common Agama *Agama agama*, Five-striped Savanna Skink *Trachylepis quinquetaeniatus* and Long-tailed Lizard *Latastia longicaudata*.

Energy content delivered to nests

We detected no differences in the energy content of prey, or in the frequency of prey deliveries in the natural vs transformed habitat (Table 4). Also, there was no relationship between the energy content of food delivered to observed nests and the asymptotic weight of both first-born (r_s = -0.18, n = 42 nestlings, P = 0.26) and second-born nestlings (r_s = -0.02, n = 13, P = 0.94).

Table 4. Total caloric content and number of prey items delivered to Grasshopper Buzzard nests (numbers indicated) with nestlings of different age classes and with different brood sizes in natural (total = 146 hours) and transformed (total = 151 hours) habitats. Comparisons included similarly-aged nestlings for nests with equal nestling numbers and similar nestling numbers for different age groups. Mann-Whitney *U*-tests and independent samples *t*-tests did not indicate significant differences between groups.

	Caloric content delivered (kJ/h)	
Nestling age/number	**Natural**	**Transformed**
0-10 days	18.8±5.39 (n = 12)	27.3±11.7 (n = 12)
11-20 days	49.1±12.2 (n =13)	46.0±10.1 (n = 13)
21-30 days	45.4±14.1 (n =13)	51.3±15.1 (n = 13)
1 nestling	34.0±9.62 (n = 12)	40.3±9.93 (n = 17)
2 nestlings	42.3±8.86 (n = 15)	44.1±10.7 (n = 16)
	Prey items delivered (prey items/h)	
0-10 days	2.08±0.51 (n = 12)	1.25±0.41 (n = 12)
11-20 days	2.69±0.75 (n = 13)	2.46±0.43 (n = 13)
21-30 days	3.00±0.58 (n = 13)	2.54±0.55 (n = 13)
1 nestling	2.59±0.46 (n = 12)	2.14±0.39 (n = 17)
2 nestlings	2.63±0.59 (n = 15)	2.06±0.41 (n = 16)

4.4 Discussion

Our results indicated that Grasshopper Buzzard diet composition differed between natural and transformed habitats during the breeding season, particularly in the incidence of the prey taxa dominating the diet: grasshoppers and reptiles. Diet shifts following human-induced habitat changes, such as cultivation, have previously been observed in temperate zone raptors (Salvati *et al.* 1999, Penteriani *et al.* 2002, Moulton *et al.* 2005), but evidence from tropical regions is scarce (Pande *et al.* 2007, Ogada & Kibuthu 2009). Although biases are inherent in analyses of prey remains and pellets (reviewed by Marti *et al.* 2007), differences in the relative importance of prey items among habitats were consistent across methods, strengthening the confidence in our results. As expected, differences in diet composition reflected differences in prey availability between habitats, reaffirming the notion that Grasshopper Buzzards are opportunistic hunters which exploit easily accessible prey resources (Thiollay & Clobert 1990).

While agricultural encroachment was associated with increased diet breadth in other avian predators (Penteriani *et al.* 2002, Ogada & Kibuthu 2009), diet breath in Grasshopper Buzzards was marginally higher in the natural habitat compared to the transformed habitat. Although wider diet breadth is expected in unproductive environments where prey availability is low and search times are high (MacArthur & Pianka 1966), lower overall prey diversity rather than higher prey availability probably caused the narrower diet breadth

in Grasshopper Buzzards in transformed habitat. Diet breadth for both habitats was greater compared to the non-breeding season, when Grasshopper Buzzards have a rather narrow, largely insectivorous diet and when a much lower proportion of reptilian prey is consumed (0.1% of total prey items; Thiollay & Clobert 1990) compared to the breeding season (5-60%; this study). The inclusion of a larger proportion of vertebrates in the diet might be a consequence of the need to limit the number of visits to the nest without sacrificing the caloric content delivered, which would also diminish the risk of nest detection by predators and subsequent predation. This is likely to be a particularly strong selective pressure in West African savannas, where small and medium-sized raptors experience a high intensity of nest predation (Thiollay 1976).

Factors associated with nestling development

We found that nestling growth parameters, including asymptotic weight, were significantly affected by land use. This effect was unrelated to other potentially confounding variables such as hatching order, gender, hatching date, rainfall, or the presence of siblings, and suggests that fledglings in natural habitat attained a superior condition compared to those from transformed habitat. Although nestling growth is typically affected by a variety of environmental factors (Ricklefs 1983), including productivity and land use (Newton *et al*. 1979, Heiss *et al*. 2009), to our knowledge this is the first study to report an effect of land use on raptor growth patterns in Africa. These results also suggest that nestling condition could be viewed as a potential tool to measure effects of land transformation on raptors in this important region.

Apart from land use, hatching order and gender were important predictors of nestling growth. In small to medium-sized raptors, reproductive effort and parental investment are normally regulated by clutch size and brood reduction through nestling starvation, as a result of which comparably little variation exists in nestling growth rates (Newton 1979). In spite of this, we recorded differential growth rates of earlier and last-hatched Grasshopper Buzzard nestlings, similar to other small to medium-sized raptors (Viñuela 1996, McDonald *et al*. 2005). Mean caloric content delivered to nests with two siblings was only 9-25% higher than those containing only a single nestling, and the number of prey items delivered was approximately similar, suggesting that food supply may have limited nestling growth, weight at fledging, and the competitive ability of second-born hatchlings. Contrary to expectations, we found no discrepancies in the caloric content of food delivered to nests in natural vs transformed habitats, and no relationship between nestling growth and the energy content of delivered prey. Since food supply to the nest is the principle determinant of growth and weight in nestlings (O'Connor 1978, Mock 1984), energy content at nests in natural habitat might have been underestimated. This might have been related, at least partly, to prey which was captured outside nest observation periods, such as predominantly crepuscular small mammals (Duplantier & Granjon 1990, McElhinny *et al.* 1997). Because the average small mammal had a caloric content *c*. 2.5 times higher than the average lizard, optimal foraging theory predicts that small mammals should be incorporated into the diet where available (Kamil *et al.* 1987). Indeed, small mammals were more commonly recorded among remains and pellets than during observations, and more frequently in

natural than transformed habitats, reflecting differences in availability between habitats. This might imply that small mammals were under-recorded during nest observations, which potentially may have underestimated energy provisioning to nests in natural habitats. In addition, categorization into size classes might have been too crude a method to detect subtle differences in prey weight between habitats. As a result, prey in similar size classes might have in fact differed in their energy content between habitats. Habitat deterioration was found to have a negative effect on lizard body condition and weight, as a consequence of behavioural strategies to cope with increased predation risk when vegetation cover is reduced (Amo *et al*. 2007). The significantly lower grass cover in the transformed habitat might have affected body condition and weight of prey items, which in conjunction with the relative scarcity of small mammals might have constrained nestling growth in transformed habitats.

We recorded a positive association between nestling growth rate and the amount of rainfall in June, which coincided with the nestling phase. This contrasts with results from studies on a variety of raptors, which reported a negative effect of rainfall on nestling growth through reduced foraging efficiency and food supply to the nest (Donazar & Ceballos 1989, Hiraldo *et al.* 1990). In arid systems, however, rainfall is an important determinant of food availability, positively affecting raptor food supply and breeding performance (Hustler & Howells 1990, Rodríguez & Bustamante 2003, Wichmann *et al.* 2003). The seasonal rains increase the abundance and/or activity of a variety of prey in West African savannas (e.g. insects, amphibians; Thiollay 1978a, Njiforti 1997), thus providing the vital food needed for successful breeding. This may be even more crucial in areas where important prey sources are relatively scarce, such as in transformed habitat.

Conclusion

Our results indicate that Grasshopper Buzzards have adapted reasonably well to anthropogenic alteration of their breeding habitat, as demonstrated by a shift in diet and the opportunistic exploitation of a wide spectrum of prey accessible during the transition between the dry and the wet season. This conclusion is further supported by analyses of nest success and productivity, which did not vary with land use in the study area (Chapter 5). Migratory Grasshopper Buzzards thus appear to be less vulnerable to habitat exploitation compared to sedentary raptors, which typically depend on productive, year-round territories with a stable supply of predominantly vertebrate prey (Thiollay & Clobert 1990). On the other hand, significant population declines have been reported within the species' West African breeding range (Thiollay 2006a), where human population growth rates are among the highest in the world, putting growing pressure on remaining breeding habitat. In this context, northern Cameroon is representative for the region; the human population here tripled between the late 1960s and present and is projected to double again by 2050 (FAOSTAT 2012). The 1700-km^2 Waza N.P. protects *c.* 5% of Cameroon's Far North Province, but increasing livestock numbers (Scholte 2003) and local deforestation rates of up to 30% in 20 years (Fotsing 2009) render vegetation cover and prey resources increasingly scarce over wide areas. Our results suggest that nestling condition at fledging is compromised under such conditions, which might negatively affect the potential for

survival and recruitment (Appleby *et al.* 1997, Arroyo 2002, McDonald *et al.* 2005), perhaps worsened by the effect of declining rainfall predicted by various climate models (e.g. Held *et al.* 2005).

Chapter 5

Breeding performance of Grasshopper Buzzards in a natural and human-modified West African savanna

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In press: *The Condor*

Abstract

Few studies have examined raptor reproduction in response to land use change in sub-Saharan Africa, hampering conservation efforts to address regional declines. To further our understanding of mechanisms underlying dramatic declines of West African raptors, we examined the relationship between environmental conditions, nest density and reproductive parameters in the Grasshopper Buzzard *Butastur rufipennis*. Analyses were based on a total of 244 nest sites divided among transformed and natural habitat in northern Cameroon. Nest density increased with the density of preferred nest trees at the landscape scale. Nests were more widely spaced in transformed than natural habitat. Dispersion was adjusted to differences in small mammal availability, which was negatively associated with nearest neighbor distance, and the area under cultivation, which was positively associated with nearest neighbor distance. We detected a positive association of productivity with rainfall, canopy shielding the nest, and grasshopper availability, and nest visibility from ground level, while canopy shielding, grass cover, rainfall, and nearest neighbor distances were positively associated with nest success. Nests in natural habitat incurred greater egg and nestling losses due to natural predators than nests in transformed habitats, while losses through human predation were small. Productivity and nest success were unaffected by land use, due to opposing effects of higher predation pressure, shorter inter-nest distances, and greater food supply in natural habitat versus transformed habitat. Our results revealed that transformed habitat may provide adequate breeding habitat for Grasshopper Buzzards, but declining rainfall and increasingly intensified anthropogenic land use are likely to impact future reproductive output.

Left: Grasshopper Buzzard nestlings in Waza National Park.

5.1 Introduction

In Africa, a range of bird species have decreased in abundance and richness with increasingly intensified land use (Sinclair *et al.* 2002, Söderström *et al.* 2003). Raptor populations stand out for some of the most dramatic declines (Thiollay 2006a,b, 2007a, Ogada & Keesing 2010, Virani *et al.* 2011), which were linked to land use change, implicating livestock grazing, cultivation, pesticide use, and human disturbance in reductions of prey availability, nest sites, and reproductive success (Ogada & Kibuthu 2009, Bamford *et al.* 2009, Virani & Harper 2009). Insectivorous raptors suffered some of the strongest declines (Thiollay 2006a), possibly through a reduction in invertebrate abundance due to high grazing pressure (Herremans & Herremans-Tonnoeyr 2000), and pesticide use (Sánchez-Zapata *et al.* 2007). However, knowledge of the exact mechanisms behind raptor declines in Africa remains scarce, which is alarming in light of the increasing rate of land transformation due to rapidly growing human populations (UN World Population Prospects 2010).

In order to examine how land use might affect nest density and reproductive success, we investigated reproductive parameters of a Grasshopper Buzzard *Butastur rufipennis* population in natural savanna, i.e. protected habitat, and transformed savanna, i.e. unprotected habitat, in northern Cameroon. The Grasshopper Buzzard is a small raptor (adult body mass: 310-408 g; Ferguson-Lees & Christie 2001), which breeds at transition of the dry to the wet season in the northern part of the Sudano-Sahelian distribution range, north to 18ºN. Over the course of the dry season, the whole population migrates as far south as 7ºN, following progressively decreasing grass cover due to grazing and fires (Thiollay 1978a) to optimize the availability of insect prey (Thiollay & Clobert 1990). Its relative abundance in West African savannas and tendency to breed in agricultural habitat make it a suitable model species to examine the relationships between environmental conditions, nest density, and reproductive output. We hypothesized that Grasshopper Buzzards selected specific nest tree characteristics in transformed and natural habitats, and that generally unfavorable food conditions and anthropogenic disturbance resulted in lower nest density and productivity in transformed compared to natural habitat.

Firstly, we examined structural characteristics of nest trees, in order to assess how anthropogenic land use influenced nest availability. An assessment of preferred nest tree features is important because trees are frequently pruned excessively in agro-ecosystems (Ruelle & Bruggers 1982), potentially reducing their suitability for breeding by influencing vulnerability to predation and weather, such as tree or trunk height (Newton 1979, Brown & Collope 2008) and canopy cover (Collias & Collias 1984, Rodríguez *et al.* 2006). We predicted that Grasshopper Buzzard selected nest trees that were less damaged, higher, sturdier, and had higher leaf cover than other trees available to breeding pairs but not used, and that these characteristics were selected in both habitats.

Secondly, we examined the role of environmental factors in driving nest density. Apart from nest site availability, raptor density may be limited by food supply, depending on which factor is in shorter supply (Newton 1979). Food availability for raptors is influenced

by abundance and accessibility of prey (Bechard 1982), and trees for perch-hunting raptors (Widen 1994). Grass cover provides vital resources for terrestrial prey populations in arid savannas (Herremans & Herremans-Tonnoeyr 2000), but a dense grass layer may also reduce foraging success of Grasshopper Buzzards (Thiollay & Clobert 1990). Apart from food supply, human persecution and disturbance have been shown to negatively affect raptor nest dispersion (e.g. Bisson *et al.* 2002, Bamford *et al.* 2009). Although raptors were shown to respond variably to the presence of important avian predators in temperate systems (Sergio *et al.* 2003), nest dispersion may be driven by spatial avoidance of centers of activity (i.e. nest sites) of the most important avian predators (Sergio & Hiraldo 2008). However, Grasshopper Buzzards establish territories at the end of the dry season (Chapter 3), which precedes a seasonal influx of migratory raptors capable of killing nestlings and adults (Thiollay 1976, 1977a), limiting options for spatial avoidance of avian predators. Therefore, we expected nest density to be positively associated with tree density and food availability, and negatively with increasing human populations and cultivation.

Thirdly, we examined potential causal factors of reproductive traits and nest success in transformed and natural habitats. Enhanced reproductive output is often associated with increased prey supply (e.g. Sergio *et al.* 2004, Pande *et al.* 2007), while rainfall may have variable effects on reproduction (e.g. Steenhof *et al.* 1999, Rodríguez & Bustamante 2003, Wichmann *et al.* 2003). During breeding, Grasshopper Buzzards incorporate a wide variety of vertebrate and invertebrate prey into the diet (Chapter 4), some of which display increased activity and availability with rainfall (e.g. amphibians, insects), potentially reducing the need for long-distance foraging flights (Selås 1997). Raptor nest success may be strongly influenced by natural predators (Sergio & Hiraldo 2008) and structural characteristics of the nest-site that increase concealment from avian and mammalian predators (Tome 2003, Rodríguez *et al.* 2006). Natural predation is likely to be important in protected areas, which provide spatial refuges for carnivores (Blaum *et al.* 2007) and large raptors (Thiollay 2006a, 2007a), whereas anthropogenic disturbance and nest harvesting are likely to be more important in agro-ecosystems (Virani & Harper 2009). Nestlings may become more conspicuous with age (Jehle *et al.* 2004), and larger brood size may similarly enhance their vulnerability to predation. Apart from predators, intraspecific competition and aggressive interactions can profoundly depress reproductive output of raptors (Newton 1979), and is likely to be higher in natural habitat where inter-nest distances are shorter than in agro-ecosystems (Thiollay 2007a). We therefore expected productivity and nest success to increase with food supply and rainfall, in addition to measures that lowered nest detectability to predators, and distance to nesting conspecifics. Based on generally impoverished resources and strong declines of raptors in transformed habitat (Thiollay 2007a), we expected more favorable reproductive parameters in natural habitat.

5.2 Materials and methods

Study area

The study area (11°00’N-11°40’N and 14°20’E-15°00’E) was roughly equally divided between Waza National Park and the cultivated area southwest of Waza N.P. in the Far

North Province of Cameroon (Figure 1). We chose the natural and transformed habitats to be adjacent to each other to ensure comparable soil type, topography and vegetation composition, making land management regime the major difference. The Sudano-Sahelian climate is characterized by a dry season (Nov-April) which precedes a wet season with the first rains in April into October (annual rainfall *c*. 500 mm). Mean annual temperature is 28 ºC and peaks from March-May when temperatures of 47 ºC are reached. The study area is generally flat with some gentle slopes and three isolated inselbergs. Open woodland savanna habitat dominates the landscape (cf. Figure 4e), and encompasses *Sclerocarya birrea* dominated woodland with *Anogeissus leiocarpus* and *Balanites aegyptiaca* locally interspersed by dense *Acacia seyal* clusters. The transformed habitat is characterized by a mosaic of cultivation, settlements and woodland under severe pressure by livestock grazing and slash-and-burn activities. Millet and sorghum are the main crops, with some maize and onions, and pesticide use is limited to herbicides at the start of the dry season (November).

Nest search and monitoring

Nest searches were conducted in nest census areas totaling 14 km^2 in natural habitat and 32 km^2 in transformed habitat from 2-17 May 2009, and in 20 km^2 in both natural and transformed habitat from 3-17 May 2010. We selected census areas based on wet season accessibility (< 13 km from a tarred road). Extensive searches for Grasshopper Buzzard's nests were conducted on foot by our team (4-8 researchers). All raptor nests discovered were included in the survey, GPS marked and their status noted. Occupied Grasshopper Buzzard nests were lined with green leaves and/or contained one or more eggs or nestlings. They were distinguished from nests of other raptors by size, shape, and characteristic features (e.g. green leaf lining; Ferguson-Lees & Christie 2001), or attending birds if present. We combined additional nest searches in the second half of May and June with visits to occupied nests. We revisited nests without eggs at 1-week intervals to determine their status, and declared nests abandoned four weeks after discovery if no eggs or attending adults were present. Nests which had failed early in the breeding season were revisited two to three times at later stages (20 May-15 June) to investigate whether renesting had occurred. In an attempt to minimize nest disturbance, we used a mirror on the end of a steel pole to reduce the time needed to check nest contents (*c*. 1-2 min per nest during incubation; Figure 3b). We revisited nests at approximately two-weekly intervals during incubation, at 7-day intervals following hatching in 2009, and at 5-day intervals following hatching in 2010. We investigated predation events by intensively searching the area < 100 m around the nest for clues such as clipped or bitten-off feathers (Figure 4a), carcasses, broken branches or claw marks on the nest tree, pieces of egg shell, bite marks on eggs, and blood marks. We recorded the number and age of the eggs or nestlings, the date, the type of evidence, and a description of the remains (feathers, body parts). Losses were recorded as "unknown cause" in case no remains were found or the identity of the predator could not be established.

Nest site selection and covariates of reproductive success

We examined characteristics of the nest site and its direct surroundings and the distance to conspecifics or sources of human disturbance, to determine potential covariates of reproductive output. Since habitat may influence raptor reproduction at multiple spatial scales (Penteriani & Faivre 1997, Sergio & Bogliani 2000), we sampled nest site characteristics at < 200 m from the nest, representing *c.* half the mean nearest nest distance (NND) and core foraging area, and at < 1 km, corresponding with the longest observed foraging flight from a nest (Chapter 3). For each nest, we determined the nest tree species (Arbonnier 2004), the diameter at breast height (DBH) and the height of the nest and the nest tree. We categorized nest tree damage in four categories based on the number of logged or broken-off branches > 20 cm diameter (0, 1, 2, ≥ 3 branches). Leaf cover was visually categorized into three categories based on the percentage of leaf cover on branches (no leaves, 1-50%, 51-100%). Nest visibility for terrestrial predators was calculated based on cumulative scores (0/1) taken from four cardinal directions at 15 m from the base of the nest tree. We visually categorized top cover from a position directly underneath the nest, based on the percentage of canopy cover in a 4-m^2 square directly over the nest (1: 0-25%; 2: 26-50%; 3: 51-75%; 4: 76-100%). We counted the number of live trees ≥ 8 m, categorized to species level, and felled trees < 200 m from the nest. Grass height and cover were recorded on four 25 m^2 squares in four cardinal directions, at 25 m from the nest tree and averaged for a mean score per nest tree. We assessed grazing pressure in five categories, from absent (0) to severe grazing (4), based on the presence of herbivore hoof prints and reduction of the grass height through grazing (visible as bitten-off grass stems) in 0, 1-25, 26-50, 51-75, and 76-100% of the surface area of a 50-m radius circle centered on the nest. Three meteorological stations located in the north, northwest and south of the study area provided the rainfall data throughout the nest period. The cumulative precipitation (mm) was considered for the months preceding (April, May) and the months following (June, July) hatching (mean hatch date 2009: 02 June; 2010: 06 June). We assessed the abundance of important prey items (Chapter 4) - grasshopper (> 40 mm), reptiles and amphibians on two pairs of parallel 6-m wide transect lines, each 200 m long (total per nest: 800 m) and 25 m apart in a northerly and southerly direction from the nest, between 07:00 and 12:00. We counted rodent burrows on 100-m sections of the transect lines, which is an effective method to estimate the relative abundance of small mammals in arid ecosystems (Vanak & Gompper 2009). The availability of reptiles, small mammals and amphibians was estimated as (adapted from Thirgood *et al.* 2003): relative prey availability = total number (individuals or burrows)/(grass height x grass cover). We adopted the grasshopper availability index proposed by Thiollay & Clobert (1990), which represents the number of grasshopper flushed along the transect line. The percentage of agriculture and woodland < 1000 m from the nest and the distance of the nest tree to the nearest village, agricultural field, tar road, and the NND were determined in ArcView GIS 3.2 software (Esri 1999) using digitized maps and satellite images of the study area (Cnes/Spot Image 2011).

We examined nest tree selection to assess whether buzzards selected specific features of trees for nesting from among those available within the range. Hereto, we recorded tree

height, tree damage, DBH, and leaf cover of unused trees within 100 m of a random subsample of 80 occupied nest trees in 2010 (equally distributed among habitats). Unused trees were ≥ 8 m high and judged capable to support a hypothetical Grasshopper Buzzard nest. These trees were selected by walking 100 m from the nest tree in a straight line towards the north and selecting the nearest tree to the nest tree.

Covariates of nest density and range size

We examined the determinants of nest density in Grasshopper Buzzards at the nest-site level, using NND as an inverse proxy measure of nest density (Newton *et al.* 1977), and at the landscape scale (4-km^2 census areas). We examined the relationship between NND and measures of food availability, including tree density, and the cover of agricultural fields < 1000 m from the nest. For analyses at the landscape scale, we measured tree density, food availability, human population size, and the area under cultivation in ArcView GIS 3.2, for the ten census areas in 2010 (Figure 1) and related those to nest density. Environmental and prey characteristics similar to those estimated for the nest sites were determined at six survey points randomly generated within each census area.

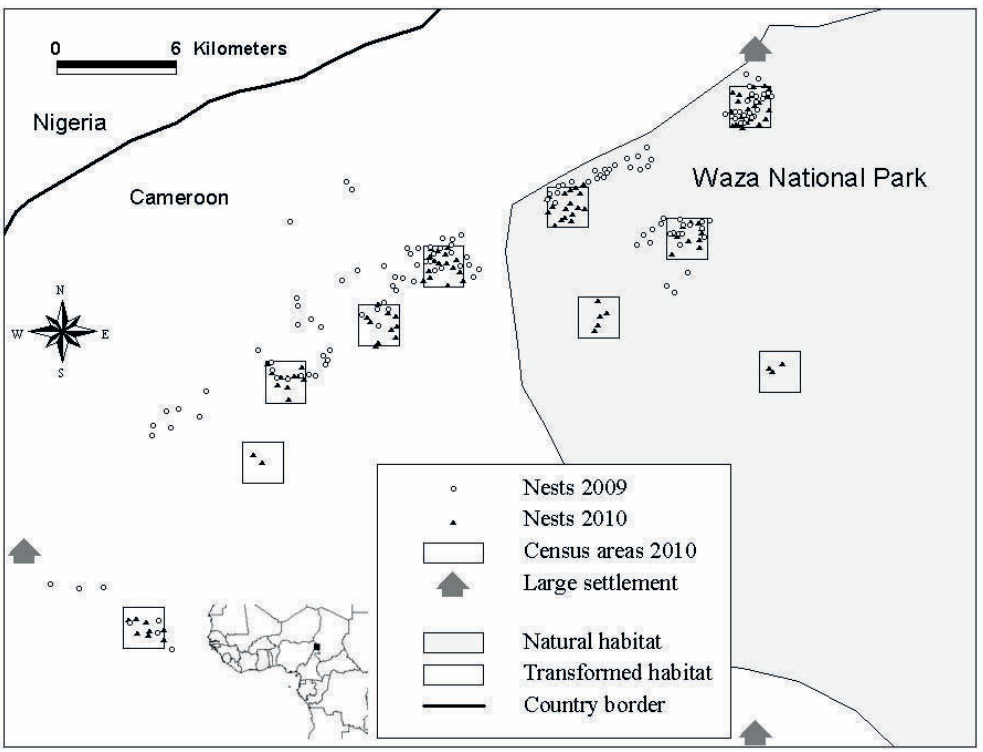

Figure 1. Location of the study area in northern Cameroon (map inserted), including the location of occupied Grasshopper Buzzard nests in 2009 and 2010 and census areas used to examine landscape correlates of nest density in 2010.

The number of potentially suitable nest trees (hypothesized as all trees ≥ 8 m) in the census areas were counted and identified to species level. Human population size was estimated by multiplying the number of houses with mean household size and verified by information gathered from village chiefs.

Statistical analyses

We built models based on *a priori* hypotheses of the influence of environmental characteristics on nest density, NND, nest success and productivity. Models were built through a backward stepwise procedure. To limit pseudoreplication, nests in the same location (nest tree; $n = 6$) were only included once in all analyses. We considered pairs of inter-correlated variables ($r > 0.60$) to be estimates of one underlying factor and excluded variables according to common sense (e.g. rainfall from June and July has no effect on clutch survival), retaining the biologically most relevant variable for analysis (Green 1979).

For analyses of covariates of NND, we employed a Generalized Linear Model (GLM) on log transformed NND and a normal distribution with an identity link function and verified model adequacy by examination of residuals (McCullagh & Nelder 1989). Independent variables included the agricultural cover < 1000 m, tree density, grass cover, and grasshopper, small mammal and reptile availability, and year (amphibian availability was excluded because of limited numbers). Standard linear and S-curve regression were used to model nest density within census areas, separately for tree density, grass cover, grasshopper, small mammal and reptile availability. Human population size and cultivation were considered only for transformed habitat. We modeled correlates of productivity with an ordinal regression model and a negative log-log link function. Apart from the predictor variables listed above, brood size and land use were used to model fledgling number, with year, top cover, and visibility as categorical factors. Tests of parallel lines were used to test model suitability.

We used MARK software (White & Burnham 1999) to estimate daily nest survival using Mayfield's method (Mayfield 1975, Johnson 1979), which has been adapted to allow for evaluation of a variety of spatial and temporal factors that might influence nest success (Dinsmore *et al.* 2002, Rotella *et al.* 2004). We carried out three different analyses, since factors affecting nest survival are likely to differ between nest stages (Rotella *et al.* 2004) and the age of most nests failing prematurely was unknown: (1) clutch survival with an assumption of constant daily survival rate (DSR; Dinsmore *et al.* 2002), i.e. a survival rate which remained constant throughout the egg phase, (2) nest survival with a variable DSR, i.e. survival which varies with nest age, for nests with nestlings, and (3) nest survival with a constant DSR for all nests. Nests for which DSR was modelled to vary with age included only those with nestlings for which body measurements were taken early in the nestling phase. A 30-day incubation period from egg laying to hatching of the last nestling, and 36-day fledging period (Chapter 3) was used to calculate overall nest success. Fail dates were assumed to be the midpoint between the last visit in which eggs or young were recorded in the nest and the next visit when the nest was empty. Eggs were deemed infertile if older than 38 days, irrespective of the presence of a breeding female. The second order Akaike's

Information Criterion corrected for small sample sizes (AICc) was used to evaluate nest survival models and to select the best model fit using a forward stepwise procedure (Dinsmore *et al.* 2002, Rotella *et al.* 2004).

We examined potential differences in reproductive parameters between habitats. Clutch size and nestling number referred to the number of eggs and nestlings recorded at a nest, respectively. Laying date was calculated by subtracting 28 days from the date of hatching of the first hatchling, corresponding with the incubation period to hatching of the first egg (Chapter 3). Hatching date was calculated by backdating nestlings from feather development using reference data on nesting development (cf. Chapter 3). Fledgling number was the number of nestlings which reached 80% of the mean fledging age (cf. Steenhof & Newton 2007), i.e. ≥ 29 days (Chapter 3), and calculated separately for all pairs and for successful pairs only. We considered a nest successful if at least one fledgling was produced. Hatching success was the nestling number divided by clutch size. Fledging and breeding success referred to fledgling number divided by nestling number and clutch size, respectively.

We used paired samples *t*-tests to test whether mean differences in height and DBH between nest trees and associated trees differed from zero, and Wilcoxon signed rank sum tests to test for differences in tree damage and leaf cover. We investigated relationships using Pearson's correlations when the data showed no violation of linearity, normality and homoscedasticity, otherwise we used Spearman's correlations. We used χ^2 contingency tables to test for an interaction between habitat and nest tree characteristics and Chi-square goodness-of-fit test to investigate whether proportional use of nest tree species differed from availability; and to investigate differences in the relative frequency of loss through predation between habitats. Mann-Whitney *U*-tests were used to test for differences in reproductive and habitat parameters between habitats. Shapiro-Wilk tests were used to test for normality and data were log transformed before analyses to adhere to normality. Analyses were conducted in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). All data are expressed as means ±S.E. and statistical significance was set at $\alpha < 0.05$.

5.3 Results

Nest site characteristics

In total, 244 occupied nest sites were fully described over the course of the study, 131 in natural habitat and 113 in transformed habitat. Grass cover and height, and the availability of small mammals and grasshoppers, were greater around nests in natural than transformed habitat, but reptile availability was higher in transformed habitat (Table 1). Grass cover around nests was associated with small mammal (r_s = 0.47, n = 244, P < 0.001), grasshopper (r_s = 0.29, n = 244, P < 0.001) and reptile abundance (r_s = 0.23, n = 244, P < 0.001), indicating decreasing prey populations along a gradient of increasing soil denudation. *Sclerocarya birrea* trees were preferred over other tree species present in the study area (χ^2_1 = 196, P < 0.001). Nest height was related to nest tree height (r = 0.49, n = 244, P < 0.001), which exceeded the height of unused trees within the range, in both

habitats (Table 2). No differences between habitats in nest visibility and top cover were recorded.

Table 1. Comparison of the vegetation and prey characteristics at nest sites in natural (n = 131) and transformed habitats (n = 113). Results of Mann-Whitney U-tests comparing the characteristics between the two habitats are indicated with asterisks (*P < 0.05, **P < 0.01, ***P < 0.001). See text for units of measurement and details of vegetation and prey characteristics.

Nest site characteristics	Natural habitat	Transformed habitat
% nests in *Sclerocarya birrea* trees	100	95[1]
Agricultural cover < 1000m***	0.00±0.00	49.4±2.79
Felled trees < 200m***	0.03±0.02	32.0±3.41
Sclerocarya birrea trees < 200m	29.8±1.60	30.2±1.72
Other trees < 200m***	7.71±0.88	12.7±0.78
Grass height***	31.1±1.76	7.67±0.77
Grass cover***	10.1±0.93	1.13±0.11
Grasshopper availability**	6.84±0.41	5.00±0.42
Reptile availability*	1.26±0.14	1.93±0.19
Small mammal availability*	8.99±1.09	5.64±0.73
Amphibian availability	0.01±0.00	0.05±0.05

[1]Other nest tree species: Karaya Gum Tree *Sterculia setigera* (n = 5), African Birch *Anogeissus leiocarpus* (n = 1).

Table 2. Characteristics measured at 40 Grasshopper Buzzards nest trees, and on paired unused trees in a 100-m radius circular plot centered on the nest tree, in natural and transformed habitat in northern Cameroon. Asterisks indicate significant differences (*P < 0.05, **P < 0.001) for paired samples t-tests to test whether mean differences in height and DBH between nest trees and associated trees differed from zero, and for Wilcoxon signed rank sum tests to test for differences in tree damage and leaf cover.

Nest tree characteristics	Nest tree	Unused tree
Natural habitat		
Height**	12.8 ±0.26	11.3 ±0.22
Damage*	0.28±0.09	0.68±0.10
DBH	54.5±1.31	51.0±1.26
Leaf cover	1.80±0.11	1.70±0.12
Transformed habitat		
Height**	12.2±0.26	9.68±0.28
Damage	0.98±0.13	1.18±0.15
DBH	50.7±10.31	48.4±15.59
Leaf cover	1.98±0.12	1.98±0.13

Covariates of nest density and NND

At the landscape level, nest density increased with the density of *Sclerocarya birrea* trees ($F_{1,8}$ = 7.09, r^2 adjusted = 0.40, P < 0.05; Figure 2). Other measures of food availability, grass cover, cultivation, and human population size did not significantly explain the variance in nest density at the landscape scale. Mean nest density was 3.25 nests/km^2 in natural habitat (± 2.55; range 0.75-7.00 nests/km^2) and 2.40 nests/km^2 in transformed habitat (± 1.35; range 0.50-4.25 nests/km^2; $U_{5,5}$ = 9.5, Z = -0.63, P = 0.55). NND differed between natural (317±117 m; range 81-838 m) and transformed habitat (449±244 m; range 131-1430 m; $U_{131,113}$ = 4496, Z = -5.36, P < 0.001). NND decreased with increasing small mammal availability, but increased with cultivation (Table 3), suggesting that depletion of

prey resources and expanding cultivation negatively influenced nest density in the transformed habitat.

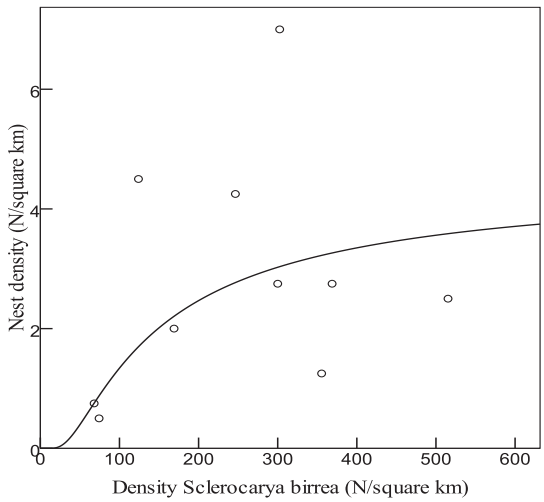

Figure 2. S-curve regression model for nest density and the number of *Sclerocarya birrea* trees ≥ 8 m inside nest census areas (cf. Figure 1 for location census areas).

Table 3. Results for a Generalized Linear Model incorporating the effect of environmental and prey variables surrounding nests in natural (n = 131) and transformed habitats (n = 113) on the distance to the nearest breeding neighbor.

Explanatory variable	***B* ±S.E.**	**Wald χ^2**	***P***
Intercept	2.57±0.03	9933	< 0.001
Small mammal availability	-0.002±0.005	21.4	< 0.001
Agricultural cover < 1000m	0.001±0.0004	7.43	0.006
Model fit: χ^2_2 = 39.7, P < 0.001			

Covariates of reproductive success

Laying date did not differ between nestlings in transformed (6 May±4 days) and natural habitats in 2009 (5 May±3.5 days; $U_{31,31}$ = 480, Z = -0.01, P = 0.99) and 2010 (resp. 9 May±8 days and 9 May±7 days; $U_{36,28}$ = 484, Z = -0.27, P = 0.79). Fledglings were produced at 43% of discovered nests (yearly range: 37-48%; n = 244), 41% (34-47%; n = 131) in natural habitat and 46% (42-49%; n = 113) in transformed habitat. The Mayfield estimate of overall nest success for 2009 and 2010 combined was 39%, based on a DSR of 0.986±0.001 (n = 244). Reproductive parameters generally did not differ between habitats, although fledgling numbers for successful pairs were higher in transformed than natural habitat in 2009 and 2010 (Table 4). An ordinal regression model indicated a positive association of fledgling numbers with April rainfall, grasshopper availability, top cover, and nest visibility (Table 5). Nest survival models showed that DSR for nests was unaffected by land use during incubation, the nest cycle, and for nests with known age (those that held nestlings), but varied with measures which were assumed to influence

predation risk, intraspecific competition, and food availability (Table 6). The most parsimonious model for daily nest survival rate included a negative effect of nest age and brood size, suggesting that older nests and those with multiple nestlings were more likely to perish than younger, single broods. Conversely, top cover was positively associated with overall nest success, and for nests that held nestlings, while tree height was positively related to clutch survival. Rainfall positively influenced clutch, nestling, and nest survival, and nest survival was positively associated with NND and grass cover. Food supply around the nest (grasshopper and small mammal availability) was positively associated with nestling survival, but small mammal availability was negatively associated with clutch survival.

Table 4. Breeding parameters of Grasshopper Buzzards nests in natural and transformed habitats in northern Cameroon, in 2009 and 2010.

Parameters	**Natural habitat**		**Transformed habitat**	
2009	Mean (*n*)	Range	Mean (*n*)	Range
Clutch size[a]	2.03±0.06 (64)	1-3	2.10±0.06 (62)	1-3
Nestling number†	1.47±0.12 (66)	0-3	1.38±0.12 (65)	0-3
Fledgling number	0.53±0.08 (66)	0-2	0.69±0.10 (65)	0-3
Fledgling number for successful pairs‡	1.13±0.06 (31)	1-2	1.41±0.06 (32)	1-3
Hatching success†	0.72±0.05 (64)	0-1	0.66±0.04 (62)	0-1
Fledging success†	0.39±0.05 (51)	0-1	0.53±0.06 (50)	0-1
Breeding success	0.27±0.04 (64)	0-1	0.34±0.05 (62)	0-1
2010				
Clutch size[a]	1.83±0.07 (60)	1-3	1.93±0.08 (44)	1-3
Nestling number†	0.71±0.11 (65)	0-3	0.81±0.13 (48)	0-2
Fledgling number	0.38±0.07 (65)	0-2	0.58±0.11 (48)	0-2
Fledgling number for successful pairs‡	1.14±0.07 (22)	1-2	1.40±0.08 (20)	1-2
Hatching success†	0.39±0.06 (60)	0-1	0.44±0.07 (44)	0-1
Fledging success†	0.61±0.07 (28)	0-1	0.70±0.08 (25)	0-1
Breeding success	0.22±0.04 (60)	0-1	0.33±0.06 (44)	0-1

[a] Only laying pairs included.
†Differences between years by means of Mann-Whitney *U*-tests (both habitats) $P < 0.05$.
‡Differences between habitats by means of Mann-Whitney *U*-tests (both years) $P < 0.05$.

Table 5. Ordinal regression model of nest site and environmental covariables on Grasshopper Buzzard nests with 0 fledglings ($n = 136$), 1 fledgling ($n = 77$), and 2 fledglings ($n = 23$) in northern Cameroon, in 2009 and 2010 (combined data). Category fledglings = 3 ($n = 2$) was omitted.

Explanatory variable	***B* ±S.E.**	**Wald χ^2**	***P***
[Top cover=1]	-1.46±0.31	22.0	< 0.001
[Top cover=2]	-0.90±0.30	9.12	< 0.001
[Top cover=3]*	0		
Grasshopper availability	0.06±0.02	6.80	0.01
Rainfall April	0.02±0.01	7.88	0.01
[Visibility=0]	-1.07±0.37	8.46	< 0.001
[Visibility=1]	-0.23±0.31	0.57	0.45
[Visibility=2]	-0.31±0.33	0.87	0.35
[Visibility=3]	0		
Model fit: $\chi^2_7 = 32.1$, $P < 0.001$			

* Top cover = 4 ($n = 6$) was excluded from the model.

Table 6. Best-supported models (ΔAICc = 0.00) describing survival of nests with constant DSR (*n* = 244), nest with known age and variable DSR (*n* = 90), and nests in the incubation stage with constant DSR (*n* = 186). Significant model terms included after model runs are presented.

Explanatory variable	*B* ±S.E.	Lower CL	Upper CL
Nest survival constant DSR[1]			
(Intercept)	2.92±0.26	2.42	3.43
Top cover	0.38±0.10	0.18	0.58
Grass cover	0.02±0.01	0.00	0.04
Rain May	0.01±0.00	0.00	0.02
NND	0.001±0.0001	0.00	0.00
Nest survival variable DSR[2]			
(Intercept)	3.87±1.85	0.26	7.49
Nest age	-0.07±0.02	-0.11	-0.03
Rain June	0.07±0.02	0.02	0.11
Top cover	0.87±0.37	0.14	1.60
Small mammal availability	0.03±0.02	-0.01	0.07
Grasshopper availability	0.12±0.08	-0.03	0.27
Brood size	-0.78±0.42	-1.60	0.05
Clutch survival constant DSR[3]			
(Intercept)	2.80±0.21	2.40	3.21
Rain May	0.04±0.01	0.03	0.05
Small mammal availability	-0.002±0.0001	0.00	0.00
Height tree	0.49±0.27	-0.04	1.02

[1] AICc weight 0.56.
[2] AICc weight 0.29.
[3] AICc weight 0.63.

Egg and nestling loss

Mammalian predation, clutch abandonment, and starvation and/or siblicide were the most commonly determined causes of failure at nests in both habitats (Table 7). Avian predation was rarely recorded (Table 7), but mammalian predation of eggs ($\chi^2_1 = 24.3$, $P < 0.001$) and nestlings ($\chi^2_1 = 13.0$, $P < 0.001$) was more common in natural compared to transformed habitat. Overall, pairs in natural habitat incurred greater egg ($\chi^2_1 = 7.33$, $P < 0.01$) and nestling losses ($\chi^2_1 = 6.03$, $P < 0.05$) due to avian and mammalian predators than nests in transformed habitats, while losses caused by human harvesting were relatively small.

5.4 Discussion

Contrary to expectations, we recorded no significant effect of land use on productivity and nest success, suggesting that the agricultural landscape in northern Cameroon provided adequate habitat for breeding Grasshopper Buzzards. This was primarily related to the opposing effects of generally more favourable resource conditions in natural habitat, versus lower losses due to natural predation and longer inter-nest distances in transformed habitat, which perhaps reduced intraspecific interference and competition (Newton 1979). The importance of natural predation for breeding Grasshopper Buzzards was supported by our observation that nest tree selection and reproductive output were strongly influenced by their vulnerability to predation. Firstly, the greater odds of failure of nests with increasing

Table 7. Egg or nestling loss (%) at nests in natural (*n* = 131) and transformed habitats (*n* = 125) in 2009 and 2010, divided by cause.

	Natural habitat		**Transformed habitat**	
Cause of loss	**Eggs (*n* = 242)**	**Nestlings (*n* = 142)**	**Eggs (*n* = 249)**	**Nestlings (*n* = 146)**
Mammalian predation[1]	12	11	5	5
Avian predation[2]	2	1	2	1
Human predation or disturbance[3]	0	0	2	4
Clutch abandonment[4]	11	-	15	-
Starvation or fratricide[5]	-	11	-	4
Other[6]	3	1	2	4
Unknown	14	36	13	24

[1]Claw marks on the nest tree (*n* = 2) implicated African Wild Cat (*Felis silvestris*) or Serval (*F. serval*). Other common potential predators in the area: Genetta sp. and African Civet (*Civettictis civetta*). Also included nestling death after the adult was killed at the nest (cf. Figure 3a) in natural (*n* = 5) and transformed habitat (*n* = 1).
[2] Pied Crow (*Corvus albus*; *n* = 6 predation events; Figure 4b), Lanner Falcon (*Falco biarmicus*; *n* = 1), Dark Chanting Goshawk (*Melierax metabates*; *n* = 1), and Red-necked Buzzard (*n* = 1) were observed preying on nestlings or eggs and/or attempting to do so.
[3]Broken branches near the nest, footprints, and/or signs of a fire underneath the nest-tree indicated nest robbery. Also included logging of the nest tree (*n* = 2).
[4]Examination of abandoned eggs showed that embryos were either little developed (*n* = 1) or eggs appeared sterile (*n* = 5).
[5]The second nestling bore wounds when last seen alive due to frequent attacks by the sibling(s) (*n* = 6; Figure 3c,d), while growth-retarded nestlings, including those with small wounds, during the last measurement suggested starvation or siblicide in other cases.
[6]Included disease or parasites and wind.

age and brood size suggests that enhanced conspicuousness of larger, and older broods, perhaps through the smell from prey remains, excrement, and heightened activity, increased the odds of detection and predation (Di Giacomo *et al.* 2011). The positive effect of tree height on clutch survival further implied that selection for relatively high trees was adaptive, possibly because it reduced access or detectability by common mammalian predators, such as African Wild Cat or viverrids. Several adults were killed at the nest by these or other mammalian carnivores, which were responsible for most egg and nestling losses in natural habitat, underlining their importance as nest predators.

Although we recorded little direct evidence of predation by avian predators, the canopy cover shielding the nest from the sky, and thus, avian predators (Tome 2003, Rodríguez *et al.* 2006) was positively associated with breeding output. This suggests that Grasshopper Buzzards could escape detection and predation by avian predators by improving nest concealment. Raptors frequently pose the greatest predation risk to small and medium-sized raptors (Sergio & Hiraldo 2008) and this also seems true in African savannas (Thiollay 1976), where seasonal migrants may be among the most important predators of Grasshopper Buzzard nestlings. Indeed, intra-African migratory Wahlberg's Eagle *Aquila wahlbergi* and Red-necked Buzzard *Buteo auguralis* were commonly recorded in the study area and frequently mobbed by Grasshopper Buzzards (R. Buij unpubl. data), suggesting they were perceived as an important threat (Coulson *et al.* 2008). Additionally, canopy shielding might have protected broods from rainstorms or excessive diurnal heat-gain from

high solar radiation, which are potentially harmful to eggs and nestlings (Collias & Collias 1984). Although this might have affected nestling survival, top cover was not significantly associated with clutch survival. Finally, the somewhat counter-intuitive positive association of productivity with increasing nest visibility might be partly explained by the low human harvesting rates, and the fact that mammalian predators primarily use olfactory and sound cues to detect prey (Selås 1997, Kleindorfer *et al.* 2005). Greater visibility from the nest might have also improved predator detection (Götmark *et al.* 1995) or nest defence (Selås 1997), benefiting productivity rather than depressing it.

Our results showed that rainfall was positively associated with Grasshopper Buzzard nest success and productivity, adding to existing evidence of the positive role of rainfall on raptor productivity in arid African savannas (Hustler & Howells 1990, Wichmann *et al.* 2003). Rainfall triggers a flux of important prey (Thiollay 1978a, Njiforti 1997), which is unpredictable at the start of breeding, limiting possibilities for opportunistic movements to other, more productive areas during the breeding season. We recorded positive associations of clutch and brood survival with rainfall at corresponding periods during the breeding season, which may point to the potential for adjustment of breeding investment through constant resource tracking, which would promote resistance to resource fluctuations (Sergio *et al.* 2011). Despite the apparent behavioural flexibility to fluctuating conditions, patterns of declining rainfall in the region since the late 1960s (Hulme *et al.* 2001) might have consistently depressed reproductive output, potentially contributing to Grasshopper Buzzard population declines between 1969 and 2004 (Thiollay 2006a). According to predictions by some climatic models (e.g. Held *et al.* 2005), the drying trend in the Sahel is likely to continue, which would aggravate breeding conditions.

Conservation implications

Although the majority of Afrotropical raptors have probably been significantly affected by land use changes in the West African savanna (Thiollay 2006a, 2007a,b), Grasshopper Buzzards in northern Cameroon showed a high degree of flexibility to the transformation of their breeding habitat. Although anthropogenic land use reduced the availability of grasshoppers and small mammals, sparse grass cover in the transformed habitat improved the accessibility of important reptile prey. Grasshopper Buzzards were dependent on *Sclerocary birrea* trees for nesting in our study area and selected relatively large trees, but such trees were as widely available in transformed as in natural habitat. Pairs even used stunted, single trees in croplands for nesting, and in five instances breeding efforts were continued when trees were heavily pruned over the course of the breeding season (cf. Figure 3f). Importantly, pairs in transformed habitat incurred lower losses due to natural predators compared to natural habitat in our study area, and this may be widely applicable, as agro-ecosystems generally support fewer mammalian and avian predators than natural habitats (Blaum *et al.* 2007, Thiollay 2006a, 2007a). Finally, we detected little evidence of nest harvesting by humans in our study area, which was mentioned as a significant factor contributing to raptor declines in West African savannas (Thiollay 2007a, Anadón *et al.* 2010). Although we suspect that our presence in the study area might have contributed to the low incidence of human harvesting, it appeared to be largely related to the unsuitability

of raptors as food for the predominantly Muslim population in the area, the majority of whom consider consumption of raptor products and their derivatives unlawful (R. Buij unpubl. data).

Despite apparently suitable breeding conditions in transformed habitat, our results showed that Grasshopper Buzzards increased inter-nest distances with increasing cultivation around nests. This may have been related to human activities on cultivated fields; although breeding pairs seemed fairly tolerant to farmers working near the nest, the concurrence of the breeding season with the start of the crop growing season might have increased the odds for disturbance and early desertion of breeding attempts in our study area. Further, small mammal availability, grasshopper availability, and grass cover, which positively influenced respectively nest density, productivity or nest success, were more favorable in natural than transformed habitat. This suggests that anthropogenic land use, in the form of livestock grazing and expanding cultivation, has the potential to negatively affect Grasshopper Buzzard populations. Such changes, which characterized the Sudano-Sahelian breeding range of the Grasshopper Buzzard during the past four decades (Wardell *et al.* 2003, Brink & Eva 2009), are likely to continue unabated as the region experiences some of the world's highest human population growth rates (*c.* 3%; UN World Population Prospects 2010) and agricultural yields generally show little sign of improvement (Njomaha 2004). Education on the potential value of raptors in pest control (Sánchez-Zapata *et al.* 2007, Sergio *et al.* 2008) might prove valuable to local initiatives for conservation of breeding populations in agro-ecosystems, which should focus on sustainable agricultural intensification and retaining native trees in croplands.

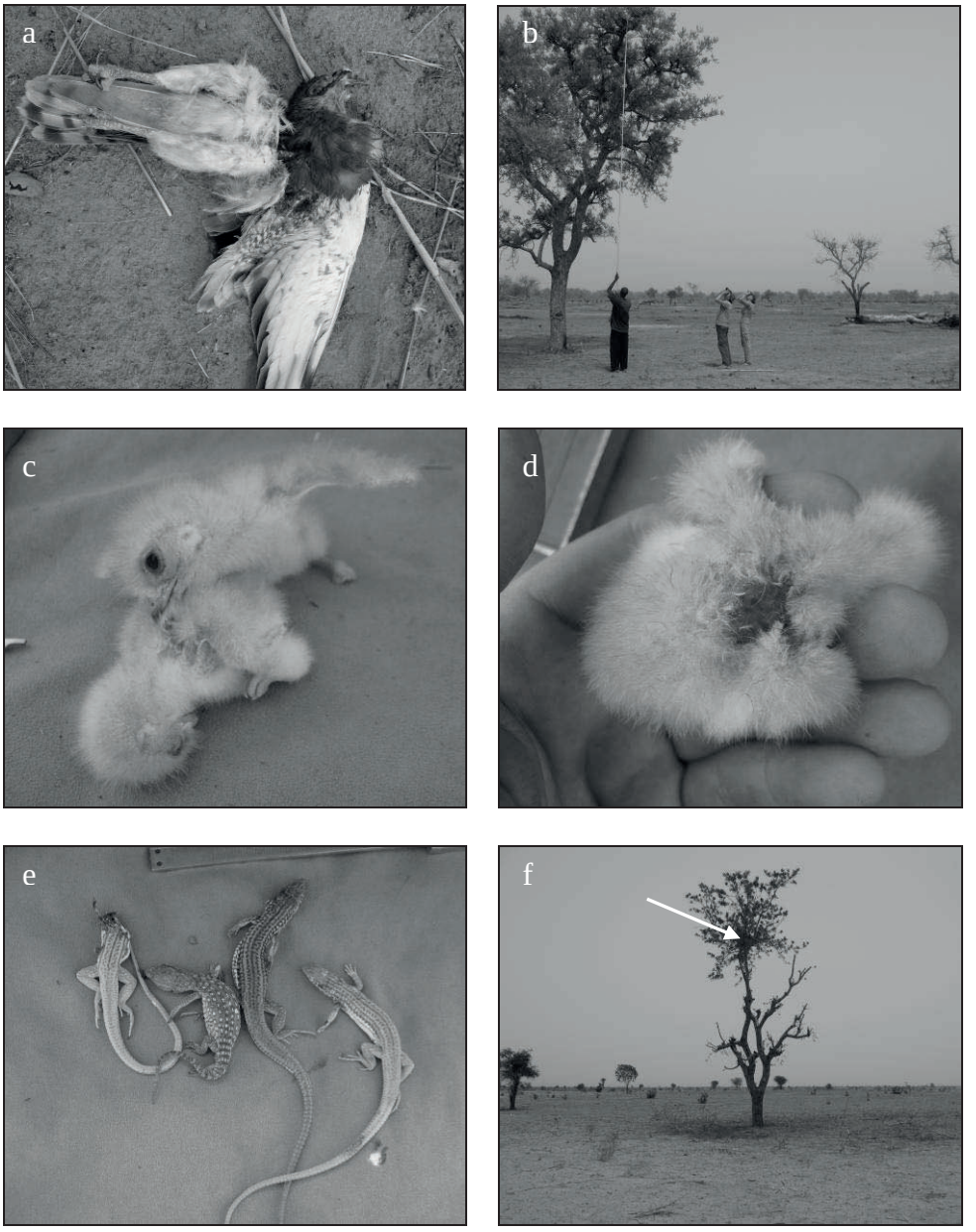

Figure 3. (a) Adult Grasshopper Buzzard killed and partly devoured by small mammalian carnivore in Waza N.P.; (b) technique used for rapid assessment of nest contents: mirror on pole; (c) Cain and Abel struggle between Grasshopper Buzzard nestlings; (d) the youngest of the two nestlings shown in (c) with a wound on its back (this nestling later perished); (e) collection of lizards from a Grasshopper Buzzard nest; and (f) heavily cropped nest tree (arrow indicates position of the nest) in transformed habitat – three nestlings fledged from this nest.

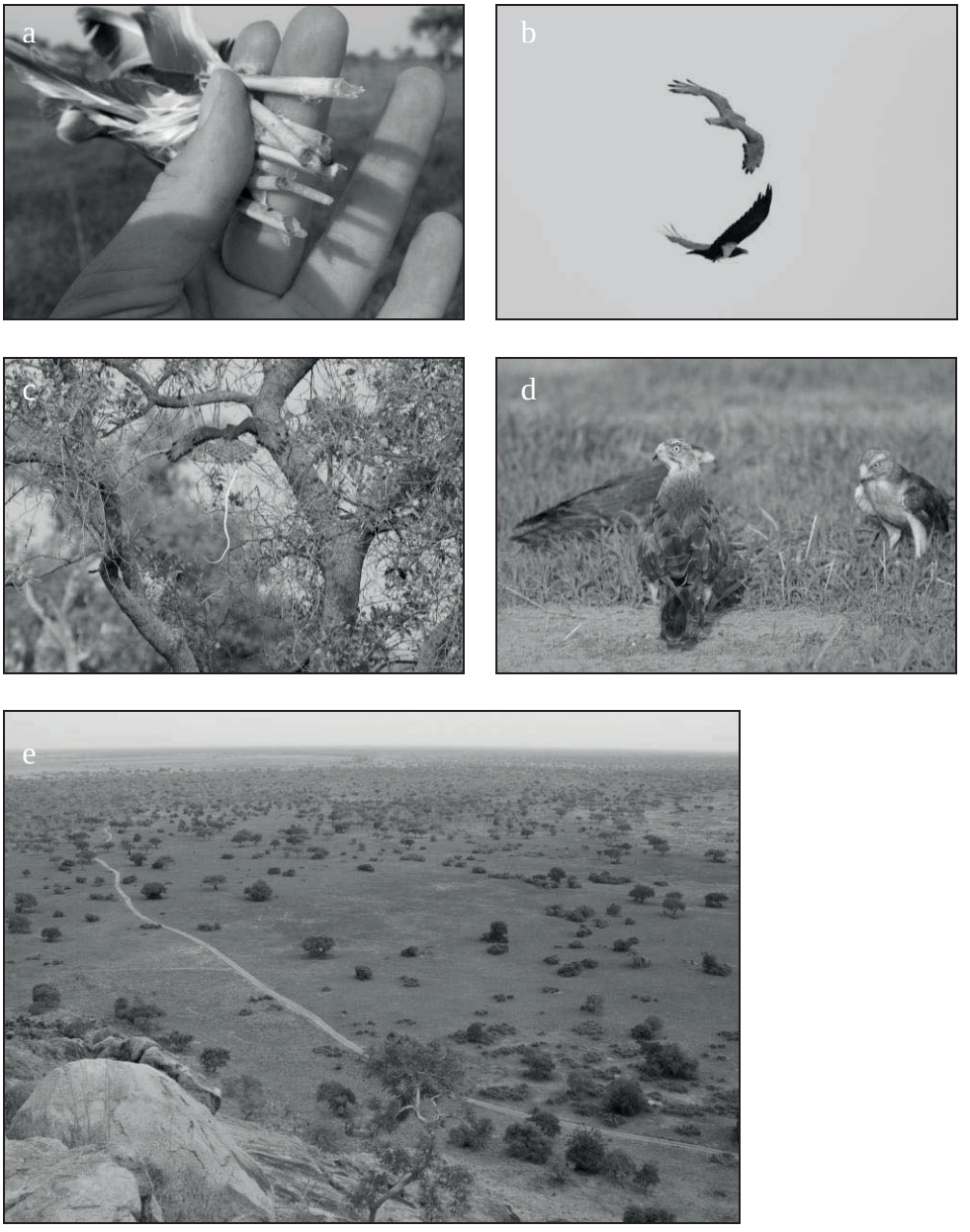

Figure 4. (a) Bitten-off flight feathers discovered underneath and in the nest indicate that a small carnivore killed this Grasshopper Buzzard nestling in Waza N.P.; (b) Grasshopper Buzzard chasing off a Pied Crow; (c) adult Grasshopper Buzzard alighting on the nest with a snake; (d) Grasshopper Buzzards feeding on termites in Waza (July 2009); and (e) breeding habitat of Grasshopper Buzzards in Waza N.P. (June 2009).

Chapter 6

Breeding biology and diet of the African Swallow-tailed Kite in Senegal and Cameroon

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In press: *Journal of Raptor Research*

Abstract

We report on the breeding biology of the African Swallow-tailed Kite *Chelictinia riocourii* in two study areas located 3400 km apart in the central (Cameroon) and western extent (Senegal) of the species' breeding range. With 110 nests in 2.8 km^2 suitable breeding habitat, Kousmar islet (23 km^2) in Senegal supports the largest documented colony of Swallow-tailed Kites to date, which was located nearby a massive winter roost. We recorded on average 7 pairs/colony in Cameroon, where nest density was 0.3 nests/km^2 in protected woodland and 0.9 nests/km^2 in cultivated habitat. In Senegal, breeding groups had on average 9 pairs. Egg-laying coincided with the end of the dry season in Cameroon, but eggs were recorded from the middle of the dry season in Senegal. Eggs hatched between April and June in both study sites in 2010, but from March 2012 in Senegal. The incubation period was estimated at 27-31 days based on two nests, and the fledging period at 32-35 days (n = 3 fledglings). Mean clutch size was 2.5 (n = 32) in Cameroon and 2.1 in Senegal (n = 29); one clutch of four eggs was recorded in Cameroon. Nest success estimated with the Mayfield method was low at 17% in Cameroon and exceptionally low at 4% in Senegal, possibly related to a combination of suboptimal food conditions, high predation pressure, intraspecific aggression and lack of experience among breeding pairs. Prey items at nests were dominated by lizards (30-54% of items) and insects (27-49%), notably grasshoppers, whereas the diet at the winter roost in Senegal was dominated by Orthoptera (55%) and Solifugids (43%). African Swallow-tailed Kites appear to cope with moderate land transformation, but widespread loss of tree cover near floodplains leads to deteriorating roost and nest availability.

Left: adult African Swallow-tailed Kite above breeding colony in Cameroon.

6.1 Introduction

The African Swallow-tailed Kite *Chelictinia riocourii* (hereafter: Swallow-tailed Kite) is a small, gregarious raptor endemic to sub-Saharan Africa largely north of the equator, from Senegambia in the west to Ethiopia and Somalia in the east, and south to Kenya. It is a slim, tern-like kite, with long pointed wings and a deeply forked tail, often recorded in groups on the wing and occasionally hovering to scan for terrestrial prey. Swallow-tailed Kites reportedly breed in the Sahelian parts of the range (between 13°N and 16°N) at the start of the rains between May and July (Thiollay 1977a, 1978a), after which populations migrate to the north (14°-19°N). Areas south of 14°N are largely vacated during the rains, but between December and April, Swallow-tailed Kites descend to the southern Sahelian and Sudan savannas (from 10°N-15°N, but as far south as 8°N; Brown & Amadon 1968; Thiollay 1977a, 1978a), while records south of West Africa's Sudan savanna zone probably occur only in very dry years (Elgood 1981). During this period, they feed predominantly on grasshoppers (Pilard *et al.* 2009, 2011, Mullié 2009), occasionally in large foraging groups (Mullié *et al.* 1992). These gather in large congregations at night roosts, such as 20,000-36,000 individuals in Senegal in January 2007-2012 (Pilard *et al.* 2011), 2480-4500 in the Office du Niger in Mali in December 2003 and January and December 2006 (Zwarts *et al.* 2005, Strandberg and Olofsson 2007, Guitard and Reynaud 2008) and > 10,000 there in February 2012 (J. Gremaud in litt.), 6000 in Cameroon (J. Thal pers. comm.) and 1300 in Niger in January 1993 (W. Mullié and J. Brouwer pers. obs.; Figure 1). Numbers are high year-round in large West African floodplain systems, such as the Inner Niger Delta in Mali (Thiollay 1978a), which constitute the principal habitat because of the high availability of grasshoppers and locusts. Duhart & Descamps (1963) found up to 30 individuals of *Locusta migratoria migratorioides* in the gizzard of a single Swallow-tailed Kite in the floodplains of the Inner Delta of the Niger.

In spite of locally high numbers, comparative road counts indicated significant population declines between 1969 and 2004 inside and outside protected areas in Burkina Faso, Mali and Niger (Thiollay 2006a), and a decreasing trend in Cameroon (Thiollay 2001). Breeding populations are threatened by unprecedented degradation of the fragile arid Sahelian ecosystems, resulting from expanding cultivation, woodcutting, and overgrazing by livestock associated with increasing human populations (Wardell *et al.* 2003, Wood *et al.* 2004). Further, Swallow-tailed Kites are suspected to be in decline owing to locust control measures and the use of pesticides in general (Ferguson-Lees & Christie 2001). Drought conditions in the Sahel from the late 1960s may have modified the principal habitats of the kites' insect prey resources, reducing the geographical distribution and duration of locust plagues (Mullié 2009). However, unprecedented grasshopper outbreaks (1974-1989, summarized in Mullié 2009) and a desert locust plague (1986-1988, US Congress OTA 1990) swept the entire Sahel in the same period, suggesting that food supply, at least locally, was not limited within the kites' breeding range.

Although Swallow-tailed Kites occupy a huge breeding range of approximately 600,000 km^2, published accounts on the breeding biology were derived mostly from short-term observations at a few nests in Kenya (Brown 1970, Davey & Davey 1980, Dewhurst &

Fishpool 1984, Sutton *et al.* 1984, Demey 2011). Reports from the much more extensive West to Central African breeding range are scarce (Bannerman 1951, Barlow *et al.* 1997, Sauvage & Rodwell 1998, Brasseur 2000, King 2000). Systematic observations of their diet during the breeding cycle are even scarcer, but we know that kites feed skinks (Squamata; Scincidae) to their young (Bates 1930). The objectives of the present study are to quantify for the first time the nest site characteristics, breeding density, reproductive success, and diet of the Swallow-tailed Kite in the central (Cameroon) and western (Senegal) parts of the breeding range. We include a diet comparison of kites at nests and roost sites and examine how breeding performance varied between populations, including an assessment of causes of nest failure.

6.2 Materials and methods

Study area

The study area in the Far North Province of Cameroon (11°00'N-11°40'N, 14°20'E-15°00'E) covers the Waza National Park (WNP) and the cultivated areas south of WNP. The area is located on sandy deposits forming the southern ridge of the former Lake Chad (6000 Before Present) and bordered to the north by *Acacia* woodlands and the seasonally inundated grasslands of the Waza-Logone floodplains. Vegetation in the study area is characterized by open woodland dominated by *Sclerocarya birrea*, *Anogeissus leiocarpus*, and *Balanites aegyptiaca*. The habitat outside WNP is characterized by a mosaic of cultivated fields (sorghum, millet), settlements, and fragments of heavily exploited woodland. Soil type and general topography of protected and cultivated land in the Cameroon study area were comparable.

The study area in Senegal (14°07'N, 16°10'W) is 3400 km west of the Cameroonian site on an uninhabited islet (area of 23 km^2), 65 km from the Atlantic Ocean in the Saloum River estuary called Kousmar, 10 km west of the town of Kaolack (Figure 3). Its conservation status is protected forest. The islet harbors a massive winter roost of Swallow-tailed Kites (20,000-36,000 individuals in January 2008-12; Pilard *et al.* 2011) and Lesser Kestrels *Falco naumanni* (21,000-29,000 individuals), which has been present at least since the 1970s (inhabitants of Ndiafate to S. Cavaillès pers. comm.) and is largely vacated from April to June each year. The habitat consists of intertidal mudflats (6.1 km^2) and degraded hypersaline areas ("tan" in Wolof, the main language in Senegal) partially covered with salt crusts at their lowest elevation, herbaceous vegetation on higher ground least exposed to spring tides (14.3 km^2), and, at the highest elevation, wooded savanna to closed woodland (2.8 km^2) in two blocks of which the largest measures 1.7 km^2. There are no permanent fresh water sources, but temporary pools form on the higher vegetated parts of the "tans" during the rainy season. There are small villages north and south of the islet. Their inhabitants exploit wood and grasses on Kousmar during the dry season. They do not graze livestock because of the lack of permanent fresh water sources, the difficulty in accessing the islet and the presence of approximately 20 Spotted Hyenas *Crocuta crocuta* and a dozen Jackals *Canis aureus* (S. Cavaillès pers. obs.). The soil of the islet consists mainly of silt.

The climate in the study areas in Cameroon and Senegal is semi-arid and characterized by a cold dry season (Nov-Feb) which precedes a hot dry season (March-May) with rains from April into October. Mean long-term annual precipitation in the Cameroon study area is 500 mm and in the Senegal study area is 610 mm.

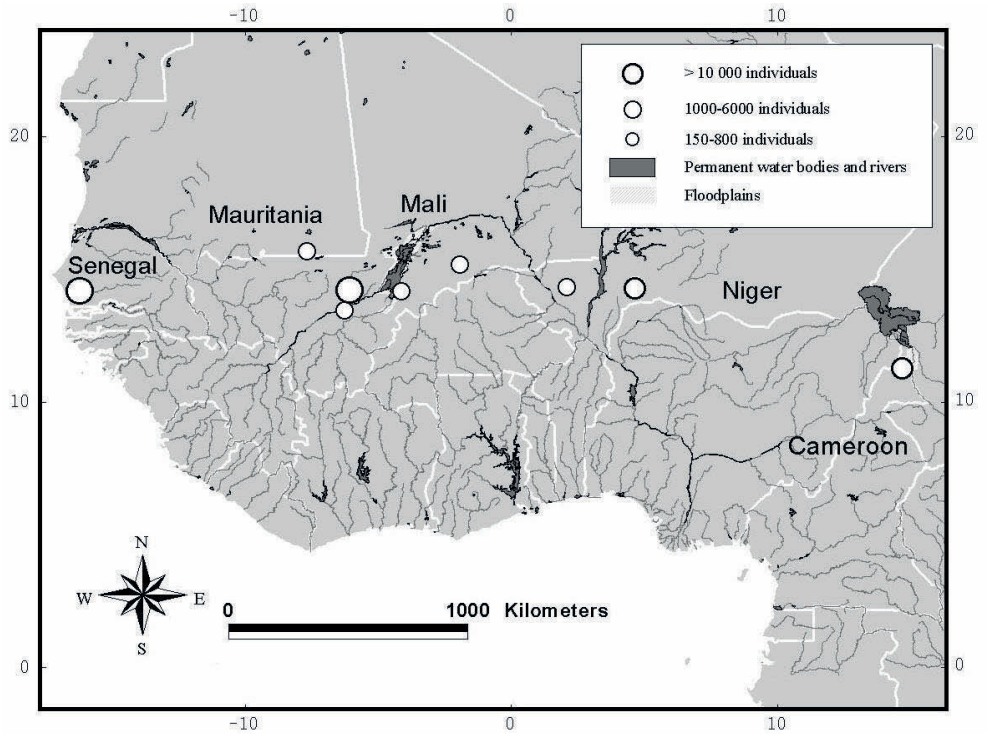

Figure 1. Locations of large Swallow-tailed Kite roosts in West Africa reported between 1980 and 2012, based on published literature and unpublished reports. Locations in Senegal and Cameroon correspond with study sites. Mali: Lamarche 1980, Strandberg & Olofsson 2007, J. Gremaud pers. obs., J. van der Kamp pers. obs.; Mauritania: Lamarche 1987; Niger: Mullié *et al.* 1992, NiBDaB; Cameroon: J. Thal pers. obs.; Senegal: Pilard *et al.* 2011, W.C. Mullié pers. obs.

Nest surveys and breeding performance

The breeding habitat in Cameroon was sampled in seven rectangular census areas totalling 14 km^2 in 2009 and 20 km^2 in 2010 in WNP, and seven rectangular areas totaling 32 km^2 in 2009 and 20 km^2 in 2010 in cultivated habitat, from 2-18 May 2009 and from 3-16 May 2010. We selected census areas based on wet season accessibility (< 13 km from a tarred road). A team of four to eight researchers searched these areas intensively on foot. In Senegal, S. Cavaillès conducted nest searches along the southern and eastern border of the forest and in the western part of the islet where open woodland prevails, from 26 March-19 June 2010. Additional nest searches were conducted from 14 January-18 February 2012 to assess the start of nest construction and laying. All nests found were recorded with GPS

coordinates and their status (e.g. nest lining, attending adults, number of eggs) noted. Nests within 2.5 km of one another were considered to be part of a single colony. The height of trees and nests was measured using extendable aluminium poles of known length. Occupied nests were defined as those nests with at least one adult present at the nest, or those nests containing one or more eggs or nestlings. A mirror on the end of an aluminium pole was used to check the contents of a nest throughout the breeding season to limit disturbance to a minimum.

In Cameroon, 20 nests were visited twice in 2009, during the incubation and nestling phases, and 29 nests were revisited at mean 5-day (3-7) intervals in 2010. In Senegal, 40 nests were visited at mean 4-day (1-9) intervals throughout the breeding cycle in 2010 and five nests were visited at mean 6-day (4-15) intervals during early breeding and egg laying in 2012. Intervals between visits in 2010 were sufficient to determine nest success without violating the assumptions of the Mayfield method (Johnson 1979). Nests that failed were revisited to verify whether re-nesting occurred. We recorded the following breeding parameters: the proportion of laying pairs among nesting pairs; hatching date, which was assessed when nests were visited during hatching or by backdating nestling age from body measurements (Mullié *et al.* in prep.); clutch size; hatching success (nestling number/egg laid); fledging success (fledgling number/nestling number); breeding success (fledgling number/egg laid); and productivity (fledgling number/nesting pair, fledgling number/successful pair). A nesting pair is defined here as pairs occupying nests, whereas laying pairs are defined as those pairs that lay eggs (Steenhof & Newton 2007). Fledgling number was the number of nestlings which reached 80% of the mean fledging age (cf. Steenhof and Newton 2007), i.e. 26 days (this study). The cause of egg or nestling loss was determined in Cameroon by intensively searching the area < 100 m around the nest and the nest cup for clues such as dead nestlings or adults, clipped or bitten-off remiges, carcasses, broken branches or claw marks on the nest tree, and pieces of egg shell. In Senegal the nest cup and the area immediately surrounding the nest (< 5 m) was searched each time a nest was visited. When evidence of predation was found, the number and age of the eggs or nestlings, the date, the type of evidence, and a description of the remains (e.g. feathers, body parts) were recorded. Losses were recorded as “unknown cause” when we found no remains or clues to the disappearance of eggs or nestlings.

Diet

We investigated nestling diet using prey remains and analyses of pellets collected at nests in May-July 2010 in Cameroon and in April-May 2010 in Senegal. Pellets were also collected monthly at the Senegal roost from October till March (2007/08 and 2008/09; W.C. Mullié & C. Riols unpubl. data), but only data from March 2008 and 2009 were used to compare the diets of breeding and roosting (i.e. non-breeding) kites, as March coincides with the onset of the breeding season and therefore would provide the least biased data set for comparison. We collected pellets and prey remains at each nest during each nest visit; remains were either discarded (insect wings, legs, etc.) or returned to the nest (fresh remains). Items (e.g., mandibles, legs, jaw bones) were identified to class or order, or if possible to family, genus, or species level using regional reference collections. The

frequency by number of prey was calculated by dividing the number of prey items by the total number of prey items identified from the combined pellet and prey remain sample. Prey numbers in each of the five prey categories were multiplied by the average mass of the prey to calculate the proportion of total biomass for each prey category. Average adult mass was available for individual Orthoptera species (Mullié & Guèye 2010) and calculated based on a locally obtained random sample of specimens for small mammals (15.3±7.5g; Rodentia, n = 12), birds (18.7±2.5g; Passeriformes, n = 3), frogs and toads (14.5±2.1g; Anura, n = 4), sunspiders (2.1±0.4g; Solifugae, n = 2), lizards (22.6±9.4g; Agamidae, n = 6; 13.8±8.3g; Scincidae, n = 6) and snakes (13.4±9.1g; Serpentes, n = 5). For other insect prey items identified to order, the average mass of the identified genera in the order was used based on the cumulative mass of 7-50 individuals of each order collected in the field divided by the number of individuals.

Statistical analyses

We used Program MARK (White & Burnham 1999) to estimate nest survival rate for nests of laying pairs, assuming a constant Daily Survival Rate (DSR; Dinsmore *et al.* 2002). Fail dates were assumed to be the midpoint between the last visit in which eggs or young were recorded at the nest and the next visit when the nest was empty. We used the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002) to evaluate models, with the lowest AICc values being selected as the best model. We used Mann-Whitney *U*-tests (SPSS 19.0, SPSS Inc, Chicago, IL, USA) to investigate differences in reproductive parameters. We used Pianka's (1973) Index to calculate diet overlap using the percentage frequency of the main prey categories in the diet. Data are expressed as means ±S.E.

6.3 Results

Nest site features and breeding density

A total of 151 occupied nest sites were described during the study from 2009-2010, 50 in Cameroon and 101 in Senegal. An additional 13 nests were discovered in 2012 in Senegal. In Cameroon, 98% of nests were in *Sclerocarya birrea* and 2% in *Balanites aegyptiaca*. We recorded up to three occupied nests in one *Sclerocarya birrea* in Cameroon. In Senegal, 32% of nests were built in *Lannea acida*, 21% in *Commiphora africana*, and 11% in *Sterculia setigera*, with 9 other nest-tree species recorded, most importantly *Mitragyna inermis* (9%), *Balanites aegyptiaca* (7%) and *Bombax costatum* (6%). In 2012 a single nest in Senegal was found in a *Borassus aethiopum* palm tree. Nests were averagely 7.4 m above the ground in Cameroon and 4.8 m in Senegal (Table 1). Nests in *Sclerocarya birrea* (Cameroon) were most often (82%) situated on side-branches < 10 cm diameter, occasionally against a larger side-branch (10-20 cm diameter; 15%), or in the tree top (3%), and usually exposed to the sky. Nests were small (18-25 cm diameter) structures of twigs and grasses, lined with feathers, pieces of white plastic, paper and/or cloth (Cameroon and Senegal). Of 20 nests in Senegal inspected throughout the breeding cycle for lining of the nest, 16 (80%) contained cloth, and 5% feathers. A single nest in 2012 had white paper

lining added at least four days after the clutch of two eggs had been completed. Outer twigs and surrounding branches became increasingly white from feces during the breeding season, conspicuously so from halfway the nestling period. Although nests may have been reused, most were newly built in Cameroon.

Seventy-six percent of nests in Cameroon were in cultivated habitat, of which 44% were located < 200 m from cultivated fields, 30% < 400 m from a Fulbe nomad camp, and 26% in heavily exploited woodland (logging, tree pruning, heavily grazed). All nests in Senegal were in mixed woodland or wooded savanna exploited by villagers for wood and grasses, and most nests (64%; n = 56/88 nests in the largest woodland block) were at the periphery of the woodland habitat. Villagers regularly cut grass under and among the nest trees and they occasionally cut branches of trees holding occupied nests.

Nesting density in nest census areas in protected, intact habitat in Cameroon was 0.34±0.19 nests/km^2 and 0.90±0.47 nests/km^2 in cultivated habitat ($U_{7,7}$ = 22.0, Z = -1.10, P = 0.27). In Senegal, nesting density in the 2.8 km^2 study area was 39.3 nests/km^2. Nearest nest distances in Cameroon and in Senegal reflected the higher nest density in the latter site (Table 1). Most Swallow-tailed Kites in Cameroon (96%; n = 50) nested in colonies of two or more nesting pairs, which had about 7 pairs on average, much smaller than the colony in Senegal (Table 1). We discovered one breeding colony in 2009 in Cameroon which was no longer present in 2010, while one colony had been re-established 1.5 km from a breeding location used in 2009. The nest trees and immediate surroundings of the abandoned breeding site had apparently remained relatively unchanged between 2009 and 2010.

Reproductive parameters and nest success

Nest building started in Senegal from 14 January in 2012 and first eggs were recorded on 14 and 18 February 2012 (n = 2 nests). Only a single clutch of four eggs was recorded (Cameroon), which was entirely lost. No immature birds were recorded among nesting pairs in Cameroon but at least three breeding individuals in Senegal in 2010 had not completed their first molt (Mullié *et al.* in prep.), indicating that immature birds were part of the breeding population. As in 2010 no special attention was given to the age of breeding birds in Senegal, on 11th April 2012 a random sample of 11 nests was more closely inspected. Of 14 birds that were observed attending these nests, five (35.7%) were in immature plumage, of which two formed a pair.

We did not record eggs at 28% of occupied nests (n = 50) in Cameroon and at 32% of nests (n = 53) in Senegal, although we could not determine whether these nests had failed prematurely, i.e. before egg laying, or whether eggs had been laid and subsequently taken by a predator. Incubation lasted 27-31 days and nestlings hatched between April and June in both study sites in 2010 (Table 1), but from March 2012 in Senegal. A small proportion of pairs (15%; n = 13) in Cameroon laid eggs before the first rains on 22 April in 2010 (total April rainfall: 3 days; 4-5 mm), but most pairs laid eggs after the first rains. In Senegal, all eggs under surveillance hatched well before the first rains on 4 June 2010. However, some laying might have continued after that date, because nests discovered after

19 June (when observations ceased) were only mapped and contents were not inspected. The nestling period (time from hatching to first flight from the nest) was estimated at 32-35 days for three nestlings in Cameroon (n = 2 nests). Nestlings were observed returning to the nest where the adults delivered food until 12 days after fledging in Cameroon (n = 2 nests). In at least one nest in Senegal, after a clutch of three eggs had been predated, new eggs were laid and two young hatched, suggesting a potential for renesting.

Table 1. Nest site and reproductive characteristics (mean ±S.E.; range) of Swallow-tailed Kites in Senegal and Cameroon in 2009 and 2010.

Parameter	Cameroon	Senegal
Nest tree height (m)	8.96±0.31 (5-13; n = 50)	6.47±0.13 (4.5-10.5; n = 94)
Nest height (m)	7.35±0.27 (4-12; n = 50)	4.80±0.12 (3-9.5; n = 94)
Nearest nest distance (m)	63.4±11.2 (4-456; n = 50)	11.3±1.6 (4.5-16.3; n = 10)
Colony size[1] (nests)	6.6±1.4 (2-13; n = 6)	110 (n = 1)
Hatching date[2]	28 May (±13.6; 26 April-19 June, n = 13)	27 April (±20.4; 05 April-31 May, n = 12)
Incubation period (days)	27-29 (n = 1)	29-31 (n = 1)

[1] Defined as a breeding aggregation with inter-nest distance < 200 m in Cameroon, and inter-nest distance < 100 m in Senegal.
[2] First-born nestlings in 2010.

The Daily Survival Rate (DSR) for nests containing eggs or nestlings in Cameroon and Senegal was 0.959±0.005 (n = 50), which raised to the number of days from initiation (first egg laid) to nest completion (first nestlings fledged; i.e. minimum of 59 days) leads to an estimated maximum nest success of 0.085±0.002. Compared with the intercept-only model, model fit improved with country (Senegal = 1, Cameroon = 2) added as a covariate (β = 0.59±0.27; ΔAICc = 2.91), and indicated that DSR was higher in Cameroon (0.970±0.006; n = 21) compared to Senegal (0.948±0.008; n = 29). Nest success thus estimated was 0.166±0.05 for Cameroon and 0.043±0.02 for Senegal, reflecting the higher productivity in Cameroon (Table 2).

Table 2. Breeding parameters (mean ±S.E.) of Swallow-tailed Kite nests in Senegal and Cameroon in 2010. Clutch size is the number of eggs laid in a nest (only for laying pairs); nesting pairs are pairs that occupied a nest; hatching success is the number of nestlings per egg laid; fledging success is the proportion of nestlings that attained 80% of the mean fledging age (cf. Steenhof and Newton 2007); breeding success is the number of nestlings that attained 80% of the fledging age, per egg laid; and productivity is the number of nestlings that attained 80% of the fledging age, per nesting pair or per successful pair.

Parameter	Cameroon	range	*n*	Senegal	range	*n*
Clutch size[‡]	2.50±0.14	1-4	32	2.10±0.13	1-3	29
Nestlings/nesting pair[‡]	1.14±0.19	0-3	44	0.64±0.14	0-3	47
Hatching success[‡]	0.60±0.09	0-1	25	0.34±0.08	0-1	29
Fledging success	0.38±0.11	0-1	18	0.22±0.10	0-1	16
Breeding success	0.21±0.05	0-1	31	0.06±0.03	0-0.7	29
Productivity for nesting pairs	0.33±0.11	0-2	45	0.19±0.07	0-2	48
Productivity for successful pairs[‡]	1.88±0.12	1-2	8	1.29±0.19	1-2	7

[‡]Differences between sites by means of Mann-Whitney U-tests P < 0.05.

Egg and nestling loss

Small carnivores were responsible for a third of nestling losses in Cameroon (Table 3). Based on the strength of branches holding the nests and their usual position at the end of the branches, genets *Genetta* spp. were the most likely mammalian predators of nestlings. African Wild Cats *Felis silvestris lybica*, which were frequently observed in the study area, might have been responsible for a portion of losses. Three nests holding six nestlings were preyed upon by a mammalian carnivore in a period of 4 days at one colony. An African Harrier Hawk *Polyboroides typus* was seen eating a 6-day old nestling at a Swallow-tailed Kite nest while being attacked by four adult kites for 4 min. Two dead adults were recorded underneath nest trees in Cameroon, in one instance two nestlings survived at least 10 days after an adult was found dead at the base of the nest tree but died before fledging.

Circumstantial evidence indicated Pied Crow *Corvus alba* predation at one nest in Cameroon (a Pied Crow was recorded perching 3 m from the nest while being attacked by two adults). One Pied Crow pair nested at 320 m from the nearest nest of the largest Swallow-tailed Kite colony (13 pairs), and was observed foraging near (< 200 m) or over the colony on 38% of visits (n = 8). In two instances, when crows perched within 100-250 m of the colony, four to seven Swallow-tailed Kites positioned themselves in trees at the edge of the colony, facing the crows. A crow flying towards the colony was chased by a group of two to eight kites uttering alarm calls until 300 m from the edge of the colony. Of the nests in this colony, 23.1% were empty at our first visit, 43.5% of eggs (n = 23) were lost before hatching, and only a single nest produced fledglings.

Table 3. Cause of egg or nestling loss in Cameroon.

Stage	Cause	Number of Eggs or Nestlings Lost	Percentage of Total
Egg	Pied crow	2	11
	Unknown	17	89
Nestling	Mammalian carnivore	9	33
	Starvation	6	22
	Pied Crow	3	11
	Wind	3	11
	Tick infestation	2	7
	African Harrier Hawk	1	4
	Unknown	3	11

Predation in Senegal was presumed to be mainly from nocturnal carnivores and Verreaux's Eagle Owls *Bubo lacteus*. Three Verreaux's Eagle Owls, probably a nesting pair with juvenile, roosted in January-February at 6.5 km from the breeding colony. Another individual roosted at 2.5 km from the nearest kite nest in 2010, and a Verreaux's Eagle Owl pair nested at this location in April 2012. During two subsequent 30-min visits each of to the three roosting Verreaux's Eagle Owls, 4-5 Swallow-tailed Kites constantly mobbed the owls, but light grey or white feather remains in two out of 18 pellets, or pellet fragments, could not with absolute certainty be attributed to Swallow-tailed Kites. Dead Swallow-tailed Kites showing signs of mammalian predation were frequently found underneath roost trees in Senegal, but few visits were made at night and, except for African Wild Cat, no small carnivores were seen, although genets may have occurred in the area. Pied Crows and

other potential avian predators were only rarely observed, mostly crossing the islet and never near the nests. An African Harrier Hawk was seen once, leaving the islet. Of 23 nests where failure was recorded, 13 nests lost eggs or young without any trace, three showed signs of egg predation, two had young preyed upon, and a hatchling died shortly after hatching at one nest. Two nests were lost because the branch on which they were constructed was cut and one adult was found taken by a predator under the nest and a nestling had fallen from another nest.

Nestling diet and comparison with roost diet

In terms of biomass contribution, > 50% of nestling diets in Cameroon and Senegal consisted of reptiles whereas diets of roosting kites were dominated by Orthopterans and Solifugids (Figure 2). Dietary overlap according to Pianka's (1973) Index based on the percentage frequency of prey numbers in the diet for nine prey categories (micro-mammals, birds, Agamid lizards, other lizards, serpents, orthopterans, solifugids, other insects, amphibians) was 0.68 for nestling diets from Senegal (n = 27 prey items) and Cameroon (n = 98 prey items). Using the same prey categories and the combined prey sample from nests (n = 125 prey items) and the Kousmar roost (n = 2660), overlap was 0.37 between roost site and nestling diets.

6.4 Discussion

With 110 nesting pairs in 2.8 km^2, Kousmar islet in Senegal supports the largest Swallow-tailed Kite breeding colony documented to date, compared with single colonies reported from Senegal (3, 5, > 15 nests; Brasseur 2000, King 2000, P. Pilard in litt.), Cameroon (2-13 nests; this study), and Kenya (two nests; Davey & Davey 1980). Based on our data and observations of inter-colony distances elsewhere (Davey & Davey 1980, Brasseur 2000), we suspect that the nest dispersion pattern in Cameroon and away from Kousmar in Senegal is probably most common. It is likely that the huge roost and breeding congregation in Senegal resulted from habitat suitability, possibly in combination with good food conditions as reported for Palearctic migratory raptors (e.g. Sánchez-Zapata *et al.* 2007). Until the 1980s, Swallow-tailed Kites were known to breed on the mainland along the border of the Saloum River, 6 km east of Kousmar (Figure 3). However, fairly recent and extensive loss of woodland in the Saloum River estuary, mainly to allow for groundnut production (Cavaillès 2010), seems to have concentrated the birds on islets, where tree diversity, density and height has been maintained to a certain extent. Other breeding nuclei in the Delta have also been recorded on islets, or relatively intact forests on peninsulas (Figure 3).

Our observations of immature birds among nesting pairs in Senegal is interesting in light of the foraging efficiency hypothesis (Beauchamp 1999), since coloniality delivers particularly strong advantages for less experienced breeding pairs (Muller *et al.* 1997, Sergio & Penteriani 2005). Possibly, these immature, inexperienced Swallow-tailed Kites cue opportunistically on the presence of successfully breeding conspecifics (Sergio & Penteriani 2005), as suggested by the settlement of new pairs in one Swallow-tailed Kite

colony which already held nests with eggs or nestlings in Senegal (Brasseur 2000). The observed communal nest defense against diurnal predators suggests that Swallow-tailed Kites may also benefit from improved predator protection at colonies during the day, although the conspicuousness of a large colony to nocturnal predators might outweigh such benefits. Frequent small carnivore predation in Cameroon suggests, however, that nocturnal predators may depress reproductive output even in small, relatively inconspicuous colonies.

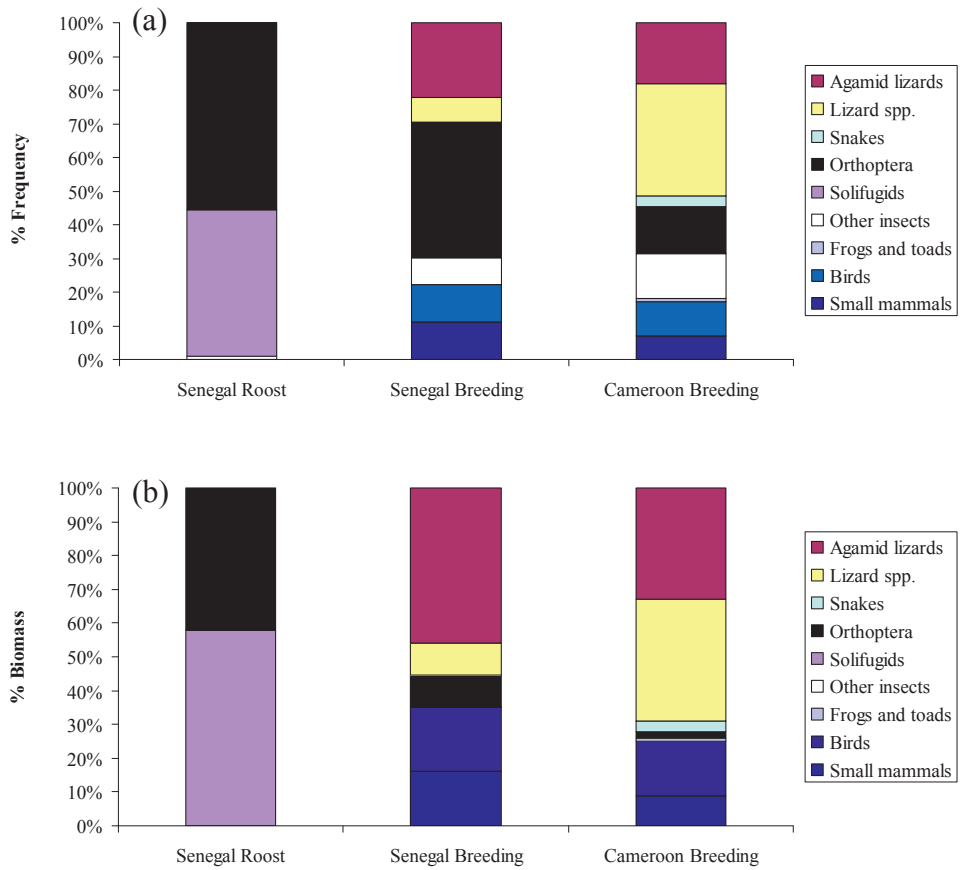

Figure 2. Diet composition based on prey remains and pellet contents of Swallow-tailed Kites in 2009-2010 at the Kousmar roost site in Senegal (n = 2660 prey items), at nests in Senegal (n = 27 prey items; five nests) and at nests in Cameroon (n = 98; 22 nests): (a) prey categories in pellets as percentage of total prey number and (b) as percentage of total prey biomass. Lizard spp. were dominated by Skinks in Cameroon (81%; n = 32), also *Trachylepis quinquetaeniatus*, *Latastia longicaudata*. Orthoptera identified at species level: *Ornithacris cavroisi*. Birds: *Oenanthe heuglini* (one juvenile). "Other insects" included: Mantidae, Termitidae, Forficulidae, Heteroptera, Lepidoptera, Hymenoptera, Coleoptera, Scolopendridae.

The proximity of breeding or roosting Verreaux's Eagle Owls, which are known to regularly prey upon raptor nestlings (Steyn 1982), might have been another important cause of nestling loss in Senegal, given the impact of large owl predation on raptor colonies elsewhere (Sergio *et al.* 2003, Coulson *et al.* 2008).

Timing of breeding and productivity

The laying dates of Swallow-tailed Kites in Cameroon were consistent with Thiollay's (1977a, 1978a) observations of breeding during the start of the rains from May-July in the southern Sahel, and 85% of pairs in Cameroon laid eggs after the first rains. Conversely, laying dates in Senegal have all been from the dry season. Although the earliest recorded laying dates during our surveys were in early March in 2010 and in mid-February in 2012, eggs and nestlings have been observed as early as 20 January at nests 38 km southwest of Kousmar (Brasseur 2000, King 2000), and eggs were recorded in two nests on 24 January 2011, 32 km northwest of Kousmar (P. Pilard in litt.). Laying thus appears to span at least four months (last week of December-first week of May) in Senegal, resembling a protracted breeding season comparable to sympatric Black-winged Kites *Elanus caeruleus* (Rodwell *et al.* 1996).

The very low frequency of clutches of four eggs (1.6%; n = 61), suggested to be the usual clutch size in this species (Brown & Amadon 1968), might reflect suboptimal breeding conditions in our study areas. We suspect, however, that Brown and Amadon's assessment of clutch size may have been based on a very low and unrepresentative sample size. Rather than reflecting the norm, it seems likely that large clutches occur mainly when feeding conditions prior to breeding are very good, as is the case in the related Black-winged Kite (Mendelsohn 1984), Letter-winged Kite *E. scriptus* (Ey 1984) and various other raptors (Dijkstra *et al.* 1982). Indeed, one clutch of four previously recorded by Bannerman (1951) and collected by Bates on 18 June 1931 north of Taoua in Niger (D. Russell in litt.), and another clutch of four collected by Bisseling at Sennar, Sudan on 16 May 1959 (M. Louette in litt.) coincided with massive Desert Locust swarms in the mentioned territories (cf. Waloff 1966, Mullié 2009). Similarly, Davey & Davey (1980) report three nests containing respectively one egg, two and four fledglings at Lake Turkana in Kenya, between 12 and 19 April 1979, when a Desert Locust upsurge occurred in SW Ethiopia (FAO 1978, 1979), immediately north of the area where the kites were nesting.

Our estimate of nest success using the Mayfield method was low at 17% for Cameroon and exceptionally low at 4% for Senegal, even in light of the generally low reproductive output of tropical raptors (Newton 1979). The extremely low reproductive output in Senegal might have resulted from frequent intraspecific interactions (Newton 1979), due to the presence of thousands of conspecifics using the breeding area and its immediate surroundings (Pilard *et al.* 2011). Additionally, high predation levels and the presence of younger, less-experienced birds might have constrained reproductive output, for example if younger. Suboptimal breeding conditions in the second half of the dry season, when we monitored nests, might also have contributed to the low reproductive success. Although this period is characterized by greatly reduced vegetation cover, facilitating capture of terrestrial prey (Thiollay &

Clobert 1990), grasshopper densities are known to decline during this time, mainly due to bird predation (Mullié & Guèye 2010). This may worsen the effect of food competition due to high numbers of conspecifics.

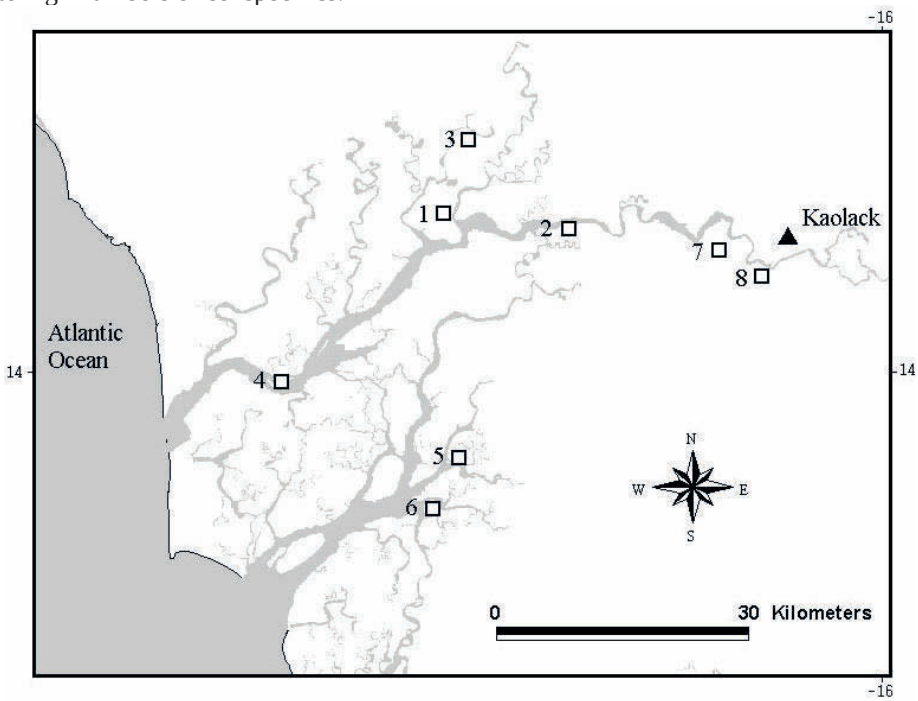

Figure 3. Breeding sites of Swallow-tailed Kites in 2000-2012 in the Saloum Delta of west Senegal. Numbers on the map correspond to 1: J. Peeters in litt. and in Brasseur 2000; 2: Petekele 2010, S. Cavaillès pers. comm.; 3: P. Pilard in litt.; 4: Il de Diable 2011, Manga pers. comm.; 5: R.E. Brasseur 2000 and in litt.; 6: Manga pers. comm.; 7: Kousmar 2010-2012 (this study); and 8: abandoned colony, S. Ndiaye pers. comm.

A prolonged breeding season and the possibility for re-nesting may allow Swallow-tailed Kites to compensate for losses incurred early in the season, as observed in various tropical raptors (Mader 1982, Delannoy & Cruz 1988, Thorstrom & Quixchán 2000), or raise multiple broods while opportunistically capitalizing on conditions of prolonged food abundance, as reported for *Elanus* kites (Mendelsohn 1984, Ey 1984). We recorded renesting at one nest in Senegal after nest predation, but follow-up studies will have to confirm the frequency at which this occurs and how it contributes to improving reproductive output.

Breeding in changing landscapes

Similar to other kites that breed in dense colonies (*Gampsonyx*, *Elanoides*, *Ictinia*; Newton 1979), Swallow-tailed Kites in Senegal and Cameroon opportunistically settled in food-rich floodplain habitats, accepting various common tree species for breeding, including relatively small trees and occasionally those stunted from frequent pruning. The importance

of floodplains for nesting and roosting Swallow-tailed Kites is in line with previous reports from western Africa (e.g. Thiollay 1978a, Pilard *et al.* 2011), which refer to congregations in or nearby floodplains, estuaries, or temporary wetlands. The ability of Swallow-tailed Kites to adapt to fluctuating resource conditions in these wetland systems may limit their vulnerability to human-induced land transformation. Colonies in Senegal relocated to islets when breeding habitats on the mainland were destroyed, and frequently settled close to cultivated fields and human habitation in Cameroon, as previously reported from Kenya (Britton 1980). Foraging kites appear to profit from reduced grass cover and height and improved prey catchability following moderate grazing or cultivation, even hunting alongside livestock to capture flushed insects (Gregory 1982; R. Buij pers. obs.), while transformation of woodland habitats into cropland mosaics may boost grasshopper prey (Mullié & Guèye 2010). Still, extensive loss of tree cover around floodplains, which are a restricted and little-protected habitat in West Africa (Zwarts *et al.* 2009), reduces availability of roost and breeding sites. The Waza-Logone floodplains experienced annual human population growth up to 5% locally in the 1990s, leading to a strong increase in firewood extraction (Scholte 2003), e.g. estimated at 10 tonnes wet mass a day for Kalamaloué N.P. north of Waza N.P. Similarly, 20% of the trees at the roost site in Senegal were lost between 2007 and 2010 due to firewood extraction (Pilard *et al.* 2011). At present, the decline of woodland cover in the Saloum River estuary exposes the islets where the kites breed to an increasing exploitation of wood (Cavaillès 2010). Such loss of woodland cover may further influence dispersion patterns and possibly drive aggregations into larger breeding colonies, possibly contributing to lower breeding output.

Chapter 7

Response to habitat modification by foraging Dark Chanting Goshawks in a West African savanna

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Abstract

Anthropogenic habitat alteration has probably contributed significantly to the decrease of raptor populations in West African savannas. To evaluate the impact of habitat degradation on foraging by sedentary Afrotropical raptors, we investigated the differences in microhabitat selection, foraging effort and energy returns between Dark Chanting Goshawks *Melierax metabates* inhabiting natural and transformed savannas in Cameroon. We expected that agro-ecosystems have become unprofitable for Dark Chanting Goshawks due to scarcity of food. In both savanna types we radio-tracked males and determined hunting effort, by time spent and distance covered between perches, and energy intake through estimation of prey energy content. Goshawks in natural habitats had smaller home-ranges and used a larger proportion of their range for foraging than goshawks in transformed habitat. Patch-level selection for relatively tall trees and high tree density, high shrub cover, and thick and extensive herbaceous cover appeared to be primarily related to optimization of prey biomass within hunting patches. Foraging effort and gains were comparable between habitats. However, herbaceous layer height and tree density within ranges, both higher in natural habitat, were negatively related to prey capture rates. Woodcutting and grazing thus favored greater prey capture rates in transformed habitat, offsetting the lower energy content of prey compared to natural habitat. Agricultural intensification-related and silvicultural practices to discourage expansion of cultivated lands, focused on conservation of trees and controlled access to pastures, would be beneficial to Dark Chanting Goshawks and other sedentary raptors.

Left: Adult male Dark Chanting Goshawk.

7.1 Introduction

Over the last 40 years unprecedented land cover and land use changes have occurred in sub-Saharan Africa, which are driven mainly by the conversion of woodlands into croplands, shrublands, and pasture (Lambin *et al.* 2003, Brink & Eva 2009). Rates of land conversion have been particularly high in West Africa's savannas (Paré *et al.* 2008, Brink & Eva 2009, Ouedraogo *et al.* 2010), where some of the highest human population densities and growth rates on the continent were reported (UN World Population Prospects 2010). The resulting habitat impoverishment was suggested to have contributed significantly to the decline of raptor populations in this region (Thiollay 2006a, 2007a), some of the most dramatic declines recorded in Africa. In light of these immense anthropogenic pressure, the West African situation offers valuable insight into the ecology, ranging and behaviour of raptors confronted with such conditions, especially since these may be representative for future conditions in many parts of the continent.

Multiple studies have examined nest site selection (Berkelman *et al.* 1999, Malan & Robinson 2001, Machange *et al.* 2005, Bamford *et al.* 2009, Virani & Harper 2009) and diet (Ogada & Kibuthu 2009) of Afrotropical raptors in habitats modified by human activities. No studies, to our knowledge, have examined foraging habitat selection at patch level scales by raptors in human-transformed landscapes. However, a thorough understanding thereof is a prerequisite to effective conservation, since maintenance of populations inside protected reserves only may not guarantee population persistence (Chape *et al.* 2005, Clerici *et al.* 2006, Brashares *et al.* 2001). Raptors concentrate foraging in habitat patches where food availability and energy gains are highest (Nishimura 1991, 1994, Ward *et al.* 1998), but morphological, ecological and behavioural adaptations underlie differential selection at the patch level (Thiollay & Clobert 1990). Generally, sedentary raptors are adapted to exploiting relatively little fluctuating, vertebrate prey populations in dense habitat and in a year-round territory. This heightens their sensitivity to anthropogenic land use, which may lead to their disappearance or decline of raptors from areas with impoverished prey populations (Herremans & Herremans-Tonnoeyr 2000), or shifts in prey abundance and diet, with potential consequences for long-term productivity (Ogada & Kibuthu 2009).

To examine the impact of habitat transformation on foraging in a sedentary Afrotropical raptor, we investigated what differences in microhabitat selection, foraging effort and energy returns existed between Dark Chanting Goshawks *Melierax metabates* inhabiting natural and transformed savannas in northern Cameroon. The Dark Chanting Goshawk is a medium-sized, generalist diurnal raptor, and among the most sedentary raptors in West African Sudan savannas (Thiollay 1977a). It is also one of the more common sedentary raptors in the region, although population declines of *c.* 51-62% were reported between 1969 and 2004 (Thiollay 2001, 2006a). Since a growing proportion of scarce natural resources is appropriated by human populations, it seems likely that agro-ecosystems have become unprofitable for Dark Chanting Goshawks due to scarcity of food. To investigate this, we radio-tracked male Dark Chanting Goshawks in natural and transformed habitats and determined hunting effort (time spent and distance covered between perches), and

energy gains. We predict that (1) in agreement with studies of sit-an-wait raptors (Nishimura 1991), the patch utilization pattern by goshawks reflects patch quality, with rich patches being visited more frequently and for longer periods than other patches; (2) Dark Chanting Goshawks in transformed habitats select similar habitat features that characterized profitable, rich foraging patches in natural habitat; (3) foraging patches are comparatively rare (i.e. further apart) in transformed than natural habitat, which will necessitate larger ranges, longer inter-perch flights and greater foraging effort in transformed habitat; and (4) differences in diet composition may result in lower energy intake in transformed than natural habitat, which together with lower foraging effort in the latter, will give rise to significantly greater foraging gains by effort in natural compared to transformed habitat.

7.2 Materials and methods

Study area

The study area (11°00'N-11°40'N and 14°20'E-15°00'E) was located inside the southern part of Waza National Park and the cultivated zone south of the park in the Far North Province of Cameroon. The degree of human influence to the habitat in the protected area (e.g. through livestock grazing, woodcutting; Scholte 2003) was negligible compared to the unprotected area. We therefore refer to Waza N.P. as "natural habitat" vs. "transformed habitat" for the unprotected area. The natural habitat was characterized by *Sclerocarya birrea* dominated woodland and *Anogeissus leiocarpus*, *Balanites aegyptiaca* locally interspersed by dense *Acacia seyal* clusters. The transformed habitat exists of a mosaic of cultivation (notably dry-season sorghum but also maize, tomatoes, groundnut, onions), human settlements, and fragments of heavily exploited woodlands, under severe pressure by livestock grazing and slash-and-burn activities for cultivation and wood selling. Traditional fields and villages were dotted with trees. Trees were absent from large crop fields, mostly to avoid settlement of colonies of Red-billed Queleas *Quelea quelea*, which are considered an agricultural pest.

Radiotracking

We captured twelve adult (> 2 years old) male Dark Chanting Goshawks in the natural (n = 6 males) and transformed habitat (n = 6) between 8 November 2009 and 9 February 2010. We repeatedly drove a predefined road network of 290 km in transformed habitat and 80 km in natural habitat and considered each detected goshawk for capture, until twelve males had been caught. We selected only mated, adult males during the non-breeding season, to minimize variability due to sex, age, and differences in reproductive status (e.g. care for female or nestlings). Goshawks were trapped with a dho-gaza net or bal-chatri trap (Bloom *et al.* 2007), and ringed, weighed to the nearest 0.1 g and equipped with a 10-g TW-3 single celled transmitter (Biotrack Ltd, Dorset, UK) mounted to the central tail feathers (Figure 2b), conform to general safety precautions (Walls & Kenward 2007).

Tagged goshawks were tracked between 5 December 2009 and 1 March 2010 from a vehicle by three observers using a 3-element Yagi antenna and 4 MHz Sika receiver,

binoculars and a telescope. Monitoring was alternated between natural and transformed habitats to minimize the potentially confounding effects of changes in vegetation, climate, and prey parameters as the dry season progressed. We tracked goshawks for three consecutive days from sunrise to sunset (*c.* 11.5-12 hrs), followed by vegetation surveys, and then tracked the next goshawk. We compiled behavior protocols and noted the time spent (in sec) on each of the following five behavior categories: (1) perching (Figure 2a): bird sitting in tree, other structures or on ground, while not engaged in feeding, (2) inter-perch flight: active flight between different perches, (3) circling: circling flight with little or no wing movement, (4) feeding: consuming prey, equivalent to meal duration for individual prey items, and (5) foraging on foot: bird walking on the ground. We also noted strikes on prey, i.e. rapid movements directed towards prey. We distinguished successful and unsuccessful strikes, although strikes occasionally had an unknown outcome when herbaceous vegetation obstructed view (20.5%; n = 337 strikes). These capture attempts involved small terrestrial prey (lizards, insects), which if captured was consumed on the ground, whereas large prey was invariably consumed at a perch.

Incremental analysis during a pilot study based on movements of a radio-tracked male goshawk indicated that 95% of the outer minimum convex polygon (MCP) range (Harris *et al.* 1990) was attained based on all locations after three days compared to the asymptotic MCP-estimate reached at day five. Therefore, we assumed a three-day survey would provide a reasonable representation of short-term range size. Observers remained inside the vehicle and the distance to the bird was kept at a minimum of 70 m or further if visual contact could be maintained. We recorded the GPS-coordinates of each perch after every displacement, and the height of the goshawk and the perch from the base of the perch, to the nearest 0.5 m. The openness of the habitat usually made relocation and identification of the perch site fairly straightforward, although birds occasionally remained out of sight (e.g. when circling). Linear flight is the most energy consuming activity of raptors (Mosher 1976); thus, to assess foraging effort, the length of linear displacements was measured using the home-range extension tool in ArcView GIS 3.2 software (Esri 1999).

Habitat measurements

The vegetation structure at patches used by hunting goshawks was compared with nearby unused patches (i.e. third-order selection; Johnson 1980), a method successfully used to provide insight into the importance of habitat elements for foraging raptors (Kenward 1982, Beier & Drennan 1997). For each goshawk, six perches were selected as the center of hunting patches, or hunting plots, which were compared to unused patches within the MCP range of the goshawk. The perches in hunting plots each had to meet the following criteria: at least one capture attempt was executed from them during the three-day observation period, and the cumulative time spent on the perch was longer than the time spent on other perches used for hunting. The hunting plot was defined as a circle with the perch as the centre. We used the average distance from their perch at which goshawks attempted to capture prey as the radius of the hunting plot. This so-called average strike distance (45 m±6.0 S.E.; range: 7-108 m) was based on 24 capture attempts by seven goshawks equally divided between natural and transformed habitats, obtained during a pilot phase prior to the

study. For each hunting plot, we allocated a paired contrast plot, north of the hunting plot. To be sure that we measured an unused area, the contrast plot was located > 90 m (i.e. twice the average strike distance) from all other used perches and > 216 m (i.e. twice the maximum observed strike distance) from the centre of each of the five other hunting plots. The centre of a contrast plot had to meet the criteria of a potentially suitable foraging perch, i.e. a woody plant of at least 3 m, representing the minimum perch height from which a successful strike at prey was observed.

For each of the 72 paired hunting and contrast plots, sampling for habitat characteristics (see Table 1) was conducted on the day following the three-day monitoring period for each goshawk. Features of the rooted herbaceous layer were measured on 4x4 m squares located at 4-m intervals along four 45-m transects positioned towards the north, east, south and west and radiating out from the centre the plot, thus giving most weight to the habitat near the centre (following Beier & Drennan 1997).

Habitat characteristics were also examined at territory level to allow comparisons of vegetation composition between territories in natural and transformed habitats. To achieve this, we positioned a 1-km transect with a fixed band width of 200 m along the territory's longest axis using ArcView GIS 3.2, adding a second transect perpendicular to the first if the longest axis did not attain 1 km. We determined tree density along the 1-km transect and shrub cover along a 200-m subsection, and herbaceous layer cover and height on sixty 4x4-m squares as described for the plots.

Table 1. Vegetation parameters measured on hunting plots and paired contrast plots.

Vegetation parameters	Description (number of measurements per plot)
Shrub cover (%)	Canopy cover of woody plants < 3 m (n = 1)
Tall tree height (m)	Height of trees > 6 m (n = 1)
Tree density (n/km^2)	Density of trees > 3 m (n = 1)
Percentage cultivation (%)	Percentage cover of active agricultural fields (sorghum and millet; n = 1)
Herbaceous layer cover (%)	Cover of the rooted herbaceous vegetation (i.e. grasses and forbs) within twenty 4x4-m squares (n = 20)
Herbaceous layer height (cm)	The height of the herbaceous layer for four points in each 4x4-m square (n = 80)[1].

[1]We used a measuring pole with a 20-cm radius circular disc dropped onto the vegetation *sensu* Holmes (1974).

Gross Energy intake

We found that in almost all cases we observed, goshawks consumed the entire prey except for one occasion (1.6%; n = 63 prey items) where a snake was only partially eaten. We therefore assumed that gross energy intake corresponded with the content of the entire prey. To enable estimation of prey body-weight, we attempted to identify prey species and genus, or family, when identification at genus level was not possible. We estimated prey dimensions through comparison with the known length of the goshawk tarsus during feeding with the use of a telescope (Marti *et al.* 2007). We estimated snout-vent length (SVL) for lizards and snakes and body dimensions (body width and length, excluding tail) of small mammals captured by goshawks. Insects were classified according to size in three categories (small: < 2 cm, medium: 2-4 cm, large: > 4 cm). To estimate the body-weight of

consumed lizards (Scincidae, Agamidae) from their size, we developed SVL-body-weight regression curves using specimens collected in the study area. For mice, we estimated body-weight based on known body dimensions and mass of specimens of different size and family collected in the study area (R. Buij unpubl. data). Mean body-weight for grasshoppers and birds was determined from specimens collected in the field. We used standard linear regression to relate body-weight estimates to meal duration (in sec), which can be used as a proxy measure for raptor prey mass (Masman *et al.* 1986). These showed that feeding time was strongly related to body-weight estimates for small mammals ($F_{1,8}$ = 38.5, r^2 = 0.82, P < 0.001) and lizards ($F_{1,29}$ = 67.0, r^2 = 0.71, P < 0.001), supporting the validity of our assessment.

Prey energy content, categorized to taxon and size, was determined for lizards, grasshoppers, birds, and small mammals using bombcalorimetry (kJ/g; Gessaman 1987). Specimens representative of prey items in the study area (same species, size), were oven dried to constant mass (± 0.0001 g) before homogenization. From each prey specimen, pellets (n = 1-4) were prepared (*c.* 1 g) using a pellet press. The pellets were dried before weighing (± 0.0001 g), and combusted in an IKA C5000 adiabatic calorimeter, which was calibrated using a benzoic acid standard (Gessaman 1987).

The energy content of snakes of different length was calculated based on body-weight-length relationships of whip and grass snakes (Colubridae; Kaufman & Whitfield Gibbons 1975), which were the most commonly captured snakes, and published energy content (Secor and Nagy 1994). Dry body-weight and caloric values for termites (Nagy *et al.* 1984, Williams *et al.* 1997) and beetles (Allen 1989, Oba *et al.* 2008) were similarly adopted from literature. To correct for small prey intake of strikes with unknown outcome, we determined the success rate of capture attempts involving small terrestrial prey with known outcome (23%; n = 56), and the average energy content of the prey items involved (22 kJ). Henceforth, a prey energy content of 5.06 kJ (i.e. 0.23 x 22 kJ) was ascribed to each capture attempt at terrestrial prey with uncertain outcome. Relaxing this assumption to a 50% deviation (-/+) from estimated consumption did not significantly affect the outcome of comparative analyses with regard to gross energy intake. To examine foraging gains per effort, gross energy intake (kJ) was expressed per strike, successful strike, distance covered (km), and time observed (hr).

Statistical analyses

Measurements of vegetation characteristics, prey energy content, gross energy intake, and foraging data were averaged for individual ranges and compared with independent samples *t*-test or Mann-Whitney *U*-tests. Standard linear and quadratic regression models were used to investigate relationships between range size and tree density, tree height, shrub cover, and herbaceous cover and height at range-level (n = 12). Similarly, we used linear and quadratic regression models to examine relationships between perch height and average tree height, herbaceous layer cover and height, and between the mean number successful strikes per hour and tree density, herbaceous layer cover and height within ranges. Models incorporating only significant terms and with the lowest AIC value were considered as final

models (Burnham & Anderson 2002). Differences in the proportional contribution of reptiles (lizards and snakes), rodents (gerbils, murid mice), and infrequent and therefore lumped "other prey" (i.e. birds, insects) to the diet were tested with Chi-square goodness-of-fit tests.

For comparisons of vegetation structure and composition between hunting plots and paired contrast plots, we constructed Generalized Linear Mixed Models (GLMMs) with bird ID as random term and plot category (0 = hunting plot, 1 = paired contrast plot) as explanatory variable, and the percentage shrub cover, active agriculture (only in transformed habitat) and the number of trees as dependent variables, with negative binomial errors and log link functions. Mean height of the tall tree stratum was modeled with normal errors and identity link functions. To investigate differences in herbaceous layer cover and height between hunting plots and paired contrast plots, we accounted for autocorrelation of measurements between plots and between squares within plots (n = 20) by incorporating bird ID and plot number (n = 12 for each goshawk) as subjects, and square number (n = 20) as repeated measures. We specified an AR-1 covariance structure since neighboring vegetation squares within plots were assumed to be more similar than those further apart (Littell *et al.* 2000). Plot category (0 = hunting plot, 1 = paired contrast plot) was included as an explanatory variable and percentage cover and height as dependent variables with negative binomial errors and log link functions.

We used GLMMs to examine differences in time budgets between habitats, for time spent on perching, inter-perch flight, circling, and foraging on foot, and for the relative contribution of each behavioral category to total observation time. Habitat was included as categorical explanatory variable in these models, and bird ID was included as random effect, with negative binomial errors and log link. The dependent variable was in the first series of models the time spent on each behavior (as defined by the period during two other behaviors; e.g. a single feeding bout), and in the second series of models the percentage time spent per day, separately for each behavioral category.

To test for differences in the length of individual linear displacements and perch time for individual perch visits between habitats, GLMMs were used with bird ID as random effect, the length of displacements or perch time as dependent variable, and habitat as explanatory variable, with negative binomial errors and log link. For differences between habitats in minimum inter-perch distance, i.e. the distance of each structure (tree, electricity pole) used as a perch to the nearest neighboring structure used as a perch during the three-day track period, bird ID was included as random effect and the log transformed inter-perch distances as dependent variable, with habitat as the categorical explanatory variable, with normal errors and identity link. To test whether frequency of perch use (total number of visits in three days) and time spent at perches were related, bird ID was taken as random effect, time spent on perches as dependent variable, the number of returns to a perch time as explanatory variable, with negative binomial errors and log link. We tested whether time spent on perches from which hunting attempts were observed was different from time spent on perches from which no attempts were observed, by incorporating time spent on perches as dependent variable, hunting attempt (yes = 1, no = 0) as categorical explanatory variable,

with negative binomial errors and log link. All statistics were implemented in SPSS 19.0 (SPSS Inc, Chicago, IL, USA), variables were log transformed as necessary to ensure normality, and all means are given ±S.E.

7.3 Results

Comparisons between transformed and natural habitat

Habitat features of goshawk ranges

Mean range size was greater in transformed compared to natural habitat (Table 2). Comparisons of vegetation structural characteristics between habitat types at the territory level indicated averagely taller trees, and higher tree density in natural than transformed habitat. Territories in transformed habitats had a higher shrub cover than those in natural habitat (Table 3). The height of the herbaceous layer was greater in ranges in natural habitat. Tree height for tall trees only and herbaceous layer cover were comparable between habitats. MCP-range size was not related to any measure of vegetation structure, but tended to decline with increasing tree density inside ranges ($F_{1,10}$ = 3.56, r^2 adjusted = 0.19, P < 0.10).

Table 2. Foraging statistics (mean ±S.E.) for twelve male Dark Chanting Goshawks in natural and transformed habitats between December 2009 and March 2010. Asterisks indicate significant differences between habitats with independent samples *t*-test; ** P < 0.01, * P < 0.05.

Foraging statistics	Natural habitat (n = 6)	Transformed habitat (n = 6)
Range size (km^2) *	1.14±0.17	1.88±0.18
Perches used (n)	70.2±10.2	64.3±7.4
Time observed (hr)	27.2±2.0	31.9±0.9
Body-weight (g)	552.2±5.2	551.7±10.3
Body-weight/wing length	17.9±0.22	18.1±0.36
Number of strikes/hr	0.94±0.08	1.03±0.08
Number successful strikes/hr *	0.12±0.03	0.23±0.03
Distance covered (km)/hr	1.25±0.15	0.97±0.13
Strike success	0.26±0.07	0.28±0.04
Energy (kJ)/strike	28.5±1.8	19.4±2.9
Energy (kJ)/successful strike *	169.8±18.3	92.8±18.8
Energy (kJ)/km	18.8±2.6	20.5±3.0
Energy (kJ)/hr	19.9±1.8	19.0±2.2

Comparison hunting plots and paired contrast plots

The number of returns to individual perches and the cumulative time spent at these perches were positively related ($F_{1, 869}$ = 705.5, P < 0.001). Also, time spent at perches from which capture attempts were observed was greater than time spent at perches from which no attempts were observed ($F_{1, 869}$ = 162.4, P < 0.001), confirming our assumption that goshawks spent more time in patches that had larger potential returns than in patches with lower potential returns. Hunting plots in both habitats were characterized by relatively tall trees and a relatively high herbaceous cover (Table 4). Hunting plots of goshawks in natural habitat were characterized by a relatively high herbaceous layer, while hunting plots in transformed habitat had a relatively high shrub cover and tree density. In transformed

habitat, the proportion of cultivated areas in hunting plots was comparable with paired contrast plots ($F_{1, 70} = 1.78$, $P = 0.19$).

Table 3. Vegetation features of six Dark Chanting Goshawk territories in both natural and transformed habitats in northern Cameroon, December 2009-February 2010. Vegetation parameters were recorded along a 1-km transect with a fixed band width of 200 m centered on the territory. Asterisks indicate significant differences between habitats with independent samples *t*-test or Mann-Whitney *U*-tests; ** $P < 0.01$, * $P < 0.05$.

Range characteristics	**Natural habitat (*n* = 6)**	**Transformed habitat (*n* = 6)**
Tree density (n/km^2) *	1189±311	467±200
Tall tree height (m)	9.91±0.37	9.00±0.33
Tree height (m) *	8.57±0.55	6.93±0.39
Shrub cover (%) **	1.27±0.15	3.96±0.44
Herbaceous layer cover (%)	8.55±1.96	6.56±2.52
Herbaceous layer height (cm) **	12.4±1.83	4.22±0.97

Movements and foraging effort

Despite larger ranges in transformed habitat, the length of individual linear displacements did not differ between habitat types ($F_{1, 1337} = 0.17$, $P = 0.68$). Relative and absolute time spent on perching, inter-perch flight, circling, and foraging on foot did not differ between habitats. Similarly, foraging efforts, i.e. the distance covered per hour and the number of strikes at prey per hour, did not significantly differ between habitats (Table 2). There was also no significant difference in the number of perches used between territories in natural and transformed habitat (Table 2), but the minimum inter-perch distance, i.e. the distance of each perch to the nearest neighboring perch, was greater in transformed than natural habitat (Table 5).

Diet and gross energy intake

Body-weight of goshawks did not significantly differ between habitats and the same was true for a proxy measure of wing load (body-weight/wing length; Table 2), suggesting that body condition and energy requirements of flight did not differ between individuals in natural and transformed habitats. Overall, the contribution of reptiles (70% of prey items recorded; $n = 63$), rodents (19%), and other prey (11%; birds and insects) to diets did not differ between habitats ($\chi^2_2 = 2.47$, $P = 0.29$). Energy content of prey specimens representing the most commonly captured taxa are presented in Appendix 7.1. The gross energy gain measured by effort or time did not differ between natural and transformed habitats (Table 2). Goshawks in natural and transformed habitat differed by a higher frequency of successful strikes in transformed than natural habitat. Conversely, gross energy gain per successful strike was higher in natural habitat as a result of the higher energy content of rodent and reptile prey items in natural than transformed habitat (Figure 1). The frequency of successful strikes declined with herbaceous layer height and tree density within ranges (Table 6), but was unrelated to herbaceous layer cover.

Table 4. GLMMs testing the effect of plot type (hunting plots or paired contrast plots) on habitat characteristics. Plot type was fitted to the models as a categorical explanatory variable and goshawk identity as a random term.

Explanatory variables	*B* ±S.E.	*t*	*P*	Model fit
Natural habitat				
a. Herbaceous layer cover[1]				
Intercept	1.55±0.30	5.22	< 0.001	$F_{1, 1438} = 41.1$, $P < 0.001$
Plot = hunting plot	0.54±0.09	6.41	< 0.001	
Plot = contrast plot	0[a]			
b. Herbaceous layer height[1]				
Intercept	2.21±0.14	15.7	< 0.001	$F_{1, 5758} = 66.7$, $P < 0.001$
Plot = hunting plot	0.37±0.05	8.17	< 0.001	
Plot = contrast plot	0[a]			
c. Shrub cover[1]				
Intercept	4.27±0.15	28.0	< 0.001	$F_{1, 70} = 1.60$, $P = 0.21$
Plot = hunting plot	0.25±0.20	1.26	0.210	
Plot = contrast plot	0[a]			
d. Tree density[1]				
Intercept	3.25±0.30	11.1	< 0.001	$F_{1, 70} = 0.16$, $P = 0.70$
Plot = hunting plot	-0.09±0.23	-0.39	0.695	
Plot = contrast plot	0[a]			
e. Tall tree height[2]				
Intercept	8.36±0.82	10.23	< 0.001	$F_{1, 70} = 13.4$, $P < 0.001$
Plot = hunting plot	3.01±0.82	3.66	< 0.001	
Plot = contrast plot	0[a]			
Transformed habitat				
a. Herbaceous layer cover[1]				
Intercept	1.39±0.26	5.39	< 0.001	$F_{1, 1438} = 37.3$, $P < 0.001$
Plot = hunting plot	0.42±0.07	6.10	< 0.001	
Plot = contrast plot	0[a]			
b. Herbaceous layer height[1]				
Intercept	1.09±0.32	3.50	< 0.001	$F_{1, 5758} = 0.01$, $P = 0.99$
Plot = hunting plot	-0.001±0.07	-0.01	0.991	
Plot = contrast plot	0[a]			
c. Shrub cover[1]				
Intercept	5.26±0.17	31.2	< 0.001	$F_{1, 70} = 5.51$, $P < 0.05$
Plot = hunting plot	0.47±0.20	2.35	0.022	
Plot = contrast plot	0[a]			
d. Tree density[1]				
Intercept	2.03±0.30	6.84	< 0.001	$F_{1, 70} = 4.62$, $P < 0.05$
Plot = hunting plot	0.56±0.26	2.15	0.035	
Plot = contrast plot	0[a]			
e. Tall tree height[2]				
Intercept	4.67±0.78	5.99	< 0.001	$F_{1, 70} = 14.4$, $P < 0.001$
Plot = hunting plot	3.75±0.99	3.80	< 0.001	
Plot = contrast plot	0[a]			

[a] Coefficient set to zero because it is redundant.
[1] Negative binomial errors and log link function.
[2] Normal errors and identity link function.

Table 5. GLMM testing the relationship between the minimum inter-perch distance and habitat. Habitat type was fitted to the models as a categorical explanatory variable and goshawk identity as a random term. Inter-perch distances were log transformed before modeling. GLMM with normal errors and identity link function.

Explanatory variables	*B* ±S.E.	*t*	*P*	Model fit
Intercept	1.86±0.03	73.6	< 0.001	$F_{1, 805}$ = 17.5, P < 0.001
Location = natural habitat	-0.15±0.04	-4.18	< 0.001	
Location = transformed habitat	0			

Table 6. Relationship between mean strike success rate (number successful strikes/hour) by Dark Chanting Goshawks (n = 12) and tree density and herbaceous layer height within ranges.

Explanatory variables	*B* ±S.E.	*t*	*P*	Model fit
Tree density	-7.508E-5±0.000	-4.051	0.003	ANOVA: $F_{2,9}$ = 16.2, r^2 adjusted = 0.73, P = 0.001
Herbaceous layer height	-0.006±0.002	-2.615	0.028	
Constant	0.29±0.025	11.682	< 0.001	

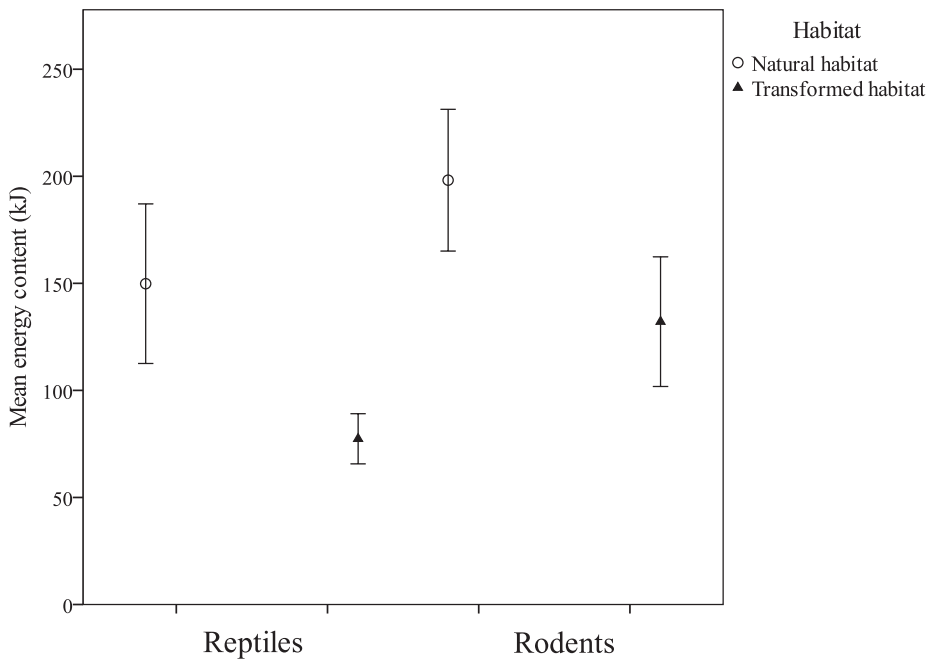

Figure 1. Mean (±S.E.) energy content of reptile and rodent prey items in natural and transformed habitat. Mean energy value of reptiles differed between habitats ($U_{12,32}$ = 99.0, Z = -2.48, P < 0.05) but not for rodents (t (11) = 1.48, P = 0.17).

7.4 Discussion

Contrary to expectations, we did not detect a dietary shift by Dark Chanting Goshawks in response to anthropogenic modification of their savanna habitat, as witnessed in other

raptors (James & Smith 1987, Pande *et al.* 2007, Ogada & Kibuthu 2009). Goshawks in the human-transformed habitat also did not adjust their activity patterns, nor did they invest more energy in foraging. Rather, goshawks in transformed habitat compensated for less profitable prey items, i.e. with a lower energy content, by higher prey capture rates compared to goshawks in natural habitat. Goshawks in natural habitat captured more profitable prey items, but they were limited in their strike success rate by a relatively thick herbaceous layer and high tree density. Thus, anthropogenic land use appeared to improve prey accessibility for Dark Chanting Goshawks, by opening up the habitat and reducing ground cover, but reduced the quality of individual prey items. Although prey size has been found to vary with land use in other raptors (Rodríguez *et al.* 2006, Cardador *et al.* 2012), this is to our knowledge the first study that demonstrates a reduction of prey energy content with land transformation in an African raptor. This seems indicative of suppressed body condition of small vertebrates in transformed habitat, assuming that goshawks will attempt to maximize their hunting returns by focusing on the most profitable prey available to them (Stephens & Krebs 1986). Terrestrial vertebrates such as rodents and lizards were found to be susceptible to loss of ground cover in transformed habitat, leading a.o. to increased activity (Vasquez *et al.* 2002, Wasiolka *et al.* 2009), negatively impacting their body condition (Amo *et al.* 2007).

Our prediction of selection for similar habitat features in natural and transformed habitats was partly confirmed, since Dark Chanting Goshawks in both habitats selected hunting patches with relatively tall trees and a high herbaceous layer cover. Goshawks further selected for high tree density (transformed habitat) and thick herbaceous layer (natural habitat) at forage patch level, which was surprising given the negative relationships of both parameters with prey capture rates. This seemed contradictory to an optimal foraging strategy (Stephens & Krebs 1986), which assumes that foragers maximize net energy intake by concentrating on optimal microhabitat, i.e. habitat which yields the greatest energy gains. Although we did not measure prey densities, patch-level selection for tall trees and high tree density, shrub cover, and a dense herbaceous cover appeared to be primarily related to optimization of prey abundance, or quality, rather than accessibility, within hunting patches. Indeed, herbaceous cover, shrubs, and large trees were shown to positively influence the abundance of lizard and rodent populations in arid savannas, by providing vital cover and food resources (Brown *et al.* 1988, Cooper & Whiting 2000, Meik *et al.* 2002, Blaum *et al.* 2007).

Dark Chanting Goshawks may only be able to persist with a minimum number of profitable hunting patches within the range, and range size is increased to meet nutritional demands where such patches are rare (Newton 1979, Kenward 1982). We found that goshawk in natural habitat utilized a larger proportion of their range than those in transformed habitat, where foraging patches and trees were more widely spaced, necessitating larger ranges. Given the current rate of vegetation loss within West Africa's heavily populated Sudan savannas, foraging habitat requirements are likely to be met in progressively fewer areas. Our results suggest that the observed decline of Dark Chanting Goshawk populations in man-altered habitats (Thiollay 2006a) is at least partly due to a worsening of foraging conditions, including declining prey quality and increasingly scarce foraging patches.

It can be argued that our results might not be broadly applicable to the Afrotropical assemblage, which is comprised of species with specific morphological and behavioral adaptations to preferred microhabitats and prey populations (Thiollay & Clobert 1990). Furthermore, foraging strategies may change over the course of the year with changing vegetation structure, prey accessibility, and the reproductive cycle (Tella & Forero 2000, Thirgood *et al.* 2003). Males and females may also be differently affected by habitat changes, resulting from inter-sexual differences in energy demands (Marti *et al.* 1993), diets (Kenward *et al.* 1981, Martínez & Calvo 2005) and foraging strategies (Opdam 1975, Marquis & Newton 1982, Thirgood *et al.* 2003). On the other hand, Dark Chanting Goshawks are likely to be representative for a range of generalist, sedentary raptors with comparable morphological traits and foraging ecology (Thiollay & Clobert 1990). Future examinations are required to confirm this and whether the observed differences in prey biomass negatively affects breeding success by constraining nestling growth rates, as reported for other raptors (Rodríguez *et al.* 2006).

Management implications

Our results suggest that the persistence of Dark Chanting Goshawk populations in agro-ecosystems is based on a trade-off between improved foraging efficiency and adequate prey quality, governed by anthropogenic activities such as livestock grazing and tree clearance. Although a moderate degree of habitat disturbance might be beneficial for foraging Dark Chanting Goshawks, they are likely to desert areas where heavy grazing and extensive woodcutting suppress prey quality. Management implications emanating from this study would be to conserve trees, notably large trees, and patches of shrubland and pasture in cultivated landscapes, thus maintaining adequate prey resources for goshawks. Unfortunately, measures to conserve vegetation cover over extensive areas are often complex to achieve, because destructive bush fallow systems are a more rational response to land saturation and a general lack of financial means to enable sustainable intensive cropping systems (Lambin *et al.* 2003, Gray 2005). Agricultural intensification-related policy initiatives to discourage expansion of cultivated lands should focus on regions where the original vegetation cover has been little to moderately affected, e.g. around national parks, and would benefit raptors and people. In most other areas, appropriate silvicultural practices encouraged, enforced, and implemented by state and traditional authorities, with designated pastures protected from heavy grazing, might represent the only alternative to the progressive impoverishment of agro-ecosystems and the gradual disappearance of their associated raptor communities.

Figure 2. (a) Adult Dark Chanting Goshawk sitting in a typical position on top of a tree while scanning for prey; and (b) a transmitter being fitted to the central tail feathers of a male Dark Chanting Goshawk.

Appendix to Chapter 7

Appendix 7.1. Dry body-weight and energetic values for prey items of Dark Chanting Goshawk. Energetic values were estimated by means of bomb calorimetry. Energy values presented for dry body-weight and Ash-Free Dry Weight (AFDW).

Order: (Sub-)Family	Dry body-weight (g)	Energy/dry body-weight (kJ/g)	Energy/AFDW (kJ/g)
Squamata: Scincidae (small)	1.63	18.20	23.03
Squamata: Scincidae (large)	6.82	17.08	23.44
Squamata: Agamidae	8.03	21.61	25.63
Rodentia: Muridae	11.70	17.83	22.76
Rodentia: Gerbillinae	16.09	20.28	24.89
Orthoptera: Acrididae	0.39	22.74	23.66
Passeriformes: Ploceidae	2.72	20.35	23.83

Chapter 8

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

Ralph Buij, Barbara M. Croes & Jan Komdeur

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.

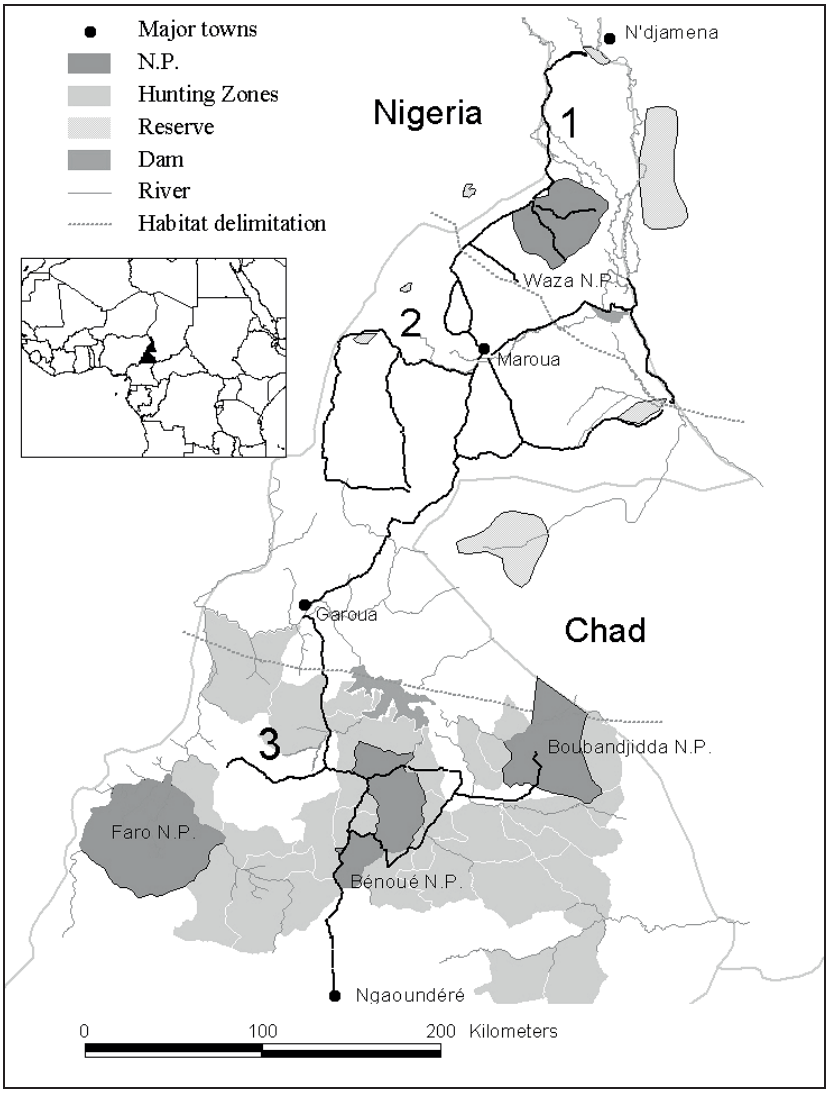

Figure 1. The study area in northern Cameroon with the delimitation of the three main biogeographical zones (1: Inundation zone, 2: Sudan savanna, 3: Guinea savanna) and the location of National Parks, hunting concessions, and forest and faunal reserves ("Reserve"). Road transects are indicated as black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

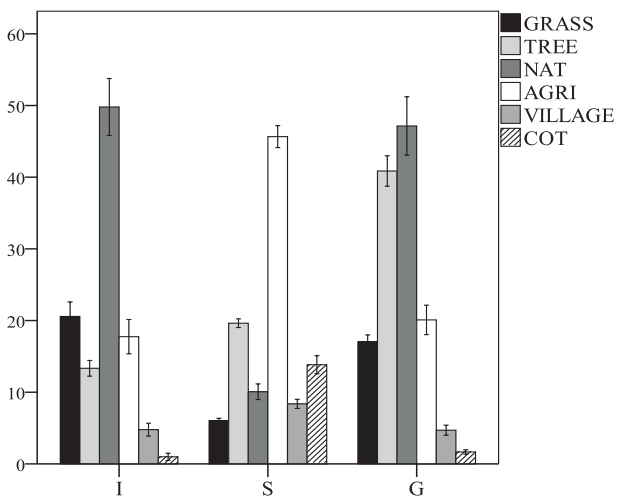

Figure 2. Habitat variables in the three biogeographical zones in Cameroon (I: Inundation zone; S: Sudan savanna; G: Guinea savanna). Value refer to percentage dry-season grass cover (GRASS), percentage cover natural habitat (NAT), percentage cover food crop cultivation (AGRI), human habitation (VIL), 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

Chapter 9

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

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In press: *Bird Conservation International*

Abstract

West African floodplains have undergone major land-use transformations in the second half of the twentieth century. To obtain insight in the effect of floodplain 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 floodplain of Cameroon: dry grasslands, cultivated grasslands, rice fields, and seasonally flooded grasslands resembling natural floodplain vegetation. We recorded 36 raptor species among 2,533 individuals, dominated by Black Kites *Milvus migrans*, which comprised 42% of counts. Although richness and diversity was 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 floodplains 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.

Left: Long-crested Eagle in a recently harvested rice field on the Waza-Logone floodplains.

9.1 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 & Calvo 1999). However, increasingly rapid processes of urbanization and agricultural intensification in developing countries may negate the adaptive response of raptors to semi-natural habitats created over longer periods by humans (Carrete & 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). Embankments of many West African floodplains in the second half of the twentieth 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 the dynamics of the floodplains, 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, 2006a).

Despite their great importance to raptor populations, particularly Palearctic raptors (Thiollay 1989), the utilization by raptors of West Africa's floodplains and their associated cultivated habitats have been relatively little studied (Thiollay 1978b, Zwarts *et al*. 2009). In the absence of studies on habitat use, it is unclear how habitat transformation on floodplains may have impacted Afrotropical and Palearctic raptors. Our aim here was to examine habitat use by raptors on the Waza-Logone floodplain in northern Cameroon, to evaluate the effect of floodplain 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 displacements 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, 2006b, Anadón *et al*. 2010), we predicted that the habitats least affected by development and human exploitation, i.e. the 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 & Herremans-Tonnoeyr 2000, Limiñana *et al*. 2012, this thesis). 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, Chapter 2), compared to flooded or dry grasslands.

9.2 Materials and methods

Study area

The study area was situated in the Waza-Logone floodplain of the Far North of Cameroon, on the inundation zone of the Logone River, which is part of the more extensive Lake Chad Basin (10º45'N-11º35'N and 14º34'E-15º05'E; Figure 1). The Waza-Logone floodplain 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. Part of the floodplain 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 floodplains and Waza National Park are Important Bird Areas (BirdLife 2011a,b,c). The climate is semi-arid, with rainfall mostly occurring between June and September (*c.* 500-600 mm/annum).

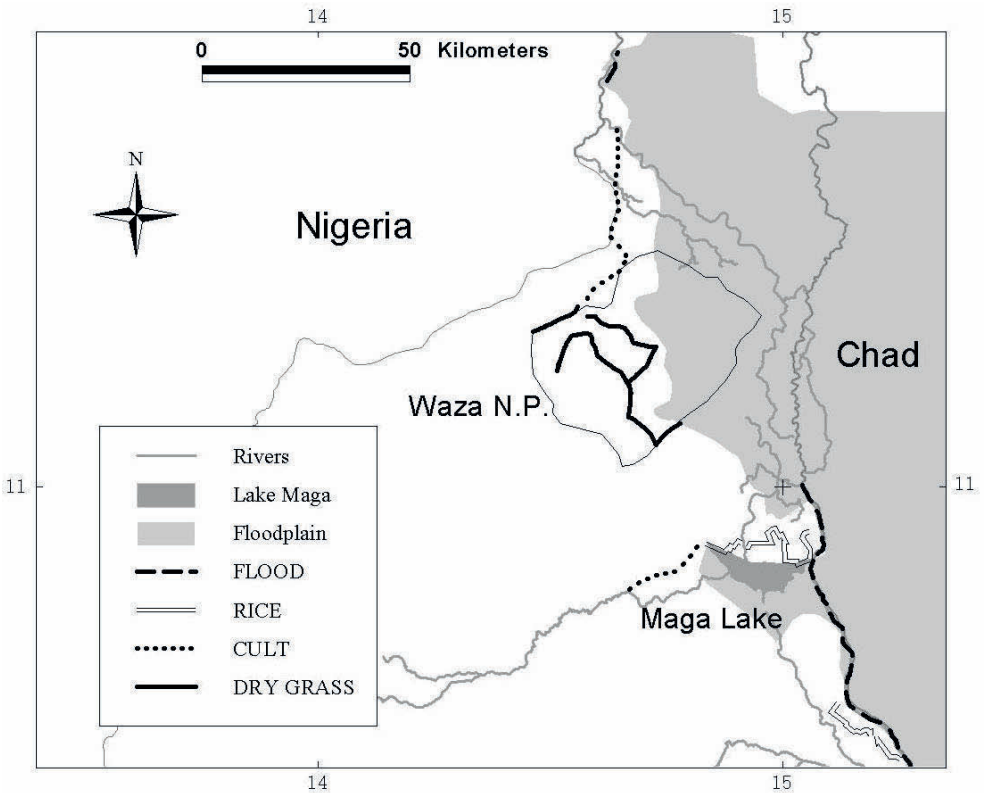


Figure 1. Location of roads used for transect surveys in the Lake Chad Basin of northern Cameroon.

The floodplains are situated along the Logone River, largely east and north of Waza National Park, with a surface area of 8000 km^2 in Cameroon. The inundation in the Waza-Logone floodplain 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 rice fields, reducing flooding on 1,500 km^2 of the floodplain. 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 others to a threefold increase in livestock numbers (Scholte 2003). The dry plains are used for sorghum cultivation in the dry season (October–April), when rice fields are mostly inactive, partly burnt, and grazed by livestock. The floodplains 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 94 and 96%, respectively, following droughts, the damming of the Logone River, and, more recently, poaching inside the park.

Habitat types

We conducted surveys along transects in four major floodplain 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 floodplain with woodlands on higher grounds, 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 depth of the floodwaters declined considerably with the construction of the 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 previous, a desiccated floodplain 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 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 at least 10 months of the year were selected. In all habitats 70–90 km of navigable roads were identified. To reduce autocorrelation 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 utilization 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). We conducted surveys 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 scanning each one side of the transect. While road surveys have proven useful for comparisons of raptor community composition between habitats (Fuller & Mosher 1981, Bibby *et al*. 1992), they were combined with spot counts because these enhance detectability of raptors hunting on the wing (Herremans & Herremans-Tonnoeyr 2000). We incorporated a 2-min spot count halfway 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 with fine weather, i.e. clear or slightly clouded skies with low to moderate winds, starting at 06:30 to 07:30 depending on the season (and the increase in air temperature). Transect surveys for a single habitat type were always conducted within 3 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 1977a). 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 1977a). 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 1977a). 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.

Statistical analyses

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 to three size categories based on mean adult body mass (small: < 300 g, medium-sized: 300–800 g, large: > 800 g; Ferguson-Lees & 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 was selected for estimation of ESW and significant differences of ESW between habitats for each size category were based on overlap of 95% confidence intervals.

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 & Colwell 2001). We used the cumulative species number on the 2-km transects (n = 10 in each category) as our units of replication. The Mau 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 & 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 favoring common or rare species such as species richness or other diversity indices (e.g. Simpson's index; Jost *et al*. 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 analyze the distribution of the most common species among the four main habitat types in SPSS 19.0 (SPSS Inc, Chicago, IL, USA). 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 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 transects surveys, and selected the final model based on the lowest QICC value. 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 & 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.

9.3 Results

A total of 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 = 2533). The most commonly recorded species, the Black Kite, comprised 42% of total numbers and 51% of Afrotropical raptors. 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 ($\chi^2_3 = 8.48$, $P < 0.05$), and was significantly higher in the floodplain than in the other habitats. Conversely, Palearctic raptor diversity, and the diversity of the entire raptor assemblage, did not differ significantly across habitats. No significant differences in species richness were recorded between habitat categories for overall, Afrotropical, and Palearctic raptor richness (Figure 2b).

Table 1. Total number of raptors detected on ten 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 (W; 4 counts; May-Oct) and dry season (D; 6 counts; Nov-April).

	CULT		**DRY GRASS**		**RICE**		**FLOOD**		
	D	W	D	W	D	W	D	W	**Tot**
Palearctic raptors									
Eurasian 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 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
African 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
Rüppell's Vulture *Gyps rueppellii*	0	0	0	2	2	0	7	1	12

Table 1. (Continued).

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
Secretary Bird *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	462	198	2533
Species number	23	13	26	16	21	10	25	14	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).

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 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 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 compared to rice fields and flooded grasslands experienced a strong decline in herbaceous cover early in the dry season (Oct–Dec; Figure 3).

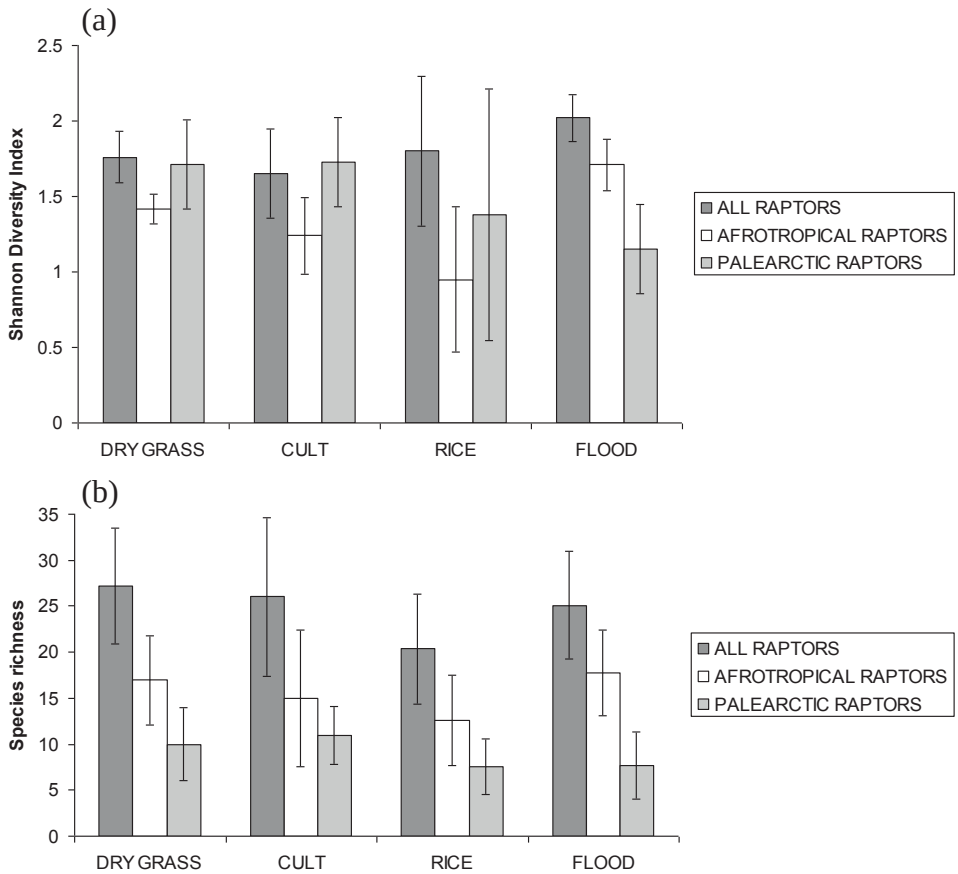


Figure 2. Raptor diversity and richness in four habitat types on the Waza-Logone floodplain. Shannon diversity indices (a) and species richness (b) are presented for all raptors, Afrotropical raptors, and Palearctic raptors. Indices were estimated at equal sampling effort. Values are presented with 95%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

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 for 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* ($\chi^2_3 = 5.92$, $P = 0.12$), Wahlberg's Eagle ($\chi^2_3 = 3.45$, $P = 0.33$), and African Swallow-tailed Kite *Chelictinia riocourii* ($\chi^2_3 = 2.56$, $P = 0.46$) were indifferent to land-use. The Black-winged Kite, a

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: floodplain) fitted as predictor variable and binomial presence data for each species as dependent variables. Model fit and mean differences (± S.E.) 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.

(I) habitat	(J) habitat	Black Kite (I-J)	Grasshopper Buzzard (I-J)	Dark Chanting Goshawk (I-J)	African White-backed Vulture (I-J)	Black-winged Kite (I-J)
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	$\chi^2_3 = 26.2$, $P < 0.001$	$\chi^2_3 = 54.6$, $P < 0.001$	$\chi^2_3 = 27.4$, $P < 0.001$	$\chi^2_3 = 21.2$, $P < 0.001$	$\chi^2_3 = 21.7$, $P < 0.001$

	(J) habitat	Gabar Goshawk (I-J)	Lanner Falcon (I-J)	Red-necked Falcon (I-J)	Hooded Vulture (I-J)
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	$\chi^2_3 = 8.47$, $P < 0.05$	$\chi^2_3 = 12.8$, $P < 0.01$	$\chi^2_3 = 23.2$, $P < 0.001$	$\chi^2_3 = 79.8$, $P < 0.001$

(I) habitat	(J) habitat	Pallid Harrier (I-J)	Booted Eagle (I-J)	Eurasian Marsh Harrier (I-J)	Long-legged Buzzard (I-J)	Steppe Eagle (I-J)
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	$\chi^2_3 = 12.5$, $P < 0.01$	$\chi^2_3 = 51.5$, $P < 0.001$	$\chi^2_3 = 34.4$, $P < 0.001$	$\chi^2_3 = 23.2$, $P < 0.001$	$\chi^2_3 = 19.1$, $P < 0.001$

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

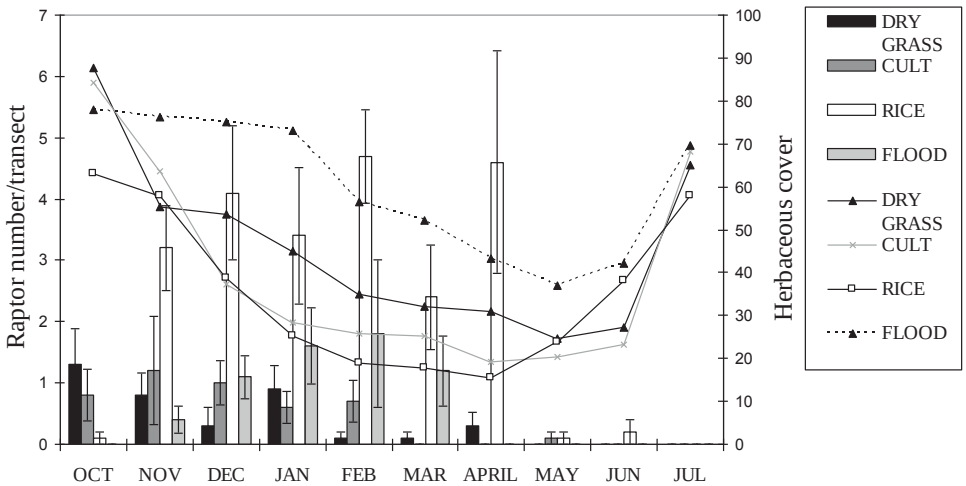


Figure 3. Mean raptor numbers ±S.E. on 2-km transects of five Palearctic raptors (Booted Eagle, Eurasian Marsh Harrier, Steppe Eagle, Long-legged Buzzard, Pallid Harrier) favoring rice cultivation (RICE) over cultivated grassland (CULT), dry grassland (DRY GRASS), and seasonal floodplains (FLOOD), from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

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.

9.4 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 & 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 (Chapter 2), but these were localized in dry, unproductive grasslands, probably lowering their attractiveness to Palearctic raptors compared to rice-dominated 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 floodplain, 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 floodplain 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 floodplain. 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 1978a), and characterized the original floodplain (Scholte *et al*. 2000). The surveyed floodplain 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 floodplain compared to the newly created cultivated habitats and dry, protected grasslands, underlining the importance of the floodplain to Afrotropical raptors. We found a preference for floodplain habitat by five Afrotropical raptors, three of which (Dark Chanting Goshawk, African White-backed Vulture, Hooded Vulture) declined significantly in the area between 1973 and 2000 (Thiollay 2001), while two other raptors (Gabar Goshawk, Red-necked Falcon) were either too infrequently recorded to evaluate population trends, or remained stable. Although wide-ranging vultures (Kendall & Virani 2011) 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 floodplain embankment, which greatly reduced the extent of floodplain 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 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 with 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 floodplain by Black Kite, Grasshopper Buzzard, and Lanner Falcon may be related to limitations on the number of breeding sites and prey availability on the floodplain. Grasshopper Buzzard and Black Kite breed at

relatively high densities during the transition from the dry to wet seasons (March–July; Chapter 5, R. Buij unpubl. data) and require adequate tree cover for nesting, thus favouring well-wooded dry grasslands over the partly treeless floodplain. In addition, prey accessibility is compromised when grass cover is high (Thiollay & Clobert 1990), as is the case during much of the year on the floodplain.

Implications for floodplain 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 floodplains have received protected status. Waza National Park protects < 10% (700 km^2) of the Waza-Logone floodplain, while regional protection of other floodplain 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, floodplains have been vulnerable to development initiatives, and rice irrigation schemes have become a common feature of floodplains the past 50 years (Zwarts *et al*. 2009). During this period, the area harvested with rice increased from 4000 to 31,000 km^2 in six Sahelian countries with large floodplain 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 & 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 & 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 floodplains 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 Secretary Bird *Sagittarius serpentarius* populations. Floodplain rehabilitation triggered a 34% increase in sedentary fisherman in two years which 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 few remaining African Fish Eagle *Haliaeetus vocifer* pairs in

the far north. Limitations to any of these exploitative utilizations will benefit raptor populations and other wildlife using the floodplains, underlining the importance for improved protection of Waza National Park and restrictions on developments that stimulate further human immigration into the area.

Chapter 10

Biogeographical and anthropogenic determinants of landscape-scale patterns in a raptor assemblage in Cameroon

Ralph Buij, Barbara M. Croes & Jan Komdeur

Abstract

We examine the role of biogeographical zonation and land use in northern Cameroon on patterns of abundance, richness, and diversity of raptors in a West African savanna, and ascertain the conservation value of West African savannas for raptors on a continental and global scale. We documented raptors along road transects from 2007-2010 on 7700 km during the dry season and 7340 km during the wet season. Transects covered three biogeographical zones differing in protected area coverage and degree of habitat modification: the relatively well-preserved Inundation and Guinea savanna zones in the north respectively the south, and the heavily exploited Sudan savanna in between. Patterns of raptor relative abundance, richness, and diversity were examined separately for Palearctic migrants and Afrotropical species. Results showed that Palearctic and Afrotropical raptor abundance was highest in the Inundation zone. Raptor diversity peaked in the Guinea zone during both seasons, while richness was higher in the Guinea zone than the Inundation zone during the wet season. Afrotropical raptor diversity was highest in the Guinea zone, and their richness higher there than in the Inundation zone, where Palearctic species density was higher compared to the other biogeographical zones. Richness and diversity of Palearctic and Afrotropical raptors did not differ between protected and unprotected areas in the same biogeographical zone. West African savannas support a comparably rich raptor assemblage on a continental and global scale. We conclude that land use, determined by protected area coverage and human exploitation, may override the dominant role of biogeographical zonation in shaping community patterns of West African raptors at the landscape scale, leading to greater abundance within potentially suboptimal habitat at the periphery of distribution ranges. Given the high raptor richness and immense pressure from human populations, West Africa's savannas should be regarded a priority region for raptor conservation.

Left: Lappet-faced Vulture (right) and Egyptian Vulture in Waza National Park.

10.1 Introduction

The current biodiversity crisis makes it imperative to understand the role of land use on landscape-scale patterns of biodiversity (Sinclair *et al.* 2002, Hoffman *et al.* 2010), and to minimize biodiversity loss by defining priority areas for conservation and efficient protected area networks (Margules *et al.* 1994, Brooks *et al.* 2006, Fjeldså 2007). Raptors, like other top predators, are among the most vulnerable taxa to environmental disturbance, and their presence often used as a proxy for high biodiversity values (Sergio *et al.* 2006, 2008). Strong raptor population declines have recently been reported throughout the African continent (Thiollay 2006a,b,c, 2007a,b, Ogada & Keesing 2010, Virani *et al.* 2011), notably in West Africa, where the pressure on wildlife and their supporting habitats is huge due to some of the highest human densities and growth rates on the continent (UN World Population Prospects 2010). Although West Africa's protected area network has a crucial role in maintaining raptor assemblages in the face of growing human pressure (Thiollay 2006a,b, 2007a), it is highly fragmented and covers a small area compared to East and southern Africa (Chape *et al.* 2005), potentially constraining the effectiveness in conserving raptor populations (Herremans & Herremans Tonnoeyr 2000), and other wildlife (Wilkie *et al.* 1998, Brashares *et al.* 2001, 2004). This is alarming given the region's importance to raptor conservation, with 69 regularly occurring species (excluding vagrants; Borrow & Demey 2001) representing 22% of the world's raptors, the majority (*c.* 91%) of which at least seasonally dependent on West African savannas. Currently, thirteen of these raptors are considered threatened ("Near Threatened", "Vulnerable", or "Endangered"; IUCN Red List 2012), including three out of twenty-three regular Palearctic migratory raptors.

An understanding of biogeographical patterns of species distribution is a prerequisite for identifying priority areas and efficient protected area systems for conservation (Ray 1984, Emanuel *et al.* 1992, Turpie 1995). The raptor assemblage inhabiting West Africa's savannas is composed of populations of Afrotropical sedentary, Palearctic and Afrotropical migratory raptors. The latter group migrates in response to changes in herbaceous layer cover and height (Thiollay 1977a, 1978a, 1989), which is the main driver of prey availability for raptors (Thiollay & Clobert 1990). As a result, raptor richness and diversity is centred on the Sudan zone, decreasing in the Sahel zone to the north because of decreasing productivity and food supply during the dry season, and in the more productive Guinea savannas to the south, where higher rainfall and a dense grass cover constrain terrestrial prey accessibility during the wet season (Thiollay 1977a, 1978a). Within the Sudan and Sahel zones, productive inundation zones offer a superabundant prey supply for Palearctic and Afrotropical migratory raptors during the dry season and at the start of the rains (Thiollay 1989, Zwarts *et al.* 2009), but floods and high grass cover limit prey accessibility during part of the year (Thiollay 1978a).

Our aim was to unravel the role of biogeographical zonation and land use in determining Palearctic and Afrotropical raptor community composition at the landscape scale in Cameroon. Significant raptor population declines in Cameroon's savannas were limited to nine out of 42 raptor species (i.e. 21% of species declined, Thiollay 2001), whereas the

majority of raptors declined significantly in central West Africa (87%; *n* = 38 species, Thiollay 2006c), suggesting that raptor populations in northern Cameroon had been comparably well preserved due to an extensive protected area network (*c*. 25% of the land surface; Figure 1). However, protected areas cover part of northern Cameroon's floodplains, and Guinea savannas of the Bénoué Valley, whereas the densely populated Sudan savannas are little protected, raising the question whether their intensive exploitation had influenced biogeographical patterns of raptor community richness and diversity. To investigate whether this was the case, we document year-round patterns of raptor species richness, diversity, and relative abundance in the Inundation zone, Sudan savanna and Guinea savanna of Cameroon, covering four years and dry and wet seasons. We expect that (1) raptor abundance peaks in the Inundation zone, whose rich grasslands attract high numbers of Palearctic and Afrotropical migrants; (2) protected areas in the Inundation and Guinea savanna zones have a higher raptor diversity and richness compared to non-protected areas in the same zone; (3) as a consequence of their better preservation, the Guinea savannas and Inundation zones of Cameroon have a higher raptor species richness, species density, and diversity than the heavily exploited Sudan savannas; and (4) the high protected area coverage of Cameroon's savannas ensures a comparably rich raptor assemblage on a continent-wide and global scale.

10.2 Materials and methods

Study area

The study area was located 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. Mean annual temperature is 24 ºC-28 ºC and peaks in March-May when temperatures of 47 ºC are reached in the Inundation zone.

Road surveys covered three main biogeographical zones with distinct vegetation composition and productivity, along a gradient of increasing rainfall from north to south (Figure 1). Zone 1. The Inundation zone. Located in the transition zone of the Sudan and Sahelian savanna belts (rainfall: 450-700 mm/annum), it supports edaphic grassland mosaics with communities of *Acacia* and broad-leaved trees (White 1983). The Waza-Logone floodplains situated along the Logone River have a surface area of 8000 km^2 in Cameroon and are part of the more extensive Lake Chad Basin. The inundation extends from August to November in average years, and duration, depth and extent of flooding varies between years (Scholte 2005). The partly flooded grasslands are fringed by open *Sclerocarya birrea* woodland with *Anogeissus leiocarpus*, *Balanites aegyptiaca*, and *Acacia seyal*. Agriculture covers < 20% of the land surface and includes mainly dry-season sorghum, millet, and rice. Human population density is low (10-25 people/km^2) but has increased following partial floodplain rehabilitation (Scholte 2003). The 1700-km^2 Waza N.P. protects part of the floodplains and small populations of herbivores, but large wildlife has been virtually exterminated in the 45-km^2 Kalamaloué N.P. (Scholte 2003). The floodplain was designated a Ramsar Wetland of International Importance in 2006.

Zone 2. Sudan zone. Located within the Sudan savanna belt (rainfall: 700-1100 mm/annum) with undifferentiated Sudanian woodlands (White 1983). The zone borders the inundation plains of the Lake Chad Basin and is characterized by hilly terrain which rises to the Mandara Mountains in the west at 500-1000 m a.s.l. with isolated peaks up to 1442 m. The entire area is densely populated (averagely *c.* 50 people/km^2, but > 100-150 people/km^2 in many areas, locally up to 350 people/km^2) and deforestation has been significant during the past 20 years (Fotsing 2009), with cultivation covering > 40% of the land and < 10% original woodland cover. Sorghum, millet, maize, beans, and groundnut are the most important food crops and cotton is cultivated throughout the zone as the main cash crop. Few patches of natural habitat remain in scattered, small (< 40 km^2) and heavily exploited forest reserves with *Isoberlinia doka*, *Balanites aegyptiaca*, *Piliostigma reticulatum* and *Combretum erythrophyllum*.

Zone 3. Guinea zone. Located largely within the Guinea savanna belt (rainfall: 1100-1600 mm/annum) but incorporating Sudanian woodland with abundant *Isoberlinia* in the north (White 1983), on undulating terrain with some scattered rocky outcrops. The Bénoué Valley encompasses a large river system and three National Parks (Bénoué, Boubandjidda, Faro) covering an area of approximately 7600 km^2. Twenty-eight sport-hunting zones cover an additional 16,000 km^2 and are managed as protected areas but with hunting quota for larger mammals and gamefowl (Mayaka 2002). The region has a low human population density (on average 13 people/km^2), which is rapidly increasing (growth rate is *c.* 5%; Mayaka 2002). Cultivation covers *c.* 20% of the zone, particularly traditional crops such as millet but increasingly cotton.

Sampling design

In each biogeographical zone, a subset of navigable roads was identified for road surveys, which were widely spaced to reduce dependency of counts, and broadly encompassed the zone within the country boundaries (Figure 1). Habitat along the roads reflected gradients of human population density, topography, and land use. Eight transects were surveyed in each zone, varying in length from 35 to 115 km. The total length of the road transects was 425 km in the Inundation zone, 897 km in Sudan savanna, and 603 km in Guinea savanna. A total of 90 km of the transect network was located inside a protected area in the Inundation zone (21% of the total transect length), and 310 km in Guinea savanna (51%). Road transects were surveyed over a 4-year period between March 2007 and December 2010 in the dry (15 October-15 April) and wet seasons (15 April-15 October). Each transect was surveyed four times in each season and a total of eight surveys for each transect. 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 species-specific activity peaks. In the Guinea zone, 90 km of the transect scheme was inaccessible during the wet season and only surveyed four times during the dry season. Overall, the distance covered by road surveys was 7700 km during the dry season and 7340 km during the wet season.

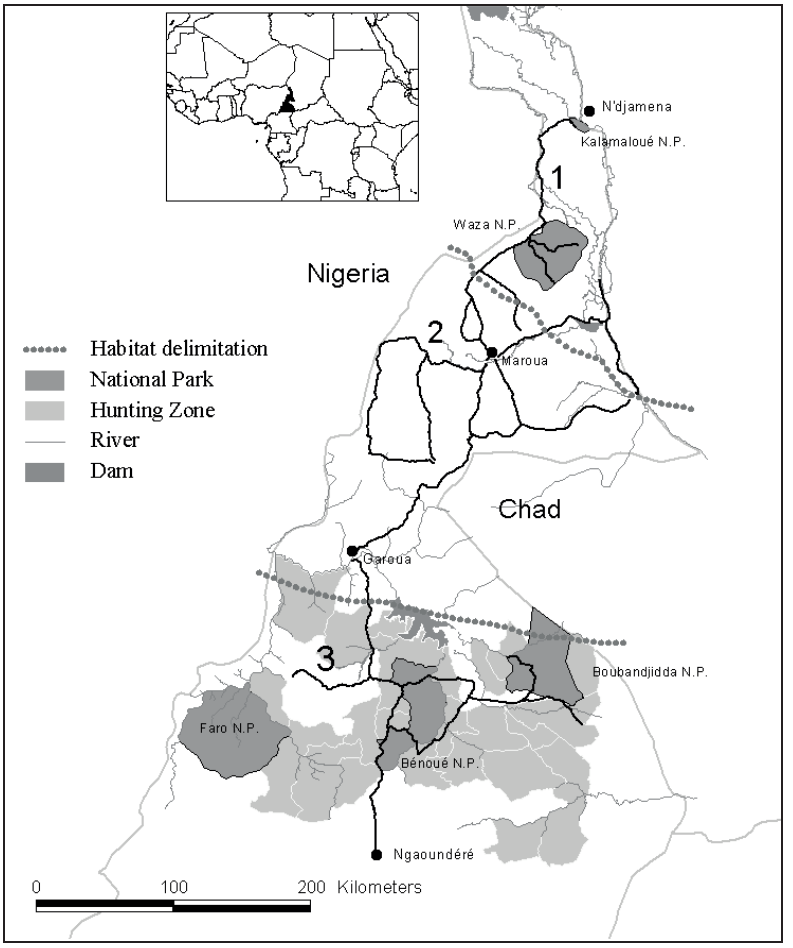


Figure 1. Study area in northern Cameroon with location of road transects. Numbers refer to the biogeographical zones: (1) Inundation zone, (2) Sudan zone, and (3) Guinea zone.

Raptors were counted by two experienced observers (one driving) from a slow-driving vehicle (average driving speed 20-25 km/hour) as widely used for raptors (Fuller & Mosher 1981, Bibby *et al.* 1992). This method provides an index of relative abundance, i.e. the number of raptors seen along a fixed transect length, that is sensitive to the behaviour of the species involved, the speed of the vehicle, the habitat, weather, hour, season, and number and experience of the observers. Since road transects often follow contours and edges, abundance estimates may be inflated as some raptors tend not to be distributed randomly across the landscape (Meunier *et al.* 2000), but comparisons of relative abundance, community composition, and large-scale habitat associations can successfully be made when potential differences in raptor detectability are accounted for (Millsap & LeFranc 1988).

All raptors perched or flying on either side of the road within eyesight range were recorded and identified with 10x42 binoculars. Stops were made at 1-km intervals to aid detectability of small and uncommon species. Additional stops were necessary to identify species and individuals spotted during stops were included in the counts. The transect length and position of each raptor along transects was recorded for each km with a geographical positioning system to the nearest 5 m. The distance from the road to the raptors was measured with a calibrated rangefinder to establish perpendicular distances for estimation of the effective strip width (Buckland *et al*. 1993). The effective strip width was estimated to assess potential differences in raptor detectability between biogeographical zones, which may bias comparisons of relative abundance. Surveys were conducted only with fine weather, i.e. clear or slightly clouded skies with low to moderate winds, starting at 06:30-07:30. Counts were finalized before 12:30-13:30 when detectability decreased due to the rise in air temperature (when raptors are either very high up or in the shade).

We examined patterns of community composition between zones and seasons for Palearctic migrants and Afrotropical species. Palearctic migrants are species which breed in Eurasia or Northern Africa and winter in sub-Saharan Africa, whereas Afrotropical species breed in sub-Saharan Africa. Black Kite *Milvus migrans*, Common Kestrel *Falco tinnunculus*, and Egyptian Vulture *Neophron percnopterus* included both Afrotropical and Palearctic populations, with distinct races for Black Kite and Common Kestrel (Ferguson-Lees and Christie 2001). For analyses at the species' level, we used the origin (Afrotropical or Palearctic) of the majority of individuals making up the population for these three species. Common Kestrel and Egyptian Vultures were separated into Afrotropical and Palearctic individuals for analyses of patterns of Afrotropical and Palearctic populations but not for Black Kite as individuals of Afrotropical or Palearctic origin could not be safely distinguished at all times.

Statistical analyses

Distance 6.0 software (Thomas *et al*. 2006) was used to estimate the strip widths of raptors detected along transects in each zone, because differences in vegetation structure and density, underlying potential differences in detectability (Buckland *et al*. 1993), might confound comparisons of relative abundance. Effective strip widths (ESW) were estimated based on the combined set of perpendicular distances to the road for flying and perching raptors, for species with > 40 observations per zone. The perpendicular distances of raptors with < 40 observations were pooled in groups of comparable size (small, medium-sized, large) to determine their zone-specific ESW. To determine ESW separately for each zone, 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 was selected for estimation of ESW and significant differences were based on overlap of 95% confidence intervals.

To calculate relative abundance, raptor counts on transects were expressed as the number of individuals per 100 km of transect, which allowed for comparisons between zones with transects of different length. To avoid losing data, the entire transect network was used for these analyses during each season, including transect sections surveyed only during the dry season. The latter was possible since the relative abundance estimates were expressed as numbers of individuals per 100 km of transect. In case of significantly different ESW between zones, we corrected relative abundance estimates to account for such differences by multiplying these with 1/ESW, and used the corrected estimates for comparisons within GEEs. Generalized Estimated Equations (GEEs; Hardin & Hilbe 2003) with robust variance estimation were used to examine the association between relative abundance estimates and biogeographical zones in SPSS 19.0 (SPSS Inc, Chicago, IL, USA), separately for raptors with > 10 observations on all transects combined, and for counts of Palearctic, Afrotropical and all raptors combined. The GEEs enabled the fitting of a log-linear model and permitted the assumption that the error distribution would follow a Poisson or Negative Binomial distribution. Biogeographical zone identity (n = 3) and transect number (n = 8) were taken as subject variables, with the period in which transects were surveyed (n = 8) as the within-subject variable. We included biogeographical zone identity and year as fixed categorical factors, the latter to control for annual variations in counts. Differences in relative abundance among zones 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.

For comparing richness of the raptor assemblages between zones for the dry and wet seasons, we followed recommendations by Gotelli & Colwell (2001) and 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 & Colwell 2001). We used 10-km transect segments that were surveyed eight times as our units of replication, totalling 39 sample units in Inundation zone, 87 in Sudan savanna, and 51 in Guinea savanna. Since every raptor observation was GPS-referenced, observations could be assigned to each 10-km segment using ArcView GIS 3.2 software (Esri 1999) and the cumulative counts in each season for each segment were used for comparisons of richness. The Mau 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 randomized 50 times for each dataset without replacement. We standardized comparisons by plotting expected species numbers against (1) the total number of road segments surveyed (a measure of species density; Gotelli & Colwell 2001) and (2) the total number of individuals observed (a measure of richness). Shannon diversity estimates were compared between zones and seasons in Cameroon in EstimateS 8.0 (Magurran 1988). We used sampling with replacement which allowed estimation of confidence intervals and comparisons of diversity between zones sampled at equal effort. The criterion used to determine whether the estimations of species richness and diversity were significantly different ($P < 0.05$) was the absence of overlap among the 95% confidence intervals (Colwell *et al.* 2004).

For comparisons of raptor richness between protected (i.e. those with frequent anti-poaching efforts: National Parks and adjoining hunting zones) and unprotected areas (all other areas), sampling was stratified according to protective status, on roads inside protected areas and/or buffer (i.e. hunting) zones and on roads outside these areas. Since counts limited comparisons for dry and wet seasons separately, we examined species richness in protected areas by combining dry- and wet-season counts on 9 sample units (10-km segments) in the Inundation zone and on 31 units in the Guinea zone. Thirty sample units in the Inundation zone and 20 units in the Guinea zone were used to examine species richness in unprotected areas. Since the Sudan zone did not have a National Park, no such assessment could be made for this zone.

For comparison of raptor richness in northern Cameroon with regional richness assessments elsewhere in the (sub-)tropics, we searched publications and unpublished reports of raptor road counts using comparable methods and data on survey effort (i.e. individuals counted; Colwell *et al*. 2004) and covering similar habitats (e.g. woodland savanna, open grasslands). Comparisons of richness estimates were standardized based on counts of individuals rather than sampling effort or area, which may compromise such comparisons (Gotelli & Colwell 2001). Only road surveys which presented detailed information on methodology, number of species and individuals counted were considered. The combined count data of 177 sample units (i.e. 1770 km) for the three biogeographical zones were used to derive a cumulative species richness curve for the study area in Cameroon. Since most published raptor surveys were conducted in a restricted period of the year (e.g., the dry season or “breeding season”), we also limited our richness estimate to the dry season to allow for meaningful comparisons between study sites.

10.3 Results

Patterns of raptor abundance

A total of 58 raptor species was identified during road surveys and 16,968 individuals were detected (Table 1). The three most commonly recorded species, Black Kite, Hooded Vulture *Necrosyrtes monachus*, and Grasshopper Buzzard *Butastur rufipennis* comprised over half of the individuals detected (53%). Booted Eagle *Hieraaetus pennatus* and Eurasian Marsh Harrier *Circus aeruginosus* represented 54% of the total number of Palearctic raptors detected, which together accounted for respectively 21%, 9% and 4% of Inundation, Sudan and Guinea zones during the dry season, and 8% of total counts. GEE model results showed a significant effect of biogeographical zone on the relative abundance of Palearctic raptors during the dry season ($\chi^2_2 = 84.3$, $P < 0.001$) and Afrotropical raptors during the dry ($\chi^2_2 = 38.6$, $P < 0.001$) and wet seasons ($\chi^2_2 = 45.8$, $P < 0.001$; Figure 2). The entire raptor assemblage was most abundant year-round in the Inundation zone, significantly less abundant in the Sudan zone and least abundant in the Guinea zone ($\chi^2_2 = 109.4$, $P < 0.001$). Five Afrotropical raptors were most abundant in the Guinea zone during the dry season, and four during the wet season (Table 2). The abundance of four Afrotropical raptors peaked on the Inundation zone during the dry and wet seasons, including two species whose relative abundance across zones remained significantly

different after corrections were made for significantly different ESWs between zones. No raptor was most abundant in the Sudan zone, and only Gabar Goshawk *Micronisus gabar*, Fox Kestrel *Falco alopex*, and Hooded Vulture were more abundant there than in another zone during the dry or wet season. Conversely, five large-bodied raptors with a distribution range centered on the Sudan zone, African Hawk Eagle *Hieraaetus spilogaster*, Brown Snake Eagle *Circaetus cinereus*, African White-backed Vulture *Gyps africanus*, White-headed Vulture *Trigonoceps occipitalis*, and Bateleur *Terathopius ecaudatus*, were more abundant in the Inundation or Guinea savanna zones during the dry or wet season.

Table 1. Species number and percentage population composition in three biogeographical zones (I = Inundation Zone, S = Sudan Zone, G = Guinea zone) in northern Cameroon, during road transect surveys between 2007 and 2010. The percentage composition relative to total numbers is presented separately for the three biogeographical zones and for dry and wet seasons.

		Dry season			**Wet season**		
	Total	I	S	G	I	S	G
Afrotropical raptors							
Black Kite *Milvus migrans* [1, 4]	**3771**	36	11	2	43	7	2
Hooded Vulture *Necrosyrtes monachus*	**3345**	7	40	3	7	43	< 1
Grasshopper Buzzard *Butastur rufipennis*[4]	**1912**	9	4	25	24	4	11
Fox Kestrel *Falco alopex*	**815**	< 0.1	9	7	< 1	11	5
Dark Chanting Goshawk *Melierax metabates*	**724**	4	4	3	4	4	6
African Swallow-tailed Kite *Chelictinia riocourii*[4]	**674**	10	3	< 1	3	1	-
Wahlberg's Eagle *Aquila wahlbergi*[4]	**574**	1	2	6	2	6	14
Black-winged Kite *Elanus caeruleus*	**567**	3	3	5	2	3	10
Rüppell's Vulture *Gyps rueppellii*	**520**	1	6	2	< 1	6	2
Lanner Falcon *Falco biarmicus*	**390**	1	3	5	2	2	3
Red-necked Buzzard *Buteo auguralis*[4]	**295**	< 0.1	1	4	1	4	5
Gabar Goshawk *Micronisus gabar*	**270**	1	2	1	2	2	< 1
African White-backed Vulture *Gyps africanus*	**195**	2	< 1	2	2	< 0.1	3
Tawny Eagle *Aquila rapax*	**187**	2	1	1	2	1	< 1
Grey Kestrel *Falco ardosiaceus*	**182**	< 0.1	1	3	< 1	2	6
Bateleur *Terathopius ecaudatus*	**174**	1	< 0.1	4	1	< 0.1	4
Shikra *Accipiter badius*[4]	**169**	< 0.1	< 1	5	< 1	1	4
Long-crested Eagle *Lophaetus occipitalis*	**156**	< 1	< 0.1	5	< 1	< 1	6
Brown Snake Eagle *Circaetus cinereus*	**107**	-	1	3	< 0.1	< 1	4
Red-necked Falcon *Falco chicquera*	**98**	1	< 1	1	1	< 1	2
African Harrier Hawk *Polyboroides typus*	**72**	< 1	< 1	2	< 1	< 1	2
Beaudouin's Snake Eagle *Circaetus beaudouini*[4]	**54**	< 1	-	< 1	1	< 1	< 1
African Hawk Eagle *Hieraaetus spilogaster*	**42**	< 0.1	< 0.1	1	< 0.1	< 1	1
Lapped-faced Vulture *Torgos tracheliotus*	**40**	< 1	-	-	1	-	< 1
Ayres's Hawk Eagle *Hieraaetus ayresii*	**38**	-	< 0.1	< 1	< 0.1	1	1
African Fish Eagle *Haliaeetus vocifer*	**37**	< 1	-	1	< 1	< 0.1	< 1
Martial Eagle *Polemaetus bellicosus*	**37**	-	< 1	1	-	< 1	1
Lizard Buzzard *Kaupifalco monogrammicus*	**36**	-	< 0.1	1	-	< 0.1	2
Western Banded Snake Eagle *Circaetus cinerascens*	**31**	-	-	1	-	< 0.1	1
White-headed Vulture *Trigonoceps occipitalis*	**23**	< 0.1	< 0.1	1	< 0.1	< 0.1	< 1
African Cuckoo Hawk *Aviceda cuculoides*	**20**	-	-	< 1	-	< 1	1
African Hobby *Falco cuvierii*	**7**	-	-	< 0.1	-	< 0.1	< 1
Ovambo Sparrowhawk *Accipiter ovampensis*	**4**	-	-	< 1	-	-	< 1
Bat Hawk *Macheiramphus alcinus*	**3**	-	-	< 1	-	< 0.1	-

Table 1. (Continued).

Secretary Bird *Sagittarius serpentarius*	**2**	< 0.1	-	-	-	-	< 1
Red-thighed Sparrowhawk *Accipiter erythropus*	**1**	-	-	< 0.1	-	-	-
Palearctic raptors							
Eurasian Marsh Harrier *Circus aeruginosus*	**491**	9	< 1	1	1	< 0.1	-
Booted Eagle *Hieraaetus pennatus*	**262**	3	3	1	-	-	-
Common Kestrel *Falco tinnunculus*[2]	**174**	1	2	1	-	1	-
Short-toed Eagle *Circaetus gallicus*	**119**	2	1	< 1	< 0.1	< 0.1	-
Montagu's Harrier *Circus pygargus*	**112**	2	1	< 1	-	-	-
Steppe Eagle *Aquila nipalensis*	**57**	1	< 0.1	< 1	< 0.1	-	-
Pallid Harrier *Circus macrourus*	**56**	1	< 1	< 1	-	-	-
Egyptian Vulture *Neophron percnopterus*[5]	**28**	< 1	< 0.1	-	< 0.1	< 1	-
Long-legged Buzzard *Buteo rufinus*	**22**	< 1	< 0.1	-	-	-	-
Honey Buzzard *Pernis apivorus*	**19**	-	< 1	< 1	-	< 0.1	< 1
Lesser Kestrel *Falco naumanni*	**18**	< 1	< 0.1	-	-	-	-
Osprey *Pandion haliaetus*	**13**	< 1	-	-	< 0.1	-	< 1
Barbary Falcon *Falco pelegrinoides*	**7**	< 1	-	-	< 0.1	-	-
Eurasian Hobby *Falco subbuteo*	**4**	-	-	-	< 0.1	-	< 1
Eastern Imperial Eagle *Aquila heliaca*	**3**	< 0.1	-	-	-	-	-
Red-footed Falcon *Falco vespertinus*	**3**	-	< 0.1	-	< 0.1	-	-
Levant Sparrowhawk *Accipiter brevipes*	**2**	-	-	-	-	-	< 1
Peregrine Falcon *Falco peregrinus*[3]	**2**	< 0.1	< 0.1	-	-	-	-
Common Buzzard *Buteo buteo*	**1**	< 0.1	-	-	-	-	-
Eleonora's Falcon *Falco eleonorae*	**1**	-	-	-	-	-	< 1
Lesser Spotted Eagle *Aquila pomarina*	**1**	< 0.1	-	-	-	-	-
Sooty Falcon *Falco concolor*	**1**	-	-	-	-	< 0.1	-
Unidentified raptors	**122**						

[1] The majority of Black Kites referred to the local race *parasitus* (Yellow-billed Kite); < 1% of dry season counts referred to the Palearctic race *migrans*.
[2] The resident race *F. t. rufescens* comprised 22% of total counts.
[3] Only the Palearctic race *calidus* was recognized on these surveys.
[4] Intra-African migrants, known for seasonal displacements (Thiollay 1978a, 2001).
[5] The local population comprised 25% of counts.

Patterns of richness and diversity

Raptor species richness and species density did not differ significantly between zones during the dry and wet seasons (Figure 3), apart from the higher species richness in the Guinea zone than the Inundation zone during the wet season. Afrotropical raptors richness was higher during both seasons in the Guinea zone than the Inundation zone (Figure 4), and Afrotropical species density was higher in the Guinea than the Inundation zone during the wet season. Although Palearctic species density in the Inundation zone surpassed species density in the other zones during the dry season, we did not find evidence of differences in Palearctic raptor richness between zones (Figure 5). Raptor diversity peaked in the Guinea zone during both seasons for Afrotropical and the complete raptor community, but no differences in Palearctic raptor diversity were detected between zones (Figure 6).

Table 2. Relative abundance (birds/100 km) of Palearctic and Afrotropical raptors recorded during road transect surveys performed in three biogeographical zones in northern Cameroon between February 2007 and December 2010. Mean values for transects in each zone ($n = 8$) are presented ±S.E. The association between biogeographical zones and relative abundance was investigated with Generalized Estimating Equations. Letters (a,b,c) indicate differences in relative abundance between zones ($P < 0.05$) using pair-wise comparisons and after Bonferroni correction.

	Afrotropical raptors											
	Dry season						Wet season					
Species	Inundation zone		Sudan zone		Guinea zone		Inundation zone		Sudan zone		Guinea zone	
African Cuckoo Hawk	-	-	-	-	0.12	±0.09	-	-	0.13	±0.08	0.55	±0.17
African Fish Eagle	1.77	±1.69	-	-	0.3	±0.23	0.25	±0.16	0.03	±0.04	0.35	±0.27
African Hawk Eagle	0.07^{a}	±0.07	0.08^{a}	±0.07	0.69^{b}	±0.22	0.08^{a}	±0.08	0.14^{a}	±0.12	0.82^{b}	±0.35
Ayres's Hawk Eagle	-	-	0.06	±0.05	0.34	±0.19	0.07^{a}	±0.07	0.45^{ab}	±0.16	0.55^{b}	±0.18
Bateleur	1.88^{ab}	±1.07	0.04^{a}	±0.03	2.39^{b}	±0.83	4.42^{ab}	±3.27	0.07^{a}	±0.07	3.22^{b}	±1.12
Beaudouin's Snake Eagle	0.54	±0.28	-	-	0.13	±0.09	1.87	±1.00	0.23	±0.09	0.36	±0.16
Black Kite[1]	107.7^{a}	±29.9	6.70^{b}	±2.18	3.05^{b}	±2.12	43.10^{a}	±15.0	9.15^{b}	±3.14	2.14^{c}	±0.86
Black-winged Kite	9.85^{a}	±2.63	3.22^{b}	±0.92	2.87^{b}	±1.12	5.94^{a}	±1.01	2.39^{b}	±0.42	4.57^{ab}	±1.30
Brown Snake Eagle	-	-	0.55	±0.17	1.77	±0.62	0.08^{a}	±0.08	0.29^{a}	±0.11	2.43^{b}	±0.66
Dark Chanting Goshawk**	15.15^{a}	±3.75	4.58^{b}	±1.41	1.80^{b}	±0.60	10.6^{a}	±2.36	3.90^{b}	±1.11	2.73^{b}	±0.80
Fox Kestrel	0.07^{a}	±0.06	7.24^{b}	±2.87	3.06^{ab}	±1.58	0.74^{a}	±0.50	9.48^{b}	±3.89	2.45^{ab}	±0.92
Gabar Goshawk	4.17^{a}	±1.10	2.05^{b}	±0.74	0.67^{b}	±0.39	3.39^{a}	±0.63	1.79^{b}	±0.45	0.67^{c}	±0.54
Grasshopper Buzzard**	29.56^{a}	±8.13	3.57^{b}	±0.93	15.3^{ab}	±6.22	56.4^{a}	±15.5	3.91^{b}	±1.00	6.23^{b}	±2.15
Grey Kestrel	0.16^{a}	±0.16	0.58^{a}	±0.24	1.77^{b}	±0.46	0.36^{a}	±0. 31	1.48^{b}	±0.32	3.35^{c}	±1.00
African Harrier Hawk	0.36^{a}	±0.18	0.18^{a}	±0.14	1.20^{b}	±0.21	0.41	±0.19	0.39	±0.14	0.94	±0.25
Hooded Vulture	26.2^{ab}	±12.9	34.9^{a}	±6.75	1.38^{b}	±1.28	23.6^{ab}	±16.8	38.8^{a}	±7.42	0.20^{b}	±0.12
Lanner Falcon	4.26	±0.94	2.48	±0.72	2.92	±0.59	4.55	±1.22	1.79	±0.55	1.44	±0.30
Lapped-faced Vulture	1.56	±0.85	-	-	-	-	1.62	±0.72	-	-	0.13	±0.10
Lizard Buzzard	-	-	0.02	±0.02	0.46	±0.28	-	-	0.04	±0.03	1.09	±0.32
Long-crested Eagle	1.17^{a}	±0.52	0.09^{b}	±0.07	2.59^{c}	±0.53	0.98^{a}	±0.63	0.09^{a}	±0.06	2.77^{b}	±0.56
Martial Eagle	-	-	0.09	±0.05	0.68	±0.15	-	-	0.33	±0.15	0.72	±0.31
Common Kestrel[2]	-	-	0.41	±0.31	0.04	±0.05	-	-	0.41	±0.37	-	-
Red-necked Falcon	3.21	±2.42	0.3	±0.17	0.48	±0.13	1.93^{a}	±0.86	0.17^{b}	±0.08	0.62^{a}	±0.19
Red-necked Buzzard**	0.38^{a}	±0.31	1.10^{ab}	±0.45	2.45^{b}	±0.81	1.44^{a}	±0.59	4.27^{b}	±1.15	2.14^{ab}	±1.16
Rüppell's Vulture	4.19	±2.26	6.6	±4.42	0.26	±0.21	1.68	±0.84	6.45	±3.71	1.41	±1.13
Shikra	0.31^{a}	±0.17	0.28^{a}	±0.13	2.43^{b}	±0.88	0.62^{a}	±0.22	1.02^{ab}	±0.30	2.06^{b}	±0.65
African Swallow-tailed Kite	42.54^{a}	±26.9	2.55^{a}	±1.30	0.08^{b}	±0.08	5.59	±2.28	1.06	±0.81	-	-
Tawny Eagle	5.87^{a}	±2.35	0.60^{b}	±0.18	0.86^{ab}	±0.38	4.38	±2.86	0.5	±0.14	0.24	±0.12
Wahlberg's Eagle	3.78	±0.84	1.51	±0.55	3.26	±1.04	4.52	±0.89	5.07	±1.11	5.23	±1.27
Western Banded Snake Eagle	-	-	-	-	0.57	±0.21	-	-	0.03	±0.03	0.62	±0.14

Table 2. (Continued).

African White-backed Vulture	5.11[a]	±3.19	0.14[b]	±0.11	0.81[ab]	±0.58	5.39[ab]	±3.75	0.07[a]	±0.05	1.65[b]	±0.78
White-headed Vulture	0.14	±0.14	0.04	±0.05	0.29	±0.21	0.19[ab]	±0.13	0.03[a]	±0.03	0.53[b]	±0.25

[1] The majority of Black Kites referred to the local race *parasitus*; *c.* < 1% of dry season counts referred to the Palearctic race *migrans*.
[2] Only includes the resident race *F.t. rufescens*.
** ESW significantly greater ($P < 0.05$) in Inundation zone and Sudan savanna compared to Guinea savanna; significant differences in relative abundance between zones as presented here not affected after correction.

	Palearctic raptors											
	Dry season						**Wet season**					
	Inundation zone		**Sudan zone**		**Guinea zone**		**Inundation zone**		**Sudan zone**		**Guinea zone**	
Booted Eagle	9.26[a]	±3.16	3.91[a]	±1.34	0.37[b]	±0.13	-	-	-	-	-	-
Common Kestrel[3]	6.11[a]	±1.66	1.69[b]	±0.47	0.67[b]	±0.28	-	-	-	-	-	-
Egyptian Vulture[4]	2.02	±1.88	-	-	-	-	0.23	±0.16	-	-	-	-
Short-toed Eagle	4.87[a]	±1.23	0.73[b]	±0.38	0.23[b]	±0.23	0.06	±0.05	0.03	±0.02	-	-
Honey Buzzard	-	-	0.19	±0.11	0.23	±0.10	-	-	0.07	±0.05	0.36	±0.20
Lesser Kestrel	0.84	±0.32	0.04	±0.04	-	-	-	-	-	-	-	-
Long-legged Buzzard	1.64	±1.34	0.03	±0.04	-	-	-	-	-	-	-	-
Eurasian Marsh Harrier	22.9[a]	±5.37	0.44[b]	±0.17	0.62[b]	±0.21	0.32	±0.20	0.03	±0.04	-	-
Montagu's Harrier	5.19[a]	±1.80	1.18[a]	±0.42	0.35[b]	±0.23	-	-	-	-	-	-
Osprey	0.66	±0.45	-	-	-	-	0.2	±0.16	-	-	0.04	±0.05
Pallid Harrier	3.22[a]	±1.21	0.33[b]	±0.28	0.13[b]	±0.06	-	-	-	-	-	-
Steppe Eagle	3.74[a]	±2.03	0.02[b]	±0.02	0.10[b]	±0.10	0.08	±0.08	-	-	-	-

[3] Only includes the Palearctic race *F.t. tinnunculus*.
[4] Excluding local breeders.

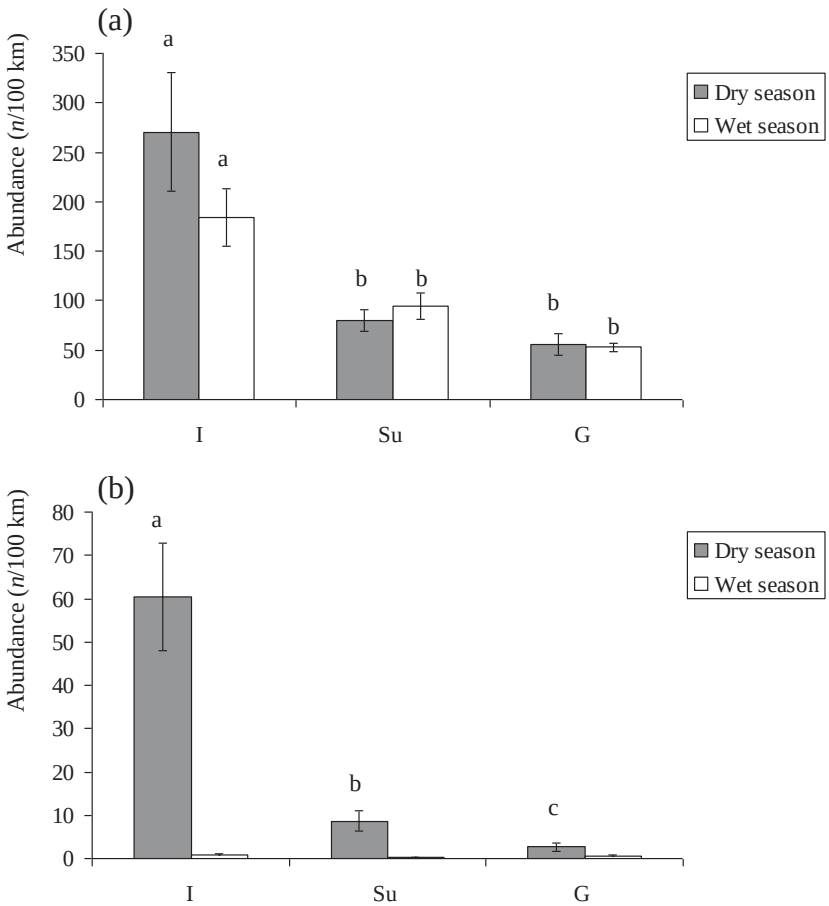


Figure 2. Relative abundance (birds/100 km) of (a) Afrotropical and (b) Palearctic raptors recorded during road transect surveys performed the Inundation zone (I), Sudan (Su), and Guinea savanna (G) of Cameroon between February 2007 and December 2010. Mean values for transects in each zone (n = 8) are presented ±S.E. The association between biogeographical zones and relative abundance was investigated with Generalized Estimating Equations. Letters (a,b,c) indicate differences in relative abundance between zones ($P < 0.05$) using pair-wise comparisons and after Bonferroni correction.

Richness and diversity in protected and unprotected areas

We did not find a significant difference in species richness and diversity (Figure 7) between protected and unprotected areas in the Inundation zone and the Guinea savannas for wet and dry season data combined, or for wet and dry seasons separately (not shown), but a trend for lower richness and diversity outside protected areas was evident for both zones and for Afrotropical and Palearctic species.

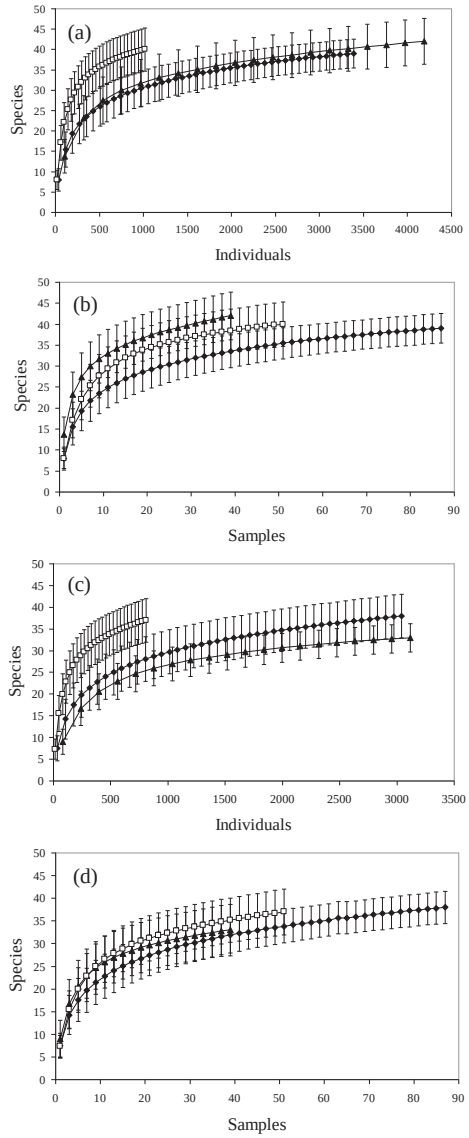


Figure 3. Sample-based rarefaction curves (with 95% CI) of raptor richness for the Inundation zone (▲), Sudan (◆), and Guinea savanna (□) in north Cameroon against (a,c) the total number of individuals detected (i.e. species richness) and (b,d) 10-km sample units (i.e. species density) during the dry (a,b) and wet seasons (c,d). Every second point is shown.

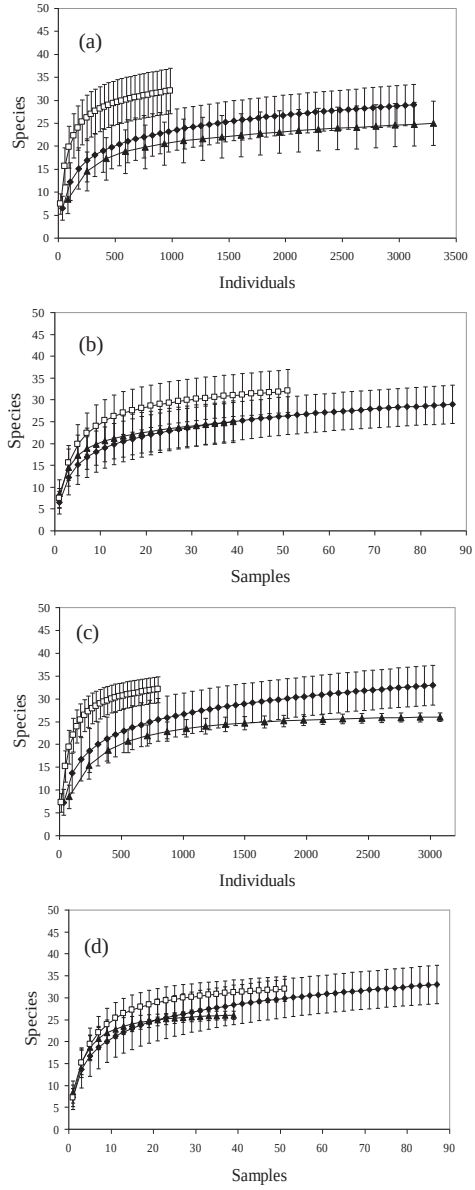


Figure 4. Sample-based rarefaction curves (with 95% CI) of Afrotropical raptor richness for the Inundation zone (▲), Sudan (◆), and Guinea savanna (□) in north Cameroon against (a,c) the total number of individuals detected (i.e. species richness) and (b,d) 10-km sample units (i.e. species density) during the dry (a,b) and wet seasons (c,d). Every second point is shown.

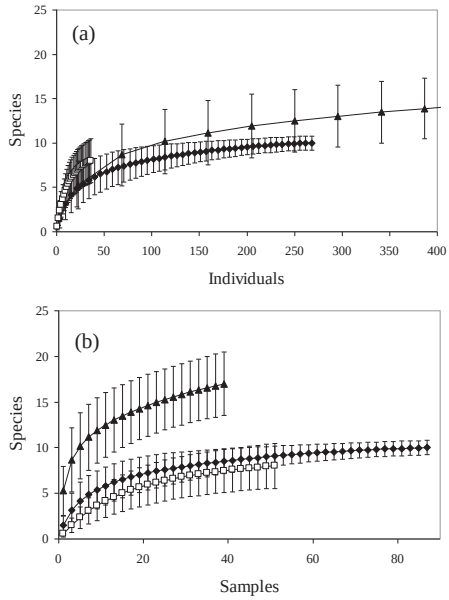


Figure 5. Sample-based rarefaction curves (with 95% CI) of Palearctic raptor richness for the Inundation zone (▲), Sudan (◆), and Guinea savanna (□) in north Cameroon against (a) the total number of individuals detected (i.e. species richness) and (b) 10-km sample units (i.e. species density), during the dry season. Every second point is shown.

Comparisons with regional, continental and global raptor richness

Most studies (one exception) conducted elsewhere in West Africa generated species richness estimates within the 95% confidence limits of our cumulative species richness curve (Figure 8), indicating comparable richness to northern Cameroon. Conversely, raptor richness estimates from comparable habitats in South America, Asia, and southern Africa were below and outside the 95% confidence limits of the richness curve of Cameroon. Raptor richness in the savannas of Cameroon thus appears to be representative for the region, but comparatively high on a continental and global scale, surpassed only by raptor richness in East African savannas.

10.4 Discussion

We detected clear patterns of raptor abundance, richness and diversity between Cameroon's biogeographical zones. Raptor diversity and richness did not peak in the heavily exploited Sudan savanna zone, previously cited as the core biogeographical zone for the West African raptor assemblage, with the highest species diversity and richness (Thiollay 1977a). Rather, diversity was highest in the dense, relatively well preserved Guinea savannas, during the wet and dry seasons, while richness was largely comparable between zones.

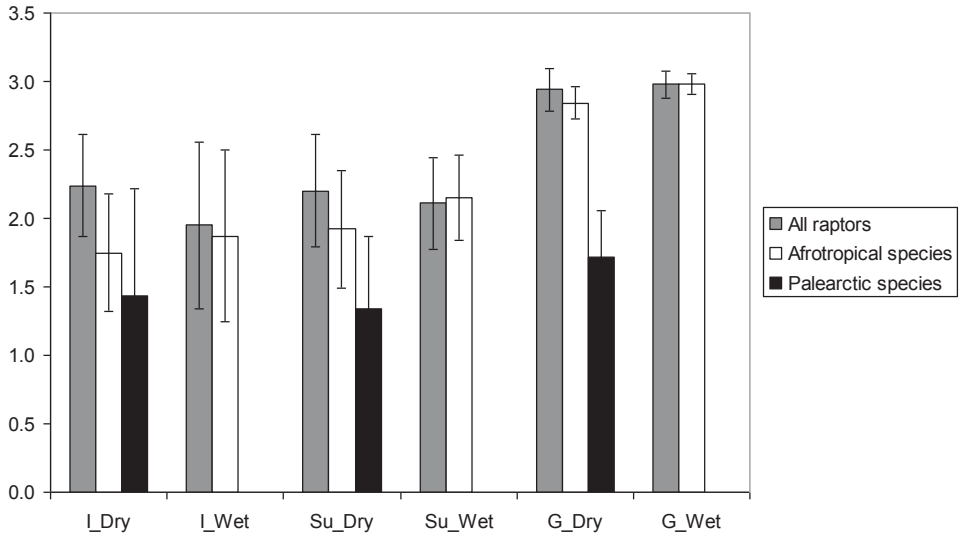
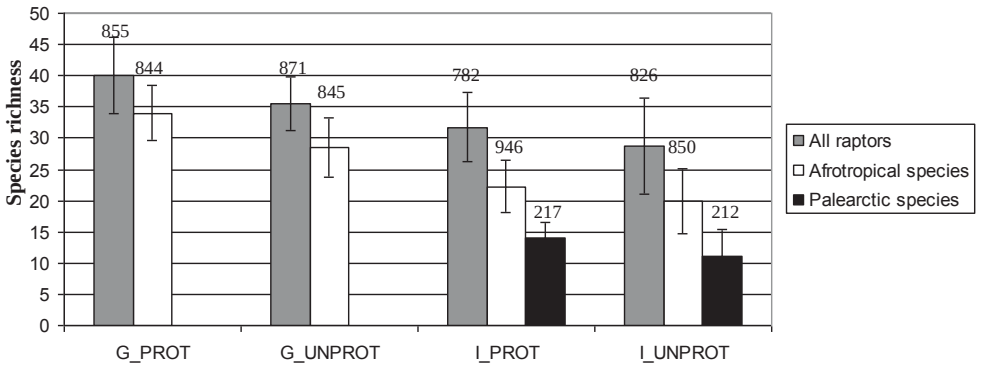


Figure 6. Shannon diversity indices (with 95% CI) for all raptors, Afrotropical raptors, and Palearctic raptors detected in the the Inundation zone (I), Sudan savanna (Su), and Guinea savanna (G), in north Cameroon, during the dry and wet seasons. Palearctic raptor diversity is presented only for the dry season since limited numbers prevented stabilization of Shannon diversity during the wet season. Diversity indices were estimated at approximately equal sampling effort (*n* = 798-850 individuals for "all raptors", *n* = 796-843 for "Afrotropical species", *n* = 37-44 for "Palearctic raptors").

Interestingly, only three Afrotropical raptors with a distribution range centered on the Sudan savannas were more common there than in biogeographical zones at more northerly or southerly latitudes. This contrast general patterns of species abundance, which tends to decline in peripheral areas of distribution ranges (Brown *et al*. 1995) where conditions are less favorable (Pulliam 2000, García & Arroyo 2001) and sensitivity to habitat alteration higher (Swihart *et al*. 2003).

Our results showed that five Afrotropical large-bodied raptors, whose distribution was centered on the Sudan zone, were more common in the Inundation zone and Guinea savannas than the Sudan zone. The higher abundance of only three raptors in the Sudan zone, compared to the other zones during either season, further underlined the impoverished state of the raptor assemblage in the Sudan savannas. These results suggest that human-induced habitat modification influenced raptor communities at the landscape scale, leading to greater abundance within potentially suboptimal habitat at the periphery of distribution ranges. It further suggests that extensive habitat modification resulting from anthropogenic land use may override the dominant role of biogeographical zonation in shaping community patterns of West African raptors.

(a)



(b)

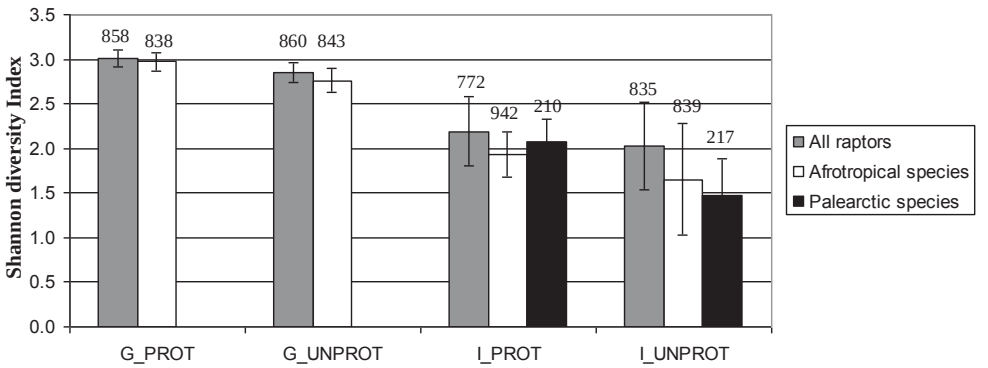


Figure 7. Species richness (A) and Shannon diversity indices (B) for all raptors, Afrotropical raptors, and Palearctic raptors in protected (PROT) and unprotected (UNPROT) areas of the Inundation zone (I), and Guinea savanna (G) in north Cameroon. Numbers of Palearctic migrants in the Guinea zone were too low for accurate comparisons and were left out. Indices were estimated at approximately equal sampling effort (*n* indicated). Values are presented with 95% CI.

Raptor richness and diversity in protected and unprotected areas

Despite a trend for lower raptor richness and diversity in unprotected compared to protected areas, these differences were not significant, which might have had several causes. First, we used lack of overlap of the 95% confidence intervals as a criterion of statistical difference, which is generally considered overly conservative (Payton *et al.* 2004), although it is the most appropriate criterion currently available for rarefaction curves (Colwell *et al.* 2012). Second, the hunting zones included in the analysis as protected areas in the Guinea zone, might have had lower raptor richness than the core conservation areas (Thiollay 2007a), but our transect coverage inside hunting zones was insufficiently extensive to test this assumption. Also, this did not play a role in the Inundation zone, where the entire protected

area network had the status of national park. Third, protected and unprotected areas were located in relative proximity, while the wide-ranging habits of raptors dependent on protected areas might make differences only apparent at greater distances (Herremans & Herremans Tonnoeyr 2000). This effect may have been enhanced by the inclusion of wet-season counts in our assessment, since rains and changes in vegetation structure may render cultivated habitats around parks interesting for migratory or nomadic raptors. Further, moderately affected woodlands around protected areas in the Inundation and Guinea zone provided breeding habitat for small to medium-sized raptors, and foraging opportunities for large raptors breeding in the park. These results suggest that protected areas might act as source areas for raptor populations, which ensured preservation of the integrity of the raptor assemblage at the landscape-scale.

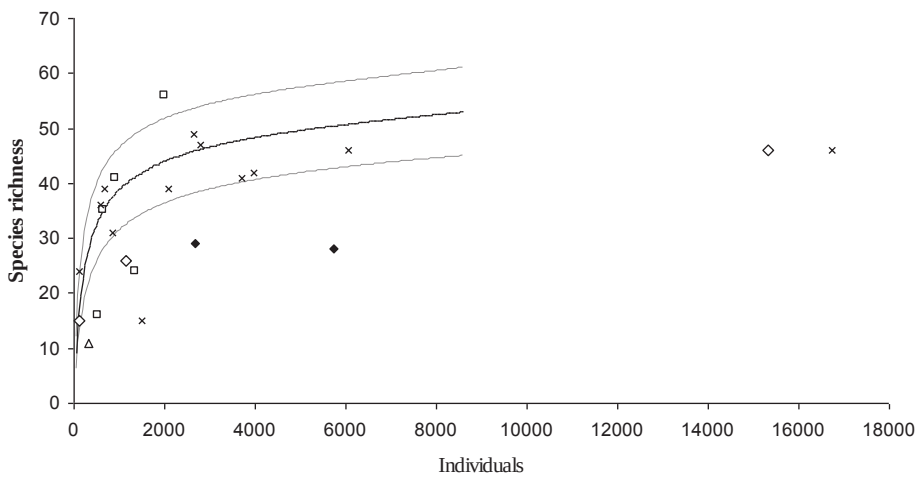


Figure 8. Raptor richness accumulation curve (solid line) with 95% confidence intervals (dashed lines) based on 7080 km dry-season road transect surveys in northern Cameroon between 2007 and 2010, compared to raptor richness recorded on road surveys in similar habitats in West Africa (X), East Africa (□), southern Africa (◊), South America (◆), and Asia (Δ). Numbers refer to published records (see Appendix 10.1).

Comparisons with regional, continental and global raptor richness

Our data illustrated the comparatively high richness of Cameroon's savanna raptor community, on a continental and global scale, which may be considered representative for raptor community richness in West African savannas. Since raptor richness is influenced by many factors, such as ecosystem productivity, topographical and vegetational diversity (Sergio *et al.* 2006, 2008), caution is needed when comparing richness estimates between widely spaced localities differing in such parameters. However, other studies used similar methods and frequently incorporated similarly diverse, productive and often partly protected areas (see Appendix 10.1), justifying our comparative assessment. As previously reported (Thiollay 1978a), the Lake Chad Basin and associated floodplains are of particular importance to Palearctic raptors, which is located on the western edge of the African winter

range for some, while others reach higher densities here compared to areas further west (Thiollay 1977a). Adding to these wintering populations are Palearctic migrants which routinely traverse Cameroon's Sudan and Guinea savannas en route to and from their winter range at more southerly latitudes (Hake *et al.* 2003, Gschweng *et al.* 2008, Strandberg *et al.* 2009). Together, the rich assemblage of Palearctic winter and passage migrants and Afrotropical raptors highlight the region's importance as a focal point for raptor conservation in Africa.

Conservation concerns

Few protected area networks in West Africa cover the range of habitats necessary to maintain the diverse assemblage of species adapted to different vegetation types and structure (Thiollay & Clobert 1990), or support migratory populations with almost constantly shifting populations along latitudinal gradients (Thiollay 1978a). Cameroon may be a positive exception in this regard, and savanna habitat preservation at different latitudes may have been instrumental in maintaining its rich raptor community. The presence of large-bodied raptors in the heavily exploited Sudan savannas contrasts the situation in central West Africa, where few or no large sedentary eagles were detected outside protected areas or their peripheral zones in the Sudan savanna zone (Thiollay 2006a,b,c). This also implies that connectivity between core populations still exists in Cameroon, which is an important prerequisite for population viability. On the other hand, poaching and increased disturbance following human population increase may have contributed to the current scarcity of Secretary Bird *Sagittarius serpentarius* and Martial Eagle *Polemaetus bellicosus*, formerly regularly encountered in the Inundation zone (Louette 1981, Scholte *et al.* 1999). Similarly, White-headed and *Gyps* Vultures, which were still recorded breeding in the 1980s and 1990s (Mundy *et al.* 1982, Scholte 1998), have declined considerably and stopped breeding in the 1990s (Scholte 1998), or more recently in Waza N.P. (R. Buij pers. obs.). This suggests that the protected area network failed to safeguard breeding populations of some of the largest, most sensitive, and threatened raptors. Similarly strong declines of eagles and vultures has been reported from various other, small (< 2500 km^2) protected areas in Burkina Faso (Thiollay 2000, 2006b), Nigeria (Tende & Ottosson 2008), and Guinea Conakry (Rondeau *et al.* 2008), whereas larger protected areas (> 4000 km^2) such as the Mole N.P. in Ghana (Dowsett-Lemaire & Dowsett 2008), the Comoé N.P. in Ivory Coast (Salewski 2000), the Bénoué Valley in Cameroon (this study), and Arli-W-Pendjari Complex in central West Africa (Thiollay 2006a) appear to retain their large raptor populations, albeit at lower densities than previously for some. Protected area size thus seems to play a crucial role in maintaining threatened raptor populations, as observed in southern Africa (Herremans & Herremans Tonnoeyr 2000), and for other vertebrate populations in West Africa (Brashares *et al.* 2001), but further studies are urgently needed to identify causes for the decline of breeding raptors inside the region's protected areas.

Appendix to Chapter 10

Appendix 10.1. List of published and unpublished reports of raptor richness estimated using road transects in western Africa, South America, and Asia.

	Reference	Country	Habitat	Cove-rage[1]	Year	S[2]
1	Jensen *et al*. 2005	Venezuela	Wetlands, agriculture, forests	R	2000-02	D,W
2	Rondeau *et al*. 2008	Guinea	Guinea and Sudan savannas, protected area	R	2006	D
3	Thiollay *et al*. 2006a	Burkina Faso, Mali and Niger	Floodplain, Sahel and Sudan savannas, protected area	R	2003–4	D
4	Thiollay *et al*. 2006a	Burkina Faso, Mali and Niger	Floodplain, Sahel and Sudan savannas, protected area	R	1969–73	D
5	Thiollay 1975a	Chad	Sudan savanna, protected area	L	1973	D
6	Cade 1969	South Africa	Woodland savanna, protected area	L	1959-65	W
7	Herremans & Herremans-Tonnoeyr 2000	Botswana	Woodland savanna, Kalahari, protected area	R	1991-95	D,W
8	Anadón *et al*. 2010	Mauritania, Mali	Sahel savannas	R	2004	D
9	Thiollay 2001	Cameroon	Sudan savanna, protected area	R	2000	D
10	Thiollay 2001	Cameroon	Sudan savanna, protected area	R	1973	D
11	Carrete *et al*. 2009	Argentina	forest, floodplain, grasslands, woodland, mountain forest, desert	R	2002-05	B
12	Sanchez-Zapata *et al*. 2003	Kazakhstan	Grassland, floodplain	R	1999	B
13	Thiollay 2007a	Burkina Faso	Sudan savanna, grassland, floodplain, woodland, protected area	R	2004-05	D
14	Weesie & Belemsogbo 1997	Burkina Faso	Sudan savanna, protected area	L	1991-92	D
15	Thiollay 1975b	Ivory Coast	Guinea savanna, protected area	L	1968-73	D
16	Thiollay 1975b	Ghana	Guinea savanna, protected area	L	1972	D
17	Ogada & Keesing 2010	Kenya	savanna woodland, protected area	L	2001-03	D,W
18	Ogada *et al*. 2010	Kenya	savanna woodland, protected area	R	2010	D
19	Njilima *et al*. 2010	Tanzania	savanna woodland, protected area	R	2010	D
20	Thiollay *et al*. 2008	Tanzania	savanna woodland, protected area	R	2008	D
21	Sorley & Andersen 1994	Kenya	savanna woodland, protected area	L	1990	D
22	Thiollay 1970	Senegal	Sudan savanna, protected area	L	1969	D
23	Barkhuysen 2004	South Africa	Grassland, agriculture, forest, protected area	R	2003	D,W

[1]Regional (R): transects covered region within a country or multiple countries; local (L): transects covered single protected areas, with or without buffer zones. [2]Season: dry (D), wet (W), breeding season (B)

Box B

Sightings of Sooty Falcon in the far north of Cameroon

Ralph Buij

Published in: *Bull ABC* (2010), 18(2): 211-215

Sooty Falcon *Falco concolor* is considered a rare Palearctic vagrant to western Africa (Borrow & Demey 2001). Confirmed records exist for eastern Chad in May and June. In addition, four to five Sooty Falcons were observed at several locations in and around the northern Aïr Mountains in Niger, between July and September; at least one was in its second calendar year (NiBDaB 2010). These constitute the only summer records for the region. The following describes observations made by the author of Sooty Falcons in northernmost Cameroon in May and July 2010.

On 1 May 2010, I photographed a Sooty Falcon south of the village of Rhumsiki in the Kapsiki Mountains (10°40'N 13°56'E; 1100 m; Figure 1a). Temperature was 35°C with clear skies; the first seasonal rains had fallen several days earlier. The falcon was hawking insects at 13:27 at 150–200 m above ground and moved off north-west. Its plumage was uniform bluish grey, including the flight feathers; the cere and feet were yellow. The ochre cheeks and chin and the dark moustachial indicate the bird was probably in its third calendar-year, or perhaps older (Forsman 1999). The habitat consisted of undulating hills and rocky outcrops with cultivation, *Combretum* and *Terminalia* shrubland and scattered villages. Several Eurasian Hobbies *F. subbuteo* were observed hawking insects in the same area that day.

Between 7 and 28 July 2010, I observed at least five Sooty Falcons near the village of Waza, south of Lake Chad and close to Waza National Park in northern Cameroon (11°40'N 14°57'E; 300 m). Photographs of at least four different individuals indicated they had barred, i.e. juvenile-type, flight feathers and relatively short wings (especially the 'hand'), suggesting they were in their second calendar-year (Forsman 1999). All observations were made near or from three granite outcrops, which constitute the only higher ground in this relatively flat area and which rise to 400–500 m. Surrounding habitat consists of seasonally flooded grassy plains, interspersed by cultivation (millet, sorghum), small villages, and higher lying *Sclerocarya birrea* and *Anogeissus leiocarpus* tree savanna, *Combretum* and *Terminalia* shrubs, and stands of *Hyphaena thebaica*. *Acacia seyal* tree savanna on black clay soils is saturated with water in the rainy season. Rainfall (peak from May–September) is irregular with an annual mean of 450-700 mm. From June, the area received above average rainfall, with rains at least every 2–3 days continuing into July. As a result, much of the surrounding grassy plains were permanently inundated.

On 7 July, two Sooty Falcons were hawking insects and 'playfully' chasing each other above the rocky outcrops. They were seen around 17:00 in overcast conditions after a day of heavy rain. Other raptors simultaneously hawking insects above the outcrops included several juvenile Lanner Falcons *F. biarmicus*, two African Hobbies *F. cuvierii* and 12 Fox Kestrels *F. alopex*. On 16–18 July, at least two Sooty Falcons were seen infrequently at the same location, mostly in the afternoon, at 16:30–18:30, when they were hawking insects together around the outcrops (Figure 1b). Once, a Sooty Falcon was seen at 07:34. On 19 July, a group of five Sooty Falcons were hawking insects together at 16:35, after a day of heavy rain.

On 24–25 July, up to three Sooty Falcons were seen together from the highest rocky outcrop in the area (500 m), which was visited for the entire day on both dates (Figures 2–4). A Sooty Falcon appeared around 14:30 on 24 July, in fine weather coinciding with the development of a distant rainstorm. It was hawking insects at very close range, pursuing prey in rapid flight among the boulders at the top of the hill, and dismembering and consuming insects in flight. Prey included dragonflies and alate termites, possibly also locusts. It often stooped at great speed from 50–70 m up, twice at dragonflies. Other raptors attracted to the insect food included two African Hobbies, a single Grey Kestrel *F. ardosiaceus* and several Lanner Falcons and Fox Kestrels. After 20 minutes, the Sooty Falcon flew off in the direction of the rainstorm. Two more Sooty Falcons appeared 30 minutes later and after some time spent hawking insects near the top of the hill, also moved off in the direction of the storm. Three Sooty Falcons - probably the same individuals - were seen higher up at 16:00, hawking insects in the rain, by which time other falcons had ceased their hunting activities. Three Sooty Falcons were again seen together at the same location on 25 July, around 13:00, in light rain. After several minutes they moved off to forage above the distant flooded grasslands.

The last observation of a Sooty Falcon was made on 28 July at 15:20; this bird was seen only briefly after it had started raining. No further visits were made to the area after 28 July. Despite five years of intensive raptor studies by myself and various year-round bird surveys by others during the past 20 years, these are the first observations of Sooty Falcons in Cameroon. Thiollay (1977a) did not observe the species during his seven years of raptor studies between Mauritania and Cameroon. The Sooty Falcons in Niger were only recorded in one out of 12 years of bird studies, following heavy rains which resulted in a superabundance of locusts (J. Newby pers. comm.). Sooty Falcons may only visit western Africa infrequently and perhaps only when heavy rains trigger a rich supply of food. Their frequency of occurrence may be under-estimated, however, due to the scarcity of observers.

It is important to note, in this respect, the paucity of observations of the ecologically similar Eleonora's Falcon *F. eleonorae* in western Africa. Intensive raptor surveys resulted in a single observation of Eleonora's Falcon in northern Cameroon (Chapter 10) and another in the south (Hivekovics & Palatitz 1998), while there are only three records elsewhere in the region: single black-morph individuals at the Banc d'Arguin, north-west Mauritania, in November and January (Lamarche 1988, Meininger *et al.* 1990), and a bird video-taped in Mount Peko National Park, Côte d'Ivoire, in March (G. Rondeau *in Bull. ABC* 8: 147). Recent satellite transmitter studies have revealed, however, that West and Central Africa - especially Niger, Nigeria, Cameroon, Chad, Central African Republic and Congo-Kinshasa - are routinely crossed by Eleonora's Falcons en route to and from their breeding grounds in the western Mediterranean (Gschweng *et al.* 2008, Lopez-Lopez *et al.* 2010). The third calendar-year Sooty Falcon seen in May in northern Cameroon was perhaps following a similar migratory route, although it was slightly west of the expected flight path, given the location of the westernmost known breeding grounds of Sooty Falcons in eastern Libya.

The Eleonora's Falcon satellite studies revealed the over-summering of juvenile Eleonora's Falcons on the African continent, away from the breeding grounds (Gschweng *et al.* 2008).

The very low proportion of subadult Sooty Falcons at some breeding colonies, such as in Oman (M. McGrady in litt.), suggests young Sooty Falcons also summer away from their breeding colonies. Similar to Eleonora's, summering Sooty Falcons may range widely on the African continent, tracking strong rains and the superabundance of prey that they bring. Observations of Sooty Falcons in eastern and southern Africa, including Madagascar, during July–October are extremely rare; only a handful were reported from Tanzania during this period, some of which may have been misidentified Grey Kestrels (N. Baker in litt.). The Sooty Falcons observed in northern Cameroon in July, and in Niger in July–August suggest that summering Sooty Falcons may be particularly attracted to good rains in this part of Africa.

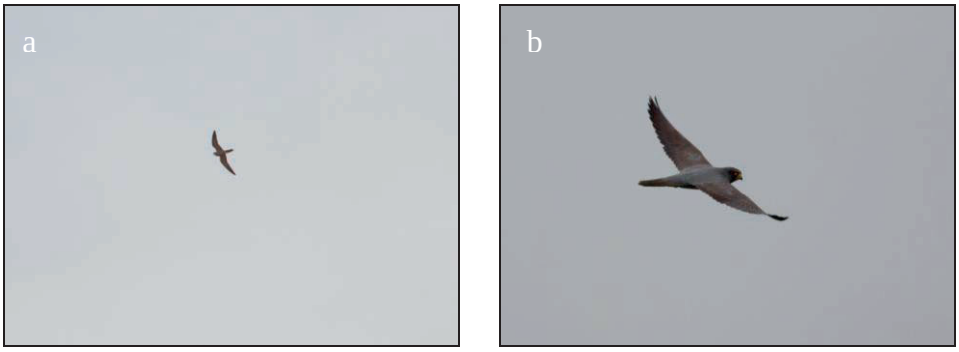


Figure 1. (a) Third calendar-year or older Sooty Falcon, 13 km south of Rhumsiki, Cameroon, 1 May 2010. Note the long wings; (b) second calendar-year Sooty Falcon; the mantle, rump and head feathers have been moulted, but note the retained juvenile upperwing-coverts, remiges and retrices, Waza, Cameroon, 17 July 2010.

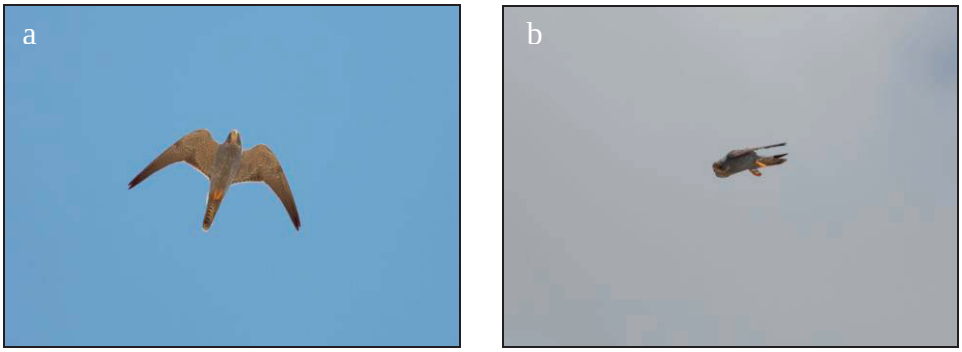


Figure 2. (a) Second calendar-year Sooty Falcon hawking insects, Waza, Cameroon, 24 July 2010; and (b) the same individual stooping at a dragonfly.

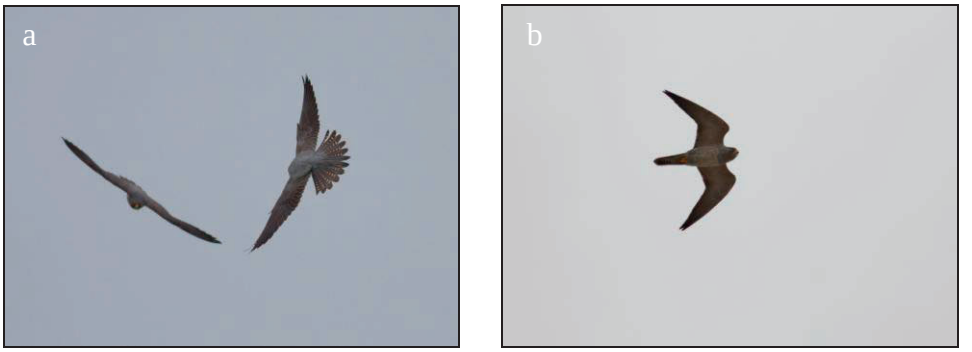


Figure 3. (a) Second calendar-year Sooty Falcon "playfully" chasing each other, Waza, Cameroon, 24 July 2010; and (b) second calendar-year Sooty Falcon; the moult of body feathers is less advanced than in the bird depicted in Figures 2a-b, Waza, Cameroon, 24 July 2010.

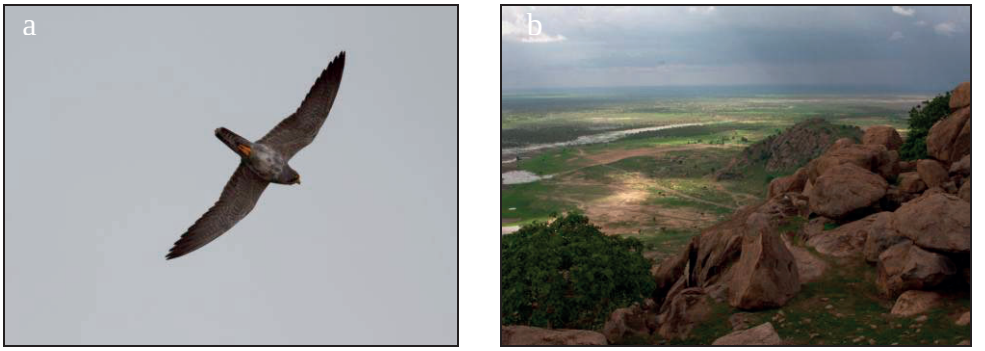


Figure 4. (a) Second calendar-year Sooty Falcon, Waza, Cameroon, 24 July 2010; and (b) Sooty Falcon habitat, a rocky outcrop of 500 m elevation in otherwise flat terrain; the falcons chased insects among the boulders and also visited the distant inundated grasslands, Waza, Cameroon, 24 July 2010.

Chapter 11

Synthesis

Ralph Buij

11.1 Introduction

Increasing evidence suggests that raptor species respond differently to alteration of their native habitats, some even increasing in numbers along gradients of transformation or remain apparently unaffected, while other species decline (Jullien & Thiollay 1996, Rodríguez-Estrella *et al.* 1998, Sánchez-Zapata & Calvo 1999, Sergio & Bogliani 2000, Anderson 2001, Palomino & Carrascal 2007, Cardador *et al.* 2011). Research in temperate and (sub-)tropical environments have revealed that 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 & Calvo 1999, Anderson 2001), particularly favoring species with high levels of behavioral and ecological flexibility to changing conditions (Suárez *et al.* 2000, Cardador *et al.* 2011). Conversely, specialist raptors of dense tropical forests may decrease even after slight modification of their habitat (Jullien & Thiollay 1996). Such results imply that raptor conservation aimed at specific species, or their use as umbrella species for conservation management, requires detailed knowledge of species-specific ecological requirements. Such knowledge is scarce for the tropical West African savannas between Senegal and Cameroon, even by African standards (Virani & Watson 1998). This region, roughly six times the size of France, is of great importance to a rich assemblage of Afrotropical sedentary and migratory raptors, as well as a wintering ground for Palearctic migratory raptors from western Europe (Zwarts *et al.* 2009) east to central Asia (Terraube *et al.* 2011), and south to southern Africa (Meyburg *et al.* 1995).

The effects of land use change on the sedentary and migratory raptors are described in more detail in this thesis, focusing on changes in prey availability and diet in response to transformation, and in-depth analyses of habitat use, breeding ecology and food intake of representatives within the Palearctic, Afrotropical migratory and sedentary raptor assemblage. Based on existing literature, I hypothesized that the largest impact of land use change would be on sedentary Afrotropical raptors, because their low mobility may limit their ability to cope with increasingly rapid and significant declines in habitat and prey availability (Carrete & Donázar 2005). Similar to some migratory raptors on European breeding grounds (Sergio & Bogliani 2000, Suárez *et al.* 2000, Cardador *et al.* 2011), I expected that Afrotropical migrants may cope better with changes in land use than sedentary species, while Palearctic migrants were expected to be most flexible and generally adapt best to changes in land use (Jones *et al.* 1996, Wilson & Cresswell 2002). I further expected that intraspecific and interspecific traits, such as sex, age, and body mass influenced vulnerability to land use change in Afrotropical and Palearctic raptors. This chapter concludes with a synthesis and an integrative discussion of the main results of the research and ends with a set of recommendations.

Response of raptors to land transformation

Foraging habitat selection by Palearctic raptors and the role of sex, age, and body mass differentiation

Dspite their hypothesized flexibility to changes in land use, I expected that interspecific (Schipper 1973, Jaksic & Braker 1983, Marti *et al.* 1993, Garcia & Arroyo 2005) or intraspecific differences (Marquis & Newton 1982, Smallwood 1988) in body mass, energy needs, and diet render large Palearctic raptors, or the larger sex of sexually-dimorphic raptors, more vulnerable to land use change than smaller raptors, or the smaller sex (Thiollay 2006a,b, 2007a). Results of the study presented in Chapter 2 confirmed my hypothesis that the vulnerability to land use change of Palearctic raptors may be influenced by gender-specific patterns of habitat selection. In addition, I found evidence for age-specific patterns of habitat selection. Intraspecific differences in foraging distribution was particularly evident in relationship to rice fields for Montagu's *Circus pygargus* and Pallid Harriers *C. macrourus*, as females of both species selected rice fields over the original, naturally flooded grassland habitat, whereas males seemed to avoid rice fields. As a result, sexual dimorphism may result in smaller males of these species being negatively affected by floodplain conversion for rice cultivation, whereas females may profit from an increase in food supply. Contrary to expectations, I recorded limited evidence for interspecific foraging segregation, although the mean prey mass differed significantly between harriers, mainly because heavier species took heavier prey items with greater frequencies, which was related to interspecific differences in body mass which determine food requirements (Nagi 1987, 2005). The interspecific food niche segregation associated with increased landscape and food resource heterogeneity suggests that floodplain development may facilitate co-existence of large numbers of harriers, supporting the general assumption that land use change may be profitable for Palearctic raptors due to increased food supply. Importantly, however, floodplain embankment and subsequent large-scale desiccation of formerly productive, inundated grasslands reduced the foraging habitat quality for harriers over an extensive area, counteracting the positive effect of increased food supply in cultivated fields.

The effect of habitat transformation on nestling diet, growth, nest density and reproductive output in Afrotropical migratory raptors

Although nestling growth in raptors was shown to be affected by productivity and land use in a temperate zone (Newton *et al.* 1979), few data are available for the tropics. As shown in Chapter 4, differences in prey availability with anthropogenic habitat transformation caused a dietary shift in a migratory Afrotropical raptor, the Grasshopper Buzzard *Butastur rufipennis*, during the breeding season. Possibly as a consequence of differences in diet quality and composition, nestling growth parameters, including asymptotic weight, were significantly affected by land use, leading to a superior condition of fledglings in natural habitat compared to those in transformed habitat. This may increase the potential for survival and recruitment of fledglings in natural habitat (Arroyo 2002, McDonald *et al.* 2005). This finding suggests that changes in food supply with habitat alteration might have rather subtle effects, with potentially important consequences for population persistence (Rodríguez *et al*. 2006). Despite the evidence for better food conditions in natural habitats, I

found no significant effect of land use on productivity and nest success in Grasshopper Buzzards (Chapter 5). This was primarily related to the opposing effects of generally more favourable food conditions in natural habitat versus lower losses due to natural predation and longer inter-nest distances in transformed habitat, the latter possibly reducing intraspecific interference and competition (Newton 1979). Thus, transformed habitats may offer particular advantages to breeding Afrotropical migratory raptors in terms of reduced natural predation pressure, which exerted a heavy toll on reproductive output of Grasshopper Buzzards and African Swallow-tailed Kites *Chelictinia riocourii* (Chapters 5, 6).

Chapters 4 and 5 also demonstrated some of the complex trade-offs between food supply and predation risk, through their impact on nestling condition and productivity, for breeding raptors in changing landscapes. Firstly, dietary analyses (Chapter 4) revealed that rodents comprised a larger proportion of the diet of Grasshopper Buzzards in natural than transformed habitat (Chapter 4). This reflected greater rodent availability in natural habitat, which contributed to denser nest spacing, suggesting rodents were an important determinant of habitat quality for Grasshopper Buzzards (Newton 1979). Although I did not find conclusive evidence, differences in rodent supply might also have contributed to the superior nestling condition at fledging in natural compared to transformed habitat (Chapter 4), which is supported by the positive association of rodent availability around nests with nestling survival (Chapter 5). On the other hand, rodent availability around nests was negatively associated with clutch survival (Chapter 5), presumably because high rodent densities attracted predators which also targeted clutches. Overall, no effect of rodent supply around nests on nest success and productivity was recorded. The combined evidence suggests that high rodent abundance in natural habitat enabled higher breeding densities and improved nestling survival compared to transformed habitat, but these advantages appeared to be countered by the greater loss of clutches.

Chapters 5 and 6 further revealed evidence for the impact of habitat transformation, through expanding cultivation and woodcutting, on nest dispersion and reproductive success of Grasshopper Buzzards and African Swallow-tailed Kites. I found that Grasshopper Buzzard nests were more widely spaced in the transformed habitat compared to protected areas, which was associated with the lower food supply and larger area under cultivation in transformed habitat. At the larger inter-nest distances, breeding raptors may experience lower intraspecific interference, or competition (Newton 1979), as suggested by the positive effect of inter-nest distance on nest success (Chapter 5). In Chapter 6, I describe the process of woodland cover loss in the Saloum River delta in Senegal, as a potential driver behind the largest breeding aggregation of African Swallow-tailed Kites known to date. Although further investigations are needed, frequent intraspecific interactions might have contributed considerably to the extremely low breeding output at this site. These results suggest that anthropogenic land transformation may have divergent effects on reproductive output by influencing nest dispersion of Afrotropical migratory raptors, by driving breeding aggregations into restricted habitats, or by lowering breeding densities and thereby the negative effects of intraspecific interactions.

The results of Chapter 4 also demonstrated a positive association between rainfall during the nestling phase, and nestling growth rate, suggesting that seasonal rains provide a crucially important food stimulus (e.g. insects, amphibians; Thiollay 1978a, Njiforti 1997) which enhanced nestling growth. In line with these results, I found a positive relationship between rainfall and Grasshopper Buzzard nest success and productivity (Chapter 5). These results add to existing evidence of the positive role of rainfall on raptor productivity in arid African savannas (Hustler & Howells 1990, Wichmann *et al.* 2003). It is interesting, in this regard, that Thiollay's transect counts were conducted at the start (1969-1973) and following (2000-2004) an exceptionally severe drought in the Sahel region, between 1968–1997, one of the most severe of the 20th century (Hulme *et al.* 2001). Although the extent of the decline caused by suboptimal rainfall is unknown, it is evident that this circumstance must have impacted the results of his surveys. My results suggest that climate change and ecological change of the wintering grounds may have acted synergistically to decrease resource availability for raptors, notably those Afrotropical migrants breeding in the Sudano-Sahelian savannas.

The impact of habitat transformation on diet and foraging in a sedentary Afrotropical raptor

Chapter 7 provides insight into the impact of habitat transformation on foraging in sedentary Dark Chanting Goshawks *Melierax metabates*. Contrary to expectations based on our studies of Grasshopper Buzzards (Chapter 4), and other raptors (e.g. James & Smith 1987, Pande *et al.* 2007, Ogada & Kibuthu 2009), habitat alteration did not prompt a dietary shift in male Dark Chanting Goshawks. Instead, habitat modification increased prey accessibility while lowering prey quality; I found that goshawks in transformed habitat compensated for smaller, less profitable prey items by higher prey capture rates compared to natural habitat. Herbaceous layer height and tree density at the range-level negatively impacted capture rates by goshawks, suggesting that anthropogenic changes to the vegetation (e.g., from livestock grazing, fires, herbicide use, wood cutting) improved prey accessibility, thus compensating for lower prey energy content in man-altered habitat. However, patch-level selection for tall trees and high tree density, shrub cover, and dense herbaceous cover by hunting goshawks appeared to be primarily related to optimization of prey biomass, suggesting that vegetation clearance negatively impacted important microhabitats for lizard and rodent prey populations (Cooper & Whiting 2000, Meik *et al.* 2002). Thus, to a certain degree, grazing and woodcutting favor Dark Chanting Goshawk foraging, but heavy and extensive wood cutting, tree pruning and grazing pressure may suppress the abundance or quality of prey resources; at a certain point, degraded landscapes may become too impoverished to sustain breeding pairs of sedentary raptors.

Sensitivity to habitat modification: the role of Afrotropical or Palearctic breeding distribution, body size and migratory behaviour

Studies of Palearctic raptors wintering in Africa have shown that winter populations can be abundant in, or even particularly attracted to, man-modified habitats (Herremans & Herremans-Tonnoeyr 2000, Anadón *et al.* 2010, Limiñana *et al.* 2012). My results (Chapters 2, 8, 9) add to various other studies which tend to support high adaptability to man-modified landscapes by some Palearctic migrants (Moreau 1972, Morel & Morel

1992, Jones *et al.* 1996, Wilson & Cresswell 2002). Conversion of floodplains, for example, may create habitat mosaics with abundant and varied food resources for Palearctic raptors, enabling the co-existence of large multi-species assemblages (Chapters 2, 9). The flexibility of Palearctic raptors to cope with changing conditions is further apparent by their shifting distributions in response to changes in prey availability (Chapter 9, Figure 3).

Despite the general indifference of Palearctic raptor community richness to land use at a 5-km scale (Chapter 8), my results illustrated that some species may profit from anthropogenic land use change, at least locally, whereas others appear mostly negatively affected. Monthly surveys on the Waza-Logone floodplains indicated that Eurasian Marsh Harrier *Circus aeruginosus* and Booted Eagle *Hieraaetus pennatus* preferably foraged over rice crops compared to other habitats (Chapter 9), Booted Eagle also responding positively to cultivation at a larger spatial scale (Chapter 8). On the other hand, the large-scale deterioration of grasslands, through heavy grazing and as a by-product of embankment for irrigated rice schemes (Chapter 2), may depress habitat quality for Palearctic raptors dependent on food resources in such grasslands. Depleted insect prey resources might particularly impact smaller, predominantly insectivorous Palearctic raptors, which appear to profit little from abundant rodent populations in cultivation (Chapters 2, 8, 9), while their high site fidelity and dependence on restricted, seasonally productive habitat, such as floodplains, increases their vulnerability to conversion of such habitats (Thiollay 1989, Limiñana *et al.* 2012, Trierweiler *et al.* in press). Increasing droughts and locust control operations add to such threats by further reducing insect prey populations (Sánchez-Zapata *et al.* 2007, Mihoub *et al.* 2010).

As hypothesized, the richness of the Afrotropical raptor assemblage was negatively associated with man-modified habitat, including croplands (Chapters 8, 9), suggesting Afrotropical raptors were generally more sensitive to habitat conversion than Palearctic raptors. This might be explained partly by their morphological adaptations, which constrain exploitation of abundant food sources in open, seasonally productive habitats (Thiollay & Clobert 1990) or as a result of human disturbance and persecution associated with cultivation (Chapter 5). However, model results did reveal that small to moderate loss of original habitat in largely untouched, dense Guinea woodlands, was positively associated with Afrotropical raptor richness, possibly because it allowed exploitation of rich prey resources to generalist raptors adapted to more open habitats (Rodríguez-Estrella *et al.* 1998, Anderson 2001). As hypothesized, I found evidence that the sensitivity of raptors to land use appeared to depend on body size, with corresponding food needs and area requirements (Newton 1979, Machange *et al.* 2005), at least in the Guinea savannas. The finding that large raptor richness decreasing with distance from protected areas supported previous results of the particular importance of the region's protected areas for sustaining populations of large eagles and vultures (Thiollay 2006a, 2007a).

The results of the habitat association models indicated that the Afrotropical migrant assemblage profited locally from moderate anthropogenic disturbance (Chapter 8), which may favor their hunting strategies (Thiollay & Clobert 1990), whereas the sedentary raptor assemblage responded negatively to anthropogenic land use across biogeographical zones.

However, the vulnerability to land modification by Afrotropical migrants varied with breeding status or landscape context, or a combination of both. For example, Afrotropical migratory Grasshopper Buzzards were positively associated with agriculture in Guinea savannas (Chapter 8), where populations spend the non-breeding season (Thiollay 1978a) and they might have profited from increased prey availability and accessibility resulting from agricultural activities. In contrast, nest density and presence was positively related to habitat preservation in the Inundation zone, where they breed (Chapters 5, 8). These results suggest that sensitivity to land use change varies seasonally and between biogeographical zones, according to the timing and location of breeding, which may confound assessments of vulnerability to habitat change if such factors are not taken into consideration.

The role of protected area coverage and land use on biogeographical patterns of abundance, richness, and diversity of raptors in West African savannas
As hypothesized, I detected clear patterns of raptor abundance, richness and diversity between Cameroon's biogeographical zones, which vary in their extent of habitat preservation (Chapter 10). My results suggest that human-induced habitat modification influenced raptor communities at the landscape scale in Cameroon, leading to greater abundance within potentially suboptimal habitat at the periphery of distribution ranges. This contrast general patterns of species abundance, which tends to decline in peripheral areas of distribution ranges (Brown *et al*. 1995) where conditions are less favorable (Pulliam 2000, García & Arroyo 2001) and sensitivity to habitat alteration higher (Swihart *et al.* 2003). I conclude that extensive habitat modification resulting from anthropogenic land use and the absence of protected areas may override the dominant role of biogeographical zonation in shaping community patterns of West African raptors.

Together, the rich assemblage of Palearctic winter and passage migrants and Afrotropical raptors highlight the importance of West African savannas as a focal point for raptor conservation, especially given the immense pressure from human populations. Protected areas have an important role in shaping landscape-scale patterns (Chapter 8, 10), and might act as source areas for raptor populations, thus ensuring preservation of the integrity of the raptor assemblage at the landscape-scale. However, the current protected area network in West Africa may not adequately cover the range of habitats necessary to maintain the diverse assemblage of species, including migratory populations with almost constantly shifting populations, and further studies are urgently needed to identify causes for the decline of Afrotropical raptors inside the region's protected areas.

11.2 Recommendations

Management recommendations emanating from this thesis would be to conserve trees or, preferably, patches of woodland, shrubland and pasture among crop fields, as they supply nest sites, foraging perches, and vital resources for prey populations exploited by raptors in agro-ecosystems. The commitment to develop more intensive agricultural strategies in Africa could limit the land converted to agriculture compared to the current low-input extensification of African agriculture (World Bank 2009), and may be seem as a favorable development. However, the introduction of new crops and changes in farm size for

commercial farm development are likely to further reduce natural vegetation cover in croplands, with detrimental consequences particularly for Afrotropical raptors. Implementations of intensive agriculture (e.g. cotton; Chapter 8) may carry additional costs for raptors exposed to heavy pesticide use, through secondary poisoning (Mullié *et al*. 1991, Keith & Bruggers 1998). Applications of pesticides toxic to birds may be particularly detrimental in areas with high raptor abundance: around National Parks and on floodplains, where Afrotropical and Palearctic raptor abundance peaks (Chapter 10), and in rice fields, with large concentrations of Palearctic raptors (Chapter 9). Although predation by raptors was shown to have little effect on the population dynamics of *Mastomys natalensis*, a major rodent pest in tropical Africa (Vibe-Petersen *et al*. 2006), raptors could be promoted as valuable predators aiding the control of grasshoppers and locusts (Fowler *et al*. 1991, Mullié 2009), and assisted through supplementation of perches (Sheffield *et al*. 2001).

Since implementation of some of the above-mentioned measures in a vast region is extremely challenging, conservation efforts for Afrotropical raptor populations should best focus on maintaining the functions of those areas which are key to their preservation at wider landscape scales: the protected areas and their peripheral zones (Chapter 5, 8, 10). Improved protection of the National Parks, with restrictions on incursions by shepherds and poachers into National Parks, is a necessity to prevent disappearance of endangered raptors from such key areas for their conservation. This would reduce disturbance at nest sites and often unsustainable harvesting of vertebrate prey resources inside protected areas (Brashares *et al.* 2001). To further accomplish this, co-management regulations pertaining to exploitative utilization of resources (e.g. wood, fish) inside protected areas, some ill-devised and little regulated (Scholte 2003), also need to be revised where appropriate, as some directly or indirectly affect raptor food availability and nest security.

Since large raptors are vulnerable to factors operating beyond protected areas, such as direct persecution (Herholdt & Kemp 1997, Ogada & Keesing 2010), a major objective should be to increase the extent of strict protected areas, although this may pose challenging given the low per-capita gross domestic product in the region (Musters *et al.* 1999, McDonald & Boucher 2011). Given such constraints, the protection of reserves needs to be integrated with compensating mechanisms that promote the economic value of the ecosystems inside and around parks for local communities (Kramer *et al.* 1997, Clerici *et al.* 2006). Hereto, buffer zone management around many protected areas may need to be re-evaluated, which includes strategies to resolve growing human-wildlife conflict (Weladji & Tchamba 2003), a more equitable distribution of wildlife revenues generated from tourism or hunting (Mayaka *et al.* 2005), and a limit to human immigration flow into buffer zones (Newmark 2008). Such measures, together with appropriate silvicultural practices encouraged, enforced, and implemented by state and traditional authorities, with limitations on agricultural expansion, might ensure continued persistence of intact raptor communities in a large part of the West African savanna region.

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Summary

Summary

Raptors in West Africa's savannas have strongly declined the past four decades and many species now survive only in a few pockets of intact habitat, mostly inside protected areas, while some species are on the brink of extinction. Little is known about the processes that sustain raptor populations within increasingly human-transformed savanna landscapes, and clues to the mechanisms and causal drivers behind population declines remain little studied. Moreover, it is unclear how changing conditions differently affect the diverse assemblage of Afrotropical and Palearctic raptors, which depend on the West Africa's savannas for part or most of their life cycle, and how vulnerability, or adaptability to changing environments, relate to life-history traits such as their mobility, sex, age, body mass, and diet. The aim of this thesis is to quantify the effects of land transformation on distribution, foraging, diet, and reproductive output of Palearctic and Afrotropical raptors, both migratory and sedentary, in West African savannas, to increase the knowledge that can support conservation efforts directed at the persistence of rich raptor populations in this part of the world.

Chapter 1 starts with a description of the study area in northern Cameroon and the research questions. Chapter 2 presents a study on foraging habitat selection by Palearctic migratory Eurasian Marsh Harrier *Circus aeruginosus*, Pallid Harrier *C. macrourus*, and Montagu's Harrier *C. pygargus* on the Waza-Logone floodplain of northern Cameroon. These and other Sahelian floodplain systems are of great importance for wintering Palearctic raptors. Aim of this study was to generate insight into the role of body mass, age, and sex in foraging habitat selection by Palearctic migratory raptors. The results showed evidence of intersexual differences in foraging preference related to land use and some evidence that juveniles exploited different habitats from adults. Although only limited evidence for interspecific differentiation of foraging habitat was found, food partitioning by prey mass was related to harrier body mass and facilitated by a diverse supply of prey on human-transformed floodplains. The comparable use of natural floodplain and cultivated habitats, and diversification of food resources with development suggest that floodplain conversion for cultivation may benefit wintering harriers to some extent. However, the avoidance of newly created rice fields and dry grasslands by certain sex- and age-groups indicated that floodplain development may have important negative consequences for a proportion of the population. Loss of habitat elements can also lead to a limitation of foraging options; Box A presents the first detailed observations of the use of certain habitat elements by bird-hunting Pallid Harriers on the African winter grounds.

To further our understanding of the mechanisms underlying dramatic declines of Afrotropical raptors, the relationship between environmental conditions, nest density, reproductive parameters, and nestling growth were examined in the Afrotropical migratory Grasshopper Buzzard *Butastur rufipennis* (Chapters 3-5). Chapter 3 provides the first detailed information of the breeding biology and nestling development of the Grasshopper Buzzard. Nests were more widely spaced in transformed than natural habitat (Chapter 5), which was related to lower rodent supply and a greater proportion of the area under cultivation in transformed habitat, while nest site availability was comparable between

habitats. Nest success and productivity were positively associated with rainfall, an important food stimulus, and the canopy shielding the nest, which limits detection by avian predators. Productivity and nest success were unaffected by land use, due to opposing effects of higher predation pressure and food supply in natural habitat compared to transformed habitat. However, loss of grass cover, prey populations and loss of woodland cover is likely to depress Grasshopper Buzzard reproductive success and nest density in the future. Additionally, land use change may have rather subtle effects. Chapter 4 shows that land use was a significant predictor of asymptotic nestling weight, when potentially confounding variables such as hatch order, gender, hatch date, rainfall, or brood size were taken into consideration. This result suggests that nestlings in transformed habitat possessed an inferior condition at fledging, possibly lowering their future survival chances. Another Afrotropical migrant, the African Swallow-tailed Kite *Chelictinia riocourii*, also appears to cope with moderate land transformation (Chapter 6), but a reduction of the extent of breeding habitat might drive populations into large breeding aggregations with potentially negative effects on reproduction.

Sedentary raptors are likely to be more vulnerable to habitat change than migratory raptors, since they depend on year-round territories for food and reproduction. To examine the effect of habitat degradation on the foraging of a sedentary species, 12 ♂ Dark Chanting Goshawk *Melierax metabates* were radio-tracked to investigate their foraging efforts and gains (Chapter 7). The results showed that Dark Chanting Goshawks in natural habitats had smaller home ranges and used a larger proportion of their range for foraging than goshawks in transformed habitat. Their selection for relatively tall trees and high tree density, high shrub cover, and thick and extensive herbaceous cover appeared to be primarily related to optimization of prey biomass within hunting patches. Foraging effort and gains were comparable between natural and transformed habitats, but herbaceous layer height and tree density within ranges, both higher in natural habitat, were negatively related to prey capture rates. Woodcutting and grazing thus favored greater prey capture rates in transformed compared to natural habitat, mediating the effect of less profitable prey items in the former, but increasingly extensive loss of vegetation cover suppress prey resources to the detriment of goshawk populations in human-transformed habitats.

Chapters 8-10 report the results of studies of habitat associations of Afrotropical sedentary, migratory, and Palearctic raptor assemblages, at different spatial and temporal scales, which provide insight into the role of environmental factors in structuring raptor populations in West African savannas. Original habitat, National Parks, cultivation, and human population size shaped patterns of raptor richness at the 5-km scale, but the importance and direction of responses differed between species groups and biogeographical zones (Chapter 8). Whereas Palearctic raptor community richness was unrelated to land use, Afrotropical raptor richness was negatively related to habitat modification and human populations in the Inundation zone and Sudan zone of northern Cameroon, but peaked at moderate levels of woodland clearance in Guinea savannas. Landscape scale analyses of raptor richness and diversity indicated that protected area coverage and human exploitation influenced biogeographical distribution patterns of Afrotropical raptors in Cameroon (Chapter 10). In the relatively well-preserved Guinea savanna zone, I found evidence for greater sensitivity

to anthropogenic impact among large raptors compared to small raptors: the richness of large raptors decreased with increasing distance to the nearest protected area, whereas the richness of small raptors was negatively correlated with the extent of natural habitat. A difference was furthermore reported in relationship to species mobility in the Guinea savanna: the richness of the sedentary Afrotropical raptor assemblage decreased with human population size, whereas the richness of Afrotropical migratory raptors increased with the area under cultivation.

Road surveys conducted at a 2-km scale on the Waza-Logone floodplain (Chapter 9) confirmed that assemblages of Afrotropical raptors responded more strongly to land use than Palearctic raptors: Afrotropical raptor diversity was higher on the naturally flooded grasslands compared to the newly created cultivated habitats and desiccated grasslands, whereas the richness and diversity of Palearctic raptors was unrelated to land use. However, Palearctic raptor abundance was highest in post-harvest rice fields, demonstrating the importance of the rice fields as foraging habitat for Palearctic raptors.

Given the globally important raptor richness and immense pressure from strongly increasing human populations, West Africa's savannas should be regarded a priority region for raptor conservation efforts (Chapter 10). Chapter 11 offers a synthesis of results and includes recommendations for conservation efforts directed at protected areas networks and their important Afrotropical raptor assemblages. Buffer zone management around National Parks needs to be re-evaluated and silvicultural practices encouraged, enforced, and implemented by state and traditional authorities, which includes limitation on the expansion of cultivation and introduction of environmentally sustainable cotton production. Management of seasonally food-rich cultivated habitats, such as rice fields, for the benefit of Palearctic raptors deserves more attention than currently the case.

Samenvatting

Samenvatting

Roofvogels in de West Afrikaanse savannes zijn sterk in aantal achteruit gegaan de afgelopen vier decennia. Op dit moment is weinig bekend over de processen die roofvogelpopulaties in de veranderende savannelandschappen beïnvloeden. Bovendien is onbekend welk effect veranderende condities hebben op roofvogels die voor een deel van hun levenscyclus van deze savannes afhankelijk zijn, en hoe hun aanpassingsvermogen gerelateerd is aan eigenschappen zoals mobiliteit, leeftijd, geslacht, lichaamsgrootte en dieet. Het doel van deze dissertatie is het kwantificeren van de antropogene impact in West Afrikaanse savannes op de distributie, foerageren, dieet, en broedsucces van Palearctische en Afrotropische roofvogels, zowel migrerende als sedentaire soorten. Zulke kennis is nodig voor het aanpassen van gebiedsbeheer ten gunste van de rijke roofvogelpopulaties in dit deel van de wereld.

Hoofdstuk 1 begint met een beschrijving van het studiegebied in noord Kameroen en van de onderzoeksvragen. Hoofdstuk 2 bevat de resultaten van een studie naar foerageerhabitatselectie van de Palearctische bruine kiekendief *Circus aeruginosus*, steppekiekendief *C. macrourus*, en grauwe kiekendief *C. pygargus* op de Waza-Logone vloedvlakte van noord Kameroen. Deze vloedvlakte is, net als andere vloedvlaktesystemen in de Sahel, van groot belang voor Palearctictische roofvogels die overwinteren in Afrika. Doel van deze studie was inzicht te verkrijgen in de rol die lichaamsgewicht, leeftijd en geslacht spelen bij de selectie van foerageerhabitat door Palearctische roofvogels in hun overwintergebied. Ik vond dat maar beperkt sprake was van inter-specifieke verschillen in habitatselectie. Echter, inter-specifieke voedselpartitie met betrekking tot prooigrootte was gerelateerd aan het gemiddelde lichaamsgewicht van drie kiekendievensoorten. Dit werd mede mogelijk gemaakt door een divers prooiaanbod op de deels ontgonnen vloedvlakte. Het vergelijkbare gebruik van natuurlijke vloedvlaktehabitat en landbouwgebieden door de kiekendieven en de diversificatie van het prooiaanbod geven aan dat de ontginning van vloedvlaktes voor landbouw geen ongunstige ontwikkeling is voor overwinterende kiekendieven. Toch is het vermijden van drooggelegde graslanden en rijstvelden door bepaalde geslacht- en leeftijdsgroepen een indicatie voor een belangrijk negatief effect van vloedvlakte-ontginning op een deel van de populatie. Ook op kleinere ruimtelijke schaal kan verlies van habitatelementen voor verlies van foerageeropties leiden - Box A illustreert het belang van bepaalde habitatelementen voor vogeljagende steppekiekendieven.

Om meer inzicht te krijgen in de mechanismen achter de sterke afname van Afrotropische roofvogels, onderzocht ik de relatie tussen omgevingsfactoren, nestdichtheid, reproductieve parameters, en groei van nestjongen in een Afrotropische migrant, de sprinkhaanbuizerd *Butastur rufipennis*. In Hoofdstuk 3 wordt de eerste gedetailleerde informatie gepresenteerd over de broedbiologie, groei en ontwikkeling van deze roofvogel. Het onderzoek naar nestdispersie in getransformeerd en natuurlijk habitat liet zien dat de afstand tussen bezette nesten groter was in getransformeerd habitat (Hoofdstuk 5), welke gerelateerd was aan lagere beschikbaarheid van knaagdieren en meer landbouwgebied in getransformeerd vergeleken met natuurlijk habitat, terwijl de beschikbaarheid van nestgelegenheid vergelijkbaar was. Nestsucces en productiviteit waren positief gerelateerd aan regenval, dat

zorgt voor grotere prooibeschikbaarheid, en de beschutting van nesten door de kroonlaag van de nestboom, van belang voor het reduceren van de detecteerbaarheid van nestjongen door grotere roofvogels. In tegenstelling tot de verwachting waren productiviteit en nestsucces niet gerelateerd aan landgebruik, door de tegengestelde effecten van hogere voedselbeschikbaarheid en hogere predatiedruk in natuurlijk habitat vergeleken met getransformeerd habitat. Desondanks lieten de resultaten zien dat een voortschrijdende afname van de grasbedekking, prooipopulaties en natuurlijk savannehabitat in onbeschermde gebieden een negatief effect zal hebben op het voortplantingssucces bij deze soort. Hoofdstuk 4 liet bovendien zien dat habitatdegradatie vrij subtiele gevolgen kan hebben voor deze soort. Landgebruik was een significante predictor van het asymptotisch gewicht van nestjongen, als rekening werd gehouden met derde variabelen zoals de nestjong volgorde, geslacht, datum van uitkomen, regenval, of broedselgrootte. Dit resultaat suggereert dat nestjongen in getransformeerd habitat over een inferieure conditie beschikken als ze uitvliegen vergeleken met nestjongen in natuurlijk habitat, met mogelijk negatieve gevolgen voor overleving of reproductie.

Een andere Afrotropische migrant, de Afrikaanse zwaluwstaartwouw *Chelictinia riocourii*, broedde net als de sprinkhaanbuizerd in vergelijkbare dichtheden in natuurlijk en gecultiveerd habitat (Hoofdstuk 6). De achteruitgang van beschikbaar broedbiotoop was echter een belangrijke factor die leidde tot een congregatie van nestparen in grote broedkolonies, zoals in Senegal, waar het erg lage broedsucces mogelijk mede gerelateerd was aan de hoge predatiedruk in de kolonie en een hoge mate van intra-specifieke interferentie.

In vergelijking met mobiele, migrerende soorten werden sedentaire roofvogels verondersteld kwetsbaarder te zijn voor veranderingen in landgebruik, omdat ze afhankelijk zijn voor hun voedsel en reproductie van territoria die ze het hele jaar bezetten. Om het effect van habitat degradatie op foerageren van een sedentaire soort te onderzoeken, werden 12 ♂ donkere zanghaviken *Melierax metabates* voorzien van een radiozender zodat hun bewegingen konden worden gevolgd (Hoofdstuk 7). Donkere zanghaviken bezetten kleinere territoria in natuurlijk habitat dan in getransformeerd habitat; bovendien gebruikten ze een grotere proportie van hun territorium in natuurlijk habitat. Toch was er geen significant verschil in de foerageerinvestering, uitgedrukt als de afgelegde lijnrechte vluchtafstand tussen foerageerplekken, van zanghaviken in de twee habitats. De selectie van jagende zanghaviken voor relatief hoge bomen en een hoge boomdichtheid, hoge dekking van de struiklaag, en een dichte, hoge graslaag leek gerelateerd aan het optimaliseren van prooibiomassa op de foerageerplekken. Door een hogere graslaag en boomdichtheid binnen territoria in natuurlijk habitat vergeleken met getransformeerd habitat, was de prooivangstfrequentie van zanghaviken in natuurlijk habitat significant lager, mogelijk omdat prooien moeilijker te detecteren en te vangen waren. Prooien in getransformeerd habitat waren echter minder energierijk dan in natuurlijk habitat, waardoor de opbrengst van het foerageren vergelijkbaar was in natuurlijk en getransformeerd habitat. Ondanks de adaptatie van foeragerende zanghaviken aan een veranderend prooiaanbod in gedegradeerd habitat leidt toenemend verlies van vegetatiebedekking tot afnemende foerageermogelijkheden.

Om inzicht te verkrijgen in het belang van omgevingsfactoren die roofvogelpopulaties structureren in West Afrikaanse savannelandschappen, werden habitatassociaties van de Afrotropische en Palearctische roofvogelgemeenschappen onderzocht. De resultaten toonden dat natuurlijk habitat, nationale parken, landbouw, en mensenpopulaties patronen van roofvogelsoortenrijkdom bepaalden op de 5-km ruimtelijke schaal, maar het belang van deze variabelen en de richting van de associaties verschilden tussen soortgroepen en biogeografische zones (Hoofdstuk 8). Hoewel de rijkdom van de Palearctische roofvogelgemeenschap niet gerelateerd was aan getoetste landgebruikvariabelen, was de rijkdom van de Afrotropische roofvogelgemeenschap negatief gecorreleerd met habitatmodificatie en met menselijke populaties in de vloedvlakte en Sudanese savannezones. De soortenrijkdom van Afrotropische roofvogels nam echter toe bij een afname van natuurlijk habitat in de Guinee-savanne zone. Op landschapsschaal gaven analyses van roofvogeldiversiteit en -rijkdom bovendien aan dat het areaal aan beschermd gebied en menselijke exploitatie van het land de biogeografische distributiepatronen van Afrotropische roofvogels in Kameroenese savannes beïnvloedden (Hoofdstuk 10). Ik vond bewijs dat grote roofvogelsoorten gevoeliger waren voor antropogene impact dan kleinere soorten in de relatief intacte Guinee-savanne zone: de soortenrijkdom van grote roofvogels nam af met afstand tot nationale parken, terwijl de soortenrijkdom van kleinere roofvogels negatief gecorreleerd was met de bedekking van natuurlijk habitat. Ook werd in de Guinee-savanne een verschil gevonden in relatie tot mobiliteit: de soortenrijkdom van sedentaire Afrotropische roofvogels nam af met een toename van menselijke populaties, terwijl soortenrijkdom van Afrotropische migranten juist toenam met het areaal landbouwgebied.

Tellingen van roofvogels langs wegtransecten op de Waza-Logone vloedvlakte en op een 2-km schaal (Hoofdstuk 9) bevestigden dat assemblages van Afrotropische roofvogels sterker reageerden op landgebruik dan die van Palearctische migranten: de diversiteit van Afrotropische roofvogels was groter op de natuurlijke vloedvlakte dan op de verdroogde graslanden en in landbouwgebied, terwijl de soortenrijkdom en diversiteit van de Palearctische soortengemeenschap geen relatie met landgebruik lieten zien. De aantallen Palearctische roofvogels waren echter significant hoger op rijstvelden dan op de vloedvlakte en deels gecultiveerde droge graslanden, waarmee het belang van rijstvelden als foerageergebied voor een belangrijk deel van de Palearctische roofvogelgemeenschap werd aangetoond.

Door het belang van de rijke roofvogelgemeenschap op wereldsschaal, en de immense druk van groeiende menselijke bevolking, zouden West Afrikaanse savannes als prioriteitsgebied moeten gelden voor natuurbeschermingsprojecten (Hoofdstuk 10). Hoofdstuk 11 bevat een synthese van de resultaten en tevens aanbevelingen voor beheer van beschermde gebieden en hun bufferzones ten behoeve van de bedreigde roofvogelpopulaties. Het beheer van bufferzones om Nationale Parken zou moeten worden gericht op een beperking van immigratie van mensen, een stop op de uitbreiding van gecultiveerd gebied, en introductie van duurzame katoenteelt. De staat en traditionele autoriteiten zouden een belangrijke rol moeten spelen in het tot uitvoering brengen van dergelijke maatregelen. Gezien hun grote aantrekkingskracht voor Palearctische roofvogels zou beheer van landbouwgebieden rijk aan prooi, zoals rijstvelden, ten gunste van roofvogels extra aandacht moeten verdienen.

Acknowledgements

At first, the research work that makes up this thesis started during weekend days away from the office. Fortunately, I could later continue my research as part of the research program of the Institute of Environmental Sciences (CML) in Cameroon. This would not have been possible without the support of my *copromotor* Hans de Iongh, who granted me time to work on these studies, and later on invested much time and effort in student supervision. I would like to make a special mention of Hans' help, not only in luring materials around when he visited Cameroon, but also allowing me to further develop these raptor studies. I am also extremely grateful to my *promotores*, Jan Komdeur of the Centre for Ecological and Evolutionary Studies at the University of Groningen, for providing such great feedback, support and providing all means possible for a highly fruitful collaboration, and Geert de Snoo of CML, for his valuable suggestions over the course of the study.

This study was financially and logistically supported by CML through its collaborative program with the University of Dschang, Cameroon, at the CEDC. Further financial support was generously provided by the Centre for Ecological and Evolutionary Studies at the University of Groningen, the Dean Amadon Grant of the Raptor Research Foundation, Inc., the Peregrine Fund, and the British Ornithologists' Union.

Many other colleagues were supportive at CML: Gerard Persoon, Paul Loth, Denyse Snelder, Maarten van 't Zelfde, Kees Musters, Patsy Haccou, Wouter de Groot, Wil Tamis, Erik Kien, Ton Brouwer, Annelies Oskam, and Edith de Roos. At Groningen University, I want to especially thank Maurine Dietz for her great help and enthusiasm, Marco van der Velde for genetic analyses, and Gertjan van Dijk, Bernd Riedstra, and Joyce Rietveld for their support and suggestions. At Wageningen University I especially thank Ignas Heitkönig and Frank van Langevelde, and at Utrecht University Max Rietkerk, for taking on student supervision in the Netherlands. I would also like to thank for fruitful discussions, comments and suggestions: Joost Brouwer, Christiane Trierweiler, Franck Noël, Christian Riols, Rob Bijlsma, Paul Scholte, Peter Weesie, Gerard Malan, Simon Thomsett, Michel Louette, Douglas Russell, Alan Kemp, Rob Davies, Bill Clarke, and Munir Virani. Sjoukje Rienks is thanked for suggestions regarding the layout of this book. I thank Wim Mullié for our pleasant collaboration and Jean-Marc Thiollay for accepting my invitation to visit Cameroon in 2007, which was a source of inspiration.

I would like to thank the students who assisted in this study, for their company and hard work: Deborah Winkel, Dirk van der Goes, Ingrid Folkertsma, Jet Salomons, Judith Brouwer, Kim Kortekaas, Leontien Cenin, Lisanne Korpelshoek, Martijn Wagemans, Nikie van Dorst, Ralph van Krimpen, Rien van Wijk, and Saskia van der Zanden. I will not forget how some managed to overcome nasty bacterial infections, malaria, cobras, typhus, heat stroke, broken vehicles *en route*, and the many hours in the baking hot sun, for the benefit of these studies. I am very grateful to all of them.

During my time in Cameroon, I had invaluable support from many people at the Centre for Environment and Development Studies in Cameroon (CEDC), without whom the already

challenging conditions may have been insurmountable. *Un grand merci* goes to Hamidou Hamadou, who was a pleasant and trustworthy person to work with throughout this period. I would further like to thank Jean-Pierre Mvondo, my counterpart at CEDC, who assisted in arranging the necessary permits. I also thank Bachirou Mohamadou, Fatima Damdam, Baba Ila, Jerôme, Ahmadou Abdoulaye, Eric Fotsing, Maurice Zeufack, Stephen Lambi, Roland Ziebe, Haman Unusa, Pricelia Tumenta, Theodore Mayaka, Charles Ndjomaha and Francis Tarla. I thank Saleh Adam, Seini Djobdi, and André Ndjidda of MINFOF, for allowing us to work in the four national parks of northern Cameroon and for arranging the necessary permits.

A special word of thanks goes to Ambassa Linis, Abba Boukar, and Amadé Ali in assisting with much of the daily work in Waza, which was is greatly appreciated. Abba and Amadé were essential in making the Grasshopper Buzzard study a success – their skills and enthusiasm were inspiring.

Finally, I thank my family for their support and for stimulating my passion for nature and raptors in particular. Last, and foremost, I thank my partner Barbara. Without her unconditional devotion to these studies, including many days of hard labour, much of the work presented here would not have been possible.

Curriculum vitae

Ralph Buij was born in Eindhoven, the Netherlands, on 12 February 1976. He started his biology study in 1994 at the University of Utrecht in the Netherlands, where he graduated in 2000. Apart from a short Masters project at the Department of Molecular Genetics, he was involved in a 14-month Masters study on the behavioral ecology of the Sumatran orangutan. He published several papers based on his work on orangutan ecology in Aceh, among others as a visiting scientist at the Behavioral Biology Department of the University of Utrecht and the Department of Biological Anthropology and Anatomy at Duke University, USA.

In 2002 he enrolled in a BSc (Honours) course in wildlife management and conservation at the University of Pretoria, South Africa. He subsequently worked as a consultant in southern Africa in 2003, on the development of natural resource management plans and environmental impact assessments. In 2004-2005, he led a research project for the Smithsonian Conservation Biology Institute, investigating the impact of oil, forestry and mining industry infrastructure on a forest elephant population in the Gamba Complex of southwest Gabon. This study supported the development of a sustainable forest management plan for an industrial corridor between two coastal national parks.

From 2006, he took over the coordination of Leiden University's research program in Africa, at the Centre for Environmental and Developmental studies in Cameroon (CEDC). He was responsible for the supervision of MSc and PhD students focusing on a range of studies, on large carnivores, nomadic pastoralism, wetland management and other natural resource management issues. Important aspects of the position were capacity strengthening of Universities and partnership development at a variety of levels, conservation project acquisition, implementation and management, and (post-)academic course and curriculum development. He initiated work on the studies that form the basis of this thesis in 2007, which included supervision of the research projects of 13 MSc students in Cameroon.