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

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Chapter 4

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

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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 $DB = 1/\sum pi^2$, 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.

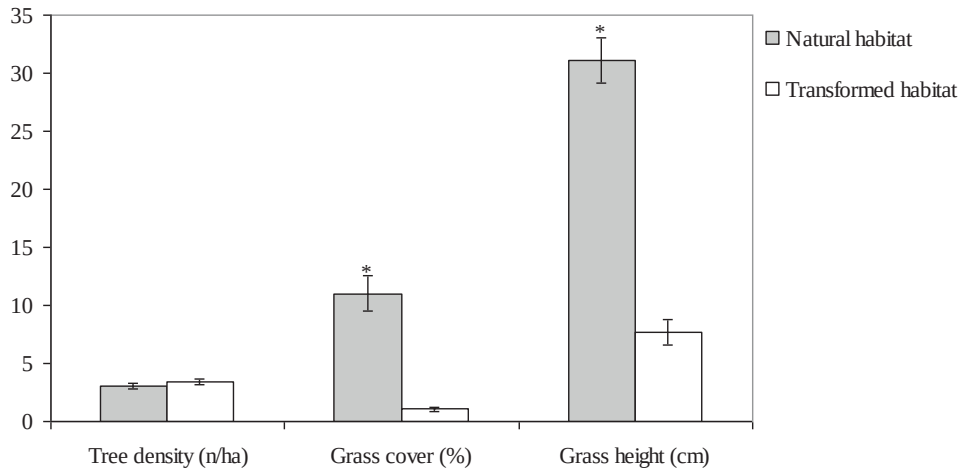

Figure 1. Mean (± S.E.) tree density, grass cover and grass height surrounding Grasshopper Buzzard nests with nestlings in natural (*n* = 62 nests) and transformed habitats (*n* = 63 nests). Asterisks indicate significant differences between habitats (Mann-Whitney *U*-tests; * *P* < 0.001).

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).