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 5

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

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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.

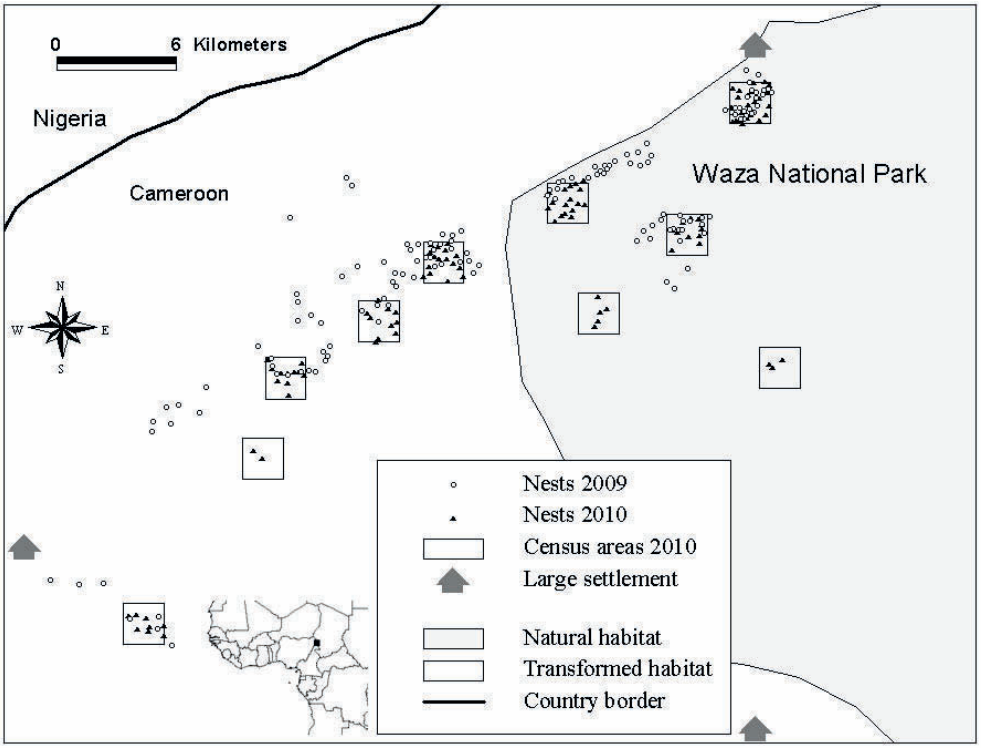

Figure 1. Location of the study area in northern Cameroon (map inserted), including the location of occupied Grasshopper Buzzard nests in 2009 and 2010 and census areas used to examine landscape correlates of nest density in 2010.

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 nests 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.

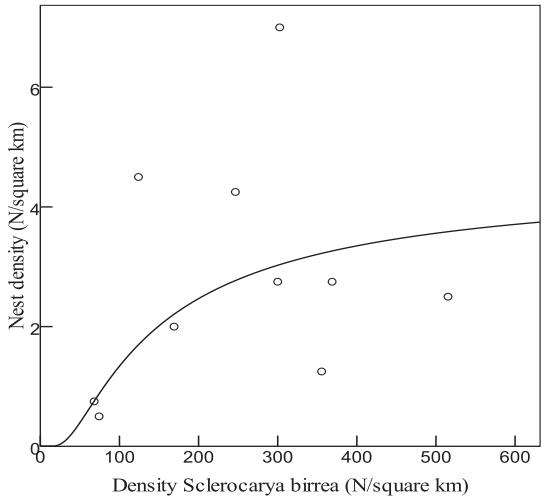

Figure 2. S-curve regression model for nest density and the number of *Sclerocarya birrea* trees ≥ 8 m inside nest census areas (cf. Figure 1 for location census areas).

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: $\chi^2_2 = 39.7$, $P < 0.001$			

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.

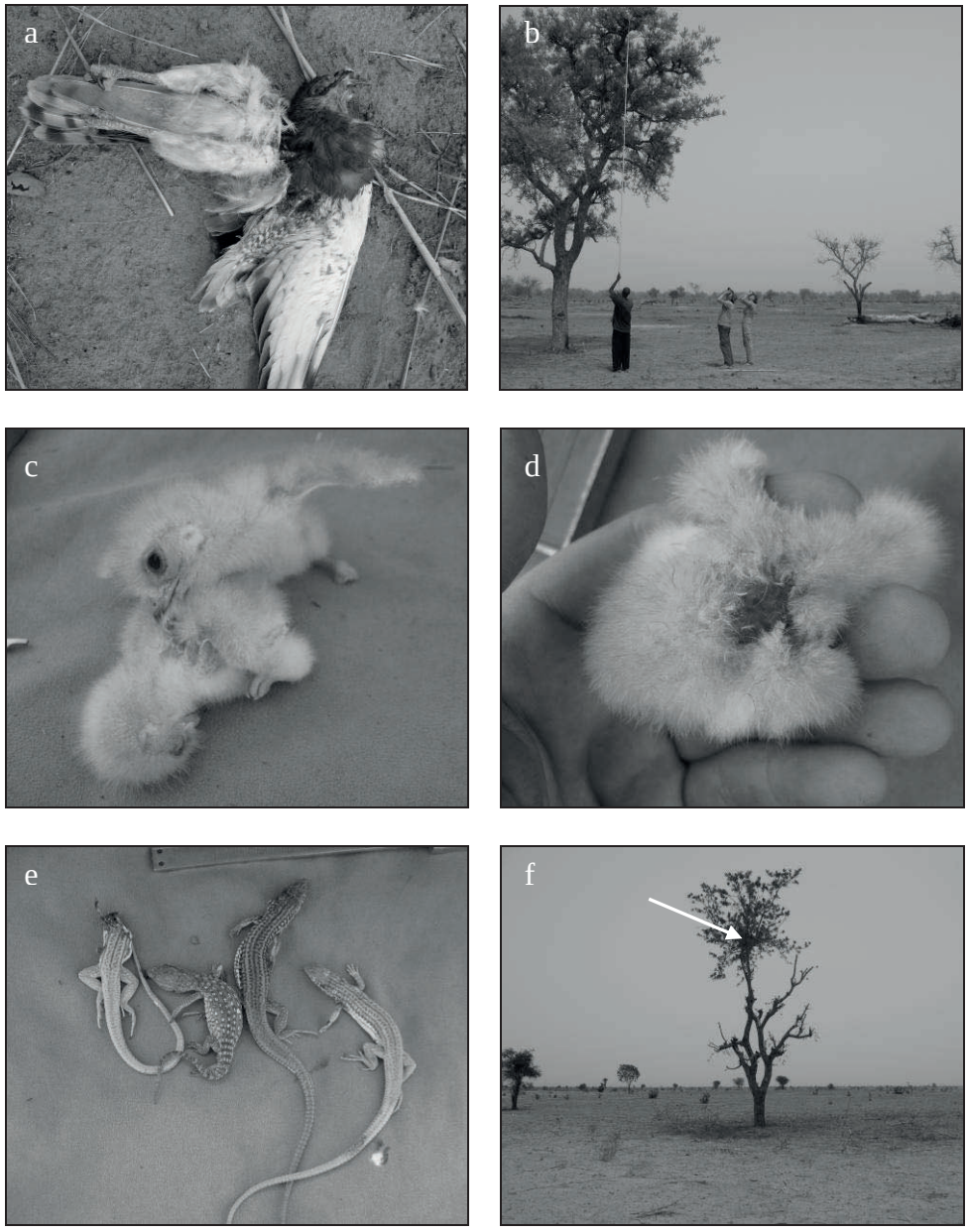

Figure 3. (a) Adult Grasshopper Buzzard killed and partly devoured by small mammalian carnivore in Waza N.P.; (b) technique used for rapid assessment of nest contents: mirror on pole; (c) Cain and Abel struggle between Grasshopper Buzzard nestlings; (d) the youngest of the two nestlings shown in (c) 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.

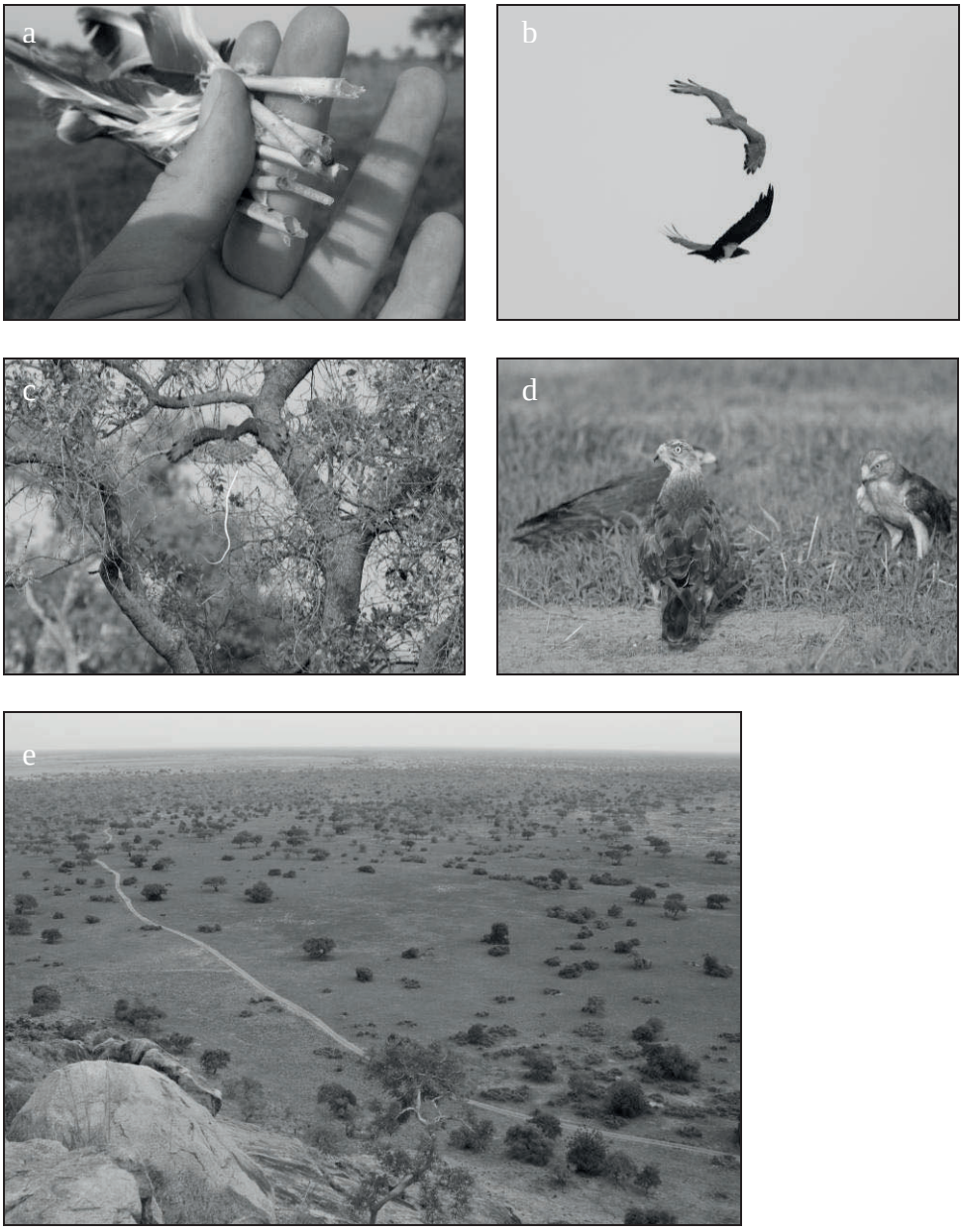

Figure 4. (a) Bitten-off flight feathers discovered underneath and in the nest indicate that a small carnivore killed this Grasshopper Buzzard nestling in Waza N.P.; (b) Grasshopper Buzzard chasing off a Pied Crow; (c) adult Grasshopper Buzzard alighting on the nest with a snake; (d) Grasshopper Buzzards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