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

Buij, R.

Chapter 7

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

Ralph Buij, Nikie van Dorst, Henriëtte F. Salomons, Barbara M. Croes, Maurine Dietz & Jan Komdeur

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	

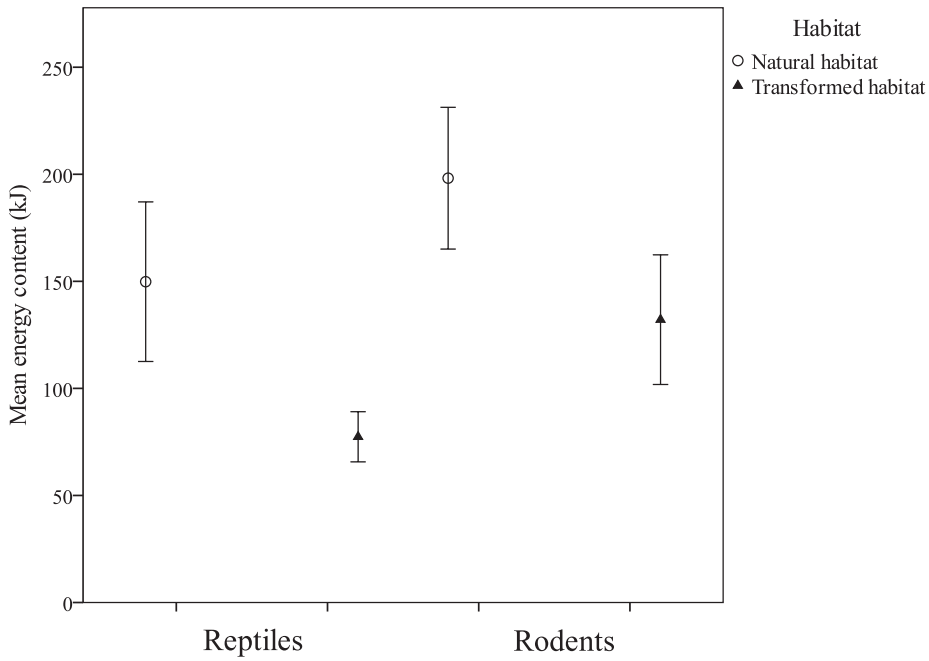

Figure 1. Mean (±S.E.) energy content of reptile and rodent prey items in natural and transformed habitat. Mean energy value of reptiles differed between habitats ($U_{12,32} = 99.0$, Z = -2.48, $P < 0.05$) but not for rodents (t (11) = 1.48, $P = 0.17$).

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