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 2

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

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

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Abstract

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

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

2.1 Introduction

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

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

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

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

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

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

2.2 Materials and methods

Study area

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

Quantifying habitat use by foraging harriers through observation plots

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

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

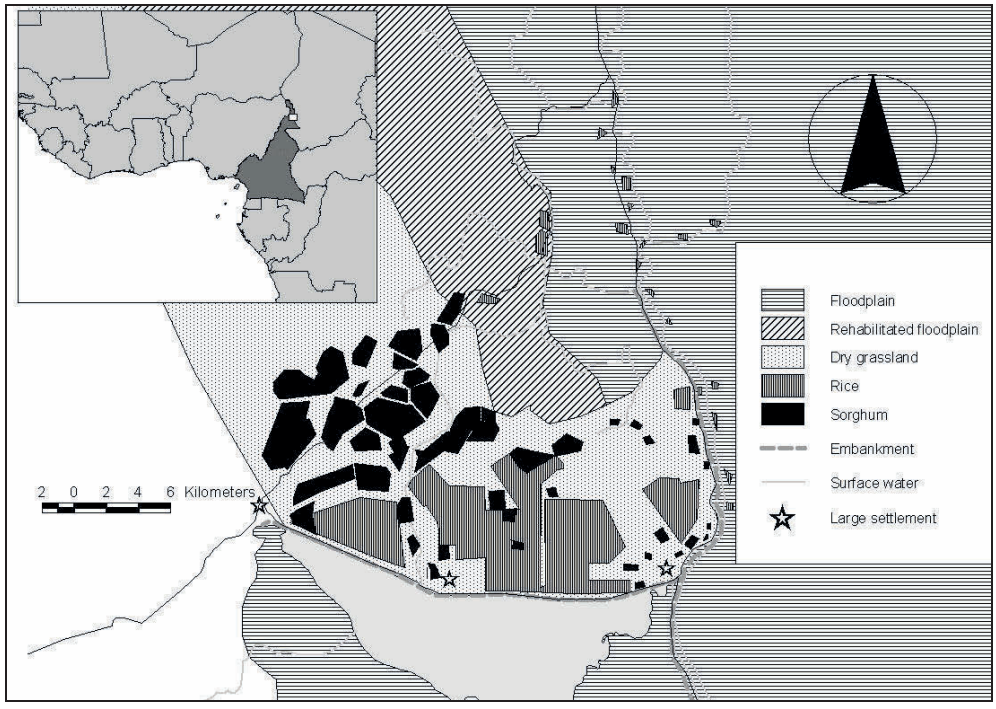

Figure 1. Location of the study area in northern Cameroon, illustrating the main habitat types and the location of the embankment and reservoir created to accommodate irrigated rice cultivation on the Logone floodplain.

Prey abundance

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

Vegetation measurements

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

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

Pellet analyses

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

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

Statistical analyses

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

2.3 Results

Habitat use by harriers

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

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

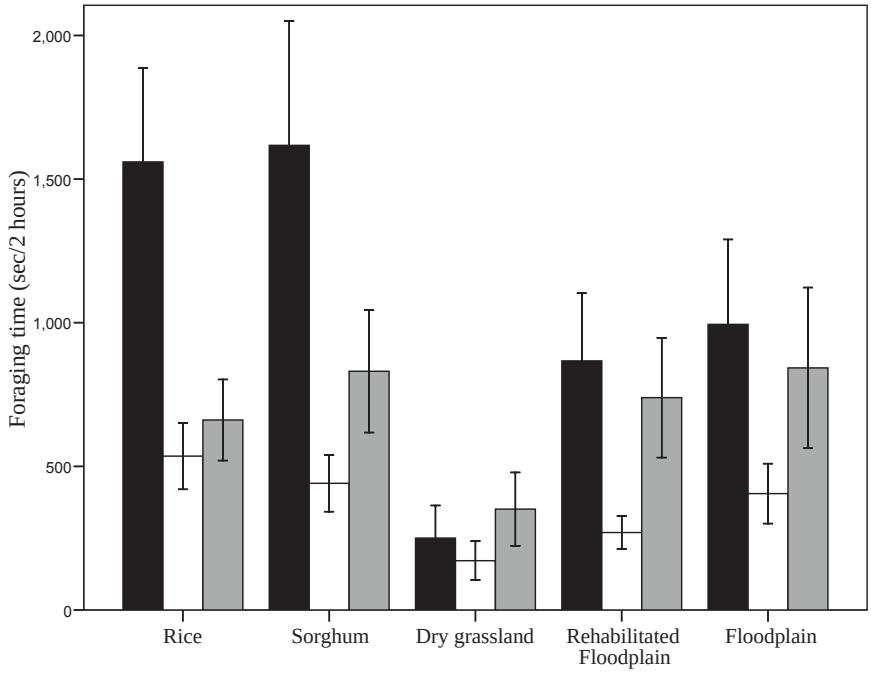

Figure 2. Harrier foraging time by habitat type on observation plots in 2009 and 2010. Foraging time given presence is indicated, for Marsh (black bars; *n* = 92 plots), Pallid (clear bars; *n* = 78), and Montagu's Harrier (grey bars; *n* = 76). Data are mean estimates ±S.E.

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

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

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

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

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

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

Habitat and prey abundance relationship

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

Harrier diet

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

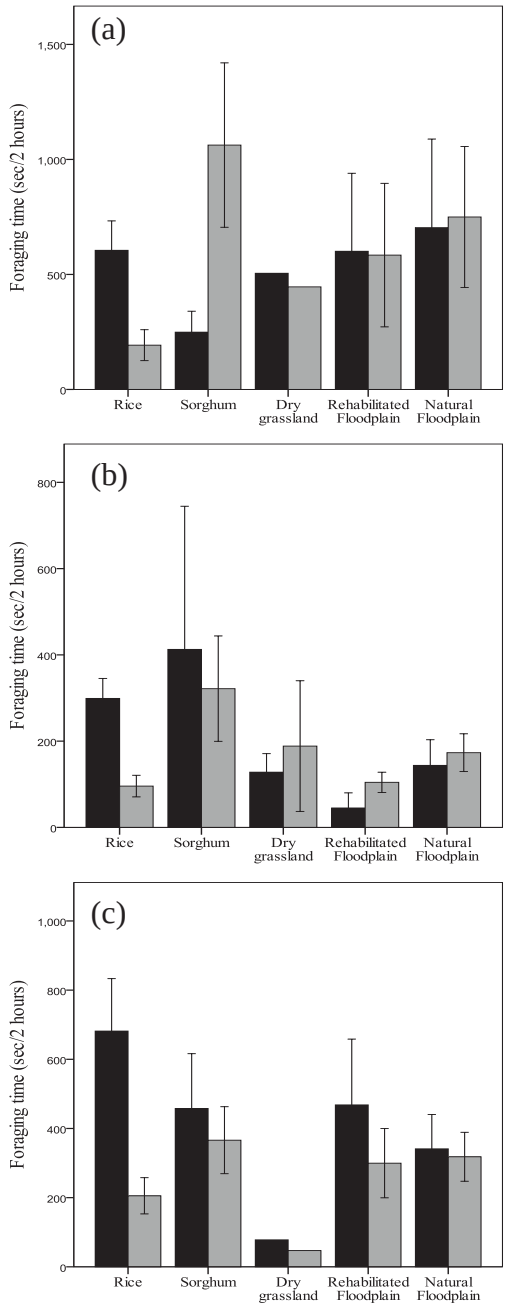

Figure 3. Harrier foraging time by habitat type on observation plots in 2009 and 2010. Foraging time given presence is indicated for female (black bars) and male (grey bars) (a) Montagu's, (b) Pallid, and (c) Marsh Harrier. Data are mean estimates ±S.E.

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

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

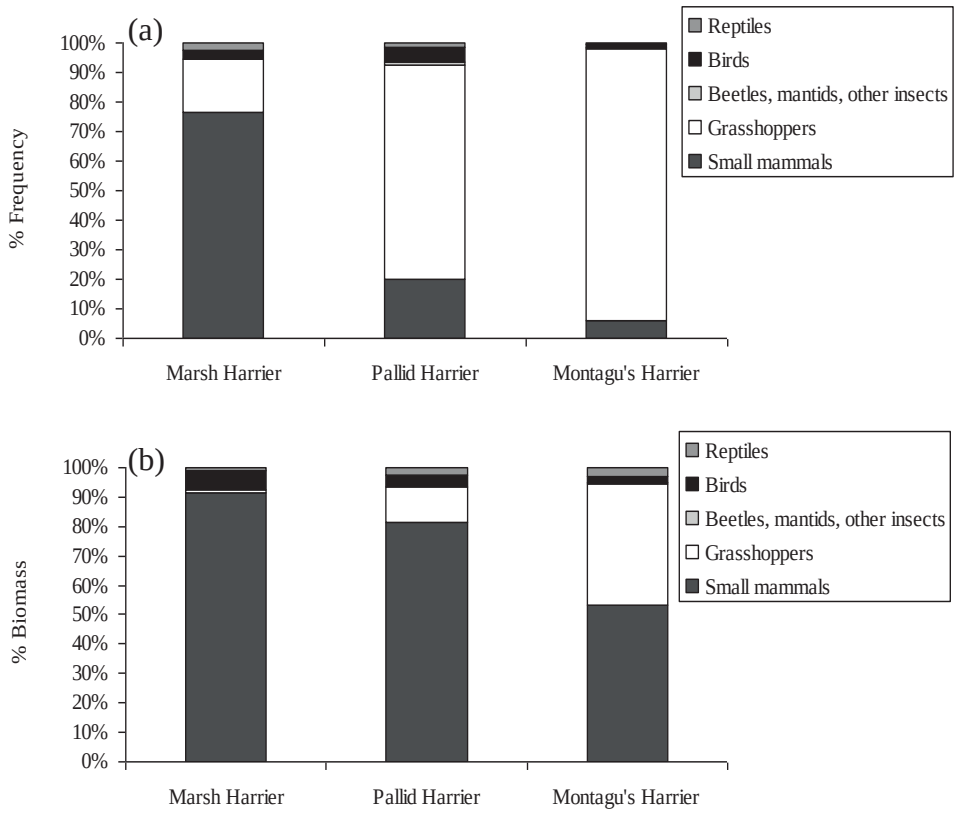

Figure 4. Pellet contents of Marsh Harriers (n = 60), Pallid Harrier (n = 51), and Montagu's Harrier (n = 90) in 2009-2010 in the Logone floodplain of northern Cameroon: (a) prey categories in pellets as percentage of total prey number and (b) as percentage of total prey biomass. Grasshoppers (includes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

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

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

2.4 Discussion

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

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

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

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

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

Conservation implications

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

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

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

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

Appendix to Chapter 2

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

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

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

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

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

Box A

Pallid Harrier bird hunting behaviour and capture success in northern Cameroon

Ralph Buij

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Abstract

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

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

Introduction

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

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

Materials and methods

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

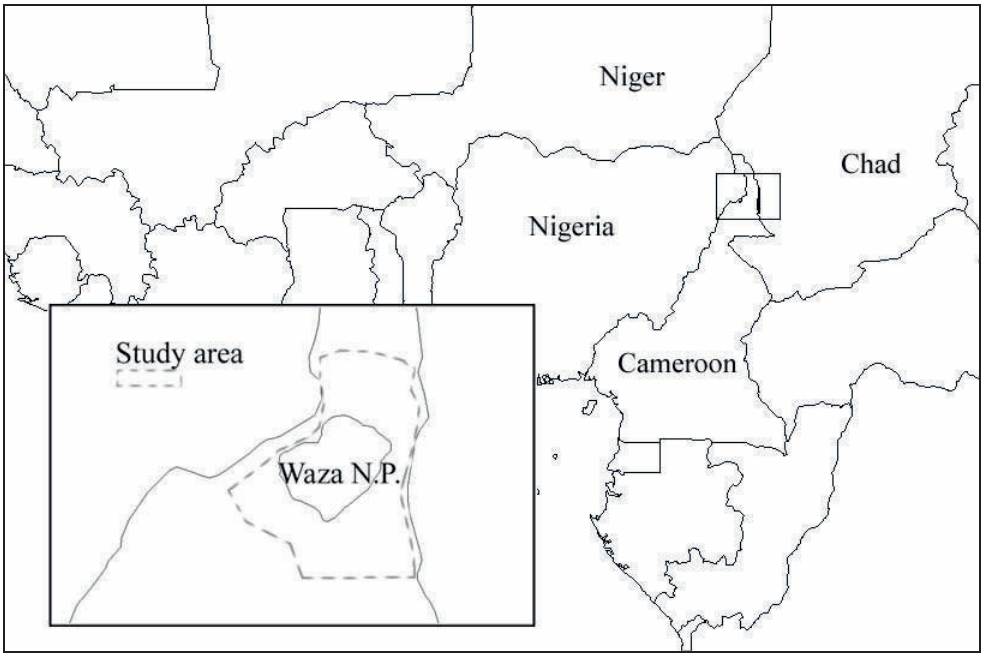

Figure 1. Map of the study area in northern Cameroon.

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

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

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

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

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

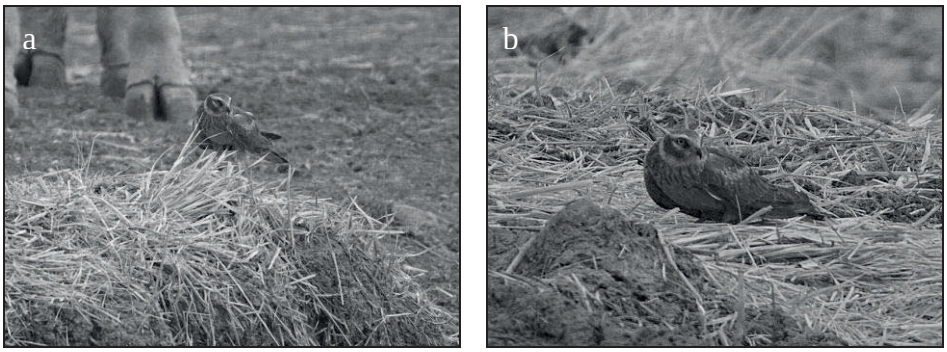

Figure 3. (a) Juvenile male Pallid Harrier waiting for Red-billed Queleas to arrive at a waterhole and (b) crouching at the arrival of a flock of birds at the waterhole

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

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

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

Results

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

Fast contour flight

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

Overt approach with rapid acceleration

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

Covert ambush

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

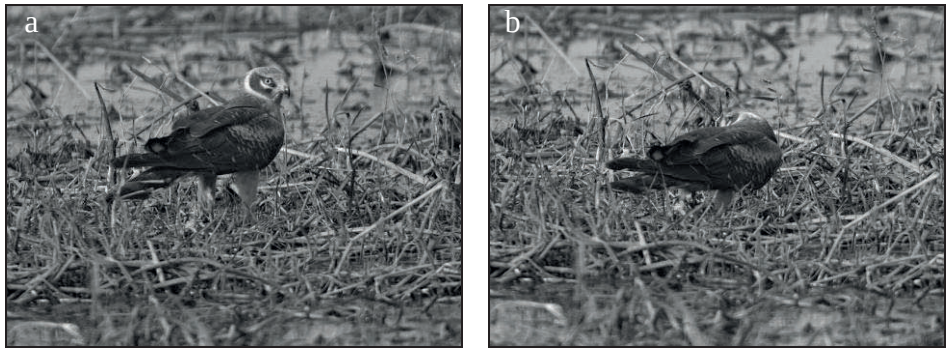

Figure 4. (a) Juvenile male Pallid Harrier scanning for birds while occasionally drinking and (b) crouching as potential prey arrives

Stoop from flight

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

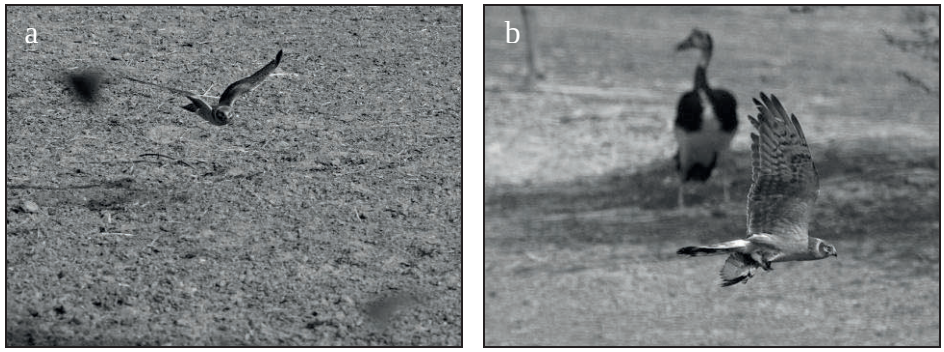

Figure 5. (a) Juvenile male Pallid Harrier in low, fast flight at Red-billed Queleas after covert ambush at a waterhole and (b) departing for cover after having caught a Namaqua Dove at a waterhole

Prey capture success with age and sex

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

Discussion

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

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

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

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

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

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

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

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