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Interspecific and intraspecific differences in habitat use and their conservation implications for Palearctic harriers on Sahelian wintering grounds

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The floodplains of the West-African Sahel region have 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 assess species, sex- and age-related habitat preferences. Sex and age have rarely been incorporated into general studies of raptor habitat associations, despite clear evidence of intrasexual and age-related differences in foraging strategies and diet composition, potentially carrying strong conservation implications. We found evidence of sexual differences in foraging preference related to land use, particularly in the most sexually dimorphic Pallid Harrier, and evidence that juveniles used different habitats to adults. This constitutes the first quantitative documentation of such differentiation by Palearctic raptors on African wintering grounds, indicating that general patterns of habitat use in wintering raptors may obscure sex- and age-specific preferences. Contrary to expectations, we found limited evidence for interspecific foraging segregation. Food partitioning by prey mass was related to harrier body mass and facilitated by a diverse availability of prey on human-transformed floodplains. Anticipated further large-scale conversion of floodplain habitat into predominantly desiccated grasslands raises concerns about the survival of wintering harriers.

Keywords: Africa, age, *Circus* spp., habitat preference, prey size, sex.

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). Severe raptor population declines throughout the Sahel since the 1960s (Thiollay 2006, 2007) coincided with extensive changes in land use, including overgrazing of grasslands, loss of soil and deforestation for agricultural expansion (e.g. Wardell *et al.* 2003, Wood

et al. 2004, Reij *et al.* 2005), suggesting that the winter range of Eurasian raptors has been 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), although trends vary regionally and between species (Thiollay 2001, 2006, 2007), 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,

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and are considered essential for the conservation of Eurasian raptors wintering in West Africa (Thiollay 1989). This is particularly true for the Palaearctic 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 with surrounding dryland savannas (Thiollay 1977a, 1978, 1989, 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 were more than halved by decreased rainfall and the expansion 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 2006). These trends largely reflected the situation on Eurasian breeding grounds (BirdLife International 2010a,b,c), and are likely to have been related to circumstances there rather than climatic conditions in the Sahel (Trierweiler & Koks 2009). However, accumulating evidence suggests that ecological conditions in the Sahel influence survival, breeding output and population numbers of Afro-Palaearctic migrants (e.g. Peach *et al.* 1991, Szép 1995, Schaub *et al.* 2005, Eraud *et al.* 2009), including raptors (Grande *et al.* 2009, Zwarts *et al.* 2009, Mihoub *et al.* 2010).

Raptors frequently exhibit sexually distinct distributional patterns on their wintering grounds, attributed to sex-specific habitat preferences with regard to foraging efficiency and preferred prey type and size (Opdam 1975, Stinson *et al.* 1981, Thirgood *et al.* 2003), or female dominance over males for the best foraging sites (Mills 1976, Bildstein & Collopy 1985, Temeles 1986, 1987). 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 with males (Storer 1966, Schipper 1973, Schipper *et al.* 1975, Kenward *et al.* 1981). 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 & Riley McClelland 1997, Bustamante *et al.* 1997, Kitowski 2003). In spite of the clear intraspecific discrepan-

cies and the important consequences that sex- and age-related differences in habitat use can have on life-history and population regulation (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 the effects of sex and age, potentially biasing estimation towards the more frequently encountered sex- or age-class. For species that exhibit strong intersexual differences in foraging behaviour, lack of discrimination between sex categories could overestimate the importance of habitat features for one sex, while underestimating them for the other (Conde *et al.* 2010).

In order to assess the impact of habitat transformation on Palaearctic harriers, we investigated 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 (Poulet 1985, Adeyemo *et al.* 2005) and grasshoppers in grasslands (Mullié & Guèye 2010). Intersexual differentiation of habitat use is likely under such conditions, as reversed size dimorphism and accompanying morphological differences are marked in harriers (Nieboer 1973, Davygora & Belik 1994, Bavoux *et al.* 2006), leading to differences in energetic requirements (Riedstra *et al.* 1998), foraging behaviour and diets (Schipper *et al.* 1975, Temeles 1986, Fritz *et al.* 2000). Based on previous studies (Schipper 1973, 1977, Bozinovic & Medel 1988, Clarke *et al.* 1993, Marti *et al.* 1993, Kitowski 2003, Garcia & Arroyo 2005), we further expected that differences in body mass would result in interspecific differentiation of habitat use, while differences in morphology and foraging tactics between age groups were also expected to influence habitat use. Therefore, we developed the following predictions: (1) that adult male and female harriers will forage in different habitats which offer differently-sized prey, and this difference will be greatest for the strongly sexually dimorphic Pallid Harrier and less evident for the least sexually dimorphic Montagu's Harrier (cf. Simmons 2000); (2) that large-bodied Marsh Harriers (530–720 g) will consume larger prey items than Pallid (310–440 g) and Montagu's Harriers (265–345 g); (3) that diet overlap will be small

between Marsh and Montagu's Harriers (body mass ratio: 2.0), large for Pallid and Montagu's Harriers (1.2), and intermediate for Marsh and Pallid Harriers (1.7), resulting in interspecific differences in habitat use depending on body mass ratios and preferred prey distribution; and (4) that juveniles will prefer different habitats from adults due to differences in foraging tactics. Based on our findings, we evaluated the impact of changes in land use in the core wintering areas, and consider the implications of future land transformation for population persistence of migratory harriers.

METHODS

Study area

Habitat use was investigated in a c. 800-km² area of the Logone floodplain in northern Cameroon (mean rainfall c. 500 mm), from January to March of 2009 and 2010. Weather conditions between January and March were fairly constant, with temperatures reaching as high as 40 °C in March with 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 ricefields was prevented, resulting in significant changes in vegetation composition and production (Scholte *et al.* 2000), partly recti-

fied by re-opening the dam in the mid 1990s (Loth 2004). Five habitat types were distinguished (Fig. 1): (1) floodplain, seasonally flooded grasslands (August–November) largely devoid of woody plants and dominated by low, perennial grasses, with inundated depressions (surface area 92 km²); (2) rehabilitated floodplain, with a vegetation similar to the pre-dam situation, except for limited recovery of tussock grasses (Scholte *et al.* 2000; 87 km²); (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 km²); (4) sorghum fields, with crops at harvest time, and a vegetation composition and structure similar to dry grassland outside the cultivated fields (56 km²); (5) rice fields, naturally flooded or irrigated between April and November, with rice stubble remaining after harvest between December and March, surrounded by canals with grassy margins and isolated woody plants (79 km²).

Quantifying habitat use by foraging harriers through observation plots

Observations of harrier foraging were conducted from the centre of an observation plot with a 350-m radius, which was the maximum area that

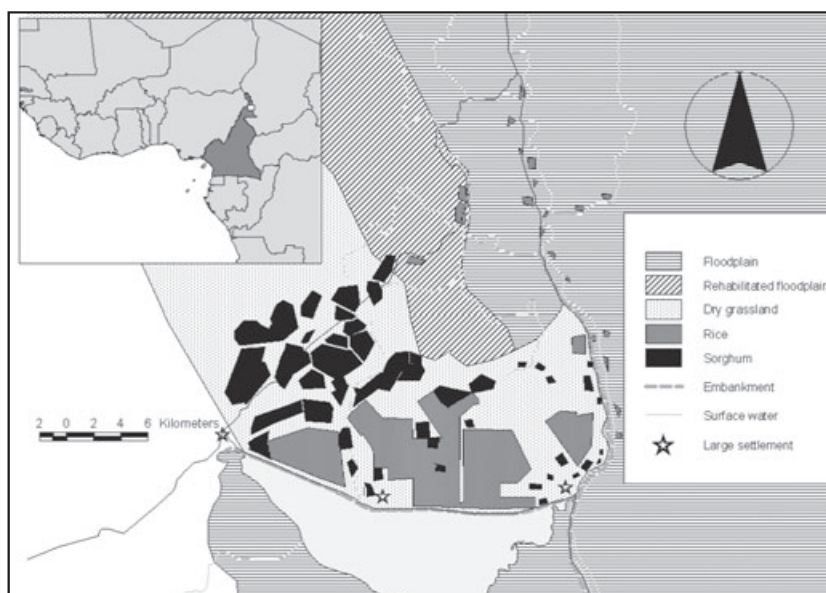


Figure 1. Location of the study area in northern Cameroon, illustrating the main habitat types and the location of the embankment and reservoir created to accommodate irrigated rice cultivation on the Logone floodplain.

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 (ESRI, Redlands, CA, USA) to discern and delineate the major habitat types, which were further validated in the field. Plots were randomly allocated within the delineated habitats using a grid, taking accessibility into account (plots > 5 km from the existing dirt road network were excluded). When visibility in any direction from the centre of the plot was < 350 m, plots were re-orientated in a northerly direction 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 wintering season of Montagu's (Trierweiler *et al.* 2007, Trierweiler 2010), Marsh (Strandberg *et al.* 2008) and Pallid Harriers (Terraube *et al.* 2011) in the Sahel.

Plot watches were randomly rotated among 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 h) and in the late afternoon (15:00–18:15 h). 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 range-finder 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 smouldering. Watches were performed simultaneously by two experienced observers, always including the first author, using 10 × 42 binoculars. To avoid missing harriers flying behind vegetation or at very low altitudes (even in ditches), observations were made from a raised location (termite mound, roof of the car) in the centre of the plot so that observer eye level was at approximately 3 m. During watches, continuous scans for harriers were

made by both observers and as harriers entered the plot, the following were recorded: species, sex, age (juvenile 2nd calendar year (cy), or adult 3rd cy or older; Forsman 1999), entry time and time spent in the plot. Harriers were photographed to 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.

Prey abundance

Abundance measures of small mammals, birds and grasshoppers were recorded for each plot between the dates in which that plot was surveyed for harriers. The relative abundance of small mammals was determined using a custom-made trap design, in which cement powder is flattened in a 30-cm circle centred on c. 20 g of peanut butter bait to allow identification of small mammal tracks. Cement traps were laid out on a rectangular grid (200 × 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 h. Tracks were categorized into diurnal rodents (dominated by Unstriped Grass Rats *Arvicanthis* spp.) and other small, predominantly nocturnal mammals, according to 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 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, starting from a

predetermined fixed compass direction from the centre of the plot. The parallel transect lines were spaced 50 m from each other. Two size-classes of grasshopper (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-h 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 (4 × 250 m) used for grasshopper abundance estimates. On each 250-m transect line, 25 squares measuring 100 m² were sampled at regular intervals for percentage surface cover of the rooted herbaceous layer (grasses including rice, and forbs). The height of the herbaceous layer was measured in a 0.30-m² circle in the middle of each square using a 2-m stick (cm-scale). The mean herbaceous layer height and cover estimates derived from 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 analysis

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 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 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. Prey remains (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, Niamey, Niger).

The frequency by number of prey in each of five main prey categories (small mammals, grasshoppers and crickets, other arthropods, birds, reptiles) was estimated by dividing the number of prey in the prey category by the total number of prey items identified from the pooled 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 the diet by their estimated mean biomass. Average adult mass was available for grasshoppers and crickets (Mullié & Guèye 2010; W.C. Mullié *in litt.* 2010) 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 (only a Red-billed Quelea was identified to species level 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 to 2010 was used to calculate bird prey mass (R. Buij, unpubl. data). For Montagu's Harriers, 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 tracking 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-km² area of the Waza–Logone floodplain in a period of several weeks in the winter of 2007/2008 and 2008/2009, incorporating the entire study area and all major habitat types (Dutch Montagu's Harrier Foundation, unpubl. data). Therefore, we assume that the pellet analysis provided a representative sample of the local diet, governed mostly by large-scale prey preferences rather than habitat directly surrounding the roost.

Statistical analysis

Analyses were performed using R (package *car*) and SPSS version 16.0 (SPSS Inc., Chicago, IL, USA). 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 analysed separately for each species and summed for the 2-h 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 analysed harrier foraging data in plots using a two-step 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; and second by modelling 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 foraging time data (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 assess inter-annual 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 correlation coefficients. Kruskal–Wallis tests were used to assess differences between the five main habitat types in 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 assess 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 assess differences in the prey biomass between the three species. Pianka's (1973) Index was used to quantify diet overlap between the harrier species using the percentage frequency by number of the five main prey categories in the diet. For all analyses, tests are two-tailed and statistical significance was accepted 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).

RESULTS

Habitat use by harriers

The cumulative harrier foraging time in 100 plots was 49.2 h 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). Harrier foraging presence differed between habitat types for Pallid Harrier ($\chi^2_4 = 14.6$, $n = 100$, $P < 0.01$) and Marsh Harrier ($\chi^2_4 = 10.9$, $n = 100$, $P < 0.05$), but none of the habitat types contributed significantly to the models ($P > 0.05$). Presence was unaffected by habitat type for Montagu's Harrier ($\chi^2_4 = 5.03$, $n = 100$, $P = 0.28$). Harrier foraging time given presence (Fig. 2) differed between habitat types for Marsh ($\chi^2_4 = 25.3$, $n = 92$, $P < 0.001$) and Montagu's Harrier ($\chi^2_4 = 9.87$, $n = 76$, $P < 0.05$), which foraged significantly less over dry grasslands than other habitat types, but not for Pallid Harrier ($\chi^2_4 = 4.97$, $n = 78$, $P = 0.29$). Significant habitat preferences were recorded for sex and age-classes of all three species based on presence data (Table 1) and time given presence (Table 2).

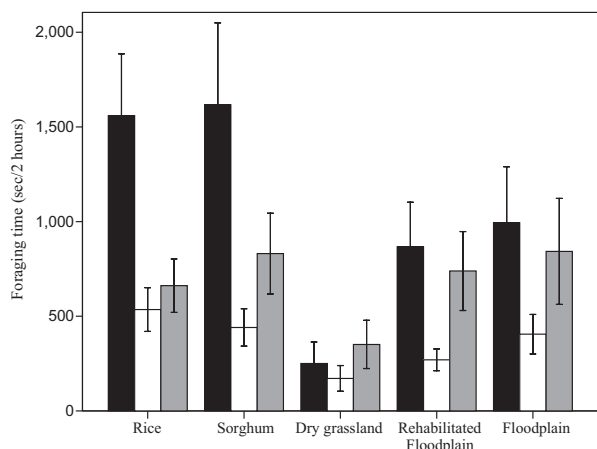


Figure 2. Harrier foraging time by habitat type on observation plots in 2009 and 2010. Mean foraging time given presence is indicated, for Marsh (black bars; $n = 92$ plots), Pallid (clear bars; $n = 78$) and Montagu's Harrier (grey bars; $n = 76$). Data are mean estimates \pm se.

Habitat and prey abundance relationships

Strong relationships were recorded between the main prey categories and habitat types (Table 3). Inter-annual differences were not apparent for prey and habitat variables ($P > 0.05$) except for mean grass cover, which was lower on plots in 2010 compared with 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 of biomass to the diet were small mammals, grasshoppers and birds (Fig. 3). Grasshopper species in the medium (e.g. *Acorypha clara*) and large (e.g. *Ornithacris cavroisi*) size-classes were recorded in pellets of all three species, large species (*Ornithacris cavroisi*, *Acanthacris ruficornis*) constituting the bulk of the grasshoppers identified (75.7%, $n = 214$). Small mammals included diurnal rodents, such as Unstriped Grass

Rats, which comprised the majority of identified small mammals in pellets of Marsh Harriers (100%, $n = 35$), Pallid Harriers (80.0%, $n = 15$) and Montagu's Harriers (78.6%, $n = 14$), and nocturnal small mammals, such as White-toothed Shrews *Crocidura* spp. and Zebra Mice *Lemniscomys* spp. No significant differences in the percentage frequency of the main prey categories (small mammals, birds, reptiles, grasshoppers and other insects) were noted between years for Marsh Harrier ($\chi^2_4 = 9.81$, $P = 0.26$), Pallid Harrier ($\chi^2_4 = 7.42$, $P = 0.13$) or Montagu's Harrier ($\chi^2_4 = 9.01$, $P = 0.27$). The same was true for pellets collected in January and March–April (Marsh: $\chi^2_4 = 5.82$, $P = 0.35$; Pallid: $\chi^2_4 = 5.41$, $P = 0.25$; Montagu's: $\chi^2_4 = 3.03$, $P = 0.58$). Mean biomass of prey consumed by Montagu's Harriers (4.97 ± 0.56 g, $n = 610$) was lower than the mean prey biomass of Pallid (13.4 ± 2.38 g, $n = 139$; $U_{610,139} = 21\,996$, $z = -9.94$, $P < 0.001$) and Marsh Harriers (68.8 ± 5.80 g, $n = 61$; $U_{61,610} = 1472$, $z = -13.8$, $P < 0.001$). The mean prey biomass of the latter two also differed significantly ($U_{61,139} = 1278$, $z = -8.10$, $P < 0.001$).

According to Pianka's (1973) Index for the five main prey categories, dietary overlap 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. The percentage contribution of the different prey categories to the diet differed, however, between Montagu's and Pallid Harriers ($\chi^2_4 = 107.1$, $P < 0.001$), Montagu's and Marsh Harriers ($\chi^2_4 = 2074.2$, $P < 0.001$), and Pallid and Marsh Harriers ($\chi^2_4 = 323.6$, $P < 0.001$).

DISCUSSION

Our results illustrate significant differences in the habitat preferences of male and female harriers, notably in the most sexually-dimorphic Pallid Harriers, but also in Marsh and Montagu's Harriers. This confirms our predictions and earlier findings from temperate regions (Schipper *et al.* 1975, Temeles 1986, Fritz *et al.* 2000) and constitutes the first quantitative documentation of such differentiation by Palaearctic raptors on African wintering grounds. Male Montagu's and Pallid Harriers avoided rice fields, which supported large concentrations of relatively heavy diurnal rodents (> 100 g), whereas females of both species preferred rice fields to flooded grassland in terms of

Table 1. Logistic regression of harrier presence/absence 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 (northern Cameroon, $n = 20$ plots per habitat type).

	<i>B</i>	<i>se</i>	Wald	<i>P</i>
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
$\chi^2 = 23.5$, $df = 4$, $n = 100$, $P < 0.001$				
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
$\chi^2 = 8.74$, $df = 4$, $n = 100$, $P = 0.07$				
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
$\chi^2 = 7.21$, $df = 4$, $n = 100$, $P = 0.13$				
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
$\chi^2 = 23.4$, $df = 4$, $n = 100$, $P < 0.001$				
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
$\chi^2 = 12.2$, $df = 4$, $n = 100$, $P < 0.05$				
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
$\chi^2 = 9.90$, $df = 4$, $n = 100$, $P < 0.05$				
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

Table 1. (Continued).

	<i>B</i>	<i>se</i>	Wald	<i>P</i>
Constant	2.20	0.75	8.69	< 0.001
$\chi^2 = 33.3$, $df = 4$, $n = 100$, $P < 0.001$				
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
$\chi^2 = 16.5$, $df = 4$, $n = 100$, $P < 0.01$				
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
$\chi^2 = 8.54$, $df = 4$, $n = 100$, $P = 0.07$				

Statistics at the bottom of each model indicate overall model fit. $df = 1$ for Wald Chi-square tests. Bold type indicates variables that contribute significantly to the predictive ability of the model. The reference habitat type is floodplain.

foraging presence and effort (i.e. time spent foraging). 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 female preference for rice fields compared with sorghum, whereas male foraging was geared toward smaller prey items (< 40 g; small mammals, large grasshoppers) relatively uncommon in rice fields. Sexual differences in habitat use were also evident in Marsh Harriers, as females significantly preferred rice fields and floodplain over other habitats, whereas males only avoided dry grasslands.

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. However, frequent observations of loosely associated foraging parties of different species, sex and age-classes (pers. obs.) suggest that opportunistic cuing on the presence of other harriers might be more common than avoidance or exclusion. We tentatively conclude, therefore, that sexual differences in preference for food, driven by energy needs (Nagy 1987, 2005), and coupled to potential differences in foraging abilities

Table 2. Generalized linear model of harrier foraging time for each of nine sex and age categories given presence on observation plots on the Logone floodplains (northern Cameroon) in 2009 and 2010.

	<i>B</i>	<i>se</i>	Wald	<i>P</i>
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
Floodplain	0	-	-	
$\chi^2 = 1.41$, <i>df</i> = 4, <i>n</i> = 32, <i>P</i> = 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
Floodplain	0	-	-	
$\chi^2 = 11.1$, <i>df</i> = 4, <i>n</i> = 51, <i>P</i> < 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
Floodplain	0	-	-	
$\chi^2 = 9.02$, <i>df</i> = 4, <i>n</i> = 54, <i>P</i> = 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
Floodplain	0	-	-	
$\chi^2 = 12.9$, <i>df</i> = 4, <i>n</i> = 40, <i>P</i> < 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
Floodplain	0	-	-	
$\chi^2 = 3.53$, <i>df</i> = 4, <i>n</i> = 43, <i>P</i> = 0.47				
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
Floodplain	0	-	-	
$\chi^2 = 1.32$, <i>df</i> = 4, <i>n</i> = 53, <i>P</i> = 0.86				

Table 2. (Continued).

	<i>B</i>	<i>se</i>	Wald	<i>P</i>
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
Floodplain	0	-	-	
$\chi^2 = 3.31$, <i>df</i> = 4, <i>n</i> = 61, <i>P</i> = 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
Floodplain	0	-	-	
$\chi^2 = 13.5$, <i>df</i> = 4, <i>n</i> = 71, <i>P</i> < 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
Floodplain	0	-	-	
$\chi^2 = 15.4$, <i>df</i> = 4, <i>n</i> = 78, <i>P</i> < 0.01				

Statistics at the bottom of each model indicate overall model fit. *df* = 1 for Wald Chi-square tests. Bold type indicates variables that contribute significantly to the predictive ability of the model. The reference habitat type is floodplain.

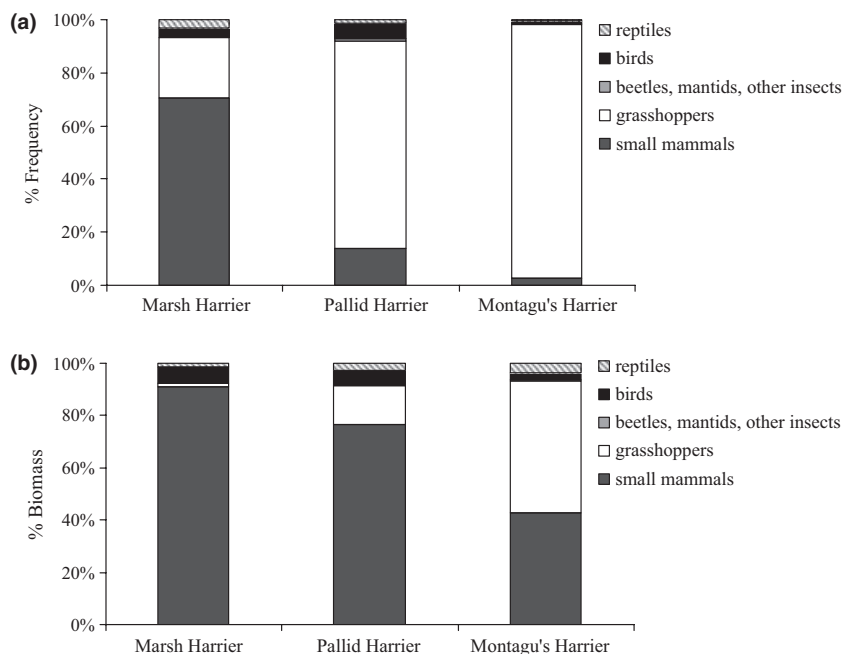
(Schipper *et al.* 1975, Davygora & Belik 1994, Clarke 1996), may have promoted the observed patterns of habitat use.

In contrast to adults, the preference for cultivated fields by juvenile Pallid and Marsh Harriers lent support to our prediction that juveniles exploited different habitats, assuming juvenile populations were approximately equally sex-balanced. It appears that the juveniles used cultivated fields as their high densities of profitable prey (i.e. diurnal rodents) were easily detected due to the limited vegetation cover (Preston 1990), as observed in juvenile raptors elsewhere (Bustamante *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 (R. Buij, unpubl. data), as such clues may guide foraging in juveniles (Ellis *et al.* 1993, Kitowski 2009, Biondi *et al.* 2010).

Table 3. Prey abundance in harrier observation plots within the five major habitat types in the Logone floodplains (northern Cameroon).

Prey type	Rice (<i>n</i> = 20)	Sorghum (<i>n</i> = 20)	Dry grassland (<i>n</i> = 20)	Rehabilitated floodplain (<i>n</i> = 20)	Floodplain (<i>n</i> = 20)	χ^2_4	<i>P</i>
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	10.70 ± 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

Abundance estimates of 'diurnal rodents' and 'nocturnal small mammals' are the proportion of traps with positive signs 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. Results of Kruskal–Wallis tests examining differences in prey abundance across habitats are presented. Letters (a, b, c) indicate significant differences (*P* < 0.05) between the habitats after pairwise comparisons using Mann–Whitney *U*-tests adjusted by sequential Bonferroni correction. Data are presented as means ± se.

**Figure 3.** Pellet contents of Marsh Harriers (*n* = 60 pellets), Pallid Harriers (*n* = 51) and Montagu's Harriers (*n* = 90) in 2009–2010 in the Logone floodplain of northern Cameroon: occurrence of main prey categories in pellets (a) as a percentage of total prey number and (b) as a percentage of total prey mass.

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. However, 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. As expected, partitioning of prey type was most evident between the species that differ most in size (i.e. Marsh and Montagu's Harrier), with high overlap between the species differing only slightly in size (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 in the Pallid Harrier diet (Appendix 1). However, we suspect this did not significantly affect diet analyses, 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 (e.g. most likely towards females and males for Marsh and Montagu's Harriers, respectively: Appendix 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 was marked in wintering harriers and that it was 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 (September–December) when prey is less patchily distributed and prey numbers are higher (e.g. grasshoppers, Mullié & Guèye 2010).

Conservation implications

Our observations suggest that patterns of habitat use in wintering raptors may be obscured by sexual 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 frequent sex or age-biased composition of non-breeding harrier populations (Thiollay 1977b, Stronach 1991, Arroyo *et al.* 1995, Clarke 1996), 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.* 1995, Trierweiler & Koks 2009, this study). The comparable use of natural floodplain and cultivated habitats suggests that floodplain embankments enabling rice and sorghum cultivation are not necessarily disadvantageous to harriers. In fact, population explosions of diurnal rodents following cultivation appear to be a rather

positive development 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 prey heterogeneity suggests that floodplain development may facilitate coexistence of large numbers of harriers. However, the avoidance of the newly created dry grasslands and rice fields by male Pallid and Montagu's Harriers, and dry grasslands by both sexes of the Marsh Harrier, indicates that floodplain development also has important negative consequences. The dry grasslands are avoided despite largely comparable prey populations to the flooded grasslands, possibly because of the poor access to prey in overgrazed, bush-encroached grasslands, where rodent and grasshopper prey may seek protection from heat and predators in the dense shrubs (Chappell & Whitman 1990, Harrison & Fewell 1995, Manson & Stiles 1998). We recorded positive relationships between grasshopper numbers and both woody plants and grass height, and between small mammals and woody plants, indicating that overgrazing and vegetation clearance negatively affected 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), while limited access of livestock protects the often marginal vegetation cover in cultivated fields until harvest time. Conversely, the high grazing pressure on dry grasslands is intensified by accessibility early in the dry season and by 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), and declines in prey populations (e.g. Fielding & Brusven 1995, Herremans & Herremans-Tonnoeyr 2000, Fabricius *et al.* 2003, Blaum *et al.* 2007) to the detriment of harriers.

The avoidance by harriers of dry grasslands is particularly important given that the area of productive floodplain habitat converted into this habitat is much larger than the area converted into rice fields. 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, leading to a large expansion of the dry, unproductive grasslands

(Loth 2004, Scholte 2005). This increase of dry grasslands at the expense of flooded grasslands thus constitutes the most important negative consequence of floodplain development for harriers. In addition to the detrimental effect of lost floodplain habitat, the often unregulated utilization of highly hazardous pesticides in rice fields is a potential threat to harriers attracted to their high rodent numbers (Mullié *et al.* 1991, Keith & Bruggers 1998).

Our results suggest 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 in order to satisfy the increasing demand for rice. 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 prompt further increases, especially of 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). The anticipated further large-scale loss of floodplain habitat, coupled with the risks of unregulated utilization of highly hazardous pesticides, raises 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.

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APPENDIX 1

Harrier pellet samples. Information on pellets collected at roost sites of Montagu's, Pallid and Marsh Harriers from January to 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 intact 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.

Species	Number of roost sites	Mean max numbers per roost (range)	Pellets collected	Pellets analyzed	Habitat	% Adult male (range)	% Adult female (range)	% Unsexed juvenile (range)
Montagu's Harrier	3	22 (9–42)	> 500	90	Dry grassland, sorghum	59 (45–73)	20 (15–22)	21 (19–33)
Pallid Harrier*	4	7 (1–15)	51	51	Rice, dry grassland, floodplain	17 (7–25)	10 (5–15)	73 (65–88)
Marsh Harrier†	2	43 (25–60)	255	60	Rice, floodplain	19 (14–23)	Unknown	Unknown

*The large roost was also visited by five male (two adults/three juveniles) Montagu's Harriers.

†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

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.

Species	2009						2010					
	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