

Winter spatial distribution of threatened acridivorous avian predators: Implications for their conservation in a changing landscape



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ABSTRACT

The Montagu's Harrier (MH) and the Lesser Kestrel (LK) are two threatened raptors overwintering in the Sahel. To ensure their conservation, it is essential to gain better knowledge on their winter ecology in order to predict their spatial distribution and estimate their respective population sizes. Combining information on raptors, their prey and habitats, collected over the 2009–2013 period in a 17,000 km² study area located in central Senegal, we assessed spatio-temporal variations of grasshopper density, and consequently estimated the abundance and distribution of MHs and LKs. The distribution of grasshoppers highlighted areas with contrasted densities, declining along a North East/South West gradient which constrained the spread of raptors. Moreover both species selected heterogeneous landscapes of savannah, mixing semi-natural and anthropogenized habitats. Population size reached 3360 and 36,000 individuals for MH and LK, which represents ~5% and 50% of their European breeding populations. The challenge for their conservation resides in their use of habitats suffering from anthropogenic perturbations, both during breeding and wintering. In Africa, this situation will be exacerbated in the near future due to interactions between food security, implying the control of grasshopper outbreaks and agricultural intensification, and to ongoing climate changes.

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1. Introduction

Within the Palearctic-Africa region, more than 25% of bird species breeding in Europe overwinter in the Sahel (Jones et al., 1996). Several studies have shown a severe decline of these Long Distance Migrant (LDM) bird species (e.g. Thiollay, 2006; Sanderson

et al., 2006). LDM birds migrate several thousand kilometres through contrasting landscapes to finally settle for almost half a year in remote areas where knowledge about their ecology is often scarce or lacunar (Walther et al., 2011). Until recently, studies focussing on European LDM birds concentrated almost exclusively on environmental conditions met by these birds on their European breeding grounds without accounting for migration or wintering. It has been shown, however, that environmental changes along migratory routes or in wintering areas may affect LDM birds through carry-over effects (e.g., Nevoux et al., 2008). Without a global approach considering both the threats in Europe and the biological and sociological factors shaping habitat suitability in wintering areas, the conservation of LDM species may be vain (Cimon-Morin et al., 2013).

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The Sahel currently faces unprecedented habitat changes induced by the development of human population and economic activities. This area, characterized 50 years ago by preserved traditional habitats, now sees the emergence of a more intensive agriculture in response to demographic constraints and needs to stabilize food resources (Powell and Williams, 1993). This has led to profound, though spatially heterogeneous, changes in the western African landscape structure. On the one hand, large areas of savannah and forest are cleared for fuel wood and converted into crop fields, or into intensively grazed areas. On the other hand, the use of chemicals, and notably pesticides, increases in order to control pests (Reij et al., 2005). Moreover, these modifications are happening concomitantly with climate changes that may lead to increased environmental alterations (Mihoub et al., 2010).

Among raptors breeding in Europe, about half are trans-saharian migrants (Gensbol, 2005) that overwinter south of the Sahara, in the Sahel (Anadon et al., 2010) or tropical Africa. Of these, most are exhibiting long-term declines supposedly originated from global changes in this region (Grande et al., 2009). Among them, two acridivorous species, the Montagu's Harriers (*Circus pygargus*; hereafter MH) and the Lesser Kestrel (*Falco naumanni*; hereafter LK) have been particularly well studied in their breeding grounds, notably in Spain, France and in the Netherlands (e.g., Arroyo and Garcia, 2002; Serrano et al., 2001; Millon et al., 2008). Recent developments in tracking systems have also greatly improved our knowledge on their migration routes and stop-over areas (Limiñana et al., 2012a; Catty et al., 2010), but we still know very little about their wintering ecology in the Sahel region.

In particular, being able to precise the relationships between environmental covariates and the abundance of birds is a crucial step towards *i* an accurate estimation of population size and *ii* the identification of hotspots, the latter being essential for planning conservation strategies. Current available estimates of the population wintering in Senegal for MH and LK are based on the counting of known roosting sites. However, these numbers are limited to the knowledge of these sites, which might lead to underestimating population size and as a consequence the importance of the area for the conservation of the species. We propose to refine these estimates by improving the knowledge of the wintering ecology of these two trans-saharian migrant raptors, using transect data collected in the field over a five years period (2009–2013). We first describe the composition in terms of sex and age-classes of these two wintering populations and investigate potential sex- or age-related biases in habitat use. Combining distance sampling observations (Buckland et al., 1993), grasshopper densities estimated from field counts and landscape data, we then assess the links between these two predator species, their main food resources and landscape structure in a more restricted area known to host large numbers of birds in important roosting sites (Mullié and Guèye, 2010). We developed a spatio-temporal model of grasshopper abundances over the study area based on field observations and a set of environmental covariates. Predictions issued from this model were then injected, along other relevant variables into a spatially explicit raptors abundance model, based on our distance sampling scheme thanks to a recently improved method, the density surface modelling (hereafter DSM, Miller et al., 2013). From the predicted abundances of the DSM models over our study area, we were able to estimate the population sizes of MH and LK, and to compare them to roost-based population estimates. We finally discuss the importance of this area for their conservation, and the future challenges that will need to be tackled in those fast changing landscapes.

2. Materials and methods

2.1. Study area

Our study area covers ~17,000 km² (14°14'N, 15°56'W, Fig. 1a and b). It is part of the Sahel region, which encompasses a band between isohyets 150 and 700 mm across Africa (Lebel and Ali, 2009). The climate is semi-arid, with a rain season occurring between June and October (Lebel and Ali, 2009). Temperatures during the studied period (January–March) ranged from 25 to 35 °C (max. 50 °C). The landscape is mainly composed of bush, ranging from herbaceous to woody savannah. The northern part is a mix of cropland dominated by groundnut (*Arachis hypogaea*) and millet (*Pennisetum glaucum*) production, with large areas of fallow and savannah. The intermediate part (Kousmar area), is characterized by shrubby or woody savannahs and intermediate formations of shrubby steppes alternating with halophytic grasslands and wetlands (details in Mullié and Guèye, 2010). In the South, areas of wooded savannas and bushlands have been converted into agricultural fields, mostly dedicated to groundnut and millet, sorghum (*Sorghum bicolor*) and maize (*Zea mays*) production, where fallows are extremely limited (see Tappan et al., 2000).

2.2. Distribution of Montagu's Harrier and Lesser Kestrel

To estimate the densities of MH & LK we applied a line transects sampling method, centred on known major roosting sites (Fig. 1a). Transects were monitored with 4-wheel drive cars on bush trails at constant speed (~25 km h⁻¹), with one driver and three observers (one in front and two at the rear on each side). A total of 143 tracks, cumulating to 9331 km, travelled during the 2010–2013, from January to early March; 2009 being a trial year, it was discarded for density estimations. The mean daily length of transects was 34 km (see Appendix A for a summary) and each transect was georeferenced. Transects were driven either outwards from or inwards toward roosting sites, and were started ~90 min after the birds had left the roosts (08.30 GMT) in order to leave them enough time to spread over the study area.

Each MH or LK observation was directly georeferenced in a database on a computer with screen interface (www.cybertracker.org). The direction of the bird (0° being in the front of the car) was assessed thanks to a compass and the distance to the bird was estimated visually. Given most observations were conducted by the same pool of observers every year, the bias inherent to such method was constant between years. Whenever possible, ancillary information on the bird were also recorded, such as sex/age (calendar years, CY), behaviour, and the habitats in which it was observed (see Appendix B). To avoid double counts, each observer was assigned a specific angle of view. The front observer being also the secretary, he contributed little to the data. All observations made outside the distance sampling protocol, in particular when the vehicle was stopped, were called “ad-libitum” and were not used in the population estimates analyses. However, they were kept in the section aiming at describing the composition of the populations.

The identification of MH individuals is straightforward and only females and young individuals can be confused with the Pallid Harrier *Circus macrourus* (hereafter PH). Regarding LK, the only other species with which it can be mistaken is the Common Kestrel *Falco tinnunculus* (CK). However, trained observers can relatively easily set apart PH and CK from MH and LK respectively, thanks to plumage characteristics and hunting behaviour. In our study area, very few PHs and CKs (4 and 165 observations respectively in 5 years) have been observed and we are thus confident that most of unidentified harriers and kestrels belong to these two species.

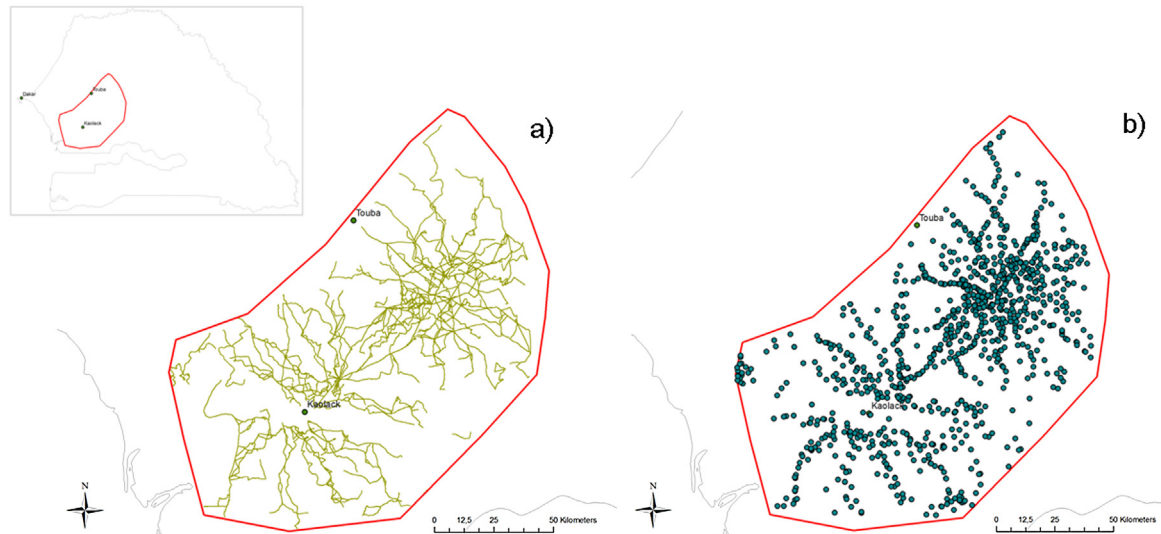


Fig. 1. a) Study area, b) Paths of all transects travelled and c) Locations of all sampling points for grasshopper density estimates.

2.3. Grasshoppers' density index

Along the birds transects conducted between 2010 and 2013, 1319 locations were sampled to estimate grasshopper abundance (Fig. 1b), on average every 7 km. Each sample consisted of two observers walking each two 100 m transects, with the four parallel transects being at least 50 m apart from each other, and at least 50 from the road. On each transect, observers noted all grasshoppers that flew from the transect line within a 2 m wide strip (1 m on each side, i.e. 200 m² transect). When shrubs were encountered within this strip, they were shaken to count resting grasshoppers. Grasshoppers were not identified at the species level but were categorized in two size classes: less or equal to 3 cm (i.e. "small", *Acorypha* and *Pyrgomorpha* genus) and larger than 3 cm (i.e. "large", *Ornithacris* genus), see Mullié and Guèye (2010). The final dataset contained 5131 individual transects (100 m length). Our index of abundance was simply the grand total of grasshoppers in the 800 m² surveyed per station which allows to model count data.

2.4. Landscape covariates

We took advantage of the MODIS dataset maintained by the NASA and downloaded from https://lpdaac.usgs.gov/data_access (Land Processes Distributed Active Archive Center, LPDAAC, 2014) which characterizes landscapes of the world at a 1 km spatial resolution. The latest image available for Senegal (2008) was used to compute environmental covariates that were further included in the density surface models. The LP DAAC was also the source of the Normalized Difference Vegetation Index images (NDVI, 250 m pixels) as well as the proportion of tree cover that were used to model the Grasshoppers' density index for the period 2010–2013. Another source of data consisted of the proportions of croplands and grasslands at a 10 km resolution available from (<http://www.glcn.org/>).

For the grasshopper statistical modelling (see below), covariates were extracted for each sampling locations at the original resolution of the data set. When predicting the response variable, values were averaged on a 1 km pixels grid. For MH and LK dsm models (see below), values of each variable were averaged on a 1 km pixels grid prior to analyses.

2.5. Statistical analyses

2.5.1. Spatio-temporal variations of grasshopper densities

The goal of this analysis was to predict grasshopper abundance over the whole study area for the period 2010–2013 (year 2009 was discarded), and to later use these predictions in the estimation of population size (see below). We built spatio-temporal (*s,t*) geo-statistical models (see e.g., Cameletti et al., 2012) thanks to Integrated Nested Laplace Approximation which allows fitting fast and accurate Bayesian approximations (Rue and Martino, 2009). The description of the methods can be found in the Supplementary material and is very similar to the one presented in Musenge et al. (2013).

As covariates, we included in initial models: the proportions of tree cover (LP DAAC, 2014), pasture and farmland, the date of the transect count (1st of January = 1) to account for within-year temporal trends, and the mean values of NDVI at sampling location for the previous autumn (September–December) and the current winter (January–February) available via MODIS NDVI products (LP DAAC, 2014). Linear and non-linear trends (modelled with a random walk of 1st order, see Illian et al., 2012) were tested as well as second order interactions between relevant terms. More than 30 different models were run and ranked thanks to their DIC values (Spiegelhalter et al., 2002). Yearly predictions were computed over the study area on a 1 × 1 km grid.

2.5.2. Distance sampling and density surface modelling

For both species, we used a two step approach: distance detection function and density surface modelling. The detection function models estimate the decrease in detection probability with increasing distance from the transect. We tested different covariates (period of the day, size of the group observed, etc.) and their interactions in order to increase the explanatory power of the model. Both half-normal and hazard-rate detection functions were fitted to data and model selection was performed with Akaike's Information Criteria (AIC). The density surface modelling consisted in combining the estimates from the best detection function model to environmental covariates, within the framework of Generalized Additive Models (GAMs) or Generalized Additive Mixed Models (GAMMs) using the dsm package (see Miller et al., 2013 for a

Table 1

Summary of all observations (combination of ad-libitum and distance transect observations), by species, sex and age ($n = 11,708$).

Species	Sex	Age	2009	2010	2011	2012	2013	Total (2009–2013)
Montagu's harrier	Female	2-3CY	7	17	55	39	14	132
		ad	43	48	275	106	112	584
	Male	2-3CY	40	43	89	46	8	227
		ad	41	114	311	176	173	815
	Ind.	<3CY	0	4	11	7	1	23
Lesser kestrel	Female	ad	—	105	139	11	51	306
		subad	—	57	14	10	6	87
	Male	ad	—	212	222	29	44	507
		subad	—	57	14	10	6	87
	Ind.	ind.	214	1502	3760	1283	1889	8648

complete description of the method and worked out examples). The method is rather flexible given that it permits modelling non-linear relationships between the response variable (number of individuals) and the covariates through splines functions (Wood, 2006). More than 30 different models were run and ranked according to their GCV scores, along with the proportion of deviance explained and r^2 (Appendix D). Model adequacy was visually assessed with QQ-plots and residuals plots.

Population size was estimated annually on a 1×1 km grid covering the study area with the following covariates: spatial position, year, julian date, period of the day, proportion of relevant habitat for each species and yearly predicted grasshopper densities. Summing over the predicted values for all grid cells resulted in an estimate of abundance over the whole study area.

All analyses were computed with the R 3.0.2 free statistical software (R Core Team, 2014).

3. Results

3.1. Species counts, sex and age class

Between January 2009 and March 2013, we accumulated 11,708 observations (transects + ad libitum), which comprised 18.5% of MH and 81.5% of LK (Table 1). Sex and age determination varied between species: only 9.4% of LK were sexed and aged, compared to 81.4% for MH. Despite the low sample size of identified LKs, we observed a higher proportion of adult males than females (respectively 62 and 38%, $\chi^2 = 10.64$, $df = 1$, $P = 0.001$). Considering all identified MH individuals, we observed 59.3% of males (46.3% of adult and 13% of 2-3CY) and 40.7% of females (33.2% of adults and 7.5% of 2-3CY, $\chi^2 = 56.2$, $df = 1$, $P < 0.001$). MH sex-ratio did not vary

between years ($\chi^2 = 8.45$, $df = 4$, $P = 0.08$), while there were significant variations between years when considering both age and sex (<3CY, male: $\chi^2 = 54.10$, $df = 4$, $P < 0.001$; female: $\chi^2 = 8.64$, $df = 4$, $P = 0.07$; adults, male: $\chi^2 = 10.97$, $df = 4$, $P = 0.03$; female: $\chi^2 = 12.38$, $df = 4$, $P = 0.015$). Finally 2.7% of all observed MH birds during transects were melanistic, and this percentage did not vary between years (2011–2013: $\chi^2 = 0.07$, $df = 2$, $P = 0.97$).

3.2. Behaviours and habitat used

Hunting behaviours was the dominant behaviour observed in 74 and 62% of cases for MH and LK respectively. MHs were observed hunting more significantly in grassy savannah (49% of observations), followed by shrub savannah (32%), arable land (14%) and finally woodland savannah with only 4% ($\chi^2 = 700.32$, $df = 3$, $P < 0.001$, Fig. 2). In contrast, LKs hunted in arable land 36% of the cases, in shrub savannah (34%), in grassy savannah (27%) and only 3% of observations were made hunting in woodland savannah ($\chi^2 = 1575.24$, $df = 3$, $P < 0.001$, Fig. 2). For both species, there was significant difference between male and female in terms of habitat used for hunting: female MH foraged equally on grassy and shrubby savannah while males tended to prefer grassy savannah ($\chi^2 = 21.94$, $df = 2$, $P < 0.001$, Fig. 2). Similarly, LK males tended to hunt more often on grassy savannah while females selected arable land ($\chi^2 = 12.31$, $df = 2$, $P = 0.002$, Fig. 2). For MH, there was no significant difference in habitat use between age classes within sex (young vs adult female: $\chi^2 = 1.83$, $df = 2$, $P = 0.40$; young vs adult male: $\chi^2 = 0.80$, $df = 2$, $P = 0.67$, Fig. 2).

3.3. Spatio-temporal variations in grasshopper densities

The best model for grasshopper density included an autoregressive term (AR1), whose estimate ($\sigma = -0.2 \pm 0.18$) suggested negative, though not significant, temporal density dependence. The range of the spatial autocorrelation of grasshopper densities for the best model was 24 km and its nugget (variance at the origin) was 0.49. The grasshopper density index was negatively affected by the proportion of croplands (-1.24 ± 0.47), while the proportion of pastures positively affected grasshopper densities, though not significantly (0.57 ± 0.29). The effect of NDVI during the fall and winter was non linear (see Appendix E). Despite year to year variations (Appendix F), the predicted values for the four years of survey highlighted two contrasted sub-areas in terms of density (Fig. 3). In the North Eastern part of the study area, the Khelkom region carried a high densities of grasshoppers (reaching over 1.25 grasshoppers/m²) while the South part of the Sine Saloum river, in the intensive ground-nuts production area, contained up to 100-fold lower abundances (0.02 grasshoppers/m²).

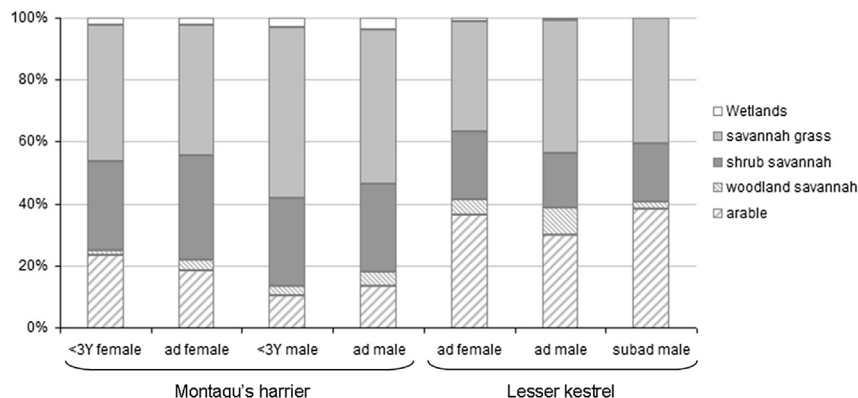


Fig. 2. Histograms of the proportion of habitats where birds were observed, by sex and age classes, for both species.

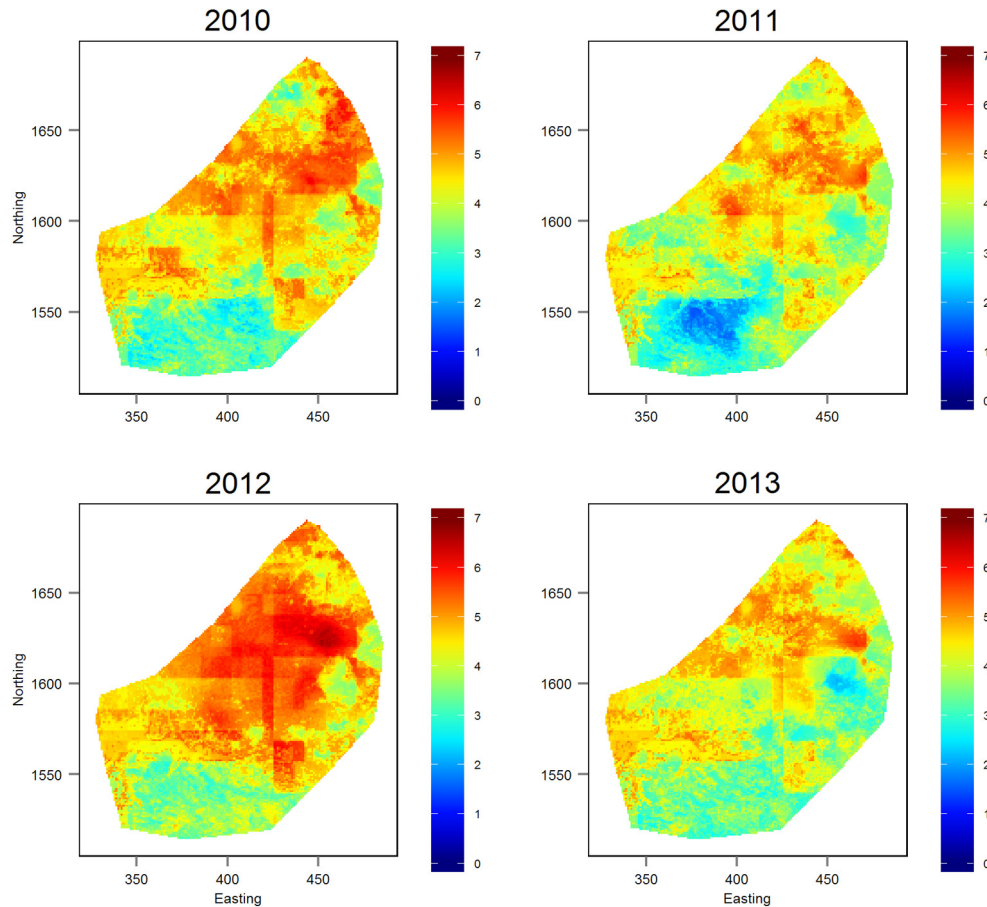


Fig. 3. Predicted values of the grasshopper index (log transformed) for the four years of the survey, computed from the best spatio-temporal model and environmental covariates.

3.4. Spatio-temporal variations of Montagu's Harrier and Lesser Kestrel densities

During the four year of survey, 972 MHs (787 observations) were of groups ranging from 2 to 18 individuals. Concerning LK (5480 birds in 1550 observations), 59% of observed birds were solitary, and 41% of the observations were of groups ranging from 2 to 90 individuals (7 records >100 were not used because it was not clear whether several different flocks were involved, due to the difficulty in assessing the depth of a group from a distance).

3.5. Detection function models

We evaluated five different models for both hazard-rate and half-normal key functions (Appendix C). Hazard-rate function showed a stronger support for both MH and LK models than the half-normal function ($\Delta AIC > 70$ for MH and > 200 for LK). The best detection function model for the two species included an additive effect of group sizes, MH's model having also a term for the period of the day of the transect count (morning vs afternoon, see Appendix C). Detection distances ranged from 0 to 992 m for MH and from 0 to 850 m for LK (Fig. 4). However, the detection probability decreased faster with increasing distance for the smaller species (LK) than for MH (respectively, $p = 0.5$ at around 150 m and $p = 0.5$ at 200 m, see Fig. 4).

3.6. Distribution modelling

The best selected model performed better for MH than for LK: adjusted- R^2 were 0.11 and 0.07 respectively and the percentages of

explained deviance were 30.3% and 20.9%. The best model for MH included year and period as factors as well as smoothing terms for the coordinates (thus accounting for medium to large scale spatial correlation), the Julian date of the transect count, grasshopper density index (one smoothing term fitted per level of the factor period) and the proportion of cropland (see Fig. 5a–d). The best model for LK included the very same terms (see Fig. 5e–h), except that the proportion of cropland was replaced by the proportion of “mosaic habitat” (cropland mixed with natural habitats). Globally, a peak of abundance was predicted around the 10th of February for MH and 25th of January for LK (Fig. 5a and e). The relationship between abundance and grasshopper density index showed two opposite patterns at low densities for MH: in the morning, the abundance of birds increased with increasing grasshopper density (Fig. 5b), while in the afternoon, the pattern became convex (Fig. 5c). The best model for LK displayed a similar pattern with a continuous increase until 0.07 grasshoppers/m² (i.e. log(4) in Fig. 5f) in the morning and 0.19 grasshoppers/m² (i.e. log(5) in Fig. 5e) in the afternoon, with an apparent threshold above this last value. Finally, we showed a quadratic effect of the proportion of cropland on MH, with a positive effect until 60% of cover, followed by a decrease (Fig. 5d). Concerning LK, we found a quasi-linear relationship between the number of birds and the proportion of croplands mixed with natural habitats (Fig. 5h).

3.7. Population size estimates

Population size estimated from both density surface models and known roosting site counts were in agreement for both species. The mean total MH population estimated from the transect counts

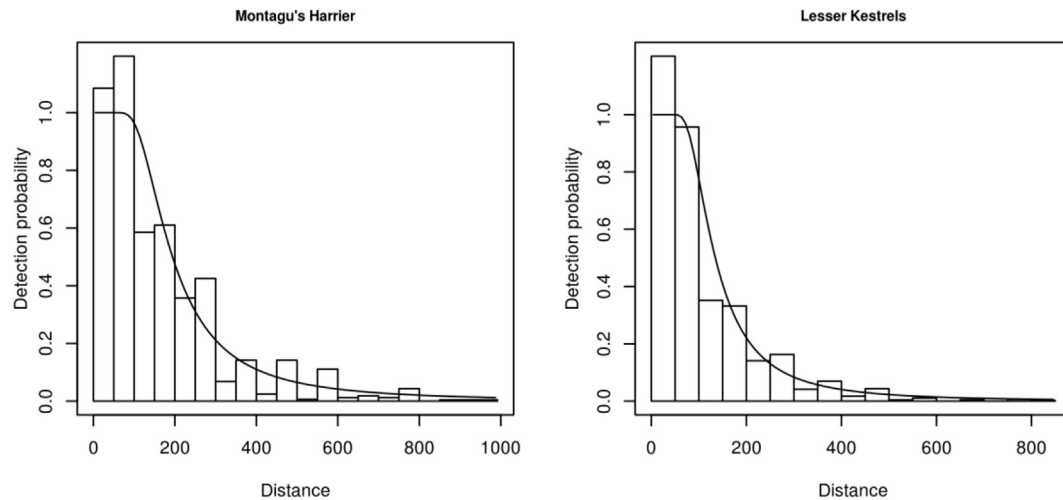


Fig. 4. Estimated detection functions for the Montagu's Harrier and the Lesser Kestrel.

ranged between 2330 and 5950 individuals (mean = 3360) while the sum of birds counted in known roosting lied between 1770 and 5270 individuals (Table 2). Similarly, the mean total LK population estimated from the transect counts ranged from 25,900 to 51,100 individuals (mean = 36,000) while the sum of known roosting birds lied between 16,300 and 31,300 individuals (Table 2).

4. Discussion

Recent progresses in telemetry and satellite imagery have greatly improved our knowledge on LDM raptors wintering ecology. However this technology comes with several drawbacks, as data collection can be limited by both technological and financial constraints. On the one hand, geolocators (GLS) have for example a relatively large spatial imprecision (e.g. Limiñana et al., 2012b) making this method pointless to investigate small scale processes. On the other hand, although miniaturized Argos PTT allows for a greater precision, their cost often limits the sample size, hence making it difficult to infer population distribution. In addition, these methods generally require the use of proxies instead of

appropriate covariates, e.g. NDVI instead of landscape or food resources variables. This can lead to spurious and undesired correlations (see e.g. Mihoub et al., 2012). Field data are thus still needed to properly address relationships between environmental factors such as food abundance and bird species' distribution (see e.g. Buij et al., 2013; Pilard et al., 2011; Mullié and Guèye, 2010). To our knowledge, the present study is the first large scale, field-based, assessment of the winter ecology of two acridivorous LDM species in this Sahelian key area. Along with their distribution and behaviours, we also carefully sampled grasshoppers, their main food resource. The large scale sampling scheme allowed predicting yearly grasshopper density over the study area, which was a prerequisite to precisely investigate the effect of food resources on the distribution of these raptors, and to improve population estimates.

Regarding the composition of populations in terms of sex and age ratio, our results are relatively limited for LK given that nine birds out of ten were unidentified. It is thus unclear whether the observed reversal of sex ratio in 2013 is an artefact, due to the difficulty of sexing birds (proper identification would require changing the distance sampling protocol, like driving speed), or has

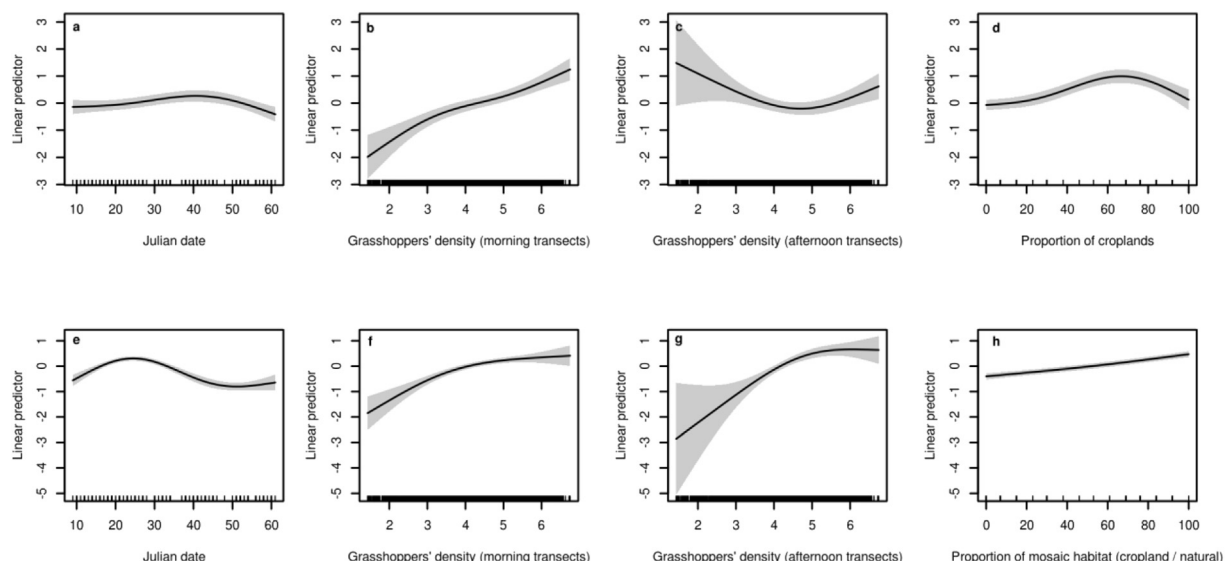


Fig. 5. Smoothing terms from the best dsM model for MH (a → d) and LK (e → g).

Table 2

Summary of the population estimates over the study area: mean, Confidence Intervals (CI) and Coefficient of Variation (CV). Averaged counts on MH roosts for January and February are presented for comparison. Similarly, the maximum number of LKs counted in January is shown.

Species	Year	Mean	CI (5%–95%)	CV	Roost size in January (N of roosts)	Roost size in February (N of roosts)
Montagu's Harrier	2010	2330	1920–2836	0.099	2390 (5)	3090 (2)
	2011	3650	3150–4430	0.075	4300 (5)	1377 (4)
	2012	5950	5080–6970	0.081	5270 (4)	NA
	2013	2810	2350–3350	0.091	1770 (4)	910 (6)
	Mean (all year)	3360	2830–3980			
Species	Year	Mean	CI (5%–95%)	CV	Maximal roost size in January (N of roosts)	
Lesser Kestrel	2010	25,900	22,900–29,300	0.063	26,620 (5)	
	2011	35,800	32,100–40,000	0.056	16,300 (5)	
	2012	31,300	27,200–36,000	0.072	31,300 (2)	
	2013	51,100	44,800–58,300	0.067	18,350 (3)	
	Mean (all year)	36,000	31,800–40,900			
	Mean (without 2013)	31,000	27,400–35,100			

a biological signification. Despite the small proportion of LKs that were sexed, our results are worth considering. First, our protocol has not changed over the years and our findings for the periods 2010–2012 are consistent with information gathered on groups of LKs resting on the ground close to the Kousmar roosting site (P. Pilard, unpublished data), from 2007 onwards: there, sex ratio were consistently male-biased (70% of males). Conversely, counts conducted in Niger during surveys in winters 2004 and 2005 underlined female-biased sex ratio (P. Pilard, unpublished data). It is thus probable that the relatively high population size estimated for 2013 combined with more females observed are the consequence of a sex-segregated wintering strategy. Groups of females would thus have moved into Senegal in 2013, as a consequence of disturbance on their original Western wintering grounds, either natural or anthropogenic. Preliminary analyses for 2013 suggests a female-biased distribution on the Eastern part of the study area. For MH, biased sex ratio might be the consequence of female-like plumage being recorded as unidentified, thus reducing the apparent number of females. However sex ratio assessed from counts on pre-roosts also suggested there were more males than females (unpublished data); moreover preliminary analysis of data from the MH French wing-tagging project begun in 2007 gave a similar trend, with a greater proportion of wing-tagged males than females observed in Senegal.

Similarly to Buij et al. (2012), we did find significant differences in habitat use between hunting males and females MH. However, given the differences in available landscape in Cameroon and Senegal, it is hard to draw any conclusions. In effect, Buij and collaborators found that males MH displayed no clear preferences while females rather used rice fields, which supported larger concentrations of a key prey, diurnal rodents. Conversely, observation data for MH in our study area did not suggest any difference in the diet, both sexes feeding on large grasshoppers (see below), a resource that appears to be plentiful in the central and north part of the study area. Thus, a possible explanation for differential hunting habitats selection could reside in sex based contrasted trade-offs between energy requirement and flight abilities, a consequence of Sexual Size Dimorphism (see e.g. Bustamante et al., 1997).

By modelling grasshopper distribution, we were able to include an *a priori* relevant covariate that may constrain the spatial variations in abundance for both species (Fig. 6). Not surprisingly, distribution models indicated that both species were positively affected by grasshopper density. As a consequence, the two species can be considered as good bio-indicators of the procession of acridivorous birds that gather in the grasshopper-rich study area and it is thus not surprising that large groups of White Storks *Ciconia ciconia*, Cattle Egrets *Bubulcus ibis*, Black Kites *Milvus migrans*, Abyssinian Rollers *Coracias abyssinicus*, or shrikes were observed along our road transects.

However the effect of prey on the spatial distribution of the two predators apparently differed. Most of the MH's population was predicted to concentrate on the Khelkom area in the North East, where the highest grasshopper densities and the largest roosts were located (Fig. 6). Conversely, LKs highest densities were predicted north of Kousmar Island (roost of ~25,000 LK) where food resources were not as high, and to a lesser extent, in the north-east part of the Khelkom area (Fig. 6). These differences might be explained by the lack of sufficiently large and suitable roosting sites for LK in the Khelkom area, principally due to deforestation, or by historical or social momentum linked to the colonial nature of LK that could *a priori* restrict their spatial distribution to a very few known/used sites. The latter would result in birds having to select habitats relatively close to their roosting sites, with more limited choices. Finally, while both species share a common prey type, namely grasshoppers, on their wintering grounds, their ecology differ in many ways (size, energy requirements, hunting strategy) and this could have consequences on the prey species selected. Indeed, the diet of MH is composed by 60% of *Acorypha clara* and 25% of *Ornithocris cravoisi* (Mullié and Guèye, 2010), while the diet of LK comprises between 24% and 86% of *O. cravoisi* and on average of 8% of *A. clara* (Pilard et al., 2011).

The population sizes predicted from the models based on transect road counts were of the same magnitude than those based on night roosts counts (Mullié and Guèye, 2010; Pilard et al., 2011; this study). During the five years of study, the study area hosted on average 3360 and 36,000 individuals for MH and LK populations respectively. When removing the year 2013 for LK, which led to surprisingly high population estimate, the mean population size for the 2010–2012 periods was estimated at 31,000 birds. These numbers represent approximately 5% and 46% of the populations breeding in Western Europe (MH: 30,000–50,000 pairs, Gensbol, 2005; LK: 25,000–42,000 pairs, BirdLife International, 2014), thus confirming the importance of the Senegal in general, for the conservation of the two species, and more particularly for LK. The concentration of LK on the Kousmar Island and to a lesser extent, in the Khelkom area, makes the species vulnerable to changes that could take place locally. The development program currently taking place aims at preserving the Kousmar Island ecosystem by involving local villagers in the management of the area, and should ensure the viability of this site for the years to come. Conversely, if some MH roosting sites appeared exceptionally large (this study but see also Cormier and Baillon, 1991), results from satellite telemetry (Limiñana et al., 2007; Trierweiler et al., 2013) showed that individuals breeding in Western Europe winter all over the Sahel region, making them less sensitive to local perturbations. Still, nowhere between Lake Tchad and Mali were such big roosts as the ones discovered in Senegal observed (B. Koks pers. comm.) and this area might require specific conservation measures.

MHs and LKs are LDM and future work will need to address the role of wintering conditions as possible drivers of carry-over effects on their survival, breeding success or frequency in breeding areas. Similarly, understanding how conditions during the breeding period affect population size or the distribution of individuals throughout the wintering ground in Africa is essential to assess

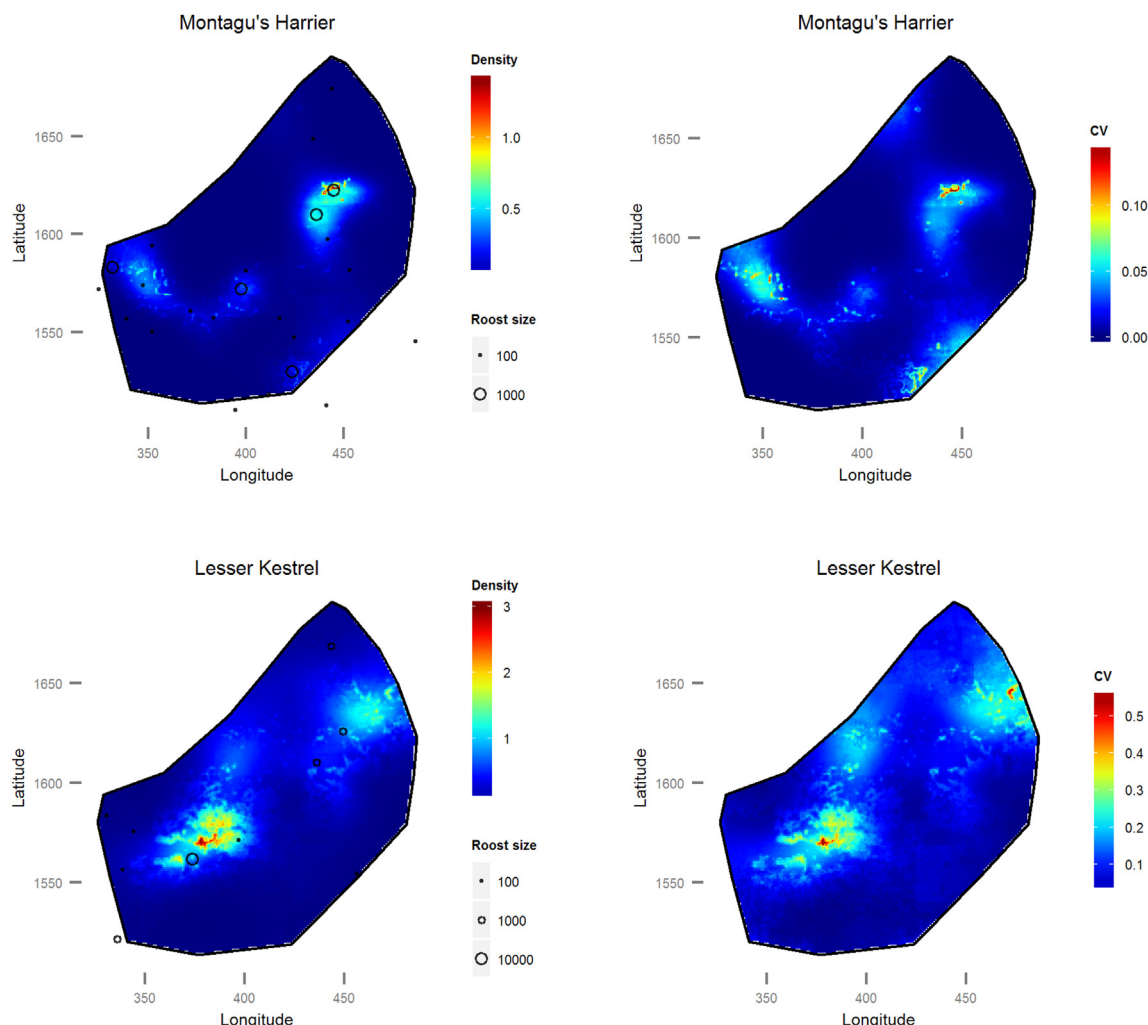


Fig. 6. Predicted densities (number of individuals per km², left panels) and coefficients of variations (CV, right panels) for MH and LK. Yearly predictions and their associated CVs were averaged for the 2010–2013 period. Known MHs' and LKs' roosting sites are represented with open dots that are proportional to roost size.

national or regional priorities that will account for the link between population of a specific nesting area and its corresponding wintering grounds. Moreover, these two species select somewhat similar habitats both on breeding and wintering grounds, i.e. landscapes that exhibit a mosaic of habitats, from natural grasslands to intensive cropfields. While the detrimental consequences of agricultural intensification in Western Europe have been highlighted for both species (Donazar et al., 1993; Arroyo et al., 2002), we lack data to tackle this issue on their African wintering grounds.

5. Conclusions

The situation there is relatively complex given acridivorous raptors could be affected concomitantly by i) landscape changes, e.g. the disappearance of habitats mosaic (Lambin et al., 2001), where the species forage or roost, ii) the control of populations that are considered as pest species when locusts outbreaks threaten food security (Lecoq, 2001), with direct mortality caused by insecticides (Keith and Bruggers, 1998), iii) climate changes that may add on top of the previous points and disrupt ecosystems functioning (Taylor et al., 2002). Maintaining healthy populations of acridivorous birds by keeping attractive roost sites through maintenance of trees and shrubs used by LKs, and natural grassland for ground roosting MHs, or a reduction of burning near roosting sites,

could constitute a good way to achieving a biological control of pest's populations while preserving biodiversity. This can only happen through a global approach accounting for the needs and concerns of local populations, as well as ecological requirements of LDM bird species.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.10.001>.

References

- Anadon, J.D., Sanchez-Zapata, J.A., Carrete, M., Donazar, J.A., Hiraldo, F., 2010. Large-scale human effects on an arid African raptor community. *Anim. Conserv.* 13, 495–504.
- Arroyo, B.E., Garcia, J.T., 2002. Alloparental care and kleptoparasitism in the semi-colonial Montagu's Harrier *Circus pygargus*. *Ibis* 144, 676–679.
- Arroyo, B.E., Garcia, J.T., Bretagnolle, V., 2002. Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Anim. Conserv.* 5, 283–290.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman & Hall, p. 446.
- Buij, R., Van Der Goes, D., De Jongh, H.H., Gagare, S., Haccou, P., Komdeur, J., De Snoo, G., 2012. Interspecific and intraspecific differences in habitat use and their conservation implications for Palearctic harriers on Sahelian wintering grounds. *Ibis*. <http://dx.doi.org/10.1111/j.1474-919X.2011.01200.x>.
- Buij, R., Cavaillès, S., Mullié, W.C., 2013. Breeding biology and diet of the African swallow-tailed kite *Chelictinia riocourii* in Senegal and Cameroon. *J. Raptor Res.* 47, 41–53.
- Bustamante, J., Donazar, J.A., Hiraldo, F., Ceballos, O., Travaini, A., 1997. Differential habitat selection by immature and adult Grey Eagle-buzzards *Geranoaetus melanoleucus*. *Ibis* 139, 322–330.
- Cameletti, M., Lindgren, F., Simpson, D., Rue, H., 2012. Spatio-temporal modeling of particulate matter concentration through the SPDE approach. *ASTA Adv. Stat. Anal.* 97, 109–131.
- Catry, I., Dias, M.P., Catry, T., Afanasyev, V., Fox, J., Franco, A.M.A., Sutherland, W.J., 2010. Individual variation in migratory movements and winter behavior of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. *Ibis*. <http://dx.doi.org/10.1111/j.1474-919X.2010.01073.x>.
- Cimon-Morin, J., Darveau, M., Poulin, M., 2013. Fostering synergies between ecosystem services and biodiversity in conservation planning: a review. *Biol. Conserv.* 166, 144–154.
- Cormier, J.P., Baillon, F., 1991. Concentration de Busards cendrés *Circus pygargus* dans la région de M'bour (Sénégal) durant l'hiver 1988–1989. *Alauda* 59, 163–168.
- Donazar, J.A., Negro, J.J., Hiraldo, F., 1993. Foraging habitat selection, land-use changes and population decline in the lesser kestrel *Falco naumanni*. *J. Appl. Ecol.* 30, 512–522.
- Gensbol, B., 2005. Guide des rapaces diurnes d'Europe, d'Afrique du Nord et Moyen-Orient. Delachaux et Niestlé editor, p. 402.
- Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Diaz-Delgado, R., Tella, J.L., Donazar, J.A., 2009. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* 118, 580–590.
- Illian, J., Sørbye, S., Rue, H., Hendrichsen, D., 2012. Fitting a log Gaussian Cox process with temporally varying effects—a case study. *J. Environ. Stat.* 3, 1–25.
- Jones, P., Vickery, J., Holt, S., Cresswell, W., 1996. A preliminary assessment of some factors influencing the density and distribution of Palearctic passerine migrants wintering in the Sahel zone of West Africa. *Bird Study* 43 (1), 73–84. <http://dx.doi.org/10.1080/00063659609460997>.
- Keith, J.O., Bruggers, R.L., 1998. Review of hazards to raptors from pest control in Sahelian Africa. *J. Raptor Res.* 32, 151–158.
- Lambin, E.F., Turner, B., Geist, H.J., Agbola, S.B., Angelsen, A., Bruce, J.W., Coomes, O.T., Dirzo, R., Fischer, G., Folke, C., George, P., Homewood, K., Imbernon, J., Leemans, R., Li, X., Moran, E.F., Mortimore, M., Ramakrishnan, P., Richards, J.F., Skanes, H., Steffen, W., Stone, G.D., Svedin, U., Veldkamp, T.A., Vogel, C., Xu, J., 2001. The causes of land-use and land-cover change: moving beyond the myths. *Glob. Environ. Change* 11, 261–269.
- Lebel, T., Ali, A., 2009. Recent trends in the Central and Western Sahel rainfall regime (1990–2007). *J. Hydrol.* 375, 52–64.
- Lecoq, M., 2001. Recent progress in Desert and Migratory Locust management in Africa. Are preventative actions possible? *J. Orthoptera Res.* 10, 277–291.
- Liminaña, R., Soutullo, A., Urios, V., 2007. Autumn migration of Montagu's harriers *Circus pygargus* tracked by satellite telemetry. *J. Ornithol.* 148, 517–523.
- Liminaña, R., Soutullo, A., Urios, V., Reig-Ferrer, A., 2012a. Migration and wintering areas of adult Montagu's Harriers *Circus pygargus* breeding in Spain. *J. Ornithol.* 153, 85–93.
- Liminaña, R., Romero, M., Mellone, U., Urios, V., 2012b. Mapping the migratory routes and wintering areas of Lesser Kestrels *Falco naumanni*: new insights from satellite telemetry. *Ibis* 154, 389–399.
- LPDAAC, 2014. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, USA.
- Mihoub, J.B., Gimenez, O., Pilard, P., Sarrazin, F., 2010. Challenging conservation of migratory species: Sahelian rainfalls drive first-year survival of the vulnerable Lesser Kestrel *Falco naumanni*. *Biol. Conserv.* 143, 839–847.
- Mihoub, J.B., Mouawad, N.G., Pilard, P., Jiguet, F., Low, M., Teplitsky, 2012. Impact of temperature on the breeding performance and selection patterns in lesser kestrels *Falco naumanni*. *J. Avian Biol.* 43, 001–009.
- Miller, D.L., Burt, M.L., Rexstad, E.A., Thomas, L., 2013. Spatial models for distance sampling data: recent developments and future directions. *Methods Ecol. Evol.* <http://dx.doi.org/10.1111/2041-210X.12105>.
- Millon, A., Arroyo, B., Bretagnolle, V., 2008. Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. *J. Zool.* 257, 349–358.
- Mullié, W.M., Guèye, Y., 2010. Does bird predation enhance the impact of Green Muscle *Metarhizium acridum* used for grasshopper control? *J. Orthoptera Res.* 19, 139–155.
- Musenge, E., Chirwa, T.F., Kahn, K., Vounatsou, P., 2013. Bayesian analysis of zero inflated spatiotemporal HIV/TB child mortality data through the INLA and SPDE approaches: applied to data observed between 1992 and 2010 in rural North East South Africa. *Int. J. Appl. Earth Obs. Geoinf.* 22, 86–98.
- Nevoux, M., Barbraud, J.C., Barbraud, C., 2008. Nonlinear impact of climate on survival in a migratory white stork population. *J. Anim. Ecol.* 77, 1143–1152.
- Pilard, P., Lelong, V., Sonko, A., Riols, C., 2011. Suivi et conservation du dortoir de rapaces insectivores (Faucon crécerellette *Falco naumanni* et Elanion Naucier *Chelictinia riocourii*) de l'île de Kousmar (Kaolack/Sénégal). *Alauda* 79, 295–312.
- Powell, J.M., Williams, T.O., 1993. Livestock, Nutrient Cycling and Sustainable Agriculture in the West African Sahel. IIED, London.
- R Core Team, 2014. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>.
- Reij, C., Tappan, G., Belemvire, A., 2005. Changing land management practices and vegetation in the Central Plateau of Burkina Faso (1968–2002). *J. Arid Environ.* 63, 642–659.
- Rue, H., Martino, S., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc.* 71, 319–392.
- Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., Van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Conserv.* 131, 93–105.
- Serrano, D., Tella, J.L., Forero, M.G., Donazar, J., 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* 70, 568–578.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van Der Linde, A., 2002. Bayesian measures of model complexity and fit. *J. R. Stat. Soc.* 64, 583–639.
- Tappan, G., Hadj, A., Wood, E., Lletow, R., 2000. Use of Argon, Corona, and Landsat imagery to assess 30 years of land resource changes in West-Central Senegal. *Photogramm. Eng. Remote Sens.* 66 (6), 727–735.
- Taylor, C.M., Lambin, E.F., Stephenne, N., Harding, R.J., Essery, R.L., 2002. The influence of land use change on climate in the Sahel. *J. Clim.* 15, 3615–3629.
- Thiollay, J.-M., 2006. The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis* 148, 240–254.
- Trierweiler, C., Mullié, W.C., Drent, R.H., Exo, K.-M., Komdeur, J., Barlein, F., Haroua, A., de Bakker, M., Koks, B.J., 2013. A Palearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. *J. Anim. Ecol.* 82, 107–120.
- Walther, B.A., Van Niekerk, A., Rahbek, C., 2011. Long-term population declines of Palearctic passerine migrant birds: a signal from the Sahel? In: *The Ecology & Conservation of Migratory Birds Conference*.
- Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. Chapman & Hall/CRC editor.