Large-scale human effects on an arid African raptor community

J. D. Anadó n[1,2], J. A. Sánchez-Zapata[1], M. Carrete[3], J. A. Doná zar[3] & F. Hiraldo[3]

1 Departamento Biología Aplicada, Universidad Miguel Hernández. Avda. Universidad, Alicante, Spain
2 Department of Ecological Modelling. Helmholtz Center for Environmental Research – UFZ, Leipzig, Germany
3 Department of Conservation Biology, Estación Biológica de Doñana, CSIC, Sevilla, Spain

Abstract

In the current scenario of biodiversity crisis there is a growing need for identifying causes of changes in biodiversity at large scales. Here we assess factors driving raptor community structure in the Sahel, a region suffering a wide range of environmental degradation and a vital area for European migrant birds. Using road surveys, we estimated the effects of population size, human settlement patterns (e.g. urban vs. nomadic) and land use on the raptor community, taking into account the major natural role played by productivity. Total raptor richness values were similar to those described for other steppe regions of the world, with one super-abundant migrant species, the black kite Milvus migrans; however, richness of resident raptors was strikingly lower than expected, with most large body-size African species (both eagles and vultures) absent. Raptor richness was strongly correlated with human activities in a scale-dependent fashion. At a 25 km resolution, raptor richness was driven by habitat and productivity, with a positive response to crops. At a smaller scale, human population was positively related with wintering species richness but negatively with richness of resident ones, perhaps as a consequence of non-agricultural activities such as direct harvesting and different forms of habitat degradation (e.g. overgrazing or firewood collection). Subsistence economies in systems with low natural environmental heterogeneity and with a human population over carrying capacity, such as the Sahel, may lead to exhausted biological systems even in the absence of intensive agricultural or urban land-use changes, as shown by the deeply impoverished sedentary raptor community. Our results suggest that, because habitat and productivity seem to play a relevant role in driving species richness, climate change may have a major effect on the raptor community of the Sahel.

Introduction

In the current context of biodiversity crisis, there is a growing need for monitoring changes in biodiversity on large scales and to identify factors causing those changes (Meffe & Carroll, 1994). However, disentangling the effects of human population on biodiversity at large scales is not a trivial task. It is well known that a number of scale-dependent correlations exist between natural and anthropogenic factors affecting biodiversity. These correlates mask and blur the real effects of human population on biodiversity, particularly at large spatial scales (Gaston, 2005; Hugo & van Rensburg, 2008).

The most supported factors controlling biodiversity (in terms of species richness) at large scales are energy availability and environmental heterogeneity (Davies et al., 2007). Furthermore, the similar positive responses of human population and species richness to energy availability (Evans & Gaston, 2005), yield a positive relationship between species richness and human population (Balmford et al., 2001). This positive relationship between human population and species richness appears to become negative as the scale is reduced (Pautasso, 2007), and the negative effects of human population on species richness, such as fragmentation, habitat loss, harvesting or pollution, yield detectable patterns at more local scales.

The spatial coincidence of human population and species richness leads to conservation conflicts (Gaston, 2005) with particularly severe negative consequences in less productive areas, where human pressure on scarce resources is high. This is the case of the Sahel, a region suffering a wide range of different forms of environmental degradation linked to the fragility of its ecosystems and to human activity (Wezel & Rath, 2002). The region's subsistence economy relies

upon extensive animal husbandry and, to a lesser extent, agriculture, and its population is doubling every 20 years (Zeng, 2003). There are three major causes likely to be threatening the biological integrity of this biome: (1) high population pressure with impacts on biodiversity such as direct harvesting (e.g. Brashares, Arcese & Sam, 2001); (2) habitat degradation mainly due to agriculture and overgrazing (e.g. Darkoh, 2003); (3) variations in system productivity due to climate change (e.g. Held et al., 2005).

Our aim here is to evaluate the relative influence of human population on the integrity of the biodiversity in the Sahel. For this purpose, as potential impacts of human population, we take into account different settlement patterns (e.g. urban and suburban vs. nomadic settlements) and land-uses, while considering the major natural role played by energy availability (measured here as primary productivity, see 'Material and methods') in this system. To address this objective we employ raptors as indicator species. This taxon has been proposed as an appropriate biodiversity indicator in humanized European landscapes (Sergio et al., 2006) as well as to track habitat transformation or human population distribution in other more natural regions (Sanchez-Zapata et al., 2003; Carrete et al., 2009). Besides their usefulness as indicators, there is also an important conservation interest regarding these species in the Sahel. Many of the European birds – and specifically raptors – are trans-Saharan migrants, many of which are considered to be of conservation concern (Tucker & Heath, 1994; BirdLife International, 2004). In general, these species are undergoing long-term population declines (Sanderson et al., 2006) that may be related to environmental changes in the Sahel (Gordo et al., 2005; Grande et al., 2009). These changes also seem to affect resident raptors and some studies indicate that there is a close link between increments in human population size and the over-exploitation of resources and trends in raptor and other vertebrate populations (Thiollay, 2006a, 2007).

Material and methods

Study area

Raptor roadside counts were carried out in southern Mauritania and northern Mali between 14126^{0}–19121^{0}N and 7112^{0}–16129^{0}E (Fig. 1). There is a marked gradient of habitats ranging from sandy and rocky deserts, to dry grasslands and open savannah. Differences in annual rainfall range from ᴏ100 mm in the deserts of Mauritania to 600 mm in the savannahs of Mali. The potential vegetation is dominated by grasses (Cymbopogon schoenanthus, Panicum turgidum, Cenchrus biflorus), and shrubs (Leptademia spartum, Calotropis procera). Trees (Acacia raddiana, Acacia seyal, Balanites aegyptiaca) are scarce and sparse in the more arid northern zones of the Sahel, but become more frequent southwards in the savannahs of Mali and Senegal, where scattered copses of baobabs Adansonia digitata appear. Human population density is very low (3 inhabitants km^{-2}; United Nations World Population Prospects; http://esa.un.org/unpp/) with a few medium-sized cities such as Nouackchott, Kiffa, Nema (Mauritania) and Kayes (Mali).

Road surveys

Raptor roadside counts were carried out during two consecutive winter seasons. In total, we followed 1 day long 25 linear transects (eight transects in January 2004 and 17 transects in December 2004), covering a total length of 3230 km (1080 km in January and 2150 in December). Within each winter season, all transects were different. Between the two winter seasons transects partially overlapped. In those areas sampled in the two seasons, overlapping samples (i.e. road stretches) were deleted in the procedures carried out to minimize data autocorrelation (see 'Autocorrelation and collinearity analysis').

Roadside counts were carried out following methods widely used in similar studies (see Sanchez-Zapata et al., 2003, 2007). Briefly, we recorded every raptor seen and its relative position (km) within the transect. Counts were done by experienced observers, from 2 h after sunrise to 1–2 h before sunset, avoiding adverse weather conditions such as intense heat, rain or fog. Average driving speed was 50–70 km h^{-1}. In a few cases it was necessary to stop the vehicle to identify the birds, but we did not record new individuals observed during these stops. All identified raptors were located ᴏ500 m away from the centre of the transect; thus, we can consider this distance as the nearest belt of our 1 km width transects. Richness of sedentary and wintering raptors as well as total richness were assigned to 5 and 25 km stretches of road, which were our sampling units for analytical purposes (Fig. 1).

Roadside counts have been criticized as a useful technique for surveying raptors because they have many inherent biases (Fuller & Mosher, 1981; Millsap & LeFranc Jr, 1988; Meunier, Verheyden & Jouventin, 2000). However, and although roadside surveys may fail to detect some secretive or rare species (Carrete et al., 2009), recent works have shown that observed species richness and that estimated using nonparametric techniques are strongly positively correlated with each other, and thus exhibit very similar, and statistically indistinguishable, macroecological spatial patterns (Evans et al., 2008). Moreover, data collected along road transects can give model performance that approaches that offered by the systematic use of quadrats, even if confounding factors such as the contiguity of distributions, detection probability, sample size and environmental data errors are present (Reese et al., 2005).

Environmental variables

Sampling units were characterized using environmental variables describing human population (types of human settlements present), land-uses and productivity along the roadside (1 km width) at two different scales: small (environmental characteristics of the 5 km sample unit, i.e. a 5 km stretch of road) and large (environmental characteristics of
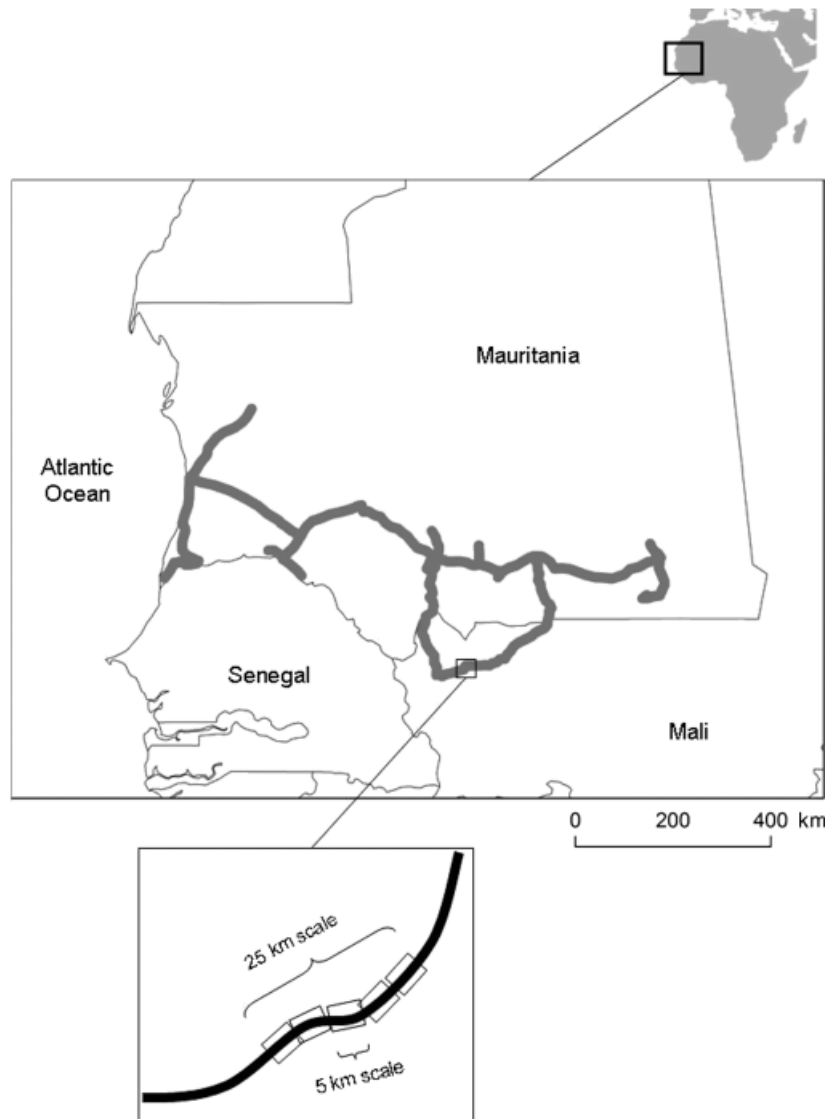
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Figure 1 Study area and location of the road transects, with a graphic description of the 5 and 25 km sampling units used in the statistical analyses (for details, see text).

the sample unit and the two previous and two subsequent units, i.e. a 25 km stretch of road, Fig. 1).

Human settlements were described using four different quantitative variables, namely: haimas (temporary emplacements used by communities of nomadic shepherds), small villages (human settlements with $\bigcirc$100 houses), towns (human settlements with $\triangleleft$100 and $\bigcirc$1000 houses) and cities (human settlements with $\triangleleft$1000 houses). The value for each variable was the number of kilometres (out of the total stretch of road considered, i.e. 5 or 25) in which haimas, small villages, towns or cities were present along the road. This information was collected during the road transects because temporary settlements change over time and are not accurately measured with geographic information systems.

Habitat was described using four different quantitative variables: desert (bare areas), very open grassland (herbaceous cover $\bigcirc$5%), open grassland (herbaceous cover $\triangleleft$5%) and crops. As with human settlement variables, each one of the habitat variables expressed the proportion of the total stretch of the road considered (5 or 25 km) dominated by desert, crops, open grassland or very open grassland. Habitat information was obtained from the Global Land Cover 2000 database (GLC2000, Mayaux et al., 2004).

Productivity was described in terms of the normalized difference vegetation index (NDVI), also at both 5 and 25 km scales. This index is frequently used as a surrogate of primary productivity and vegetative growth in terrestrial ecosystems (Box, Holben & Kalb, 1989). The variable described the mean NDVI value along the roadside. We used the average NDVI values obtained from the Famine Early Warning System Network (FEWS NET; http://earlywarning.usgs.gov/adds/) during the months in which

field work was carried out. Both productivity and habitat maps have a resolution of 1×1 km and thus adequately describe the road transects.

Analytical procedures

Autocorrelation and collinearity analysis

Before modelling, we checked for autocorrelation in each of the response variables by means of the Moran's I coefficient. For this purpose, we assessed the significance of the Moran's I values of the residuals from a full model containing all predictor variables (e.g. Rhodes et al., 2009). In all cases, significant autocorrelation values were detected. To minimize autocorrelation, we calculated nearest neighbour distance between all pairs of samples (5 and 25 km road stretches) and randomly deleted one of the samples of the pair with the smallest nearest neighbour distance. This procedure was repeated iteratively until no significant autocorrelation was detected in the residuals of the full models for the six dependent variables, yielding a non-autocorrelated dataset for analysis of 378 for 5 km stretches and 105 for 25 km stretches.

All predictor variables were checked for collinearity by calculating all pair-wise Spearman's rank correlation coefficients. When pairs of predictor variables were strongly correlated ($|r_s| > 0.7$) we discarded one of the redundant variables (e.g. Rhodes et al., 2009). For every pair of correlated predictors, we retained those with the lowest Akaike information criteria from univariate models of the two predictors (Burnham & Anderson, 2002). This approach led us to discard productivity and the four habitat variables measured at 5 km scale.

Deviance-partitioning analysis and modelling procedures

We performed deviance-partitioning analyses to explore the relative influence of human population, land-uses and productivity on the richness patterns at the two spatial scales (Anadon et al., 2006; Carrete et al., 2007). This analysis allowed us to separate the pure from the joint effects of the three groups of explanatory variables on raptor richness. For this purpose, we first constructed generalized linear models relating the three group of variables (population, land-uses and productivity) to raptor richness (wintering, sendentary and total raptor richness), considering variables taken at the 5 and 25 km scales. Secondly, we performed models in which the joint effect of two groups of variables were simultaneously considered: human settlements and habitat (HS+H), human settlements and productivity (HS+P) and habitat and productivity (H+P). Then, we built general models summarizing the total deviance explained in the datasets (i.e. HS+H+P). Lastly, we calculated the pure and joint effects (deviance explained) of human settlements, land-uses and productivity using basic algebra (Anadon et al., 2006; Carrete et al., 2007). Once deviance-partitioning analyses assessed the relative influ-

ence of population, land-uses and productivity on the raptor richness at the two spatial scales, we identified the variables relevant within each group and their relationship (i.e. positive or negative) with our dependent variables by checking multivariate models.

At the large scale (25 km), we used the logarithmic as link function and the Poisson as error distribution. At the smallest scale (5 km), due to the high number of zeros in the dataset, we used zero-inflated Poisson models (Lambert, 1992; Welsh et al., 1996). A zero-inflated model can be viewed as a two-part model, in which (1) the probability of species presence; (2) the abundance, given its presence, are modelled from the same data. These models assume two latent groups in the dataset: an always-zero group (inflation group) and a not-always-zero group. This procedure yields two separate models that can be interpreted independently, but with a joint value of explained deviance and AIC values. The first model (logistic link function, binomial error distribution) describes the probability of belonging to the always-zero group or to the not-always-zero group whereas the second model (logarithmic link function, Poisson error distribution) describes the mean richness in the not-always-zero group. Models were built by means of a step-wise approach, using their AIC value (Burnham & Anderson, 2002) as model selection criteria (Murtaugh, 2009). However, to increase the parsimony of our multivariate models, variables were added only if they resulted in a $> 1\%$ increase in the explained deviance. All 5 and 25 km models included the year of sampling to control for potential annual variability. The linear and the quadratic form of all explanatory variables were tested.

Results

We detected 15 raptor species, eight of which were resident and seven trans-Saharan winter migrants (Table 1). Wintering species were > 20 times abundant than residents (45 vs.

Table 1 Results of road raptor surveys

Species	n	n/100 km
Black kite Milvus migrans	1298	40.2
Egyptian vulture Neophron percnopterus	31	1.0
Montagu's harrier Circus pygargus	23	0.7
Marsh harrier Circus aeruginosus	50	1.5
Hen harrier Circus cyaneus	1	O0.1
Short-toed eagle Circaetus gallicus	40	1.2
Peregrine falcon Falco peregrinus	1	O0.1
Total wintering raptors	1444	44.7
Bateleur Tetrathopius eucaudatus	1	O0.1
African swallow-tailed kite Chelictinia riocourii	7	0.2
Lizard buzzard Kaupifalco monogrammicus	1	O0.1
Dark chanting-goshawk Melierax metabates	1	O0.1
Grasshopper buzzard Butastur rufipennis	14	0.4
Wahlberg's eagle Aquila wahlbergi	2	0.1
Common kestrel Falco tinnunculus	21	0.7
Lanner falcon Falco biarmicus	12	0.4
Total resident raptors	59	1.8

n = total number of individuals along the 3230 km surveyed.

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2 individuals $100 \, \text{km}^{-1}$, respectively). This was largely because of black kites Milvus migrans by far the most common bird of prey. Not taking into account this species, wintering species abundance dropped to 5 individuals $100 \, \text{km}^{-1}$. Small falcons such as Falco tinnunculus and Falco biarmicus were the most abundant sedentary species.

The deviance partitioning reveals a scale-dependent relationship between raptor richness and our explanatory variables (Fig. 2). At a large scale (25 km), richness of sedentary, wintering and total raptors were mostly related to the pure effect of land-uses and its joint effect with productivity. The effect of population was nearly null at this scale. At a smaller scale (5 km), there were strong differences among the response of the three richness indexes. As shown by the total explained deviance values, the richness of resident raptors was much more influenced by the explanatory variables considered in our study (c. 44%) than richness of wintering and total raptors (17 and 19%, respectively). Moreover, resident raptor richness was strongly affected by the pure

effects of population (47% of the explained deviance) followed by the pure effects of habitat and its joint effect with productivity (18 and 19%, respectively), whereas the richness of wintering species was mainly related to the joint effect of land-uses and productivity (55%), followed by the pure effects of land-uses (24%) and population (15%) (Fig. 2). Small negative values ($O 2\%$) were obtained for three components of the deviance-partitioning analysis at 5 km scale, suggesting an slight synergic relationships among environmental factors (e.g. the explanation power of two variables considered together is higher than the sum of the explanation power of these variables by their own).

In relation to the particular variables relevant at a large scale (25 km), land-use models varied among the three richness indexes, all showing a positive response toward the proportion of crops (Table 2). For wintering and total raptor richness, land-use models also included a negative response to the proportion of deserts, whereas for resident raptors these models included a negative response to
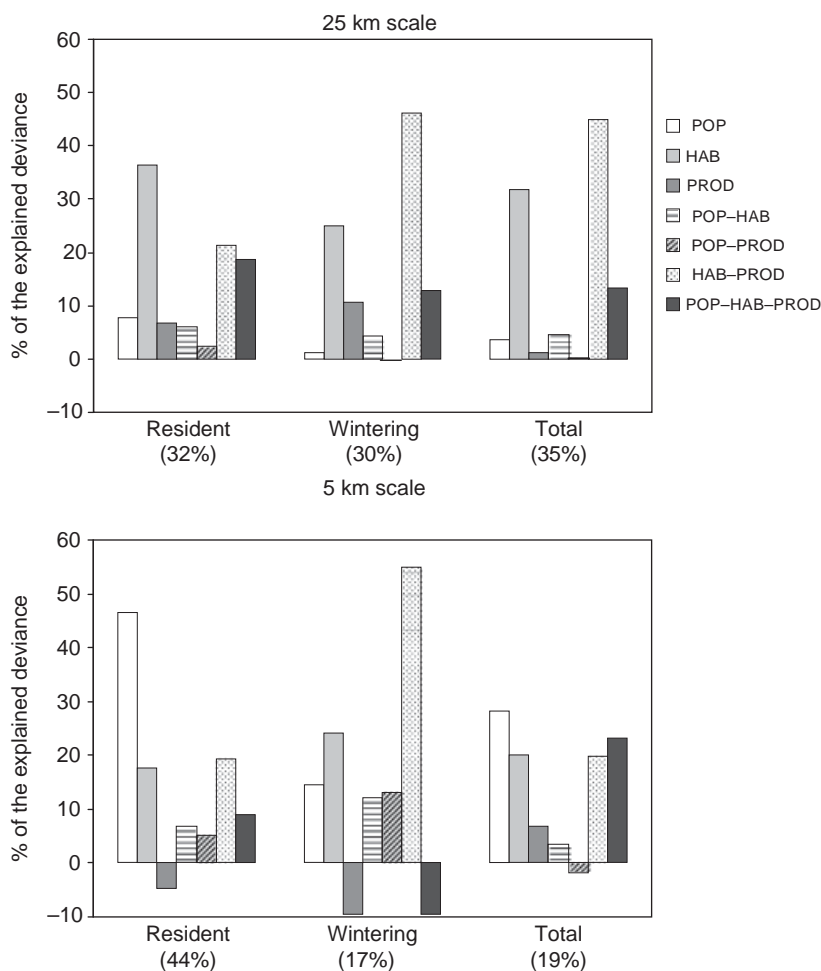

Figure 2 Results of the deviance partition analysis for resident, wintering and total raptor richness at the 25 km (top) and 5 km scale (bottom). It should be noted that 5 km models mainly include predictors at 25 km scale. Explained deviance values (in % of the total explained deviance) are shown as bars. In parentheses, total explained deviance for each richness index. POP, Human population variables; HAB, habitat variables; PROD, productivity (normalized difference vegetation index).

Table 2 Multivariate models employed in the deviance partition analysis

		Rich resident			Rich wintering			Rich total		
		Variable	D^2	Type	Variable	D^2	Type	Variable	D^2	Type
25 km	Population	Haimas25	11.4	−	Haimas25	5.4	−	Haimas25	7.8	−
	Habitat	Crops25	17.7	+	Desert25	19.8	−	Crops25	19.1	+
		Very Open Grass.25^2	26.7	++	Crops25	26.6	+	Desert25	28.2	−
								Very open grass.25^2	33.7	++
	Productivity	NDVI25^2	16.0	++	NDVI25^2	21.0	++	NDVI25^2	21.2	++
5 km	Population	Village25	14.8	+	Town25	5.2	+	Town25	6.4	+
		Town25^2	23.3	(−)				Haimas25^2	9.9	(−)
		Village^2	29.5	(+)						
	Habitat	Crops25^2	18.2	(−)	Desert25	9.8	−/+	Crops25	8.9	+/−
		Open grass.25	23.0	+	Crops25	12.2	+	Open grass.25	12.4	+/−
					Open grass.25^2	14.0	(+)			
	Productivity	NDVI25	12.6	+	NDVI25	8.4	+/−	NDVI25	8.8	+/−

D^2, explained deviance. Type of response: '−', negative; '+', positive; '++', hump-shaped quadratic. A sign response between brackets indicates a quadratic non-hump-shaped response (general positive or negative). For 5 km analysis, two signs are given for Poisson/Binomial model. If both signs match, only one sign is given. All responses are significant (P○0.05).
NDVI, normalized difference vegetation index.

proportion of very open grassland. Regarding productivity, the quadratic relationship with all indexes of raptor richness indicates maximum values of species at intermediate values of productivity (Table 2).

At a smaller scale (5 km), the three richness indexes were also mainly related to variables measured at a 25 km resolution (Table 2). All population models included the proportion of towns at a 25 km scale, with a negative response in resident raptors and a positive response in wintering and total raptor richness. The resident raptor richness model also included the proportion of villages at 25 and 5 km scales with a positive response whereas the total raptor richness model included a negative response to the proportion of haimas at a 25 km scale. Finally, richness of sedentary raptors was positively related to productivity. Productivity was negatively related to the probability of the presence of wintering and total raptors, but positively related to their richness (Table 2).

Discussion

Richness of the raptor community in the Sahel

Overall richness (15) and abundance (47 individuals 100 km^{-1}) of raptors in the Sahel was similar to that found in other arid and semiarid ecosystems such as the Patagonian Monte, the central Asia steppes, or Baja California (Ellis, Glinshi & Smith, 1990; Donazar et al., 1993; Rodrıguez-Estrella, Donazar & Hiraldo, 1998; Sanchez-Zapata et al., 2003; Carrete et al., 2009). However, this result can be misleading because of the presence of a very abundant migrant species, the black kite. Indeed, when excluding this species from analysis, total abundance drops to 7 individuals 100 km^{-1}. Furthermore, even not taking into account black kites, most of the raptors censused were trans-Saharan wintering species (5 individuals 100 km^{-1}; six species), in contrast with the lower

abundance of resident raptors (2 individuals 100 km^{-1}; eight species). The richness of residents raptors was thus much lower than expected, considering the large-bodied resident birds of prey that, although potentially present in the Sahel (hooded Necrosyrtes monachus, African white-backed Gyps africanus, Ruppell's Gyps rueppellii, lappet-faced Torgos tracheliotus, white-headed vultures Trigonoceps occipitales and martial eagles Polemaetus bellicosus, Thiolay, 2006a,b, 2007), were totally absent from our roadside counts despite the significant sampling effort and the high visibility of these species. These absences were unlikely due to sampling bias, because road transects have been successful in detecting large-bodied raptors in many other studies carried out in open systems such as our one (Donazar et al., 1993; Sanchez-Zapata et al., 2003; Thiolay, 2006a,b, 2007; Carrete et al., 2009). The increasing rarity of large vertebrates was also reported in other parts of the western Sahel (Mali, Burkina Faso and Niger), where the persistence of large raptors, ungulates and carnivores is restricted to a few protected areas (Thiollay, 2006a,b, 2007) and reflects the deep impoverishment suffered by biological communities in this area. As discussed below, this decline could be linked to the increasing density of human population. This effect may be more serious in the case of sedentary species that complete their whole life cycle in the Sahel and thus suffer more constant human pressure than the wintering species that breed in the Western Palaearctic.

Factors driving raptor richness in arid landscapes

Environmental available energy and environmental heterogeneity are major drivers of species richness at macroecological scales (Davies et al., 2007). In our study, patterns at a large scale (25 km resolution) between people, productivity and species richness only partially agree with expected patterns. The raw explicative power of productivity over raptor richness (16–21%) was larger than values reported by

other works for taxa with these characteristics (i.e. high mass, top predator; Evans, Greenwood & Gaston, 2005). However, as revealed by deviance-partitioning analysis, this effect was mainly due to a combined effect of productivity and land-uses. Actually, the positive effects of crops and the negative effect of deserts (independent of habitat productivity) were the main factors shaping raptor richness at macroecological scales in the Sahel. This result is remarkable taking into account our current knowledge about species–energy relationships. Many studies dealing with this subject implicitly assume that, because descriptors of environmental available energy (e.g. temperature, NDVI) likely affects basic resources or conditions, the detected species–energy relationships reflect ecological processes (e.g. Evans et al., 2005; but see Chase & Leibold, 2002 and Evans, James & Gaston, 2006). Our results thus support studies suggesting that part of the influence of productivity on species richness arises from its correlation habitat type (Evans et al., 2005, 2006).

At a smaller scale (5 km resolution), deviance-partitioning analysis showed that population, land-uses and productivity show a higher explanatory power for sedentary compared with wintering species, the latter being rather low (17%). Different macroecological responses depending on species attributes and scale have been described previously (e.g. Evans et al., 2005, 2008). In our case, it is likely that the distribution of wintering species may be more loosely related to environmental factors and resources, largely responding to unpredictable abundant feeding sources (Sanchez-Zapata et al., 2007). On the other hand, the lower percentage of deviance explained by population variables highlights the lower vulnerability of wintering species to continuous human pressure compared with sedentary species (Thiollay, 2007), that undergo their entire life cycle in the Sahel. In sedentary raptors, we detected a larger effect of people compared with land-uses and productivity. The increase in human effects on species richness as we scale down agrees with described general patterns (Pautasso, 2007).

Habitat, measured here as land-uses, played a central role in raptor richness similar to that described for other arid ecosystems (Rodrıguez-Estrella, 2007; Carrete et al., 2009). Crops are positively related to wintering raptor richness at both macroecological and more local scales, whereas the response of resident raptors to crops was less consistent, shifting between scales. These patterns generally agree with those found by Thiollay (2006b) at a 5 km scale in Burkina Faso and are also similar to that described for raptors in European landscapes, where trans-Saharan migrant raptors are more abundant in extensive agroforestal mosaics and resident raptors more common in more natural areas (Sanchez-Zapata & Calvo, 1999). The presence of wintering raptors was also linked to deserts, probably because black kites, the most abundant species, were common in arid landscapes. Overall, the response of richness to deserts was negative.

At the smaller scale (5 km), where the effects of human population are relevant, resident raptor richness showed a negative response to towns. This result indicates a negative effect of human population, particularly at higher densities. The effect of human population relying on subsistence economies and the extensive use of the territory, independent of land-uses, is likely to be a major force shaping the distribution of sedentary raptors in the Sahel. The main processes behind this negative effect on biodiversity could be direct persecution of raptors as well as harvesting of their main basic resources such as prey or nesting material (Thiollay, 2006b). Indeed, bushmeat for human consumption is a key contributor to local economies throughout the developing world (Milner-Gulland, Bennett & the SCB 2002 Annual Meeting Wild Meat Group, 2003; Brashares et al., 2004). Other activities such as overgrazing or firewood collection have also been pointed out as leading causes of degradation of dry-lands, and thus, as having a negative effect on biodiversity (Wezel & Rath, 2002; Darkoh, 2003). This scenario resembles the situation in rural Europe before industrialization, when high densities of dispersed human populations and, more importantly, their negative effects through persecution and poisoning of wild animals, increased extinction rates at both local and global scales (Thompson & Jones, 1999; Brashares et al., 2001; Carrete et al., 2007). This situation might be exacerbated in the Sahel by the lack of natural refuges for wildlife, others than a few protected areas.

Once the most sensitive species to human perturbations have become virtually extinct (i.e. vultures and eagles), the resulting community of resident raptors mainly includes medium and small body-size species. This impoverished community may find adequate habitats in landscapes with low to intermediate human disturbance, as shown by the positive response of resident raptors to villages (◯ 100 houses). Finally, opposite to resident species, wintering raptors were positively related to towns, likely indicating the lower impact of harvesting on wintering species, because they do not complete their annual cycle in the Sahel, and thus are not dependent on territories and nests, which are extremely vulnerable.

Furthermore, most birds related to towns are to some extent scavengers, and thus are not intensively harvested because they are considered impure as a food source by the Muslim culture (e.g. Levitic 11, 13–19). Additionally, this result may be magnified by black kites, by far the most common species in our transects (Table 1), which is a scavenger partially relying on human waste and refuse and thus linked to human centres and their surroundings (Sanchez-Zapata et al., 2007).

General conservation insights

Much attention has been focused on habitat loss and fragmentation and on urbanization as major drivers of biodiversity loss due to human population growth (Millennium Ecosystem Assessment, 2005). Our work indicates that subsistence economies in systems with low natural environmental heterogeneity and with human populations over carrying capacity, such as the Sahel, may alone lead to exhausted biological systems even in the absence of significant agricultural or urban land-use changes, as shown by the striking impoverishment of our sedentary raptor community. This

situation is likely to be occurring in many systems of developing countries with high population growth and low carrying capacity, a situation particularly common in the arid and semiarid portions of Africa (Le Blanc & Perez, 2008).

Reductions in species richness, particularly of large body-size vertebrates and top predators, are also likely to have far-reaching consequences on the ecosystem (Rooney et al., 2006) and on the services provided to humans (Sekercioglu, Daily & Erhlich, 2004). Non-scavenger raptors may play an important role in controlling prey populations and thus in the control of pest outbreaks (Crooks & Soule, 1999; Sergio et al., 2008). Particularly in the Sahel, raptors seem to act as a biological control of locust outbreaks (Sanchez-Zapata et al., 2007). Scavenger raptors are mainly responsible for the disposal of carcasses and their functional extinction may yield increases in small scavenger-opportunist species and disease outbreaks (Pain et al., 2003). The current extreme rarity of large vultures in the Sahel detected in this work supports the severe decline of this group in many areas worldwide (Koenig, 2006).

In light of the devastating droughts and famines that occurred between the late 1960s and early 1990s, there has been sustained interest in recent decades in the study of environmental change in the Sahel (e.g. Zeng, 2003; Olsson, Eklundh & Ardo, 2005). Some authors highlight that climate change and plant cover decrease may yield an scenario of expansion of the Sahara desert (Zeng, 2003; Zeng & Yoon, 2009). Because habitat and productivity seem to play a relevant role in driving species richness, our results suggest that changes in climate, and thus in the distribution of habitats and productivity, may have a major effect on this raptor community.

Acknowledgements

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