

Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain

L. Cardador¹, M. Carrete^{2,3} & S. Mañosa¹

¹ Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Barcelona, Catalonia, Spain

² Department of Conservation Biology, Estación Biológica de Doñana (CSIC), La Cartuja, Sevilla, Spain

³ Department of Physical, Chemical and Natural Systems, Ecology Area, Universidad Pablo de Olavide, Ctra. Utrera, Sevilla, Spain

Keywords

agriculture; arable; artificial ecosystems; conservation; habitat change; preference; wetlands.

Correspondence

Laura Cardador, Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Catalonia, Spain.
Email: lcardador@ub.edu

r

Abstract

Agricultural intensification over the last 60 decades has been linked to decreases in biodiversity and in the breeding populations of several avian species in farmlands. However, agricultural intensification has not affected all species in the same way and transformed landscapes can still provide suitable habitats for species tolerant to some degree of anthropogenic change. Understanding habitat selection in man-made landscapes is a pre-requisite to effective management and conservation of the species that use them. However, habitat-related choices made by individuals occupying these landscapes are often difficult to explain, as the cues they use may be decoupled from the ecological context in which they evolved. Here, we investigated nesting habitat selection in a ground-nesting raptor breeding mainly in wetlands, which, unlike many other species occupying farmlands, has experienced a population increase in some agricultural regions. We used multivariate analysis to assess the extent to which habitat characteristics, human disturbance or proximity to other occupied sites influenced nesting-site occupancy. Our results indicate that Marsh harriers occupied breeding sites according to habitat cues obtained at two complementary spatial scales (i.e. the breeding site and the foraging area). This study indicates that a raptor species that uses human-made structures such as ponds for breeding while exploiting their surrounding crops for hunting can take advantage of agricultural intensification. Environmental disturbances are often viewed only in terms of their harmful impacts on the affected species. However, human activities are causing many types of alterations in natural landscapes that can be exploited by certain species with positive responses towards these transformations. The adaptation of some raptors to human-altered environments, such as the Marsh harrier in our study area, raises doubts regarding the appropriateness of using such species as indicators of natural habitat quality.

Introduction

Agricultural intensification over the last six decades has been linked to decreases in biodiversity and in breeding populations of several avian species in farmlands (Tucker & Heath, 1995; Chamberlain *et al.*, 2000; Donald, Green & Heath, 2001). Contributing factors to the overall impact of intensification include pesticide use, removal of hedges and other uncultivated areas to produce larger fields, earlier harvesting dates and an increase in monocultures (Newton, 2004). Generally speaking, such agricultural practices have resulted in losses of habitat quality and heterogeneity that have negatively affected avian species directly through increments in mortality or reproductive failures or indirectly by reducing or degrading their hunting and nesting habitats (Benton, Vickery & Wilson, 2003; Newton, 2004). In this context, studies of habitat selection in farmlands have been central in conservation biology and have been described as

an essential tool to assess the habitat requirements of a species and to develop effective management strategies (e.g. Blanco, Tella & Torre, 1998; Tella *et al.*, 1998; Arroyo, García & Bretagnolle, 2002; O'Connell & Yallop, 2002; Carrete & Donazar, 2005; Arroyo *et al.*, 2009).

Agricultural intensification has not affected all species in the same way, and transformed landscapes still provide suitable habitats for species tolerant to anthropogenic alterations. For example, in intensively managed lands, where artificial ponds and irrigated crops have replaced natural wetlands or created new ones, some bird species have benefitted through the creation of new foraging or breeding habitat (Czech & Parsons, 2002; Tourenq *et al.*, 2004; Sánchez-Zapata *et al.*, 2005; Moreno-Mateos, Pedrocchi & Comín, 2009; Sebastián-González, Sánchez-Zapata & Botella, 2010). The Marsh harrier *Circus aeruginosus* is a medium-size raptor that breeds mainly in wetlands and behaves as an open-habitat hunter (Cramp &

Simmons, 1994). The European Marsh harrier population underwent a dramatic population decline from 1960 to 1980 due to drainage of wetlands, contamination and direct persecution, but recovered in recent decades, when the species underwent a moderate increase, <10%, (Cramp & Simmons, 1994; BirdLife International, 2004). Contrary to other species occupying farmlands, the recovery of this species has been very noticeable in some agricultural regions, even in areas dominated by intensified crops. Within some of these regions such as the Iberian Peninsula, the increase in the Marsh harrier population has been accompanied by an increase in its geographic range, with some pairs occupying artificial ponds and reservoirs related to agricultural practices. However, the extent to which these recent occupations are due to habitat characteristics, to the proximity of other occupied sites or to a combination of these factors, is unclear. Understanding the attractiveness and quality of wetlands for wildlife in human-transformed environments is vital to the success of attempts to reconcile development and biodiversity conservation (Froneman *et al.*, 2001; Moreno-Mateos *et al.*, 2009; Sebastián-González *et al.*, 2010). Furthermore, the expanding Marsh harrier population provides an opportunity to identify some of the anthropogenic factors involved in apparently natural invasion processes that are currently favouring worldwide biotic homogenization (McKinney & Lockwood, 1999; Rice & Pfennig, 2008).

Here, we investigate the factors influencing nesting-site occupancy in an expanding population of Marsh harriers located in an agricultural area in the Iberian Peninsula, the Catalan Ebro Basin (Fig. 1a), where the species has increased from eight breeding pairs in 1997 to 53 in 2008 (Fig. 2). For this purpose, we establish the relative importance of habitat characteristics and social behaviour in the occupancy rate of breeding sites at two spatial scales. The results are discussed within the current scenario

of agriculture intensification and its potential effects on biodiversity.

Materials and methods

Study area and field procedures

The study area comprises 7300 km² within the Catalan Ebro Basin, north-eastern Spain (Fig. 1a and b). The landscape is mostly low-lying and flat, broken by discrete ranges of small hills (0–400 m a.s.l.), and has a semiarid Mediterranean climate. The annual precipitation is 300–500 mm, with most rain occurring in spring and autumn, and an annual thermal amplitude of 19–20 °C (Bosch, 2004). Traditional agriculture in this area comprises extensive cultivation of cereal crops separated by field margins, where harvested fields remain uncultivated for 1 or more years (fallow system) and are grazed extensively by livestock (Suárez, Naveso & de Juana, 1997). During the 20th century, agriculture in this area underwent several dramatic changes, including the replacement of traditionally cultivated cereals (e.g. spring-sown wheat and barley) with a variety of alternative crops (e.g. winter-sown wheat and barley, alfalfa, maize, sunflowers, deciduous fruit trees, horticultural crops and rice), the establishment of irrigation systems and the disappearance of the fallow system and field margins (Tella *et al.*, 1998). Now, the study area is an agricultural mosaic composed of arable, non-irrigated cereal crops (mainly winter-sown wheat and barley), irrigated fields (mainly alfalfa, winter-sown wheat, winter-sown barley and some sweet corn), dry fruit trees (mainly olive and almond trees) and irrigated fruit trees (mainly peach, pear, apple and nectarine trees). A total of 617 wetlands have been described over the study area, of which *c.* 92% are artificial ponds and reservoirs related to agricultural irrigation (A. Varea, unpubl. data).

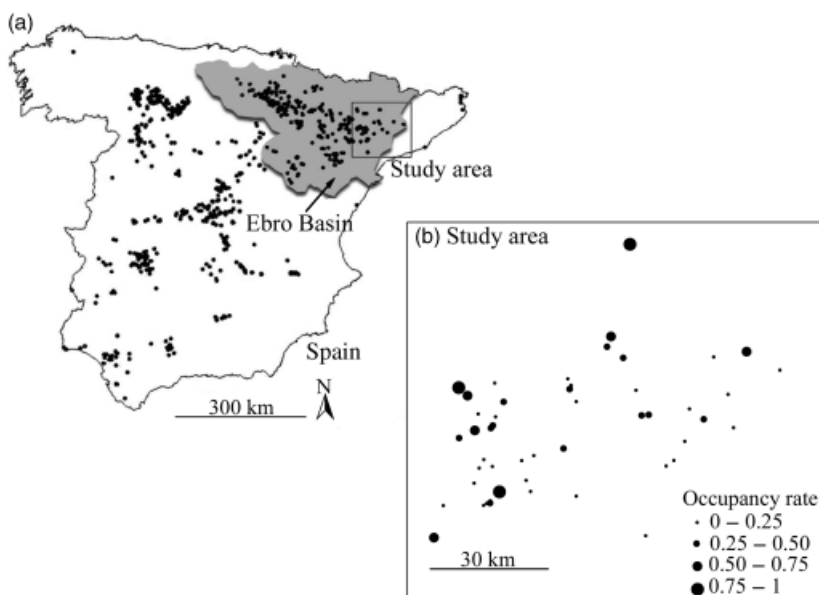


Figure 1 (a) Distribution of the breeding population of the Marsh harrier *Circus aeruginosus* in Spain in 2006 (Molina & Martínez, 2008). The Ebro Basin is shown in grey; (b) occupancy rate of monitored breeding sites in the study area (Catalan Ebro Basin, Spain, 1997–2008).

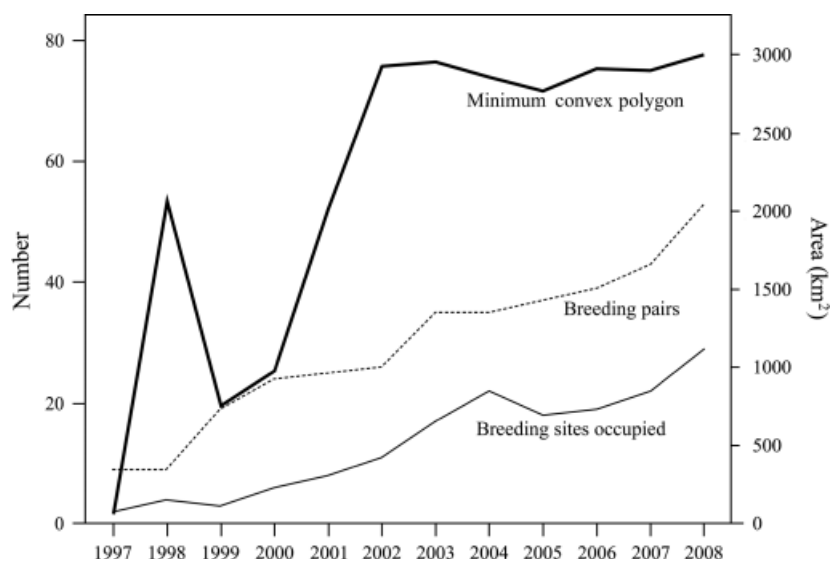


Figure 2 Population trend for the breeding population of Marsh harrier *Circus aeruginosus* in the Catalan Ebro Basin, Spain, showing the number of breeding pairs, the number of breeding sites occupied and the minimum convex polygon area including the occupied breeding sites recorded each year (Source: Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya and own data).

The breeding population of Marsh harriers in the study area was systematically monitored from 1997 to 2008 (Fig. 2). Each year, known breeding sites and other areas potentially suitable for breeding were visited repeatedly to determine occupancy, looking for signs of breeding behaviour (i.e. territorial displays or deliveries of nest material or prey items to the nest). Potentially suitable breeding sites were considered to include all wetlands (defined as artificial ponds, reservoirs, marshes and parts of rivers or watercourses; see Table 1) with the presence of tall standing reeds *Phragmites australis*, reed-mace *Typha angustifolia* or other dense emergent aquatic vegetation (Cramp & Simmons, 1994). Visits began in early April, when nest building started, and continued until fledging (May–July). A breeding site was considered to be occupied when at least one breeding pair laid eggs.

Characteristicsofthebreedingareas

The location of monitored breeding sites and associated habitat variables were entered into ArcView 3.2 Geographic Information System. We measured a total of 14 habitat variables within each monitored wetland and within a 3 km radius around the wetland to describe nest site and landscape characteristics, respectively (Table 1). Three kilometres is the average home-range size of breeding Marsh harriers estimated on the basis of radio-tracking data (Cardador *et al.*, 2009).

Variables measured at the wetlands were obtained from 1:5000 aerial photographs from 2005 (Institut Cartogràfic de Catalunya) ground-truthed in the field during 2006 (Table 1). The type of wetland was assessed in the field, while land uses and variables describing human disturbance such as distance from wetlands to the nearest villages, roads and paths were obtained from 1:50 000 digital land-use maps (Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya; Table 1).

Proximity to other occupied sites was estimated as the linear distance from wetlands to the nearest occupied

site (NND), and through an isolation index (S) describing the relative position of a given wetland within the spatial distribution of the breeding population (Carrete *et al.*, 2006). Because our Marsh harrier breeding population was the continuation of a larger breeding population located in the west of the Ebro basin (Fig. 1a), for calculations of NND and S values, we took into account Marsh harrier breeding locations both within and outside of our study area. The NND of each wetland could be calculated annually, and we used their average value as the input data. The S was taken from metapopulation theory relating to connectivity, and calculated for wetland i as $S_i = \sum \exp(-d_{ij}) \times A_j$ (with $i \neq j$), where d_{ij} is the linear distance between wetland i and j , and A_j is the number of breeding pairs in the wetland j , j representing all known occupied wetlands. Because this index is formulated to describe connectivity (Moilanen & Hanski, 1998), smaller values indicate increasing isolation. Because accurate information of the whole Marsh harrier breeding population outside the study area was only available for 2006 (data from Dirección General de Desarrollo Sostenible y Biodiversidad, Zaragoza, and SEO/BirdLife) and because the global geographic distribution of the population (and thus S) has remained unchanged during recent years (based on the comparison between distribution maps of the Marsh harrier breeding population from 1998 and 2006; Martí & Moral, 2003; Molina & Martínez, 2008), we used S from 2006 as a single estimate of isolation. This approach is justified by the fact that, for the territories in this study, estimates of S in 2006 were correlated with estimates of this parameter in all other years (Spearman's rank correlation range = 0.263–0.944; P -value range: <0.0001–0.031).

Analysis

We used logistic regressions (using the genmod procedure of SAS 8.0; SAS Institute, 2004), with a stepwise procedure, to analyse the factors affecting occupancy of wetlands by

Table 1 Variables used in models to analyse the occupancy of Marsh harriers *Circus aeruginosus* in Catalanian Ebro Basin, Spain, 1997–2008

Variables	Definition
Habitat variables	
Breeding-site level	
Type	Artificial pond (included constructions of small dimensions < 13 ha to store water related to agricultural practices), reservoir (included water bodies originated by a floodgate), river (included junctions of rivers and meanders of permanent rivers), watercourse (included reedbeds in natural channels through which water flows only occasionally, during periods of maximum rain), inland natural wetland (included inland marshy terrains and salt marshes where water availability drastically decreases or even dries completely during spring and summer).
Vegetation	Area of emergent vegetation at the wetland (ha)
Shape	Length of emergent vegetation edge per surface of emergent vegetation (m ha^{-1})
Water	Area of open water (ha)
Landscape level	
Intensified-herbaceous	Extent of intensified, irrigated herbaceous crops within 3 km of the wetland (%)
Intensified-tree	Extent of intensified, irrigated fruit trees within 3 km of the wetland (%)
Traditional-herbaceous	Extent of traditional, non-irrigated herbaceous crops within 3 km of the wetland (%)
Traditional-tree	Extent of traditional, non-irrigated fruit tree crops within 3 km of the wetland (%)
Vineyard	Total extent of intensified vineyards within 3 km of the wetland (%)
Other	Total extent of unsuitable habitats for the species (i.e. urban areas and forest) within 3 km of the wetland (%)
Village	Distance to the nearest village (m)
Road	Distance to the nearest road (m)
Path	Distance to the nearest path (m)
Proximity to other occupied sites	
NND	Distance to the nearest occupied wetland (km)
S	Isolation of the wetland with respect to the other occupied ones

NND, nearest neighbour distance.

Marsh harriers (binomial error distribution; logit-link function). As wetland sites comprise only emergent vegetation and open water, the inclusion of these two variables means that the size of the entire site was accounted for in the

models (Table 1). We used the occupancy rate (number of years occupied/total years monitored) as the dependent variable. For each significant model ($P < 0.05$), we calculated the percentage of deviance explained ($100 \times (\text{deviance}_{\text{null model}} - \text{deviance}_{\text{model}}) / \text{deviance}_{\text{null model}}$). As neighbouring wetlands could have similar environmental conditions due to their spatial autocorrelation, we added, in every model, a spatial term composed of the X and Y coordinates (UTM Projection), and all of their interactions terms up to the third order (Legendre & Legendre, 1998). However, to avoid artificial increases in the explained variation, we first tested the nine explanatory terms in our logistic regression models using a stepwise procedure and we only retained the significant ones (Borcard, Legendre & Drapeau, 1992).

Following Carrete *et al.* (2007), we used deviance partitioning to take account of co-linearity between spatially related variables. Deviance partitioning entails the calculation of incremental improvement in models due to the inclusion of a variable in every possible model incorporating that variable. This allows the ‘pure’ effect of each explanatory variable to be separated from joint effects that cannot unambiguously be attributed to one variable or another (Fig. 3a). For a more detailed description of this method, see Carrete *et al.* (2007).

Finally, we tested whether the relationship between area of emergent vegetation (vegetation) and occupancy rate could be accounted for by a null model involving only random settlement with respect to vegetation area. Following Gillings & Fuller (2001), we used a randomization procedure that produced the expected occupancy rate for locations of different sizes (for each location, this procedure was repeated 100 times). Thus, our database included a set of observed values of occupancy rates (one for each locality) and a set of expected values derived from random settlement (100 for each locality). A generalized linear model (GLM) (binomial error distribution; logit-link function) with occupancy rate as the dependent variable was used to determine whether there was a significant difference in the relationship between vegetation area and occupancy rate for the observed set and the random set of data. Specifically, we tested the potential interaction between ‘vegetation’ and ‘type of data’ (a categorical variable with two levels: observed/random).

Results

Wetlands characteristics and occupation pattern of the breeding population

In total, 51 wetlands within the study area had the minimum requirements described for Marsh harrier (i.e. the presence of dense emergent aquatic vegetation) and were monitored during the study period (Fig. 1b). Wetland sizes ranged from 0.5 to 287 ha, but 88% of them were smaller than 15 ha, with an average size of 4.9 ± 4.1 ha. Only 32% of monitored wetlands were of a natural origin, while 39% were artificial ponds and 29% were reservoirs related to intensive

agriculture (for definitions of artificial ponds and reservoirs, see Table 1). Emergent vegetation was mainly composed of a mixture of reed and reedmace, with reed being the dominant species in c. 90% of wetlands. Thirty-five out of the 51 monitored wetlands were occupied at least once from 1997 to 2008 (Fig. 3, Table 2). During this period, we recorded 375 breeding attempts, 354 of which resulted in egg laying. For wetlands occupied at least once during the study period, the mean number of breeding pairs per year of occupation was 1.45 ± 1.79 (range 1–11.50, $n = 35$).

Occupancy models for the breeding population

Our results show that Marsh harriers occupied breeding sites using habitat cues obtained at two complementary spatial scales. Proximity to other occupied sites seemed not to strongly affect occupancy rates (NND: $\chi^2 = 0.04$, $P = 0.84$; S : $\chi^2 = 0.09$, $P = 0.76$).

The habitat model explained 67% of the deviance in the dataset, a value that increased to 71% when the latitude (Y) was also included. The deviance partitioning analysis shows that the area of emergent aquatic vegetation had the greatest effect on the occupancy rate of wetlands by Marsh harriers, its pure effect accounting for c. 65% of the total deviance explained (Fig. 3b). A GLM showed that the observed relationship was significantly greater than a null model would predict (interaction vegetation \times type of data: $\chi^2 = 6.20$, $P = 0.013$), indicating that the observed increase in the occupancy rate with vegetation area was steeper than expected and could not arise solely by a random settlement pattern (Fig. 4). The pure effects of the type of wetland (25%) and the percentage of intensified herbaceous crops in the surroundings (17%) were also important in explaining variability in occupancy (Fig. 3b). A smaller amount of

deviance (< 5%) was explained by each of the joint effects of these variables (d, e, f and g). Thus, the occupancy rate of wetlands by Marsh harriers increased with their area of emergent aquatic vegetation and the percentage of irrigated herbaceous crops in their surroundings, with a minimum at inland-natural wetlands (see Table 3).

Analysis of changes in mean productivity of locations with respect to the habitat characteristics measured in the study suggested that no significant relationships existed between this demographic parameter (i.e. mean number of young fledged per breeding pair) and habitat attributes

Table 2 Characteristics of breeding sites occupied at least once during the study period, Catalan Ebro Basin, Spain, 1997–2008

Variable	Mean \pm SD	Range	Units
Habitat variables			
Breeding-site level			
Vegetation	8.4 \pm 19.6	0.5–103.2	ha
Shape	551 \pm 290	105–1268	m ha ⁻¹
Water	18.5 \pm 49.8	0–224	ha
Landscape level			
Intensified-herbaceous	41.4 \pm 31.5	0.0–99.5	%
Intensified-tree	18.3 \pm 22.4	0.0–83.4	%
Traditional-herbaceous	20.0 \pm 27.4	0.4–94.8	%
Traditional-tree	3.0 \pm 5.4	0.0–16.9	%
Vineyard	4.8 \pm 11.4	0.0–41.4	%
Other	12.6 \pm 17.3	0.0–74.8	%
Human pressure			
Village	2348 \pm 1107	75–4235	m
Road	66 \pm 129	0–631	m
Path	40 \pm 79	0–280	m
Proximity to other occupied sites			
Distance	13.8 \pm 8.6	3.8–32.2	km
Isolation	0.13 \pm 0.26	0–1	

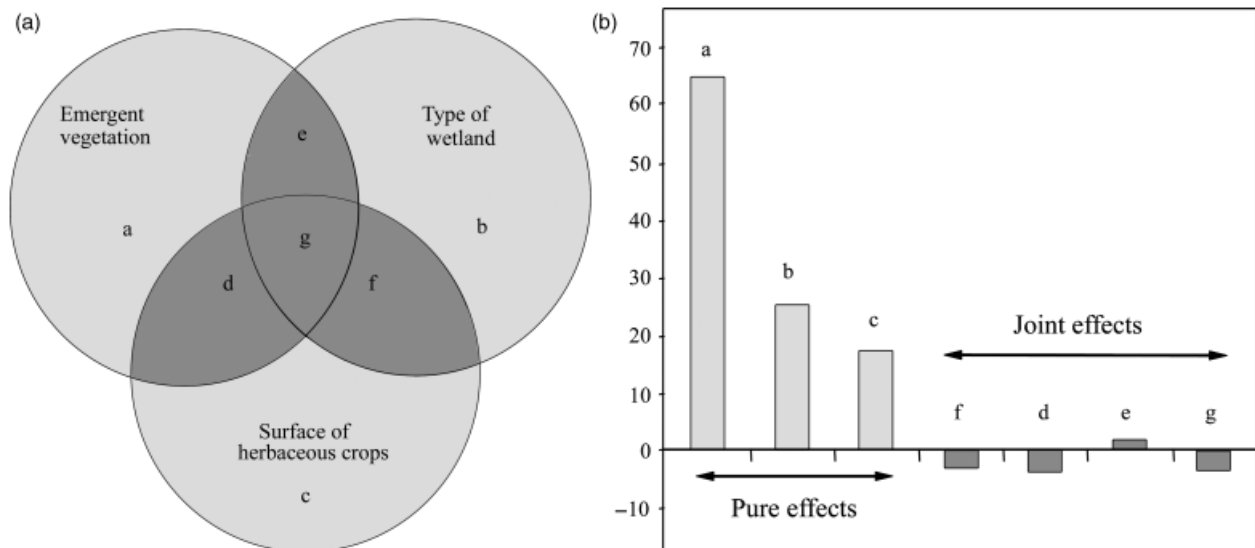


Figure 3 (a) Deviance partitioning analysis for the occupancy rate of breeding sites by Marsh harriers *Circus aeruginosus*. (b) Percentage of variability in occupancy rate explained by the pure and joint effects of habitat variables.

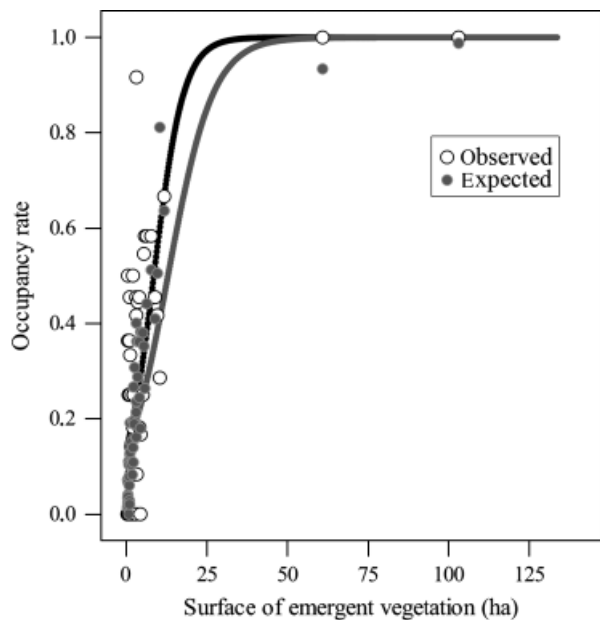


Figure 4 Effect of surface of emergent vegetation on the occupancy rate, derived from fitted values from GLM estimates (binomial error distribution, logit-link function). The observed trend is shown with a black line. The grey line indicates the expected trend under a null model in which occupancy rate variation arises solely by individuals settling randomly with respect to vegetation area. Observed occupancy rates and mean expected occupancy rates from 100 replicates (see "Materials and methods") are also shown.

(GLMs, normal error distribution, identity link function: all $P > 0.45$).

Discussion

Factors affecting occupancy rate: can human-made landscapes provide suitable breeding habitat for Marsh harriers?

When choosing a site at which to settle, individuals need to simultaneously consider the quality of available sites in terms of their environmental conditions, resource availability and the presence of predators and/or parasites (Martin, 1993; Penteriani, Gallardo & Roche, 2002). However, this quality can be modulated by the presence of conspecifics, which may either decrease or enhance the appeal of a site (Stephens & Sutherland, 1999). In our study model, the occupancy rate of wetlands by Marsh harriers was mainly explained by the independent effect of habitat features acting at two spatial scales, that is, the breeding site (area of emergent aquatic vegetation and type of wetland) and the foraging area (percentage of intensified, irrigated herbaceous crops in the surroundings). Neither human pressure variables nor proximity to other occupied sites seemed to be important determinants of occupancy rates in this expanding population.

Table 3 Generalized linear model obtained for the occupancy of breeding sites by Marsh harriers *Circus aeruginosus* in the Catalanian Ebro Basin, Spain (1997–2008)

Parameter	Estimate	SE	χ^2	P
Intercept	-148.06	48.85	9.19	0.0024
Y	0.00003	0.00001	8.89	0.0029
Type (inland-natural wetland)	-3.69	0.92	16.18	<0.0001
Type (artificial pond)	-0.06	0.37	0.03	0.8743
Type (reservoir)	-0.47	0.37	1.59	0.2068
Type (river)	-1.07	0.73	2.13	0.1443
Type (watercourse)	-	-	-	-
Vegetation	0.28	0.05	27.3	<0.0001
Intensified-herbaceous	0.02	0.01	22.01	<0.0001

d.f. = 41.

Nest protection and food availability are key determinants of habitat selection patterns in different avian species (Martin, 1993; Penteriani *et al.*, 2002; Sergio, Pedrini & Marchesi, 2003). In our study species, both factors seem to influence occupancy. Indeed, occupancy rate increased with emergent vegetation area steeper than expected by a random settlement pattern. This relationship was particularly apparent in wetlands with small and intermediate surfaces of emergent vegetation (up to *c.* 50 ha). The occupancy rate was higher in wetlands with larger surfaces of emergent vegetation, perhaps because harrier breeding attempts in such sites experience lower rates of failure due to terrestrial predators, disturbance by humans or local flooding events (Bavoux *et al.*, 1989; Fernández & Azcona, 1993; Buczek & Keller, 1994; Stanevicius, 2004; Eglington *et al.*, 2009). At a landscape scale, harriers responded positively to the area of irrigated herbaceous crops, suggesting that they offer a larger abundance or accessibility to prey (Preston, 1990). This interpretation is reinforced by a previous finding showing how radio-tracked Marsh harriers occupying intensified habitats tended to have smaller home ranges than birds nesting within non-irrigated ones (Cardador *et al.*, 2009). Intensified farmlands in our study area included cereals (basically irrigated wheat and barley), alfalfa and some maize crops. Some of these crops, such as intensified cereals and maize, are used infrequently by Marsh harriers, probably because the height and uniformly dense growth that characterize these crops for much of the summer result in low availability of prey to hunting harriers (Cardador & Mañosa, in press). However, Marsh harriers may be taking advantage of regularly mowed fields (intensively managed alfalfa), which offer an adequate vegetation structure for hunting during a major part of the year (Ursúa, Serrano & Tella, 2005; Kitowski, 2007). Furthermore, intensified herbaceous crops in our study area, mainly alfalfa fields, seem to hold higher densities of small mammal prey, especially Mediterranean Pine Vole, than do more extensive crops (A. Varea and A. Folch, unpubl. data). More specific studies on hunting habitat selection are necessary to determine whether and to what extent managed herbaceous crops are preferred hunting habitats of Marsh harriers.

The occupancy rate at natural wetland sites was lower than for any other habitat type, and may be a consequence of their drainage pattern. In the study area, water reserves at natural wetlands decrease drastically, or even dry out completely, during spring and summer, when harriers breed. Thus, their emergent vegetation is less developed compared with that of other wetlands (i.e. reservoirs, artificial ponds, rivers and watercourses), offering less suitable breeding sites for nesting.

Agricultural intensification and changes in bird communities: winning and losing species in a world of change

Agricultural intensification has had deleterious effects on farmland bird populations at a scale that is comparable to deforestation and global climate change, thus being a major anthropogenic threat to biodiversity (Donald *et al.*, 2001). The key to explain this phenomenon seems to be the loss of ecological heterogeneity, which is important in maintaining resources for species-rich communities of organisms (Benton *et al.*, 2003). Examples of steppe and pseudo-steppe bird species declining after the intensification of agricultural practices are numerous in Spain, which is the western European stronghold of many of these species (Rodríguez & de Juana, 1991; Tella, Torre & Sánchez, 1996; Suárez *et al.*, 1997; Blanco *et al.*, 1998; Tella *et al.*, 1998). However, there are also some cases of species gaining new habitat opportunities due to the development of intensive crops and the associated agricultural infrastructure. The abundance of some waterbirds at artificial ponds, for example, seems to be larger in comparison with their populations in natural (but degraded) wetlands (Sebastián-González *et al.*, 2010). Our results indicate that a raptor species using wetlands for breeding while relying on the surrounding vegetation for feeding can also take advantage of agricultural intensification, at least when food availability is not compromised. Given what is known about other European Marsh harrier populations, many of which have undergone recent expansion (BirdLife International, 2004), our results suggest that this bird could be a winning species in a world of change.

Direct anthropogenic introductions are not the only mechanism favouring the spread of species towards new environments. Human activities are causing many types of alterations in natural landscapes that can be exploited by certain species with positive responses towards these transformations (McKinney & Lockwood, 1999). However, the benefits of transformation on some widespread species (referred to as 'winning species'; McKinney & Lockwood, 1999), such as waterbirds in our study area (Estrada *et al.*, 2004), and the harmful effects on others (referred to as 'losing species'; McKinney & Lockwood, 1999), such as pseudo-steppe birds in our study area (Estrada *et al.*, 2004), could lead to biotic homogenization processes that can be considered an unprecedented form of global change (Ricciardi, 2007) and one of the most important forms of biological impoverishment world-wide (Olden *et al.*, 2004).

Raptors have been proposed as appropriate indicators for monitoring changes at an ecosystem scale because they are at the top of food chains, occurring across a broad gradient of anthropogenic disturbance, from pristine wilderness to metropolitan areas, and because individual species are often associated with particular habitat types (e.g. Tella *et al.*, 1998; Sánchez-Zapata *et al.*, 2003; Carrete & Donazar, 2005; Carrete *et al.*, 2009). Moreover, in some biological systems, these top predators are strongly associated with high biodiversity values (Sergio *et al.*, 2008). However, the adaptation of some raptors to human-altered environments (Anderson, 2001; Panasci & Whitacre, 2002; present results) makes their widespread potential use as valuable indicators of natural habitat quality controversial (Rodríguez-Estrella, Donazar & Hiraldo, 1998; Carrete *et al.*, 2009). Our results suggest that Marsh harriers respond positively to some degree of intensification, which reduces their usefulness as an indicator species of natural habitat quality. Moreover, preliminary analysis of changes in productivity with respect to the habitat characteristics measured in this study suggests that no significant relationships exist between this demographic parameter and habitat attributes, suggesting that none of the habitats occupied in this area are population sinks. However, further research is needed to determine whether finer cues such as individual survival can indicate other forms of ecosystem degradation such as water pollution or pesticide use during crop development.

Acknowledgements

We wish to thank A. Varea, who inventoried wetlands within the Catalanian Ebro Basin; J. Bonfil, F. Pont and P. Cerralbo, who assisted in fieldwork; Ajuntament de Torres de Segre (Lleida, Spain) for the logistic support. Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya (Barcelona, Spain) provided data on census of the breeding population studied. Direcció General de Desenvolupament Sostenible y Biodiversidad (Zaragoza, Spain) provided data on census of breeding population in Aragon in 2006. SEO Birdlife provided data on census of breeding population in Spain in 2006. S. Young kindly revised English language. The comments of A. Amar, J.A. Sánchez-Zapata and M. Wilson greatly contributed to improve previous versions of the paper. L.C. was supported by a postgraduate grant from Ministerio de Ciencia e Innovación (MICINN) of Spain. This paper was partially written during a pre-doctoral stay of L.C. in the EBD (CSIC).

References

- Anderson, D.L. (2001). Landscape heterogeneity and diurnal raptor diversity in Honduras: the role of indigenous shifting cultivation. *Biotropica* **33**, 511–519.
- Arroyo, B., Amar, A., Leckie, F., Buchanan, G.M., Wilson, J.D. & Redpath, S. (2009). Hunting habitat selection by

- hen harriers on moorland: implications for conservation management. *Biol. Conserv.* **142**, 586–596.
- Arroyo, B., García, J.T. & Bretagnolle, V. (2002). Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Anim. Conserv.* **5**, 283–290.
- Bavoux, C., Burneleu, G., Leroux, A. & Nicolau-Guillaumet, P. (1989). Le busard des roseaux *Circus a. aeruginosus* en Charente-maritime (France). II – Chronologie et paramètres de la reproduction. *Alauda* **57**, 247–262.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188.
- BirdLife International. (2004). *Birds in Europe: population estimates, trends and conservation status*. Cambridge: BirdLife International (BirdLife Conservation Series No 12).
- Blanco, G., Tella, J.L. & Torre, I. (1998). Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrhocorax* conservation in a Spanish pseudo-steppe landscape. *J. Appl. Ecol.* **35**, 232–239.
- Borcard, D., Legendre, P. & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology* **73**, 1045–1055.
- Bosch, A. (2004). Clima. In *Els ocells de la Plana de Lleida*: 37–45. Calvet, J., Estrada, J., Mañosa, S., Moncasí, F. & Solans, J. (Eds). Lleida: Pagès Editors.
- Buczek, T. & Keller, M. (1994). Breeding ecology of the Marsh Harrier *Circus aeruginosus* in eastern Poland. Part 1. Causes of brood losses. *Acta Ornithol.* **29**, 81–87.
- Cardador, L. & Mañosa, S. (in press). Foraging habitat use and selection of western Marsh-harriers (*Circus aeruginosus*) in intensive agricultural landscapes. *J. Raptor Res.*
- Cardador, L., Mañosa, S., Varea, A. & Bertolero, A. (2009). Ranging behaviour of Marsh Harriers *Circus aeruginosus* in agricultural landscapes. *Ibis* **151**, 766–770.
- Carrete, M. & Donazar, J.A. (2005). Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. *Biol. Conserv.* **126**, 582–590.
- Carrete, M., Grande, J.M., Tella, J.L., Sánchez-Zapata, J.A., Donazar, J.A., Díaz-Delgado, R. & Romo, A. (2007). Habitat, human pressure, and social behaviour: partialling out factors affecting territory extinction in the Egyptian vulture. *Biol. Conserv.* **136**, 143–154.
- Carrete, M., Sánchez-Zapata, J.A., Tella, J.L., Gil-Sánchez, J.M. & Moleón, M. (2006). Components of breeding performance in two competing species: habitat heterogeneity, individual quality, and density-dependence. *Oikos* **112**, 680–690.
- Carrete, M., Tella, J.L., Blanco, G. & Bertelotti, M. (2009). Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes. *Biol. Conserv.* **142**, 2002–2011.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubbs, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**, 771–788.
- Cramp, S. & Simmons, K.E.L. (eds) (1994). *Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. Vol. II. Hawks to bustards*. Oxford: Oxford University Press.
- Czech, H.A. & Parsons, K.C. Agricultural wetlands and waterbirds: a review (2002) *Waterbirds* **25**, Special publication 2: 56–65.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. Roy. Soc. Lond.* **268**, 25–29.
- Eglington, S.M., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Bolton, M. (2009). Habitat management and patterns of predation of Northern Lapwings on wet grasslands: the influence of linear habitat structures at different spatial scales. *Biol. Conserv.* **142**, 314–324.
- Estrada, J., Pedrocchi, V., Brotons, L. & Herrando, S. (2004). *Atlas dels ocells nidificants de Catalunya 1999–2002*. Barcelona: Institut Català d'Ornitologia (Ico)/Lynx Edicions.
- Fernández, C. & Azcona, P. (1993). Human disturbance affects parental care of marsh harriers and nutritional status of nestlings. *J. Wildl. Manage.* **57**, 602–608.
- Froneman, A., Mangnall, M.J., Little, R.M. & Crowe, T.M. (2001). Waterbird assemblages and associated habitat characteristics of farm ponds in the Western Cape, South Africa. *Biodivers. Conserv.* **10**, 251–270.
- Gillings, S. & Fuller, R.J. (2001). Habitat selection by Skylarks *Alauda arvensis* wintering in Britain in 1997/98. *Bird Study* **48**, 293–307.
- Kitowski, I. (2007). Inter-sexual differences in hunting behaviour of Marsh Harriers (*Circus aeruginosus*) in Southeastern Poland. *Acta Zool. Lit.* **17**, 70–77.
- Legendre, P. & Legendre, L. (1998). *Numerical ecology*. Amsterdam: Elsevier.
- Martí, R. & Moral, J.C. (Eds.). (2003). *Atlas de las Aves Reproductoras de España*. Madrid: Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología.
- Martin, T.E. (1993). Nest Predation and Nest Sites. *BioScience* **43**, 523–532.
- McKinney, M.L. & Lockwood, J.L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14**, 450–453.
- Moilanen, A. & Hanski, I. (1998). Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* **79**, 2503–2515.
- Molina, B. & Martínez, F. (2008). *El aguilucho lagunero en España. Población en 2006 y métodos de censo*. Madrid: Seo/BirdLife.
- Moreno-Mateos, D., Pedrocchi, C. & Comín, F.A. (2009). Avian communities' preferences in recently created agricultural wetlands in irrigated landscapes of semi-arid areas. *Biodivers. Conserv.* **18**, 811–828.

- Newton, I. (2004). The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**, 579–600.
- O'Connell, M. & Yallop, M. (2002). Research needs in relation to the conservation of biodiversity in the UK. *Biol. Conserv.* **103**, 115–123.
- Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* **19**, 18–24.
- Panasci, T.A. & Whitacre, D.F. (2002). Roadside hawk breeding ecology in forest and farming landscapes. *Willson Bull.* **114**, 114–121.
- Penteriani, V., Gallardo, M. & Roche, P. (2002). Landscape structure and food supply affect eagle owl (*Bubo bubo*) density and breeding performance: a case of intra-population heterogeneity. *J. Zool.* **257**, 365–372.
- Preston, C. (1990). Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* **92**, 107–112.
- Ricciardi, A. (2007). Are Modern Biological Invasions an Unprecedented Form of Global Change? *Conserv. Biol.* **21**, 329–336.
- Rice, A.M. & Pfenning, D.W. (2008). Analysis of range expansion in two species undergoing character displacement: why might invaders generally 'win' during character displacement? *J. Evol. Biol.* **21**, 696–704.
- Rodríguez, J.M. & de Juana, E. (1991). Land-use changes and the conservation of dry grassland birds in Spain. In *Farming and birds in Europe*: 43–78. Pain, D. & Pienkowsky, M.W. (Eds). London: Academic Press.
- Rodríguez-Estrella, R., Donázar, J.A. & Hiraldo, F. (1998). Raptors as indicators of environmental change in the scrub habitat of Baja California Sur, Mexico. *Conserv. Biol.* **12**, 921–925.
- SAS Institute. (2004). *SAS/STAT 9.1. User's guide*. Cary: SAS Institute.
- Sánchez-Zapata, J.A., Anadón, J.D., Carrete, M., Giménez, A., Navarro, J., Villacorta, C. & Botella, F. (2005). Breeding waterbirds in relation to artificial pond attributes: implications for the design of irrigation facilities. *Biodivers. Conserv.* **14**, 1627–1639.
- Sánchez-Zapata, J.A., Carrete, M., Grivilov, A., Sklyarenko, S., Ceballos, O., Donázar, J.A. & Hiraldo, F. (2003). Land use changes and raptor conservation in steppe habitats of Eastern Kazakhstan. *Biol. Conserv.* **111**, 71–77.
- Sebastián-González, E., Sánchez-Zapata, J.A. & Botella, F. (2010). Agricultural ponds as alternative habitat for waterbirds: spatial and temporal patterns of abundance and management strategies. *Eur. J. Wildl. Res.*, **56**, 11–20.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K. & Hiraldo, F. (2008). Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Ann. Rev. Ecol. Evol. Syst.* **39**, 1–19.
- Sergio, F., Pedrini, P. & Marchesi, L. (2003). Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. *Biol. Conserv.* **112**, 351–362.
- Stanevicius, V. (2004). Nest-site selection by marsh harrier (*Circus aeruginosus*) in the shore belt of helophytes on large lakes. *Acta Zool. Lit.* **14**, 47–53.
- Stephens, P.A. & Sutherland, W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405.
- Suárez, F., Naveso, M.A. & de Juana, E. (1997). Farming in the dry-lands of Spain: birds of the pseudosteppes. In *Farming and birds in Europe*: 297–330. Pain, D. & Pienkowsky, M.W. (Eds). London: Academic Press.
- Tella, J.L., Forero, M.G., Hiraldo, F. & Donázar, J.A. (1998). Conflicts between lesser kestrel conservation and European agricultural policies as identified by habitat use analyses. *Conserv. Biol.* **12**, 593–604.
- Tella, J.L., Torre, I. & Sánchez, C. (1996). Habitat availability and roost-site selection by the stone curlew *Burhinus oedicnemus* in an arid cultivated landscape (los Monegros, NE Spain). *Rev. d'Ecol.* **51**, 153–159.
- Tourenq, C., Benhamou, S., Sadoul, N., Sandoz, A., Mesléard, F., Martin, J. & Hafner, H. (2004). Spatial relationships between tree-nesting heron colonies and rice fields in the Camargue, France. *Auk* **121**, 192–202.
- Tucker, G.M. & Heath, M.F. (1995). *Birds in Europe. Their conservation status*. Cambridge: BirdLife International (BirdLife Conservation Series no. 3).
- Ursúa, E., Serrano, D. & Tella, J.L. (2005). Does land irrigation actually reduce foraging habitat for breeding lesser kestrels? The role of crop types. *Biol. Conserv.* **122**, 643–648.