13 November 2019

National Infrastructure Planning
Cleve Hill Solar Park

BY EMAIL

Deadline 7 – Research into the Impacts on Marsh Harrier

Dear Hefin,

On behalf of GREAT I am submitting our concerns about the potential negative impacts on the marsh harrier population should this proposal be approved.

As stated by Natural England in ISH 6 (11 September 2019), there is still uncertainty that the marsh harrier's may consider the changes to the site so great that they won't use the area. Although the applicant considers this unlikely, their opinion should not be considered due to a clear conflict of interest and lack of expertise in this matter.

At the same hearing, Kent Wildlife Trust stated that the solar panels will make it more difficult for marsh harriers to survey to hunt, and that this is a unique project with no experience elsewhere to draw on.

The ExA pointed out the fundamental disagreement between some parties and asked the applicant to respond. Mr Phillips suggested that the law only requires them to be sure beyond scientific doubt, yet they have not provided any research evidence to suggest 'beyond scientific doubt' has been proved.

Whilst there is very limited research on the marsh harrier in the UK, there is a significant amount of research on the marsh harrier in Spain, examples of which are included below:

- **Effect of prey on a predator's breeding success** (Appendix A) - This research found a direct correlation between the populations of nesting pairs on the availability of common voles during spring. This demonstrates that a reduction in foraging area on the agricultural land for the marsh harriers could have negative impacts on the breeding success of the species.

- **Ranging behaviour of the marsh harrier in agricultural landscapes** (Appendix B) – This research found the increase and spread of the marsh harrier population has been noticeable in some agricultural regions, including those dominated by intensified farmlands. Male home-range intensive-use areas were generally single areas, including the fields around the nest. This demonstrates the importance of retaining the current area of intensified farmland.

- **Factors affecting the expansion success of bird populations in human- transformed environments: The case of the Marsh Harrier Circus aeruginosus in the Ebro Valley** (Appendix C) – This research found that land-use changes, habitat fragmentation, environmental pollution, invasive species and nutrient enrichment have been reported to be some of the major human-induced global changes that negatively affect population growth and species' geographic ranges. As the solar park will introduce significant land use changes, and there is an intention to enrich some of the areas with nutrients, these must be considered as potential negative impacts for the marsh harriers. Additionally, contrary to other farmland species, the marsh harriers' recovery has been pronounced in regions dominated by agricultural habitats, including regions of intensive croplands. The marsh harrier seems to be an example of a native species that has benefited from this transformation and still rely on traditional extensive cereal farmland for foraging. Unlike most farmland birds, intensive agricultural areas represent higher quality habitat for marsh harriers than extensive croplands. Indeed, the abundance of small mammals, a chosen and high-quality prey, seems to be greater in intensive agricultural areas. On a large scale, spatial constraints such as geographic barriers (e.g. a solar park) can limit the ability of a species to fully occupy its potential habitat. These points demonstrate that it is vitally important for this land to remain as intensive farmland to protect the marsh harrier and approval of this application will be detrimental to their survival in this area.

- **Can intensive agricultural landscapes favour some raptor species? The Marsh Harrier in north-eastern Spain**. (Appendix D) – This research states the marsh harrier breeds mainly in wetlands and behaves as an open-habitat hunter. This open habitat would be removed by the solar park development, reducing it instead to thin strips of green between array tables.

- **Predicting off-site impacts on breeding success of the marsh harrier** (https://wildlife.onlinelibrary.wiley.com/doi/pdf/10.1002/jwmg.21266) – This research highlights that this species is negatively impacted by artificial land use within 2 km of their range. As the Cleve Hill development will be within this distance we believe that, should it be approved, this will be detrimental to the continued success of the marsh harrier at this site.

- **Human Disturbance Affects Parental Care of Marsh Harriers and Nutritional Status of Nestlings** (https://www.jstor.org/stable/3809289?socuuid=9651e34d-b28d-4e5b-aeb0-078af1ae5ad7&socplat=email&seq=1#page_scan_tab_contents) – This research found minor human disturbances may cause long-term effects on lifetime

> reproductive success of marsh harriers by increasing energy and time expenditure in non-reproductive activities and by reducing condition of nestlings. The number of food items delivered and the time spent by males and females in the nesting area and on the nest decreased during disturbed periods, especially during incubation, whereas behaviours related to stress (alarm calls, chases against other intruding birds, and percentage flying time) increased. As the expected disturbance of the solar park will be significant, both in terms of duration and change, the negative impact will be much greater than that found in this report which is unacceptable.

In view of this and other available research, which the applicant has not provided, we do not believe that this case has been proven ‘beyond scientific doubt’ and ask that the ExA consider this during their review.

Kind regards,

Marie King

Effect of prey on a predator's breeding success. A 7-year study on common vole (Microtus arvalis) and ....

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Effect of prey on a predator's breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's harrier (*Circus pygargus*) in a West France marsh

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Abstract

The results obtained during the seven years of this study on the Saintongeais marshes showed that the population of the common vole, *Microtus arvalis*, displays episodic outbreaks in the study site.

The reproductive biology of the Montagu's harrier, *Circus pygargus*, was studied in close relation to the dynamics of this rodent. All the breeding parameters of harriers showed significant variations from year to year. Some of them (nest density, production of young) were correlated to the available vole densities during the course of the breeding season.

The settlement of nesting pairs was directly correlated with yearly changes in the availability of common voles during spring.

A mean difference of up to two fledglings per nest could be observed between years with a high and low summer vole density. This latter result differs from those reported by certain authors on other harrier species and validates the hypothesis that such cyclic populations of voles directly affect the productivity of specialized populations of this raptor species in this kind of habitats.

Keywords: Breeding success, *Circus pygargus*, *Microtus arvalis*, vole cycle, specialist predator.

Résumé

Les résultats obtenus au cours de ces sept années d'étude dans les marais Saintongeais ont permis de mettre en évidence des explosions démographiques épisodiques de la population de campagnol des champs, *Microtus arvalis*.

La biologie de reproduction du busard cendré, *Circus pygargus*, a été étudiée en étroite relation avec la cinétique de population de ce rongeur. Nous observons des variations interannuelles significatives de tous les paramètres de la reproduction des busards. Certains d'entre eux (densité de nicheurs, production en jeunes) sont corrélables aux densités de campagnols disponibles au cours des diverses phases de la saison de reproduction.

La fixation des couples nicheurs sur le site d'étude était directement corrélable aux variations interannuelles de disponibilité des campagnols au printemps.

Une différence moyenne atteignant deux jeunes à l'envol par nid a pu être observée entre les années de forte et de faible densité estivale de campagnols. Ce dernier résultat diffère des observations rapportées par certains auteurs sur d'autres espèces de busards. Il nous permet de

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valider l'hypothèse du caractère "spécialiste" de ce rapace et d'une influence directe des populations cycliques de ce campagnol sur le succès reproducteur de ce prédateur dans ce type de milieu.

INTRODUCTION

The French Atlantic marshes cover an area of about 240 000 ha. The small mammal community of these marshes is dominated by the common vole (*Microtus arvalis*) which displays important cyclic variations in population density (SPITZ, 1974; BUTET & LEROUX, 1989, in press). A large community of raptors is also observed and these marshes are one of the most important nesting sites for the French population of the Montagu's harrier, *Circus pygargus* (LEROUX, 1987).

Montagu's harrier has a narrow prey spectrum but particular populations differ sometimes extremely in prey choice (SCHIPPER, 1973; KROGULEC, pers. com.). THIOLLAY (1968) found that this raptor was specialized on small mammals and mainly on common vole in western France marshes. Such predator-prey relationships provide good models for studying food-influenced reproduction since generalist predators are supposed to be less affected by cyclic fluctuations in a single prey. Consequently, diurnal and noctural raptors feeding on microtine species are the most commonly cited avian-mammal examples investigated to evaluate variations in nesting densities as well as breeding success and adaptive behavioural responses to prey fluctuations (LOCKIE, 1955; HAGEN, 1969; GALUSHIN, 1974; HAMERSTROM, 1979; VILLAGE, 1981; SIMMONS *et al.*, 1986).

Main studies on harriers reported no reliable correlation between food availability and the number of young produced (HAMERSTROM, 1979; SIMMONS *et al.*, 1986). During this 7-year field study, we used a large prey sampling scale to obtain reliable local vole density data during successive harrier breeding seasons. Comparative analysis of these data with harrier nesting densities and various other breeding parameters enabled us to test the hypothesis of food-influenced breeding biology in this predator-prey model.

STUDY AREA

The study area (Saintongeais marshes) (45°57' N, 0°55' W) is situated on both sides of the Charente river (Charente-Maritime, France). The sampling area extended over 300 km^2 and its spatial structure comprised parts with different histories: old salting marshes abandoned for several centuries and drained flat marshes. The soil, with this surface heterogeneity and associated differences in hydromorphy, supports various plant communities from reed swamp to grassland. A dense ditch network delimits the parcels where extensive grazing represents the most common land use. Currently both an extension of the fallow land due to the abandonment of pastures and an intensification of wheat cultures on recently drained areas are observed.

This heterogeneity of land use offers various nesting sites for raptors characterized by dense and tall herbaceous communities (*Carex spp.*, *Scirpus spp.*...) and ungrazed or old abandoned pastures. Wheat fields constitute new nesting sites.

METHODS

The dynamics of the vole population was sampled by the line live trapping method using the live traps model (INRA, Aubry, 1950). We used 20 trap lines randomly located on different parcels respecting the relative importance of agricultural land use within the study area. In practice, there were 4 trap lines in cultivated fields, 4 in herbaceous fallows and 12 distributed on both grazed and ungrazed pastures. Trap lines were about 2 kilometers apart to avoid problems of variations in local prey abundance and comprised 51 traps spaced 2 meters of each others and placed for 48 hours (equivalent to 2040 trap nights per trapping session). The number of trapping sessions varied between years but sampling was always maintained during spring (end of April or early in May) at the arrival of harriers, during summer (July) corresponding to the intensive provisioning phase, in autumn (October) when generally the vole population is at its yearly peak and in winter to appreciate the winter decline. A mean local relative abundance of the vole population can then be expressed by the trap night index (*i.e.* number of animals caught per 100 trap nights) which is commonly used. For the common vole, the number of captures can be converted into density per hectare using a standardized method (Spitz *et al.*, 1974), based on different conversion factors of capture numbers. These correction factors were obtained from differences in vole activity according to season, sex, age for both sexes, and sexual activity of females. We collected these biological parameters to use these trap line coefficients which, for the western French common vole population, have been previously tested and described by Spitz (1977). Vole age was estimated using the lens weight method (Martinet, 1966). The sex-ratio and the sexual activity of females was estimated during autopsies.

164 potential nesting sites were recorded over the 300 km^2 of the study area by an air survey. They were visited one to three times during the breeding season. The nest searching method has been described in detail by Leroux (1987). Depending on searching difficulties, the areas prospected ranged from 0.5 to 10 km^2 per half-day. Nesting densities were recorded by the general census method for raptors (Thiollay, 1968; Leroux, 1987) and expressed as the number of nesting pairs per 10 km^2 including both located nests and settled oairs exhibiting typical nesting behaviour such as male food provisioning and/or territorial defence. Clutch size, hatching and fledging success were noted for each located nest. The fledging success was assessed both from the mean fledging success of all nests and mean fledging success of successful pairs (*i.e.* raising at least one fledgling). A one way analysis of variance was used to analyse the yearly variations of the various breeding parameters and their relationship with the vole density fluctuations was assessed by a Spearman rank correlation (r_s) using a two-tailed hypothesis.

We considered that only food conditions in spring (May) could influence the first events of breeding and may be related to nest numbers as well as to laying and hatching efficiency. On the other hand, fledging success should be more closely related with prey availability in summer (July), since breeding pairs of harriers had large nestlings dependent on provisioning conditions at that time (Simmons *et al.*, 1986).

RESULTS

Variations in vole density

Figure 1 shows vole densities during successive harrier breeding seasons. When harriers arrived in the study site in spring (end of April), the estimated mean vole densities varied between 1 (spring 1986) and 85 (spring 1990) voles/ha. The changes in vole density also differed between the seven breeding seasons. The outbreaks observed in 1987 and 1992 were characterized by a rapid increase in mean local density. During these two years densities increased up to 325 ind./ha and 170 ind./ha at the autumn peaks. In contrast, low vole densities were observed in 1986, 1988, 1989 and 1991, autumn peaks being between 30 and 70 voles per hectare. We observed an intermediate vole density in 1990 with an autumn density around 120 voles per hectare. These results indicate that the vole population in this region displays periodic fluctuations and may be considered a cyclic one. The mean increase rates of the vole population differed between years and there was no significant correlation between vole density in spring and autumn ($r_s=0.61$, $n=7$). This indicates that sampling must be maintained in spring and summer to evaluate food conditions for harriers during their breeding season. The necessity for large scale sampling on the various types of land was confirmed by the differences in density observed within trapping sessions. For example in October 1987 density varied from 560 voles per hectare in one abandoned old field to 150 voles per hectare in the least populated parcel.

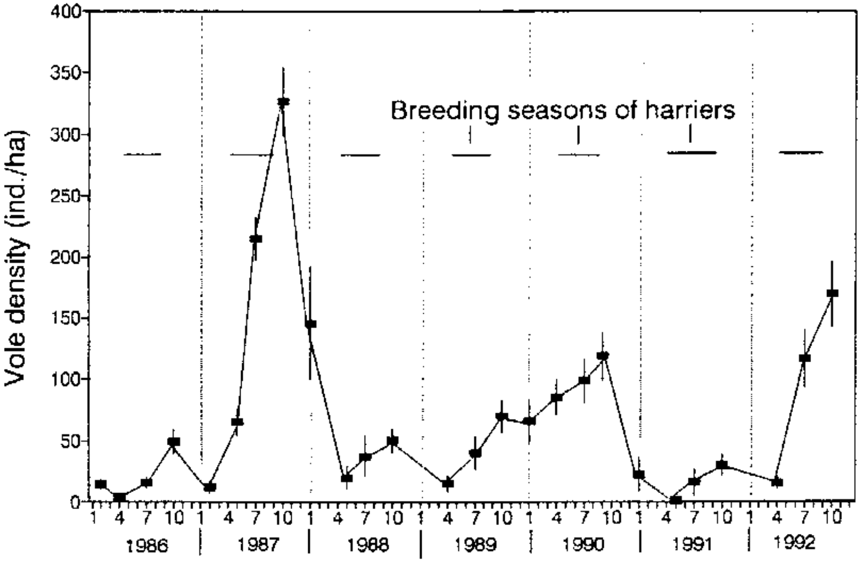

FIG. 1. – General pattern in fluctuations of the mean vole density during seven successive years (1986-1992) in the "Saintongeais marshes". Plotted values with standard error were obtained at the end of April or early in May, July, October and some winter values in January or February.

Harrier breeding parameters

217 nests were used for analysis during the seven years of the study. The nesting density ranged between 0.6 and 3.0 nests / 10 km^2 (table I). Fluctuations in nest numbers were correlated with spring vole densities over 7 years ($r_s=0.88$, $n=7$, $p<0.05$, fig. 2 *a*).

During the seven years of the study 162 nests were inspected for clutch size (table I). The mean values ranged from 2.8 eggs to 4 eggs and varied significantly between breeding seasons ($F_{6,40}=2.82$, $p < 0.05$). Mean clutch size was not correlated with spring vole density ($r_s=0.67$, $n=7$).

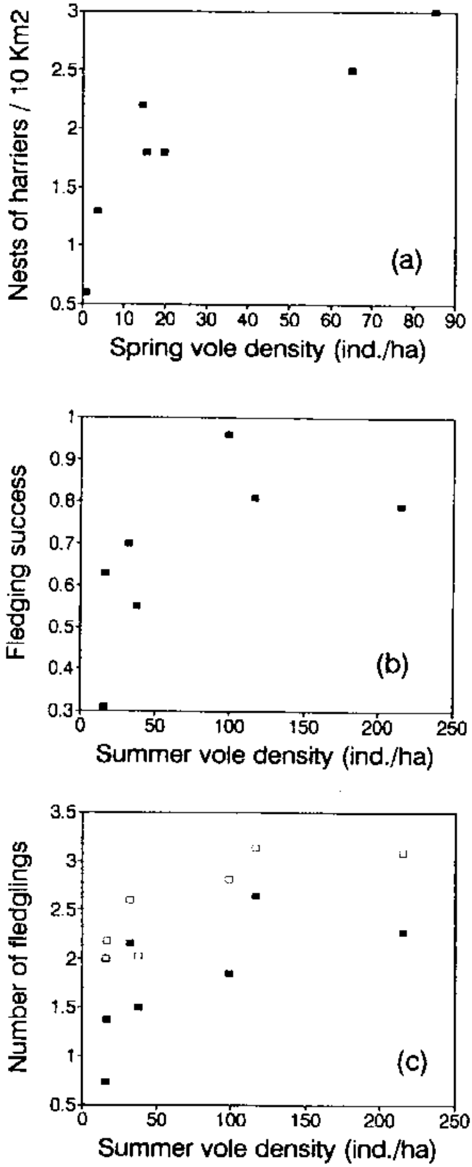

FIG. 2. — Various breeding parameters of harriers plotted against vole density during 1986-1992. (*a*) Nests/10 km^2 versus spring vole density ($r_s = 0.88$, $p < 0.05$). (*b*) Fledging success versus summer vole density ($r_s = 0.75$, $p < 0.05$). (*c*) Number of fledglings versus summer vole density, on all nests (black squares, $r_s = 0.85$, $p < 0.05$), on successful nests (empty squares, $r_s = 0.85$, $p < 0.05$).

As for clutch, we observed a significant variation in the mean number of hatchlings during the seven years of the study ($F_{6,38} = 3.5$, $p < 0.05$). Differences between breeding seasons exceeded one hatched young per nest (table I). The mean number of hatchlings was not significantly correlated with spring vole densities ($r_s = 0.18$, $n = 7$).

Hatching and fledging success varied significantly (table I) between years ($F_{6,43} = 2.28$, $p < 0.05$ and $F_{6,37} = 5.17$, $p < 0.05$, respectively). Hatching success was neither correlated with spring vole density ($r_s = -0.04$, $n = 7$) nor summer vole density ($r_s = 0.43$, $n = 7$). Only fledging success showed a significant correlation with summer vole density ($r_s = 0.75$, $n = 7$, $p < 0.05$, fig. 2 *b*).

The mean number of fledglings calculated with all breeding pairs or with only successful nests showed significant variation over the seven breeding seasons ($F_{6,60} = 4.45$ and $F_{6,44} = 5.76$ respectively, $p < 0.05$). The difference in the mean production of youngs by all pairs could reach two birds. There was a significant relationship of these two parameters with summer vole densities ($r_s = 0.86$, $n = 7$, $p < 0.05$, fig. 2 *c*).

Nest failures varied greatly from year to year (table I) but were not correlated with summer vole density ($r_s = -0.27$, $n = 7$).

Table I. – *Variations in breeding density, nest failures and mean values of clutch, hatch and young harriers produced during 1986-1992. Mean values with standard error and sample size.*

	1986	1987	1988	1989	1990	1991	1992
Nests/10 km^2	1.3	2.5	1.8	2.2	3.0	0.6	1.8
Clutch size	3.43	3.80	3.48	3.61	3.80	2.81	4.05
	0.16 (23)	0.15 (40)	0.17 (25)	0.14 (18)	0.21 (25)	0.40 (11)	0.18 (20)
Nb. of hatchlings	2.37	3.26	2.71	3.46	2.25	2.09	3.65
	0.33 (27)	0.24 (38)	0.32 (24)	0.19 (15)	0.34 (20)	0.48 (11)	0.27 (20)
Nb. of fledglings							
– all nests	1.37	2.27	1.50	2.16	1.85	0.73	2.64
	0.21 (35)	0.22 (60)	0.18 (42)	0.29 (18)	0.29 (26)	0.38 (11)	0.29 (25)
–successfull nests	2.18	3.09	2.03	2.60	2.82	2.00	3.14
	0.17 (22)	0.17 (44)	0.16 (31)	0.21 (15)	0.20 (17)	0.70 (04)	0.20 (21)
Hatching success	0.68	0.77	0.73	0.89	0.61	0.64	0.96
	0.08 (24)	0.05 (43)	0.07 (29)	0.07 (15)	0.09 (18)	0.13 (11)	0.02 (18)
Fledging success	0.63	0.79	0.55	0.70	0.96	0.31	0.81
	0.11 (19)	0.05 (37)	0.07 (24)	0.09 (14)	0.03 (14)	0.12 (08)	0.06 (18)
Nest failures (%)	9.1	15.4	19.3	16.6	33.3	84	16.6

DISCUSSION

Newton (1979) mentioned several studies reporting that vole cycles influenced certain breeding parameters of various raptor species (*Circus cyaneus, Falco tinnunculus, Buteo buteo*). For example, Balfour (1962), Cavé (1968), Hamerstrom (1979), Rockenbauch (1969), Village (1979) and Simmons *et al.* (1986) reported that prey abundance affected nesting density in different raptor species. Our data suggest that density of harriers in our study area was also influenced by yearly variations in vole abundance at the onset of harrier breeding. Hamerstrom (1979) pointed out that nesting of harriers (*Circus cyaneus*) in central Wisconsin was strongly linked to vole (*Microtus pennsylvanicus*) abundance during 3 out of 4 peak years within a 16-year period. This strong relationship is surprising considering the more eclectic diet of this harrier species (Hamerstrom, 1979; Simmons *et al.*, 1986). The frequency of presentation of prey to females by males may be an important explaining mechanism. When voles are abundant, males often present females with small tidbits. When voles are scarce, harriers turn to larger quarry (birds) and the female is less often stimulated (Hamerstrom, 1979). Sexual urge and provisioning rate should be interrelated (Balfour, 1963, *in* Hamerstrom, 1979).

The clutch size in the Saintongeais marshes is one of the smallest observed in Europe (5.15 in Great Britain, Brown, 1976; 4.25 in Poland and 4.13 in Andalusia, Kroguleс, pers. com.; 4.24 in the Netherlands, Schipper, 1978; 3.6, Cormier, 1985 at Noirmoutier France; 3.64 for 162 nests in the present study). Prey-dependent clutch size variations were found in the European buzzard *Buteo buteo* (Mebs, 1964). On the other hand, Simmons *et al.* (1986) reported that harrier females appeared to be in a better condition for egg laying in years with high food abundance. We observed important variations of the clutch size between years but differences were not significantly correlated with prey abundance and the small clutch size in our study area is probably dependent on other factors than prey availability.

Simmons *et al.* (1986) reported that breeding success of northern harriers was positively, but not significantly, related to availability of meadow voles. Hamerstrom (1979) reported no reliable correlation when studying the same species in Wisconsin. Simmons *et al.* (1986) explained this trend by a prey shift at harrier hatch. Northern harriers in New Brunswick fed mainly on voles during the breeding season, but nestling and fledgling birds in mid-June constitute a new available prey source and have a boosting effect on harrier reproduction, especially when voles are scarce. This prey shift confers a more generalistic character to northern harriers and consequently disturbs the expected vole-related effects. A similar explanation can be given for Hamerstrom's (1979) findings.

Our preliminary observations on nest provisioning after hatching (Butet & Leroux, 1989), showed that voles remained the main prey even when density was low and only feeding rates seemed to vary slightly according to microtine availability. This agrees with Thiollay (1968) who observed that Montagu's harrier fed almost exclusively upon the common vole in another nearby breeding site. The significant vole-related fledging success observed in the Saintongeais marshes probably reflects this single prey dependency.

Simmons *et al.* (1986) reported that predation rates on nests were lower when vole densities were high. Within the Saintongeais marshes, predation is responsible for about 45% of nest failures (Leroux, 1989) but we did not observe a close relationship between prey availability and nest failures.

Newton (1979) mentioned several studies showing that breeding parameters affected by voles cycles varied according to raptor species. For example, an increase of young productivity has been demonstrated in the case of *Buteo buteo* (Rockenbauch, 1975) and *Falco tinnunculus* (Village, 1979) but never reported for harrier species. Recently, Korpimäki (1992) studied the breeding success of long-eared owls in west Finland. This raptor appeared to be specialized on common vole *Microtus epiroticus* and its density, clutch size and production of youngs was clearly dependent on spring density of this rodent. This demonstrates that Montagu's harriers are food-specialized raptors in west France marshes and supports the idea of a food-influenced breeding success in this kind of habitat where the common vole is the most dominant and cycling prey species.

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Ranging behaviour of Marsh Harriers Circus aeruginosus in agricultural landscapes

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INTRODUCTION

Studies of ranging behaviour can provide valuable information on the ecological requirements of a species. They may be an essential tool in designing conservation policies (Sutherland 1998, Tella et al. 1998) as they provide the information needed to predict the consequences of land-use change on species' habitat use, especially in regions subject to major habitat transformations. In particular, knowledge of the temporal and spatial variation in ranging behaviour is needed to understand space-use patterns over species' complete annual cycles and over a range of habitats (Blanco et al. 1998, Tella & Forero 2000, Peterjohn 2003). However, this sort of information is available for only a few species, and even then does not usually cover the non-breeding season (Suárez et al. 1997).

Marsh Harriers Circus aeruginosus occur within a wide range of open habitats, including agricultural landscapes. After a dramatic population decline during 1960–80, mainly due to drainage of wetlands, contamination and direct persecution, the European population has recovered in recent decades and is currently classified as 'Secure' (Cramp & Simmons 1994, BirdLife International 2004). Within the Iberian Peninsula, the increase and spread of the Marsh Harrier population has been noticeable in some agricultural regions, including those dominated by intensified farmlands. This is the case in the Catalan Ebro Basin (Spain), where the breeding population increased from eight breeding pairs in 1997 to 51 in 2008 (Departament de Medi Ambient I Habitage de la Generalitat de Catalunya unpubl. data). However, little is known about the ranging behaviour ofthe Marsh Harrier in these agricultural areas. The objective of our study was to investigate the ranging behaviour and foraging-area requirements of the Marsh Harrier throughout the complete annual cycle in a representative agricultural area within the Iberian Peninsula.

METHODS

Study Area and radio-tagging

Our research was conducted in the Catalan Ebro Basin, in northeast Spain. This is a flat region below 400 m asl. It has a semi-arid Mediterranean climate with an annual precipitation of 300–500 mm and a median temperature of 14ºC (Bosch 2004). Almost one-third of the area is covered by farmland. Harriers were captured and tracked in two different farmland regions, some 30 km apart: a 170-km2 area (41º73'N, 0º38'E) mostly covered by intensified-herbaceous irrigated crops, mainly alfalfa, wheat, barley and some sweet corn; and a 280-km2 area of more heterogeneous land use (41º51'N, 0º52’E), dominated by a large central area of nonirrigated cereal crops, surrounded by dry fruit trees (olive and almond trees) in the south and irrigated fruit trees in the north.

We captured and tagged two Harriers in the irrigated farmland (nesting by two small artificial ponds) and seven in the non-irrigated farmland (all nesting around the Utxesa reservoir) between June 2000 and June 2003. Marsh Harriers were captured in breeding areas using bal-chatri traps (n = 8) or bow traps (n = 1). We determined the sex and age of each captured bird from Bavoux et al. (1988) and Forsman (1999). Each Harrier was fitted with a numbered leg band, two round dorsal plastic patagial tags and a back-pack transmitter: 10-g AYAMA-Segutel (Mataró, Spain) transmitters or 12-g Biotrack (Wareham, UK) transmitters. Transmitters were attached using harnesses made with four nylon threads covered by silicon tubes (n = 6) or with four Teflon ribbon pieces (n = 3) joined as an ‘X’ under the breast (Kenward 2001).

Sampling scheme

Radiotagged Harriers were tracked using AYAMA or TELEVIT- 900 receivers and a three-element Yagi antenna. Tracking of the birds was carried out from a car during sessions of an average of 6 ± 2 h (n = 282). We began each tracking session from an elevated vantage point located near the breeding site (< 1000 m) and followed the transmitter signals until the bird was located. Roads and paths were abundant, meaning that access was effectively unrestricted. We plotted the geographical position of each location with an estimated precision of c. 100 m on 1 : 25 000 aerial photographs. The minimum interval between successive locations of a single bird was 2.5 h and, on average, 2.31 ± 1.02 relocations per Harrier per tracking day (n = 340) were obtained. Harriers were monitored during periods ranging from 1 to 15 months and were located 1.7 ± 1.4 days per week (n = 197).

Home-range estimates

Home-ranges were estimated using the Animal Movement extension for ARCVIEW GIS 3.2. We used Fixed Kernel methods (FK) with least squares cross-validation (Seaman & Powell 1996); 90% isopleths (FK90) were taken as an estimate of total home-range estimates and 50% isopleths (FK50) as intensive-use-area estimates. Because our aim was to obtain the best estimate of hunting ranges, locations within a radius of 100 m of the nest were eliminated from the analysis to avoid excessive influence of nest locations in the FK estimates.

For home-range calculations, locations were classified to four periods according to the species' biology: pre-laying (February–March), nesting (April–July), postfledging (August–September) and winter (October– January).

RESULTS

Home-range variation

Male home-range size exhibited large variation between Harriers (Table 1). The intensive-use areas (FK50) represented 10–28 % of the total home-range and, generally, they were single areas, including the fields around the nest (Fig. 1). Home-ranges of the two females in our study were smaller than those of males (Table 1). There was no evidence that home-range size was merely a reflection of sampling effort because the number of locations of each bird and their home-range were not related (FK90 $r_{18} = 0.068$, $P = 0.77$; FK50 $r_{18} = -0.10$, $P = 0.66$), and thus home-range calculations were not an artefact of variation in sampling effort.

In the nesting period, partial or total overlap was observed among the home-ranges of individuals nesting close to each other: in 2000, Harriers tracked in nonirrigated farmlands, which nested in the same colony, shared between 20% and c. 100% of their home-ranges (Fig. 2a); in the irrigated farmland, male SM1 and male TM1, which nested 5 km from each other in 2003, shared 47% and 8% of their home-ranges, respectively (Fig. 2b).

No consistent pattern of male home-range size variation throughout the annual cycle was detected (Table 1). A trend was observed for shortest distances occurring during the pre-laying period (Table 1). Home-range position tended to be very similar throughout the annual cycle (Fig. 1).

DISCUSSION

The Marsh Harrier, as with other birds of prey, is a long-lived species, usually having large home-ranges (Zachariah 2000) and few studies have attempted to determine its foraging area requirements. Early estimates were based on direct sightings and ranged from 80 to 2800 ha in different regions of Europe (Salamolard 1997). However, comparisons were confounded by differences in methods, as home-range estimates based on direct sighting are known to be underestimated (Salamolard 1997). Our results are consistent with the few previous home-range estimates based on radiotracking data, although in general they fall within the upper range of variability described for the species: from 480 to 2000 ha for three adult Harriers tracked on grasslands during winter (Bavoux et al. 1994) and 349 ha for breeding and 1603 ha for non-breeding Harriers tracked on grasslands (Sternalski et al. 2008). The differences observed may be related to habitat. The use of smaller home-ranges on grasslands may reveal a higher habitat quality in grasslands compared with our study (cultivated areas), as home-range size in raptors mainly depends on prey availability (Kenward 1982, Marquiss & Newton 1982, Village 1982). In fact, conversion of grasslands into cultivated areas has been linked with impoverished food supplies (Butet & Leroux 2001). These differences agree with that found for Montagu's Harrier Circus pygargus, where hunting ranges for individuals occupying cultivated lands tended to be larger than those of individuals occupying grasslands (Salamolard 1997).

As expected from their different roles during breeding (Cramp & Simmons 1994), female Marsh Harriers had smaller home-ranges than males and remained closer to the nest during the nesting period. This behaviour also has been reported for other European harriers (Schipper 1977, Salamolard 1997, Arroyo et al. 2009). We observed a large variation in home-range size for male Harriers, which may be related to age or habitat factors, but the small sample size prevented further analysis of these effects.

During the nesting period, as with other raptors having large home-ranges, radiotagged Marsh Harriers in our study, nesting in the same breeding area or nearby, showed partial or total overlap of their home-ranges (Newton 1979). Hunting alone and moving from one place to another over time may have allowed them to decrease intraspecific interactions, although sharing some areas within their home-ranges; home-range overlap and the absence of aggressive interactions between individuals within hunting ranges have already been reported for Montagu's Harriers (Salamolard 1997).

Variation in home-range size throughout the annual cycle for radiotagged Harriers in our study showed high individual variability; however, they tended to be smaller in the pre-laying period. Within individuals, home-range position tended to be similar throughout the annual cycle. This result supports that found for other sedentary populations of Marsh Harriers in France (Sternalski et al. 2008). Suitable food supplies around breeding areas throughout the annual cycle may explain this fact, as the ultimate reason for birds leaving their breeding areas for part of the year is likely to be food shortage (Newton 1979). Furthermore, territorial behaviour may also be involved: remaining close to the breeding areas and maintaining home-ranges over the complete annual cycle may provide an advantage by preventing other harriers occupying the site at the beginning of the breeding period (Amar & Redpath 2005). Remaining close to breeding areas is especially important in the pre-laying period, when territorial displays, pair formation and breeding-territory establishment start, and such behaviour may therefore relate to the likelihood of pairing successfully (Marquiss & Newton 1982).

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Table 1. Home-range size by the 90% and 50% isopleths of the fixed kernel (FK) and mean distance from locations to the nests (MD ± standard deviation), Catalonian Ebro Basin, Spain, 2000-2004. N is the number of locations and days is the number of days one harrier was detected.

Harrier	Sex	Age	Habitat	Year	N	Days	FK 90 (ha)	FK 50 (ha)	MD (m)
Nesting									
UF1	Female	Adult	Non-irrigated	2000	8	6	1.2	0.2	153±65
UF2	Female	Adult	Non-irrigated	2000	23	10	271	61	1066±1194
UM1	Male	Adult	Non-irrigated	2000	9	8	946	264	1714±1498
UM2	Male	First adult	Non-irrigated	2000	25	11	6269	692	5015±4114
UM3	Male	First adult	Non-irrigated	2000	29	17	864	246	2017±2643
UM4	Male	Adult	Non-irrigated	2001	44	29	6353	661	5359±4265
UM4	Male	Adult	Non-irrigated	2002	27	16	5497	604	4444±3676
UM5	Male	Juvenile	Non-irrigated	2001	7	7	5359	1146	4391±3819
SM1	Male	Adult	Irrigated	2002	52	22	341	106	2491±1804
SM1	Male	Adult	Irrigated	2003	112	44	371	40	1281±987
TM1	Male	Adult	Irrigated	2003	71	29	2075	289	2747±2678
Mean ± SD ♀♀							**136±191**	**31±43**	**609±646**
Mean ± SD ♂♂							**3287±2865**	**484±381**	**3070±1487**
Post-fledging									
UM4	Male	Adult	Non-irrigated	2001	31	16	6859	1064	6190±4480
SM1	Male	Adult	Irrigated	2002	28	9	245	47	1614±460
TM1	Male	Adult	Irrigated	2003	72	27	3184	587	4208±3457
Mean ± SD ♂♂							**3430±3314**	**566±509**	**4004±2295**
Winter									
UM4	Male	Adult	Non-irrigated	2001-02	27	15	7812	2727	5987±3186
SM1	Male	Adult	Irrigated	2002-03	33	12	417	68	1817±1011
TM1	Male	Adult	Irrigated	2003-04	64	21	411	116	1442±2017
Mean ± SD ♂♂							**2880±4271**	**970±1522**	**3082±2523**
Pre-laying									
UM4	Male	Adult	Non-irrigated	2002	6	5	1660	460	4329±1925
SM1	Male	Adult	Irrigated	2003	12	4	830	180	2238±1864
TM1	Male	Adult	Irrigated	2004	24	6	14	4	209±338
Mean ± SD ♂♂							**835±823**	**215±230**	**2260±2060**

Figure 1. Marsh harrier home-range variation throughout the annual cycle, Catalan Ebro Basin, Spain, 2000-2004. For each harrier (UM4, SM1 and TM1), successive home ranges, from first nesting period tracked to the end of tracking, are shown. FK90 (——) and FK50 (——) are shown. Breeding areas are indicated in grey.

Figure 2. Overlap among marsh harrier home ranges during the nesting period, Catalan Ebro Basin, Spain, 2000-2004. Locations and FK90 for harriers UM1(☆,–··–), UM2 (▲, ——), UM3 (●,·····), UF2 (■,——) and UF1 (○) in nesting period 2000 (a); and harriers TM1 (●,——) and SM1 (○, ——) in nesting period 2003 (b) are shown. In grey, breeding areas.

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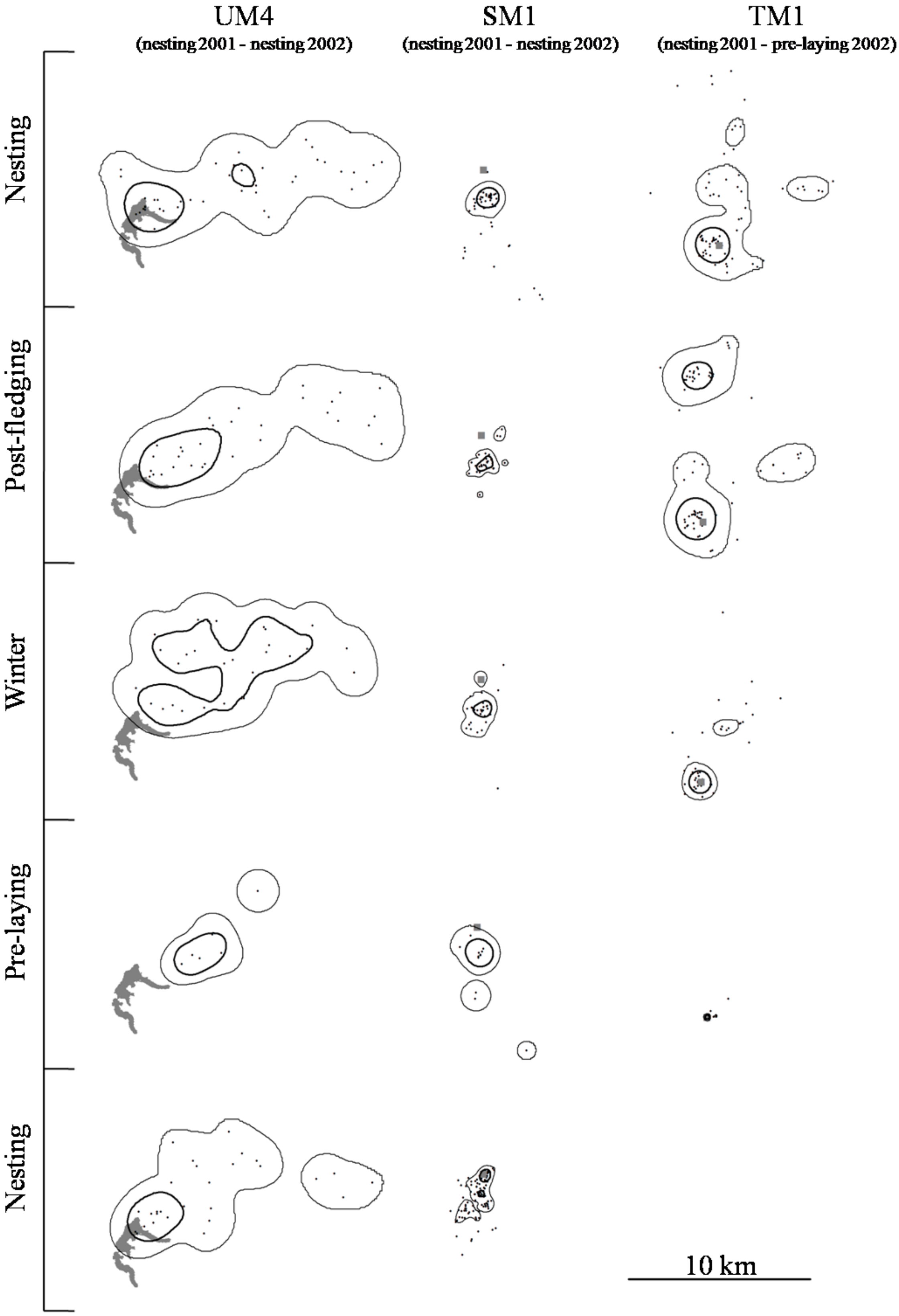

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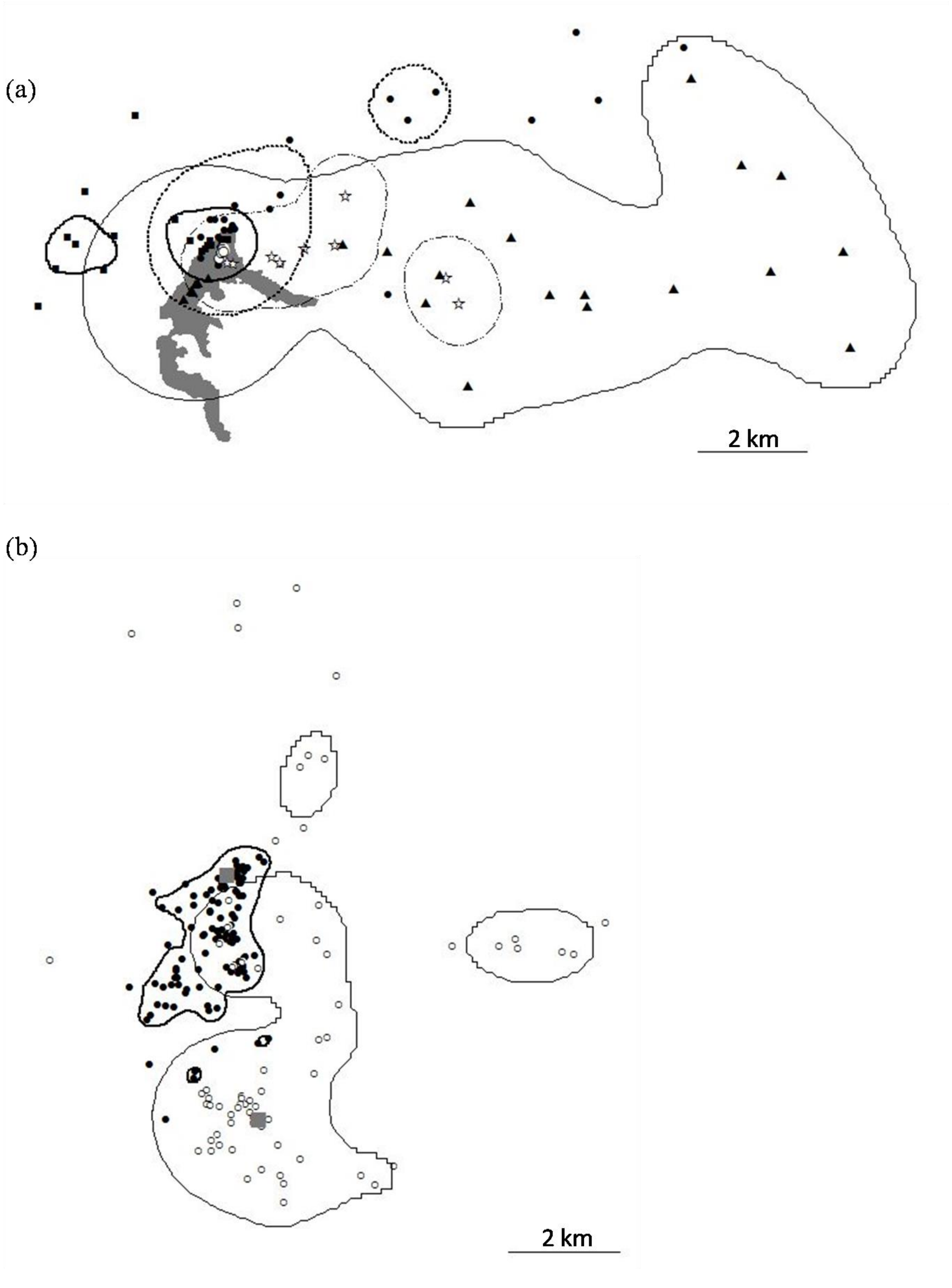
Figure 2.



Factors affecting the expansion success of bird populations in human-transformed environments: The case of the Marsh Harrier Circus aeruginosus in the Ebro Valley

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Focus

Factors affecting the expansion success of bird populations in human-transformed environments: the case of the Marsh Harrier *Circus aeruginosus* in the Ebro Valley

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Understanding the factors that limit the current distribution of species and populations is crucial not only for ecological and theoretical research but also for predicting the impact of global change on biodiversity and its consequences for effective management and conservation. Using as a study model an expanding population of Marsh Harrier *Circus aeruginosus* in Spain, this review shows that environmental factors, sociability, dispersal constraints and density-dependent mechanisms may all play an important role in the distribution of common native species. Marsh Harrier breeding numbers fell greatly between 1960 and 1980 mainly due to organochlorine pesticides, the drainage of wetlands and direct persecution. Its recent population recovery may be attributable in part to less use of organochlorine pesticides and less direct persecution. However, this species may also have benefitted from the increase in number of artificial structures such as irrigation ponds and reservoirs in areas of intensive agriculture, which are used as breeding sites and their surrounding croplands as hunting areas. At a local scale, individual variation in density dependence in productivity and settlement patterns may have favoured the dispersal of some individuals to new empty habitat patches, while other birds have aggregated around traditional breeding areas. However, on a large scale (i.e. peninsular Spain), the breeding population of Marsh Harriers seems also to be spatially constricted by factors other than environmental variables. This indicates that potential unoccupied habitat for Marsh Harriers still exists and further expansion in the Iberian Peninsula could occur (at least at the spatial resolution of available studies that do not, however, take into account small-scale processes such as food abundances or pesticides that may restrict the species' distribution). The potential consequences of this expansion for other species should be taken into account in order to ensure the conservation of overall biodiversity in a world of change.

Key words: Marsh Harrier, *Circus aeruginosus*, agriculture, habitat, steppe lands, Spain

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Although changes in species' geographic ranges are natural phenomena, the rate and magnitude of these changes have increased significantly as a result of anthropogenic action (Vitousek *et al.* 1997). The rate at which a population spreads or contracts spatially is determined by the rates of population growth and dispersal, coupled with density dependence (Holt *et al.* 2005). Human-induced environmental changes can lead to variations in local birth and/or death rates through deterministic processes such as an impoverishment or an increase in species-specific habitat and food resources, which drive populations toward positive or negative growth. Moreover, spatial range constraints such as dispersal may limit the ability of a species either to resist reductions in available appropriate habitat (particularly where these reductions lead to habitat fragmentation) or to exploit expansions, and thus cope with this type of environmental change (Moore *et al.* 2008, Martínez-Morales *et al.* 2010). Like environmental characteristics, density dependence may also limit population growth and range expansion. For example, in cases of strong negative density dependence, a population stops growing at low absolute population size and thus may become vulnerable to extinction due to demographic or environmental stochasticity (Holt *et al.* 2005).

Land-use changes, habitat fragmentation, environmental pollution, invasive species and nutrient enrichment have been reported to be some of the major human-induced global changes that negatively affect population growth and species' geographic ranges (Chapin *et al.* 1997, Vitousek *et al.* 1997). Current trends in range and abundance in many taxa suggest that over 50% of species in most groups are declining as a result of some of these human activities (Mckinney & Lockwood 1999). However, human activities do not affect all species in the same way and transformed landscapes still provide suitable habitats for species tolerant of anthropogenic alterations. Some of these species are not only able to resist demographic and geographic range declines in human-transformed environments, but can even increase their numbers and expand their geographic ranges (Mckinney & Lockwood 1999). Thus, human activities are able to create new suitable habitats that can be exploited by species that thrive in human-altered environments (e.g. Carrete *et al.* 2010, Carrete & Tella 2011).

The negative and positive impacts of human activities tend to be non-randomly distributed among taxa and ecological groups (McKinney & Lockwood 1999). Thus, human-induced environmental change acts as a non-random filter, selecting for those species best able to survive in modified ecosystems. Broadly speaking, the general pattern of expansion of widespread species (the so-called 'winners') and the contraction of rare, often endemic, native species (the 'losers') may lead to a process of biotic homogenization, which could represent an unprecedented form of global change (McKinney & Lockwood 1999, Ricciardi 2007) and one of the most important forms of biological impoverishment worldwide (Olden *et al.* 2004).

Population expansions related to human disturbances have recently gained notoriety as major conservation and management concerns in natural and semi-natural ecosystems. Many examples exist of non-native species spreading through ecosystems (i.e. exotic invasions) that provoke new threats to native wildlife populations (e.g. Marchetti 1999, Smith 2005). However, invasions by native species, which take advantage of human disturbance, have been generally ignored as a potential component of change in biodiversity, probably because they are considered more *natural* processes than exotic invasions (Garrott *et al.* 1993, Valéry *et al.* 2009, Carrete *et al.* 2010). However, expanding populations of native, human-resistant species may represent an important threat to other, more human-sensitive species, which could be superior competitors in natural areas but not always in transformed areas (Didham *et al.* 2007, Carrete *et al.* 2010). On the other hand, these expanding populations may offer useful information applicable to other species that are not able to spread in human-transformed environments. Thus, under the current scenario of global change in which human disturbance plays a major role, understanding not only why some species are declining but also the main factors that lead others to expand are important conservation challenges. In this review we use agricultural systems and an expanding population of Marsh Harrier *Circus aeruginosus* in the Ebro Valley (N Spain) as a study model to explore the role played by ecological factors such as habitat and food availability, spatial range constraints and density dependence in the expansion of a species in human-transformed environments and to discuss its potential consequences.

Agricultural intensification and changes in bird communities

Agricultural intensification is one of the most severe forms of land-use modification that occur in Europe over the past six decades (Donald *et al.* 2001). Farmland has been profoundly altered in many industrialized countries as a result of increased demand for food and, above all, the subsequent intensification of farming techniques aimed at increasing food production (Figure 1) and other related changes in land use (Bouma *et al.* 1998). These changes in agricultural landscapes have led to a decrease in biodiversity and in the breeding populations of several farmland species (Chamberlain *et al.* 2000, Donald *et al.* 2001, Benton *et al.* 2003), thereby making agricultural intensification one of the most important threats to biodiversity in Europe — comparable to deforestation and global climate change (Donald *et al.* 2001).

Factors that contribute to the overall impact of intensification on biodiversity include the increased use of pesticides and fertilizers, the mechanization of harvesting and other agricultural operations, the removal of hedgerows and other uncultivated areas to create larger fields, the irrigation of dry habitats, earlier harvesting dates and an increase in monocultures (Newton 2004). These agricultural practices have led to losses in habitat quality and heterogeneity, which are important factors that help maintain resources for species-rich communities (Benton *et al.* 2003).

Of particular note is the recent decline in farmland bird populations (Figure 2). Close relationships between changes in bird populations and temporal and/or spatial variation in agricultural intensity have been shown to occur across Europe (e.g. on a European scale the change in cereal yields alone accounts for 30% of the decline in farmland bird numbers; Donald *et al.* 2001), as well as in individual countries and regions (e.g. Chamberlain *et al.* 2000). Such declines have been rapid, massive and widespread and some species have fallen in number and range by over 80% in less than 20 years (Chamberlain *et al.* 2000, Newton 2004).

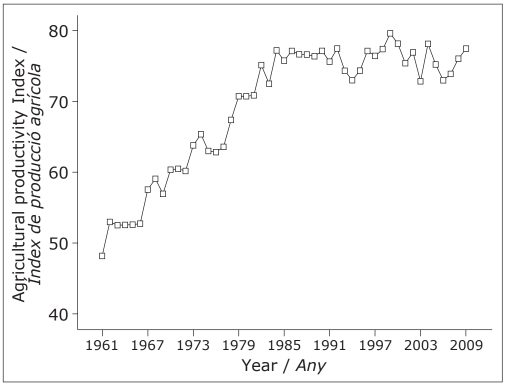

Figure 1. Changes in the index of overall agricultural productivity in Western Europe from 1961 to 2009. This index is based on the sums of price-weighted quantities of different agricultural products after the quantities used as seed and feed have been deducted. This index is expressed in millions of international dollars. Data from the FAOSTAT database (http://faostat.fao.org/). *Canvis en l'índex de productivitat agrícola a Europa occidental entre 1961 i 2009. Aquest índex està basat en la suma de les quantitats de diferents productes agrícoles ponderades pel seu preu (deduint-ne les quantitats destinades a llavors o aliment) . S'expressa en milions de dòlars. Dades de FAOSTAT (http://faostat.fao.org/).*

However, agricultural intensification has not affected all bird species in the same way (Figure 2) and some transformed landscapes are suitable habitats for species that are tolerant of anthropogenic alterations. For example, on intensively managed land, where artificial ponds and irrigated crops have replaced natural wetlands, some bird species now thrive as a result of the creation of new foraging and/or breeding habitats (Sebastián-González *et al.* 2010, 2013).

Population expansion in agricultural habitats: the Marsh Harrier as a study model

The Marsh Harrier *Circus aeruginosus* is a semi-colonial, medium-sized raptor that occurs in the mid-latitudes of the western Palearctic. This ground-nesting raptor, which breeds mainly in wetlands and hunts over open habitat (Cramp & Simmons 1994), underwent a dramatic population decline in Europe in the period 1960–1980 due to the drainage of wetlands, contamination and direct persecution (Cramp & Simmons 1994). However, it has recovered on a European

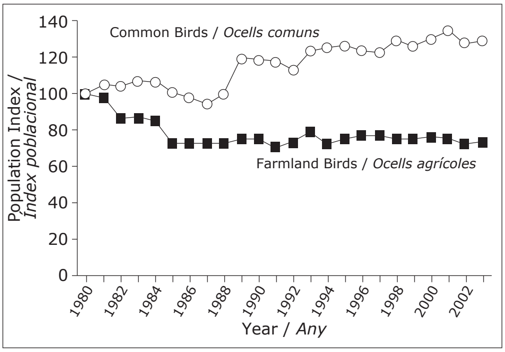

Figure 2. Trends in common bird populations in the European Union since 1980. The composite population trend of 19 common farmland species (i.e. open-country specialists, the bulk of whose populations are found in open farmed habitats) and of 25 common species (generalist species that occur across a range of varied habitats) are shown. The indexes are calculated in relation to a value of 100 given for 1980 (PECBM, 2005). *Tendències de les poblacions d'ocells comuns als països de la Unió Europea des de 1980. La tendència dels ocells de medis agrícoles (quadrats) és el resultat de combinar 19 espècies especialistes de medis oberts majoritàriament cultivats, mentre que la tendència dels ocells comuns (cercles) resulta de 25 espècies comunes generalistes que es troben en un ampli ventall d'hàbitats. Els índexs s'han calculat de manera que el valor de 1980 sigui 100 (PECBM, 2005).*

scale in recent decades (an increase of over 10% in numbers), although declines are still reported to be occurring in south-eastern Europe (BirdLife International 2004). Currently, the species is widespread across much of Europe and its European breeding population is estimated at 93,000–140,000 breeding pairs. It status is given as 'Secure' (BirdLife International 2004).

Contrary to other farmland species, this species' recovery has been pronounced in regions dominated by agricultural habitats, including regions of intensive croplands in peninsular Spain (Molina & Martínez 2008). Within areas such as the Ebro Valley (NE Spain, Figure 3), the increase in Marsh Harrier populations has been accompanied by an increase in the number of locations used for nesting, and some pairs now occupy artificial ponds and reservoirs linked to agricultural practices (Cardador *et al.* 2011). The expanding Marsh Harrier population thus provides an opportunity for identifying some of the anthropogenic factors involved in apparently natural invasion processes that are currently favouring worldwide biotic homogenization (McKinney & Lockwood 1999).

Factors affecting expansion success

Changes in availability of species-specific resources

Nest-site and food availability have been described as key limiting factors in birds (Newton 1994, Sergio *et al.* 2003). Several examples exist of avian species whose breeding numbers and distribution increase or decrease in relation to food availability or the number of suitable nesting sites (Newton 1998). Agricultural intensification has been linked to habitat impoverishment and food depletion for many species occupying agricultural areas (e.g. Blanco *et al.* 1998, Tella *et al.* 1998). The Marsh Harrier, however, seems to be an example of a native species that has benefited from this transformation. As in many areas of its range, the Marsh Harrier in NE Spain is expanding after a period of dramatic decline (Cramp & Simmons 1994, BirdLife International 2004). In the Catalan Ebro Valley, this expansion is taking place in parallel with the use of a newly available habitat type, intensive herbaceous croplands (Cardador *et al.* 2011, Cardador & Mañosa 2011). As in other species that select habitat features at multiple spatial scales (Sergio *et al.* 2003), the Marsh Harrier could be taking advantage of the numerous artificial ponds constructed in recent years in areas of intensive agriculture as breeding sites, while still relying on traditional extensive cereal farmland for foraging. However, radio-tracked individuals breeding in both intensive and extensive agricultural landscapes in the Ebro Valley used the herbaceous fields near their nest sites as foraging areas (Cardador & Mañosa 2011), thereby indicating that this species is exploiting both new nesting and foraging habitats. Moreover, individuals occupying and using intensified habitats for foraging tended to have smaller home ranges than birds foraging within more traditional habitats (Cardador *et al.* 2009), which suggests that, unlike for most farmland birds, intensive agricultural areas represent higher quality habitat for Marsh Harriers than extensive croplands. Indeed, the abundance of small mammals, a chosen and high-quality prey for *Circus* species (e.g. Butet & Leroux 1993, Sternalski *et al.* 2010), seems to be greater in

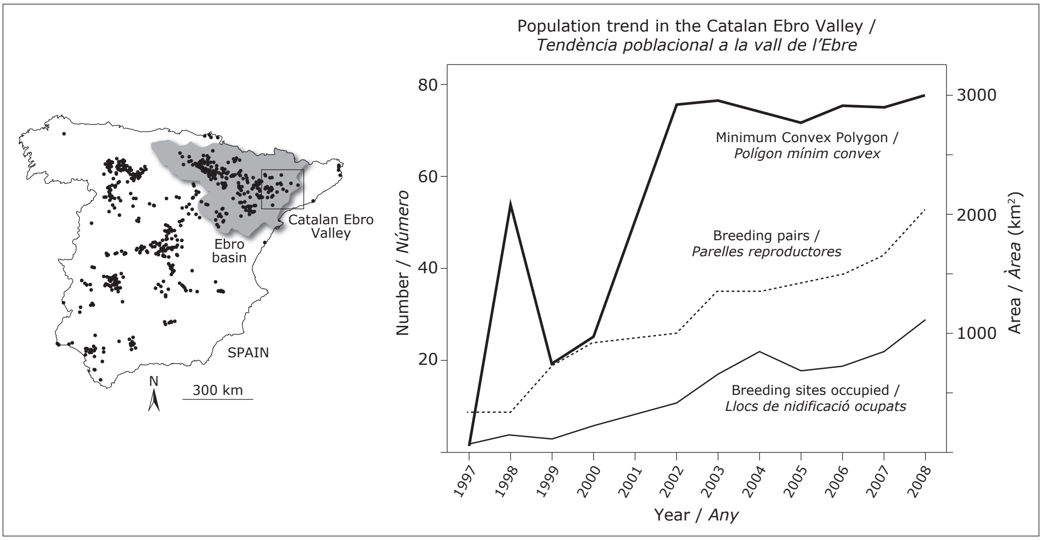

Figure 3. Distribution of the breeding population of the Marsh Harrier *Circus aeruginosus* in Spain in 2006 and the population trends for the breeding population of the Marsh Harrier in the Catalan Ebro Valley (Cardador *et al*. 2011).
Distribució de la població reproductora d'Arpella Vulgar Circus aeruginosus *a Espanya el 2006, i tendència de la població reproductora a la part catalana de la vall de l'Ebre (Cardador* et al. *2011).*

intensive agricultural areas in the Ebro Valley and is good evidence of the benefits derived from the occupation of this new habitat by this species (Cardador *et al.* 2012a).

Results obtained from radio-tracked individuals in the Ebro Valley largely agree with those obtained by analysing the factors affecting the species' occupancy rate of breeding sites in the area. The occupancy rate of breeding sites has been described as an indicator of habitat quality in raptors (Sergio & Newton 2003). The occupancy of wetlands by Marsh Harriers in agricultural areas in the Ebro valley is mainly explained by the independent effect of habitat features acting at two spatial scales: the breeding site (area of emergent aquatic vegetation and type of wetland) and the foraging area (percentage of intensified, irrigated herbaceous crops in the area surrounding the nest site). Neither human pressure variables nor proximity to other occupied sites seemed to be important determinants of occupancy rates in this expanding population (Cardador *et al.* 2011). The occupancy rate of artificial wetlands such as ponds or reservoirs was not significantly different from that of rivers or watercourses but was greater than that of inland natural wetlands (Cardador *et al.* 2011), suggesting that the emergent vegetation in these human-made structures provides new suitable breeding habitat for nesting Marsh Harriers. At a landscape scale, Marsh Harriers have responded positively to new areas of intensified herbaceous crops, probably because (as mentioned above) they offer more – and more accessible – prey items (Cardador *et al.* 2012a). Lower competition as a result of declining populations of other predator species in intensive croplands could also be related to this positive selection pattern, although this hypothesis has not to date been fully assessed. Preliminary analysis of changes in productivity in relation to habitat characteristics suggests that no significant relationships exist between this demographic parameter and habitat attributes, suggesting that none of the habitats occupied in the Ebro Valley are unsuitable nesting habitats.

Intrinsic features such as body size, genetic variability, life-history traits and dispersal behaviour can also influence whether or not species are 'winners' or 'losers' in a human-dominated world (Bennett & Owens 1997, Mckinney & Lockwood 1999). For example, the niche specialization concept has been shown to be useful in tackling this question since more specialized species are expected to be more sensitive to environmental transformations (Devictor *et al.*

2008). The studied population of Marsh Harrier appeared to behave as a generalist species in relation to farming practices, using both intensive and traditional herbaceous crops for hunting (Cardador & Mañosa 2011). Furthermore, it seemed to be able to adapt to temporal variations in resource availability. Tracked individuals changed their relative use of different crops (i.e. alfalfa, winter-sown wheat and barley or maize) during the year, probably in relation to their height and density (Cardador & Mañosa 2011). Diet composition and delivery rates also differed in terms of food availability in farmlands with different degrees of intensification (Cardador *et al.* 2012a). In intensive croplands in the Ebro Valley, Marsh Harriers prey mostly on voles, probably due to their greater abundance, and prey delivery rates increase during the breeding season as the food demands of their broods also increase (Figure 4). On the other hand, in traditional farmland, where voles seem to be less abundant, Marsh Harriers had more diverse diets and preyed mostly on birds and mice, but responded to increases in energy demands late in the season by turning to larger prey items (but with no increased delivery rates) (Figure 4) (Cardador *et al.* 2012a). All of these results suggest that, like other generalist predators, Marsh Harriers may be able to exploit transient resources in intensive agricultural habitats and may be less sensitive to habitat degradation than other, more specialized species (Siriwardena *et al.* 1998).

The importance of spatial range constraints

Species-specific niche requirements are not the only factors that determine the range of a species. On a large scale, spatial constraints such as time-limited dispersal or geographic barriers can limit the ability of a species to fully occupy its potential habitat (Moore *et al.* 2008, Martínez-Morales *et al.* 2010), thereby leading to discrepancies between suitable environmental habitat and a species' geographic distribution (Pinto & MacDougall 2010). Indeed, the equilibrium between habitat and species distribution should only be expected to occur under conditions of unlimited dispersion or when dispersion occurs as fast as the generation of suitable habitat for occupation (De Marco *et al.* 2010).

The spatial distribution of Marsh Harriers in peninsular Spain is largely determined by environmental variables (both climatic and habitat) during both the breeding and the wintering seasons (Cardador *et al.* 2014). However, there is evidence that Marsh Harrier distribution is also spatially constrained by factors other than environmental variables during the breeding season (Cardador *et al.* 2014). These spatial constraints seem to be consistent with the idea of limited dispersal from areas occupied in previous years since, in general, reduced probability of occurrence of the species occurs in environmentally suitable (in terms of climate and habitat variables) areas that are furthest from previously occupied areas (Cardador *et al.* 2014). Limited dispersal may be related to the short natal dispersal distance described for the species (Sternalski *et al.* 2008), which is perhaps associated with social factors such as conspecific attraction that are known to affect colonial species (Serrano *et al.* 2004, Cardador *et al.* 2012b).

Raptors are long-lived species that may move over large areas for several years before entering into the breeding population (Newton 1979). When they settle to breed, individuals must optimize their fitness by increasing their foraging, mating, breeding and survival prospects. Settling near natal areas or close to conspecifics minimizes the costs of gaining good knowledge of breeding sites and foraging areas, and also increases mating opportunities (Brown *et al.* 1990, Arroyo *et al.* 2001, Serrano *et al.* 2005). Indeed, many colonial bird species have high levels of both natal philopatry and conspecific attraction (Sternalski *et al.* 2008, Serrano *et al.* 2004). These demographic mechanisms may impede or delay the colonization by Marsh Harriers of empty suitable patches located at great distances from previously occupied areas in peninsular Spain. For a fraction of the population, a positive effect of conspecific aggregation on settlement patterns and productivity has indeed been found (Cardador *et al.* 2012b). Additionally, although the least competitive breeders seemed to occupy the most isolated locations and thus promote range expansion at regional scales (Cardador *et al.* 2012b), this pattern may not translate immediately to larger scales and so a colonization lag in terms of the most distant areas may exist (De Marco *et al.* 2010).

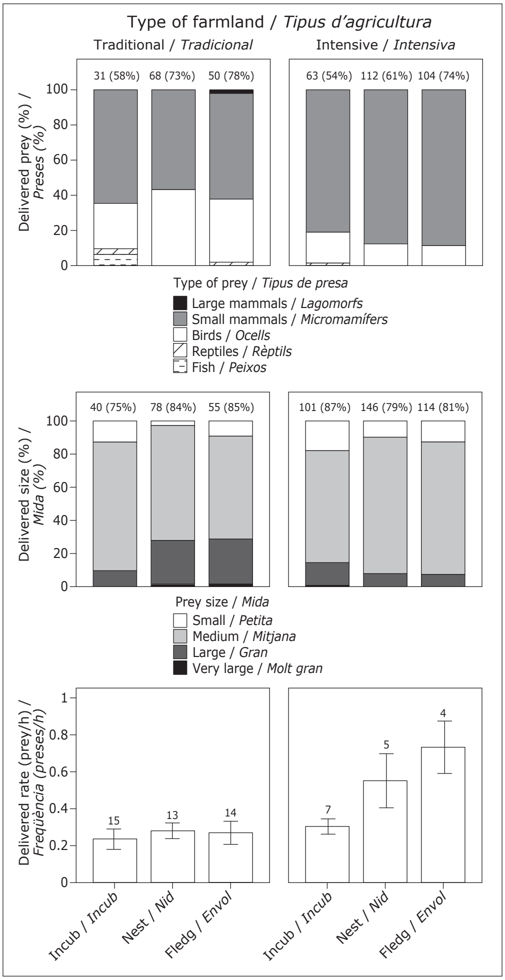

Figure 4. Comparative data on diet composition, prey size and delivery rate according to agricultural landscapes (traditional or intensively managed) and period of the breeding cycle (incubation, nesting and post-fledging) of male Marsh Harriers in the Catalan Ebro Basin (Spain), 2001–03. For diet composition and prey size, number of identified prey and percentage that it represents from total observed deliveries (in parentheses) are shown. For delivery rates, mean ± SE and sample sizes (number of harriers observed delivering food at least once in each period) are shown. Size categories: very large (e.g., lagomorphs or Mallards *Anas platyrhynchos*); large (e.g., rats *Rattus* spp. or Red-legged Partridges *Alectoris rufa*); medium (e.g., rodents or Sparrows *Passer domesticus*); and small (e.g., shrews or Orthoptera).

Dades comparatives de la dieta, la mida de presa i la freqüència d'aportaments de preses al niu en relació al tipus de paisatge agrícola (tradicional o intensiu) i al període del cicle reproductor (incubació, nidificació i envol) per a individus mascle d'Arpella vulgar a la part catalana de la vall de l'Ebre (anys 2001-2003). Per a la composició de la dieta i la mida de presa es mostra el total de preses identificades i el percentatge que representen respecte el total d'observacions fetes (entre parèntesi). Per a la freqüència d'aportaments de preses al niu es mostra la mitjana ± DT; la mida mostral correspon al número de mascles d'arpella observats fent aportaments al niu almenys un cop a cada període. Categories de mida de presa: molt gran (p. ex., lagomorfs o Ànec collverd Anas platyrhynchos*); gran (ex., rates* Rattus *spp. o Perdiu roja* Alectoris rufa*); mitjana (p. ex., ratolins o pardals* Passer domesticus*); i petita (p. ex., mussaranyes o ortòpters).*

Density dependence, individual traits and species' range distributions

The presence of conspecifics may also severely modulate the quality of a breeding site. Given that conspecifics are competitors, the addition of a new individual to a patch may decrease its suitability (Fretwell & Lucas 1969) or even prevent its occupation by other individuals (Rodenhouse *et al.* 1997, Oro 2008). However, conspecifics can also provide advantages for settlers that include the transmission of information about food, earlier predator detection, better defence efficiency and/or more mating opportunities (Arroyo *et al.* 2001, Serrano *et al.* 2005, Parejo *et al.* 2007), all of which should have benefits for individual fitness (Courchamp *et al.* 1999). Both positive and negative effects of the presence of conspecifics will act on the same individual and the final balance in the costs and benefits will depend on individual characteristics.

A particular case of inter-individual variation found in many avian species is chromatic variability in plumage. Plumage colouration can co-vary with morphology, physiology and behaviour (see Roulin 2004, Ducrest *et al.* 2008 for a review), as well as with age (Forsman 1999). Colour variability might thus modulate intraspecific interactions, leading to differential cost-benefit balances of conspecific presence for individuals with different colourations. In the case of the Marsh Harrier, males can be easily classified into three colour categories, 'dark brown', 'light brown' and 'grey' according to the presence or absence of grey feathers on the upper-wing, and whether the under-wing appears completely dark brown or light (Forsman 1999, Sternalski & Bretagnolle 2010). Females can also be easily classified as 'dark' or 'light' according to whether the upper-wing is completely dark brown or light brown with very large obvious white shoulder patches. It has recently been demonstrated that the productivity of Marsh Harriers varies between breeding pairs in terms of the phenotype of the breeders (i.e. plumage colouration) and their relative spatial position within the breeding population (Cardador *et al.* 2012b). Specifically, in northern Spain, the productivity of brown males (both dark and light) decreased along the breeding density gradient, an effect that was more marked when these birds were paired with dark females. By contrast, the productivity of lighter breeders (i.e. breeding pairs formed by grey males and light females) did not change with conspecific density. This suggests that not all individuals have the same expectation of success at a given population density. Variability in aggressiveness between individuals of different plumage colouration (Sternalski & Bretagnolle 2010, Sternalski *et al.* 2012), associated with melanin-based plumage differences (Roulin 2004, Vergara *et al.* 2007) or age (Forsman 1999, Vergara *et al.* 2013), may explain these inter-individual differences (Carrete *et al.* 2006, Margalida *et al.* 2008). In northern Spain, this pattern gives rise to an uneven occupation of localities by individuals with different plumage colouration (Cardador *et al.* 2012b): less aggressive dark individuals avoid high-density situations by colonizing new patches, which promotes the expansion of the species.

In this sense, density-dependence processes, combined with differences in niche requirements between individuals, could have important consequences for species' range expansions. In the Marsh Harrier population in northern Spain, positive density dependence acting on a part of the population could explain the existence and maintenance of areas supporting greater population densities, even if they are not consistently of higher habitat quality than surrounding areas (Cardador *et al.* 2012b). Conversely, the negative density dependence in other individuals would, through intraspecific competition, increase the probability that empty, but otherwise suitable patches, are occupied. For these latter, less competitive birds, the benefits of settling in traditional areas may be counterbalanced by the costs of intraspecific competition and thus make dispersal to new unoccupied areas advantageous (Balzik *et al.* 2010).

The potential consequences for other species of the expansion of a 'winner' predator

The alteration of biotic communities by major anthropogenic stressors (e.g. eutrophication, land-use changes and fragmentation) affects not only the number of species in most ecosystems but also the relative abundance of species and of biomasses (i.e. evenness). More importantly, the exogenous modification of the environment can unbalance ecosystems, thereby leading to changes in competition regimes between species (Valéry *et al.* 2008) long before species are actually driven to extinction (Chapin *et al.* 2000). Thus, under the current scenario of global change and biotic homogenization, the establishment and spread of some of the species that benefit from anthropogenic changes may represent an important threat to other more human-sensitive species that could be superior competitors in more natural areas but not always in transformed areas (Didham *et al.* 2007, Carrete *et al.* 2010).

Several studies have discussed the inexorable risk that the invasion of exotic organisms entails to native biota due to competition (e.g. Vitousek 1997, Ricciardi 2007). Invasive species can reduce natural diversity by monopolizing resources, introducing or spreading infectious diseases and parasites, or by changing community composition and the relative abundance of sympatric species, and thus may lead eventually to local extinctions (Soulé 1990). However, predation by introduced species is a far more important cause of extinction. It is listed as being responsible for the extinction of more than 40% of vertebrate species (Sax & Gaine 2008). Although less attention has been given to locally overabundant or expanding native species (Garrott *et al.* 1993), these species could have similar impacts on natural and semi-natural ecosystems to those caused by exotic invasive species (Valéry *et al.* 2008, Carrete *et al.* 2010).

For example, the nesting success of some species in certain areas has been correlated with local predator densities, and predator removal programmes have led to increased nesting success and breeding density in several species (see Newton 2004 for a review). This situation could become even more critical if human-induced environmental changes lead to greater accessibility to nests (Whittingham & Evans 2004). The potential consequences of the expansion of the Marsh Harrier on other more human-sensitive species have not yet been addressed. However, in some areas within its distribution range, such as the Ebro Valley, there are several threatened species such as pseudo-steppe birds (e.g. Little Bustard *Tetrax tetrax*, Black-bellied *Pterocles orientalis* and Pin-tailed *P. alcahata* Sandgrouses) that are potential prey species for generalist Marsh Harriers (Suárez *et al.* 1997, Tella *et al.* 1998, Blanco *et al.* 1998). The potential effects of the expansion of certain native species on other native species is an additional factor that is worth examining in the Marsh Harrier and in other expanding native species.

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Resum

Factors que afecten l'èxit d'expansió de poblacions d'aus en medis transformats per l'home: l'Arpella vulgar *Circus aeruginosus* a la vall de l'Ebre

Entendre els factors que limiten la distribució de les espècies i les seves poblacions és de vital importància des d'un punt de vista teòric, però també per predir correctament les conseqüències del canvi global en la biodiversitat i prendre decisions de gestió i conservació eficaces. Aquesta revisió mostra que els factors ambientals, la sociabilitat, les limitacions en la dispersió i els mecanismes denso-dependents poden tenir un paper important en la distribució d'espècies autòctones comunes, utilitzant com a model d'estudi una població en expansió d'Arpella vulgar *Circus aeruginosus* a Espanya. Els efectius reproductors d'Arpella vulgar s'havien reduït considerablement en les dècades anteriors (1960-1980), a causa principalment dels plaguicides organoclorats, el drenatge d'aiguamolls i la persecució directa. Així, almenys una part de la recuperació de les poblacions d'Arpella vulgar ha pogut ser deguda a la reducció en l'ús d'organoclorats i la persecució directa. No obstant això, l'espècie també s'ha beneficiat de l'expansió d'estructures artificials, com ara estanys artificials i basses de reg, relacionades amb la intensificació de l'agricultura, i que han servit com a nous territoris de cria i els seus cultius adjacents com a zones de caça. A escala local, la variació individual en els patrons denso-dependents de productivitat i assentament pot haver afavorit la dispersió d'alguns individus a noves parcel·les d'hàbitat buides, mentre que altres s'han agregat al voltant de les àrees tradicionals. Tot i això, a gran escala (o sigui, a nivell de l'Espanya peninsular), la població reproductora d'Arpella vulgar sembla estar espacialment limitada més enllà de les variables ambientals. Aquest resultat indica que encara hi ha hàbitat potencial perquè l'Arpella vulgar efectuï noves expansions a la península Ibèrica, almenys, en la resolució espacial dels estudis duts a terme. Malauradament, aquesta resolució no permet tenir en compte els processos a petita escala que poden restringir la distribució de les espècies, com ara l'abundància local d'aliment o els pesticides. S'han de tenir en compte les possibles conseqüències d'aquesta expansió per d'altres espècies per tal de conservar adequadament la biodiversitat en un món canviant.

Resumen

Factores que afectan el éxito de expansión de poblaciones de aves en medios transformados por el hombre: el Aguilucho lagunero *Circus aeruginosus* en el valle del Ebro

Entender los factores que limitan la distribución de las especies y sus poblaciones es de vital importancia desde un punto de vista teórico, pero también para predecir correctamente las consecuencias del cambio global en la biodiversidad y tomar decisiones de gestión y conservación eficaces. Esta revisión muestra que los factores ambientales, la sociabilidad, las limitaciones en la dispersión y los mecanismos denso-dependientes pueden desempeñar un papel importante en la distribución de especies autóctonas comunes, utilizando como modelo de estudio a una población en expansión de Aguilucho lagunero *Circus aeruginosus* en España. Los efectivos reproductores de Aguilucho lagunero se habían reducido considerablemente en las décadas

anteriores (1960-1980), debido principalmente a los plaguicidas organoclorados, el drenaje de humedales y la persecución directa. Así, al menos parte de la recuperación de sus poblaciones ha podido deberse a la reducción en el uso de organoclorados y la persecución directa. Sin embargo, la especie también se ha beneficiado de la expansión de estructuras artificiales, tales como estanques artificiales y balsas de riego, relacionadas con la intensificación de la agricultura, y que han servido como nuevos territorios de cría y sus cultivos adyacentes como zonas de caza. A escala local, la variación individual en los patrones densodependientes de productividad y asentamiento puede haber favorecido la dispersión de algunos individuos a nuevos parches de hábitat vacíos, mientras que otros individuos se han agregado alrededor de las áreas tradicionales. No obstante, a gran escala (o sea, a nivel de la España peninsular), la población reproductora de Aguilucho lagunero parece estar espacialmente limitada más allá de las variables ambientales. Este resultado indica que todavía existe hábitat potencial para que el Aguilucho lagunero efectúe nuevas expansiones en la península Ibérica, al menos, a la resolución espacial de los estudios llevados a cabo. Por desgracia, esta resolución no permite tener en cuenta los procesos a pequeña escala que pueden restringir la distribución de las especies, tales como la abundancia local de alimento o los pesticidas. Se deben tener en cuenta las posibles consecuencias de esta expansión para otras especies a fin de conservar adecuadamente la biodiversidad en un mundo cambiante.

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

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

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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 & Donázar, 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 & Pfenning, 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 km^2 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).

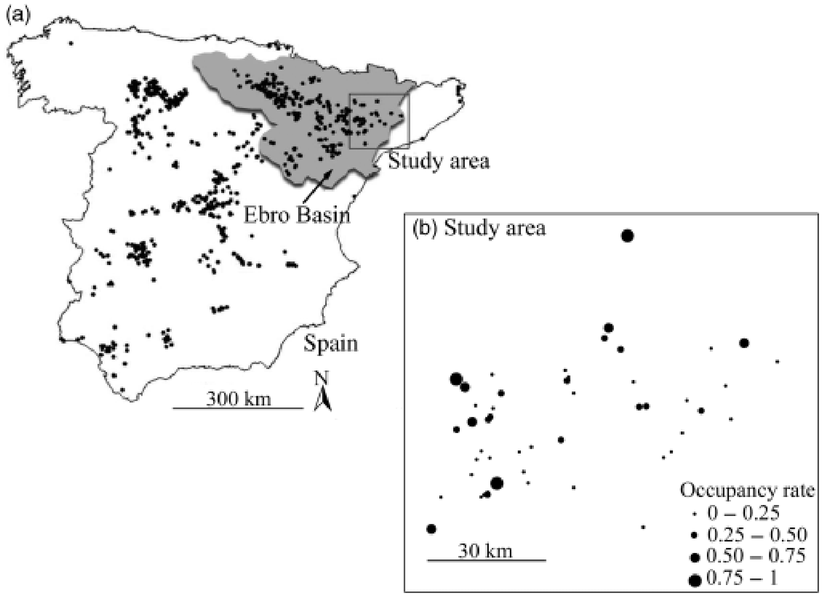

Figure 1 (a) Distribution of the breeding population of the Marsh harrier *Circus aeruginosus* in Spain in 2006 (Molina & Martínez, 2008). The Ebro Basin is shown in grey; (b) occupancy rate of monitored breeding sites in the study area (Catalan Ebro Basin, Spain, 1997–2008).

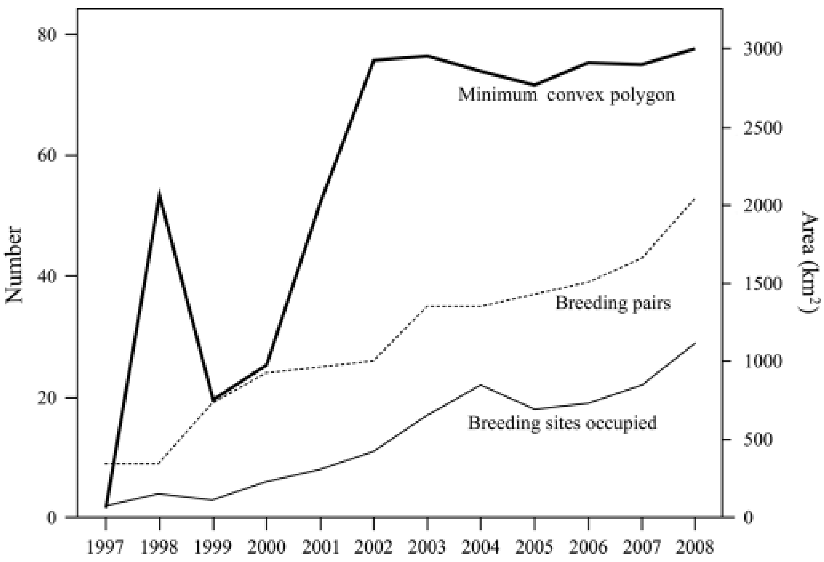

Figure 2 Population trend for the breeding population of Marsh harrier *Circus aeruginosus* in the Catalan Ebro Basin, Spain, showing the number of breeding pairs, the number of breeding sites occupied and the minimum convex polygon area including the occupied breeding sites recorded each year (Source: 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*, reedmace *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.

Characteristics of the breeding areas

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 $S_i = \Sigma \exp(-d_{ij}) \times A\mathrm{j}$ (with $i \neq j$), where d_{ij} is the linear distance between wetland i and j, and Aj 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 Catalonian 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 × 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 ± SD	Range	Units
Habitat variables			
Breeding-site level			
Vegetation	8.4 ± 19.6	0.5–103.2	ha
Shape	551 ± 290	105–1268	m ha^{-1}
Water	18.5 ± 49.8	0–224	ha
Landscape level			
Intensified-herbaceous	41.4 ± 31.5	0.0–99.5	%
Intensified-tree	18.3 ± 22.4	0.0–83.4	%
Traditional-herbaceous	20.0 ± 27.4	0.4–94.8	%
Traditional-tree	3.0 ± 5.4	0.0–16.9	%
Vineyard	4.8 ± 11.4	0.0–41.4	%
Other	12.6 ± 17.3	0.0–74.8	%
Human pressure			
Village	2348 ± 1107	75–4235	m
Road	66 ± 129	0–631	m
Path	40 ± 79	0–280	m
Proximity to other occupied sites			
Distance	13.8 ± 8.6	3.8–32.2	km
Isolation	0.13 ± 0.26	0–1	

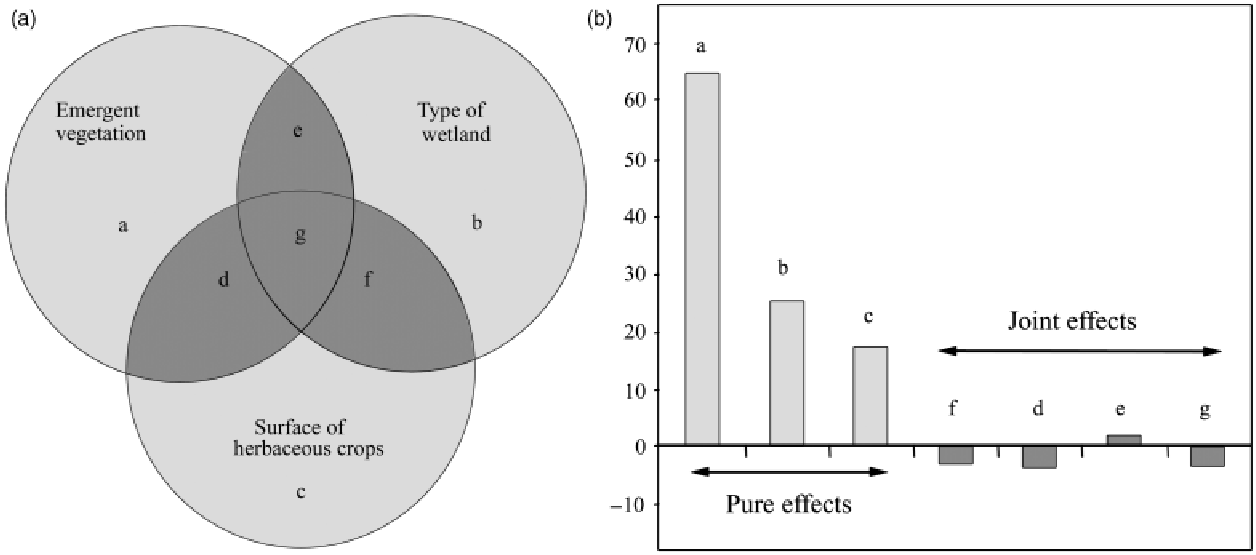

Figure 3 (a) Deviance partitioning analysis for the occupancy rate of breeding sites by Marsh harriers *Circus aeruginosus*. (b) Percentage of variability in occupancy rate explained by the pure and joint effects of habitat variables.

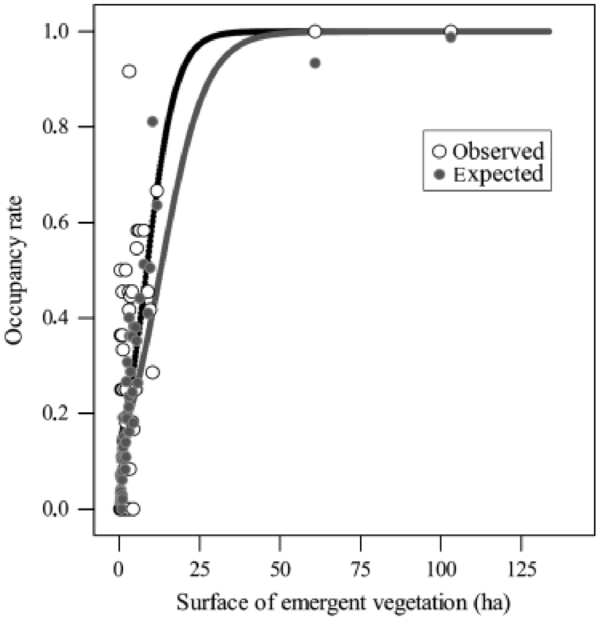

Figure 4 Effect of surface of emergent vegetation on the occupancy rate, derived from fitted values from GLM estimates (binomial error distribution, logit-link function). The observed trend is shown with a black line. The grey line indicates the expected trend under a null model in which occupancy rate 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 Catalonian 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 & Donázar, 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, Donázar & 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.

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