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

Factors affecting expansion success of bird populations in human-transformed environments: the marsh harrier *Circus aeruginosus* in the Ebro Valley

Laura Cardador Bergua

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Factors affecting expansion success of bird populations in human-transformed environments **Laura Cardador** **PhD Thesis**

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A mis mujeres valientes, mis abuelas
A los padres perfectos
A Olga

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Contents

INTRODUCTION AND OBJECTIVES

INTRODUCTION

Change in species geographic ranges is a natural phenomenon, but the rate and magnitude of such change has significantly increased due to anthropogenic causes (Vitousek et al. 1997). The rate at which a population spreads/contracts through space is a function of the rates of population growth and dispersal, coupled with density dependence (Holt et al. 2005). Human-induced environmental changes can lead to variation in density-independent components of local birth or death rates through deterministic process (e.g. impoverishment/increase of habitat and food resources), thus pushing populations toward positive/negative growth. Moreover, spatial range constraints, such as dispersal, may limit the abilities of a species to cope with such environmental changes, either in resisting reductions in available suitable conditions (particularly where these cause habitat fragmentation) or in exploiting expansions (Moore et al. 2008, Martínez-Morales et al. 2010). Density-dependence may also limit population growth and range expansion, beyond environmental characteristics. For example, with strong negative density-dependence a population stops growing at low absolute population size and may be vulnerable to extinction because of demographic or environmental stochasticity (Holt et al. 2005). On the other hand, the presence of the 'Allee effect' (i.e., an increase of per capita growth rates with population density, Stephens et al. 1999) can be involved in sudden population expansions (Holt et al. 2005).

Winning and losing species in a world of change

Human activities cause many types of alterations to ecosystems with important effects on their biodiversity. Land-use changes, habitat fragmentation, environmental pollution, invasive species or nutrient enrichment have been described as some of the major human-induced global changes leading to biodiversity loss (Chapin et al. 1997, Vitousek et al. 1997, Sala et al. 2000). Current trends in range and abundance of many taxa suggest that over 50% of species in most groups are declining as a result some of these human activities (see Mckinney and Lockwood 1999). In this context, studies of ecological requirements of species in human-transformed environments and of the causal factors underlying their population declines have been central in conservation biology and have been described as an essential tool for developing effective management strategies to conciliate development and biodiversity conservation (e.g. Blanco et al. 1998, Tella et al. 1998, Arroyo et al. 2002, 2009, O'Connell and Yallop 2002, Carrete and Donázar 2005).

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 also increase their population numbers and expand their geographic range (Mckinney and Lockwood 1999). In this sense, human activities can create new suitable habitats that can be exploited by some species that thrive in human-altered environments (e.g. Carrete et al. 2010, 2011, Martínez-Morales et al. 2010). Negative and positive impacts of human activities tend to be non-randomly distributed among taxa and ecological groups (McKinney and Lockwood 1999). Thus, human-induced environmental change acts as a non-random filter, selecting for those species best able to survive within modified ecosystems (Smart et al. 2006). Broadly, the general pattern of expansion of some widespread -usually non-native but also native- species (so-called 'winners') and the contraction of rare, often endemic, native species (so-called 'losers') could lead to a biotic homogenization process, which can be considered as an unprecedented form of global change (McKinney and Lockwood 1999, Ricciardi 2007) and one of the most important forms of biological impoverishment worldwide (Olden et al. 2004).

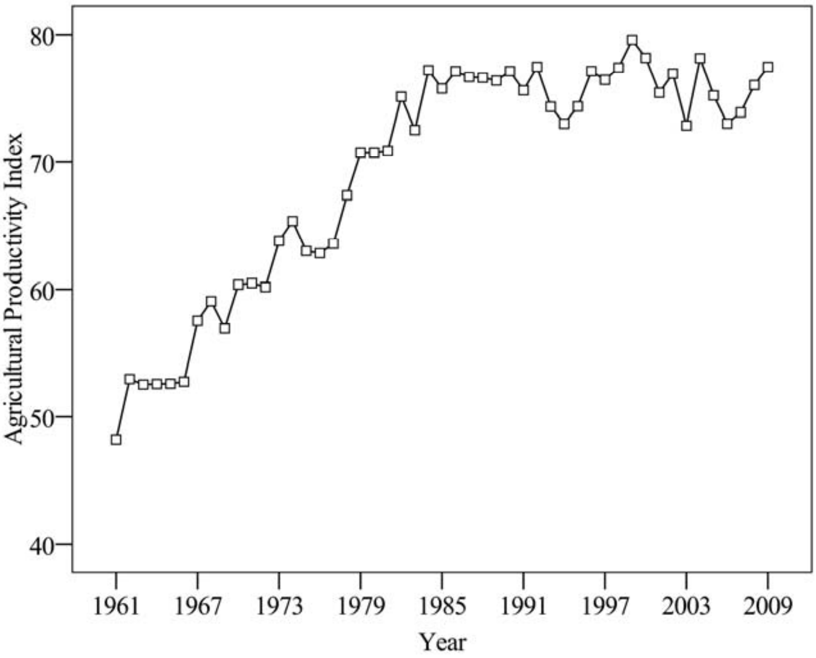
Population expansions related with human disturbances have recently gained notoriety as a major conservation and management concern in natural and semi-natural ecosystems. Many examples exist of non-native species expanding across ecosystems (i.e., exotic invasions) and causing native wildlife endangerments (e.g. Griffis and Jaeger 1998, Marchetti 1999, Smith 2005). However, invasions by native species have been scarcely studied as a potential component of biodiversity change, probably because they are considered *natural* processes compared to 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 that could be superior competitors in natural areas but not always in the transformed ones (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, in the current scenario of global change, in which human disturbance plays a major role, understanding not only why some species are declining but also which are the main factors leading others to expand remain important conservation challenges.

Agricultural intensification and changes in bird communities

Agricultural intensification can be considered one of the most severe forms of land-use modification occurring across Europe over the last six decades (Donald et al. 2001). Farmland in many industrialized countries has been profoundly altered as a result of increased food demand, mainly through the intensification of farming techniques to increase food production (Fig. 1) and related changes in land-uses (Bouma et al. 1998). Those changes in agricultural landscapes have lead to decreases in biodiversity and in breeding populations of several species in farmlands (Chamberlain et al. 2000, Donald et al. 2001, Benton et al. 2002), thus making agricultural intensification one of the major threats to biodiversity in Europe, comparable to deforestation and global climate change (Donald et al. 2001).

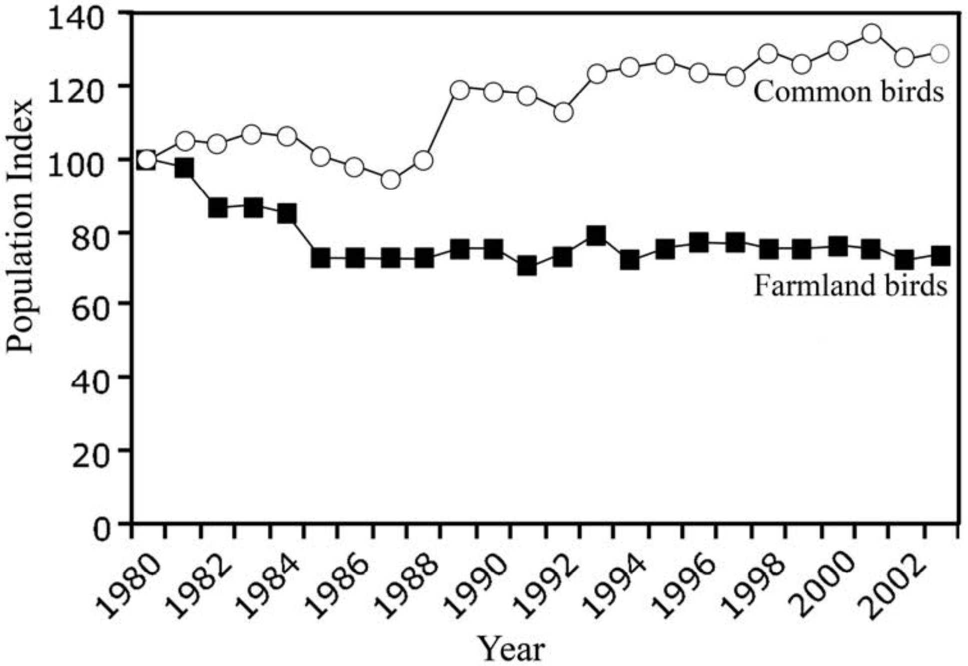
Contributing factors to the overall impact of intensification on biodiversity include increased pesticide and fertilizer use, mechanization of harvesting and other agricultural operations, removal of hedges and other uncultivated areas to produce larger fields, irrigation of dry habitats, earlier harvesting dates and an increase in monocultures (Newton 2004, Sanderson et al. 2005). These agricultural practices have resulted in losses of habitat quality and heterogeneity, which are important in maintaining resources for species-rich communities of organisms (Benton et al. 2003).

Figure 1. *Changes in an index of overall agricultural productivity in Western Europe from 1961 to 2009. The index is based on the sums of price-weighted quantities of different agricultural products produced after deductions of quantities used as seed and feed-weighted in a similar manner and is expressed as millions of international dollars. Data from the FAOSTAT database (http://faostat.fao.org/).*



Of particular note, and of recent concern, has been the decline in populations of bird species in farmlands over recent decades (Fig. 2). Strong relationships between changes in bird populations and temporal and/or spatial variation in agricultural intensity have been demonstrated across Europe (e.g., the change in cereal yield accounts for 30% of the decline in farmland bird numbers alone, on a European scale, Donald et al. 2001) and in individual countries and regions (e.g. Chamberlain et al. 2000, Benton et al. 2002). Such declines have been rapid, massive and widespread, with some species experiencing more than an 80% reduction in former numbers and range in less than 20 years (Tucker and Heath 1994, Chamberlain et al. 2000, Newton 2004). At present, major species with an unfavourable conservation status within Europe use lowland farmlands during some periods of their annual cycles (Tucker and Heath 1994).

Figure 2. *Trends in common bird species populations in European Union countries since 1980. Composite population trend of 19 common farmland species (i.e. open-country specialist species, the bulk of whose populations are found in open farmed habitats) and composite population trend of 25 common species (generalist species that occur across a range of varied habitats) are shown. The indexes are calculated such that values for 1980 average 100. Source: EBCC/RSPB/Birdlife/Statistics, the Netherlands.*



The process by which birds have been negatively affected by agricultural change varies between species but is generally associated with either reduction and degradation of their hunting and nesting habitats or direct mortality of birds through harvesting processes (Benton et al. 2003, Newton 2004). However, agricultural intensification has not affected all bird species in the same way (Fig. 2), and transformed landscapes provide suitable habitats for species tolerant of 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 habitats (Sánchez-Zapata et al. 2005, Sebastián-González et al. 2010).

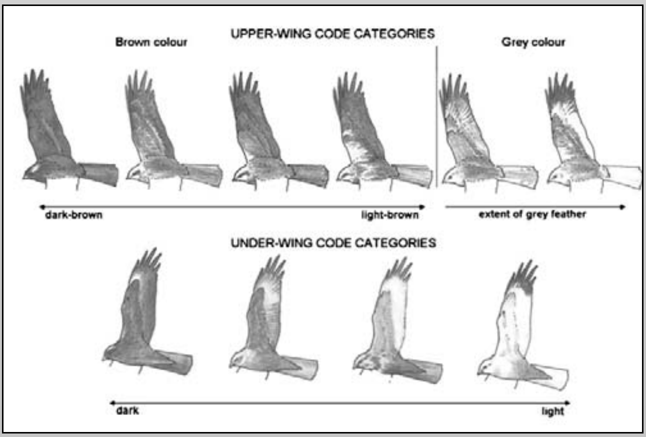
Population expansions in agricultural habitats: the marsh harrier as a study model

Studies dealing with factors that jeopardize the long-term persistence of species are numerous and of unquestionable importance for conservation (e.g. Blanco et al. 1998, Tella et al. 1998, O'Connell and Yallop 2002). Conversely, the ecology of expanding native species is sometimes less stimulating for conservation ecologists, even when understanding factors driving species success in a world where extinction rates are reaching their historical maximum could be equally fascinating and important to predicting future biodiversity changes (Garrott et al. 1993). One such native and expanding species is the marsh harrier (*Circus aeruginosus*), a semicolonial, medium-sized raptor that occurs in the middle latitudes of the western Palearctic (see Box 1 for details on the species).

From 1960 to 1980, the marsh harrier underwent a dramatic population decline in Europe due to drainage of wetlands, contamination and direct persecution (Cramp and Simmons 1994). However, it recovered in recent decades with a moderate general increase (>10%), although there were some declines in south-eastern Europe (Fig. 3). Currently, the species is widespread

BOX 1. The marsh harrier

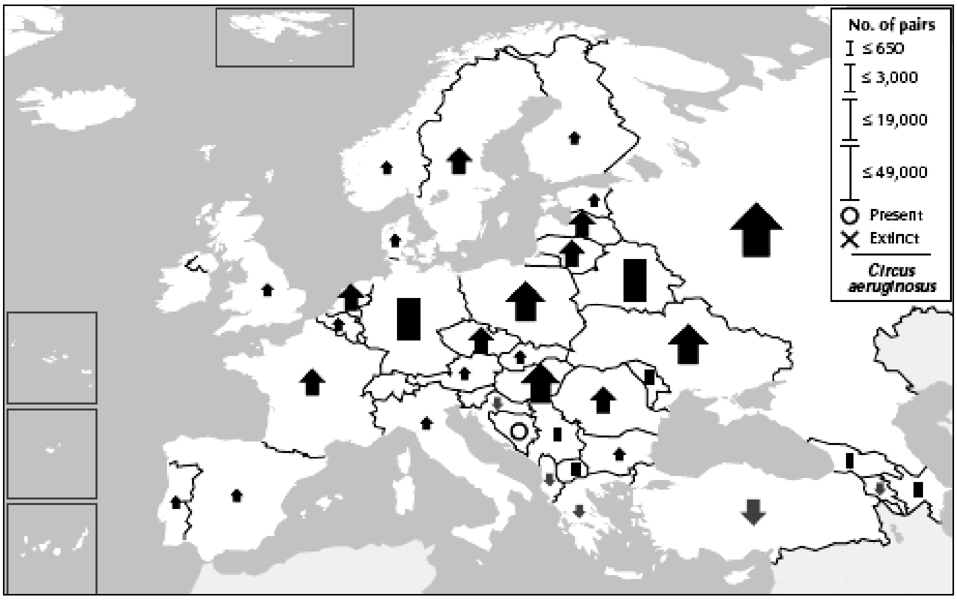
The marsh harrier (*Circus aeruginosus*) is a semicolonial, medium-sized raptor (length: 48-56 cm; wing-span: 115-130 cm; weight: ♂ 405-667g, ♀ 540-800g) that occurs in the middle latitudes of the western Palearctic. Individuals nest on the ground mainly within wetlands and behave as open-habitat hunters (Cramp and Simmons 1994). They use a wide range of open habitats, including agricultural landscapes, while avoiding mountainous, forested and wooded areas. The species show a wide trophic niche. Birds and small mammals (especially rodents) are the most consumed prey but marsh harriers also consume carrion and wounded animals, insects, frogs, snakes and fish, depending on local circumstances (Cramp and Simmons 1994). Outside the breeding season, individuals often roost communally on the ground at night. Northern populations are migratory while populations from the Mediterranean areas are resident. Main wintering ranges extend from the north of the Mediterranean Basin to Sub-Saharan Africa (Cramp and Simmons 1994, Strandberg et al. 2008). Individuals show sexual dimorphism, with females being 10-15% larger than males. This species has also evolved strong sexual dichromatism, with females usually darker than males, as well as plumage colour polymorphism (Forsman 1999, Sternalski and Bretagnolle 2010a).



Colour variation in flying marsh harriers.
Source: Sternalski and Bretagnolle (2010a).

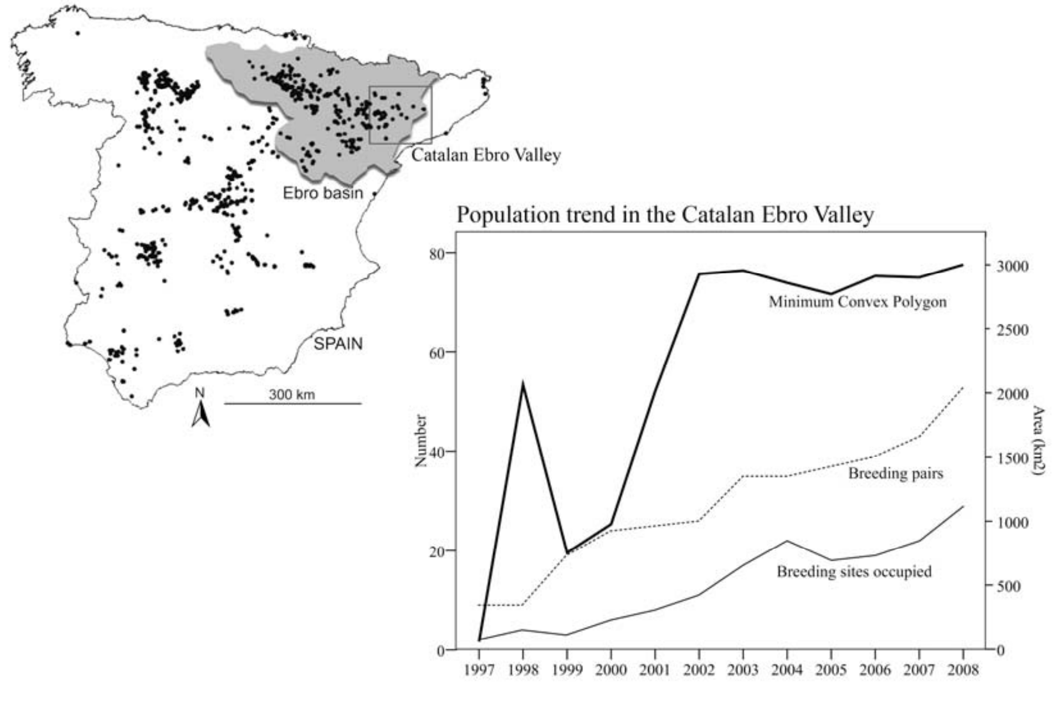
across much of Europe. The European breeding population is estimated at 93,000-140,000 breeding pairs and is evaluated as 'Secure' (BirdLife International 2004).

Figure 3. *Breeding population trends of marsh harrier over Europe during 1990-2000. Upwards, downwards and no arrows indicate positive, negative or non-significant trends of population growth, respectively. Arrow size indicates breeding population numbers. Source: BirdLife International (2004).*



Contrary to other species occupying farmlands, the recovery of this species has been very noticeable in some regions dominated by agricultural habitats -even in regions of intensified crops, such as peninsular Spain (Molina and Martínez 2008). Within some areas such as the Ebro Valley (NE Spain, Fig 4), the increase in the marsh harrier population has been accompanied by an increase in the number of locations used for nesting, with some pairs occupying artificial ponds and reservoirs related to agricultural practices. However, the extent to which these recent occupations are due to foraging and nesting habitat characteristics, the presence of conspecifics or to a combination of all these factors is unclear. Understanding the attractiveness and quality of breeding and foraging sites for wildlife in human-transformed environments is vital to the success of attempts to reconcile development and biodiversity conservation (Sánchez-Zapata et al. 2005, 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 and Lockwood 1999, Rice and Pfenning 2008).

Figure 4. *Distribution of the breeding population of the marsh harrier Circus aeruginosus in Spain in 200), (Molina and Martínez 2008) and population trend for the breeding population of marsh harrier in the Catalan Ebro Valley.*



OBJECTIVES

The main goal of this thesis is 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 through human-transformed environments. For this purpose, I use as a study model an expanding population of the marsh harrier living in an agricultural landscape of north-eastern peninsular Spain.

Particular objectives of this thesis are:

1. To investigate the foraging habitat use and selection in this expanding population across human-dominated landscapes
2. To explore its ranging behaviour and foraging-area requirements throughout the complete annual cycle
3. To compare its diet composition and food provisioning patterns in two localities with different degrees of human transformation
4. To assess factors influencing its nest-site occupancy pattern
5. To evaluate changes in the occupancy pattern associated with conspecific presence and individual differences
6. To evaluate the effect of pure spatial range constraints (i.e. dispersal processes) in the distribution of the species within its potential suitable habitat

Each one of these particular objectives is presented as a chapter of this thesis taking the form of a scientific paper (i.e., with the corresponding sections: introduction, methods, results, discussion, and references), which allows readers to understand each one independently of the others. However, and to address the main goal of the thesis, results of different chapters are linked together in a general discussion.

Chapter 1. Foraging habitat use and selection of marsh harriers in a human-dominated landscape[1]

Land-use change from extensive dry agriculture to intensive farmlands has been described as a major cause leading to impoverishment of food resources and reduction or degradation of foraging habitats for many declining open-habitat birds occupying farmlands (Tella et al. 1998, Newton 2004). Contrary to these species, marsh harrier populations are expanding in many agricultural areas, including intensified ones.

Little is known about foraging habitat use and selection of the marsh harrier in agricultural areas (Kitowski 2007, Luo et al. 2010). Territories located within intensified areas could actually be suitable for breeding but not for hunting purposes, forcing individuals to forage on patches of extensive fields. However foraging at distant patches increases energy costs (Amar and Redpath 2005). So, individuals occupying this new breeding habitat could do it because they can also find food resources in the intensive cultivated surroundings. Thus, I hypothesize that marsh harriers could be taking advantage of both habitat types, with those individuals occupying intensified landscapes using the surrounding intensified areas for hunting while individuals occupying extensive agricultural areas are using extensive areas for hunting.

[1] *Cardador L, Mañosa S (2011) Foraging habitat use and selection of Western Marsh-Harriers (Circus aeruginosus) in intensive agricultural landscapes. Journal of Raptor Research 45.*

Chapter 2. Ranging behaviour and foraging-area requirements throughout the complete annual cycle of marsh harriers in a human-dominated landscape[2]

Food is one of the main limiting factors for raptors (Newton 1979, 1998), and their breeding densities and breeding success can vary in relation to food availability (Salamolard et al. 2000, Redpath et al. 2002). Human-induced changes in habitat composition and structure can lead to changes in food availability (Newton 2004). Thus, determining the location and the size of foraging areas used by a species throughout the complete annual cycle, particularly in regions subject to major habitat transformations, is needed to determine where and when food resources are more exposed to human disturbances and to predict the potential consequences of these disturbances on species population dynamics.

At an intraspecific level, home range sizes decrease with increasing food availability (Kenward 1982, Saïd et al. 2009). Considering that the study population is composed of breeding pairs occupying agricultural habitats with different degrees of intensification, differences in home range sizes among individuals can be considered as indicative of the quality of these habitats (Kenward 1982, Saïd et al. 2009). If marsh harriers are occupying intensive crops as a secondary habitat because of the saturation of their preferred one, breeding pairs in this new location should show higher home ranges than pairs breeding in traditional extensive agricultural lands. Conversely, if intensive crops are good quality areas, in terms of food supply, home range sizes of individuals in these areas should be equal to or even smaller than those in extensive crops.

[2] *Cardador L, Mañosa S, Varea A, Bertolero A (2009) Ranging behaviour of marsh harriers Circus aeruginosus in agricultural landscapes. Ibis 151: 766-770.*

Chapter 3. Diet composition and food provisioning patterns of marsh harriers in two localities with different degrees of human transformation[3]

Organisms differ in their susceptibility to anthropogenic impacts depending on their degree of specialization (Devictor et al. 2008). At a population level, trophic generalists may be less susceptible to impoverished food supplies because of their ability to shift among alternative food resources (Purvis et al. 2000). However, not all prey types that a species can use are qualitatively equal (Salamolard et al. 2000). For *Circus* species small mammals have been described as a preferred and high-quality prey (e.g. Butet and Leroux 1993, Sternalski et al. 2010b). I explore here whether food availability varies between two areas in the Ebro Valley with different degrees of intensification and whether the marsh harrier is able to change their feeding and foraging behaviour in response to such differences. I hypothesize that if the marsh harrier is taking advantage of intensified habitats in terms of food availability, this should be reflected in diet and diversity and composition (i.e., especially in the percentage of small mammals consumed), as well as in provisioning patterns.

[3] *Cardador L, Planas E, Varea A, Mañosa S (2011) Feeding behaviour and diet composition of the marsh harrier in agricultural landscapes. In prep.*

Chapter 4. Factors influencing nest-site occupancy patterns in the marsh harrier in a human-dominated landscape[4]

Nest-site quality is a major determinant of individual fitness and can act as an important limiting factor of population growth and range expansions (Newton 1979, 1998). The creation of new nesting habitat opportunities related to human-induced environmental changes may favour the settlement and spread of some species. Occupancy rates have been described as a reliable method of habitat quality assessment (Sergio and Newton 2003). I investigated variations in nest-site occupancy rates in relation to habitat characteristics and distance to previously occupied sites to evaluate whether the creation of artificial ponds and reservoirs linked to irrigation practices in intensified agricultural landscapes may be benefiting this expanding species, which breeds mainly in wetlands. I hypothesize that if human-made agricultural ponds provide suitable breeding habitat for the marsh harrier, they should show equal or even higher occupancy rates than natural wetlands.

[4] *Cardador L, Carrete M, Mañosa S (2011) Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain. Animal Conservation, in press (doi: 10.1111/j.1469-1795.2011.00449.x).*

Chapter 5. Effect of density-dependence on the occupancy pattern and breeding behaviour of marsh harriers in a human-dominated landscape[5]

Apart from habitat characteristics, density-dependence can also act as an important ecological factor regulating populations. Both positive and negative effects of the presence of conspecifics (Fretwell and Lucas 1969, Rodenhouse et al. 1997, Stephens et al. 1999, Courchamp et al. 1999) can occur in the same population, even acting on the same individuals; thus, a trade-off between the costs and benefits of conspecific presence would exist (Brown et al. 1990, Arroyo et al. 2001, Serrano et al. 2005, Balkiz et al. 2010). Interestingly, individual differences in age or quality can modulate the way in which conspecifics affect fitness and the costs and benefits derived from their presence and abundance. For example, differences in age or aggressiveness among individuals can affect their competitive skills, changing the ways in which they interact with conspecifics and thus their fitness at similar breeding densities. In this sense, I hypothesize that less competitive individuals should avoid high conspecific densities to increase their fitness, thus increasing the probabilities of occupying empty suitable patches. This situation can have profound consequences for the whole distribution of the population.

[5] *Cardador L, Carrete M, Mañosa S (2011) Inter-individual variability and conspecific densities: consequences for population regulation and range expansion. In prep.*

Chapter 6. Effect of pure spatial range constraints on marsh harrier distribution models during different periods of its annual cycle in a human-dominated landscape[6]

Spatial range constraints (e.g. physical geographical barriers or time-limited expansions from place of origin; Moore et al. 2008, Blach-Overgaard et al. 2010) can limit the abilities of a species to cope with global environmental changes (Moore et al. 2008, Martínez-Morales et al. 2010). Thus, in the current scenario of global change and biotic homogenization, a better

understanding of the importance of pure spatial factors such as range controls of species distributions is needed for robust conservation planning, as these pure spatial range constraints may indicate the extent to which a given species will be able to track rapid environmental changes. Specifically, I examined whether current distributions of the marsh harrier in the Iberian Peninsula can simply be explained in terms of habitat availability and preferences or whether spatial filters, probably accounting for dispersal limitations, need to be considered. I hypothesized that if the species is expanding and has not yet occupied all of its potential range in terms of habitat availability, spatial filters should be significant descriptors in species distribution models.

[6] *Cardador L, Sardà-Palomera F, Carrete M, Mañosa S (2011) Incorporating spatial constraints in marsh harrier distribution models during different periods of its annual cycle. In prep.*

INFORME DELS DIRECTORS

La doctoranda Laura Cardador Bergua presenta en la seva tesi doctoral titulada "Factors que afecten l'èxit d'expansió de poblacions d'aus en medis transformats per l'home: l'arpella *Circus aeruginosus* a la Vall de l'Ebre" una sèrie de treballs de gran qualitat científica publicats o pendents de ser sotmesos en revistes científiques internacionals de gran prestigi incloses en el *Science Citation Index*. A continuació es detalla la contribució científica que ha realitzat la doctoranda en cada un dels articles, així com els seu factor d'impacte (*Thomson Institute for Scientific Information*):

- Foraging habitat use and selection of Western Marsh-Harriers (*Circus aeruginosus*) in intensive agricultural landscapes.
  L Cardador, S Mañosa (2011)
  Journal of Raptor Research 45
  Factor d'impacte (2009): 0,435
  La doctoranda L.C.B ha contribuït en el disseny del treball, en l'anàlisi de dades i en la redacció científica.

- Ranging behaviour of marsh harriers *Circus aeruginosus* in agricultural landscapes.
  L Cardador, S Mañosa, A Varea, A Bertolero (2009)
  Ibis 151: 766-770
  Factor d'impacte (2009): 2,123
  La doctoranda L.C.B ha contribuït en el disseny del treball, en l'anàlisi de dades i en la redacció científica.

- Feeding behaviour and diet composition of the marsh harrier in agricultural landscapes.
  L Cardador, E Planas, A Varea, S Mañosa (2011)
  Article en preparació, pendent de ser enviat a *Bird Study*
  Factor d'impacte (2009): 0,966
  La doctoranda L.C.B ha contribuït en el disseny del treball, en l'anàlisi de dades i en la redacció científica.

- Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain.
  L Cardador, M Carrete, S Mañosa (2011)
  Animal Conservation, in press (doi: 10.1111/j.1469-1795.2011.00449.x)
  Factor d'impacte (2009): 2,358
  La doctoranda L.C.B ha contribuït en el disseny del treball, en la recollida i anàlisi de les dades i en la redacció científica.

- Inter-individual variability and conspecific densities: consequences for population regulation and range expansion.
  L Cardador, M Carrete, S Mañosa (2011)
  Article en preparació, pendent de ser enviat a *PLoS ONE*
  Factor d'impacte (2009): 4,351
  La doctoranda L.C.B ha contribuït en el disseny del treball, en la recollida i anàlisi de les dades i en la redacció científica.

- Incorporating spatial constraints in marsh harrier distribution models during different periods of its annual cycle.
  L Cardador, F Sardà-Palomera, M Carrete, S Mañosa (2011)
  Article en preparació, pendent de ser enviat a *Ecography*
  Factor d'impacte (2009): 4,385
  La doctoranda L.C.B ha contribuït en el disseny del treball, en l'ànalisi de dades i en la redacció científica.

Tanmateix, informem que cap dels co-autors participants en els articles que composen aquesta tesi han utilitzat, implícita o explícitament, cap d'aquests treballs per a l'elaboració de la seva pròpia tesi doctoral.

Barcelona, a 10 de juny de 2011
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DISCUSSION AND CONCLUSIONS

DISCUSSION

There is a close link between environmental variables, intrinsic rate of increase and distribution of populations (Holt et al. 2005). In its broadest sense, the range of a species is the spatial expression of its niche (i.e. the set of environmental factors, both abiotic and biotic, which allows populations to persist, Brown 1984). Changes in environmental factors can, thus, promote changes in species distributions, either contracting or increasing their ranges. In this respect, human-induced environmental changes are often viewed in terms of their harmful impacts on the affected, usually endangered species, whose population numbers and distribution has decreased as a consequence of these changes (e.g. Suárez et al. 1997, Newton 2004). However, there are many types of alterations in natural and semi-natural landscapes that can be exploited by certain species with positive responses towards these transformations (Mckinney and Lockwood 1999). There is a growing recognition that species are not equally at risk when facing global changes (Mckinney and Lockwood 1999, Devictor et al. 2008). Variation in susceptibility to extinction may be related to external factors, such as how these human-induced environmental changes affect habitat suitability or food resources for particular species (Holt et al. 2005), or to intrinsic factors such as niche specialization or dispersal (Mckinney and Lockwood 1999, Devictor et al. 2008). Understanding the relationship between those factors and the degree of endangerment of a species is a key point in reconciling human development with biodiversity conservation.

Here, I used as study model a population of a long-lived species showing a marked increment in breeding numbers and range distribution throughout agricultural environments, to focus on the role played by ecological factors such as habitat and food availability, density-dependence and spatial range constraints on this expansion. This study model is particularly interesting when taking into account that many avian species inhabiting these human-dominated landscapes are of conservation concern (Tucker and Heath 1994) and that most papers dealing with the effects of agriculture on wildlife often highlight only this negative relationship (e.g. Benton et al. 2003, Tella et al. 1998).

Can human-induced environmental changes favour native species? The expansion of the marsh harrier in the Ebro Valley as a case study

Nest-site and food availability have been described as key limiting factors in avian species (Martin 1993, Penteriani et al. 2002, Sergio et al. 2003). Several examples exist of avian species increasing or decreasing their breeding numbers and distribution in relation to food availability or number of suitable nesting sites (e.g. Newton 1994). 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; see Newton 2004 for a review). The marsh harrier, however, seems to be an example of a native species benefiting from this transformation. As in many areas of its range, the marsh harrier in northeastern Spain is expanding after a period of dramatic decline (Cramp and 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, the intensified herbaceous crops (Chapter 1). As in some other species selecting habitat features at multiple spatial scales (Sergio et al. 2003, Martínez et al. 2007), the marsh harrier could be taking advantage of the numerous artificial ponds constructed in intensified areas in recent years for breeding, while still relying on traditional hunting habitats, in this case, the patches of extensive cereal farmland. However, radio-tracked individuals breeding in both intensive and extensive agricultural landscapes the herbaceous fields near their nests as hunting areas (Chapters 1), indicating that the species is not only exploiting a new breeding habitat but also a new hunting habitat. Moreover, individuals occupying intensified habitats tended to have smaller home ranges than birds nesting within more traditional ones (Chapter 2), also suggesting that, contrary to most farmland birds, marsh harriers found the intensive agricultural area to be a higher quality habitat than the extensive crops. Indeed, the abundance of small mammals, a preferred and high-quality prey for *Circus* species (e.g. Butet and Leroux 1993, Sternalski et al. 2010b), seems to be higher in intensive agricultural areas, giving strong support for the potential benefits derived from the occupation of this new habitat by the species (Chapter 3).

Habitat heterogeneity has profound consequences in population dynamics (Korpimäki 1988, Siikamäki 1995), so correctly identifying high quality areas is of interest for both theoretical and applied purposes. In this sense, occupancy rate of breeding sites has been described as an indicator of habitat quality among raptors (Sergio and Newton 2003). 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, i.e. 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 (Chapter 4). Occupancy rate at artificial wetlands such as ponds or reservoirs was not significantly different from that at natural wetlands such as rivers or watercourses, and was even larger than at inland natural wetlands (Chapter 4), suggesting that emergent vegetation from these human-made structures have provided new suitable breeding habitats for nesting marsh harriers. At a landscape scale, harriers responded positively to the area of intensified herbaceous crops, probably because they offer a larger abundance and greater accessibility to prey (Chapter 3). Preliminary analysis of changes in productivity with respect to the habitat characteristics suggests that no significant relationships exist between this demographic parameter and habitat attributes, suggesting that none of the habitats occupied in this area are unsuitable nesting habitats.

Apart from land uses, other factors such as the presence and abundance of conspecifics can modulate the quality of a site (Serrano et al. 2005, Soutullo et al. 2006). Site quality is a major determinant of fitness, although its effect can be confounded by individual quality (Carrete et al. 2008), particularly when individuals do not distribute at random through sites of differing quality. In this sense, phenotypic differences among marsh harriers, presumably linked to competitive skills, seem to be affecting individual settlement pattern within the breeding population. Such differences in settlement patterns seem to be related to differences in positive and negative density-dependence effects on productivity. Individuals with darker plumage had lower productivity when occupying highly populated breeding areas, while individuals with lighter plumage increased their productivity in these areas (Chapter 5). Variability in aggressiveness among individuals with different plumage colourations (Sternalski and Bretagnolle 2010), associated with melanin-based plumage differences (Roulin 2004) or age (Forsman 1999), may explain these inter-individual differences (Sol et al. 1998, Carrete et al. 2006, Margalida et al. 2008). Interestingly, this variability in density-dependence on productivity between individuals could be forcing less competitive individuals to move into empty breeding sites at a regional scale, thus favouring the expansion of the population (Chapter 5).

However, is the species reaching its maximum distribution or will it continue its expansion? When modelling the spatial distribution of the species, I found evidence that marsh harrier distribution at the scale of peninsular Spain is not only limited by climate and habitat availability but also by spatial constraints during the breeding season (Chapter 6). Limited dispersal from previously occupied areas, perhaps associated with social factors such as the benefits of conspecific density on productivity for the bulk of the breeding population (the lighter birds; Chapter 5) and/or the short natal dispersal distances described for the species (around 1-2 km, in a sedentary population of marsh harriers in France, Sternalski et al. 2008), is probably behind these spatial constraints. Although at a regional scale, less competitive, dark brown individuals looking for the most isolated sites for breeding may favour the expansion of the species, this pattern did not appear to be occurring at a larger scale, thus the species would continue to expand in the surrounding area of its range limits, and less likely by colonizing distant habitats.

Intrinsic features such as body size, genetic variability, life-history traits or dispersal behaviour can also influence whether species are winners or losers in a human-dominated world (Bennett and Owens 1997, Mckinney and 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 marsh harrier in the study area appeared to behave as a generalist species in relation to farming practices, using both intensive and traditional herbaceous crops for hunting (Chapter 1). Furthermore, it seemed to be able to adapt to temporal variations in resource availability. Tracked individuals changed the relative use of different crops (i.e. alfalfa, winter-sown wheat and barley or maize crops) during the year probably in relation to their height and density (Chapter 1). Its diet composition and delivery rates also differed in accordance with food availability in farmlands with different degrees of intensification (Chapter 3). In the intensified area, harriers prey mostly on voles, probably responding to their higher abundances and increased prey delivery rates throughout the breeding season as food demands of the broods increase. On the contrary, in traditional farmlands, where voles seemed to be less abundant, marsh harriers had a more diverse diet, preying mostly on birds and mice, and responded to increases of energy demands by turning to larger prey but late in the season with no increased delivery rates. 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 incorporating spatial constraints into habitat models

Species-specific niche requirements are not the only factors determining the range distribution of a species. At a large scale, spatial constraints, such as time-limited dispersal or geographical barriers, can limit the abilities of a species to fully occupy its potential habitat (Moore et al. 2008, Martínez-Morales et al. 2010), leading to mismatches between suitable environmental habitats and species geographic distribution (Pinto and MacDougall 2010). Indeed, equilibrium between environment and species distribution –the main assumption of most species distribution models- could be expected only under unlimited dispersion or when dispersion is as fast as the generation of suitable habitat for occupation (De Marco et al. 2010).

The spatial distribution of marsh harriers across peninsular Spain was largely explained by environmental variables (both climatic and habitat variables) during both the breeding and the wintering seasons. However, by including spatial filters in models (Diniz-Filho and Bini 2005, De Marco et al. 2010), there is evidence that marsh harrier distribution was also spatially constrained beyond environmental variables during the breeding season, but not during wintering (Chapter 6). These filters seemed consistent with the idea of a limited dispersal from areas occupied in previous years since, in general, they reduced the probability of occurrence of the species in distant but otherwise suitable areas (Chapter6). Limited dispersal may be related to the short natal dispersal distance described for the species (Sternalski et al. 2008) but also to social factors such as the benefits derived from conspecific density for individual fitness (Chapter 5). Further research is needed to correctly assess the relative role of both processes in the distribution of the species, as well as the existence of potential links between them (i.e., density-dependent dispersal rates, Blakiz et al. 2010, Serrano et al. 2004). Finally, it is worth noting that at smaller scales mismatches between environmental characteristics and species distribution at particular sites could be related to local processes, such as food abundances or pesticide use, which cannot be detected at the spatial resolution of these analyses.

Raptors are long-lived species that may move over large areas for several years before entering into the breeding population (Newton 1979). At that time, i.e. when settling for reproduction, 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 appropriate knowledge of breeding sites and foraging areas as well as increases mating opportunities (Brown et al. 1990, Arroyo et al. 2001, Serrano et al. 2005). Indeed, in colonial birds, many species present a high level of natal philopatry and high levels of conspecific attraction (Sternalski et al. 2008, Serrano et al. 2004). This could be occurring with marsh harriers in peninsular Spain, a demographic mechanism that can impede or delay the colonization of empty suitable patches located at great distances from previously occupied areas. In fact, for a fraction of the population (light breeders), a positive effect of conspecific aggregation on productivity was found (Chapter 5). On the other hand, though at a regional scale, poor competitive dark breeders seemed to occupy most isolated locations and promote range expansion, this pattern could not translate immediately to a larger scale, and a colonization-lag to most distant areas could exist (De Marco et al. 2010).

Contrary to the breeding period, spatial constraints seemed to have a negligible impact on marsh harrier distribution during winter. One possible explanation may be related to the arrival of migrant marsh harriers from central and northern-Europe during winter (Molina and Martínez 2008), joining the local resident population. Migrants can move long distances (Strandberg et al. 2008) and may be able to reach suitable patches where breeders from local populations, which show high site fidelity throughout the year (Chapter 2), are not present. On the other hand, censuses at roost sites during winter may also allow us to detect juvenile dispersers from local populations, which may move long distances and have a different geographic distribution with respect to the breeding population, as in other birds of prey (Real and Mañosa 2001). More specific studies on ranging behaviour of resident and migrant populations throughout the year are necessary to determine whether and to what extent spatial filters may be reflecting actual differences in spatial distribution between local and migrant birds and/or temporal movements of individuals from the local population.

Density-dependence, individual traits and species range distributions: lessons from an expanding population of marsh harriers

Density-dependence can modulate intrinsic rates of population growth and migration and can thus have important effects on species range expansions (Holt et al. 2005). As most in population processes, explanations for species range expansion usually make the inferred assumption that species traits are fixed among individuals. However, in most species, there is likely to be individual variation in niche requirements or dispersal propensities. Species ranges can thus potentially reflect ecological or evolutionary processes associated with such individual variation (Thomas et al. 2001, Holt 2003, Simmons and Thomas 2004).

A particular case of variability between individuals found in many avian species is phenotypic variation in colour 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), and thus modulate intraspecific interactions leading to differential cost-benefit balances of conspecific presence for individuals with different colourations. My results showed that the productivity of this marsh harrier population varied among breeding pairs, depending on the phenotype of breeders (i.e. plumage colouration) and their relative spatial position within the breeding population (Chapter 5). This pattern coincided with an uneven occupation of localities in relation to conspecific aggregation by individuals with different plumage colouration. Most likely, individual phenotype combined with local breeding densities seems to be the main determinant of breeding output in this species, beyond habitat heterogeneity, suggesting that not all individuals had the same expectation of success at a given population density. Segregation of birds of different phenotypes in large or small breeding cores found in the study area can thus be the result of individuals sorting themselves to maximize their own expected fitness (Brown et al. 1990).

Differences in niche requirements among individuals could have important consequences for species range expansion. In the studied population, positive density-dependence acting on a part of the population could explain the existence and maintenance of areas supporting high population densities, even if they are not of consistently higher quality than the surrounding areas (Muller et al. 1997). Conversely, negative density-dependence on the other individuals would, through intraspecific competition, increase the probability that empty, but otherwise suitable patches, became occupied. For these latter, less competitive birds, the benefits of settling in traditional areas may be counterbalanced by the costs of intraspecific competition, and make dispersal to new unoccupied areas advantageous (Balzik et al. 2010).

Populations cannot become established beyond their potential range because they have negative growth rates in these suboptimal or non-adequate habitats. However, it is clear that species can adapt to inhospitable conditions over long time periods, and there is abundant evidence for adaptation to different environments within the range of a species, sometimes over short timescales (Schluter 2000). Phenotypic plasticity, i.e. the capacity of a given genotype to produce different phenotypes under different environmental conditions, has been the focus of much research (e.g. Thompson 1991, Via et al. 1995, DeWitt et al. 1998). In particular, behavioural flexibility has been proposed as one of the main mechanisms to explain the invasion of novel habitats by invasive species because it provides them with the ability to expand or change their ecological niche (Sol et al. 2000, 2002, Wright et al 2010). Recently, however, behavioural flexibility has been reinterpreted as a specific trait encompassing variability among individuals, but not necessarily within individuals (Carrete and Tella 2011). One prominent contribution of this research is that the behaviours of individuals, but not the average behaviour at the level of species, are important during the invasion process. Linked with the recognition of individual consistency and inter-individual variability in adaptive behaviours, two similar hypotheses proposed that individuals may distribute themselves among breeding sites to settle in those places that best match their phenotype (Edelaar et al. 2008, Carrete and Tella 2010), causing directed gene flow which can promote population differentiation and adaptation (Edelaar et al. 2008). A similar situation can be portrayed in the case of the expansion of the marsh harrier, if colour differences are actually related to melanin-based plumage polymorphism (Sternalski and Bretagnolle). Less aggressive individuals avoid high-density situations by colonizing new patches, which promotes the expansion of the species.

An alternative explanation to this pattern could be related to variation in competitive skills with age. Adult birds could counterbalance the negative effects of crowding by taking advantage of communal defence (Arroyo et al. 2001), while younger individuals would suffer more the cost of crowding than its benefits. Expanding populations are commonly characterized by a high proportion of non-adult breeders (Newton 1998), a phenomenon explained by a high resource availability resulting from a change in the carrying capacity of the system (in this case, high food availability associated with a new habitat type). This could be the case of the large proportions of brown males found in our population (approximately 50%). Also in this case, variability in animal behaviours might contribute to variation in age-specific fecundity across individuals, if reproduction at an early age is not only the result of ecological factors acting on individuals, but is also the result of intrinsic and genetic differences between individuals (inter-individual variability in animal behaviours, so-called personalities). The high reproductive output expected for individuals occupying these new opportunities can favour the selection of individuals breeding at younger ages (Biro and Stamps 2008), thus increasing the proportion of the population looking for this new habitat type. Although more research is needed to actually understand the expansion process, evolutionary processes at range limits combined with density-dependent dispersal should be considered as important drivers of distribution changes in this and other species (Bridle and Vines 2006, Travis et al 2009).

Potential consequences of the expansion of a predator winner for other species

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

Several studies have discussed the inexorable risk that invasion of exotic organisms may entail to native biota (e.g. Vitousek 1997, Ricciardi 2007). Invasive species can reduce natural diversity by monopolizing resources, introducing or spreading infectious diseases and parasites, changing the species composition or relative abundance of sympatric species, and even causing local extinctions (Noss 1990, Soule 1990). However, predation by introduced species has been a far more important species interaction in causing extinction. Indeed, predation alone is listed as being responsible for the extinction of more than 40% of vertebrate species (Sax and Gaine 2008). Although less attention has been given to locally overabundant or expanding native species (Garrott et al. 2003), these species could have similar impacts on natural and semi-natural ecosystems to those caused by exotic ones (Valéry et al. 2008, Carrete et al. 2010).

Apart from possible threats derived from competition with functionally similar species, expanding populations of predators could also threaten the persistence of scarce or endangered populations by increases in predation (Sinclair et al. 1998). For example, nest success of some species in different areas has been correlated with densities of predators, and predator removal studies have led to increased nest success and breeding density in several species (see Newton 2004 for a review). This situation could be even more critical, if human-environmental changes lead to greater accessibility to nests (Whittingham & Evans 2004). In this thesis, I have not addressed the potential consequences of the expansion of the marsh harriers on other, more human-sensitive species. However, in the study area there are several species with an unfavourable conservation status (Suárez et al. 1997, Tella et al. 1996, Blanco et al. 1998), such as pseudo-steppe birds, which are potential prey species for generalist marsh harriers. The potential threats of the expansion of some native species on other native species is perhaps one additional factor worth examining in this and other expanding native species.

Summary of findings

In this thesis, I have achieved new insights on the biology of a common native raptor species, the marsh harrier, in human-transformed environments of the Iberian Peninsula and I have related them to possible causes of its recent range expansion. Understanding the factors that limit the current distribution of species and populations is crucially important for ecological and theoretical research (Dumbrell et al. 2010, Pinto and MacDougall 2010), but also to correctly predict the consequences of global changes for biodiversity and to take effective management and conservation decisions (Pearson and Dawson 2003, Blach-Overgaard et al. 2010). Although limited, these results show that environmental factors, sociability, dispersal constraints and density-dependent mechanisms may play an important role in the distribution of a common native species. Marsh harrier breeding numbers had been greatly reduced in previous decades (1960-1980) mainly due to organochlorine pesticides, drainage of wetlands and direct persecution (Cramp and Simmons 1994).

Thus, at least part of their increase may represent population recovery following reductions in organochlorine use and direct persecution. However, the species may also have benefited from the spread of human-made structures such as artificial ponds and reservoirs related to agricultural intensification, for breeding and from their surrounding crops for hunting. At a local scale, individual variation in density-dependence for productivity and settlement patterns may have favoured dispersal of some individuals to new empty habitat patches, while others aggregated around traditional areas. However, at a large scale (i.e., across peninsular Spain), the breeding population of marsh harriers seems to be spatially constricted beyond environmental variables. This result indicates that potential habitat for marsh harriers still exists for further expansions in the Iberian Peninsula (at least at the spatial resolution of our analyses, which does not allow us to consider smaller scale processes that may restrict the species distribution such as local food abundances or pesticides). Potential consequences of this expansion for other species should be considered in order to properly conserve biodiversity in a world of change.

CONCLUSIONS

- Human-induced environmental transformations can promote the creation of new suitable habitats for some native species that thrive in human-transformed landscapes. In this sense, we showed that the marsh harriers in our study area can take advantage of human-made structures, such as artificial ponds and reservoirs related to agricultural practices, for breeding, while exploiting their surrounding herbaceous crops, both traditional and intensified, for hunting.

- Probability of occurrence of marsh harriers at foraging sites decreased with the distance to the nesting site and increased in wetlands and herbaceous crops (both those with high-intensity agricultural practices and those with low-intensity agriculture). Tagged harriers in intensified farmlands did not use all crop types equally throughout the year; they selected different crops in relation to the crop stage (growing, plowed, and stubble) and to particular agricultural practices (irrigated, unirrigated).

- Male marsh harriers tracked in our study area used home ranges of 9-63 km^2 during the breeding period, with high variation among individuals. These home-range sizes were of the same order of magnitude than the few previously published estimates available for the species. Individuals show high site fidelity to nesting areas throughout the annual cycle. Size of home ranges in intensified farmlands in our study area tended to be smaller than those in the traditional farmland.

- Marsh harriers in intensified areas took higher percentages of small mammals (86% of the diet) than harriers in traditional farmlands (48% of the diet), suggesting that intensified areas offered higher availability of such prey. Moreover, harriers in traditional and intensified farmlands did not prey equally on different small mammal species (Mediterranean pine voles in intensified farmlands and mice in traditional ones). Marsh harriers in intensified farmlands responded to increased energy demand of the growing chick throughout the breeding season by increasing feeding rates. On the contrary, in traditional farmlands, where harriers had access to more diverse prey, they turned to larger prey late in the season.

- Occupancy rate of wetlands by marsh harriers in the Ebro Valley was mainly explained by the independent effect of habitat features acting at two spatial scales, i.e. 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 nor proximity to other occupied sites seemed to be important determinants of occupancy rates in this expanding population.

- Spatially-structured social aspects, such as the presence and the numbers of conspecifics, are an important source of spatial heterogeneity that affect both occupancy patterns and breeding performance. Productivity of our marsh harrier population varied among breeding pairs, depending on plumage colouration of breeders and their relative spatial position within other breeding pairs at local scales. In this way, individual variability combined with local breeding densities seems to be the main determinant of breeding output in this species, beyond habitat variables, suggesting that not all individuals had the same expectation of success at a given density. Accordingly, our results showed an uneven occupation of localities by individuals of different plumage colouration, with lighter harriers breeding in more aggregated groups than dark brown birds.

- At a population scale, differences in settlement patterns among individuals could have important consequences for the spatial distribution of a population, particularly when expanding. Indeed, in the expanding marsh harrier population, while positive density-dependence in settlement patterns, acting on a part of the population, could explain the existence and maintenance of areas supporting high population densities, negative density-dependence in settlement patterns, acting on another fraction of the population, could increase the probability that empty, but otherwise suitable patches, become occupied.

- The distribution of the marsh harrier at the scale of peninsular Spain seemed to be spatially constrained beyond environmental variables during the breeding season but not during winter, suggesting that the breeding population still has access to potential habitat for further expansions. These results highlight that factors determining species distribution vary throughout the annual cycle, and spatio-temporal dynamics of species should be taken into account when modelling species distributions.

RESUM EN CATALÀ

INTRODUCCIÓ

El canvi en la distribució geogràfica de les espècies és un fenomen natural, però el seu ritme i magnitud ha augmentat considerablement com a conseqüència de causes antropogèniques (Vitousek et al. 1997). La velocitat a la que s'estén o contrau una població a través de l'espai depèn de les seves taxes de creixement i dispersió, així com de fenòmens de denso-dependència (Holt et al. 2005). Els canvis ambientals produïts per l'home poden conduir a processos deterministes (com per exemple, l'empobriment o l'augment de recursos alimentaris o de l'hàbitat) que poden donar lloc a variacions en les taxes de naixement o mortalitat d'una població, empenyent-la, així, a un creixement positiu o negatiu. A més, les constriccions espacials, com per exemple les causades per limitacions dispersives, poden determinar la capacitat d'una espècie per respondre a aquests canvis ambientals, ja sigui en resistir reduccions en la disponibilitat d'hàbitat (en particular aquelles causades per la fragmentació de l'hàbitat) o en expandir-se (Moore et al. 2008, Martínez-Morales et al. 2010). Més enllà de les característiques ambientals, els processos de denso-dependència també poden jugar un paper clau en limitar el creixement demogràfic i l'expansió geogràfica d'una població. Per exemple, davant d'una denso-dependència negativa marcada, una població deixa de créixer a mides poblacionals absolutes baixes, sent més vulnerable a extincions degudes a processos estocàstics (Holt et al. 2005). D'altra banda, la presència de l'efecte "Allee" (és a dir, un augment de les taxes de creixement a mesura que augmenta la densitat d'una població, Stephens et al. 1999), poden contribuir a l'expansió sobtada de certes poblacions (Holt et al. 2005).

Espècies guanyadores i perdedores en un món de canvi

Les activitats humanes causen molts tipus d'alteracions en els ecosistemes, amb efectes importants sobre la seva diversitat biològica. Els canvis en els usos del sòl, la fragmentació de l'hàbitat, la contaminació del medi ambient, les espècies invasores o l'eutrofització han sigut descrits com alguns dels principals canvis globals produïts per l'home que condueixen a pèrdues de biodiversitat (Chapin et al. 1997, Vitousek et al. 1997, Sala et al. 2000). Les tendències actuals en l'àrea de distribució i abundància de molts taxons suggereixen que més del 50% de les espècies en la majoria dels grups estan disminuint com a resultat d'algunes d'aquestes activitats humanes (vegeu McKinney i Lockwood 1999). En aquest context, els estudis sobre els requeriments ecològics d'espècies que ocupen ambients alterats per l'home, així com dels factors causants de la seva disminució han estat centrals en la biologia de la conservació i s'han descrit com una eina essencial per desenvolupar estratègies efectives de gestió per conciliar el desenvolupament i la conservació de la biodiversitat (per exemple, Blanco et al. 1998, Tella et al. 1998, Arroyo et al. 2002, 2009, O'Connell i Yallop 2002, Carrete i Donázar 2005).

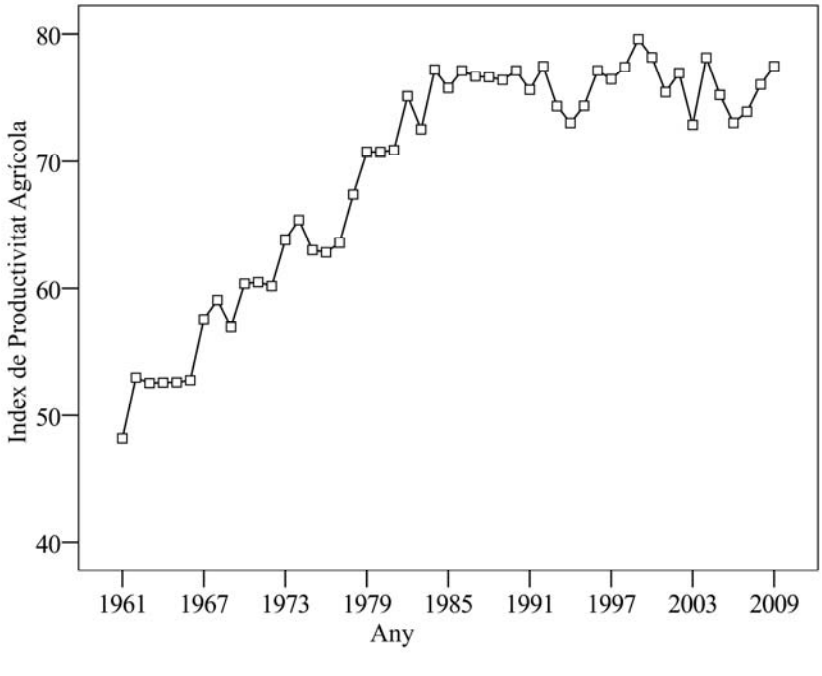
No obstant això, les activitats humanes no afecten a totes les espècies de la mateixa manera. Els ambients transformats poden proporcionar un hàbitat adequat per a moltes espècies tolerants a les alteracions antropogèniques. Algunes d'aquestes espècies no només no disminueixen demogràfica i geogràficament en ambients transformats, sinó que també poden augmentar la seva mida poblacional i ampliar la seva àrea de distribució (McKinney i Lockwood 1999). En aquest sentit, les activitats humanes poden crear noves extensions amb hàbitats adequats per algunes espècies que prosperen en ambients alterats per l'home (per exemple, Carrete et al. 2010, 2011, Martínez-Morales et al. 2010). Els impactes negatius i positius de les activitats humanes sobre les espècies tendeixen a no estar distribuïts a l'atzar entre diferents tàxons i grups ecològics (McKinney i Lockwood 1999). D'aquesta manera, els canvis ambientals d'origen humà poden actuar com un filtre, seleccionant aquelles espècies més capaces de sobreviure en els ecosistemes modificats (Smart et al. 2006). En termes generals, el patró general d'expansió d'algunes espècies comunes- natives o no natives- (anomenades "guanyadores") i la contracció d'altres espècies poc freqüents (anomenades "perdedores") pot donar lloc a un procés d'homogeneïtzació biòtica, que es pot considerar com una nova forma de canvi global (McKinney i Lockwood 1999, Ricciardi 2007) i una de les formes més importants d'empobriment biològic a tot el món (Olden et et al. 2004).

Les expansions poblacionals relacionades amb pertorbacions humanes han guanyat, recentment, interès per a la conservació i gestió de molts ecosistemes naturals i semi-naturals. Existeixen molts exemples d'espècies no autòctones en expansió (invasions exòtiques) que constitueixen una amenaça per a molts ecosistemes (per exemple, Griffis i Jaeger 1998, Marchetti 1999, Smith 2005). Contràriament, les invasions causades per espècies natives han estat poc estudiades com un component potencial de canvi de la biodiversitat, probablement perquè aquestes expansions semblen més "naturals" enfront de les invasions exòtiques (Garrott et al. 1993, Valéry et al. 2009, Carrete et al. 2010). No obstant això, l'expansió d'algunes espècies natives, resistents a les transformacions humanes, pot representar una amenaça important per a altres espècies, més sensibles a les alteracions humanes, que podrien competir de forma superior en àrees naturals, però no sempre en les àrees transformades (Didham et al. 2007, Carrete et al. 2010). D'altra banda, aquestes poblacions en expansió poden oferir informació útil i aplicable a altres espècies que no són capaces de prosperar en ambients alterats per l'home. És per tot això, que en la situació actual de canvi global, on la intervenció humana juga un paper clau, la comprensió no només de perquè algunes espècies estan disminuint, sinó també de quins són els factors principals que condueixen a altres a augmentar constitueixen un element clau per a la conservació.

La intensificació agrícola i els canvis en les comunitats d'aus

La intensificació agrícola ha sigut una de les formes més severes de canvi global que s'ha produït a tota Europa en les darreres sis dècades (Donald et al. 2001). Com a conseqüència d'un augment en la demanda d'aliments, les zones agrícoles de molts països industrialitzats s'han vist profundament alterades a través de la intensificació de les seves tècniques de cultiu, per tal d'augmentar la producció (Fig. 1), així com per canvis en els usos del sòl (Bouma et al. 1998). Aquests canvis en els ambients agrícoles han conduit a la disminució poblacional de moltes espècies i a una pèrdua de biodiversitat en aquests ecosistemes (Chamberlain et al. 2000, Donald et al. 2001, Benton et al. 2002) i han fet de la intensificació agrícola una de les principals amenaces per a la biodiversitat a Europa, comparable a la desforestació i el canvi climàtic global (Donald et al. 2001).

Figura 1. *Canvis en l'índex de productivitat agrícola a Europa occidental des de 1961 fins al 2009. L'índex es basa en la suma dels preus ponderats de diversos productes, després d'haver restat les quantitats usades com a llavors i pinsos, i s'expressa en milions de dòlars internacionals. Fot de les dades: base de dades de FAOSTAT (http://faostat.fao.org/).*

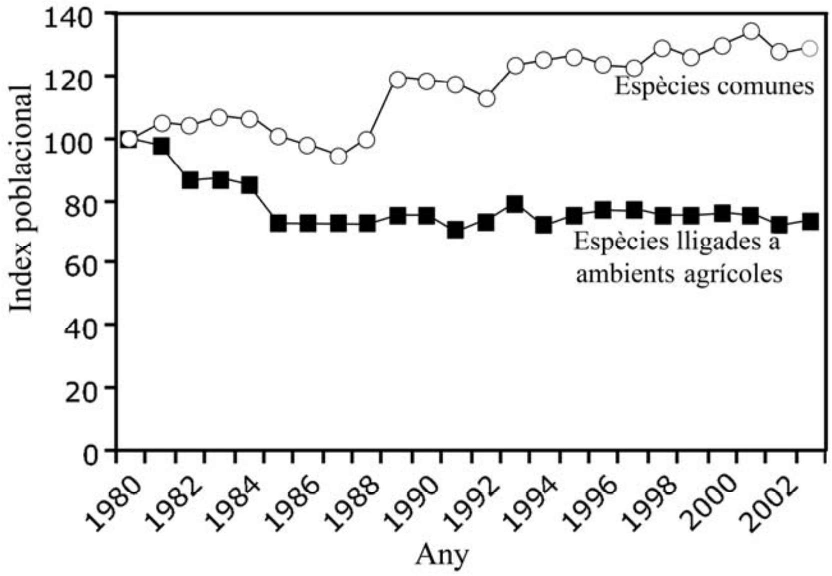


Els factors que han contribuït a l'impacte de la intensificació sobre la biodiversitat inclouen l'augment en l'ús de pesticides i fertilitzants, la mecanització de la collita i altres operacions agrícoles, l'eliminació de marges i altres àrees sense conrear entre conreus per produir camps més extensos, l'establiment de sistemes de regadiu en ambients àrids, l'avançament de les dates de collita i un augment dels monocultius (Newton 2004, Sanderson et al. 2005). Aquestes pràctiques agrícoles han provocat pèrdues de l'heterogeneïtat i qualitat de l'hàbitat, necessàries per al manteniment de comunitats riques en espècies d'organismes (Benton et al. 2003).

Particularment notable ha estat la disminució de nombroses poblacions d'aus de zones agrícoles durant les últimes dècades. La relació entre els canvis en les poblacions d'aus i la variació temporal i/o espacial en la intensificació agrícola s'ha demostrat a tota Europa (per exemple, el canvi en la producció de cereals explica el 30% de la disminució en el nombre d'aus de zones agrícoles, a escala europea, Donald et al. 2001) i a determinats països i regions (per exemple, Chamberlain et al. 2000, Benton et al. 2002). Aquestes disminucions han estat ràpides, massives i generalitzades. Algunes espècies han reduït en més d'un 80% els seus efectius i la seva distribució en menys de 20 anys (Tucker i Heath 1994, Chamberlain et al. 2000, Newton 2004). Actualment, la major part d'espècies d'aus amb un estat de conservació desfavorable a Europa utilitza zones agrícoles en algun període del seu cicle anual (Tucker i Heath 1994).

El procés pel qual les aus s'han vist negativament afectades pels canvis en les pràctiques aerícoles varien entre espècies, però en general estan associats a la reducció i degradació dels seus hàbitats de nidificació i caça o a la mortalitat directa deguda als processos de sega (Benton et al. 2003, Newton 2004). Tot i això, la intensificació agrícola no ha afectat a totes les espècies d'aus de la mateixa manera (Fig. 2), i els ambients transformats proporcionen un hàbitat adequat per a algunes espècies tolerants a les alteracions antropogèniques. Per exemple, a zones intensificades, on els estanys i basses de reg artificials i els cultius de regadiu han substituït els aiguamolls naturals o n'han creat de nous, algunes espècies d'aus lligades a medis aquàtics s'han beneficiat degut a que aquestes zones han representat la creació de noves zones d'alimentació i/o de cria (Sánchez-Zapata et al. 2005, Sebastián González et al. 2010).

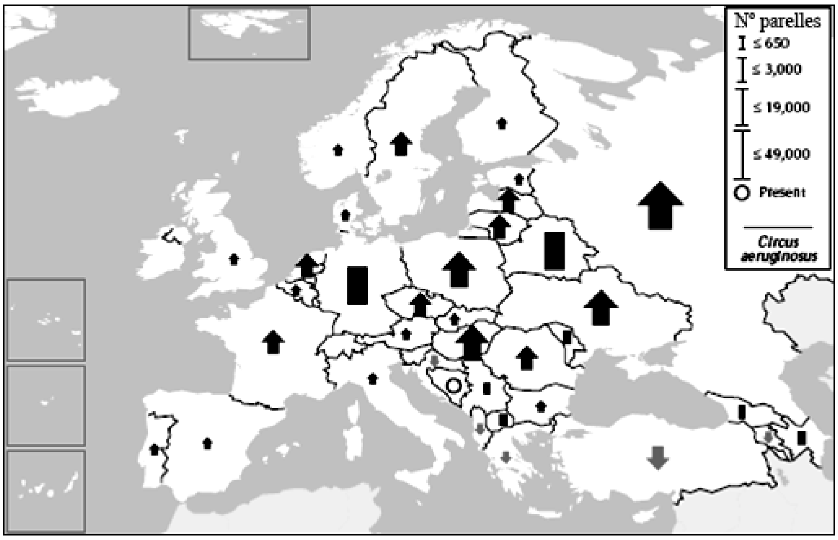
__Figura 2.__ Tendència poblacional d'ocells comuns als països de la Unió Europea des de 1980. Es mostra l'índex d'abundància basat en 19 espècies estretament lligades als medis agrícoles (és a dir, espècies especialistes d'hàbitats oberts, amb la major part de les seves poblacions reproductores distribuïdes a medis agrícoles) i l'índex d'abundància basat en 25 espècies comunes (és a dir, espècies generalistes que poden utilitzar una gran varietat d'hàbitats). Els índexs es calculen considerant que els valors per a 1980 representen el 100% de la població. Font de les dades: EBCC / RSPB / BirdLife / Estadística, els Països Baixos.



Poblacions en expansió en ambients agrícoles: l'arpella com a model d'estudi

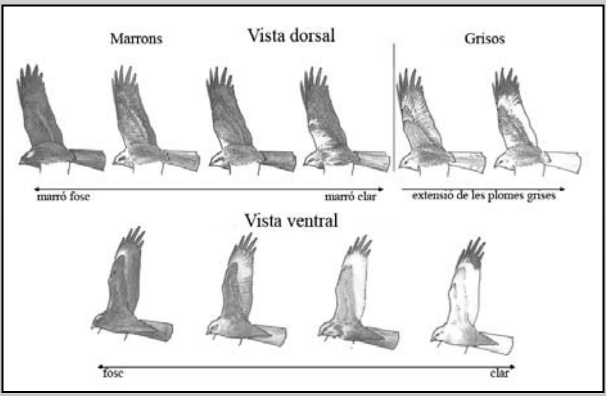
Els estudis sobre els factors que posen en perill la persistència a llarg termini d'una espècie són nombrosos i d'indubtable importància per a la conservació (per exemple, Blanco et al. 1998, Tella et al. 1998, O'Connell i Yallop 2002). Per contra, l'ecologia d'espècies natives comunes o en expansió sembla a vegades menys estimulant per als ecòlegs de la conservació (Garrott et al. 1993), tot i que comprendre els factors que poden conduir a l'èxit d'una espècie en un món on les taxes d'extinció estan arribant al seu màxim històric, pot ser igualment fascinant i important per a predir canvis futurs en la biodiversitat. Una espècie en expansió és l'arpella (*Circus aeruginosus*), un rapinyaire semi-colonial, de mida mitjana que ocupa les latituds mitges de la regió paleàrtica occidental (vegeu el Requadre 1 per obtenir detalls sobre l'espècie). Entre els anys 1960 i 1980, l'espècie va patir una forta davallada poblacional a Europa, principalment com a conseqüència de la dessecació de les zones humides on l'espècie criava, de la contaminació i de la persecució directa per part de l'home (Cramp i Simmons 1994). No obstant això, l'espècie s'ha recuperat en les últimes dècades amb un augment general moderat (> 10%), encara que hi ha hagut algunes disminucions al sud-est d'Europa (Fig. 3). En l'actualitat, l'espècie s'estén per la major part d'Europa. La població reproductora europea s'estima en 93.000-140.000 parelles reproductores i l'espècie està catalogada com a "segura" (BirdLife International 2004).

***Figura* 3.** *Tendències poblacionals de les poblacions reproductores d'arpella a Europa durant el període 1990-2000. El sentit de les fletxes (amunt, avall, sense fletxa), indiquen les tendències positives, negatives o no significatives del creixement poblacional. La longitud de la fletxa indica la mida de la població reproductora. Font: BirdLife International (2004).*



Requadre 1. L'ARPELLA

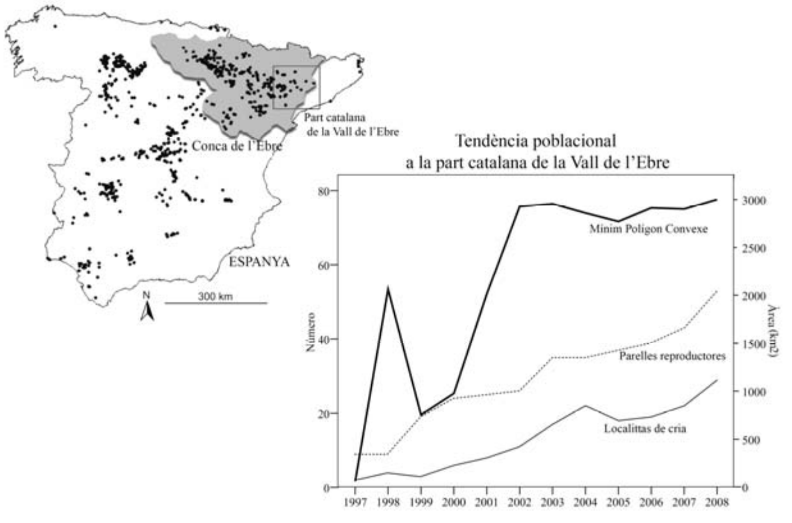
L'arpella (*Circus aeruginosus*) és un rapinyaire semi-colonial, de mida mitjana (longitud: 48-56 cm, envergadura: 115-130 cm; pes: ♂ 405-667g, ♀ 540-800g) que es distribueix a latituds mitjanes de la regió paleàrtica occidental. Nidifica a terra, principalment a zones humides i utilitza hàbitats oberts per caçar (Cramp i Simmons 1994). Utilitzen una gran varietat d'hàbitats oberts, incloent zones agrícoles, i eviten les zones muntanyosos i les zones boscoses. La espècie mostra un ampli espectre alimentari. Les aus i els micromamífers (especialment els rosegadors) representen les preses més consumides, però també poden consumir carronya i animals ferits, insectes, amfibis, rèptils i peixos, depenent de les circumstàncies locals (Cramp i Simmons 1994). Fora de la temporada de cria, els individus sovint formen joques comunals a terra. Les poblacions septentrionals són migratòries mentre que les poblacions més meridionals són residents. L'àrea d'hivernada s'estén des del nord de la conca Mediterrània fins a l'Àfrica subsahariana (Cramp i Simmons 1994, Strandberg et al. 2008). Els individus mostren dimorfisme sexual, les femelles són un 10-15% més gran que els mascles. També presenten un dicromatisme sexual marcat, les femelles solen ser més fosques que els mascles, així com polimorfisme en la coloració del plomatge (Forsman 1999, Sternalski i Bretagnolle 2010a).



Variació en vol del color del plomatge de l'arpella.
Font: Sternalski i Bretagnolle (2010a).

Contràriament a altres espècies, la recuperació de l'arpella ha estat molt notable en algunes regions dominades per paisatges agrícoles, fins i tot intensificats, com algunes zones de la Península Ibèrica (Molina i Martínez 2008). En algunes regions, com la vall de l'Ebre (NE d'Espanya), l'augment de la seva població s'ha vist acompanyat d'un augment en el nombre de localitats de cria (Fig. 4), amb algunes parelles que ocupen embassaments i basses de reg artificials relacionats amb les pràctiques agrícoles. No obstant això, la mesura en que aquestes ocupacions recents es deuen a les característiques de l'hàbitat de nidificació i de caça, a la proximitat a zones prèviament ocupades o a una combinació d'aquests factors no està clara. Comprendre l'atractiu i la qualitat dels hàbitats d'alimentació i de cria en ambients transformats per l'home és molt rellevant per tal de poder conciliar el desenvolupament i la conservació de la biodiversitat (Sánchez-Zapata et al. 2005, Sebastià-González et al. 2010). D'altra banda, la població en expansió de l'arpella ofereix una oportunitat per identificar alguns dels factors antropogènics que poden estar contribuint a processos d'invasió, aparentment naturals, que afavoreixen processos d'homogeneïtzació biòtica (McKinney i Lockwood 1999, Rice i Pfenning 2008).

Figura 4. *Distribució de la població reproductora d'arpella Circus aeruginosus a Espanya l'any 2006 (Molina i Martínez 2008) i tendència poblacional a la part catalana de la Vall de l'Ebre entre els anys 1997 i 2008.*



OBJECTIUS

L'objectiu principal d'aquesta tesi és explorar el paper que desenvolupen factors ecològics com l'hàbitat i la disponibilitat d'aliments, les limitacions espacials i la denso-dependència en l'expansió d'una espècie a través d'ambients transformats per l'home. Amb aquesta finalitat, es fa servir com a model d'estudi la població en expansió d'arpella de la Vall de l'Ebre.

Els objectius específics d'aquesta tesi són:

1. Investigar l'ús i selecció d'hàbitat de caça d'aquesta població en expansió en paisatges transformats per l'home.
2. Estudiar els seus patrons d'ús de l'espai al llarg del cicle anual.
3. Comparar la composició de la dieta i els patrons d'aprovisionament d'aliments en dues localitats amb diferents graus de transformació humana.
4. Avaluar els factors que influeixen en el seu patró d'ocupació de les localitats de cria.
5. Avaluar els canvis en el patró d'ocupació associats a la presència d'individus de la mateixa espècies i a diferències individuals.
6. Avaluar l'efecte de les constriccions espacials (processos de dispersió) en la distribució de l'espècie al llarg del seu hàbitat potencial.

Cadascun d'aquests objectius particulars es presenta com un capítol en format d'article científic (és a dir, amb les corresponents seccions: introducció, mètodes, resultats, discussió i referències), el que permet una comprensió dels mateixos de forma autònoma a la resta. Malgrat això i per abordar l'objectiu general de la tesi doctoral, els resultats dels diferents capítols és relacionen entre sí en una discussió general.

DISCUSSIÓ

Existeix una estreta relació entre les variables ambientals, la taxa intrínseca de creixement d'una població i la seva distribució (Holt et al. 2005). En el seu sentit més ampli, l'àrea de distribució d'una espècie és l'expressió espacial del seu nínxol ecològic (és a dir, el conjunt de factors ambientals, tant biòtics com abiòtics, que permeten a una població persistir, Brown 1984). Els canvis en els factors ambientals poden promoure, doncs, canvis en la distribució de les espècies, és a dir, la contracció o expansió de les àrees ocupades. En aquest sentit, els canvis ambientals produïts per l'home sovint són considerats en termes dels seus efectes negatius en les espècies afectades, en general en perill d'extinció, l'àrea de distribució de les quals s'ha reduït com a conseqüència d'aquests canvis (per exemple, Suárez et al. 1997, Newton 2004). No obstant això, hi ha molts tipus d'alteracions en els paisatges naturals i semi-naturals que poden ser aprofitats per algunes espècies, que responen positivament a aquestes transformacions (McKinney i Lockwood 1999). Hi ha un creixent reconeixement que no totes les espècies tenen el mateix risc quan s'enfronten a canvis globals (McKinney i Lockwood 1999, Devictor et al. 2008). La variació en la susceptibilitat a l'extinció, per part d'aquestes, pot estar relacionada amb factors externs com poden ser canvis antropogènics que afecten directament als seus recursos tròfics o d'hàbitat (Holt et al. 2005), o a factors intrínsecs com el grau d'especialització o les habilitats dispersives d'aquestes espècies (McKinney i Lockwood 1999, Devictor et al. 2008). Comprendre la relació entre aquests factors i el grau d'amenaça d'una espècie és un element clau per conciliar el desenvolupament humà amb la conservació de la biodiversitat. En aquesta tesi doctoral, s'utilitza com a model d'estudi una població d'una espècie de llarga vida (l'arpella en la Vall de l'Ebre) que ha experimentat un marcat increment en els seus efectius i àrea de distribució en un ambient agrícola en els darrers anys, per investigar la importància que poden tenir certs factors ecològics com l'hàbitat i la disponibilitat d'aliments, processos de denso-dependència i les constriccions espacials (limitacions dispersives) en la seva expansió. Aquest model d'estudi és particularment interessant si es té en compte que moltes espècies d'aus que habiten aquests paisatges agrícoles, són d'interès per a la conservació (Tucker i Heath 1994) i que bona part dels treballs centrats en l’efecte de l’agricultura sobre l’avifauna sovint han fet èmfasi, només, en la seva relació negativa (Benton et al. 2003, Tella et al. 1998).

L’hàbitat de nidificació i la disponibilitat d'aliments s’han descrit com uns dels principals factors limitadors per a les poblacions d'aus (Martin 1993, Penteriani et al. 2002, Sergio et al. 2003). Existeixen nombrosos exemples de poblacions que han augmentat o disminuït el seu èxit reproductor i àrea de distribució, en relació amb la disponibilitat d’aliments i llocs de nidificació (Newton 1994). La intensificació agrícola s'ha relacionat amb l'empobriment de l'hàbitat i l'esgotament dels recursos tròfics clau de moltes espècies d’aus que ocupen ambients agrícoles (per exemple, Blanco et al 1998, Tella et al 1998, vegeu Newton 2004 per una revisió). Contràriament, l’arpella sembla ser un exemple d’una espècie nativa que s’està beneficiant d’aquestes transformacions. Com en moltes altres àrees del seu rang, l’arpella a la Península Ibèrica està en expansió després d'un període en el que els efectius poblacionals i la seva distribució van disminuir de manera dramàtica (Cramp i Simmons 1994, BirdLife International 2004). A la Vall de l'Ebre, aquesta expansió ha tingut lloc en paral·lel a l’ús d'un nou tipus d'hàbitat disponible, zones agrícoles dominades per conreus herbacis intensificats (Capítol 1). Com en altres espècies que seleccionen l’hàbitat a diferents escales (Sergio et al. 2003, Martínez et al. 2007), l'arpella podria estar utilitzant les nombroses zones humides artificials, relacionades amb el reg dels conreus intensius, d’aquestes àrees per criar, però dependre, encara, de zones agrícoles més tradicionals per caçar, en aquest cas, els camps extensius de cereal de secà. No obstant això, els individus marcats i seguits durant la present tesis doctoral van utilitzar sempre les àrees més properes al niu, ja fossin cultius intensius o extensius (Capítol 1), el que indica que l'espècie no només estaria explotant un nou hàbitat de cria, sinó també un nou hàbitat de caça. D'altra banda, les arpelles marcades que ocupaven hàbitats intensificats tendien a tenir àrees de caça més petites que les d'ambients extensius (Capítol 2), suggerint que, contràriament a moltes altres aus que ocupen ambients agrícoles, les arpelles podrien trobar en les zones intensificades estudiades, hàbitats de major qualitat que en les zones més tradicionals. De fet, l'abundància de petits mamífers, una presa preferida i d'alta qualitat per a les espècies del gènere *Circus* (per exemple, Butet i Leroux de 1993, Sternalski et al. 2010b), semblava ser major en les zones d'agricultura intensiva estudiades, donant suport als possibles beneficis derivats de l'ocupació d'aquest nou hàbitat per l'espècie (Capítol 3).

La qualitat de l'hàbitat té conseqüències importants en la dinàmica poblacional de les espècies (Korpimäki 1988, Siikamäki 1995), de manera que poder identificar correctament àrees d'alta qualitat és d'interès, tant des de un punt de vista teòric com aplicat. En aquest sentit, la taxa d'ocupació de les localitats de cria ha estat descrita com un indicador adequat de la qualitat d'un hàbitat pels rapinyaires (Sergio i Newton 2003). Els resultats de la present tesi, mostren que la taxa d'ocupació de zones humides per part de l'arpella s'explica principalment per l'efecte independent de les característiques de l'hàbitat a dues escales espacials: a nivell de la zona de cria (superfície de vegetació aquàtica emergent i tipus de zona humida) i a nivell de la zona d'alimentació (percentatge de cultius herbacis intensificats a l'entorn de les zones humides). Ni les variables de pressió humana, ni la proximitat a altres llocs ocupats semblava afectar les taxes d'ocupació en aquesta població en expansió (Capítol 4). La taxa d'ocupació de zones humides artificials, com embassaments i basses de reg, no va diferir de la de zones humides naturals, com rius o barrancs, i va ser encara major que la d'aiguamolls naturals d'interior (Capítol 4), suggerint que la vegetació emergent d'aquestes estructures creades per l'home hauria proporcionat un nou hàbitat de nidificació propici per a l'arpella. A escala de les zones d'alimentació, les arpelles van respondre positivament al percentatge de cultius de regadiu herbaci intensificat a l'entorn de les zones humides, probablement pel fet que oferirien una major abundància o accessibilitat a les preses (Capítol 3). Anàlisis preliminars de la variació de la productivitat (numero de polls que volen per parella reproductora) en relació a les característiques de l'hàbitat van suggerir que no existia un vincle significatiu entre aquest paràmetre demogràfic i els atributs de l'hàbitat, el que suggereix que cap dels hàbitats ocupats en aquesta àrea eren hàbitats inadequats per a l'espècie.

A part dels usos del sòl, altres factors com la presència i l'abundància d'individus de la mateixa espècie, poden determinar la qualitat d'un hàbitat (Serrano et al. 2005, Soutullo et al. 2006). La qualitat de l'hàbitat és un factor determinant de l'eficàcia biològica d'un individu, encara que els seus efectes poden ser confosos per la pròpia qualitat individual (Carrete et al. 2008). En aquest sentit, es va trobar que l'efecte de la presència i abundància d‘altres individus de la mateixa espècie a les zones de cria no afectava igual a individus amb fenotips diferents, presumptament vinculats a diferències en les habilitats competitives, dintre de la població estudiada. La productivitat dels individus de plomatge fosc disminuïa quan aquests criaven més agregats, mentre que la productivitat dels individus clars augmentava en relació a l'agregació (Capítol 5). La variabilitat en l'agressivitat entre els individus amb diferents coloracions del plomatge (Sternalski i Bretagnolle 2010a), associades amb polimorfismes basats en la melanina (Roulin 2004) o amb l'edat (Forsman 1999), podrien explicar aquestes diferències inter-individuals (Sol et al. 1998, Carrete et al. 2006, Margalida et al. 2008). En concordança amb aquestes diferències, els individus amb plomatges diferents també van mostrar patrons d'ocupació diferents, on els individus foscos criaven menys agregats a escala local. De forma interessant, aquesta variabilitat en l'efecte de la densitat en la productivitat podria estar obligant als individus menys competitius a ocupar localitats de cria buides i més aïllades també a escala regional, afavorint l'expansió de la població (Capítol 5).

Però, ha ocupat l'arpella tota la seva distribució potencial o encara pot continuar la seva expansió? Modelant la distribució espacial de la població reproductora d'arpella a escala de la Península Ibèrica es va trobar evidència que la seva distribució no només estava limitada per variables de clima i hàbitat sinó que també estava constreta per limitacions espacials. Aquestes constriccions espacials semblarien consistents amb limitacions dispersives des de les àrees prèviament ocupades i podrien estar relacionades amb factors socials, com l'atracció per individus de la mateixa espècie (Serrano et al. 2004) i/o amb les baixes distàncies de dispersió natal descrites per poblacions sedentàries de l'espècie (al voltant de 2.1 km, en una població sedentària d'arpella a França, Sternalski al. 2008). D'altra banda, l'efecte positiu causat per l'agregació sobre la productivitat d'una fracció de la població (els individus de plomatge més clar) podria reforçar aquesta tendència. Encara que a escala regional, la cerca de llocs aïllats per criar per part dels individus menys competitius (els més foscos), podria afavorir l'expansió de l'espècie, aquest patró semblaria no estar passant a una escala major. Per tant la situació prevista a partir d'aquest model de distribució seria que l'espècie continuarà la seva expansió ocupant noves àrees properes a la seva distribució actual, amb menors probabilitats de que colonitzi hàbitats més llunyans.

Les característiques intrínseques d'una espècie, com ara la mida corporal, la variabilitat genètica, la fecunditat o les habilitats dispersives també poden determinar si una espècie serà guanyadora o perdedora en un món de canvi (Bennett i Owens 1997, McKinney i Lockwood 1999). Per exemple, el grau d'especialització de nínxol pot afectar al grau de susceptibilitat d'una espècies a les transformacions de l'hàbitat (Devictor et al. 2008). L'arpella en l'àrea d'estudi es va comportar com a una espècie generalista en relació al grau d'intensificació de l'hàbitat, utilitzant tant els cultius herbacis intensius com els tradicionals per a la caça (Capítol 1). D'altra banda, també semblava ser capaç d'adaptar-se a les variacions temporals en la disponibilitat de recursos. De fet, els individus marcats i seguits canviaven l'ús relatiu que feien de diferents tipus de cultius (alfals, cereals d'hivern i blat de moro) al llarg de l'any, probablement en relació amb la seva alçada i densitat (Capítol 1). La composició de la dieta i les taxes d'aportaments de preses per part dels adults reproductors al niu també van diferir, probablement en relació a la disponibilitat i accessibilitat de les preses, en dues localitats amb diferent grau d'intensificació agrícola (Capítol 3). A la zona de cultius intensius, les arpelles consumien principalment talpons, i augmentaven les taxes de lliurament de preses al niu al llarg del període reproductor, probablement en resposta a la creixent demanda d'aliments per part de les cries. Contràriament, a la zona de cultius extensius, on els talpons semblaven ser menys abundants, les arpelles presentaven una dieta més diversa, consumien mes quantitat de ratolins i ocells, i augmentaven la mida de les preses consumides al llarg del període reproductor, però no la taxa de lliurament de preses al niu. Tots aquest resultats suggeririen, que igual que altres espècies generalistes, l'arpella podria ser capaç d'explotar els recursos transitoris en les zones agrícoles intensificades, sent menys sensibles a les transformacions de l'hàbitat que altres espècies més especialistes (Siriwardena et al. 1998).

CONCLUSIONS

1. Els canvis ambientals creats per l'home poden promoure la creació d'hàbitats adequats per a algunes espècies natives. En aquest sentit, es va mostrar que l'arpella en l'àrea d'estudi podia utilitzar estructures artificials, com embassaments i basses de reg artificials, per criar i explotar els conreus herbacis del seu entorn per caçar.

2. La probabilitat d'ocurrència de l'arpella a les àrees de caça disminueix amb la distància al niu i augmenta en zones de vegetació palustre i conreus herbacis (tant de secà com de regadiu). Les arpelles marcades a zones intensificades no van usar amb la mateixa freqüència els diferents cultius al llarg del any, sinó que els va seleccionar en funció del seu estadi (en creixement, rostoll o llaurat) i de determinades pràctiques agrícoles (camps regats o no regats).

3. La mida de les àrees de caça usades pels mascles d'arpella a l'àrea d'estudi oscil·la entre 9 i 63 km^2, encara que existeix una gran variabilitat entre

els individus. La mida de les àrees de caça de les arpelles seguides a la Vall de l'Ebre és del mateix ordre de magnitud que les poques estimes publicades amb anterioritat per a l'espècie. Els individus mostren una elevada fidelitat a les àrees de cria al llarg del cicle anual. La mida de les àrees de caça dels individus marcats que usaven conreus intensius tendeix a ser inferior que la dels que usaven conreus més tradicionals, suggerint que les zones intensificades de la vall de l'Ebre podrien oferir una hàbitat de caça adequat per a l'espècie, inclús superior al de zones més tradicionals.

4. Les arpelles que crien a la zona intensificada de l'àrea d'estudi presenten un major percentatge de petits mamífers a la dieta (85% de la dieta) que les que crien a la zona més tradicional (49% de la dieta), que inclouen un major percentatge d'ocells. A més, es van observar diferències a nivell de les espècies de petits mamífers consumides. A la zona intensificada les arpelles consumien preferentment talpons comuns *Microtus duodecimcostatus* (aproximadament el 60% dels petits mamífers identificats), una espècie estretament lligada amb sòls humits. Contràriament, a la zona tradicional els talpons només representava un petit percentatge de les preses consumides (10%), mentre que els ratolins del gènere *Mus* eren els mamífers més consumits. A la zona intensificada les arpelles responien a la creixent demanda d'aliments dels polls al llarg del període reproductor, augmentant la freqüència d'aprovisionaments al niu. Contràriament a la zona més tradicional, on les arpelles presentaven dietes més diverses, els individus augmentaven la mida de les preses aportades però no la freqüència d'aportaments.

5. La taxa d'ocupació de les zones humides a la Vall de l'Ebre respon a l'efecte independent de les característiques de l'hàbitat a dues escales espacials diferents: a nivell de la zona de cria (percentatge de vegetació aquàtica emergent i tipus de zona humida) i a nivell de l'àrea d'alimentació (percentatge de conreus herbacis intensificats a l'entorn de la zona de cria). Ni les variables de pressió humana, ni la proximitat a altres llocs ocupats semblen ser determinants importants de les taxes d'ocupació en aquesta població en expansió.

6. Els aspectes socials espacialment estructurats, com la presència i el nombre d'individus de la mateixa espècie, són una font important d'heterogeneïtat espacial que afecta als patrons d'ocupació i a la productivitat de l'espècie (número de polls volats per parella reproductora). A més afecta de forma diferent a individus fenotípicament diferents. La productivitat de la població d'arpella de la Vall de l'Ebre variava en funció de la coloració del plomatge dels individus reproductors i de la seva posició relativa dintre de la resta de parelles reproductores a escala local. D'aquesta manera, la variabilitat individual combinada amb la densitat d'individus a l'àrea de cria sembla ser el principal determinant de la productivitat d'aquesta població, independentment de les variables d'hàbitat, el que suggereix que no tots els individus tenen les mateixes expectatives de criar amb èxit a una determinada densitat. En concordança, els nostres resultats mostren una ocupació desigual de les localitats per individus amb coloracions diferents del plomatge, amb els individus més clars criant més agregats que els individus foscos.

7. A escala poblacional, les diferències inter-individuals en els patrons d'assentament en relació a la densitat d'individus de la mateixa espècie, podrien tenir conseqüències importants per a la distribució espacial d'una població, especialment si aquesta s'està expandint. De fet, a la població d'arpella de la Vall de l'Ebre l'efecte positiu de la densitat sobre una part de la població podria explicar l'existència i manteniment de nuclis amb elevades densitats, mentre que els seus efectes negatius sobre altres individus, podria augmentar la probabilitat que altres localitats buides, però adequades per a l'espècie, siguin ocupades.

8. La distribució actual de l'arpella a escala de la Península Ibèrica sembla estar espacialment limitada, més enllà de les variables ambientals, durant l'època reproductora però no durant l'hivern. Aquests resultats suggereixen que la població reproductora encara tindria hàbitat potencial per expandir-se (com a mínim a la resolució espacial de les nostres anàlisis, que no permetrien considerar processos a menor escala com l'abundància local d'aliments o de contaminants). Aquests resultats també posen de manifest que els factors que

determinen la distribució de les espècies varien al llarg del cicle anual i que, per tant, la dinàmica temporal d'una espècie s'ha de tenir en compte quan es modela la seva distribució.

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CHAPTERS / PUBLICATIONS

Chapter I

Foraging habitat use and selection of marsh harriers in a human-dominated landscape

Cardador L, Mañosa S (2011) Foraging habitat use and selection of Western Marsh-Harriers (Circus aeruginosus) in intensive agricultural landscapes. Journal of Raptor Research 45: 168-173.

Ús i selecció d'hàbitat de caça de l'arpella *Circus aeruginosus* en paisatges agrícoles intensius

Laura Cardador · Santi Mañosa

Resum Es va estudiar l'ús i selecció d'hàbitat de caça de l'arpella *Circus aeruginosus* en una zona agrària mitjançant la ràdio-telemetria de 7 individus mascles d'arpella a la Plana de Lleida (al nord-oest de la península Ibèrica). L'aplicació de models lineals generalitzats mixtes va mostrar que la probabilitat d'ús d'un punt dintre de l'àrea d'estudi depenia tant de l'hàbitat com de la distància a la zona de nidificació. La probabilitat d'ocurrència va disminuir amb la distància al niu i va augmentar en zones humides i cultius herbacis (tant en camps poc intensius de secà com en camps d'ús molt intensius de regadiu). En zones dominades per cultius herbacis intensius (panís, cereal i alfals), les arpelles (n = 2) no van utilitzar tots els cultius per igual al llarg de l'any. A més van seleccionar diferents tipus de cultius en relació al seu estadi (creixement, sembrat, rostoll) i de determinades pràctiques agrícoles (amb o sense reg).

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Chapter II

Ranging behaviour and foraging-area requirements throughout the complete annual cycle of marsh harriers in a human-dominated landscape

Cardador L, Mañosa S, Varea A, Bertolero A (2009) Ranging behaviour of marsh harriers Circus aeruginosus in agricultural landscapes. Ibis 151: 766-770.

Patrons d'ús de l'espai de l'arpella *Circus aeruginosus* en paisatges agrícoles

Laura Cardador · Santi Mañosa · Anna Varea · Albert Bertolero

Resum Es van estudiar els patrons d'ús de l'espai i la mida de les àrees de caça de l'arpella al llarg del seu cicle anual en un paisatge agrari representatiu situat al nord-oest de la península Ibèrica (La Plana de Lleida) mitjançant el marcatge i radio-seguiment de 9 individus. La mida de les àrees de caça dels mascles va variar molt entre individus amb una mitjana de 3.287 ± 2.865 ha (n = 7) durant el període reproductor. Les àrees d'ús intensiu (on els individus eren localitzats el 50% del temps) van representar entre el 10 - 28% de l'àrea total usada i en general incloïen els camps més propers a la zona de nidificació. Les àrees de caça usades per les femelles (n = 2) durant el període reproductor van ser de mida inferior a la dels mascles amb un promig de 136 ± 191 ha. Durant el periode reproductor els individus criant en zones properes (≤ 5 km) van mostrar solapament parcial o total de les àrees de caça usades. No es va observar un patró consistent de variació en la mida de les àrees de caça usades pels mascles (n = 3) al llarg de l'any; tot i que es va observar una tendència a que fossin menors durant el període pre-reproductor (febrer – març). La posició de les àrees de caça va ser molt semblant al llarg de l'any.

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Chapter III

Diet composition and food provisioning patterns of marsh harriers in two localities with different degrees of human transformation

Cardador L, Planas E, Varea A, Mañosa S (2012) Feeding behaviour and diet composition of the Marsh Harrier Circus aeruginosus in agricultural landscapes. Bird Study 59: 228-235.

Composició de la dieta i patrons d'aportaments de preses al niu de l'arpella a paisatges agrícoles

Laura Cardador · Enric Planas · Anna Varea · Santi Mañosa

Resum Es va avaluar la composició de la dieta i la freqüència d'aportaments de preses al niu de l'arpella durant el període reproductor en dues zones agrícoles situades a la Plana de Lleida (al nord-oest de la península Ibèrica) que diferien en el seu grau d'intensificació agrícola. Les arpelles de la zona més intensificada van presentar un major percentatge de micromamífers en la dieta (86% de la dieta) que les de les zones de cultius més tradicionals (48% de la dieta), que presentaven un major percentatge d'ocells (46% de la dieta). Dintre dels micromamífers, el talpó comú *Microtus dueodecimcostatus* va ser la pressa més consumida a la zona més intensificada (aproximadament el 60% dels micomamífers identificats). Contràriament, aquesta espècie només va representar un petit percentatge (10%) en la zona de cultius tradicionals, on els ratolins del gènere *Mus* van ser els micromamífers més consumits. Censos de micromamífers realitzats a l'àrea d'estudi van suggerir que la composició de la dieta de les arpelles podia estar reflectint diferències reals en l'abundància de micromamífers en aquestes àrees. La freqüència d'aportaments al niu va augmentar al llarg del període reproductor a la zona més intensificada, contràriament aquest patró no es va observar en la zona més tradicional, on els individus augmentaven la mida de les preses consumides al llarg del període reproductor.

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Chapter IV

Factors influencing nest-site occupancy patterns in the marsh harrier in a human-dominated landscape

Cardador L, Carrete M, Mañosa S (2011) Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain. Animal Conservation 14: 382-390.

Poden els ambient agrícoles intensificats oferir hàbitat adequat per algunes espècies d'aus rapinyaires? L'arpella al nord-est d'Espanya

Laura Cardador[1] · **Martina Carrete**[2,3] · **Santi Mañosa**[1]

Resum En aquest capítol s'investiga la selecció d'hàbitat de nidificació de l'arpella a la Plana de Lleida (NE Península Ibèrica). Mitjançant anàlisis multivariants s'avalua la importància de les característiques de l'hàbitat, la proximitat a altres localitats de cria ocupades i les pertorbacions humanes en els patrons d'ocupació de les localitats de cria de l'espècie. Els nostres resultats mostren que l'arpella ocupa els llocs de cria en relació a les característiques de l'hàbitat a dues escales espacials complementaries (l´hàbitat de nidificació i l'hàbitat de caça del seu entorn) i indiquen que un rapinyaire que utilitza estructures artificials creades per l'home, com basses de reg i embassaments, i els cultius herbacis del seu entorn per caçar, podria beneficiar-se de la intensificació agrícola. Sovint només es consideren els efectes negatius que les activitats humanes ocasionen en algunes espècies. Malgrat això, les activitats humanes estan causant, també, molts tipus d'alteracions en els paisatges naturals i semi-naturals, que poden ser explotades per altres espècies amb respostes positives a aquestes alteracions. L'adaptació d'algunes aus rapinyaires als ambients alterats per l'home, com l'arpella en la nostra àrea d'estudi, planteja dubtes sobre la conveniència d'utilitzar aquestes espècies com indicadores de la qualitat i grau d'alteració d'un hàbitat.

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Chapter V

Effect of density-dependence on the occupancy pattern and breeding behaviour of marsh harriers in a human-dominated landscape

Cardador L, Carrete M, Mañosa S (2011) Inter-individual variability and conspecific densities: consequences for population regulation and range expansion. PLoS ONE 7: e33375.

Variabilitat inter-individual i densitat: conseqüències en la dinàmica poblacional i processos d'expansió

Laura Cardador[1] · Martina Carrete[2] · Santi Mañosa[1]

Resum La presència de coespecífics pot modular notablement la qualitat d'un lloc. La densitat de coespecífics en les localitats de cria, pot tenir efectes positius i negatius sobre els individus que les ocupen, amb el balanç final entre els seus costos i beneficis depenent de les pròpies característiques individuals. Un cas particular de variació inter-individual que es dóna en moltes espècies és la variabilitat cromàtica. Les diferències en color poden co-variar amb la morfologia, fisiologia i el comportament dels individus, així com amb l'edat. De forma interessant, les diferències en la qualitat individual i en edat poden modular l'efecte que la presència de coespecífics té en l'eficàcia ecològica dels individus. Es va investigar si la variabilitat en el color del plomatge afectava els processos de regulació poblacional i d'expansió en una en una espècie de vida llarga. Els nostres resultats van mostrar que existia una forta variació en l'efecte final de la densitat en la productivitat de parelles reproductor integrades per individus amb diferent coloració. La productivitat de les parelles més clares va augmentar al llarg del gradient de densitat, mentre que la de les més fosques disminuïa. De manera similar, es donava una ocupació desigual de les localitats en relació a la densitat, amb les parelles més clares criant més agregades. El mateix patró es va donar a escala poblacional, on la probabilitat de colonitzar localitats noves i aïllades també variava en funció del color de les parelles.

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Chapter VI

Effect of pure spatial range constraints on marsh harrier distribution models during different periods of its annual cycle in a human-dominated landscape

Cardador L, Sardà-Palomera F, Carrete M, Mañosa S (2011) Incorporating spatial constraints in marsh harrier distribution models during different periods of its annual cycle. In prep.

Importància de les constriccions espacials en els models de distribució de l'arpella en diferents períodes del cicle anual

Laura Cardador[1] · **Francesc Sardà-Palomera**[2] · **Martina Carrete**[3] · **Santi Mañosa**[1]

Resum Quan es modela la distribució espacial de les espècies, sovint s'assumeix que aquestes estan en equilibri amb el medi ambient. No obstant això, aquesta assumpció podria no complir-se si existeixen limitacions dispersives. Es van analitzar dades de presència d'una població en expansió d'arpella a la Península Ibèrica, durant el període reproductor i l'hivern, per analitzar si la seva distribució podia explicar-se només en termes de variables ambientals (clima i hàbitat) o si altres limitacions espacials no ambientals s'havien de tenir en compte. Per a això, es van construir models de distribució considerant només variables ambientals o incloent també vectors propis (com a variables descriptores de limitacions espacials no ambientals, com limitacions dispersives). Els nostres resultats van revelar que les variables ambientals jugaven un paper clau en determinar la distribució de l'arpella durant el període reproductor i l'hivern. Tant les variables de clima com d'hàbitat semblaven importants. Malgrat això, quan es van afegir els vectors propis als models, es va trobar evidència que, a part de les variables ambientals, altres constriccions espacials limitaven la distribució de la població d'arpella durant el període reproductor, però no durant l'hivern.

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ORIGINAL ARTICLE

Incorporating spatial constraints in marsh harrier distribution models during different periods of its annual cycle

Laura Cardador[1] · Francesc Sardà-Palomera[2] · Martina Carrete[3] · Santi Mañosa[1]

Abstract When modelling spatial distribution of species, it is often assumed that species are in equilibrium with the environment. However, this assumption can be violated under limited dispersal conditions. We analyzed occurrence data of an expanding population of the marsh harrier in peninsular Spain, during the breeding and wintering seasons, to address whether its current distribution can simply be explained in terms of environmental variables (climate and habitat) or whether non-environmental spatial constraints need to be considered. We did so by implementation of species distribution models constructed with environmental variables alone and with the inclusion of eigenvectors (to capture non-environmental spatial constraints). Our results revealed strong responses to environmental variability during both the breeding and the wintering seasons. Both habitat and climatic factors appeared to be important range controls. However, by including eigenvectors in models, we found evidence that marsh harrier distribution was spatially constrained beyond environmental variables during the breeding season, but not during its wintering.

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Introduction

Individuals can have non-random, aggregated spatial distributions. Species-specific environmental responses or pure distance effects can be involved in generating these patterns (Rominger et al. 2009, Dumbrell et al. 2010). Under deterministic models, species distribute based on defined niche spaces, and their probabilities of occurrence are expected to change linked to environmental variables (Snyder and Chesson 2003). By this way, distributions can be patchy at the population level because the environment tends to be spatially autocorrelated, with nearby sites being more ecologically similar than distant ones (Legendre 2003). Climate has often been proposed as the main range-limiting factor within environmental variables, especially at large spatial scales (Huntley et al. 2007). Besides, non-climatic environmental factors such as topography, land uses or soil types are thought to increase in importance at increasingly finer scales (Pearson and Dawson 2003, Anadón et al. 2006). Nevertheless, distribution patchiness may also arise as a result of pure spatial constraints such as stochastic events or dispersal limitations (e.g. physical geographical barriers or time-limited expansions from place of origin; Moore et al. 2008, Blach-Overgaard et al. 2010). Species can be present and persist at particular locations not because of higher habitat quality but because individuals mostly recruit near their natal areas or close to conspecifics (Pinto and MacDougall 2010). Furthermore, distance- and environment-based dispersal limitations may also operate simultaneously, and their relative strengths can vary at different spatial scales (Pinto and MacDougall 2010).

Understanding the relative roles of environmental factors and pure spatial constraints as determinants of the geographical distribution of species has ecological and theoretical interest (Dumbrell et al. 2010, Pinto and MacDougall 2010) but also applied relevance (Blach-Overgaard et al. 2010). Spatial constraints can limit the abilities of a species to cope with global environmental changes, either in resisting reductions in available suitable conditions (particularly where these cause habitat fragmentation) or in exploiting expansions (Moore et al. 2008, Martínez-Morales et al. 2010).

Environmental changes are a natural phenomenon, but the rate and magnitude of such changes have being significantly increased during recent decades because of anthropogenic causes (Donald et al. 2001, Carrete et al. 2009). Thus, a better understanding of the importance of pure spatial factors as range controls of species distributions is needed for robust conservation planning, particularly in the current scenario of global change, as these pure spatial range constraints may indicate the extend by which a given species will be able to track these rapid environmental changes.

Species distribution models (SDMs) have provided a popular analytical framework for predicting species distributions and are applied across a range of biogeographical scales (Guisan and Thuiller 2005). SDMs represent an empirical method to draw statistical inferences about the drivers of species' ranges under different conservation, ecological and evolutionary processes (Zimmermann et al. 2010). However, although empirical evidence indicates that patterns of species distribution are often constrained by pure spatial limitations (Pinto and MacDougall 2010), most SDMs assume equilibrium between species' distribution and the environment, ignoring potential consequences of spatial limitations (Guisan and Thuiller 2005).

The marsh harrier *Circus aeruginosus* is a semi-colonial, ground-nesting raptor that mainly breeds in wetlands and hunts on open habitat (Cramp and Simmons 1994). Northern populations are migratory while populations from the Mediterranean areas are resident. Main wintering ranges extend from the north of the Mediterranean basin to the Sub-Saharan Africa (Cramp and Simmons 1994, Strandberg et al. 2008). During winter, individuals roost communally on the ground. The European marsh harrier population underwent a dramatic population decline from 1960 to 1980 due to wetland drainage, contamination and direct persecution, but recovered in recent decades, when the species underwent moderate increase (ca. 10%; Cramp and Simmons 1994, BirdLife International 2004). The same tendency was experienced in other local populations, such as the Spanish one, where the breeding population of the species also increased in recent decades (Molina and Martínez 2008), although the area occupied remained nearly unchanged (Fig. 1). Absence of more sites with suitable habitat for the species or pure distance effects could be limiting this range expansion. Here, we study whether the current distribution of the expanding population of marsh harrier in our study area can simply be explained in terms of environmental variables or whether non-environmental spatial constraints need to be considered. We did so by implementation of SDMs constructed with environmental variables alone and with the inclusion of eigenvectors. The inclusion of eigenvectors (so-called *spatial filters*) in SDMs has recently been shown to effectively capture non-environmental spatial constraints caused by dispersal-limited, non-equilibrium range dynamics (Griffith and Peres-Neto 2006, De Marco et al. 2010). We fitted a separate model for the breeding and wintering seasons, since for highly mobile organisms, temporal variation in ecological factors determining their distributions in different periods of the annual cycle may occur (Blanco et al. 1998, Tella and Forero 2000). Incorporating spatial constraints in SDMs during different periods of the annual cycles can lead to an improvement of model accuracy while also providing relevant information about the potential drivers of the spatial dynamics of species.

Methods

Occurrence data

The study area covered peninsular Spain (493,770 km^2). Occurrence data of marsh harriers during the breeding and wintering periods were obtained from a national census performed in 2006 (SEO/Birdlife 2006). In this census, marsh harriers were surveyed by standardized nest searching and detection of territorial pairs in potential breeding areas during the breeding period and counts of individuals entering roost sites during winter (Molina and Martínez 2006). In total, 1,278 nests/territories and 308 active roost sites were detected. The location of nests/territories and the central coordinates of roost sites were incorporated into a Geographic Information System (GIS) using Universal Transverse Mercator (UTM) grid of 1-km^2.

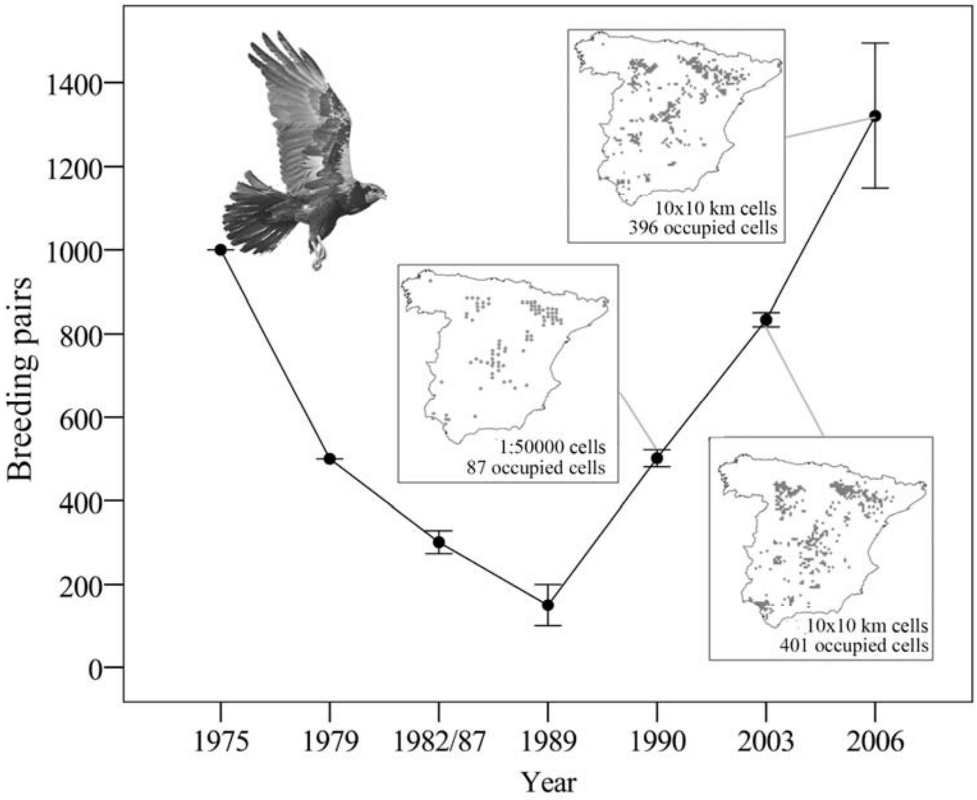

Figure 1. Evolution of the breeding population of marsh harrier in Spain from 1975 to 2006. Data were compiled from various sources (revised data from 1975 to 2003: Jubete 2003; data on 1990: Martínez et al. 1996; data on 2006: Molina and Martínez 2008). Mean, maximum and minimum estimates are shown. Available maps showing the distribution of the species are also shown.

Environmental range controls

We used four climatic variables commonly used in species distribution modelling to represent the climatic controls (mean annual temperature T_{AN}, minimum temperature of the coldest month T_{MIN}, maximum temperature of the warmest month T_{MAX} and mean annual precipitation AP, Supplementary material Fig. S1). These variables were obtained with a resolution of 180 m from the "Atlas Climático Digital de la Península Ibérica" (Ninyerola et al. 2005), a climatic model constructed with historical data series (1951-1999) from 2,285 climate stations belonging to the Servicio Nacional de Meteorología of Spain.

The habitat variables representing the environmental variability of the area were slope (SLO, derived from the WorldClim 1.4 digital elevation model with a resolution of 1 km^2, Hijmans et al. 2005), percentage of suitable habitat (in this case, open vegetation; Cramp and Simmons 1994), and the normalized difference vegetation index (NDVI, an index of primary productivity commonly used as a descriptor of potential food supply for many raptor species; Carrete et al. 2007, Grande et al. 2009) (see Supplementary material Fig. S1 for details). NDVI and VEG were derived from remote sensing with a resolution of 250 m. VEG was obtained by pooling 7 original categories (i.e., arable land, pastures, natural grasslands, moors and heathlands, scrub with sclerophyllous vegetation, sparsely vegetated areas and wetlands) of the CORINE land cover 2006 (European Agency of Environment 2006). NDVI came from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Terra (EOS AM) satellite data as a series of monthly mean values for 2000-2006. These values were averaged to derive an annual mean to use for analyses. As we were interested only in NDVI from habitats suitable for the species, we only used NDVI values from cells defined as open habitat at a resolution of 250 m in the Corine Land Cover.

All layers were reprojected to the Universal Transverse Mercator projection (UTM) and resampled to 1 km^2 grid size using the bilinear resampling technique. Previous information has shown that the pattern of habitat selection of marsh harriers is highly influenced by habitat characteristics at the scale of the foraging area (Cardador et al. 2011). So, for each variable, we took as the value for the 1x1 km cells the mean value of that variable in a square of 10 x 10 km centred in the 1x1 km cells, by using focal statistics. This way, values of each variable for the 1x1 km cells integrated information of the landscape composition at a larger scale (100 km^2), encompassing the average foraging area of marsh harriers estimated on the basis of radio-tracking data (Cardador et al. 2009). All GIS operations were conducted in ArcGIS 9.2.

Spatial range controls

To account for non-environmental spatial constraints on the marsh harrier distribution, we used spatial filters (eigenvectors) as spatial constraint variables. Filters could be considered as different and independent propositions of how cells were geographically related or connected to each other, expressed as new variables derived from geographical distances and indicating the spatial relationships among cells at different spatial scales (Diniz-Filho and Bini 2005). The inclusion of spatial filters in the models allowed us to account for the effect of subjacent spatial structures that were not captured by environmental factors at these scales (De Marco et al. 2010).

Due to computational limitations and following Blach-Overgaard et al. (2010), the filters were computed at a coarse resolution (20x20 km), but subsequently interpolated to 1x1 km resolution using the Inverse Weighted Distance method in ArcGIS. We computed the spatial filters in SAM 3.0 (Rangel et al. 2006) by constructing a pairwise distance matrix amongst all grid cells using their Universal Transverse Mercator coordinates (latitude and longitude). The distance matrix was subsequently truncated at the maximum distance that connected all the study area under the minimum spanning tree criterion (default settings in SAM 3.0), and from this modified distance matrix 444 spatial filters were computed using principal coordinate analysis (Borcard and Legendre 2002). Since we were interested in assessing the relative importance of environmental factors and non-environmental spatial constraints, it was of paramount importance not to introduce bias in the modelling towards either environment predictors or spatial filters. So, following Blach-Overgaard et al. (2010) and because a fixed number of predetermined environmental predictors were used, we included the same number of spatial filters in the models (the first 6 filters, *see results*). These filters possessed strong clinal patterns (Filter 1 portrayed a north-south gradient and Filter 2 and east-west gradient), containing two major clusters of similar values positioned at opposite ends of the map (Supplementary material Fig. S2). Subsequent spatial filters (Filters 3-6) became more fragmented and created a more oscillatory pattern across peninsular Spain, representing spatial effects at finer spatial scales (distance between clusters around 700-500 km approx., Supplementary material Fig. S2).

Distribution modelling

We built models to estimate the probability of occurrence of marsh harrier using the Maximum Entropy modelling approach, via the Maxent 3.1 software (Phillips et al. 2006, Phillips and Dudik 2008). We selected Maxent because of its consistently high performance compared to other predictive algorithms in a recent comparative methodological study (Elith et al. 2006). Maxent does not require absence data points for the modelled distribution; instead, the probability distribution is defined only on species presences (Phillips et al. 2006). To address the study questions, we ran Maxent with five models based on different combinations of the predictors: 1) a full environmental model that included all the climatic and habitat predictors (clim+hab), 2) an environment and filter model (clim+hab+filters) that included all environmental predictors and spatial filters. The remaining models included single groups of predictors in isolation: 3) climate (clim), 4) habitat (hab) and 5) the spatial filters. The default settings for Maxent were used (Phillips et al. 2006), except for the response types (we only test the linear and quadratic response types). Duplicate samples (i.e. two or more records within the same pixel) were removed and handled as single observations. We evaluated the contribution of the environmental variables to the Maxent models by examining the contribution of each predictor to the regularized training gain in the best performing model.

Statistical analysis

Model performance was assessed by dividing the species occurrence data into random training (70%) and test (30%) datasets, and using 10,000 randomly selected pseudoabsences from the whole study area. A given model was calibrated on the training data and evaluated on the test data using the Area Under the receiver operating characteristics Curve (AUC) as a threshold-independent assessment measure. AUC has been used extensively in the species distribution modelling literature and can be interpreted as the probability that a model discriminates correctly between presence and absence sites (Phillips et al. 2006). AUC values range 0–1, where 1 indicates perfect model performance and 0.5 indicates predictive discrimination no better than random. To reduce uncertainty caused by sampling artefacts (generated during the random resampling of presence localities), we conducted 25 replicate models for each predictor set. We used Mann-Whitney *U*-tests to assess how model performance (measured by means of AUC values) varied between predictor sets.

Results

Selection of predictor variables

After performing a first correlation analysis, we eliminated T_{AN} from modelling owing to their high correlation with T_{MAX} and T_{MIN} ($r > 0.8$; Supplementary material Table S1). Then, to avoid biases in the modelling towards either environment predictors (i.e.: climate and habitat) or spatial filters, we only used six spatial filters for analyses (the same number as environmental variables, *see Methods*).

Breeding season distribution model

Environmental variables (i.e. climate plus habitat) and spatial constraints were both important controls of marsh harrier distribution during the breeding period. The clim+hab+filters model had superior predictive ability than the clim+hab ($U = 39$, $n = 50$, $P < 0.001$), and the filter ($U = 0$, $n = 50$, $P < 0.001$, Fig. 2) models. Models including just climatic and habitat variables also performed worse than the full environmental model, i.e. the clim+hab model, (all $P < 0.001$). These results indicate that the breeding distribution of marsh harriers was not only limited by environmental factors (both climate and habitat characteristics), but also by spatial constraints, as shown by the mapped predicted distributions of the species (Fig. 3).

Variables with the highest contribution to the training gain in the clim+hab+filters model were slope (36.6% of contribution to the Maxent model), suitable vegetation (28.8% of contribution to the Maxent model), and the spatial filters (30.1% of contribution to the Maxent model; Fig. 4). The other environmental variables contributed less to the model, with all climatic variables together and NDVI contributing a 4.5% to the model.

Wintering season distribution model

Environmental variables, both climate and habitat, were the most important range controls for the wintering distribution of marsh harriers. The environmental model including both habitat and climatic variables (clim+hab) performed better than models including just climatic ($U = 1$, $n = 50$, $P < 0.001$) or habitat ($U = 118$, $n = 50$, $P < 0.001$) predictors. Contrary to the breeding scenario, no significant differences between the clim+hab model and the clim+hab+filt models were found ($U = 238$, $n = 50$, $P = 0.151$, Fig. 2). These results indicate that the distribution of roost sites during winter was mainly limited by environmental factors, with no significant additional effect of spatial filters (Fig. 3).

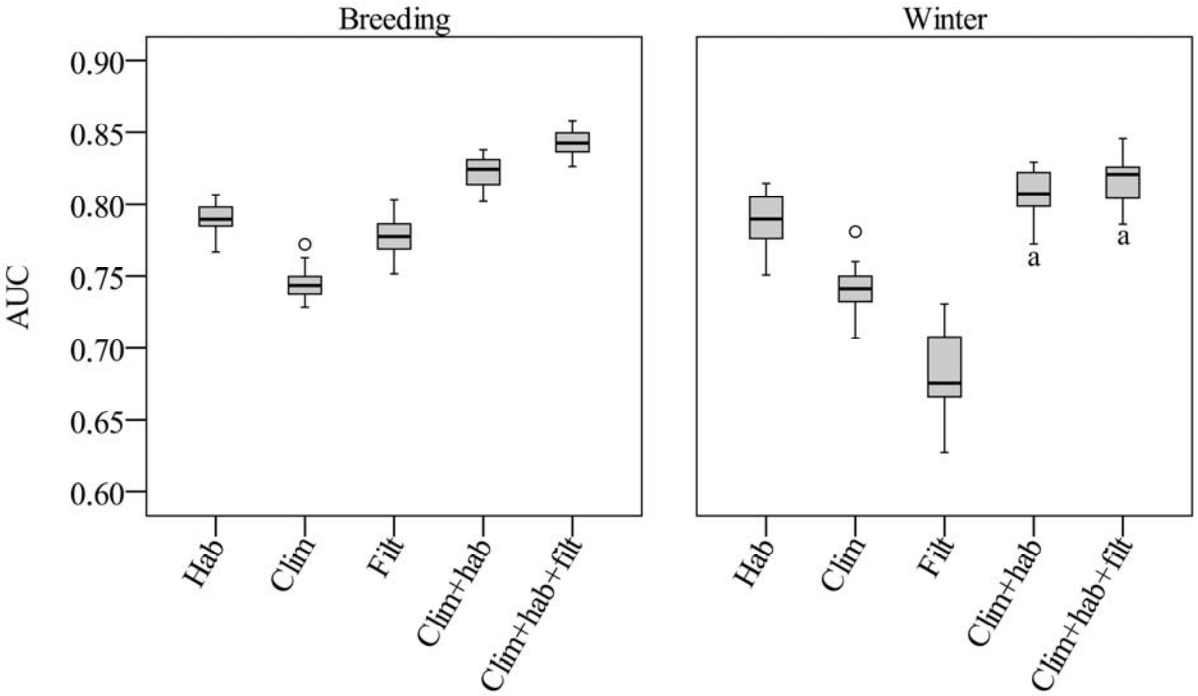

Figure 2. Differences in predictive ability among marsh harrier' distribution models based on different sets of predictors for the breeding and the winter periods. Note that for each set of predictors and season 25 replicate models with different subsets of total data were conducted. The length of the box is the interquartile range (IQR) and the line inside mark the medians of the 25 replicate models conducted for each predictor set. Letter *a* indicate models which were not significantly different based on Mann-Whitney U-tests (p > 0.05). All other models significantly differed at p < 0.0001. Values more than 1.5 IQR's from the ends of the box are labeled as outliers (o).

The most important range controls (i.e., variables with the highest contribution to the training gain in the clim+hab model) were slope (59.6% of contribution to the Maxent model), and suitable vegetation (18.5% of contribution to the Maxent model; Fig. 4), followed by minimum temperature of the coldest month, mean annual precipitation, NDVI and maximum temperature of the warmest month, which together contributed a 21.9 to the model (each of them < 10% of contribution).

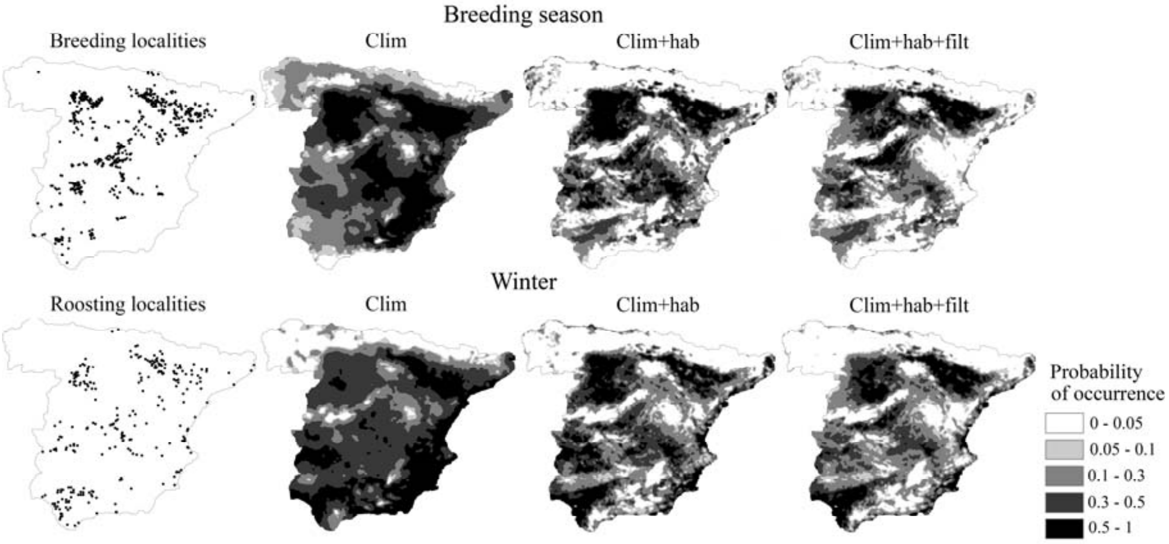

Figure 3. Observed and averaged predicted distributions of the marsh harrier in Spain in the breeding and wintering periods. Predicted distributions are based on Maxent models using different sets of predictors: climate (clim), both climate and habitat predictors (clim+hab) or climate, habitat and spatial filters (clim+hab+filt). Note that models developed for each set of predictors were calibrated using 25 different randomly selected subsamples of total data (averaged predictions are shown).

Discussion

In this paper, we examined the relative influence of pure spatial-range constraints and environmental factors on the breeding and wintering distributions of a long-lived raptor species in peninsular Spain. Our results revealed strong responses to environmental variability during both the breeding and the wintering seasons, as shown by the high values of AUC. However, by including spatial filters in models (Diniz-Filho and Bini 2005, De Marco et al. 2010), we found evidence that marsh harrier distribution was also spatially constrained beyond environmental variables during the breeding season, but not during its wintering.

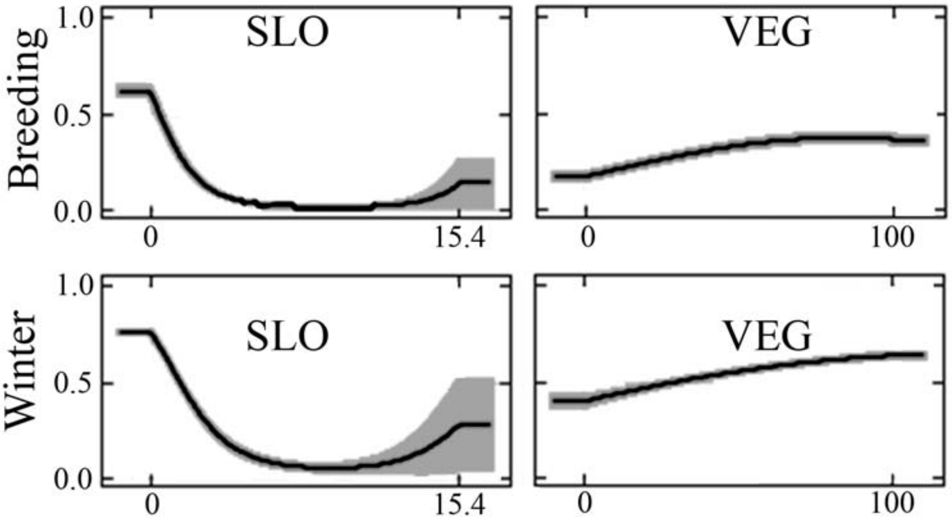

Figure 4. Response curves illustrating the relationships between probability of occurrence of marsh harriers and our set of predictors. These curves show how the shape of the response changes for a particular variable while all other variables are held at their mean sample value. Only response curves for environmental variables that contributed a minimum of 10% to the regularized training gain in the best performing model are shown. Mean response curve of the 25 replicate Maxent runs (black) and standard deviation (grey) are shown.

Within environmental variables, both habitat and climatic controls appeared to be important determinants of marsh harrier distribution during both the breeding and the wintering seasons. However, when used alone, habitat variables shaped better the distribution of marsh harrier (higher AUC) than climatic variables, suggesting that marsh harrier were more dependent on habitat than on climate at the scale of peninsular Spain. Although the good fit of a model does not necessarily imply correct inference of causation (James and McCulloch 1990), our explanatory models suggested that the most suitable areas for this species, in both the breeding and wintering seasons, were flat terrains (lower slopes) with high percentages of open vegetation. This result is consistent with the previously described dependence of the species on these habitats (Cramp and Simmons 1994).

Contrary to the equilibrium postulate (i.e., the species are in equilibrium with the environment, Guisan and Thuiller 2005), the significant effect of spatial filters on the marsh harrier distribution during the breeding period suggested that this distribution was not only limited by environmental controls but also by spatial constraints. As spatial filters simply capture spatial range constraints of any nature (Borcard and Legendre 2002), we cannot firmly establish the mechanisms behind them. But taking into account that spatial filters reduced probability of occurrence of the species at most isolated suitable areas with respect to the distribution of the species in previous years (Figs. 1 and 3), they could be consistent with limited dispersal from source areas. Indeed, the areas at which higher probabilities of occurrence were predicted by the model, coincided in general, with the early distribution of the species in 1990. Limited dispersal from source areas could be related with the high philopatry and short natal dispersal distances described for the species (Sternalski et al. 2008), maybe associated with social factors, such as conspecifics attraction, which are known to affect colonial species (Serrano et al. 2004).

Contrary to the breeding period, spatial filters seemed to have a negligible impact on marsh harrier distribution during winter. One possible explanation may be related with the arrival of migrant marsh harriers from central and northern-Europe during winter, which join the local resident population (Molina and Martínez 2006). Migrants can move long distances (Strandberg et al. 2008) and may be able to reach suitable patches where breeders from local populations, which show high site fidelity over the year (Cardador et al. 2009), should not be present. This could be the case, for example, of suitable areas from eastern peninsular Spain (one of the most overpredicted areas by the clim+hab model during the breeding season), which hold large populations of marsh harriers in winter (with at least some individuals having a European breeding origin, based on ring recoveries, Molina and Martínez 2006). In fact, migration routes described for northern populations covered the eastern (i.e. Mediterranean) region of peninsular

Spain, ensuring accessibility of migrant birds to these areas (Strandberg et al. 2008). On the other hand, censuses at roost sites during winter may also allow us to detect juvenile dispersers from local populations, which may move long distances and have a different geographic distributions with respect to the breeding population, as in other birds of prey (Real and Mañosa 2001). More specific studies on ranging behaviour of resident and migrant populations over the year are necessary to determine whether and to what extent spatial filters may be reflecting actual differences in spatial distribution between local and migrant birds and/or temporal movements of individuals from the local population.

Understanding the factors that limit current distributions of species and populations is crucially important in building effective management and conservation strategies. In the present study, we have achieved new insights on the determinants of a raptor species distribution in two different periods of its life cycle (wintering and breeding season) by the novel implementation of SDM developed by De Marco et al. (2010). Although limited, our methodological approach illustrates that it is possible to use these models in conjunction with additional historical and ecological information, to point out alternative hypothesis about the recent distribution of a species. However, the selection of environmental predictors to be included in these models remain a critical step to avoid that variation attributed to the spatial filters can simply represent a correlated environmental factor not included as a predictor in the model. In our model approach, for example, information on the presence of tall standing emergent vegetation (the principal roosting and nesting habitat of the species, Cramp and Simmons 1994, Cardador et al. 2011) was not available. However, taking into account that emergent vegetation should be a limiting factor in both the breeding and winter seasons but spatial filters only seems to play an important role during the breeding period, it seems difficult that the effect of spatial filters could be related to this variable. In relation to predictor selection, our model approach also limited collinearity problems. Although, there were fairly high correlations among some of the predictor variables (Supplementary material Table 1), Maxent has the ability to deal with such cases, in a way that overall model performance will not be affected (Phillips et al. 2004). More importantly, in our case, only one variable T_{AN} was highly correlated with other variables (T_{MAX} and T_{MIN}) and it was eliminated from analysis.

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SEO/BirdLife provided data on census of the breeding and wintering populations of the marsh harrier in Spain in 2006. Original photo of marsh harrier provided by Marcos Lacasa.

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Table S1. Pearson correlation coefficient of the environmental variables and spatial filters. Correlation is based on 10000 randomly picked cells. Correlation with $P < 0.05$ are shown in bold letters.

	Filter 6	Filter 5	Filter 4	Filter 3	Filter 2	Filter 1	TMIN	TMAX	TAN	SLO	AP	VEG
Filter 6												
Filter 5	-0.012											
Filter 4	0.014	-0.017										
Filter 3	**0.021**	0.004	-0.006									
Filter 2	-0.001	0.007	-0.015	0.008								
Filter 1	**0.027**	-0.014	0.005	0.002	0.005							
TMIN	**-0.184**	**-0.038**	-0.012	**-0.239**	**0.047**	**0.479**						
TMAX	0.008	**-0.063**	**-0.388**	**0.182**	**-0.155**	**0.633**	**0.418**					
TAN	**-0.097**	**-0.033**	**-0.185**	**-0.101**	**-0.100**	**0.625**	**0.896**	**0.762**				
SLO	**0.178**	**0.044**	**0.179**	**-0.205**	**-0.036**	**-0.095**	**-0.385**	**-0.511**	**-0.499**			
AP	**-0.147**	**0.124**	**0.205**	**-0.258**	**0.285**	**-0.139**	**-0.023**	**-0.675**	**-0.356**	**0.463**		
VEG	**0.082**	**-0.116**	**-0.110**	**0.158**	**0.086**	**-0.154**	**-0.133**	**0.111**	**-0.047**	**-0.211**	**-0.328**	
NDVI	**-0.092**	**0.137**	**0.103**	**-0.280**	**0.330**	**-0.173**	**-0.033**	**-0.587**	**-0.314**	**0.428**	**0.792**	**-0.357**

Figure S1. The distribution of the six environmental variables: AP, annual precipitation; TMIN, minimum temperature of the coldest month; TMAX, maximum temperature of the warmest month; SLO, slope; VEG, percentage of open vegetation; NDVI, normalized difference vegetation index.

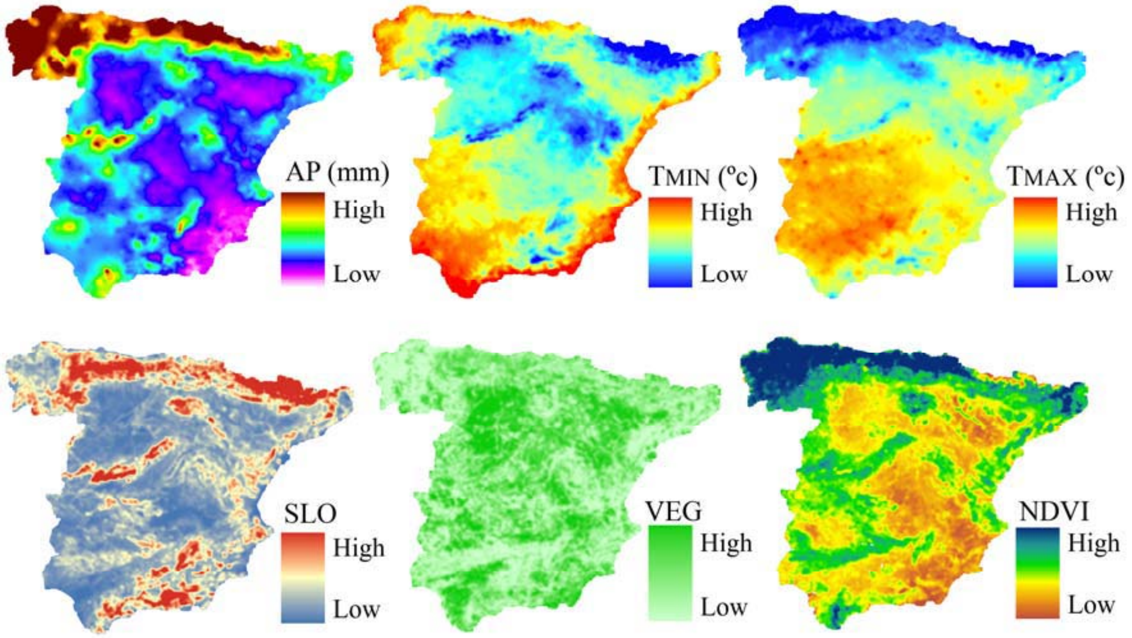

Figure S2. The geographic patterns of the 6 spatial filters showing the spatial relationship amongst cells (1 × 1 km grids). Increasingly lighter (white) colours indicate larger numerical values of the eigenvectors. The spatial pattern of Filter 1 shows two major clusters of high and low values, respectively, more or less portraying a north-south gradient in Spain, while Filter 2 captures an east-west gradient. Subsequent filters portray more oscillatory patterns across Spain.