Focus

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

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

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

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

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

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

in human-transformed environments and to discuss its potential consequences.

Agricultural intensification and changes in bird communities

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

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

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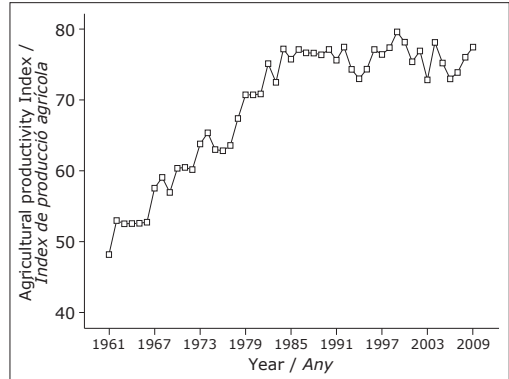

Figure 1. Changes in the index of overall agricultural productivity in Western Europe from 1961 to 2009. This index is based on the sums of price-weighted quantities of different agricultural products after the quantities used as seed and feed have been deducted. This index is expressed in millions of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

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

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

The Marsh Harrier *Circus aeruginosus* is a semi-colonial, medium-sized raptor that occurs in the mid-latitudes of the western Palearctic. This ground-nesting raptor, which breeds mainly in wetlands and hunts over open habitat (Cramp & Simmons 1994), underwent a dramatic population decline in Europe in the period 1960–1980 due to the drainage of wetlands, contamination and direct persecution (Cramp & Simmons 1994). However, it has recovered on a European
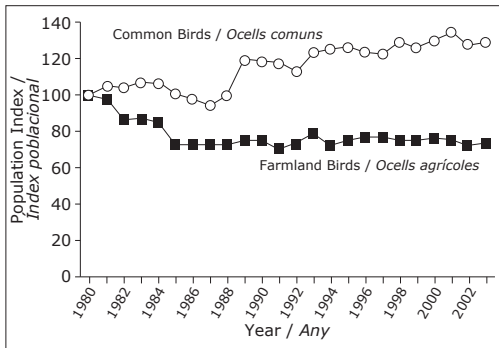
Figure 2. Trends in common bird populations in the European Union since 1980. The composite population trend of 19 common farmland species (i.e. open-country specialists, the bulk of whose populations are found in open farmed habitats) and of 25 common species (generalist species that occur across a range of varied habitats) are shown. The indexes are calculated in relation to a value of 100 given for 1980 (PECBM, 2005). *Tendències de les poblacions d'ocells comuns als països de la Unió Europea des de 1980. La tendència dels ocells de medis agrícoles (quadrats) és el resultat de combinar 19 espècies especialistes de medis oberts majoritàriament cultivats, mentre que la tendència dels ocells comuns (cercles) resulta de 25 espècies comunes generalistes que es troben en un ampli ventall d'hàbitats. Els índexs s'han calculat de manera que el valor de 1980 sigui 100 (PECBM, 2005).*

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

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

Factors affecting expansion success

Changes in availability of species-specific resources

Nest-site and food availability have been described as key limiting factors in birds (Newton 1994, Sergio *et al.* 2003). Several examples exist of avian species whose breeding numbers and distribution increase or decrease in relation to food availability or the number of suitable nesting sites (Newton 1998). Agricultural intensification has been linked to habitat impoverishment and food depletion for many species occupying agricultural areas (e.g. Blanco *et al.* 1998, Tella *et al.* 1998). The Marsh Harrier, however, seems to be an example of a native species that has benefited from this transformation. As in many areas of its range, the Marsh Harrier in NE Spain is expanding after a period of dramatic decline (Cramp & Simmons 1994, BirdLife International 2004). In the Catalan Ebro Valley, this expansion is taking place in parallel with the use of a newly available habitat type, intensive herbaceous croplands (Cardador *et al.* 2011, Cardador & Mañosa 2011). As in other species that select habitat features at multiple spatial scales (Sergio *et al.* 2003), the Marsh Harrier could be taking advantage of the numerous artificial ponds constructed in recent years in areas of intensive agriculture as breeding sites, while still relying on traditional extensive cereal farmland for foraging. However, radio-tracked individuals breeding in both intensive and extensive agricultural landscapes in the Ebro Valley used the herbaceous fields near their nest sites as foraging areas (Cardador & Mañosa 2011), thereby indicating that this species is exploiting both new nesting and foraging habitats. Moreover, individuals occupying and using intensified habitats for foraging tended to have smaller home ranges than birds foraging within more traditional habitats (Cardador *et al.* 2009), which suggests that, unlike for most farmland birds, intensive agricultural areas represent higher quality habitat for Marsh Harriers than extensive croplands. Indeed, the abundance of small mammals, a chosen and high-quality prey for *Circus* species (e.g. Butet & Leroux 1993, Sternalski *et al.* 2010), seems to be greater in
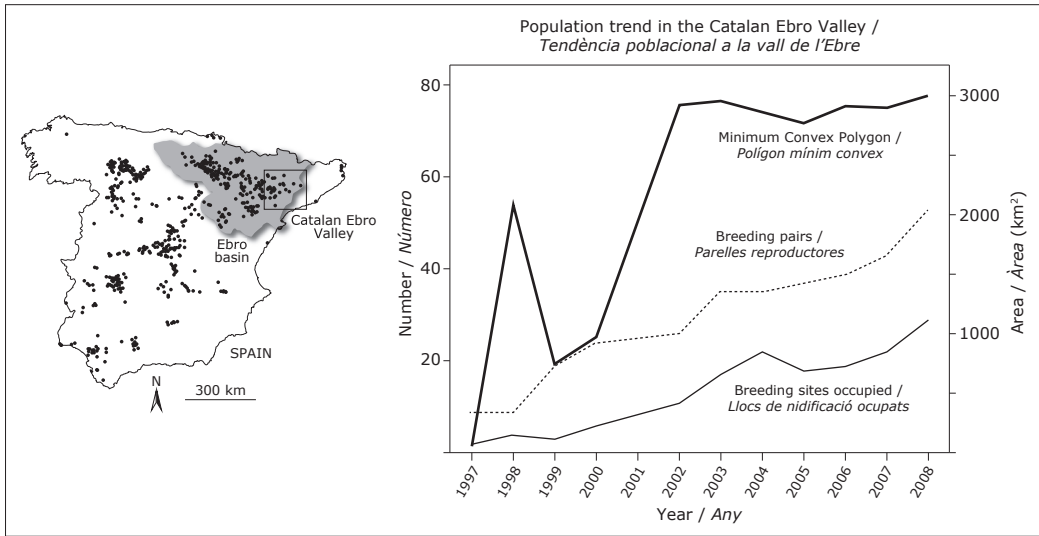
Figure 3. Distribution of the breeding population of the Marsh Harrier *Circus aeruginosus* in Spain in 2006 and the population trends for the breeding population of the Marsh Harrier in the Catalan Ebro Valley (Cardador *et al*. 2011).
Distribució de la població reproductora d'Arpella Vulgar Circus aeruginosus *a Espanya el 2006, i tendència de la població reproductora a la part catalana de la vall de l'Ebre (Cardador* et al. *2011).*

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

Results obtained from radio-tracked individuals in the Ebro Valley largely agree with those obtained by analysing the factors affecting the species' occupancy rate of breeding sites in the area. The occupancy rate of breeding sites has been described as an indicator of habitat quality in raptors (Sergio & Newton 2003). The occupancy of wetlands by Marsh Harriers in agricultural areas in the Ebro valley is mainly explained by the independent effect of habitat features acting at two spatial scales: the breeding site (area of emergent aquatic vegetation and type of wetland) and the foraging area (percentage of intensified, irrigated herbaceous crops in the area surrounding the nest site). Neither human pressure variables nor proximity to other occupied sites seemed to be important determinants of occupancy rates in this expanding population (Cardador *et al*. 2011). The occupancy rate of artificial wetlands such as ponds or reservoirs was not significantly different from that of rivers or watercourses but was greater than that of inland natural wetlands (Cardador *et al*. 2011), suggesting that the emergent vegetation in these

human-made structures provides new suitable breeding habitat for nesting Marsh Harriers. At a landscape scale, Marsh Harriers have responded positively to new areas of intensified herbaceous crops, probably because (as mentioned above) they offer more – and more accessible – prey items (Cardador *et al*. 2012a). Lower competition as a result of declining populations of other predator species in intensive croplands could also be related to this positive selection pattern, although this hypothesis has not to date been fully assessed. Preliminary analysis of changes in productivity in relation to habitat characteristics suggests that no significant relationships exist between this demographic parameter and habitat attributes, suggesting that none of the habitats occupied in the Ebro Valley are unsuitable nesting habitats.

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

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

The importance of spatial range constraints

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

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

Raptors are long-lived species that may move over large areas for several years before entering into the breeding population (Newton 1979). When they settle to breed, individuals must optimize their fitness by increasing their foraging, mating, breeding and survival prospects. Settling near natal areas or close to conspecifics minimizes the costs of gaining good knowledge of breeding sites and foraging areas, and also increases mating opportunities (Brown *et al.* 1990, Arroyo *et al.* 2001, Serrano *et al.* 2005). Indeed, many colonial bird species have high levels of both natal philopatry and conspecific attraction (Sternalski *et al.* 2008, Serrano *et al.* 2004). These demographic mechanisms may impede or delay the colonization by Marsh Harriers of empty suitable patches located at great distances from previously occupied areas in peninsular Spain. For a fraction of the population, a positive effect of conspecific aggregation on settlement patterns and productivity has indeed been found (Cardador *et al.* 2012b). Additionally, although the least competitive breeders seemed to occupy the most isolated locations and thus promote range expansion at regional scales (Cardador *et al.* 2012b), this pattern may not translate immediately to larger scales and so a colonization lag in terms of the most distant areas may exist (De Marco *et al.* 2010).
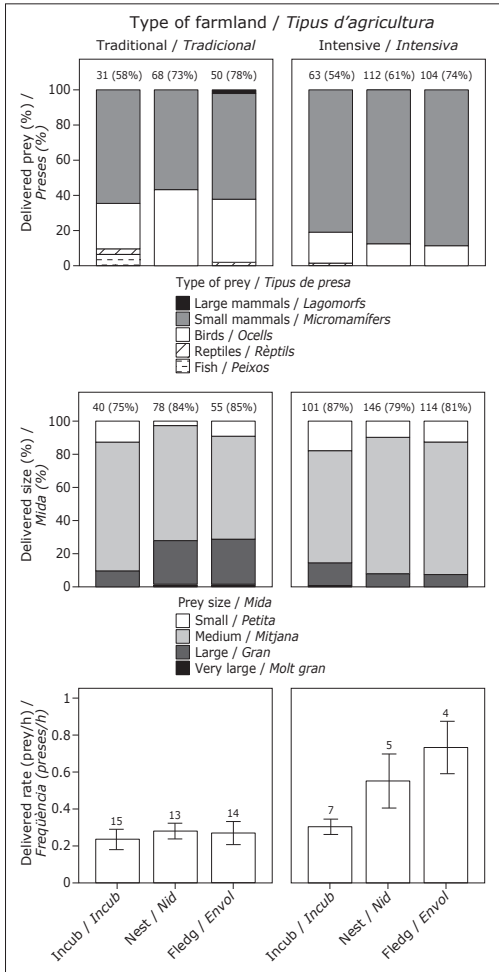
Figure 4. Comparative data on diet composition, prey size and delivery rate according to agricultural landscapes (traditional or intensively managed) and period of the breeding cycle (incubation, nesting and post-fledging) of male Marsh Harriers in the Catalan Ebro Basin (Spain), 2001–03. For diet composition and prey size, number of identified prey and percentage that it represents from total observed deliveries (in parentheses) are shown. For delivery rates, mean ± SE and sample sizes (number of harriers observed delivering food at least once in each period) are shown. Size categories: very large (e.g., lagomorphs or Mallards *Anas platyrhynchos*); large (e.g., rats *Rattus* spp. or Red-legged Partridges *Alectoris rufa*); medium (e.g., rodents or Sparrows *Passer domesticus*); and small (e.g., shrews or Orthoptera).

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

Density dependence, individual traits and species' range distributions

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

positive and negative effects of the presence of conspecifics will act on the same individual and the final balance in the costs and benefits will depend on individual characteristics.

A particular case of inter-individual variation found in many avian species is chromatic variability in plumage. Plumage colouration can co-vary with morphology, physiology and behaviour (see Roulin 2004, Ducrest *et al.* 2008 for a review), as well as with age (Forsman 1999). Colour variability might thus modulate intraspecific interactions, leading to differential cost-benefit balances of conspecific presence for individuals with different colourations. In the case of the Marsh Harrier, males can be easily classified into three colour categories, 'dark brown', 'light brown' and 'grey' according to

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

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

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

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

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

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

Acknowledgements

Resum

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

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

Resumen

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

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

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

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