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ROLES OF RAPTORS IN A CHANGING WORLD: FROM FLAGSHIPS TO PROVIDERS OF KEY ECOSYSTEM SERVICES

EL PAPEL DE LAS RAPACES EN UN MUNDO EN CAMBIO: DE ESPECIES BANDERA A PROVEEDORES DE SERVICIOS ECOSISTÉMICOS

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Summary.—Birds of prey have been, in comparison to other avian groups, an uncommon study model, mainly due to the limitations imposed by their conservative life strategy (low population density and turnover). Nonetheless, they have attracted a strong interest from the point of view of conservation

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biology because many populations have been close to extinction and because of their recognised role in ecosystems as top predators and scavengers and as flagship species. Today, after more than a century of persecution, and with the exception of some vultures still very much affected by illegal poisoning, many populations of birds of prey have experienced significant recoveries in many regions of Spain and the European Mediterranean. These changes pose new challenges when addressing the conservation of raptors in the coming decades. On this basis, and from a preferentially Mediterranean perspective, we have focused our attention on the need of describing and quantifying the role of these birds as providers of both regulating (rodent pest control and removal of livestock carcasses) and cultural ecosystem services. Moreover, we revisited persisting conflicts with human interests (predation of game species) and call attention to the emergence of new conflicts with a strong social and media component such as the predation on live cattle by vultures. Also, the rampant humanization of the environment determines the need for new solutions to the growing, yet scarcely explored, problem of accidents in new infrastructures such as mortality in wind farms. Finally, we explored in depth the ecological response of birds of prey to large-scale habitat changes such as urbanisation and abandonment of marginal lands that are also expected to increase in the near future. We urgently need more scientific knowledge to provide adequate responses to the challenge of keeping healthy populations of avian predators and scavengers in a rapidly changing world.

Key words: animal ecology, birds of prey, conservation, cultural services, global change, human-wildlife conflicts, pest control, predation, regulating services, rewilding, supporting services, urban habitats.

RESUMEN.—Las aves de presa han sido, en comparación con otros grupos de aves, más raramente utilizadas como sujeto de estudios en ecología en razón de las limitaciones que impone su estrategia de vida (baja densidad de población, alta longevidad y baja natalidad). Por el contrario, han suscitado un gran interés desde el punto de vista de la biología de la conservación, debido a que sus poblaciones en muchos casos se han aproximado a la extinción, así como al reconocimiento de su papel en los ecosistemas como superpredadores y carroñeros como especies bandera. Hoy en día, tras más de un siglo de persecución, y con la excepción de algunos buitres todavía muy afectados por envenenamientos ilegales, muchas especies de aves de presa han experimentado importantes crecimientos poblacionales en muchas regiones de España y del Mediterráneo europeo. Este escenario plantea nuevos desafíos para abordar la conservación de las rapaces en las próximas décadas. Sobre esta base hemos focalizado nuestra atención en la necesidad de describir y cuantificar el papel de estas aves como proveedores de servicios ecosistémicos, tanto reguladores (control de plagas de roedores y eliminación de restos de ganado) como culturales y de apoyo. Por otra parte, llamamos la atención hacia el reavivamiento de conflictos con intereses humanos (predación sobre especies cinegéticas) y a la aparición de nuevos conflictos con un fuerte componente social y mediático como la predación de aves carroñeras sobre ganado vivo. De igual modo, la creciente humanización del medio y de las poblaciones de aves de presa de mayor tamaño determinan que haya que buscar nuevas soluciones a problemas ya conocidos como los accidentes en infraestructuras, pero que tienen nuevas facetas complejas y aun poco exploradas como la mortalidad en parques eólicos. Finalmente, nos adentramos en la respuesta de las aves de presa a cambios a gran escala en el hábitat, como la urbanización y el abandono de tierras marginales que ya están ocurriendo y se prevé que se incrementen en las próximas décadas. Debe generarse más conocimiento científico para poder dar adecuada respuesta al reto que supone mantener poblaciones sanas de aves predadoras y carroñeras en un mundo que cambia vertiginosamente.

Palabras clave: aves de presa, cambio global, conflictos con fauna salvaje, conservación, control de plagas, ecología animal, hábitats urbanos, predación, resilvestramiento, servicios culturales, servicios de apoyo, servicios de regulación.

Introduction: Raptors multiplying and its ecological and conservation aftermath

Anthropogenic activities are leading to broad-scale non-random changes in bird community compositions (Bonebrake *et al*., 2010; Le Viol *et al*., 2012). This is not a new phenomenon as human pressures, mainly through persecution and modification of habitats, have had historical consequences for bird populations all around the world. For example, it is estimated that up to 1,300 avian species could have been wiped out in only a few centuries by the colonising Pacific islanders (see among others Steadman, 1995; Duncan *et al*., 2013). What is new is the current speed of the process. The rampant humanization of the planet following the industrial revolution has led to a new epoch, the "anthropocene", which involves the rapid disappearance of species, the so-called "sixth extinction" (Barnosky *et al*., 2011; Dirzo *et al*., 2014). Although bird extinctions have been exceptional in Europe during the last century generalised declines are evident in many groups. For instance, those birds associated with farmlands and/or the transaharan migrants have suffered clear declines since the middle of the XXth century. In contrast, forest birds have been relatively well conserved, due to the widespread tendency of land abandonment in marginal areas (Donald *et al*., 2001; Gregory *et al*., 2007; BirdLife International, 2013; Reif, 2013).

Within this general scenario of biotic homogenisation, environmental impoverishment and decline of many primary consumers it would be expected that predatory birds also would show negative population trends. However, this is not so. In fact, birds of prey (Accipitriformes and Strigiformes) have shown striking changes during the last few decades, switching in many cases from an almost "terminal" status (see e.g., Geroudet, 1964) to spectacular recoveries in both numbers and distribution ranges (see below). It is well-known that since the end of the XIXth century, birds of prey were intensively persecuted in Europe to which was added the mode of the scientific collecting (see e.g., Chapman and Buck, 1893, 1910; Hiraldo *et al*., 1979). In Spain, it was in the middle of the XXth century, following the creation of the "*Juntas de Extinción de Animales Dañinos*" (Boards for the extinction of harmful animals), when slaughtering was implemented as a systematic practice (Garitacelaya, 2003; Paulos, 2006). A similar picture was found in the rest of Europe and in many regions of North America and Australia (Bijleveld, 1974; Newton, 1979; Olsen, 2006). Following the legal protection of all species of birds of prey, many populations have shown a notable recovery in Europe (Deinet *et al*., 2013) with the notable exception of some scavenger species whose decline still continues, especially in the Eastern Mediterranean, mainly due to illegal poisoning (Donázar *et al*., 2009). The shift is clearly linked to the stopping of non-natural mortality by direct killing and the progressive correction of other limiting factors, such as the banning of some pollutants and the correction of intrusively positioned power lines (Newton, 1979), as well as to broad-scale habitat protection and the adoption of species-specific conservation measures and broad-scale habitat protection (Donald *et al*., 2007; Williams *et al*., 2012; Kolecek *et al*., 2014) (fig. 1).

But the struggle continues. During the last half century raptor populations have suffered successive crises with potentially very negative consequences such as the irruption of the European wild rabbit haemorrhagic disease at the end of the XXth century and the restrictive EU sanitary measures limiting the disposal of livestock carcasses to scavengers at the beginning of the XXIth century (Tella, 2001; Donázar *et al*., 2009) which

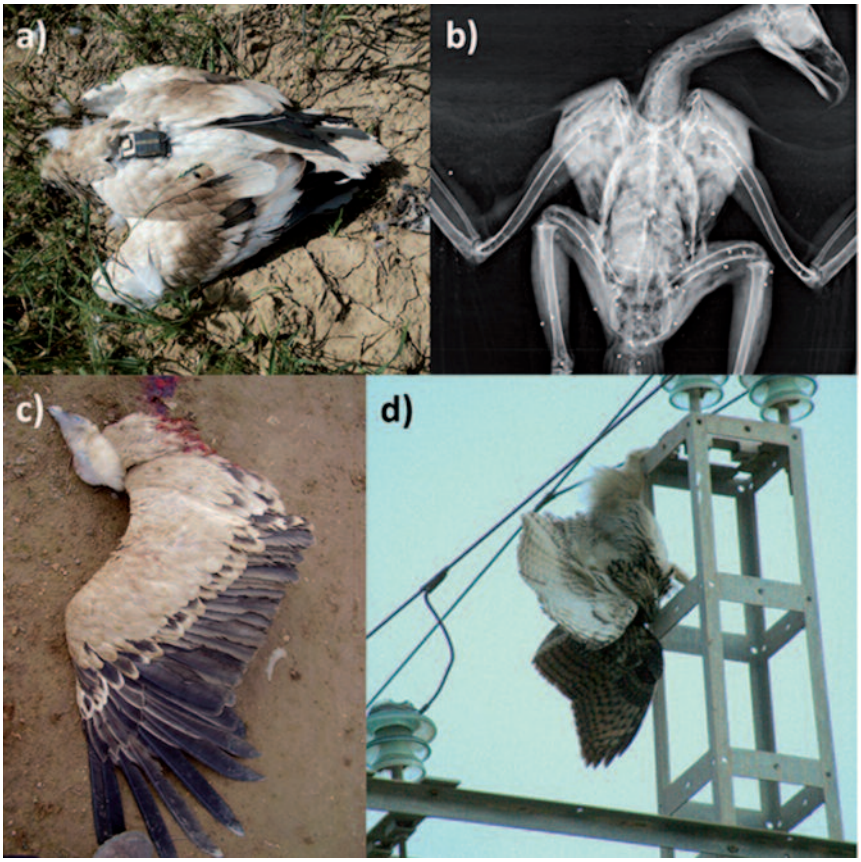

FIG. 1.—Non-natural mortality caused by human activities is the main limiting factor for birds of prey populations in Europe. Poisoning is causing the precipitous regression of different scavenger species (a. a poisoned Egyptian vulture) whereas direct killing is losing relative importance but still is a menace factor for some migratory routes (b, radiography of a shot Spanish imperial eagle). New developments such as wind farms are gaining importance during the last decades, being responsible now for the deaths of thoushands of birds of prey (c. a griffon vulture mutilated by a wind turbine) and other flying vertebrates. Accidents in power lines are still probably the main factor of mortality for many species of raptors (d. an electrocuted eagle owl). Credits: a: EBD-CSIC; b: Centro de Análisis y Diagnóstico de la Fauna Silvestre-C.A.D. Consejería de Medio Ambiente y Ordenación del Territorio; c: Eugenio Montelío; d) Juan M. Pérez-García.

[La mortalidad no natural causada por actividades humanas es el principal factor limitante para poblaciones de rapaces en Europa. Los envenenamientos son causa del abrupto declive de varias especies de carroñeros (a. alimoche común envenenado), mientras que la persecución directa ha perdido importancia relativa pero es todavía un factor de amenaza en algunas vías migratorias (b, radiografía de un águila imperial ibérica tiroteada). Nuevos desarrollos como los parques eólicos están ganado importancia durante las últimas décadas, siendo responsables de la muerte de miles de grandes rapaces (c. a buitre leonado mutilado por una turbina eólica). Los accidentes en tendidos eléctricos son todavía el principal factor de mortalidad para muchas especies de rapaces (d. búho real electrocutado). Creditos: a: EBD-CSIC; b: Centro de Análisis y Diagnóstico de la Fauna Silvestre-C.A.D. Consejería de Medio Ambiente y Ordenación del Territorio; c: Eugenio Montelío; d) Juan M. Pérez-García.]

required the immediate reaction of scientists, managers and conservationinsts (Margalida *et al*., 2012). For future decades the main challenge is to determine how populations of birds of prey, along with other organisms, will envisage their fitting into a world shaped by anthropogenic activities and how healthy populations of raptors and human interests can coexist. This is our main objective in this essay (fig. 2). Within a global scenario, our perspective focuses mainly on the Mediterranean basin, where, as in the rest of the world, studies of ecology and conservation of raptors flourished from the mid-90s of the last century, but that currently shows a certain delay that requires correction (fig. 3). First,

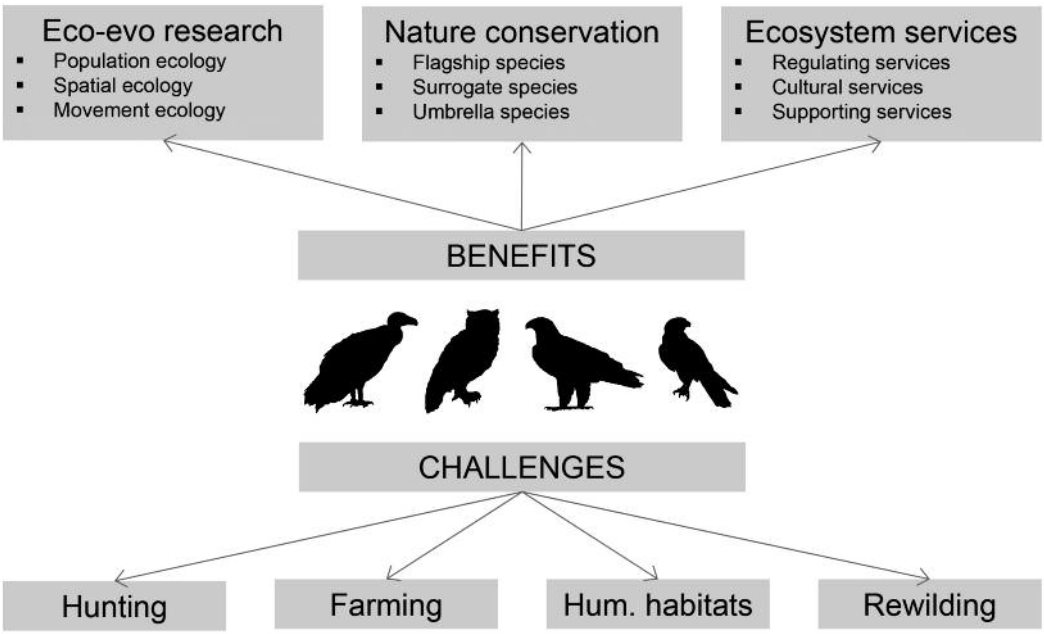

FIG. 2.—Main benefits and challenges for conserving raptors in a changing world. Raptors are fruitful study models for several ecological and evolutionary disciplines, are key elements in many biodiversity conservation schemes that can exert positive effects to a wide array of organisms and perform crucial ecosystem functions that translate into important ecosystem services. On the other hand, conflicts with hunters and, to a lesser extent, farmers may compromise the future of some raptor populations. Also, raptors living in Mediterranean countries will need to cope with changes in their habitats due to increasing urbanization around big cities and abandonment of rural areas.
[Principales beneficios y retos en la conservación de aves de presa en un mundo en cambio. Las rapaces son buenos modelos de estudio en determinadas disciplinas dentro de la ecología y evolución, son además elementos clave en muchas estrategias dentro de la biología de la conservación, ejerciendo efectos positivos sobre muchos otros organismos ecológicos y de conservación, y llevan a cabo funciones ecosistémicas clave que se traducen en servicios ecosistémicos. Desde otro punto de vista, los conflictos con cazadores y, en menor medida, con ganaderos, pueden comprometer el futuro de algunas poblaciones de aves de presa. Las rapaces que viven en países mediterráneos deben afrontar fuertes cambios de hábitat asociados a la urbanización en torno a grandes ciudades y al abandono de áreas rurales.]

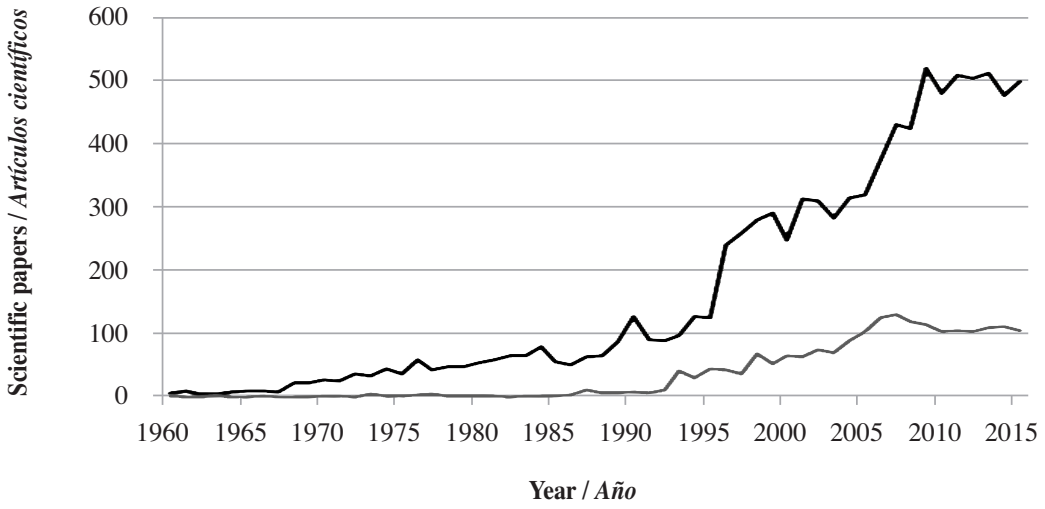

FIG. 3.—Number of raptor-related papers published in peer-reviewed journals between 1960 and 2015. It is distinguished between total (black) and those focused in the Mediterranean region (grey). Based on a compilation from the Scopus search engine.
[Número de artículos sobre aves rapaces publicados en revistas científicas con revisión por pares entre 1960 y 2015. Se distingue entre el total (línea negra) y aquellos que se centran en la región mediterránea (línea gris). Basado en una búsqueda a través de Scopus.]

and because successful conservation must be based on scientific knowledge, we examine the position of raptor research in the field of vertebrate ecology. Then we examine in depth the role played by birds of prey as flagship and umbrella species within general nature conservation strategies. After, a review of the role of raptor as ecosystem services providers is followed by an analysis of the conflicts arising between raptor conservation and human interests. Finally, we approach the future of birds of prey in light of the prospective changes in ecosystems and landscapes.

RAPTORS IN ANIMAL ECOLOGY RESEARCH

Birds of prey might not seem the most ideal study models in animal ecology as they often occur at low densities over large ranges, breed in sites of difficult access, show elusive behaviour, and have long generation times, all of which which makes it difficult to obtain large sample sizes, follow entire cohorts of marked individuals, and apply experimental designs. At the same time, they encompass very different lifestyles, from territorial to colonial, strictly sedentary to vagile or migratory, or from arthropod- or snail-eaters to obligate scavengers, opening substantial opportunities for the study of a wide range of ecological and evolutionary questions. Animal ecology in its classical sense deals with the relationships between animals and the environment and how these relationships shape animal distribution and abundance, with fundamental contributions of birds of prey in the literature (e.g. trophic ecology and predator-prey dynamics, factors shaping abundance and distribution, population dynamics of long-lived animals).

Nowadays, this discipline includes many functional and evolutionary aspects that exceed its initial meaning, and birds of prey have been employed as study models to advance decisively in some of them (e.g. signalling, sexual selection, sibling competition, parental and sexual investment, life-history strategies). However, it is the traditional view of animal ecology that has a more direct and obvious link with applied aspects such as management and conservation, and therefore it is within this context that we focus our attention in this review.

The first ecological studies on raptors emerged in parallel with the advent of animal ecology as a formalised discipline (see e.g. Breckenridge, 1935). However, raptor ecology actually began to flourish after the pesticide crisis in the 1950s and 1960s and the inspiring book by Ian Newton (Newton, 1979). In this book, Newton addressed many aspects of raptor ecology and paved the way for most modern research. Many of these aspects were then in its infancy and are much better known nowadays, while others remain rather underinvestigated. In this section, we briefly discuss some of the most significant advances and promising avenues in three fundamental and related areas of animal ecology: population, spatial and movement ecology.

Population ecology and dynamics

Understanding population dynamics and regulation is pivotal in animal ecology. Pattern-oriented approaches (Coulson *et al*., 2000) investigate what regulates raptor populations by studying the feedback between density and population size or fecundity (e.g. Ferrer and Donázar, 1996; Krüger and Lindström, 2001). Whether the frequently reported negative relationship is due to the preemptive occupation of the best sites (the habitat heterogeneity hypotheses), to interference between individuals (the individual adjustment hypothesis), or to other causes such as changes in the age-structure of populations is however difficult to infer without additional information, making this approach controversial (Balbontín and Ferrer, 2008; Beja and Palma, 2008; Carrete *et al*., 2008; Ferrer *et al*., 2008). Clearly, experimental approachess are needed, but they are often ethically inadmissible or hardly feasible in raptors. Fruitful ways of further advance in this field should include more detailed behavioural information on habitat selection, territory defence and social interactions (Serrano and Tella, 2007), as well as information on how territory size and quality change with density and population size (Both and Wiser, 2000; Carrete *et al*., 2006), and to what extent variations in fecundity are motivated by intrinsic properties of habitats and/or to phenotypic traits of individuals (Krüger *et al*., 2012). In addition, floaters (the non-breeding fraction of the population) may play a key but largely overlooked role in the regulation of breeding populations (Penteriani *et al*., 2005), not only because they compensate any population decrease by moving to a breeder position, but also by potentially affecting fecundity of breeders in multiple ways (e.g. by decreasing feeding rates or increasing stress or exposure to predators of territory owners, see López-Sepulcre and Kokko, 2005). However, it should be noted that regulatory processes do not only act throughout productivity, but the key regulatory mechanisms (e.g. density dependent competition by interference) may also operate on survival, even in the presence of density-dependent fecundity depression (Nevoux *et al*., 2011). For these reasons, progress in our understanding of population regulation and limitation in raptors will be only possible if we effectively move from a pattern- to a process-oriented framework in which the responsible mechanisms of density-dependent feedbacks are directly investigated.

In practice, this change of paradigm implies that emphasis should be put on how intrinsic (population composition in terms of age, morphology, behaviour or any other phenotypic trait) and extrinsic (food, predators, competitors, diseases, parasites, weather) factors affect demographic rates (survival, recruitment, reproduction, dispersal) that will ultimately explain population dynamics (Frederiksen *et al*., 2014). This approach requires high-quality longitudinal data on known-age individuals, which means in practice that marking and monitoring programs need to be maintained in the long-term. Once the determinants of vital rates are known, they can be integrated in population models that provide estimates of deterministic and stochastic population growth rates. Stage- and age-structured matrix models (Caswell, 2001) have been among the most popular, particularly, to assess the effect of current and future limiting factors on population trajectories and long-term viability (e.g. Altwegg *et al*., 2006; Millon *et al*., 2014; Sanz-Aguilar *et al*., 2015), and to identify the most influential demographic parameters (e.g. Hiraldo *et al*., 1996). Although the time is long past when populations were considered geographically closed, *sensu lato* metapopulation dynamics remains largely underinvestigated in raptors. This is a key element in ensuring effective conservation actions, as the scarce evidence to date have proven that connectivity plays a critical role in the persistence of both local populations and the entire metapopulation, and that local management decisions may have range-wide consequences (Kauffman *et al*., 2004; Schaub, 2006; Hernández-Matías *et al*., 2013; Schumaker *et al*., 2014). Finally, new mathematical models are fuelling a more efficient and effective use of data and we will certainly see more progress in the future. Integrated population models are a powerful tool that make use of multiple and independent data (e.g. annual population counts and demographic data), providing more precise parameters and projections with the full range of uncertainties (Frederiksen *et al*., 2014). These models have proved useful in furnishing robust evidence about the paramount role of immigration on raptor population growth and persistence (Abadi *et al*., 2010; Altwegg *et al*., 2014; Tempel *et al*., 2014; Lieury *et al*., 2015).

Spatial ecology: raptor-habitat relationships

Habitat use, preference, and selection have been usually confounded in the literature (Johnson, 1980), although the goal of most studies, regardless of the scale of analysis, is to characterise habitat suitability. This has been usually approached by modelling data on presence-absence, presence only, density, and/or abundance as a function of environmental covariates (see e.g. Donázar *et al*., 1993; Meyer *et al*., 1998). Inspired by the complexity and dynamic nature of animal distributions and abundances, some studies have dealt with this topic at multiple temporal and spatial scales or at different activity-specific environments for nesting, roosting or feeding (e.g. Thompson and McGarigal, 2002; Martínez *et al*., 2003; D'Elia *et al*., 2015). These approaches have generated an important body of knowledge with a wide range of applied uses, such as understanding the ecological requirements or biogeography of species, predicting species distributions, identifying reintroduction sites and priority conservation areas, and predicting the response of populations to climate change or habitat loss (Franklin, 2009). However, distribution and ecological niche models have limitations because underlying mechanisms are indirectly inferred from patterns of distribution or habitat use, so they may be confounded and are not always clear or generalizable (Martínez *et al*., 1999;

Bamford *et al*., 2009). For example, a given species may be absent in some localities because individuals avoid certain habitat features, but also because they are systematically killed by man or predators. Further, in avoiding competition or disturbance birds may be forced to use habitats they do not actually prefer, decoupling distribution from habitat preferences. In some circumstances, the behaviour and use of habitat resources may be directly observed by recording habitats where individuals forage or roost (Bakaloudis *et al*., 1998; Ursúa *et al*., 2005), although biases associated with, for example, habitat-mediated detectability are sometimes unavoidable. These problems can be circumvented with telemetry-based data which are being incorporated routinely in to the study of raptor-habitat relationships since the pioneer work of Southern (1964). Telemetry has provided a pile of information on habitat use and selection since then to study, for example, daily and seasonal variations, amplitude of home ranges in relation to territory quality, prey abundance or habitat fragmentation, and differences between sex- and age-clases (e.g. Bechard, 1982; Tella *et al*., 1998; Carrete and Donázar, 2005; Sunde and Redpath, 2006; Fernández *et al*., 2009; Campioni *et al*., 2013; Tanferna *et al*., 2013; Rivers *et al*., 2014). The understanding of the mechanisms underlying individual variability in habitat use is however poorly known and very limited as yet. A few studies on raptors have shown individual differences in settlement areas depending on previous experience during the wandering stage (Delgado *et al*., 2010), or in prey selection and diet breadth in relation to foraging habitat selection (Terraube *et al*., 2014). Davis and Stamps (2004) proposed that experience in the natal habitat may shape habitat selection during adulthood, but information on birds of prey is controversial (Mannan *et al*., 2006; Delgado *et al*., 2010). Apart from this scarce evidence, very little is known about whether genetic, cultural or ontogenic factors shape between and within individual differences and to what extent they may be flexible in their habitat preferences. This may well be one of the most promising and productive areas of research on raptor-habitat relationships in the future.

Movement ecology: dispersal and migration

Dispersal and migration involve the longest movements performed by birds throughout their life-cycles. Dispersal is the glue that binds populations and allows the expansion of distribution ranges and colonization of new areas, with a key role in population dynamics and evolutionary processes. Most research on dispersal in birds of prey has focused on the causes motivating it and on the cues used by individuals to settle in a new location, both in natal and breeding dispersal contexts.

Using capture-recapture techniques, a wide array of individual, environmental and social correlates has been identified (e.g. Korpimäki, 1993; Wiklund, 1996; Serrano *et al*., 2001), but few studies have evaluated comprehensively the fitness payoffs of adopting different dispersal strategies (Forero *et al*., 2002; Serrano and Tella, 2012). Additionally, molecular methods have increasingly been used to infer effective dispersal and connectivity among subpopulations (Martínez-Cruz *et al*., 2004; Brito, 2007; Hull *et al*., 2008; Alcaide *et al*., 2009). Although both capture-recapture and molecular data provide valuable information on realised dispersal patterns, their main handicap is that they rarely give in-depth insight into the underlying movement process. For this reason, one of the major gaps of knowledge about raptor dispersal is the transient stage separating emigration from a site and immigration to another (see Penteriani

and Delgado, 2009). This is particularly important in natal dispersal of long-lived raptors with delayed sexual maturity because they usually spend several years in non-breeding areas in which they may be exposed to differential pressures. Much progress in this respect has been made possible thanks to the advent of modern tracking tools, showing that in some species, such as large eagles and territorial vultures, pre-breeders wander over vast geographic areas and settle temporarily in sites with high food resources, usually located far away from breeding grounds (Balbontín, 2005; Cadahía *et al.*, 2010; Margalida *et al.*, 2013). In other species, such as large owls, young individuals try to settle as soon as possible in well-defined home ranges, and temporary settling areas used are often located near breeding territories of conspecifics (Rohner, 1997; Delgado *et al.*, 2010; Penteriani and Delgado, 2012). Further, floaters and failed-breeders may prospect different areas to gather information on habitat quality to optimise future settlement decisions (Serrano *et al.*, 2003; Sergio and Penteriani, 2005), although the precise pathways covered and the cues used during prospecting remain poorly known (Nathan *et al.*, 2012; Therrien *et al.*, 2015).

Biotelemetry and experimental approaches have also been useful to demonstrate that dispersal in birds of prey is determined by the interplay between endogenous factors (e.g. hormones and body condition) and the social environment or the spatial configuration of the landscape (see Belthoff and Dufty, 1998; Delgado *et al.*, 2010).

Migratory raptors are in turn exposed to different environmental conditions during breeding, migration and wintering, so patterns observed at one stage may be affected by conditions experienced in another (Grande *et al.*, 2009; Mihoub *et al.*, 2010). New tracking devices and other technological innovations have provided detailed information on migration routes, wintering, summering and stopover areas, causes and rates of mortality experienced en route, and migration strategies that would have been unthinkable until recently (Rodríguez *et al.*, 2009; Bohrer *et al.*, 2012; Klaassen *et al.*, 2014; Therrien *et al.*, 2014). Moreover, they have provided information on within and between individual variability in speed and amplitude of movements, flying performance in relation to food resources and weather conditions (Lanzone *et al.*, 2012; Dodge *et al.*, 2014), timing and routes of migration (López-López *et al.*, 2014), and their link with life-history strategies and demographic issues (Sergio *et al.*, 2014).

However, carry-over effects, i.e. processes occurring in one season that affect individual performance in another season (Harrison *et al.*, 2011), remain largely unknown in birds of prey, although they have been well documented in other migratory birds (e.g. Norris *et al.*, 2004) and constitute an interesting field of open research. Finally, it has been shown that resident and migrant raptors may segregate spatially in sympatry (e.g. Cardador *et al.*, 2015), so another promising line of research is partial migration (populations composed of a mixture of resident and migratory individuals). Partial migration is ubiquitous in animals but has been scarcely explored in spite of its potential to further our understanding of the evolution of migratory behaviours, its ecological consequences, and its applied implications in a context of global change (Chapman *et al.*, 2001).

From a general point of view, movement ecology is a growing field with an increasingly better established theoretical framework (Nathan *et al.*, 2008). From the first studies of long-distance dispersal and migratory movements investigated by following radio-tracked raptors with aircraft (Cochran, 1975; Beske, 1982), the use of satellite telemetry has revolutionised the study of movement ecology in birds of prey. Now the challenge is to visualise and analyse the overwhelming

volume of available data (Gurarie *et al*., 2016), as well as to identify how individuals take movement decisions under different environmental conditions depending on their own state and previous experience. This will certainly enrich our understanding of raptor ecology and conservation in the years ahead.

THE ROLE OF RAPTORS IN NATURE CONSERVATION

Raptors within modern progress in wildlife conservation

Nature conservation has experienced a continued transition in relation to the commitments of authorities to promote it worldwide. After the first private initiatives funded by global organizations for the protection of nature (i.e. IUCN, WWF, ICPB) that took place in the mid twentieth century, it was not until the 1970s when environmental awareness acquired a legal status in Europe (De Klemm and Shine, 1993). The milestone that initially launched these global environmental commitments came in 1972 with the UN Convention on the Human Environment and the establishment of the United Nations Environmental Program (www.unep.org/); further, the endorsement of the first international conventions and treaties on the protection of species and habitats (RAMSAR, OSPAR, Barcelona) was triggered. The decade ended with the adoption of the Convention on the Conservation of European Wildlife and Natural Habitats in Europe (Bern Convention www.coe.int/en/web/bern-convention/home). It was the first to include a list of strictly protected species establishing a new and binding approach, and forcing countries to take active measures to protect them. The Convention on the Conservation of Migratory Species (Bonn Convention www.cms.int/) and the Birds (2009/147/EC) and Habitats (43/92/EEC) Directives also deepen the need for protecting some species, prioritised against others depending on their conservation status, scientific interest, rarity or cultural value.

Within these different conventions, treaties and regulations, birds of prey have had a notorious presence almost monopolising the lists of protected species. Along with waterfowl (Kirby *et al*., 2008) and reptiles, raptors have been the group with a higher level of protection at the European level in different reference texts (table 1). Thus, there are significant differences in the proportion of protected species between raptors and other taxonomic groups in both the Bern Convention ($\chi^2_7 = 20{,}532.4$; $p < 0.001$) and the European Directives ($\chi^2_7 = 20{,}764.3$; $p < 0.001$). Likewise, birds of prey have also been the subject of priority conservation and recovery projects. Taking as reference the 740 LIFE projects awarded by the EU between 1992 and 2014 for species of wild flora and fauna (http://ec.europa.eu/environment/life/project/Projects/), 14.0% were aimed to one or several species of raptors, being these projects about a third (31.9%) of those devoted to the protection of birds.

Raptors as flagship species and other surrogate concepts

Why do protection and devotion are so strongly biased to raptors? Why do raptors enthral society to become a priority group? Several reasons have been highlighted within this regard that could justify their importance: 1) the attractiveness that their behaviour provokes in people, their aesthetic attributes and symbolism (Douglas and Verísimo, 2013), 2) the traditional persecution that raptors have suffered due to interactions with anthropic interests, and the resulting environmentalist awareness awakened in different social sectors (Redpath

TABLE 1

Number and percentage (in brackets) of species of different taxonomic groups, protected under the Bern Convention and the Birds 2009/147/CE and Habitats 92/43/CEE Directives, in relation to the total number of existing species. Sources: *Flora*: Euro + Med PlantBase, 2006-2011 http://www.emplantbase.org/home.html; *Invertebrates*: Wieringa, 1995; *Fishes*: Freyhof and Brooks, 2011; *Amphibians*: Temple and Cox, 2009; *Reptiles*: Cox and Temple, 2009; *Birds*: BirdLife International, 2015; *Mammals*: Temple and Terry, 2007.
[Número y porcentaje (paréntesis) de especies pertenecientes a diferentes grupos taxonómicos protegidos bajo la Convención de Berna y las Directivas de Aves (2009/147CE) y de Hábitats (92/43/CEE) en relación con el número total de especies existente. Fuentes: Flora: Euro + Med PlantBase, 2006-2011 http://www.emplantbase.org/home.html; Invertebrados*: Wieringa, 1995;* Peces*: Freyhof and Brooks, 2011;* Anfibios*: Temple and Cox, 2009;* Reptiles*: Cox and Temple, 2009;* Aves*: BirdLife International, 2015;* Mamíferos*: Temple and Terry, 2007.]*

Taxonomic group		Total species in Europe	Species in Bern Convention (Appendices I, II)*	Species in Birds Directive (Annex I) or Habitats Directive (Annex IV)
Flora		20000	703 (3.5%)	691 (3.4%)
Fauna	Invertebrates	100000	104 (0.1%)	142 (0.1%)
	Fishes	546	18 (3.3%)	13 (2.4%)
	Amphibians	85	52 (61.1%)	70 (82.3%)
	Reptiles	151	84 (55.6%)	149 (98.6%)
	Birds	533	314 (58.9%)	181 (33.9%)
	Raptors	47	47 (100%)	42 (89.3%)
	Mammals	260	126 (48.4%)	166 (63.8%)

* Estimated number in function of the number of species considered as whole families are included in App. II

et al., 2013), 3) their rarity or the overall unfavourable conservation status of several species (Burfield, 2008), and 4) their role as top-predators and their ecological requirements whose fulfilment depends on the environmental health of the ecosystems they inhabit (Sergio *et al*., 2008).

The leading role of raptors in active conservation initiatives during the last 40 years granted them the tag of "*flagship species*" (Sergio *et al*., 2008), being organisms for which protection has been prioritised by all public administrations, NGOs and media, similar to the level of large carnivore mammals (Sergio *et al*., 2006). As a result, a large number of actions have been developed like reintroduction projects, land stewardship, scientific research, solving threatening factors or environmental awareness (see "Other search options" in www.iucnredlist.org). These great investments and efforts towards raptor protection in Europe has had positive effects on those species with a more unfavorable conservation status and prioritised in

TABLE 2

Population status (breeding pairs) of the 24 diurnal and nocturnal raptors included in priority lists of European protected species ("Source": a = IUCN Red List, in the categories NT; VU; EN; CR; b = European Union's Species Action Plans for Birds; c = Spanish Catalogue of Threatened Species; and d = Other flagship raptor species), between first available global census and most recent ones, and their trend (+: positive; –: negative; stable or unknown according to BirdLife International, 2005).
[Estatus poblacional (número de parejas) de las 24 rapaces diurnas y nocturnas incluídas como prioritarias en las listas europeas de especies protegidas. ("Source": a = Libro Rojo de la UICN, en las categorías NT; VU; EN; CR; b = Planes europeos de acción para aves; c = Catálogo español de especies amenazadas; y d = otras rapaces "paraguas"). Se muestra el cambio entre el primer censo global disponible y el más reciente, así como la tendencia (+: positiva; –: negativa; estable o desconocida; de acuerdo con BirdLife International, 2005).]

Species	Source	Population 1 (year)	Population 2 (year)	Trend	References
Aegolius funereus	c		90900-309000 (2015)	stable	1
Aegypius monachus	c	250 (1973)	2128 (2012)	+	2, 5
Aquila adalberti	a, b, c	38 (1974)	407 (2014)	+	4
Aquila chrysaetos	d	4971-6151 (1990)	9300-12300 (2014)	+	1, 6
Aquila fasciata	b, c	862-1072 (1990)	1100-1200 (2014)	stable	1, 3
Aquila heliaca	b	400 (1992)	1178-1387 (2010)	+	2
Circus cyaneus	a		30000-54000 (2012)	–	1
Circus pygargus	c	35000-65000 (2004)	54500-92200 (2013)	unknown	1
Circus macrourus	a		300-1100 (2012)	unknown	1
Clanga clanga	a, b	874 (1996)	770-1000 (2012)	–	1, 3
Clanga pomarina	b	10244 (1996)	16400-22100 (2012)	stable	1, 3
Falco biarmicus	b	330-429 (1990)	430-840 (2014)	+	1, 3
Falco cherrug	a, b	300 (1990)	350-740 (2012)	+	1, 2
Falco eleonorae	b	6250 (1990)	14300-14500 (2012)	+	1, 3
Falco naumanni	b	23000 (1970)	26000 (2012)	+	2
Falco peregrinus	d	6000 (1970)	13900 (2013)	+	2
Falco rusticolus	b	1650-2650 (1990)	1100-1900 (2012)	stable	1, 3
Falco vespertinus	a		30300-63400 (2013)	–	1
Gypaetus barbatus	a, b, c	95 (1999)	200 (2013)	+	2
Gyps fulvus	d	2500 (1980)	27000-28000 (2013)	+	2
Haliaaetus albicilla	d	2200 (1970)	8600-10900 (2012)	+	2
Milvus milvus	a, b	21000 (1970)	23600 (2010)	stable	2
Neophron percnopterus	a, b, c	3300-5050 (2008)	3000-4700 (2012)	–	1, 3
Pandion haliaetus	c		8400-12300 (2012)	+	1

1 = BirdLife International, 2015; 2 = Deinet *et al*., 2013; 3 = European Union's Species Action Plans for Birds; 4 = Spanish official working groups; 5 = SEO/BirdLife's national census (www.seo.org/2012/07/02/monografias-seguimiento-de-aves/); 6 = Watson, 1992.

different regulations. Thus, of the 24 endangered species of bird of prey at the European level and/or with ongoing EU action plans, more than half have improved their status in the last 20-40 years, 29.1% are stable or no clear information on their trend is available, and 16.6% show a declining trend (table 2).

An important body of scientific literature has been published regarding the effects that active raptor conservation has had on other components of the environment, following the "*surrogate*" concept (i.e. species used as sensitive indicators of a conservation problem, to track population changes of other species or to locate areas of high biodiversity; Caro and O'Doherty, 1999). There are heterogeneous results regarding the relationships between presence and relative abundance of birds of prey and geographically co-occurring environmental indices such as diversity, species richness and threatening factors. On the one hand, several authors have demonstrated the role of raptors as "*biodiversity indicators*", establishing a positive and direct relationship between richness and abundance of raptors and other animal or plant species in the same areas (Sergio *et al*., 2006; Martín and Ferrer, 2013; Burgas *et al*., 2014). However, this principle is far from being widespread because some biomes such as semidesert do not show any of the mentioned relationships with raptors (see Estrada and Rodríguez-Estrella, 2016). Also, links between raptors and species with different habitat requirements or with less inter-specific attraction seem lower (Senzaki and Yamaura, 2015). Otherwise, raptors properly act as "*sentinels*" of different local and large-scale environmental changes and global threats to biodiversity, such as the dynamic of their prey populations, the levels of pollutants and illegal poaching activities (García-Fernández *et al*., 2008; Helander *et al*., 2008, Molina-López *et al*., 2011). However, a direct effect on the performance of raptor populations from change and habitat alteration processes when they occur in low or moderate intensity has been analysed and ruled out (Rodríguez-Estrella *et al*., 1998), possibly due to their plasticity in satisfying several of their ecological requirements (Donázar *et al*., 2010; Sullivan *et al*., 2016). Finally, less clear is their role as "*umbrella species*" (Branton and Richardson, 2011). There is a small number of conclusive studies (i.e. Senzaki *et al*., 2015), and therefore a lower overall consensus on the reliability of considering birds of prey such as drivers that meet the complete needs of all co-occurring species in all ecosystems and habitats, given the difficulty in standardising their ecological requirements (land use, ecosystem functionality, ecological processes, etc) generically (Carrete and Donázar, 2005; Sergio *et al*., 2008). Overall, the diversity of life strategies of raptors and the different conservation status within the same species at the regional level make their role as sentinel, indicator or umbrella species highly context-dependent.

In any case, conservation plans based on raptors presence have shown positive effects in providing global environmental benefits derived from the increase in the land surface covered with management plans, the enhanced environmental awareness and the fight against global threats for biodiversity. Thus, their consideration as "*flagship species*" allows that the protection and proper management of the territory inhabited by raptors also impact on a large amount but not all the species and habitats, thus optimising efforts and performance of the financial investment prioritised towards these top-predators and the achievement of global environmental goals (Sergio *et al*., 2008). In relation to adaptive management (Salafsky *et al*., 2001), the accurate knowledge of the ecology and threats of birds of prey (table 2) in comparison to other taxa has been widely used as a tool for updating the assessment

of their conservation status (i. e. BirdLife International, 2015) and, as a consequence, the application of a wide range of protection techniques regularly assessed from a scientific perspective (i.e. power line retrofitting, poisoning prosecution, habitat management; Balbontín, 2005; Margalida *et al*., 2014; Chevallier *et al*., 2015; Hernández-Matías *et al*., 2015; Matthiopoulos *et al*., 2015).

Raptors as providers of ecosystem services

Biodiversity loss and alteration of the environment are increasingly threatening ecosystem functions and associated ecosystem services worldwide (e.g. Loreau *et al*., 2001; Hooper *et al*., 2005). Ecosystem services can be defined as the benefits people obtain from ecosystems and the species that make them up (MEA, 2003). Millennium Ecosystem Assessment establishes four broad types of ecosystem services: *provisioning services* that relate to the products obtained from ecosystems including for example water or food; *regulating services* that are the benefits obtained from the regulation of ecosystem processes, for instance, climate regulation; *cultural services*, that refer to the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences; and *supporting services*, which are those that are necessary for the production of all other ecosystem services, such as soil formation or nutrient cycling (MEA, 2003). Although the idea that humans can benefit from nature is not new, the concept of ecosystem service, which is increasingly used by scientists, managers, and general public (Daily *et al*., 2009), has allowed us to better understand the consequences of ecosystems change and biodiversity loss for human well-being.

Avian scavengers as providers of supporting, regulating and cultural services

Birds are an ideal study models in ecosystem services research (Şekercioğlu *et al*., 2004; Şekercioğlu, 2006; Whelan *et al*., 2008; Green and Elmberg, 2014). Within this field, a "classical" example are the ecosystem services provided by vultures and avian facultative scavengers, but it has received little scientific attention until recently (Moleón *et al*., 2014), when the number of studies has raised (see Markandya *et al*., 2008; Gangoso *et al*., 2013) partially due to the precipitous decline of vultures and other avian scavengers in many regions of the world and specially in Africa and Asia where they were formerly extremely abundant (Ogada *et al*., 2012, 2016).

Quantification, not only in economic terms, of ecosystem services provided by avian scavengers will be a major future challenge (Wenny *et al*., 2011). In the Indian subcontinent, the catastrophic vulture decline led to increases in the abundance of mammal scavengers, i.e. rats *Rattus* sp. and feral dogs *Canis lupus familiaris* (e.g. Pain *et al*., 2003; Markandya *et al*., 2008), which are important reservoirs of pathogens causing bubonic and rabies diseases, respectively. This also increased rates of infection to humans and domestic species (Markandya *et al*., 2008; Ogada *et al*., 2012). In this scenario, health costs attributable to vulture declines, i.e. the loss of regulating services, were estimated at more than $2 billion per year (Markandya *et al*., 2008). In Europe, the outbreak of bovine spongiform encephalopathy (BSE) led to the approval of a sanitary regulation that forced the collection and transport of carcasses of extensive livestock from farms to be destroyed in authorised plants. Apart from negative impacts on vulture behaviour and populations (Donázar *et*

al., 2009; see below), this measure led to the decline of the services provided by vultures (Margalida and Colomer, 2012). In Spain, for instance, it was estimated that the Spanish vulture populations removed between 134 and 200 t of bones and between 5551 and 8326 t of rotten meat every year (Margalida and Colomer, 2012). In addition, supplanting carrion consumption by scavengers with artificial removal of livestock carcasses meant the emission of over 77,000 metric tons of CO_2 eq. to the atmosphere per year and the annual payment of ca. $50 million to insurance companies by farmers and administrations (Morales-Reyes *et al*., 2015).

Humans and vultures have been closely related to each other during the course of human history, especially since the rise of agriculture and animal domestication around 10,500 years ago (Moleón *et al*., 2014). Since then, vultures have been revered and become part of religious symbolism of numerous human cultures, as derived from the ancient Egyptian goddesses Mut (a woman with vulture's wings) and Nekhbet (a vulture), and monuments from the Maya civilisation (Morelli *et al*., 2015). Even today, the Parsees in Asia depend upon funeral services provided by vultures, which remove their dead relatives placed in the 'Towers of Silence' (Pain *et al*., 2003).

Recently, the observation of birds (i.e. birdwatching) has become one of the most promising branches of ecotourism, which provides important economic profits and may favour conservation of natural areas (Şekercioğlu, 2002). However, the economic benefits of these cultural services have been rarely quantified. In the United States there were 47 million birdwatchers in 2011. They spent $41 billion in trip and equipment expenditures, generating $107 billion in total, and creating 666,000 jobs (Carver, 2013). Specifically, the observation of vultures and other large raptors is an increasing activity and supplies important recreational services. For example, in a natural reserve of Israel, the griffon vulture *Gyps fulvus* watching provided benefits around $1.1-1.2 million per year (Becker *et al*., 2005).

Scavenging plays a fundamental role in the maintenance of the stability, structure and dynamics of the food-webs (Wilson and Wolkovich, 2011). Although supporting services provided by scavengers still remain relatively unexplored it seems clear that avian carrion eaters may contribute to the nutrient redistribution among ecosystems (DeVault *et al*., 2003; Beasley *et al*., 2015) thanks to their ability to travel great distances. Nutrient cycling benefits plants that then produce oxygen, food, medicine or erosion control (MEA, 2003; Wenny *et al*., 2011). Finally, carcass recycling implies an increase in nutrient availability in the soil (Melis *et al*., 2007), which could have effects on microbes, plants and invertebrates.

Biological control of rodent agricultural pests by raptors

The size and growth rate of human population has required huge environmental transformations from heterogeneous landscapes with complex ecological interactions to homogeneous and ecologically simplified areas devoted to food production, settlement and rubbish treatment-deposition. These new ecosystems are almost free of predators, competitors, parasites and pathogens and represent optimal breeding grounds plenty of food for a number of human commensal organisms, such as some rodent species. The high capacity of adaptation of microtine voles, murine rats and mice favoured by their high intrinsic reproductive potential has promoted the rapid colonisation of these novel habitats. In addition, current agricultural practices, such as cropping intensification, increasing irrigation and cultivation of green herbaceous plants throughout the

year, create ideal conditions for rodents to expand and breed continuously (Singleton *et al*., 2010; Jareño *et al*., 2015). Consequently, many small, extremely fertile, rodent species have experienced population outbreaks becoming pests in agricultural areas and villages. These rodent pests have provoked considerable damage in crop production and caused human health problems (Singleton *et al*., 2010; Buckle and Smith, 2015).

Rodent pest control

The first strategies used to combat rodent pests were developed in the 1950s and were based on the use of chemical poisons, including anticoagulants (Hadler and Buckle, 1992). This was followed by a period of reassessment of chemical procedures due on the one hand to the resistance developed by rodents to chemicals and, on the other hand, to the social awareness about the environmental impact of chemical poisons (Singleton *et al*., 2010). Although some old-fashioned minds leading regional administrations persist in the use of this technique, pest-control experts recognise that the use of rodent-killing materials alone is not enough to control rodent pests (Meyer and Kaukinen, 2015). The recent action lines for rodent pest control are based on a set of simultaneous methods. The idea of integrating different methods (including biological control) to combat rodent pests goes back a long way (Howard, 1967), although it began to create interest in the 1990s through the so-called Integrated Pest Management (IPM) scheme (Kogan, 1998; Singleton *et al*., 2010). The IPM plan aims to find durable strategies that combine biological and cultural controls with limited pesticide use. From this scheme arises what was called the Ecologically Based Rodent Management (EBRM; Singleton, 1999).

Raptors as biological control of rodent pests

One of the measures pursued by the IPM and EBRM is the increase of rodent predator populations. Both diurnal and nocturnal raptors are avian predators whose abundances seem to play a significant role in the population dynamics of rodents (Lima *et al*., 2002; Fargallo *et al*., 2009). Furthermore, there are abundant empirical studies about how raptor abundance or raptor rodent consumption relates to rodent population density (e.g. Korpimäki, 1985; Salamolard *et al*., 2000; Bernard *et al*., 2009; Millon *et al*., 2014). Thus, it is plausible to think that raptors have the potential to regulate or limit rodent abundance (Şekercioğlu, 2006). However, the evidence and the number of studies finding causation are notably scarce. Experimental studies are not conclusive (Norrdahl and Korpimäki, 1995; Torre *et al*., 2007; Maron *et al*., 2010) and recent reviews about predation effects have shown that whereas experimental mammalian predator removal clearly increases prey population densities, the effect is not so clear in the case of avian predators (Holt *et al*., 2008; Salo *et al*., 2010). Similar conclusions can be extrapolated to technical and scientific studies aimed to evaluate the effectiveness of the biological control by raptors (BCR) in rodent pests. Raptors, and particularly barn owls *Tyto alba*, have a long tradition in their use as a management technique to control rodent pests in palm and rice plantations of Asia (Fall, 1977; Duckett, 1991). The relatively easy methods to attract raptors to plantations by providing artificial nest sites and perches facilitate the direct predation of rodents (Askham, 1990; Duckett, 1991; Motro, 2011). Yet, the efficiency of this measure has been questioned. Criticisms come from the scarcity of reports showing measurable effects of BCR on rodent numbers and/or crop damage (Marsh, 1998; Hygnstrom *et*

al., 1994; Wood and Fee, 2003). The truth is that even today there are very few properly designed studies performed to evaluate the efficiency of BCR. Nevertheless, there are also promising results in the application of BCR to diminish both plantation damage (Murua and Rodríguez, 1989; Hafidzi and Mohd, 2003) and rodent densities in reduced areas around the nests and perches (Paz *et al*., 2013). These few and contrasting results highlight the need to undertake more properly designed studies to evaluate the efficiency of BCR as an applicable management technique in agro-sylviculture.

To assess the effectiveness of BCR on rodent pests a deep knowledge about the raptor-rodent population dynamics is needed as the capacity of raptors to regulate rodent populations will depend upon the relative abundance of the prey species (Sinclair *et al*., 1990). Furthermore, the efficiency of biological control techniques has been favoured by the increasing landscape complexity in agricultural systems through the integration of croplands with natural habitats to help the persistence of populations and guilds of predators that reduce pest densities (see Bianchi *et al*., 2006; Maas *et al*., 2015), but again this measure has not been investigated in the case of raptors. Therefore information about the predator community composition, its trophic ecology, intraguild competition and habitat requirements is also needed.

Current agricultural view in many developed countries still makes its commitment to cropping intensification and overuse of chemical phytosanitaries (herbicides, fungicides, insecticides, rodenticides, etc) and fertilizers. It is expected that predators will leave the area if they succeed in reducing the population of the only prey species (targeted rodent species) inhabiting the place, as there are no other resources abundant enough to sustain predator populations. The modern IPM scheme offers a valuable framework within which to think about agriculture as a less aggressive environmental exploitation able to maintain a reasonable level of biodiversity, to exploit other economical resources, such as hunting or tourism and benefit from ecological services.

HUMAN-RAPTOR CONFLICTS

Predation on game species

Background

Hunters and raptors preying on game species represent one of the more pervasive human-wildlife conflicts (fig. 4). The general assumption behind this conflict is that raptors compete with hunters for a shared resource, i.e. game species, which could lead to reduced quotas and subsequent economic losses to the hunting lobby (Kenward 1999; Thirgood *et al*., 2000a; Valkama *et al*., 2005; Park *et al*., 2008). Tensions are mainly associated to small-game hunting, an important socio-economic activity in rural areas of developed countries (Grado *et al*., 2001; Virgós and Travaini, 2005). The perceived (and mostly unfounded, see below) role of birds of prey in depleting hunting resources entails conservation consequences: raptor persecution (e.g., in the form of poisoning or intentional shooting) has been common practice among hunters for decades (e.g., Whitfield *et al*., 2003), which strongly ignores national and international regulations regarding the protection of raptor populations (e.g., European "Bird Directive" no. 79/409/CEE and "Habitat Directive" no. 92/43/CEE). This is of special concern for the most endangered species, for which continued killing contributed to reduce their populations to the point of local and regional extermination in some cases (Whitfield *et al*., 2004; Carrete *et al*., 2007). Unfortunately, species not feeding on game may also suffer from poisoning, as well as from direct killing by indiscriminate

shooting (e.g., Villafuerte *et al*., 1998). Thus, political and social action, as well as scientific attention, has often been encouraged to reconcile raptor conservation and hunting interests (Valkama *et al*., 2005; Moleón, 2007a; Thirgood and Redpath, 2008).

Assessing the impact of raptor predation on game populations

The key question from a scientific perspective is whether predation exerted by raptors is *compensatory* or *additive* to other prey losses (Moleón, 2012). Raptor predation would be compensatory if raptor-induced mortality does not entail a net increase in the mortality rate of the prey population. This may occur when mortality by raptors is rapidly compensated by a parallel reduction of deaths caused by other factors, or by enhanced reproduction, longevity and recruitment of prey species (Krebs, 2002). In this case, preyed individuals are usually of low quality (e.g., ill, injured, young or old) and constitute the so called "doomed

FIG. 4.—Conflicts between hunters and conservationists are still present and deteriorate because game populations have decreased in many regions of Europe whereas birds of prey populations recover. Booted eagle *Aquila pennata* with red-legged partridge *Alectoris rufa*. Credit: Eugenio Martínez-Noguera.
[Los conflictos entre cazadores y conservacionistas son todavía habituales e incluso empeoran porque las poblaciones de especies cinegéticas han declinado en muchas regiones de Europa mientras que las rapaces se recuperaban. Aguililla calzada Aquila pennata *con una perdiz roja* Alectoris rufa. *Crédito: Eugenio Martínez-Noguera.]*

surplus" of the population (Errington, 1946). In contrast, raptor predation would be additive if raptor-induced mortality results in a parallel increase of net mortality (Krebs, 2002). However, rather than fully compensatory or additive, predation exerted by raptors is likely characterised by a mixture of both components (Aebischer, 1991).

But, how can we empirically assess the impact of raptor predation on game prey populations? Predator-removal experiments could provide excellent insights. In practice, however, manipulation of raptor densities is largely prevented due to ethical and logistic reasons, especially on large spatiotemporal scales. An alternative approach consists of calculating the *predation impact*, i.e., the number of individuals (*kill rate*) or the proportion of the prey population (*predation rate*) taken by the predator (e.g., Valkama *et al*., 2005; Moleón *et al*., 2012). However, although the assessment of both parameters may be an important basic step, it results insufficient to infer limitation by the studied predator on the prey population because the nature of predation (i.e., what percentage is actually additive) remains unresolved. Answering this crucial question requires a profound knowledge of prey demography (including mortality rates and causes). Predation patterns and demographic information can then be integrated into prey population dynamics models to estimate changes of the hunting bag (which is highly dependent on the hunting form and socio-economical context) in relation to raptor abundance and predation rates (Marcström *et al*., 1988; Thirgood *et al*., 2000a). To accurately do this, we should recognise that raptor abundance and predation rates might change according to prey density. Thus, a recommended first step is to estimate the raptor's *total response* (i.e., how the total prey consumed by the total raptor population varies with changing prey densities), which results from summing the *functional response* (a function of the per capita intake) and the *numerical response* (a function of the total raptor population; Gilg *et al*., 2006). Correlational methods, e.g., comparing prey population with predator population and diet over different years or regions, could also provide an indication of the influence of raptor predation on small-game prey population dynamics (Moleón *et al*., 2008, 2013; see Park *et al*., 2008 for a list of advantages and disadvantages associated with different methods).

Impact of raptor predation on game populations: scientific evidences

Several reviews have dealt with the issue of raptor predation on game populations (Newton, 1993, 1998; Kenward, 1999; Valkama *et al*., 2005; Park *et al*., 2008). In Europe, ca. 62% of diurnal and nocturnal raptor species do not include (or do so only occasionally) gamebirds in their diets (Valkama *et al*., 2005). For the other 20 species, few studies have addressed the limiting potential of raptor predation on game breeding populations, and even less on game pre-harvest numbers, which is the main concern of hunters. The main conclusion that can be taken from these studies is that the impact of raptors on game populations and hunting bags is low in general, with some possible exceptions at the local level for certain raptor-gamebird systems (Valkama *et al*., 2005; Park *et al*., 2008). Scientific evidence on the best-known case study, i.e., that represented by hen harrier *Circus cyaneus* and red grouse *Lagopus lagopus scoticus* in Scotland (Thirgood *et al*., 2000a; Thirgood and Redpath, 2008), indicate that: a) harriers show a sigmoidal, type III functional response (typical of generalist predators) to changing red grouse densities, but harrier breeding density is primarily determined by the abundance of passerines and rodents, not red grouse (Redpath and

Thirgood, 1999); b) predation by hen harriers can reduce grouse harvests when the former are present at high densities and the latter at low densities, but hardly otherwise (Thirgood *et al*., 2000b; 2000c), which results in annual commercial losses of ca. £100,000 (estimation for 1996; Redpath and Thirgood, 1997); and c) several science-based management measures, including diversionary feeding, could significantly reduce the conflict (e.g., Redpath *et al*., 2001). Unfortunately, this profound scientific knowledge has been insufficient to date to reconcile conservationist and hunting interests in Scottish grouse moors because the lack of political willingness to implement solutions and, especially, the entrenched position of game managers, so hen harrier persecution is still widespread there (Thirgood and Redpath, 2008).

What is the state of the art in other systems? Studies in the Mediterranean Basin are scarcer and largely limited to Spain. Here, the system formed by Bonelli's eagle *Aquila fasciata* and two of its main prey in W Europe, the European rabbit *Oryctolagus cuniculus* and the red-legged partridge *Alectoris rufa* (Moleón *et al*., 2009), has received recent attention. In an area of SE Spain, Bonelli's eagle showed a hyperbolic, type II functional response to rabbit and partridge density changes, thus behaving as a specialist predator (Moleón *et al*., 2012). Although no numerical response to rabbits or partridges was found in this study, another work considering additional study areas and a longer temporal series found a positive relationship between the proportion of rabbits in the diet and Bonelli's eagle productivity at the territory scale. On the population scale, greater consumption of rabbits also improved productivity, adult survival and population growth rate (Resano-Mayor *et al*., 2016). A positive effect between rabbit availability and demographic parameters has been recorded in other diurnal (e.g., golden eagle *Aquila crysaetos*; Fernández, 1993) and nocturnal (e.g., Eurasian eagle owl *Bubo bubo*; Martínez and Zuberogoitia, 2001) Iberian raptors.

Mean kill rate per Bonelli's eagle territory (i.e., breeding pair plus fledglings) during the 100-day reproductive season (i.e., when the eagles' food requirements are higher) was ca. 49 rabbits and ca. 40 partridges in SE Spain. This resulted in a mean predation rate of 7.6-18.5% (rabbit) and 4.6-22.4% (partridge), depending on the considered territory radius of the eagle (Moleón *et al*., 2012). At the population level, the predation rate by Bonelli's eagle was $< 2.5\%$ for both prey, either for the breeding or the non-breeding period. This suggests that predation by Bonelli's eagles could scarcely affect the number of rabbits and partridges available for shooting in autumn, as well as the partridge population in spring hunted using call lures. In fact, Bonelli's eagle predation rates on partridge were notably lower than those reported for other European raptor-gamebird systems, probably because of the lower population density of Bonelli's eagles due to their greater territories (Moleón *et al*., 2011a). In an area of NE Spain, Northern goshawk *Accipiter gentilis* predation was estimated to reduce the partridge huntable stock by 22%, although it was unclear how much of these losses was additive. Moreover, goshawk predation hardly provoked changes in partridge breeding numbers between consecutive years (Mañosa, 1991). Given the lower pair density of large eagles in relation to smaller raptors (Newton, 1979) and the superpredation events by the former on the latter (Sergio and Hiraldo, 2008; Lourenço *et al*., 2011), small game populations in hunting states with breeding eagles could be subject overall to less predation pressure if compared with those in which eagles have been exterminated (Moleón *et al*., 2011a).

Although the predation impact by Bonelli's eagle was very low in general, the enhanced

predation pressure exerted by all shared predators (i.e., those species preying on both rabbits and partridges) on partridges after rabbit haemorrhagic disease (RHD) had decimated rabbit populations 25 years ago was probably enough to force a subsequent partridge population decline in Spain (Moleón *et al*., 2008; 2013). The population crash of these important small game species caused by RHD, either directly via infection (rabbit) or indirectly via hyperpredation (partridge), led to increased predator persecution in Spain (e.g., red kites *Milvus milvus*; Villafuerte *et al*., 1998).

Finally, it is interesting to note that not all preyed individuals are similar in quality. For instance, Penteriani *et al*. (2008) found that Eurasian eagle owls prefer to capture substandard rabbits. Also, unpaired sex ratios in prey populations could enhance or buffer the negative effects of raptor predation. In spring, Bonelli's eagle and eagle owl predation on partridges is biased towards males (Donázar and Castién, 1989; Moleón *et al*., 2011a). However, female partridges are probably easier to capture by terrestrial predators during this period, which could counteract the effects of raptor predation on the sex ratio of partridge populations (Moleón *et al*., 2011a). In addition, prey can exhibit behavioural responses to avoid excessive predation. In dispersal areas of the Spanish imperial eagle *Aquila adalberti* in Spain, the continued presence of foraging immature individuals in reduced areas induced changes in the activity and space use pattern of rabbits, which forced dispersing eagles to abandon the area after a few days (Ferrer, 1993).

The main lesson learned after decades of research effort is that determining the impact of raptor predation on small-game populations, with particular emphasis on quantifying the additive component of predation, and offering efficient tools for sport hunting management is a complex issue that cannot be resolved by using simple and partial approaches. We need fine estimations of game bag loss, which could be accompanied by associated economic quantification. However, this is not the last step.

Let us imagine that raptor predation is identified as an important limiting factor of a given game prey population. In such a case, a new key question would arise: can we conclude that removing raptors is the most efficient management measure to guarantee sustained hunting profitability? Apart from legal and ethical considerations, the response is not, because several factors other than predation (mostly, human-induced factors such as habitat degradation, overhunting and the spread of emerging infectious diseases) can exert a much higher limiting effect on the game prey population (e.g., Newton, 1998). It is also pivotal to differentiate between the proximate and ultimate causes of prey declines in order to design the most efficient measures (Moleón *et al*., 2013). Thus, improved scientific arguments, together with responsible attitudes among policy makers, stakeholders and hunters are indispensable ingredients to reduce human pressure on raptors while maximising hunting profitability.

Finally, we should bear in mind that raptors need healthy prey populations to persist in the wild, while sport hunting in general is not a vital activity for humans. This is not a trivial question, especially in light of the large amounts of money and huge efforts that Europe is nowadays devoting to the conservation of raptors (see above).

Scavengers and livestock

Although human-wildlife conflicts likely have an ancient origin (Anderson, 1997), it is during the recent decades, coinciding with the increase of the human population and the need to give value to natural resources, that the confrontations between wildlife and hu-

mans are becoming habitual, increasing the interest of environmentalists, managers and policy-makers (Treves *et al*., 2009; Gehring *et al*., 2010). Among the conflicts between wildlife and humans, the commonest scenario is related to the coexistence between herbivores of economic importance and threatened predators (mainly carnivores and raptors) (Peterson *et al*., 2010; Redpath *et al*., 2013, Redpath *et al*., 2015). However, when the conflict arises in an unexpected scenario as, for example, with species not considered a menace for human interests, the management actions to solve this interaction are unknown and difficult to implement. This is the case of the attribution of attacks of Eurasian griffon vultures on livestock, an apparent emerging conflict that was identified in southern Europe during the 1990s and which has increased progressively during the subsequent decade (Margalida *et al*., 2011; Margalida *et al*., 2014). This conflict causes major unrest among farmers but has received scarce attention from the scientific community (Margalida *et al*., 2011; Margalida *et al*., 2014). The opportunistic killing of small and medium-sized vertebrates has been reported as relatively frequent in some New World vulture species (Lowney, 1999; Avery and Cummings, 2004) but has only been reported occasionally in the Old World vultures (Houston, 1994).

The temporal context of the conflict

The first reports of vultures attacking livestock were documented in northern Spain in the middle of 1990s (Navarra, western Pyrenees) but it was not until middle of the 2000s when the conflict was generalised across Spain and southern France (see the review in Margalida *et al*., 2014). In general, most of the presumed attacks took place in spring (from April to June), coinciding with birthing dates in areas of extensively reared livestock (mainly sheep and cows that constitute 80% of the livestock affected, see Margalida and Campión, 2009; Margalida *et al*., 2014). Analysing the temporal pattern, most of the complaints took place from 2006 onwards, coinciding with the food shortages provoked by the sanitary policies after the bovine spongiform encephalopathy (BSE) (Donázar *et al*., 2009; Margalida *et al*., 2010). This facilitated that the general social perception of the problem, also misinterpreted by the media and people, attributed immediately a causal relationship between food shortages and vulture behaviour. Indeed, the sudden trophic reduction provoked some shifts in the diet (Donázar *et al*., 2010), behaviour (Zuberogoitia *et al*., 2010), demographic parameters (Margalida *et al*., 2014) and foraging movements of vultures. However, some preliminary results suggested that there is no relation between the frequency of complaints of alleged attacks and both the spatial availability of trophic resources and the density of vulture populations (Margalida and Campión, 2009). To support this, it must also be taken into account that many complaints took place before food shortage regulations (1996-2006, see Margalida *et al*., 2014). Thus, the link between "vulture attacks" and a reduction in food availability is unclear, at least with respect to the breeding population.

A magnification of the problem

Despite the relatively low economic cost of the conflict (Margalida *et al*., 2014), the social and media impact has been substantial. This provoked pressure on administrations that were obliged to explore the problem with more detail. Figure 5 shows the trend of the between 2006 and 2015. As we can see from the figure, this trend increased suddenly from 2006 to 2010, then diminished from 2011 onwards (fig. 5) coinciding with the

approval and application of new and more flexible regulations that allowed access to more food resources by avian scavengers (Margalida *et al*., 2012). However, the real application was effective after 2013 when most of the administrations returned to a pre-BSE scenario, providing more natural food (livestock losses) and creating feeding stations for vultures. Thus, probably with the approval of new regulations, the social alarm diminished and the importance of the conflict showed the regressive trend observed. However, as occurs with the previous hypothesis that "food shortages" equals "increase of attacks", other explanations are possible. It seems that after the important increase in the number of complaints between 2006 and 2010, a more rigorous control and assessment of the complaints by administrations increased the percentage of rejection. For example, in Catalonia, as a case model that applied specific and rigorous controls during 2010-2015, the complaints compensated by administration decreased from 40-62% during 2008-2010 to only 2-9% during 2011-2015. Thus, a careful monitoring showed that the problem was overestimated and most of the complaints were independent of the vultures' behaviour in the scenario of the problem. In this regard, some preliminary conclusions obtained during *in situ* visits to disentangle the true factors explaining the presumed attack were obtained. Firstly, changes in husbandry practices in areas in which livestock range freely or remain unattended in large fenced enclosures even at the time of lambing has been considered as one of the main factors. These circumstances increase the chance of predation by other animals such as common ravens

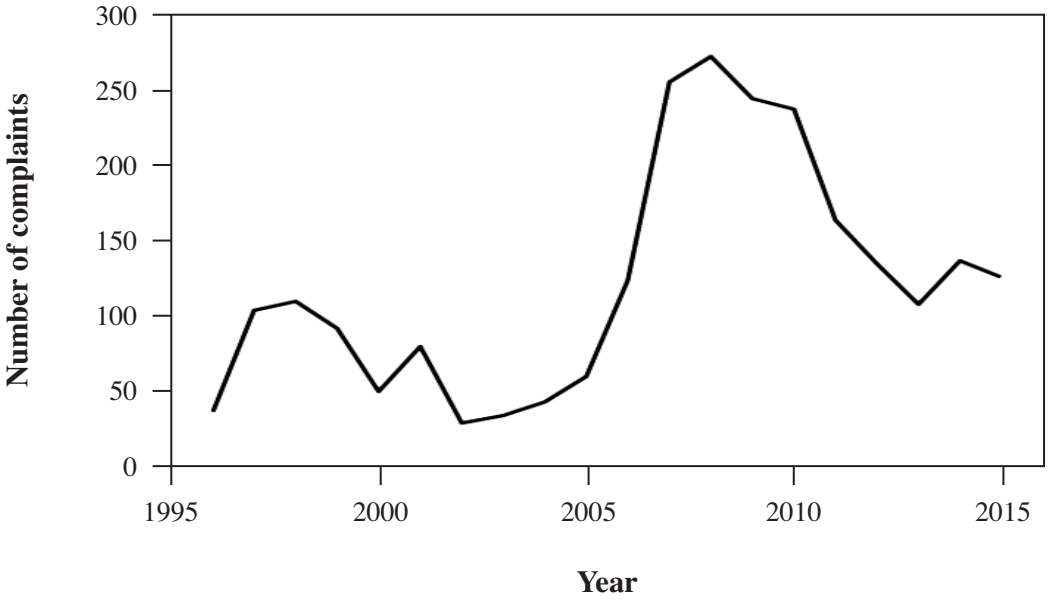

FIG. 5.—Trend in the number of complaints related with European griffon vulture attacks to livestock in Northern Spain (Catalonia, Aragón, Guipuzcoa and Álava) during the period 1996-2015.
[Tendencia en el número de reclamaciones relacionadas con ataques de buitres leonados a ganado en el norte de España (Cataluña, Aragón, Guipúzcoa y Álava) durante el periodo 1996-2015.]

Corvus corax, which have been considered responsible of several aggressions. Secondly, individuals were mainly affected during calving and most of them presented problems (young individuals with first birth, breech birth...). Finally, in most cases, the complaint is plainly argued by showing pictures with the rests of the livestock presumably attacked (skin debris and bone remains), but with direct observation or additional evidence, just relying on the only affirmation that "vultures were present in the livestock carrion".

Raptors and human infrastructures

Transport and energy infrastructures are growing exponentially worldwide. Their increases derive from such human demand of resources and are also pointed out as drivers of global change (Vitousek *et al*., 1997). The development of infrastructures has been exponential in Mediterranean Europe during the last decades as a result of the growing financial support of EU development funds. For example, France has the largest network of roads (10^6 km) and Spain the largest network of motorways (14,000 km) in Europe (http://www.irfnet.eu/images/Statistics/ER_Statistics_Final_2012.pdf). Thus, the major socioeconomic changes in the Mediterranean are driving a shift in the mortality factors affecting birds of prey from direct persecution to casualties associated to infrastructures (Martínez-Abraín *et al*., 2009) (fig. 1).

Transportation: Roads, railways and airports

The increasing network of roads for the transportation of people and goods has important effects on habitats, mainly through fragmentation (Forman and Alexander, 1998; Trombulak and Frissel, 2000; Meunier *et al*., 2000) but also on the behaviour and survival of raptors and owls (Bautista *et al*., 2004; Lambertucci *et al*., 2009). Although other terrestrial vertebrates such as reptiles and mammals suffer higher road mortality rates (Glista *et al*., 2007), some diurnal raptors and owls might also follow population declines because of reduced survival. For example, in Mediterranean habitats two declining owl species, barn owls and little owls *Athene noctua*, might be particularly sensitive to road casualties (Hernández, 1988; Frías, 1999; Fajardo, 2001). In contrast, different raptor species such as common kestrels *Falco tinnunculus*, black kites *Milvus migrans* or common buzzards *Buteo buteo* are attracted to road verges that provide with food resources (small mammals and rabbits) and perches (Meunier *et al*., 2000), but nevertheless these species as well as other forest-dwelling raptors suffer a significantly lower vehicle collisions (Zuberogoitia *et al*., 2015). On the other hand, increasing traffic load has been described as a factor influencing foraging behaviour of raptors affecting particularly large and endangered species such as the Spanish imperial eagle and cinereous *Aegypius monachus* and griffon vultures that decrease their activity close to roads on weekends (Bautista *et al*., 2004). Surprisingly although the Mediterranean region holds dense railway networks including the largest high-speed railway network in the world (UIC, 2014), there are no published studies on its potential effects on raptors.

Interactions between birds of prey and airports have been mainly assessed from the perspective of bird collision with aircrafts. Although raptors only constitute a minor percentage of the airfield's avifauna, this group caused the majority of fatal accidents in the Mediterranean region (Thorpe, 2005; Kitowski, 2011). Due to its large size and low flight maneuverability, griffon vulture

was the species that caused the most serious accidents (Kitowski, 2011). Other species involved were Eurasian kestrels, common buzzards, marsh harriers *Circus aeruginosus* or Montagu's harriers *C. pygargus*. Among owls, little owls are particularly sensitive to this type of of accidents, being involved in half of all the bird strikes reported in some airports (Kitowski, 2011). Most of the bird strike reports remain unavaible to the public due to airport policies which prevent the study of their incidence. Despite this, the relative importance of mortality from collision with aircraft seems likely to be low, but precise studies focussing on its effect on bird of prey populations are needed. Mitigation measures for bird of prey strikes included vegetation management and habitat modification to make airfield less desirable for their prey species (ICAO, 2012; DeVault *et al*., 2013) and real time radar surveillance to monitor bird movements and manage air traffic (Leshem *et al*., 2010). So far, the effectiveness of other widely used methods as bird deterrents or falconry has not been properly assessed. In recent years, some hazard bird strike models based on the structure of landscape, abundance and sensitivity of bird species or aircraft movements have been implemented (Soldatini *et al*., 2010; Coccon *et al*., 2015). This could be an effective tool to evaluate and manage the risk of bird collision with aircrafts.

Energy production: power lines, wind farms and solar facilities

Electrocution and collision with power lines are among the main causes of population declines for many bird species (Lehman *et al*., 2007) and are considered a major source of human induced mortality for raptors in Southern Europe since the pioneering studies in late 1980's (Ferrer *et al*., 1991; Ferrer and Negro, 1992; Rubolini *et al*., 2005). In fact, electrocution might be considered as the major modern source of non-natural mortality for an array of medium and large-sized birds of prey such as the Spanish imperial eagle (González *et al*., 2007; López-López *et al*., 2011), Bonelli's eagle (Real *et al*., 2001; Hernández-Matías *et al*., 2015), booted *Aquila pennata* and short-toed snake *Circaetus gallicus* eagles (Martínez *et al*., 2016) or the Eurasian eagle owl (Sergio *et al*., 2004; Martínez *et al*., 2006). Retrofitting of power lines has been proved to reduce mortality and improve population viability of endangered species (López-López *et al*., 2011; Chevallier *et al*., 2015).

Wind farms are also a major source of mortality for birds and bats worldwide (Sánchez-Zapata *et al*., 2016). In Mediterranean habitats there is increasing concern on the demographic consequences of collisions in wind farms for long lived raptors such as Egyptian *Neophron percnopterus*, cinereous and griffon vultures (Carrete *et al*., 2009, 2012; Sanz-Aguilar *et al*., 2015; Vasilakis *et al*., 2016). Other raptor species such as short-toed snake eagles and common kestrels are also frequently found dead in wind farms although their effects on population dynamics are unknown.

Solar facilities are relatively new and their effects on biodiversity have been scarcely documented (DeVault *et al*., 2014). On a local scale, impacts are mostly associated with habitat transformation and to a lesser extent with wildlife mortality (Lovich and Ennen, 2011; Hernández *et al*., 2014). There are no detailed published results on the effects of these infrastructures on raptors in Mediterranean habitats although steppe raptors such as Montagu's harriers and lesser kestrels *Falco naumanni* are more likely to be affected because of the spatial coincidence of these infrastructures with their breeding and foraging habitats.

BIRDS OF PREY IN NOVEL HABITATS: ADAPTATIONS AND CONSEQUENCES OF LIVING IN CITIES

Habitat alteration and loss are one of the major threats for biodiversity and unfortunately their effects are reaching a global scale (see i.e. Donald *et al*., 2013). Nonetheless, the same processes that are causing the habitat loss are simultaneously originating novel ecosystems, defined as ecosystems created deliberately or inadvertently by human activity that show a species composition and abundance previously unknown in that bioma (Hobbs *et al*., 2006). Urbanization involves one of the most extreme forms of landscape change, since natural habitats are fragmented, isolated and finally lost by urban development at varying spatial scales, which generally lead to a deep restructuring of affected communities (Marzluff *et al*., 2001; Alberti, 2005; González-Oreja, 2011). Species diversity is lower in animal communities inhabiting urban landscapes, although human habitation offers a variety of intentional or incidental subsidies to wildlife, such as provision of supplementary foods (Fuller *et al*., 2008); and some well-adapted species opportunistically exploit such resources and reach high abundances. These high densities of potential prey attract birds of prey to hunt and even to breed in urban environments (Chace and Walsh, 2006; Rutz, 2008; Solonen and Ursin, 2008). While it is evident that urbanization is causing the restructuration of faunal assemblages, the effect of urbanization on individual species is more complex than initially perceived (González-Oreja, 2011; Isaac *et al*., 2014).

High prey concentrations act as powerful attraction for predators, mainly raptors and owls, which are able to occupy surrounding natural areas and move into urban areas for hunting (Zuberogoitia *et al*., 2002). Raptors breeding near urban areas largely increase the consumption of certain species included in the range of optimal prey mass, which positively affect breeding success and brood size (Drewitt and Dixon, 2008; Zuberogoitia *et al*., 2013; Martínez-Hesterkamp, 2015). The abundance of feeding resources also attracts floaters, wintering and non-territorial birds, which directly occupy cities (Pirovano *et al*., 2000; Cade and Burnham, 2003; Isaac *et al*., 2014). However, urban environments may not contain the full complement of resources required by a species (Chace and Walsh, 2006). Nest site availability is one of the main limiting factors in urban areas and those that already exist are usually of poor quality (Altwegg *et al*., 2014). One of the consequences may be the establishment of long-term non-breeding territories, which would act as ecological traps (see Battin, 2004; Isaac *et al*., 2014; Fasciolo *et al*., 2016), ultimately reducing fitness components (Schlaepfer *et al*., 2002; Remes, 2003).

In some cases, birds of prey are able to find nesting resources in cities, because they reuse stick-platforms of corvids, occupy old structures or artificial ledges, or are intentionally favoured by setting nest-boxes (Cade *et al*., 1996; Ranazzi *et al*., 2000; Solonen and Ursin, 2008; Fiuczynski, 2011; Zuberogoitia, 2011; Lövy and Riegert, 2013; Rodríguez *et al*., 2013; Altwegg *et al*., 2014). Some raptor species produce fewer eggs and fledglings in urban habitats than they do in rural ones (Tella *et al*., 1996). However, other species respond with higher reproductive success (Bird *et al*., 1996) (fig. 6). In urban environments, breeding tawny owls *Strix aluco* seem to be relatively free from the pronounced regional abundance fluctuations of small mammals, and probably gain from the relatively stable food resources (such as rats and common pigeons *Columba livia*), as well as the warmer microclimate of towns compared to rural habitats that largely govern the breeding of owls elsewhere (Solonen and

Ursin, 2008). The abundance and stability of prey species and the behavioural adjustments to human disturbance result in higher breeding success and productivity in urban goshawks *Accipiter gentilis* and sparrowhawks *Accipiter nissus* (Papp, 2011; Solonen, 2014a). However, some breeding urban raptors, mainly cliff-nesting species, suffer conflicts with the human occupants of the building on which the birds have decided to breed and are expelled as a consequenc, reducing their reproductive performance (Atwegg *et al*., 2014).

Home ranges of urban raptors and owls are larger than those monitored in natural areas, because they probably enlarge territories for exploiting suitable hunting grounds, which are sparsely distributed within urbanised areas and surrounded by a high proportion of unused developed areas (Tella *et al*., 1996; Henrioux, 2000; Riegert *et al*., 2007; Lövy and Riegert, 2013). However,

FIG. 6.—Peregrine falcon *Falco peregrinus* breeding in a building in Valladolid (central Spain) where it preys mainly on domestic pigeons *Columba livia*. Urban raptors may have comparatively higher breeding success in relation to rural areas thanks to the exploitation of locally abundant food resources. Credit: Juan Sagardía.
[Halcón peregrino Falco peregrinus *nidificando en un edificio de Valladolid (España central) donde preda fundamentalmente sobre palomas domésticas* Columba livia. *Las rapaces urbanas pueden tener éxitos reproductores comparativamente altos en relación con zonas rurales gracias a la explotación de recursos localmente abundantes. Crédito: Juan Sagardía.]*

this is not a regular rule for every species; avian forest-dwelling predators seem to have lower home ranges in cities than non-urban con-specifics, possibly due to high concentrations of prey species, mainly birds, of optimal size in parks (Bloom and McCrary, 1996; Warkentin and Oliphant, 1990; McGrady, 1991; Sodhi and Oliphant, 1992; Rutz, 2006; Fiuczynski, 2011; Sulkava *et al*., 2014). Moreover, urban raptors exhibit higher levels of hunting success and lower flight activity than non-urban ones (Rutz, 2006).

Birds born in urban environments seem prone to reoccupy these habitats; even secretive species such as goshawk and sparrowhawks show a remarkable tolerance to human disturbance (Rutz, 2003; Papp, 2011). However, fear of humans remains highly constant throughout the adult lifespan of a bird species (i.e. burrowing owl, *Athene cunicularia*; Carrete and Tella, 2013) and there is strong individual consistency in the response to disturbances (Carrete and Tella, 2010). Thus, it is more likely that a permanent perturbation factor like human disturbance would be selecting those individuals that are able to better tolerate humans (Rebolo-Ifrán *et al*., 2015). Therefore, differences among urban and rural populations are more probably a consequence of selective pressures (Carrete and Tella, 2013). Urbanised areas may be selecting individuals with adaptive abilities (so called behavioural syndromes or personalities) which are able to deal with urban challenges, human presence included (Rebolo-Ifrán *et al*., 2015). The contribution of captive bred birds in reintroduction programmes may also affect individual behavioural adjustments and favour changes in the relationships between raptors and humans in cities (Cade and Burnham, 2003; Cugnasse, 2004).

From a negative point of view, urban raptors are frequently affected by risks associated with vehicle and window collisions as well as electrocutions (Chace and Walsh, 2006; Hager, 2009), by premature fledging and by direct persecution (Cade and Bird, 1990). Riegert *et al*. (2010) conclude that the apparent advantage of suitable nesting sites for common kestrels in the city centre can be counterbalanced by new possible risks, such as threats from humans. Moreover, the high population densities of some prey species that positively affect raptors can elevate contact rates within and among species, and favour the spread of parasites by direct contact or oral-fecal routes (Bradley and Altizer, 2006). Increased interspecific competition in some reduced urban areas (i.e. foraging and resting sites) has been linked to chronic stress, which can lower resistance to infection and intensify the harmful effects of pathogens through effects on the host immune system (Sol *et al*., 1998; Padgett and Glaser, 2003). Furthermore, some heavy metal and pesticide pollutants become concentrated in the surroundings of developed areas and can be highly detrimental to vertebrate health (Bradley and Altizer, 2006) and adversely affect urban raptors (e.g. Newsome *et al*., 2010).

Overall, the combined effect of these various factors in many modern cities seems to be positive for peregrine falcons *Falco peregrinus*, goshawks, sparrowhawks, long-eared owls *Asio otus*, tawny owls and others (Cade *et al*., 1996; Rutz, 2008; Solonen, 2014a, b; Lövy and Riegert, 2013). However, there are still open questions related to the medium- and long-term consequences of living in urban habitats. On one hand, it is not clear that the urban population may maintain a stable trend without immigration. On the contrary, demographic data from a long-term monitored population of urban peregrines suggest that the population would have declined in the absence of immigration (Atwegg *et al*., 2014). Finally, reproductive performance is high in most species, but further research is needed in order to assess the effects on survival and long-term inter-

generational fitness. Lövy and Riegert (2013) also suggested that it would be of interest to clarify raptors' use of habitat networks in urban environments, i.e. how fragmentation and/or connectivity of focal habitats influence patterns of birds' movement.

The challenge of rewilding for raptors

As we have previously emphasised throughout the text, besides direct and indirect persecution, degradation and the loss of natural habitats remain as one of the major threats for raptors conservation worldwide. Nonetheless, the projections on land-use changes modelled for Europe reveal a different picture (Pereira *et al*., 2010). After centuries of deforestation, the continent has followed a trend of land abandonment and consequently an increase of scrub and forested areas (Kaplan *et al*., 2009; van Vuuren *et al*., 2006). Although frequently linked to the idea of releasing charismatic species (see details in Deinet *et al*., 2013; Stokstad, 2015) a "rewilding" process is more properly understood as the passive management of ecological succession through the reduction of human control of landscapes. This encompasses opportunities to restore natural ecological processes, as well as species and the ecosystems services that might be provided (Gillson *et al*., 2011; Navarro and Pereira, 2012; Pereira and Navarro, 2015). During the last decade this issue is motivating a great deal of interest among scientists and policy makers who are trying to predict the response of species and the capacity to adapt to new environments on the basis of the different projections of socio-economic alternative scenarios.

According to Navarro and Pereira (2012), rewilding triggers profound biodiversity changes with some loser and winner species (see below). In this context raptors are not an exception. The study of the effects of land-use abandonment and its consequences on the viability of the ecosystems (and the species inhabiting there) is a challenge in environmental sciences. On the one hand, rewilding processes reduce human presence in many areas thus increasing the availability of suitable habitat for those species being historically persecuted (Enserik and Vogel, 2006; and see above). Conversely, farmland abandonment may have negative consequences on species historically linked to traditional agro-grazing exploitations and rural constructions (Fuller, 1987; Labaune and Magnin, 2002; Laiolo *et al*., 2004; see below). Within this context, European raptors are a paradigmatic study case due to their position within food webs as top predators and scavengers. However, there is little knowledge on how raptors would face rewilding. Focusing on carrion-eaters, it seems likely that land-abandoment process may affect important fractions of the populations of vultures living in the Iberian Peninsula in the coming decades (fig. 7; see also García-Barón, 2014). It has been argued that rewilding may favour the availability of carrion for large avian scavengers thanks to both the expansion of wild ungulates (and their abundances) and the recovery of large predators. Both issues would represent an increase in the availability of carcasses in the wild (Selva *et al*., 2003; Wilmers and Post, 2006). However, although rewilding occurs in some mountain ranges of southern Europe it must be taken into account that large scavengers forage over huge areas so they may be still very dependent on livestock carcasses and food supply at artificial feeding stations (Margalida *et al*., 2011).

Many raptor species (especially large eagles) and some scavengers like the cinereous (*Aegypius monachus)* and Egyptian vultures are very dependent on wild rabbits, a keystone species of the Mediterranean biome (Delibes-Mateos *et al*., 2008). Re-

wilding future scenarios predict the dominance of closed forest and scrubland undermining this lagomorph which prefers mixed habitats of scrubs-forest and open grassland for concealment and feeding (see references in Smith and Boyer, 2008). Thus, García-Barón (2014) showed that up to 50% of the breeding and potential foraging areas for

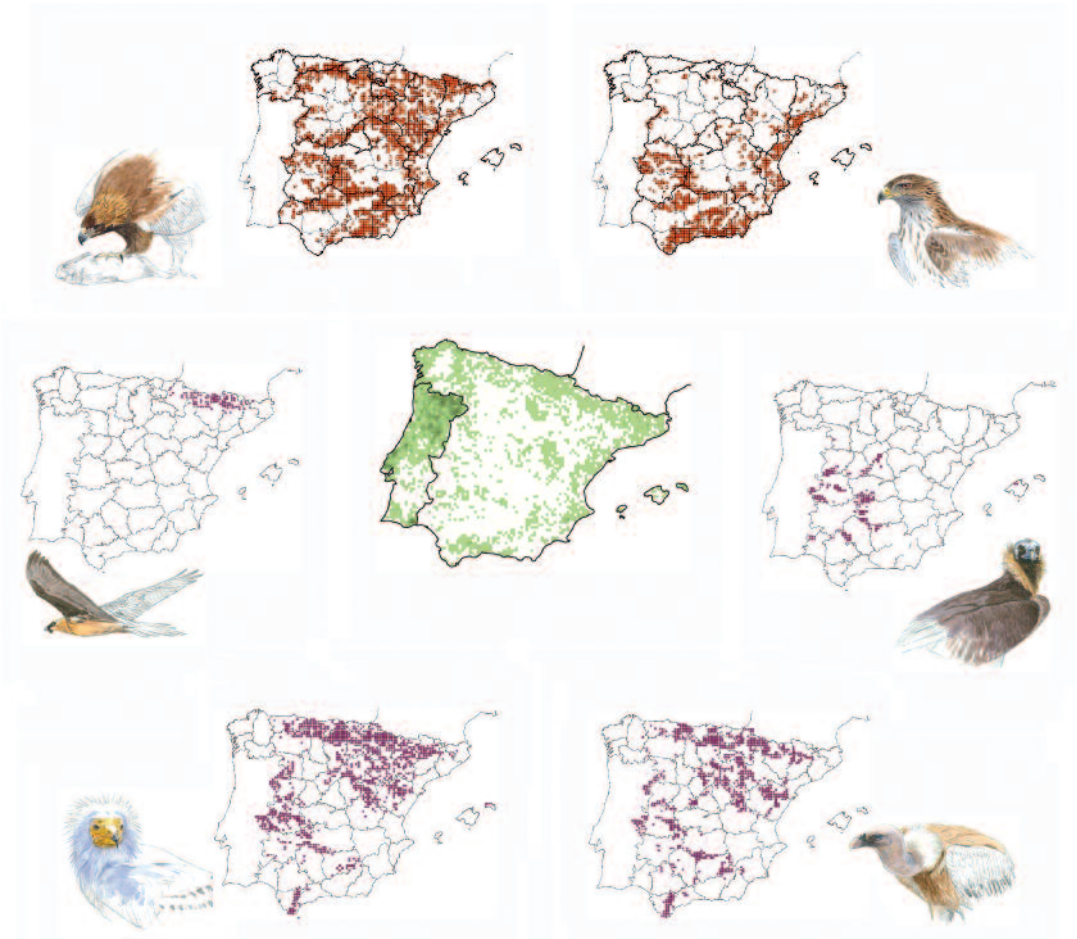

FIG. 7.—Hotspots of land abandonment (in green) vs. the distribution of the breeding areas of four vultures (griffon, Egyptian, cinereous and bearded) and two eagles (Bonelli's and golden) based on information available in the *Spanish Atlas of Breeding Birds* (del Moral and Martí, 2004). The map in the centre shows areas categorized as "agriculture" in 2000 that are projected to become abandoned or afforested in 2030 (Verburg and Overmars, 2009). (Species drawings: Juan Varela). Figure modified from Cortés-Avizanda, *et al*. (2015).

[Mapas de abandono de usos del suelo (en verde) vs la distribución de las zonas de reproducción de los cuatro buitres ibéricos (alimoche, quebrantahuesos, buitre negro y leonado) y dos águilas (perdicera y real) basados en la información disponible en el Atlas Español de Aves Reproductoras *(del Moral y Martí, 2004). El mapa en el centro muestra las áreas categorizadas como "agricultura" en el año 2000 que se prevé que se convertirán en abandonadas o de expansión forestal para 2030 (Verburg y Overmars, 2009). (Dibujos de especies: Juan Varela). Figura modificada a partir de Cortés-Avizanda,* et al. *(2015).]*

cinereous vultures in the Iberian Peninsula may be affected by predicted land abandonment under variable socio-economic scenarios. Conversely, and because the rewilding processes would favour the size and the number of patches of woodland, a higher number of old and tall trees would also increase and thus enhance the availability of suitable breeding areas for forest-breeding raptors (Zuberogoitia *et al*., 2013).

In general, it can be expected that land abandonment and the subsequent changes in the abundance and distribution of resources will have asymmetrical effects on birds of prey (and other organism) populations. How these processes can shape the structure of raptor assemblages and communities remains an outstanding question. Besides, diffuse competition (Bock *et al*., 1992; Piana and Stuart, 2012), a scarcely-studied process, competitive exclusion may determine that most aggressive and/or social species can displace other birds of prey from preferred breeding areas (Krüger, 2002; Sergio *et al*., 2005) although high variability can be expected depending on site-specific contexts (see e.g. Treynis *et al*., 2011). Also, when a group of species exploits simultaneously the same food resource, as happens with avian scavengers, monopolisation by dominants (e.g., Eurasian griffon vultures) may appear when their relative abundance increases (Donázar *et al*., 2010; see also Carrete *et al*., 2010), and negative effects on populations of the subordinate avian scavenger species, as well as on other organisms, are predicted (De Vault *et al*., 2003; Shivik, 2006; Selva and Cortés-Avizanda, 2009; Cortés-Avizanda *et al*., 2012). Finally, intraguild predation (the killing of species using the same resources) appears as a generalised phenomenon having potential consequences at individual and population levels, but also having the potential of shaping predator communities (Sergio and Hiraldo, 2008). For example, the spread of forests may benefit the larger body-sized tawny owl in detriment of smaller species as barn and little owls which are more associated with open areas (Mikkola, 1983).

The counterpart of land-use abandonment is the intensification of agricultural practices in much more cost-efficient other areas. This fact leads to an increase of contrasting landscapes of large surfaces covered by dense forests and scrublands and intensively cultivated crops. These changes in the landscape are not new but has accelerated in recent decades when the process also directly affects many birds of prey species linked to environments under agro-grazing traditional practices which are not as hostile (Donázar *et al*., 1996). The abandonment of traditional practices may negatively affect species such as the threatened lesser kestrel because of the disappearance of older, rural buildings for breeding. Similarly, great interest has arisen in the study of the effects of rewilding on the abundance of arthropods (an important item in the diet of these and other open-habitat birds) where population fluctuations could be largely influenced by both the modification of land uses.

In general, the abandonment of the rural areas would reduce human presence and thereby relax human disturbance, thus enabling breeding success of raptors as well as modifying their feeding or foraging behaviours (see review in Martínez-Abraín *et al*., 2009, 2010). However, the abandonment of traditional agro-grazing activities does not necessarily mean the disappearance of all forms of humanisation and their impact. In fact, those wilder areas would become of interest for recreational activities which are currently considered as an increasing concerning topic in wildlife conservation (Martínez-Abraín *et al*., 2010). In addition, after the abandonment of the land, owners can search profitability by installing certain industries, such as wind farms that can have serious consequences on popu-

lations of raptors, other birds and bats (Sánchez-Zapata *et al*., 2016). Consequently, it seems erroneous to establish a linear relationship between land abandonment and human intervention on landscapes and life assemblages.

Future avenues

The paradigm of nature protection through the prioritisation of threatened or flagship species has had valuable results in Europe over the last 40 years benefiting specifically most birds of prey species occupying the continent. Thus, most of the emblematic taxa have experienced spectacular recoveries so that they have substantially expanded both the areas of distribution and population sizes. However, it is necessary to advance new approaches which improve the conservation status of both birds of prey as well as other elements of biodiversity. Increasing awareness of general public and policy-makers in this subject would overcome the dilemma between protected vs. non-protected territories, improving the capacity for sectorial policies integration –especially the agricultural ones (Hodge *et al*., 2015)–, the mobilisation of financial resources and the achievement of the objectives derived from the international legal commitments on wildlife protection and sustainable development.

It seems desirable to highlight the role of raptors as ecosystem services providers with clear benefits to human welfare and ecosystems sustainability (Whelan *et al*., 2015). It is increasingly acknowledged among scientists that avian scavengers yield important regulatory and cultural services but its quantification remains to be addressed in detail. In addition, studies aimed at the mapping of ecosystem services on a large scale would be very helpful (Naidoo *et al*., 2008). Moreover, additional research about supporting services (i.e., nutrient cycling) provided by scavengers is necessary. Studies about the perception of stakeholders (i.e., shepherds) and evaluation of the ecosystem services and providers (i.e., vultures and facultative scavengers) would be essential for the establishment of management proposals for the conservation of the scavenger populations and the maintenance of the services provided. Also, higher social recognition of these benefits seems desirable (Daily *et al*., 2009). This is particularly true for Spain where the bulk (> 90%) of the European vulture populations are found (Margalida *et al*., 2010).

Birds of prey also provide regulating services through pest control (chiefly rodents) in agricultural systems. There is however, a striking paucity of studies in this field, mainly because reliable investigation needs long-term experimental approaches in large predator-excluded and control areas with replicates, which is time- and personnel-demanding and expensive, thus unaffordable for local small research groups. IPM (integrated pest management) and BCR (biological control by raptors) implementation requires the involvement of regional and national administrations to provide areas, personnel and funds for investigation on these promising, non-aggressive, cheap and sustainable procedures of agricultural pests more and more demanded by the public.

Increasing populations of birds of prey may result in conflicts with human interests. Perhaps the most entrenched is that arising from the predation on game species which often results in direct killing and indirect persecution (poisoning) (Villafuerte *et al*., 1998). Available scientific evidence indicates that raptors are rarely able to limit game prey populations (see reviews in Valkama *et al*., 2005; Park *et al*., 2008). However, current scientific knowledge on this topic is still very scarce and suffers from serious biases that prevent inferring robust conclusions. The methodological complexity

(including considerable field effort) of determining the impact of predation on game populations, which increases in complex ecosystems, probably deters further advance in this field (Valkama *et al*., 2005; Park *et al*., 2008; Moleón, 2012). Future research is particularly desirable in Mediterranean regions, which combine high hunting pressure and important raptor populations (Valkama *et al*., 2005; Moleón *et al*., 2011a). Studies that explore simultaneously the raptor functional and numerical responses are rare (Valkama *et al*., 2005; Moleón *et al*., 2012), as well as multi-scale (e.g., population plus territories within the population) approaches of predation rates (Moleón, 2007b). Also, mammalian game species, which can be highly valuable for hunters (e.g. European rabbit is the most frequently killed game species in Spain; Moleón *et al*., 2011a) have received much less attention than gamebirds (e.g., Newton, 1993, 1998; Kenward, 1999; Valkama *et al*., 2005; Park *et al*., 2008; Thirgood and Redpath, 2008). Moreover, studies including the floating segment of the raptor population are virtually absent. This is a relevant gap in the case of species such as large eagles because floaters concentrate in large numbers in juvenile dispersal areas during the non-breeding period (e.g., Moleón *et al*., 2011b), which normally coincides with the main hunting period. Floater persecution in such areas and period is elevated, which may result in negative demographic effects for the raptor whole raptor population (Penteriani *et al*., 2008). The impact of raptor-caused mortality on game species releases for population reinforcement (Kenward *et al*., 2001), as well as the effect of raptors on game prey behaviour (Ferrer, 1993), also provide ample room for further research. Finally, multi-species approaches, preferably considering the whole raptor (and mammalian carnivore) community, are highly encouraged against one predator-one prey approaches (Valkama *et al*., 2005).

Damages blamed on raptors are not limited to game species but also reach the binomial vultures-livestock. This emergent conflict is widely publicised and magnified by the broadcast media (Margalida *et al*., 2014) and its mitigation requires dialogue between scientists, farmers, managers, policy-makers and disseminators. The lack of scientific data and the role of the media increased the social alarm and political pressures to take management decisions not based on scientific evidence. Practitioners generally have centred their attention on reducing negative interactions, rather than on increasing positive relations between humans and wildlife (Frank, 2016). In the case of griffon vultures, taking into account the important services provided by these species (Margalida and Colomer, 2012; Morales-Reyes *et al*., 2015) and the lack of sound evidences of a true and well defined problem, we need to face the issue under this angle to reduce the uncertainty of an overestimated conflict.

Conflicts between raptors and human interests are not uni- but bidirectional. It is largely known that raptors may be killed in power lines but new infrastructures such as wind farms charge a growing toll on birds of prey populations. Adequate planning and adoption of mitigation measures should be, in this order, the main strategies aimed to minimize these undesirable effects. Fortunately, raptors are among the best studied group of vertebrates in Europe and elsewhere with detailed information on the distribution and status for most of the species (Sánchez-Zapata, 2012). Besides, some of them (particularly large eagles and scavengers) have been long-term monitored so population viability analyses could be applied to evaluate the effects of infrastructures (Hernández-Matías *et al*., 2013; Chevallier *et al*., 2015; Sanz-Aguilar *et al*., 2015). Raptors might be used as indicators and/or umbrella species useful for both for planning new infrastructures and for evalu-

ating and managing mitigation measures (Moleón *et al*., 2007; Pérez-García *et al*., 2011, 2016). Further research is required on the impact of emergent infrastructures such as wind and solar facilities, on the conflicts with transportation (particularly air and rail) but also on the effectiveness of the mitigation measures undertaken.

One of the most challenging prospective questions is how birds, and raptors in particular, will be affected by the impending changes in the European landscapes. Because novel ecosystems, (like large cities and conurbations) result from human actions, management is required to guide their development. How we manage these new ecosystems effectively is a point for debate: what should the goals be and how should these systems fit with other systems along the wild-intensively managed gradient (Atwegg *et al*., 2014)? What is even more interesting, does a new combination of species maintain similar functional properties with respect to the old species pool? Do they alter the original network of mutualistic and antagonistic interactions, and what are the consequences for community organisation (Hobbs *et al*., 2006)? On the other hand, concentration of humans in urban areas leads to the progressive depopulation of rural regions and the loss of traditional agro-grazing systems. In a Europe under severe global change, land abandonment might be an opportunity to preserve specific habitats and therefore to conserve specific organisms and ecological processes.

Overall, a multidisciplinary approach is required in order to get further understandings on the responses of raptors to different land-abandonment "rewilding" scenarios, to define new research avenues, addressing the costs and benefits and developing monitoring schemes within those future divergent landscapes. Future perspectives should rely on to couple the numerous studies about the biology, habitat selection, diet, concerns, etc. (as well as the historical information accumulated on raptor distribution and abundance) with the socio-economic projections on future land-uses which, from our point of view, will allow researchers and policy managers to know how populations and species fit into new habitats and landscapes. Indeed, we consider that those studies would facilitate the establishment of future conservation measures guarantying the preservation of raptors and their relationship with humans.

At the end, and it can not be otherwise, advances in the conservation of birds of prey within the context of current global change can hardly be dissociated from ecological knowledge. As in many areas of science, important conceptual advances in animal ecology have been stimulated by technological innovations combined with a parallel increase of statistical and mathematical methods tools (Cagnacci *et al*., 2010; Börger, 2016). Modern technologies not only allow collecting data on precise location of individual animals on the planet, but a plethora of sensors can be used to collect information on physiology and behaviour, and animals themselves can be used as sampling platforms to measure external variables as they move (Wilmers *et al*., 2015). Bio-logging innovations and practical analytical methods are increasingly formalising the close relationship between individual behaviour, habitat selection, species abundance, and population dynamics (Morales *et al*., 2010; Matthiopoulos *et al*., 2015; Van Moorter, 2015). This integrated and comprehensive framework will fuel the incorporation of new ideas and theories relating within- and between-individual variation to (meta) population-level consequences. For example, studies on vertebrates have shown the great importance of consistent individual differences in key personality traits such as boldness or aggressiveness on immediate survival prospects and dispersal propensity (e.g. Dingemanse *et al*., 2003;

Bremner-Harrison *et al*., 2004), and how the coupling of some of these components have far-reaching consequences for range expansions and the colonisation of novel environments (Duckworth *et al*., 2007). This kind of integrative approach is of crucial importance for understanding eco-evolutionary dynamics at all scales from individuals to (meta) populations, and probably is the most fertile ground for future research in raptor ecology.

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