Wildlife Research Monographs 6

Fabián Casas
Jesús T. García *Editors*

The Future of the Red-legged Partridge

Science, Hunting and Conservation

Springer

Wildlife Research Monographs

Volume 6

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Editors

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ISSN 2366-8733 ISSN 2366-8741 (electronic)
Wildlife Research Monographs
ISBN 978-3-030-96339-2 ISBN 978-3-030-96341-5 (eBook)
https://doi.org/10.1007/978-3-030-96341-5

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Foreword

I had a dream! An international scientific synthesis concerning the Red-legged Partridge. My colleagues, the younger ones, who specialize on the subject, have made it come true.

This extremely exhaustive work brings together all the new methods (genetics, biological analysis, from diseases to predators, field descriptions, modeling…) in order to fully understand how natural populations will thrive in a perpetually changing environment that challenges the adaptability of this species.

All these research teams allow us to have a global picture of the situation of the species throughout South-Western Europe: 90% of the breeding population can be found on the Iberian Peninsula (Spain and Portugal—including Madeira—and Andorra). France, Great Britain, where the species was successfully introduced in the XVIIIth century, and Italy represent the remaining 10%.

The Red-legged Partridge should attain the status of "rural patrimony" species, due to the large range they occupy and its eco-ethological adaptability to open and diversified landscapes, often highly managed by man for agriculture and livestock; a true biodiversity indicator in human-modified landscapes. The results laid down here prove this diversity and, therefore, make further research indispensable in order to comprehend more fully the life history of partridge populations in such different environments.

There are several reasons why the Red-legged Partridge' status has evolved from "moderate decline" in the years 2000, to species "Near Threatened" today throughout Europe.

Firstly, genetic progress should allow to reduce the large amount of hybrid birds (*Alectoris rufa x Alectoris chukar*), both in the wild and in the partridge farming. The first steps have been taken, but the problem is still far from being resolved. It is now necessary to do extensive genetic tests between extant and ancient populations (individuals preserved in museums), in order to understand better the evolution of its genetic pool over time.

More worrying are the changes in their habitat. The tendency to simplify our agroecosystems does not encourage the Red-legged Partridge to settle, as it prefers a diversified agricultural environment. Also, it needs open space, and Mediterranean scrub (garrigue-matorral) invasion is becoming the norm. Solutions need to be found in the countries involved within the European Union.

It is not yet possible to judge the results of global warming in the species, but a significant amount of birds has settled further north in France and in high altitude locations (Alps and Pyrenees). This is not only due to re-introductions of birds, which were in fact more frequent during the 1990s. Who Knows? Maybe the species is reconquering its old haunts, which stretched from Northern Brittany and Jersey to the Rhine area in Germany and even Switzerland.

Finally, hunting management methods that have been successfully tested, need to be put into motion over the largest possible area involving as many game estates as possible. Quantitative management by assigning daily quotas or restricting the number of hunting days is necessary, but not sufficient, as it ignores the ethological profile of this highly sociable species. For example: if hunting would only be allowed in the morning, family units could regroup at the end of the day and thus avoid some of the nocturnal dangers of predators. Also, if the minimum size of a group at the end of the hunting season was allowed to be 4 to 5 birds, this would allow the birds that survive the hunting season to settle and reproduce in the next spring with more guarantees than for smaller groups.

In order to ensure a favorable outcome for the Red-legged Partridge, we advise an "eco-etho responsible" and knowledge-based way of hunting, thus we can preserve a renewable resource essential for the maintenance of biodiversity.

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About the Editors

Fabián Casas Ph.D. in 2008 from the Universidad de Castilla-La mancha (UCLM). My background combines an interdisciplinary and applied approach to evaluate the effect of different human activities in wildlife and to develop sustainable management strategies for wildlife that would allow the conservation of biological diversity, especially of threatened species, and its compatibility with a rational use of natural resources by humans. I have mostly worked in agricultural ecosystems evaluating the effects of hunting and farming practices for threatened species as great and little bustards, pin-tailed and black-bellied sandgrouse, and gamebirds as the red-legged partridges. Recently, I have focused my research on the relation between habitat, food availability, and diet of red-legged partridge chicks, in order to disentangle the relationship between arthropods and habitat on red-legs.

Jesús T. García Ph.D. in Zoology and Physical Anthropology (2003) from the Universidad Complutense de Madrid. I currently work as a scientific holder in the Spanish National Research Council (CSIC). My interests are constantly evolving and have included conservation of wild species and populations, population and community ecology, evolutionary ecology, natural history, resource partitioning, reproductive tactics, foraging theory, species diversity, invasive species, genetics of dispersal, avian parasites, population genetics, conservation genetics, and phylogeographic analyses. I have used a variety of animal models in my research, essentially birds but also mammals, mostly linked to steppes or agrarian environments. Currently, I am working on several projects that use molecular approaches and involve fieldwork, labwork, analysis of large datasets, and applied conservation activities.

The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting

Miguel Ángel Farfán, Jesús Duarte, Alberto Meriggi, Luis Reino, Javier Viñuela, and Juan Mario Vargas

A Review of Historical Changes of Distribution: What Are the Main Contributing Factors?

The Red-legged Partridge is endemic to the Mediterranean region. It is a resident species from southwestern Europe and native to Portugal, Spain, France, Corsica, northern Italy and western Germany (Cramp and Simmons 1980). Historically, it has been successfully introduced in the UK and Azores and Madeira archipelagos. The world population of the species is estimated between 2 and 4.5 million pairs (BirdLife International 2004), with the Iberian population roughly estimated at 2.5 million pairs (Aebischer and Lucio 1997; Blanco-Aguiar 2007), where historically it occupied almost the entire territory. Thus, in Spain, it is reported as a breeding species in 86.3% of the UTM 10 × 10 km^2 (Blanco-Aguiar et al. 2003), and it is

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_1

Table 1 Densities of the red-legged partridge in its geographical range

Country	Dominant density	High density
England	<2 pairs/100 ha	2–8 pairs/100 ha
France	<1 pairs/100 ha	10–35 pairs/100 ha
Italy	<2 pairs/100 ha	2–16 pairs/100 ha
Portugal	<3 pairs/100 ha	15–20 pairs/100 ha
Spain	<5 pairs/100 ha	15–50 pairs/100 ha

present from sea level to an elevation of 2500 m (Díaz et al. 1996), although it is rare in the Cantabrian Mountain range and may even be absent in some specific areas due to local weather conditions or lack of suitable habitat. In the Canary and Balearic Islands, it has been introduced, while in the central and southern regions of peninsular Spain, the species occupies many habitats and reaches higher natural densities (Aebischer and Lucio 1997; Vargas et al. 2006) (Table 1). In Portugal, the Red-legged Partridge occupies most of the territory, although it is more abundant in the eastern fringe of the country and in the southern half (Equipa Atlas 2008). It appears mainly linked to agricultural lands (Borralho et al. 1997a; Beça 2005; Ribeiro 2006).

In Italy, the range of the Red-legged Partridge has undergone major changes since the first half of the twentieth century. Before the Second World War, the Red-legged Partridge's range extended mainly along the northern Apennine chain from the Southern Alps to the west to the province of Modena in the Emilia-Romagna region to the east, both on the southern and northern slopes. In central Italy, the presence of the species was mainly recorded in Tuscany, Umbria and Marche regions (Martorelli 1906; Arrigoni degli Oddi 1929; Spanò 1992, 2010; Massetti 2003). From the 1960s, the Red-legged Partridge showed a marked range contraction and population isolation, although since the end of the 1980s, it has shown a very important expansion of the range, even outside the original one, caused by several reintroduction projects started in northern and central Italy and releases from game farms (Spanò et al. 1987, Meriggi et al. 1992; Spanò 1992, Massetti 2003; Lasagna et al. 2013; Primi et al. 2013; Tizzani et al. 2013). Today, the Red-legged Partridge is present in the northern half of Italy, and its current range extends over a surface of 56,356 km^2, representing 18.7% of the country's area.

In France, the Red-legged Partridge occupies two thirds of the southern part of the country, and it is present from sea level to an elevation of 1200 m. Its range is limited on the north by the isotherm of 8 °C in March (SEOF 2016). The two national surveys developed in 1970–1977 and in 1977–1981 confirmed a stability range during this period. However, between 1985 and 1989, the national atlas showed an expansion to the north (Eure-et-Loir, Yonne, Seine-et-Marne and Aube) caused by the significant releases of birds from breeding farms (SEOF 2016) and probably by the increase in global average temperature worldwide caused by climate change.

In the UK, the Red-legged Partridge is not native. It was introduced in East Anglia around 1770 using stock from France (Game and Wildlife Conservation Trust 2016). After successive releases, they became fully settled by the end of the century. However, its spread was slow and a maximum range was not reached until the 1930s, followed by a decline and slight contraction of range. This trend has reversed since about 1959, and the distribution by 1972 was probably the most widespread extent of the self-sustainable range of the Red-legged Partridge in Britain (Sharrock 1976; Parkin and Knox 2010) and represents the area offering the continental-type climate and land-use characteristics that are typical of its natural range in mainland Europe (Holloway 1996). Since then, populations and range have fluctuated considerably throughout the years. Currently, the Red-legged Partridge is essentially a south-easterly bird in Britain.

Overall, we can observe a general pattern in the abundance of the Red-legged Partridge along its range characterized by low abundances in areas with a wet climate such as the northern fringe of the Iberian Peninsula and the Atlantic coast of Portugal, France and the UK, and high abundances in areas with a Mediterranean climate such as southwestern regions in Portugal and central and southern regions of peninsular Spain.

The variations from the historic to current range of the Red-legged Partridge in Europe are caused by historical, environmental and, particularly, human-related factors that have large geographical scale impacts. As discussed below, these factors are related to habitat loss, overhunting and releases of farm-reared birds.

In most European countries, the intensification of agriculture has transformed large areas of traditional farming landscapes (Fernández-Alés et al. 1992). Agricultural intensification of the most productive areas has resulted in an increase in average crop area and a decrease in edge and marginal area per property in Spain (Andrés et al. 2002). At the opposite extreme, many areas dedicated to marginal agriculture with poor competitive value were abandoned and subsequently occupied by scrubland and forest (Romero-Calcerrada and Perry 2004). These transformations in the landscape have caused important changes in the distribution of the Red-legged Partridge, which is restricted to agricultural plains and some agro-forestry areas (Acevedo et al. 2006; Ribeiro 2006; Gortázar et al. 2007; Vargas et al. 2007; Delibes-Mateos et al. 2009).

The dramatic increase of hunter numbers in Europe from the 1960s and their ability to move caused a marked range contraction and population fragmentation in diverse regions of its distribution area. By contrast, the decline observed in wild populations of the Red-legged Partridge and the contraction of its range as a consequence of overhunting have been countered by restocking with farm-reared birds (Baillie et al. 2006). Sometimes releases also occurred in areas outside the historic range, causing some alterations of the original species distribution (Spanò 2010; Lasagna et al. 2013; Tizzani et al. 2013).

Conservation Status: Is a Revision Needed?

The Red-legged Partridge still has a very large range, but their populations underwent a large decline and range contraction starting in the twentieth century and particularly marked since 1970. Although populations were stable in Portugal and Italy during 1990–2000, the species continues to decline across most of its European range to date (Rocamora and Yeatman-Berthelot 1999; Birdlife International 2004, 2016).

During the past 30 years, the Red-legged Partridge has experienced a significant population decline that has become severe in some areas of the Iberian Peninsula. Blanco-Aguiar (2007) conducted an in-depth analysis on the available data for Spain and concluded that the population decline was over 50% during that period. According to the Spanish Ornithological Society (SEO in Spanish) (SACRE-Spring program), this decline rose to 19% of their populations in Spain during the period 1998–2010 (Escandell et al. 2011). This estimate for the past decade reaches values of up to 33% in the central region of Spain. In the mid-1980s, the whole post breeding population of the Red-legged Partridge in Italy was estimated at 9639 individuals (Spanò et al. 1987; Meriggi et al. 1992). The current Red-legged Partridge population in Italy is estimated at 3000–4000 mature individuals, a population size similar to that registered in 2003 (BirdLife International 2004).

The reasons for the population decline of the Red-legged Partridge throughout its range are related to the loss of habitat caused by agricultural intensification (land use and farming practices changes), the risk of hybridization with individuals released from farms and questionable genetic purity, excessive hunting pressure and poor management on use of biocides and pesticides (Ricci 1985; Lucio and Purroy 1992; Capelo and Castro-Pereira 1996; Borralho et al. 1997b; Tapper 1999; Blanco-Aguiar 2007; Blanco-Aguiar et al. 2008; Vickery et al. 2009; Birdlife International 2016).

Habitat loss is the main threat to the Red-legged Partridge populations (Lucio and Purroy 1992; Tucker and Heath 1994; Blanco-Aguiar et al. 2003) and is a consequence of both the intensification of agriculture and the abandonment of marginal areas and the progressive changes occurring in the partridge range. Agricultural intensification and mechanization relegate the Red-legged Partridge to rural areas with increasingly lower quality, causing potential changes in demographic parameters (for example, higher reproductive failure and high rates of predation by opportunistic predators or those associated with degraded media). The agricultural intensification also tends to increase the average size of plots, to reduce the boundaries and the herbaceous cover and to use herbaceous varieties of short cycle (Casas and Viñuela 2010; Duarte 2012). Also, it involves increasing the use of agricultural technology (tractors, harvesters) versus other more traditional forms of agriculture management and the massive use of pesticides, whose main effects on the Red-legged Partridge are mortality increase and productivity decrease (López-Antia et al. 2015a, b, 2018, 2021).

The increased use of agricultural technology and conflicts of interest between agricultural production and biological cycles of species also cause direct problems for the Red-legged Partridge. These factors together reduce habitat quality and the carrying capacity for the Red-legged Partridge. In recent years, a direct relationship between agricultural management models, changes in land use and hunting yields of the species has been observed (Fernández-Alés et al. 1992; Vargas et al. 2006).

In other areas, the loss of purchasing power and profitability of small farms have produced a progressive rural exodus and agricultural/rural abandonment, both in demographic terms and in aspects of traditional farming practices, which has led to changes in land uses that have affected the overall biodiversity (Fernández-Alés et al. 1992; Romero-Calcerrada and Perry 2004). Traditional farming has given way in recent years to a widespread increase of forests and other forms of natural vegetation. In Andalusia, in southern Spain, from 1991–2007, the area covered by dense woodland increased by 48% and that covered by dense scrub experienced an increase of 69%. In the same period, agricultural land was reduced by 6% (Consejería de Medio Ambiente 2012). The optimum habitat for small game species has evolved into a habitat more favourable for big game species. As a result of the reforestation of abandoned farmlands and the increase of scrub areas caused by the abandonment of traditional ranching, forest areas have increased as opposed to the mosaics of pastures, grasses and scrubs. Consequently, species such as wild boar and red deer have proliferated at the expense of small game species (Delibes-Mateos et al. 2009, 2012; Acevedo et al. 2011). The increase of ungulate densities in forested areas negatively affects the Red-legged Partridge abundance as a consequence of a reduction in food resources and an increase in nest predation rates (Carpio et al. 2014, 2015).

Moreover, the shortage of partridge has led many hunters to try to find quick solutions. The spread of restocking of Red-legged Partridge to reinforce wild populations is a consequence of the decline perceived by hunters (Caro et al. 2014). This perception is accompanied by the need to find short-term solutions, by distrust in the management of the Administration and lack of understanding among landowners and farmers to implement other measures related to habitat improvement. However, restocking is a practice that carries a potential health risk to wild populations (Gortázar et al. 2006; Villanúa et al. 2008) due to disease transmission and introduction of parasites in the environment. Apparently, a guaranteed genetic quality does not exist for most released farm animals (Casas et al. 2013), so that the problem of hybridization with wild Red-legged Partridges remains, among other reasons because the survival and breeding of farm Red-legged Partridges with wild specimens has been demonstrated (Duarte and Vargas 2004; Barbanera et al. 2005). This process applied to large-scale carries a clear genetic risk (Blanco-Aguiar et al. 2008; Barbanera et al. 2009; Negri et al. 2012) for the wild populations of Red-legged Partridge. In addition, the release of Red-legged Partridges reared on farms can produce a ‘calling effect’ for predators and cause an increase of predation on wild populations. This ‘calling effect’ has been shown by Duarte et al. (2007) during restocking with the Common Pheasant (*Phasianus colchicus*) in a Mediterranean environment.

In addition to the above-mentioned factors, excessive hunting pressure on the Red-legged Partridge is also occurring as a consequence of several factors. For example, the severe decline suffered by the wild rabbit as a result of diseases (Delibes-Mateos et al. 2008) has led to increased hunting pressure on other species such as the Red-legged Partridge. Other factors that could cause overhunting are an inadequate adjustment between availability and hunting yields and an adjustment of harvest made in relation to the number of released birds (Arroyo et al. 2012; Díaz-Fernández et al. 2012; Casas et al. 2016) regardless of the fact that restocked

Red-legged Partridges have a high mortality rate during the first days after their release (Gaudioso et al. 2011). Finally, sometimes the excessive hunting pressure occurs due to the long hunting season of the Red-legged Partridge in relation to other species. This is the case in Spain where the hunting season of the Red-legged Partridge is longer than other species due to the hunting method named ‘reclamo’, which employs a male bird decoy (Vargas et al. 2012).

Despite the situation described in the preceding paragraphs, the Red-legged Partridge is currently listed as ‘Near Threatened’ worldwide (Birdlife International 2020) because this species has a very large range and even though the population trend appears to be decreasing, the decline is not believed to be sufficiently rapid to approach the thresholds for ‘Vulnerable’ under the size range and population trend criteria considered by IUCN. In contrast, in Europe this species was recently classified as a Species of European Conservation Concern (Aebischer and Potts 1994), but not in the last editions about conservation status of European birds where it has been downgraded to Least Concern because the same IUCN criteria are used (Birdlife International 2004, 2016). However, its wide distribution and seemingly still large global population may be masking a very precarious situation with a high genetic risk of extinction of pure Red-legged Partridge, as argued by Aebischer and Potts (1994). Recent information supports this view, for example, Blanco-Aguiar et al. (2008) have shown the existence of a high number of wild populations with allochthonous genetic lineages. The consequences of hybridization on the conservation of wild Red-legged Partridge, the clear negative population trends, both short- and long-term, and the still scarce knowledge of the current genetic situation are enough factors to justify a review of the conservation status of the Red-legged Partridge worldwide.

Environmentalists, game managers and government officials are currently more aware of the real situation of the Red-legged Partridge. Thus, considering both the uncertainty about the species’ future and its socio-economic importance has led to naming the species as ‘Priority’ in Castilla-La Mancha, southern Spain. Considering the current status of this species, Vargas et al. (2006) suggested that there is a need to create protected areas to ensure maintenance of high density groups and the genetic characteristics of wild populations of Red-legged Partridge in Andalusia (southern Spain). Management measures in these areas would involve maintenance of habitat heterogeneity, controlling hunting pressure and thorough quality control regarding restocking practices (Pépin and Blayac 1990; Borralho et al. 1997b; Lucio 2002).

Hunting Importance in Europe

Red-legged Partridge hunting is an important economic activity in many areas of Western Europe (ADAS 2005; Beja et al. 2009; Bicknell et al. 2010; Díaz-Fernández et al. 2012). In Spain, it is one of the most emblematic small game species (Vargas and Muñoz 1996; Garrido 2002), and its commercial use has important socioeconomic effects in several rural areas where other agrarian uses are only marginally important (López-Ontiveros and García-Verdugo 1991; Delibes 1992; Lucio and Purroy 1992). Both directly and indirectly, Red-legged Partridge hunting generates an important economic flow that involves hostelry activity, services and all the auxiliary industries that accompany its hunting (Arroyo et al. 2011; Garrido 2012). For example, according to PACEC (2006), in the UK, there are nearly half a million (480,000) hunters and the shooting industry is worth £2 billion each year and supports 70,000 full time jobs. While in Spain, the number of hunting licences is approximately 769,500 (MITERD 2020) and hunting activities generate annually around 6.5 billion euros and support 187,000 jobs (Andueza et al. 2018).

The Red-legged Partridge comprises 13.4% of all the small game animals harvested in Spain, a proportion only surpassed by European wild rabbits, thrushes and pigeons (in order of importance) (MITERD 2020). In 2018–2019 in Andalusia, southern Spain, one of the main hunting areas in the country, more than 476,948 Red-legged Partridges were captured, representing 9.8% of the game species individuals captured (Junta de Andalucía 2021). It is the fourth highest game species capture, only preceded by thrushes, European wild rabbits and pigeons (in order of importance).

The hunting importance of the Red-legged Partridge in Europe is also reflected in the number of authorized game farms. In Andalusia alone, the number of authorized farms engaged in the production of the Red-legged Partridge in 2019 was 74 (Junta de Andalucía 2017). In the UK, there are approximately 400 rearing farms (Bicknell et al. 2010).

The number of Red-legged Partridges released per year is directly linked to the number of game farms. According to the Ministry of Agriculture, Fisheries and Food (MAPA 2016), 1,829,592 Red-legged Partridges were released in Spain in 2016, although some authors affirm that since 2000 between 4 and 5 million Red-legged Partridges have been released annually (Gortázar et al. 2000; Arroyo and Beja 2002). This figure is lower than numbers of Red-legged Partridges releases in the UK, 10 million per year (Aebischer 2019), but higher than that in France, 2 million per year (Arroyo and Beja 2002; Caro et al. 2014), and Italy, 450,000 per year. Taking into account that the price of Red-legged Partridges reared in farms is between 4.5 and 5 euros per unit (Bicknell et al. 2010), it is easy to determine the financial significance of business linked to farm-reared Red-legged Partridge and its importance for some local economies.

However, the Red-legged Partridge is also attractive from a strictly social viewpoint. On the Iberian Peninsula, the social demand to hunt is distributed almost evenly throughout the region. For example, in the southern half of Spain (Castilla-La Mancha, Extremadura and Andalucía) the Red-legged Partridge is the most attractive small game species (Vargas and Muñoz 1996). This social aspect is also shown in the different hunting methods used to capture it. In Spain, for example, it is the species with the largest number of authorized capture methods (jumping, coursing, driven shooting and using a live male bird decoy, called ‘reclamo’) (Vargas et al. 2012).

Relevant Multidisciplinary and International Research in the Past 50 Years

Efforts made in recent decades to research the Red-legged Partridge have produced results of direct importance in the conservation and management of this species. Some of the most important results are discussed below.

Release and restocking programmes using farm-reared animals are among the most commonly used management tools employed with game species in Europe (Gortázar 1998; Gortázar et al. 2006; Mustin et al. 2011). Therefore, while wild Red-legged Partridge populations have recently suffered marked declines in most of the species' range (BirdLife International 2016), releasing of farm-reared Red-legged Partridges has increased and become more widespread since the 1990s (Blanco-Aguiar et al. 2008; Sánchez-García et al. 2009). The main stated objective of the releases is to benefit wild populations, while increasing or maintaining hunting quotas when population densities are low (Sokos et al. 2008). However, the release of farm-reared partridges may have an opposite effect on wild populations by increasing overall mortality induced by hunting both released and wild birds and by reducing the production of wild partridge populations (Casas et al. 2016; Guzmán et al. 2020). In addition, Cabodevilla et al. (2020) have shown that the release of farm-reared partridges could have negative effects on sympatric wild species such as the Little Bustard (*Tetrax tetrax*).

Different authors have shown that release of farm-reared Red-legged Partridges for the purpose of supplementation without monitoring genetic quality has a dramatic impact on wild Red-legged Partridges, and it has led to the existence of a high number of wild populations with allochthonous lineages (Blanco-Aguiar et al. 2008; Barbanera et al. 2005, 2011; Barilani et al. 2007). If we consider that release is a widely used technique in the management of the Red-legged Partridge, it is evident that this management tool in the absence of genetic quality standards of individuals released is one of the main conservation problems facing the wild Red-legged Partridge at present.

Sexual selection of the Red-legged Partridge has been an aspect widely studied in recent decades. Among the most noteworthy advances is the apparently important role of carotenoids as honest quality signals in the sexual selection of this species. Thus, Pérez-Rodríguez (2008) showed that the eye ring pigmentation and bill redness, which are carotenoid-based, reach maximum intensity in April–May, coinciding with the end of the reproduction season of the Red-legged Partridge (Vargas et al. 2012), and that these traits are positively associated to body condition and, consequently, to the foraging efficiency and nutritional status (Pérez-Rodríguez and Viñuela 2008).

Research on the Red-legged Partridge at the biogeographical scale has provided a different view about environmental and anthropogenic factors that determine its distribution. Throughout its range, the Red-legged Partridge appears to be linked mainly to cropland areas, while dense forested areas and dense scrublands are avoided. An example of this pattern is shown by Vargas et al. (2006) in the southernmost region of its distribution area (Fig. 1). The results show that the most favourable areas for the Red-legged Partridge, according to the hunting yields (number of individuals/100 ha), are mainly located in plain areas covered by croplands, while the least favourable areas are located in the mountain ranges. This situation seems to be a consequence of the transformations that have occurred in the landscape over the past few decades, both the intensification of agriculture and the abandonment of marginal areas and the progressive changes occurring in the country (Delibes-Mateos et al. 2009, 2012). In brief, we can say that at present the Red-legged Partridge is doomed to live in a habitat that is not optimal for it, agricultural areas, but the least bad among the areas available. A very interesting aspect of the biogeographical approach to the study of the Red-legged Partridge is that the assessment of how landscape changes affect the distribution of the species at the geographical level can be used to identify general population patterns and, additionally, to design further complementary works at smaller scales.

Scientific Topics Not Sufficiently Covered

It is surprising that despite efforts over the past 30 years to research the Red-legged Partridge, this species is catalogued as insufficiently known in Spain (Madroño et al. 2004). This fact could be considered somewhat nonsense taking into account the number of studies conducted on this species. It is true, however, that important gaps in knowledge remain related to reproductive details, incidence of predation in population dynamics, metapopulation dynamics and winter dispersal, responses to habitat management and other management measures effective to reverse the population decline of the species.

Further work is clearly required in order to evaluate the time needed to recover a wild population that is not subject to hunting activity based on the influence of game management, habitat structure and predators. For example, although projects involving re-introductions have become increasingly popular in the past 30 years, only a very small proportion of re-introductions used an experimental approach. In order to improve the success of releases, as well as to understand the general biological mechanisms involved in this field of conservation biology, more experiments are needed evaluating different releasing techniques (Seddon et al. 2007). Recently, Aebischer et al. (2015) have shown that combining habitat management with predator control generates large local increases in numbers of farmland birds over

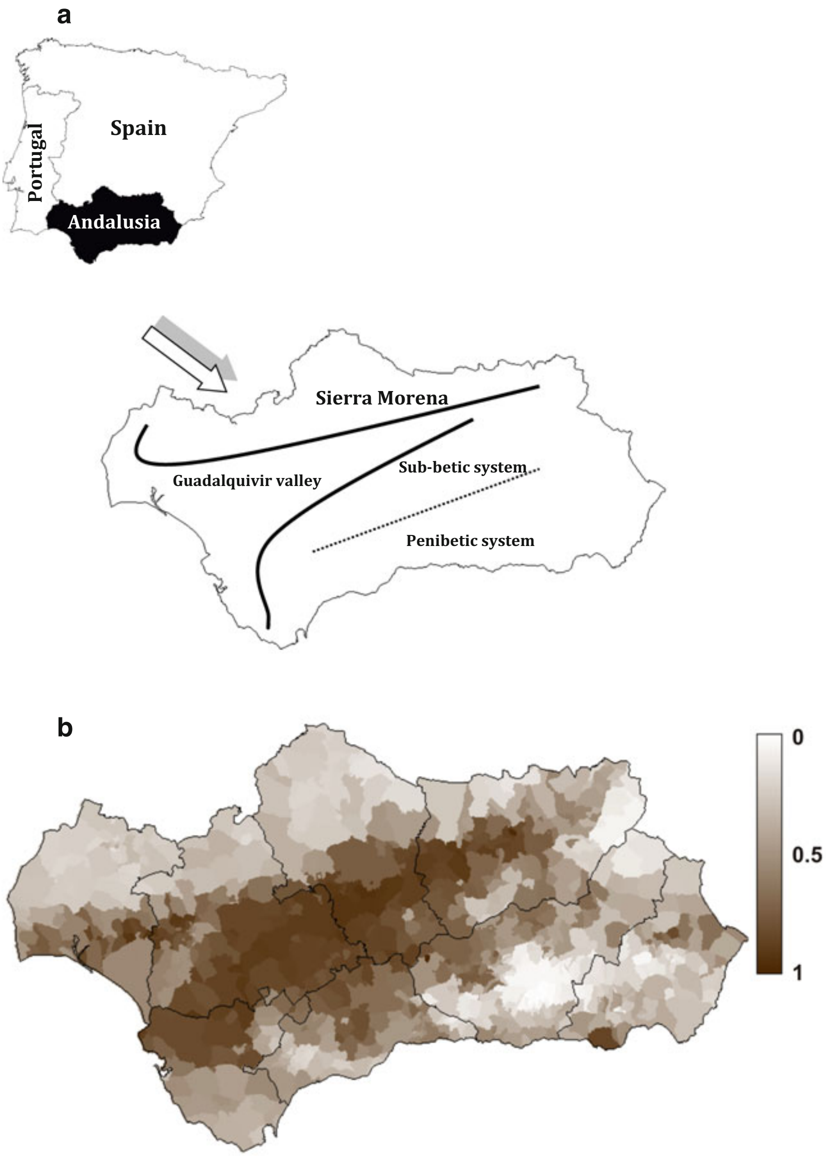

Fig. 1 (**a**) Schematic form of the main mountain ranges (Sierra Morena and the Betic System, subdivided into two ranges, Sub-Betic and Penibetic) and the most important plain (Guadilquivir valley) in Andalusia, southern Spain. (**b**) Hunting yield favourability model (number of red-legged partridges/100 ha). 0 represents minimum and 1 represents maximum favourability. Taken from Vargas et al. (2006)

relatively short-time periods. However, this local result should be confirmed in other areas under the same management such as in southern France (Ricci et al. 1990), though the implementation of this management tool at larger-scales may not be feasible.

Regarding releases of the Red-legged Partridge, further research is also needed at the national level. Release of captive-reared individuals is a management tool increasingly used in Europe (Gortázar et al. 2006; Park et al. 2008; Champagnon et al. 2012). However, in countries where the Red-legged Partridge is a native species, the proportion of animals released relative to wild individuals is unknown. There is not accurate quantitative and spatial information on releases, but according to Caro et al. (2014), in Spain the number of Red-legged Partridges released each year is higher than that of the Spanish wild breeding population and the geographical variation in release intensity is significantly related to areas where historically the Red-legged Partridge had been more abundant. To advance in this area, continued cooperation among governments, hunters and land-owners of hunting farms is necessary to improve monitoring of individuals released. A practical way to do this is marking released Red-legged Partridges (Caro et al. 2014).

Another aspect poorly studied is the overhunting of wild Red-legged Partridge populations caused by the release of farm-reared individuals. Casas et al. (2016) have shown a direct relation between restocking and increase of hunting mortality of wild individuals. Guzmán et al. (2020) have shown a negative relation between release intensity and young/adult ratios in release areas. However, these results should be confirmed in other regions where releases are used as a main management tool.

Also, there is a lack of knowledge about the particular ecology of the species in very specific habitats such as woody crops and ‘dehesa/montados’ (savannah-like habitats). Duarte (2012) and Borralho et al. (1996, 1999) have provided information on reproductive phenology, breeding success and habitat selection of the Red-legged Partridge in olive groves, a widespread habitat in the southern Iberian Peninsula. Locally, olive groves are a suitable habitat that provides cover and food for the species. Although there is scant information at the biogeographical scale, several authors have shown that olive groves are favourable areas for the Red-legged Partridge (Borralho et al. 2000; Vargas et al. 2006; Delibes-Mateos et al. 2012). Therefore, agricultural practices realized in the olive groves throughout the year have a negative effect on the Red-legged Partridge and this habitat can become an ecological trap for the species. For these reasons, future research aimed at improving the landscape for farmland birds should be encouraged to conserve Red-legged Partridges wild populations.

Blanco-Aguiar et al. (2008) have shown the existence of a high number of wild and game farm populations with allochthonous lineages. From the point of view of conservation biologists, hybridization should be of special concern because it may also result in the loss of unique genetic, morphological, behavioural or ecological characteristics that have evolved in local populations over time. In this regard, further work is needed to determine basic aspects such as success of hybrids in the wild, the consequences of hybridization on fitness and its potential implications for Red-legged Partridge conservation.

Another aspect scarcely investigated is the effect of climate change on the distribution of the Red-legged Partridge. To plan conservation and to design adequate management programmes at the biogeographical scale, it is necessary to predict their distributional response to climate change, especially under the current situation of rapid change. In a similar form to that of Muñoz et al. (2013), we modelled the distribution of the Red-legged Partridge in mainland Spain with respect to a combination of different general circulation models (GCM) and Special Report on Emissions Scenarios (SRES). We used four different circulation models: CGCM2 from the Canadian Climate Centre for Modeling and Analysis, ECHAM4 from the Max Planck Institut für Meteorologie, and HadAM3H and HadCM2SUL from the Hadley Centre (U.K.). The circulation models CGCM2 and ECHAM4 were run with the conditions forecasted by the SRES A2 and B2, HadAM3H was run with the scenario A2, and HadCM2SUL was run with the scenario IS92a (Nakicenovic et al. 2000; Leggett et al. 1992). Scenarios A2 and B2 represent an intermediate position of the range of projected temperature change scenarios for Spain, A2 being medium-high and B2 medium-low (Brunet et al. 2007). We use the Favourability Function (Real et al. 2006; Acevedo and Real 2012) to develop distribution models:

$$F = (((P)/(1 - P))/((n1/n0) + (P/(1 - P)))),$$

F being the favourability value in each 10 km × 10 km UTM square; $n1$ and $n0$ being the number of UTM squares with presences and absences, respectively; and P being the probability of Red-legged Partridge presence in each UTM square. P was calculated with a multiple logistic regression, using the presence and absence of Red-legged Partridge in each UTM square as the dependent variable.

Our results showed that depending on the circulation model and scenario considered, the distribution of the Red-legged Partridge will be maintained, increased or reduced in mainland Spain (Fig. 2). It would be advisable to continue research in this line of work.

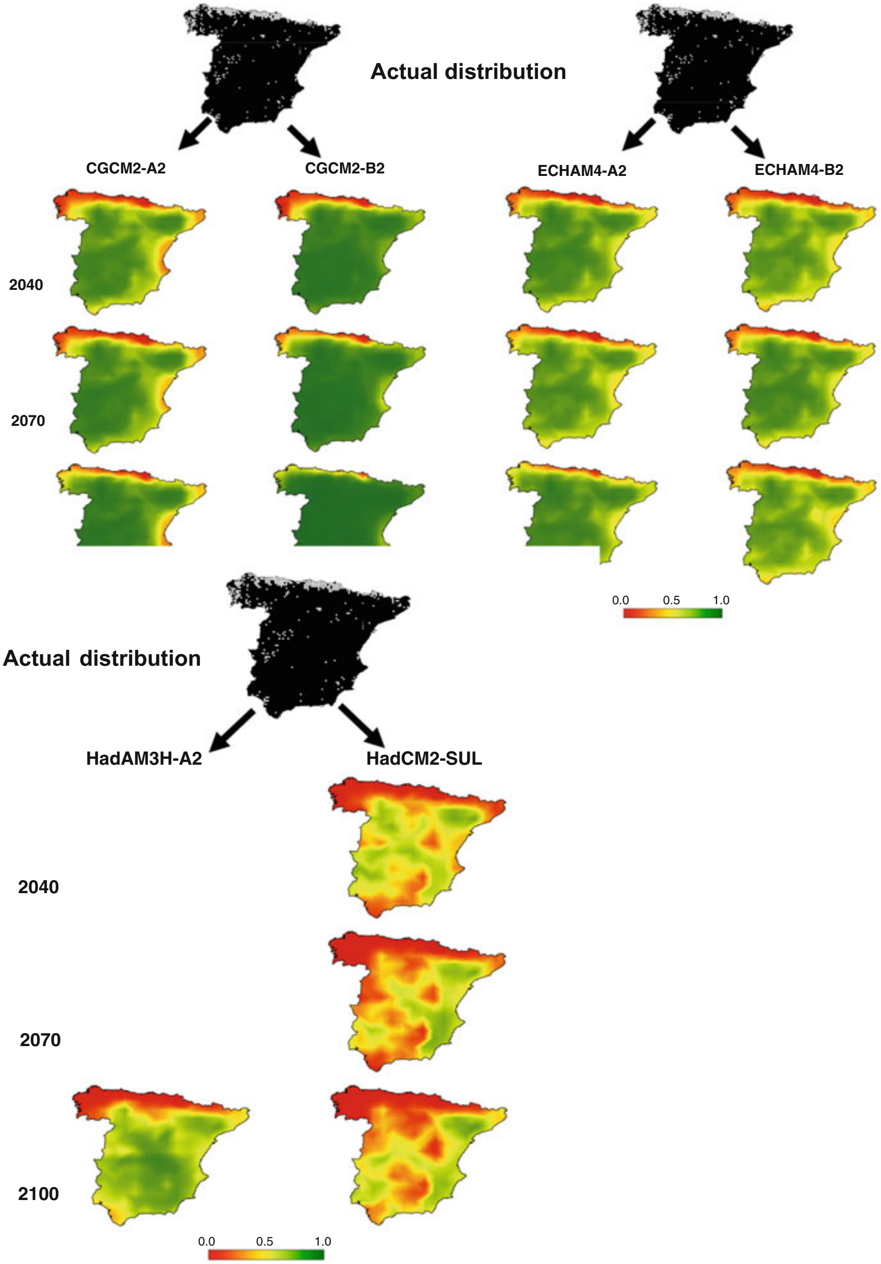

Fig. 2 Favourability values forecasted at each 10 km × 10 km UTM square of mainland Spain for red-legged partridge, according to each circulation model (CGCM2, ECHAM4, HadAM3H and HadCM2SUL) and Special Report on Emissions Scenarios (A2 and B2) for each considered period. 0 represents minimum and 1 represents maximum favourability. Actual distribution: black = presence; white = absence

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Advances in Research on Ecophysiology and Evolutionary Ecology: The Red-Legged Partridge as a Study Model

Lorenzo Pérez-Rodríguez

Introduction: From Game Species to Evolutionary Ecology Starlet

Most scientific research on the red-legged partridge produced during the twentieth century was focused on the basic breeding biology, spatial ecology or sanitary aspects of this species (see Chaps. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?" and "Health Monitoring and Disease Control in Red-Legged Partridges"). In many cases these studies were purely descriptive and closely related to game management. Nevertheless, with the advent of the new century, a relevant shift occurred, with a series of studies where the red-legged partridge was used to address relevant aspects of evolutionary biology and in particular of the sub-discipline of evolutionary ecology. This field of research explores how evolution shaped the genotype and phenotype of the species, as well as the way they interact with the environment and with other organisms. Nowadays, the red-legged partridge is increasingly recognized as a useful model system for addressing burning questions in evolutionary ecology, which at the same time is contributing to unravel some aspects of its behaviour, ecology and physiology that remained ignored.

There are several intrinsic features that make the red-legged partridge an interesting model for research in evolutionary ecology and ecophysiology. It is a socially monogamous and slightly sexually dimorphic species, and both sexes collaborate in clutch and brood attendance, although offspring care and breeding investment is higher in females (Cramp and Simmons 1980). Also, significant rates of extra-pair paternity and intraspecific brood parasitism have been described (Casas et al.

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_2

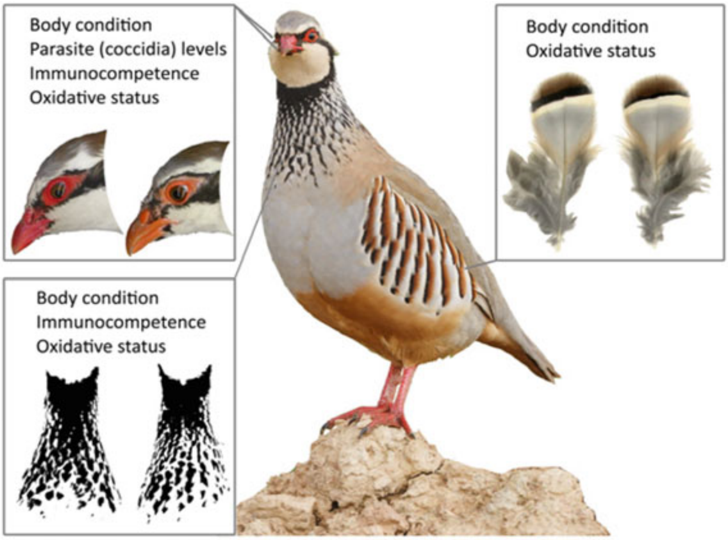

Fig. 1 Ornaments of the red-legged partridge and their relationship with quality-related traits. Boxes contain illustrative images of the variability of each character and the specific quality-related traits for which a connection has been empirically established. *Carotenoid-based colouration*: beak and eye ring redness are considered together because they tend to respond to the same sources of variation, although their responsiveness and dynamism differ (higher for the eye ring). The informative potential of leg colouration has not been addressed yet, although its biochemical basis is similar to that described for eye ring and beak. *Black bib*: the box contains two bibs with similar eumelanin-pigmented areas but whose patterns exhibit high (left) and low (right) fractal dimensions; the area covered by the trait is related to the oxidative status during moult, whereas the fractal dimension is related to the body condition and immunocompetence of the individual. *Barred pattern of the flanks*: the size of the black band (specifically, of the black area of the ventral portion of each feather) is related to the body condition of the individual, whereas the size of the brown and black bands is indicative of the oxidative status during feather growth. Central picture: José Ardáiz. Boxes' pictures: Lorenzo Pérez-Rodríguez

2006a, b), indicating that the sexual conflict within a pair remains even though the social pair bond is maintained. Such breeding system is somehow representative of the vast majority of bird species (Ligon 1999). The red-legged partridge is also a good model species for studying the function and evolution of ornamental pigmentation, as it displays two of the most widespread colourations among animals: carotenoid and melanin-based traits (Fig. 1). Interestingly, these colourations, besides their likely role as social signals of quality, are not displayed in a conspicuous or flashy fashion. Instead, the redness of the beak, eye rings and tarsi and the shape and size of the flank bands and black bib can only be fully perceived at a short distance. From medium and long distances, birds remain mostly cryptic thanks to the mimetic olive dorsal plumage, which is particularly useful against aerial predators that rely on visual cues to detect their prey. Therefore, the colour ornaments of the red-legged partridge seem to have evolved as a product of the compromise between signalling and predation avoidance. When studying the evolution of life-history and phenotypic traits, extreme cases (e.g. strictly polygamous species, lek mating systems, highly conspicuous or bulky ornaments) are often preferred as models because the trade-offs show up more easily. However, most avian species are far from these extreme strategies, having evolved intermediate strategies as a result of environmental and evolutionary constraints. Study systems like the red-legged partridge are therefore required to get a more representative, generalizable, balanced and unbiased view of adaptive and evolutionary processes.

The red-legged partridge shows some clear phenotypic (e.g. carotenoid-based teguments and melanin-based patterns in the bib and flanks, slight sexual dimorphism) and behavioural (e.g. socially monogamous pair bonding, biparental care) parallelisms with the unquestionable major avian model system for evolutionary biology studies in captivity, the zebra finch (*Taeniopygia guttata*) (Griffith and Buchanan 2010). The vast knowledge on the zebra finch biology and genome as well as simple practical issues like its handy small size and perfect adaption to captive conditions results in an unparalleled potential for captivity experiments with no need of large infrastructures. However, the red-legged partridge possesses some characteristics that, from a logistic perspective, are useful for designing experiments. For instance, partridges are relatively large birds. Although this might impose some space requirements for housing, it also presents some advantages, for example, the possibility to collect higher volumes of blood for different analyses and the use of radio-tagging techniques for field studies. The large number and size of eggs laid by females enable manipulative studies of maternal effects, and the precocial nature of the species allows isolating pre- and postnatal parental effects following simple farming procedures. In fact, partridge farming has led to the development of useful housing and rearing protocols and to the commercial availability of specific equipment. Finally, unlike other bird species commonly used as captive study systems in evolutionary biology —Japanese quail (*Coturnix japonica*), common pheasant (*Phasianus colchicus*), zebra finch— the red-legged partridge is an autochthonous species in most of the geographic areas where it is commercially bred. This is a great opportunity for scientists to combine studies in captivity and wild conditions while settled in the same geographic location.

Most research on evolutionary ecology using this species as a model has focused on the function of carotenoid and melanin-based ornamental colourations, with a particular emphasis in the physiological mechanisms regulating their expression. Below I will summarize some of the main results from these studies. Also, I will identify key questions and unexplored areas that warrant special attention of the research community in the near future.

The Redness of the Red-Legged Partridge as a Study System of Carotenoid-Based Ornamentation

The red colourations of the beak, eye ring and tarsi of the red-legged partridge are probably the most distinct and characteristic traits of this species, as highlighted by its Latin name as well as by its common name in most languages (although, ironically, its "red legs" remain poorly studied as compared to its other two red traits). This kind of showy traits usually plays a role in signalling individual quality during mating or in social interactions in many taxa but particularly in birds (Hill and McGraw 2006; McGraw 2006a). A direct and experimental assessment of the role of these traits in mate choice and intra-sexual interactions in the red-legged partridge is still pending, but there are some indirect evidences supporting such a signalling role. For instance, experiments in captivity have shown that females paired with males whose eye rings and beaks were artificially intensified by means of red paint tended to start laying eggs earlier and produced significantly a higher number of eggs than females mated to un-manipulated males (Alonso-Álvarez et al. 2012). Also, females mated with these "made-up" males varied the allocation of key components of the egg yolk (carotenoids, androgens) as compared to control females. These results indicate that females actually use the redness of their mates as cue for key reproductive decisions, as expected from traits used as signals of quality in sexual selection processes. Another set of indirect evidences of the signalling value of these traits comes from field studies reporting an assortative mating based on beak redness in this species, a pattern that would arise from a reciprocal mate choice based on this character (Casas et al. 2010).

The characteristic red colouration of the beak, eye rings and legs of the red-legged partridge results from the accumulation of carotenoids (Pérez-Rodríguez and Viñuela 2008; García-de Blas et al. 2011, 2013). Carotenoid pigments are a series of large lipophilic compounds produced by photosynthetic organisms and certain bacteria and fungi (Goodwin 1984). Partridges, like the rest of animals, cannot synthesize carotenoids de novo but have to obtain them from their diet (Goodwin 1984). Importantly, this colour production mechanism is not exclusive at all of the red-legged partridge: carotenoid-based colouration is widespread in the animal kingdom, resulting in yellow, orange or red striking visual displays in many fishes, amphibians, reptiles and birds. During the last decades, evolutionary and behavioural ecologists have become increasingly interested in these traits because they often play key roles in communication, being used as signals of bearer quality in social and mate choice contexts (Goodwin 1984; Hill 2002; McGraw 2006a; Pérez-Rodríguez et al. 2013a, b). Theory predicts that signal expression must be linked to the intrinsic characteristics of the bearer, implying that signal development (i.e. extension or intensity of the colour) could be used as a visual cue to assess individual quality. The key functional question is as follows: what determines the variability in colour expression among individuals? In other words, what factors limit the deposition of carotenoids in beaks, skin, scales or feathers to maximize their colour? The answer to these questions demands a deep understanding of carotenoid physiology and metabolism (McGraw 2006a; Pérez-Rodríguez 2009; Pérez-Rodríguez et al. 2016). Avian species, like the above-mentioned zebra finch, the European greenfinch (*Carduelis chloris*) or the house finch (*Haemorhous mexicanus*), have been widely used to address these questions (McGraw 2006a). Although the red-legged partridge is a newcomer to that list of avian study models, it has provided really useful insights into the factors regulating carotenoid metabolism and carotenoid-based colourations.

Carotenoids in Teguments and Blood: Sources of Variation

The red colour of the beak, legs and eye rings of the red-legged partridge results, respectively, from the accumulation of red carotenoids in the ramphoteca and epidermis (Pérez-Rodríguez and Viñuela 2008; García-de Blas et al. 2011, 2013, 2014). Several red carotenoids (ketocarotenoids) can be found in these integuments. The most abundant is astaxanthin followed by papilioerythrinone, lutein and canthaxanthin (García-de Blas et al. 2013, 2014). Both astaxanthin and papilioerythrinone are mostly present (>80%) in esterified forms (mono- and diesters) (García-de Blas et al. 2013). By contrast, there are only two carotenoids in the plasma and internal tissues (liver, fat) of the red-legged partridge: lutein and zeaxanthin (García-de Blas et al. 2015, 2016). These two carotenoids are the most abundant in the diet of partridges and other granivorous and herbivorous birds (McGraw 2006a).

These descriptive data provided very relevant basic information about the carotenoid metabolism in the red-legged partridge. For instance, the fact that none of the main ornamental red carotenoids appear in the bloodstream or in internal organs implies that partridges metabolize dietary (yellow) precursor carotenoids into ornamental (red) carotenoids. Specifically, the most likely metabolic pathway for astaxanthin and papilioerythrinone production is the transformation of zeaxanthin and lutein, respectively (García-de Blas et al. 2014) (Fig. 2). More importantly, the lack of these two red ornamental carotenoids in blood or the liver indicates that the biotransformation of ingested dietary precursors into ornamental carotenoids takes place directly at the red integuments (García-de Blas et al. 2015). Interestingly, supplementation experiments have shown that increasing astaxanthin or canthaxanthin levels in the diet of partridges did not enhance, but reduced ornamental trait redness (García-de Blas et al. 2016; Alonso-Álvarez et al. 2018). Indeed, whereas canthaxanthin was absorbed and deposited in the red teguments, internal organs and egg yolks of partridges, dietary astaxanthin was not. The negative effect of dietary intake of these two ketocarotenoids on trait redness is probably due to an interference with the absorption of lutein and zeaxanthin and probably also vitamin E. This is interesting from an ecological perspective, as lutein and zeaxanthin (but not astaxanthin and canthaxanthin) form a significant part of the natural diet of this species in the wild. Thus, the metabolic pathway towards an intense red colouration in this species does not admit shortcuts: only increasing the intake of the dietary

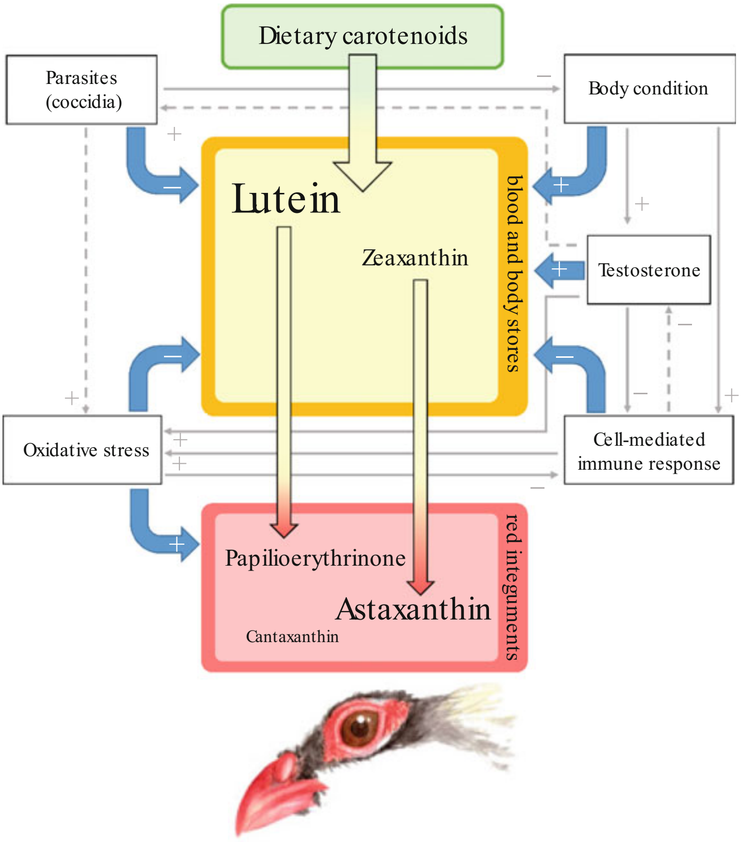

Fig. 2 Physiological pathway of carotenoid-based colouration in the red-legged partridge and factors that affect the different phases. The size of the name of each carotenoid type represents its relative abundance in each compartment. Solid grey arrows indicate interactions between factors that have been proved in this species, either by experimental or correlational evidence; dashed grey lines represent interactions found in similar species but still untested in the red-legged partridge. See the main text for details. Illustration credit: Lorenzo Pérez-Rodríguez

precursors of the main ketocarotenoids pigmenting their legs, beaks and eye rings can allow partridges to maximize their colouration. This is consistent with the "carotenoid limitation" —or "foraging ability"— hypothesis for the evolution of carotenoid-based traits as signals of individual quality (Endler 1983; Hill 1990; McGraw 2006a). According to this hypothesis, carotenoids are a limited resource for most animals, and better foragers would be able to obtain a higher amount of carotenoid precursors to maximize the colour intensity of their ornaments. In this way, ornament colouration would directly reflect foraging efficiency and nutritional status, serving as an honest indicator of these relevant fitness-related traits. Consistently with this idea, at least in captive conditions, the overall nutritional condition of red-legged partridges is positively related to the red pigmentation of their beaks and eye rings and negatively to the physiological stress experienced by the individual (Pérez-Rodríguez and Viñuela 2008; Mougeot et al. 2009). Confirmatory evidence that the same holds true under natural scenarios —where the carotenoid content of diet is probably higher— is still pending.

The detailed knowledge on biochemical pathways leading to the red traits also allows for a further refinement of the carotenoid limitation hypothesis (García-de Blas et al. 2014; Pérez-Rodríguez et al. 2016). Thus, astaxanthin, the most abundant carotenoid in the red teguments of the red-legged partridge as well as the main responsible of the redness of the trait (García-de Blas et al. 2013, 2014), results from the transformation of zeaxanthin, the least abundant carotenoid in the partridge diet (García-de Blas et al. 2015, 2016). This might impose an extra handicap to the ornament pigmentation, reinforcing the honesty of red ornaments. Also, the metabolic pathways implicated in the synthesis of red carotenoids would entail certain physiological costs (see below), contributing to make the reddest colouration unaffordable for low-quality birds. Importantly, astaxanthin is the main carotenoid in red colourations in many animal species (not just in birds), which would make the conclusions obtained for the red-legged partridge applicable to many other groups (e.g. Wedekind et al. 1998; Pérez-Rodríguez et al. 2016).

Wild and farm-reared partridges often differ in the intensity of their red colouration, as largely known by hunters and gamekeepers and as supported by scientific evidence (García-de Blas et al. 2013). These differences do not result from the presence of different carotenoids in their internal organs and ornaments, but mostly from differences in the relative and absolute concentrations of the two ketocarotenoids mentioned above (García-de Blas et al. 2013, 2015). Unfortunately, a detailed description of the carotenoid composition of the red-legged partridge's diet in the wild is still pending. Therefore, we do not know if the redder colouration of wild birds as compared to captive ones is due to the higher overall carotenoid content of their diet, to a relatively higher proportion of zeaxanthin over lutein, to a higher absorption capacity and carotenoid metabolism efficiency of wild birds, or to a summed effect of all these factors. In any event, absolute and relative ketocarotenoid concentration in ornamental red traits may not be the only factor contributing to colour differences between wild and captive partridges. For instance, it has been observed that ornamental carotenoids are present in higher levels of esterification in wild than in farm-reared birds, which could also contribute to enhance the colour stability and intensity in the former (García-de Blas et al. 2013).

Although dietary carotenoid intake is a major determinant of carotenoid-based colouration, variability in colour expression remains when carotenoid intake is constant. For instance, higher levels of carotenoids are found in the blood of males as compared to females fed the same diet (Negro et al. 2001; Pérez-Rodríguez 2008; Pérez-Rodríguez and Viñuela 2008), which results in subtle but detectable differences in colouration between sexes (Villafuerte and Negro 1998; Pérez-Rodríguez 2008; Pérez-Rodríguez and Viñuela 2008). Also, circulating carotenoids and carotenoid-based colouration vary seasonally, peaking during the mating season and decreasing afterwards (Pérez-Rodríguez 2008; Alonso-Álvarez et al. 2008), thus reflecting the dynamic nature of these traits (Pérez-Rodríguez 2008). Such decrease in plasma carotenoid levels is particularly marked in females, who must allocate a great amount of these pigments to the egg yolk production (Bortolotti et al. 2003; Pérez-Rodríguez 2008). However, similar—but less marked—temporal dynamics are observed in males, reflecting seasonal changes in the allocation and/or requirements of these pigments. Also, some studies have reported age-related variations, with lower circulating carotenoids and duller carotenoid-based colouration in older birds, at least in captivity (Alonso-Álvarez et al. 2009, 2010; García-de Blas et al. 2013).

The high degree of inter-individual variability in carotenoid-based colouration not attributable to the diet is not restricted to the red-legged partridge, but has been widely reported in many species of birds and other animals. This was identified by researchers as a clear evidence that additional factors (other than carotenoid access) mediate the expression of carotenoid-based signals, which would ultimately imply that these traits would signal *something else* than foraging ability and nutritional status (Lozano 1994; von Schantz et al. 1999). For that reason and considering that carotenoids have many biochemical roles apart from serving as integumentary pigments, researchers have formulated a series of new hypotheses trying to explain the function and evolution of these traits as signals of quality (Lozano 1994; von Schantz et al. 1999; McGraw 2006a; Pérez-Rodríguez 2009; Hill and Johnson 2012) (Fig. 1). In this context, the red-legged partridge has served as a very useful model for the study of honest colour signals.

Physiological Regulation of Carotenoid-Based Signals

Once carotenoids have been acquired through diet, carotenoid-based signal expression can be constrained in at least three main ways. First, carotenoid absorption, mobilization or transformation would require the activation of certain mechanisms (e.g. endocrine, metabolic) that would, in turn, entail certain costs for the individual, decreasing its fitness. Second, the use of carotenoids for integument pigmentation would consume a relevant portion of the physiological stock of these molecules, potentially impairing the functionality of other processes that also require the participation of carotenoids. This situation would represent a trade-off in the use of carotenoids for colour signalling versus self-maintenance, and only high-quality individuals would satisfy adequately both branches of the dilemma. The third pathway is related to external factors or internal processes that would cause, as a side effect, a reduction in carotenoid bioavailability or carotenoid metabolism efficiency, ultimately resulting in a reduction of carotenoid deposition in the ornament (Pérez-Rodríguez 2009; Hill 2011). These hypotheses are not mutually exclusive; in fact, they share common mechanisms and processes (e.g. action of the endocrine system, immune function, redox balance), with dynamic interactions that are difficult to disentangle (Pérez-Rodríguez 2009). However, it is necessary to assess the relative importance of each physiological mechanism separately because the theory predicts that the information provided by a given signal must be unavoidably related to its production costs and constraints. Studying the physiological mechanisms implicated in carotenoid bioavailability and use is therefore essential to fully understand the evolution of carotenoid-based signals. The advent of the red-legged partridge as a valuable study model for carotenoid-based traits coincided with the emergence of these physiological hypotheses. For this reason, much of the research done on this species addressed these topics, resulting in highly relevant contributions to this field of research (see review in Pérez-Rodríguez et al. 2013a).

A pivotal concept in all these physiological mechanisms linked to carotenoid colouration is oxidative stress. Oxidative stress results from the imbalance between production of reactive oxygen species and the antioxidant defences of the organism in favour of the former (Halliwell and Gutteridge 2007). The main source of reactive oxygen species is the aerobic metabolism, although other sources like immune response or pollutants can also contribute significantly. Importantly, oxidative stress results in relevant damages to biomolecules such as DNA, lipids and proteins, impairing their functionality. Oxidative stress has become a popular concept for the general public in the last years due to its involvement in ageing and several degenerative diseases (Ahmad 1995; Barnham et al. 2004; Halliwell and Gutteridge 2007). But beyond its biomedical interest, oxidative stress has drawn the attention of evolutionary biologists due to its role in many biological processes, which makes it a good candidate for mediating different life-history trade-offs (von Schantz et al. 1999; Costantini 2008, 2014; Monaghan et al. 2009). This is particularly remarkable in the case of carotenoid-based signals, as carotenoids can be involved in redox status in several ways, either acting as antioxidants or just because they are particularly susceptible to oxidation by reactive oxygen species (Lozano 1994; von Schantz et al. 1999; Hartley and Kennedy 2004; Pérez-Rodríguez 2009; Simons et al. 2012).

Carotenoid-Based Traits as Indicators of Oxidative Stress and Immune Function

Studies addressing the links between carotenoid-based colouration and health-related variables (i.e. oxidative stress, immunocompetence or parasite levels) in the red-legged partridge have focused on the redness of the beak and eye rings. Given that sexual signals are expected to be particularly sensitive to diseases and infections (Hamilton and Zuk 1982; Balenger and Zuk 2014), special attention has been paid to the relationship between the redness of these traits and certain parasites, like coccidia. Coccidia are parasitic protozoa that infect the caeca and small intestine of their hosts. Coccidiosis is a common infection in poultry but also affects wild avian populations. High levels of coccidia cause a reduction of circulating carotenoids in the red-legged partridge, thus decreasing the carotenoid pigmentation of the eye rings and beak (Mougeot et al. 2009). Similar negative impacts of coccidia on carotenoid-based colouration have also been reported in other bird species (e.g. Brawner et al. 2000; McGraw and Hill 2000; Horak et al. 2004; Martinez-Padilla et al. 2007). The most likely explanation for this negative effect is that coccidia infection damages the intestinal epithelium, thereby reducing carotenoid absorption (Allen 1987), with a subsequent fading in colouration. However, the negative impact of parasites on carotenoid-based colouration may also result from another indirect pathway. Infections elicit an immune response from the host, which may itself consume carotenoids. In fact, experiments in the red-legged partridge have revealed that cell-mediated immune responses reduce circulating carotenoids (Pérez-Rodríguez et al. 2008), which would potentially decrease redness of the teguments if the immune challenge is maintained in time. This is attributed to the direct implication of available carotenoids on immune responses, as these molecules exhibit immunostimulant properties (Simons et al. 2012). Again, observational evidence in the red-legged partridge supports this hypothesis, as cellular immunity is positively related to circulating carotenoid levels and redness in this species (Blas et al. 2006; Pérez-Rodríguez et al. 2008; Mougeot et al. 2009). Altogether, these results indicate that carotenoid-based ornamentation in the red-legged partridge—at least eye rings and beak colouration—would be informative of the sanitary state of the individual and the ability to face future immune challenges (Pérez-Rodríguez et al. 2008, 2010; Mougeot et al. 2009) (Fig. 1). Indeed, a long-term study in captivity showed that the intensity of the red colouration predicted both longevity and lifetime fecundity in male partridges (Cantarero et al. 2019), supporting the idea that red ornaments reflect the overall health and viability of individuals.

Much of recent research on carotenoid physiology produced in the last years has focused on the potential antioxidant role of carotenoids (Pérez-Rodríguez 2009). In fact, the mentioned link between carotenoids and immune response in the partridge —in consistence with results from other species— could also be attributed to a mediating role of oxidative stress. Immune responses entail a release of reactive oxygen species, and carotenoids would be consumed as antioxidants during the challenge (Halliwell and Gutteridge 2007; Costantini and Moller 2009). Evidence from the red-legged partridge offers some support for such an antioxidant role. Although circulating carotenoids are mostly unrelated to oxidative damage biomarkers in observational studies (Alonso-Álvarez et al. 2008, 2010; Pérez-Rodríguez et al. 2008), experimental setups revealed a different picture. When partridges are fed with high vs. low doses of carotenoids, high carotenoid intake seems to confer some protection against an oxidative challenge elicited by a regular intake of diquat—a free radical generator—at least in females (García-de Blas et al. 2016). It seems therefore that carotenoids can offer some antioxidant protection in this species. But, does the reverse hold? Does oxidative stress impair carotenoid availability, subsequently fading colouration? The empirical evidence in this sense draws a more complex scenario (Fig. 2). Experiments exposing red-legged partridges to oxidative challenges via diquat administration have reported contrasted results. In juveniles, oxidative challenge leads to a decrease in circulating carotenoids and carotenoid-based colouration (Alonso-Álvarez and Galván 2011). However, a similar oxidative challenge applied to adults produced no effects on carotenoid levels in blood or internal tissues, but increased ketocarotenoid concentration in ornamental traits, enhancing their redness (García-de Blas et al. 2016). These contrasted results would arise from a higher susceptibility to oxidative stress of juveniles, whose antioxidant system would still be relatively immature. But more interestingly, the unexpected positive effect of oxidative challenge on redness found in the second study led to a novel hypothesis (García-de Blas et al. 2014, 2015, 2016). Given that the transformation of lutein and zeaxanthin into papilioerythrinone and astaxanthin requires some oxidation steps, researchers proposed that a certain level of oxidative stress favours the in situ biotransformation of dietary into ornamental carotenoids (García-de Blas et al. 2016). This may also require the activity of the oxygenase CYP2J19, an enzyme that is part of the P450 cytochrome, which is involved in many detoxification reactions (Lopes et al. 2016; Mundy et al. 2016). This would support the hypothesis that carotenoid-based colouration could be a sign of the capacity of a given individual to manage oxidative stress, as both carotenoid metabolism and detoxification ability would share common pathways (Hill and Johnson 2012; Johnson and Hill 2013). Interestingly, it has been shown that the eye ring redness predicts the resistance to future immune challenges in the red-legged partridge, as redder individuals suffer less oxidative damage when mounting an immune response (Pérez-Rodríguez et al. 2010). The results obtained in red-legged partridges could be extrapolated to other species also displaying red carotenoid-based ornaments with the similar biochemical profile (e.g. Pérez-Rodríguez et al. 2016).

Testosterone-Mediated Control of Carotenoid-Based Traits

The steroid hormone testosterone plays a key role in regulating the expression of sexual characters, enhancing the development of typical male traits and behaviours that are often displayed as signals of quality (Adkins-Regan 2005). However, such signal-enhancing effect may entail costs, as high levels of testosterone would lead to immunosuppression (Folstad and Karter 1992). These contrasted effects of the hormone are the two pillars underpinning the immunocompetence handicap hypothesis, which suggests that only high-quality individuals are able to afford the immunosuppressive effects of testosterone while showing the most elaborated sexual displays (Folstad and Karter 1992). There is a large body of literature testing this hypothesis, which is still a subject of debate (Roberts et al. 2004). Furthermore, some modifications of the original hypothesis have been put forward, like the so-called oxidation handicap hypothesis, which proposes that oxidative stress, rather than —or in addition to— immunosuppression, would be a plausible cost of testosterone level ultimately ensuring the reliability of sexual signals (Alonso-Álvarez et al. 2007).

An experiment in captivity has provided compelling evidence of the viability costs of testosterone for male partridges (Alonso-Alvarez et al. 2020). In that study, 1-year-old males were treated with testosterone-filled subcutaneous implants, whereas others (controls) were treated with empty implants. The experiment was repeated every following breeding season, for 6 years. Males treated with testosterone lived shorter than controls, since they were more prone to die from a natural bacterial infection. Whether this effect is due to a direct immunosuppressive effect of the hormone or to an indirect effect of oxidative stress is unknown, however.

Although apparently unrelated, testosterone and carotenoids share many common features: both are usually higher in males as compared to females and in adults as compared to juveniles, and their levels are usually higher during the mating season. Also, as mentioned, both compounds are linked to social signalling and to immunocompetence. Despite such strong similarities, it was not until 2006 when a general connection between both compounds was established and experimentally demonstrated, precisely, using the red-legged partridge as study model (Blas et al. 2006). Working with captive partridges, researchers found that an experimental increase in testosterone levels was mirrored by an elevation of circulating carotenoids (Fig. 2). Interestingly, such an increase did not result from a mobilization of carotenoids from body stores but, apparently, from an increase in absorption capacity. Other studies have proposed that such increase in circulating carotenoids would also be favoured by a testosterone-mediated enhancement of transport molecules in the bloodstream, like cholesterol (McGraw et al. 2005). Irrespective of the proximate mechanism, carotenoid surplus may enhance the ability of individuals to develop an effective immune response under high testosterone levels. Such a link between carotenoids and testosterone underpins a new perspective for the honesty of carotenoid-based signalling, as high-quality individuals would need to allocate fewer proportions of these carotenoids to compensate for the immunosuppressive actions of testosterone, providing grounds to advertise their quality by devoting the carotenoid surplus to ornaments (Blas et al. 2006). Since the formulation of this hypothesis in the red-legged partridge, the regulation of carotenoid physiology by testosterone has received further support in other species (e.g. McGraw and Ardia 2007; Mougeot et al. 2007; Casagrande et al. 2011; Peters et al. 2012).

But we can still give another turn to the screw to the story. Testosterone upregulates metabolic rates, which may increase the production of reactive oxygen species and, ultimately, lead to oxidative stress (von Schantz et al. 1999; Alonso-Álvarez et al. 2007; Hill 2014). This, added to mentioned connections between testosterone, carotenoids and immunity, seems to support the central role of oxidative stress in mediating honesty of carotenoid-based colouration. Research conducted with the red-legged partridge has paid particular attention to the interplay among these factors. Experimental evidence in this species supports the existence of oxidative cost associated with high testosterone levels in males during mating (Alonso-Álvarez et al. 2008). Carotenoid bioavailability and colour expression are influenced by such costs, but, interestingly, the impact of these costs largely depends on the quality of the individual (as expected, in fact, from a reliable signalling system; Zahavi 1975). Thus, 2-year-old partridges, which are likely at the apogee of their vigour, responded to an experimental increase in testosterone levels by elevating their circulating carotenoids and enhancing the redness of their eye rings (Alonso-Álvarez et al. 2009). By contrast, old males—presumably at the decline of their somatic integrity—were negatively affected by increased testosterone levels, showing decreased circulating carotenoids and ornament redness when exposed to high levels of the hormone. Furthermore, whereas middle-aged males showed no adverse effects of the treatment, old males treated with exogenous testosterone elicited weaker immune responses (Alonso-Álvarez et al. 2009). Circulating carotenoids and the higher levels of oxidative stress experienced at old ages apparently mediated these age-dependent effects of testosterone on red ornamentation. Senescence is characterized by a deterioration of somatic condition. Thanks to these age-dependent effects of testosterone on oxidative stress and immunocompetence, a testosterone-mediated mechanism of colour expression would maintain the honesty of the signal, which would reliably mirror the current state of the individual.

In summary, current evidence suggests that the honesty of carotenoid-based traits in the red-legged partridge depends on several mechanisms (resource allocation trade-offs, hormonal mediators that impose physiological handicaps, shared pathways, side effects of the functionality of vital pathways, i.e. Hill 2011) whose relative importance may vary across life stages and environmental contexts.

Melanin-Based Traits of the Red-Legged Partridge Plumage

Although carotenoids have attracted a great interest of behavioural ecologists for decades, they are not the main pigment in animals. This pre-eminent position is occupied by melanins, which are responsible for many of the black, brown, grey and rufous patterns observed in animals (as well as plants and fungi). This wide array of colours is the result of variations in the relative and absolute concentrations of the two main types of melanins: eumelanin (black) and pheomelanin (reddish-brown) (McGraw 2006b). However, unlike carotenoid-based colourations —which are supposed to evolve mostly as signalling traits—, melanin-based colourations often entail multiple functions unrelated to communication, including thermoregulation, camouflage or enhancement of the mechanic endurance of teguments. Nonetheless, melanin-based traits also play a significant role as signals (McGraw 2006b), but the mechanisms regulating their reliability are still poorly known (Jawor and Breitwisch 2003; McGraw 2006b) as compared to carotenoids. One key difference between carotenoids and melanins is that the later are synthesized by animals. This has led to the largely sustained assumption that melanins are relatively inexpensive to produce (Jawor and Breitwisch 2003; McGraw 2006b), apparently discarding the condition-dependent expression of melanin-based traits. However, several non-mutually exclusive hypothetical mechanisms would explain a quality-dependent expression of melanin-based traits: the social control of traits used as badges of status (Senar 2006), the pleiotropic effects of the physiological pathways involved in melanin synthesis (Ducrest et al. 2008), the potential oxidative costs of eumelanin synthesis (Galván and Alonso-Álvarez 2008; Galván and Solano 2009) or the condition-dependent expression of melanin-based patterns (Bortolotti et al. 2006; Griffith et al. 2006; Pérez-Rodríguez et al. 2013b; Pérez-Rodríguez et al. 2017).

As said at the beginning of this chapter, the plumage of the red-legged partridge is composed of a combination of drab tones and conspicuous badges that likely reflect an evolutionary trade-off between camouflage and signalling. Chemical analyses of the melanin composition of the different plumage patches are still pending (Toral et al. 2008), but their perceived colour can be used as a raw approximation to its composition (Galván and Wakamatsu 2016). Brownish olive hues of the back plumage likely result from a balanced content of eu- and pheomelanin in the feathers. By contrast with the mimetic back, the red-legged partridge shows an orange belly (based on pheomelanin), a black bib (based on eumelanin) and a conspicuous lateral barred pattern composed of an alternation of whitish, black and brown bars—unpigmented, eumelanin- and pheomelanin-based, respectively—within each feather. The study of the lateral barred plumage and, specially, the black bib has revealed significant links with individual quality, which suggests a potential role as signals of quality (e.g. Bortolotti et al. 2006; Pérez-Rodríguez et al. 2013b) (Fig. 1). Interestingly, both plumage traits are conspicuously displayed by individuals during mating and agonistic interactions (Cramp and Simmons 1980), which is consistent with their putative role in social signalling.

Melanin-Based Plumage Patches: Signals of Oxidative Stress and Condition?

There is evidence that some melanin-based plumage ornaments of the red-legged partridges are connected to nutritional status. For instance, the size of the black bar of the flank feathers is related to the body condition of the individual (Bortolotti et al. 2006), suggesting a potential role of this trait as a signal of nutritional status (Fig. 1). However, the mechanistic link between condition and melanin production remains elusive (Griffith et al. 2006; McGraw 2006b). A constraint based on the relative scarcity of some essential micronutrients required for eumelanin synthesis or the existence of certain allocation trade-offs has been proposed, but sound and general empirical evidence of these mechanisms is still missing (McGraw 2008).

Although much less developed than in the case of carotenoids, a physiological link between oxidative stress and melanin-based colour expression has also been proposed (Galván and Alonso-Álvarez 2008; Galván and Solano 2009). According to this framework hypothesis, the melanogenic pathway involves a relatively complex series of interactions among different compounds, where glutathione plays a central role (Galván and Alonso-Álvarez 2008; Galván and Solano 2009). Glutathione is a peptidic molecule that inhibits the eumelanin pathway (Galván and Solano 2009). Thus, the levels of this key molecule seem to regulate the synthesis (amount and type) of melanin within the melanocyte. But, importantly, glutathione also plays a central role in other processes. For instance, glutathione is the main endogenous nonenzymatic antioxidant in the cell, protecting its functional integrity against free radicals (Halliwell and Gutteridge 2007). This dual role of glutathione is the basis of the hypothesised physiological link between melanin pigmentation and oxidative stress: high oxidative stress would deplete glutathione levels, thus favouring eumelanin synthesis, whereas low oxidative stress levels will lead to high glutathione levels, inhibiting eumelanin synthesis. Thus, according to this hypothesis, eumelanic signals would be expressed at their highest intensity only when the individual is able to counteract the cost of low glutathione levels by activating alternative antioxidant mechanisms. In other words, eumelanin-based traits would evolve as honest signals of the functionality of the antioxidant system. The hypothetical mechanism assuring pheomelanic signalling is however less evident and dependent on resource allocation trade-offs as this melanin depends on cysteine availability in the diet (Galván and Solano 2009).

This mechanism thus sets the ground for a context-dependent reliability of eu- and pheomelanin colourations that still awaits experimental support (Galván and Solano 2009). So far, the red-legged partridge constitutes one of the best examples supporting the connection between oxidative stress and melanin-based pigmentation. In an experiment performed on partridge chicks of approximately 1 month of age, researchers found that increasing individual oxidative stress by administration of an exogenous source of free radicals (diquat) reduced glutathione levels and led to larger eumelanin plumage ornaments, i.e. increased size of the black bib and average area of the black band of flank feathers. By contrast, the same treatment reduced the area of the brown-reddish pheomelanin-based band of the flank feathers (Galván and Alonso-Álvarez 2009). Thus, these results support the proposed link between oxidative stress and plumage pigmentation, with glutathione levels as a key mediator of the process. Given the close links between oxidative stress and individual performance (see above), this opens a window to consider the size or intensity of melanin-based traits of the red-legged partridge as an indicator of individual oxidative status. Note, however, that the connection is not simple and intuitive, as situations of high oxidative stress might *facilitate* the production of black (eumelanin-based) traits, making them relatively affordable for all individuals, i.e. less reliable signals. This contrasts with the above-mentioned positive links between eumelanin-based pigmentation and condition found in this species. Therefore, the potential context-dependent meaning of these traits deserves further research.

A Matter of Pattern Expression?

The traditional approach to the evolution of colour signals assumes that pigment acquisition or production and its allocation to external teguments are the main constraints of signal expression. This implicitly assumes that colour intensity and the size of the patches are the key features conveying information on individual quality. However, this traditional paradigm has been recently challenged, as evidence from diverse taxa suggests that the actual pattern (i.e. shape of a patch, uniformity of the borders, regularity or complexity of the design) would equally behave as a reliable signal of individual quality in contexts of social communication (Pérez-Rodríguez et al. 2017). Some empirical evidence on this emerging research line has resulted from research on the red-legged partridge. As said before, the lateral barred pattern of this species results from the perfect alignment of flank feathers. Although there can be notable variations in the width of the bands, a detailed study of this trait reported that the number of bands remains relatively invariable among individuals (8–9 in more than 90% of individuals of either sex) (Bortolotti et al. 2006). Interestingly, despite covering a relatively large body area (ca. 84 cm^2), the feathers creating the pattern (roughly 45–50) emerge from a small piece of the skin about 1x4 cm on the upper breast. This implies that some of these ornamental feathers —particularly those covering the rear section of the patch— are notably long, exceeding 9 cm. The alignment of the bands and their position during courtship and agonistic behaviours are regulated by muscular contraction acting on feather follicles, creating a dazzling visual display. The offset of such display architecture is its susceptibility to alterations due to feather loss. Flank feathers —particularly the longest ones— are in fact loosely attached to the bird's body and therefore can be easily lost during agonistic encounters or when eluding a predator grasp, through a kind of autotomy strategy (Moller et al. 2006). The presence of such composite barred pattern might have evolved as an amplifier of somatic integrity, whose alterations can be used as cues for individual quality assessment (Pérez-Rodríguez et al. 2017). Interestingly, when any of these flank feathers is lost, replacement feathers do not perfectly fill these gaps. As a result, the pattern reveals long-lasting traces of recent traumatic events that would otherwise remain unnoticed by conspecifics and cannot be repaired until the next natural moult (Bortolotti et al. 2006).

The spatial configuration of the black bib of the red-legged partridge also conveys information on individual quality (Pérez-Rodríguez et al. 2013b). In a study combining observational and experimental data from captive partridges, researchers found that birds displaying bibs with higher fractal dimension —characterized by a smooth transition between the uniform black throat patch and the lower spotted region of the trait— showed better body condition and stronger immune responses within the study population. Also, when individual body condition was experimentally impaired during moult, new bibs showed a lower fractal dimension than bibs previously displayed by the same birds, while control (ad libitum-fed) individuals moulted bibs with a similar fractal dimension (Pérez-Rodríguez et al. 2013b). These results in captivity have been complemented by evidence from wild birds during the mating season. Thus, mated birds of both sexes showed higher bib fractal dimension than unmated ones (Cantarero et al. 2018). Moreover, paired individuals showed assortative mating according to the fractal dimension of their bibs, which can be considered as an indirect evidence of the implication of this character in mate choice (Cantarero et al. 2018). These results indicate that, irrespective of the size of the bib (a proxy of the amount of melanin deposited in the trait), the pattern of this trait conveys information about individual quality and is actively used as a social signal in this species. It remains unknown, however, what is the mechanistic and functional link between individual quality (i.e. nutritional status, immunocompetence) and pattern expression. Creating colour patterns requires a tight control over multiple mechanisms that must be synchronized at very different spatial and temporal scales. One possibility is that factors affecting developmental stability or homeostasis during moult may alter this machinery, resulting in changes in the expression of the pattern. Complex colour patterns, like the bib of the partridge, may therefore act as indices of the individual capacity to buffer stressors that alter these vital processes, thus linking individual quality and trait expression (Pérez-Rodríguez et al. 2017).

Future Research Directions

Although a newcomer to the evolutionary ecology scene, the red-legged partridge has contributed to the advance of this field of research by serving as an ideal study model for several sub-disciplines. Most of these contributions have focused on the physiological regulation of carotenoid-based colouration, particularly on its links with oxidative stress and androgens. In this sense, the findings obtained in this species have challenged the long-standing paradigm of the resource allocation trade-off as the main physiological way to explain the honesty of carotenoid-based signals. More recently, research on melanin-based traits has contributed to improve our understanding of the factors affecting the expression of these colour traits in vertebrates. However, we are only beginning to grasp the potential of this species as a model for research on these and other fields within evolutionary ecology. Unfortunately, the fast advance in these topics contrasts with the limited attention paid to other key issues that deserve proper assessment in order to allow a sound scientific progress. For instance, in contrast with our understanding of the biochemical basis and the mechanisms regulating carotenoid physiology, empirical evidences supporting the actual use of these traits in social interactions (i.e. mate choice or intra-sexual competition) are limited and rather indirect (Casas et al. 2010; Alonso-Álvarez et al. 2012). Experimental tests specifically designed for addressing the signalling value of these traits are needed to fully assess the biological relevance of the above-mentioned physiological framework. The same applies to melanin-based plumage traits, as evidence supporting their role in social communication is only indirect and correlational (Cantarero et al. 2018). Obtaining such relevant information is feasible since mate choice trials and male-male dominance tests can be easily applied in partridges (e.g. Alonso et al. 2008; Prieto et al. 2018).

Although carotenoid- and eumelanin-based traits have attracted most attention from researchers interested in social signalling, other conspicuous traits of the red-legged partridge that may also play a significant role in communication have been overlooked. The orange belly plumage, for instance, shows a considerable degree of variability in chroma (*pers. obs.*), but whether this relates to age, sex or any aspect of individual quality remains unknown. The presence of such conspicuous pheomelanin-based trait that is jointly expressed with other eumelanin-based plumage patches mentioned above makes the red-legged partridge a perfect model species to evaluate contrasted responses for both types of melanins under different physiological and environmental contexts (Galván and Solano 2009). Apart from chromatic traits, this species presents another trait that is widespread among Galliformes: the spurs. Spurs are present in males as well as in some female partridges. However, to date, no study has explored the sources of variation of this trait. Behavioural tests are also required to assess their use as armaments or ornaments. Finally, the red-legged partridge exhibits a large set of ritualized behavioural displays and vocalizations (Pintos et al. 1985) whose signalling potential has been largely ignored and deserves a detailed research programme.

As shown in this chapter, different aspects of social signalling in the red-legged partridge have been thoroughly studied by evolutionary ecologists. However, it is necessary to broaden the scope of future studies to address additional aspects of the ecology and life history of the species. Understanding the factors underlying the observed variability in mating and breeding strategies of partridges (Green 1984; Casas et al. 2006a, 2009) is essential to fully understand the biology of the species. Also, such a broad picture will allow us to better interpret the relevance of the results reported in this chapter in an integrative ecological context. An extra effort to connect key life-history traits of the red-legged partridge with other relevant aspects, like its spatial ecology and sanitary issues (see Chaps. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?" and "Health Monitoring and Disease Control in Red-Legged Partridges"), will ultimately allow a more efficient and integral design of management and conservation policies.

To date, most research on the evolutionary ecology of the red-legged partridge has been performed in captivity. The easy adaptation of this species to captive conditions and the existence of optimized protocols and adapted facilities derived from commercial breeding have facilitated long-term research programmes that addressed different aspects of its biology. However, the availability of these experimental setups and rearing facilities may also allow more ambitious studies that have been neglected to date. For instance, the establishment of selection lines for some of the physiological or phenotypic traits mentioned in this chapter would be of great interest for the study of the trade-offs associated with their expression, shedding light on the forces shaping their evolution. Similarly, the fact that several closely related *Alectoris* species can be easily maintained in captivity and cross-bred sets the ground for empirical setups to study the evolution of different traits within the genus. In any case, despite the great potential for captivity studies, the main challenge in the short term is to validate and calibrate the conclusions obtained in captivity with studies performed in the wild (e.g. García-de Blas et al. 2013). Comparison of partridge populations subjected to different management conditions —from unmanaged populations in relatively well-conserved natural habitats to highly managed populations in areas of intensive agriculture— may allow to test the potential context-dependent expression of the traits of interest.

Evolutionary ecology research using the red-legged partridge as a model species faces the challenge of dealing with a crossroad of diverse collectives with contrasted interests and perspectives. However, researchers must turn need into virtue and spotting the windows of opportunity that this situation offers, some of which have been highlighted above. Finding ways to interconnect the basic and applied research on this species also requires the involvement of other sectors of the society and governments. In this sense, the case of an emblematic game-bird species in the United Kingdom, the red grouse (*Lagopus lagopus scoticus*), is a good model to follow. In that case, scientists, hunters, gamekeepers and other stakeholders have collaborated for a long time in research programmes aimed at simultaneously resolving the basic evolutionary ecology questions as well as understanding key aspects of grouse biology of interest for population management, such as ecophysiology, sanitary status, behaviour, population dynamics or predator-prey interactions. This long-term intersectoral collaboration has been essential to implement a more efficient and science-guided management practices and conservation policies. The example of the red grouse is a proof that determined willingness for dialogue and cooperation, even though hard to reach, can generate highly beneficial synergies for all the involved sectors.

Acknowledgements I am grateful to Carlos Alonso-Álvarez for his insightful comments to an early draft of this chapter and to Elisa Pérez-Ramírez for carefully reviewing the last version. During the writing of this manuscript, I was supported by a SECTI postdoctoral contract from the University of Castilla-La Mancha and by the research project SBPLY/17/180501/000468 from the JCCM (co-financed with the European Regional Development Fund (ERDF)).

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Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?

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F. Casas, J. T. Garcia (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_3

Habitat Requirements

The red-legged partridge (*Alectoris rufa*) is a Mediterranean endemic species associated mostly with varied (semi-)open-land habitats. Red-legged partridge wild population range is mainly restricted to Spain, Portugal, France and Italy, but it has been introduced successfully in the United Kingdom and some Atlantic islands (Azores, Canary and Madeira archipelagos; see Chap. "The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting"). Habitat quality is one of the main factors to determine the density and distribution of species (Cody 1985). Therefore, understanding the role of habitat use and selection is key for establishing a relationship between habitat requirements and population dynamics, particularly important for planning effective management and conservation measures, especially relevant in game species as red-legged partridge of high socio-economic interest (Viñuela et al. 2013; Sánchez-García et al. 2020) and conservation concern (recently classified as Near Threatened; BirdLife International 2021). In fact, the first scientific studies on the red-legged partridge were mainly on habitat use and selection (e.g. Potts 1980; Ricci 1985; Lucio and Purroy 1987; Peiró et al. 1993).

Red-legged partridge is considered a very adaptable species, and it can be found in a wide variety of habitats and climates, from hot and dry semi-deserts to open woodland areas or even at cold and wet uplands in a broad altitudinal range, from sea level to over 1500 m a.s.l. (Blanco-Aguiar et al. 2003; Potts 2012). In fact, a family covey with chicks younger than 1 week has been recently observed around 3000 m a.s.l. in Sierra Nevada National Park (Granada, Spain; Pimentel, C., personal communication). Moreover, its range reaches northern areas, or even typically Atlantic areas in Spain, where their densities are lower (Lucio and Purroy 1992), and it has adapted to different environmental and weather conditions in their introduced populations in the United Kingdom (Chap. "The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future"). Nonetheless, it is in agrarian landscapes of the Mediterranean basin where partridges reach their highest densities (Vargas et al. 2006; Potts 2012), specifically in mosaic landscapes with high diversity of crops, mainly cereal fields, with interspersed patches of fallows, olive groves, vineyards, natural vegetation (mainly Mediterranean shrubland) and a well-conserved network of field boundaries (linear vegetation strips between fields and adjacent tracks and fields), formed mostly by hedgerows in Northern Spain, France and the United Kingdom or by annual non-cropped herbaceous strips of unploughed land in Central and Southern Spain and Portugal (Rands 1986a; Lucio and Purroy 1992; Borralho et al. 1999; Fortuna 2002; Vargas et al. 2006; Casas and Viñuela 2010; Viñuela et al. 2013). Therefore, in extensive landscapes, red-legged partridge can choose among a high variability of habitats, which they might use, in a greater or lesser grade, to satisfy their ecological requirements over the year, which would vary according to the availability of shelter and food (Morales and Traba 2009; Casas et al. 2014; see below).

Red-legged partridge habitat use and selection during the non-breeding season vary among regions (depending on habitat availability mostly), but in general, it selects areas dominated by a mosaic of crops with longer availability of field boundaries and small interspersed patches of natural vegetation (Ricci 1985; Rands 1986a; Lucio and Purroy 1992; Aebischer and Lucio 1997; Fortuna 2002; Vargas et al. 2006; Buenestado et al. 2008; see also Sects. “Red-Legged Partridge Habitat Requirements in Italy”, “Red-Legged Partridge Habitat Requirements in France” and “Red-Legged Partridge Habitat Requirements in Mainland Portugal”). In highland areas, red-legged partridges select areas with steeper slopes and less dense scrubland during spring, while during autumn-winter they prefer shrublands (*Crataegus* sp., *Prunus* sp., *Rosa* sp.), avoiding rocky areas (Lucio 1991; Lucio and Purroy 1992). By contrast, in lower areas (transition zones between highland and lowland), red-legged partridges use areas with low natural vegetation, like thymes during spring, but they prefer areas with greater vegetation cover during autumn-winter (Lucio and Purroy 1992).

In agrarian ecosystems, during the breeding season, Fortuna (2002) found that red-legged partridges positively selected field boundaries and Mediterranean scrubland patches but avoided fallow fields. This last habitat has been pointed as a potentially important habitat for partridges, because it could be a resource of food (weed seeds) and refuge. However, the importance of this habitat for red-legged partridges is not clear, and contrasting results have been found. Borralho et al. (1999) found a positive correlation of fallow fields (abandoned rice fields and of unharvested olive tree groves) with partridges’ density. Nevertheless, the availability of fallows, low landscape heterogeneity and agricultural intensification are interrelated factors, and these would be one of the main causes behind the greater home range size in areas where average size of cropped fields is greater and there are lower availability of field boundaries and higher perturbation by agricultural practices (Buenestado et al. 2008) that might affect their survival (Buenestado et al. 2009). In any case, fallow fields have significantly decreased since 2002 owing to agricultural intensification (Traba and Morales 2019), so we cannot rule out that fallow could be positive for partridges, as it is for other farmland species (Traba and Morales 2019).

On the other hand, the Mediterranean climate is characterized by dry and hot summers, and red-legged partridge habitat use and spatial distribution during summer are strongly influenced by the location of artificial water ponds (Borralho et al. 1998), so water provisioning is one of the main hunting management practices applied by game managers and hunters which would affect abundance and modify their habitat selection patterns (Borralho et al. 1998; Díaz-Fernández et al. 2013).

Nesting Habitat Use and Selection

The selection of appropriate habitat for nesting is key to maximize the probability of nesting success (Taylor et al. 1999; Tirpak et al. 2006). This is especially significant for ground-nesting bird species, due to the high predation rate that they may have to cope with (Potts 2012; Roos et al. 2018; McMahon et al. 2020) and because that can affect population dynamic in Galliformes (Potts 1980).

Red-legged partridges look for nesting places with dense and tall vegetation cover (Rands 1988; Ricci et al. 1990), where they can hide their nests, and both females and males can also stay hidden during the incubation. Besides, a positive correlation between breeding density and the availability of suitable nesting cover in red-legged partridge has been shown (Rands 1986a). Therefore, the habitat chosen for placing their nests might vary according to the availability of most suitable nesting places (those habitats with higher vegetation cover and an appropriate height) and population density (due to competition for the best nesting places) but may also be influenced by predator abundance (Potts 1980, 2012; Cody 1985; Rands 1988; Ricci et al. 1990; Herranz 2000; Casas and Viñuela 2010; Chaps. "Is Predation the Key Factor of Partridge Ecology and Management?" and "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes").

Field boundaries have been considered the most important nesting habitat for red-legged partridges along their range from the Iberian Peninsula to the United Kingdom (Rands 1986a, 1988; Berger 1987; Ricci et al. 1990; Casas and Viñuela 2010; Villanúa et al. 2011), regardless of the type of vegetation (annual plants or hedgerows) and floristic composition forming these vegetated non-cropped linear strips (see Sect. "Habitat Requirements" for a further description). Moreover, partridges positively select field boundaries, and generally a higher nesting success on nests placed in this habitat has been found (Rands 1986a, 1988; Ricci et al. 1990; Casas and Viñuela 2010; Potts 2012). Nevertheless, the low availability of well-vegetated field boundaries suitable for nesting, or even its absence in many areas, due mostly to agricultural intensification (Pain and Pienkowski 1997; Potts 2012), may leave partridges with no alternative but to nest in crops or other less suitable habitats (e.g. Casas and Viñuela 2010), which may undermine red-legged partridges' nesting success. In fact, partridges might use other habitats for nesting (e.g. herbaceous crops) if permanent habitats are poor or lacking (Potts 2012). For example, red-legged partridges in agricultural areas use mostly cereal fields for placing their nests (over 50% of nests in Central Spain; Casas and Viñuela 2010), although this habitat has been found to be negatively selected in areas dominated by this cropped habitat and has a lower nesting success mainly due to harvesting (Casas and Viñuela 2010; Villanúa et al. 2011). Moreover, most of the nests placed in cereal fields are usually located in the first 5 metres from the field boundary (almost 60% of nests; Casas and Viñuela 2010), which enhances the importance of field boundaries as important nesting places (Ricci et al. 1990; Casas and Viñuela 2010).

On the other hand, in areas where permanent crops are the main habitat, nests can also be located in field boundaries, such as in areas where olive groves (more than 80% of nests; Duarte 2012) or vineyards (20% of nests; Meriggi et al. 1991) can be found. In some areas of Southern Spain, where olive groves dominate the landscape, habitat management during the nesting period is considered key for the maintenance of sustainable populations (Duarte 2012, but see Sect. "Olive Groves and the Red-Legged Partridge" for further details).

Brooding Habitat Use and Selection

Red-legged partridge chicks leave the nest a few minutes after hatching, and from then on, they are able to forage for themselves, although sometimes the adults would show them the food (Cramp and Simmons 1980). Food availability and shelter are crucial during the first weeks of life for red-legged partridge chicks to fulfil their high metabolic demands and to avoid predation (Rands 1986b; Duarte 2012; Potts 2012). If food and shelter availability are scarce in the areas close to the nest location, family coveys would be forced to do longer movements, which could increase predation risk (Green 1984; Potts 1986; Duarte 2012).

Chicks feed mostly on arthropods during the first 3 weeks after hatching (Green 1984; Rueda et al. 1993), so that habitats with higher availability of insects and greater vegetation cover are preferably used (Green 1984). In arable lands, Green (1984) found that red-legged partridge chicks used field boundaries and closer surroundings (52% of locations were within 25 m of the nearest field boundaries) as foraging areas. Similarly, Duarte (2012) found in a landscape dominated by olive groves that family flocks with chicks younger than 6 weeks old used habitat according to insect availability, selecting field boundaries and areas where habitat variability is greater. Nevertheless, family flocks with chicks older than 6 weeks keep selecting heterogeneous areas with greater occurrence of ecotones but where insect availability is not an important factor (Duarte 2012). Differences between these two age-classes chicks are related to diet requirements, owing to that arthropods are an important part of their diet for younger chicks (mostly during the first month of life), while older chicks feed mostly on seeds and vegetation (Green 1984; Rueda et al. 1993). Therefore, because chicks have different biological requirements and moving capabilities from hatching until they reach adult size, they might show differences in habitat use between different age-classes chicks, e.g. family flocks with younger chicks used tracks (dirt roads, habitat with no vegetation cover) more frequently than those with older chicks (Casas et al. 2020).

Microhabitat Selection of the Red-Legged Partridge in Agrarian Landscapes

Morales and Traba (2009) and Traba et al. (2015) examined red-legged partridge microhabitat selection at a small scale examining niche partition with other coexisting medium- to large-sized steppe birds in cereal steppes of Central Spain. More precisely, they characterized the spatial structure of vegetation preferred by the species during the breeding season, regardless of the particular vegetation formation in which individuals were found. Such a microscale approach allowed for the analysis of variables related to refuge and food availability for the red-legged partridge and other steppe birds, which are directly involved in evolutionary trade-offs between survival (shelter from predation), on the one hand, and breeding

Table 1 Mean (± standard deviation) values of microhabitat variables selected by red-legged partridges in Mediterranean agrarian systems. Data represent cover (percentage) and vertical structure (number of contacts at different heights) or mean height in red-legged partridge and control locations. *N* red-legged partridge = 42, *N* control = 178. Statistics come from GLMM with site and year as random factors and observation as fixed factor. See Traba et al. (2015) for more information on data analyses

	Control	Partridge	*F*	*p*
Bare ground	50.6 ± 37.32	46.4 ± 34.75	1.72	0.415
Litter	8.1 ± 17.45	23.2 ± 22.42	16.21	0.155
Plant cover	45.6 ± 37.23	50.4 ± 37.25	1.65	0.421
Green plant cover	32.4 ± 37.82	50.0 ± 37.53	1.79	0.409
Weed cover	11.2 ± 22.94	28.4 ± 32.03	187.94	**<0.05**
No. of contacts below 5 cm	0.8 ± 0.87	0.9 ± 0.86	1.16	0.476
No. of contacts 5–10 cm	0.8 ± 0.87	0.8 ± 0.69	0.21	0.728
No. of contacts 10–30 cm	1.4 ± 1.48	1.4 ± 1.55	0.7	0.557
No. of contacts above 30 cm	1.3 ± 1.85	1.1 ± 1.29	9.22	0.203
Mean plant height	40.2 ± 32.21	47.6 ± 30.02	0.02	0.92

Bold indicates significative differences between control points and partridge locations

success, on the other (Morales et al. 2008; Morales and Traba 2009; Traba et al. 2015).

Most microhabitat characteristics selected by the red-legged partridge were not statistically different from habitat availability in the study sites. Only weed cover was significantly higher at partridge locations than at random control points (Table 1), suggesting a preference of breeding red-legged partridges for particularly food-rich locations.

Figure 1 shows the microhabitat preferences of the red-legged partridge and other coexisting medium- to large-sized steppe birds in agricultural landscapes of Central Spain in relation to two main ecological gradients: variation in shelter and food availability. The position in such microhabitat space of different agrarian fields (habitats) found in the study sites is also shown, which provides an idea of their availability in terms of food and shelter. Red-legged partridge preferences are close to general habitat availability (control). This is particularly for shelter availability, whereas for food availability partridges selected statistically higher values, in consistency with the mentioned preference for higher weed cover locations. These preferences are also close to the centroid of a triangle whose vertices correspond to the availability of shelter and food of cereal crops, ploughed fields and long-term fallows. Such results indicate that the mosaic dry cereal farmland of Central Spain is particularly suitable for red-legged partridge in terms of microhabitat, coinciding with the preferences of some typical steppe birds like the little bustard (*Tetrax tetrax*, particularly female; see Fig. 1). They also suggest that, within those landscapes, red-legged partridges tend to occupy locations with relatively high refuge availability and larger amounts of food resources than those generally available.

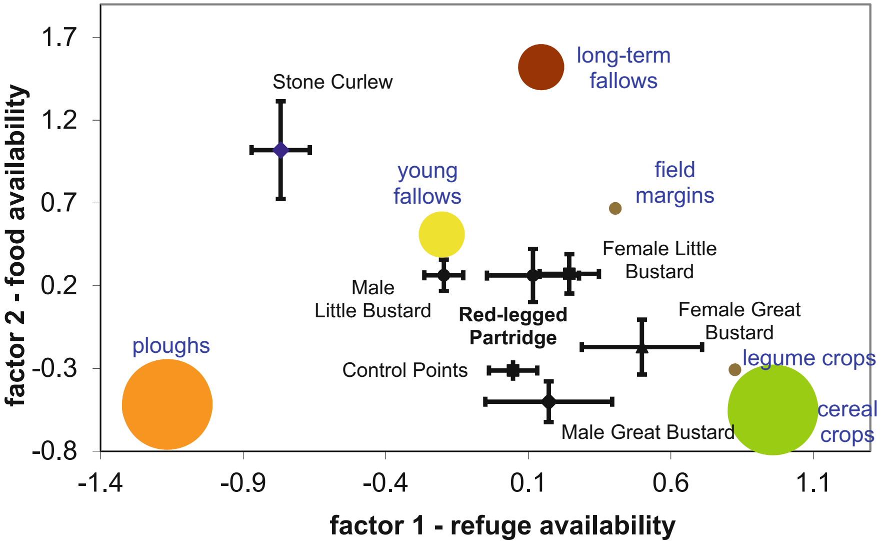

Fig. 1 Species and control point centroids (± SE in both axes) in the space defined by the two PCA axes representing two main microhabitat gradients in agricultural landscapes of Central Spain occupied by the red-legged partridge and other medium- to large-sized steppe birds (original microhabitat variables are presented in Table 1). Axes can be interpreted as ecological gradients. General values for the main agricultural fields (habitats) are also shown, the size of the circle being associated to variability in both axes. Based on Morales and Traba (2009), see Traba et al. (2015) for more details on statistics

Olive Groves and the Red-Legged Partridge

Olive groves are an agricultural environment resembling open forest with different management and structural characteristics from arable crops. Olive groves are a very important crop in the whole Mediterranean basin because of the biodiversity they hold (Atauri and De Lucio 2001; Duarte et al. 2009) as well as the extension they occupy. In Spain, they occupy around 2,751,255 hectares (55% of the whole olive grove surface in Europe), mainly distributed in Andalusia (60.5%), where olive groves represent 18.9% of Andalusia's surface (ESYRCE 2020).

Olive production (oil and olives) has changed since the 1970s in response to progressive intensification models that have implied increasing plantation density from 80–100 to 200–500 trees per hectare (Saavedra and Pastor 2002). Management of the herbaceous vegetation, irrigation, application of herbicides and fertilization has increased at the same pace as production. As a result, olive grove plots are now concentrated to be more cost-effective, with a loss of landscape diversity and boundaries as a consequence.

Olive groves usually show a vertical structure with three different parts depending on herbaceous cover through seasons (Duarte 2012). Parallel tree rows define the presence of "grove streets", which width is the distance between trees; the existing space below the treetop is the "ruedo"; and the crop boundaries with other crops or shrubland constitute its borders. Natural herbaceous cover is present in the streets only from October to January, the rainy season. The rest of the year, herbaceous cover is usually removed using mechanical or herbicide treatments, resulting in almost bare soil. In the "ruedos", natural vegetation withstands somewhat longer (October–May), but it is finally controlled by the end of spring and throughout all summer. Borders show a more stable herbaceous cover during most of the year.

One of the characteristics of olive groves is that management requires some action practically every month of the year. Ground herbaceous vegetation of the streets and the "ruedos" is controlled almost monthly, but fertilization is also necessary, pruning, removing branches (new tree shoots) and acting on the olive trees in general. Therefore, this requires human presence in the groves almost permanently, which may have a huge impact on wildlife.

Since the beginning of the first decade of the twenty-first century, olive groves have experienced a great conversion, from dry to irrigated farming. In 2020 the area covered by irrigated olive groves, mainly with drip irrigation, was around 818,000 hectares (31% of the total olive grove surface in Spain; ESYRCE 2020). Even though initially the existence of irrigation could be considered a positive factor for the fauna in need of water during the summer season because the presence of water could imply herbaceous growth and the presence of insects, drip irrigation is also used to apply fertilizers or pesticides (see Chap. "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes"). This way of applying fertilizers that benefits from a system that is extensively distributed all over the grove could then suppose a massive agrochemical distribution vehicle, a very important risk factor for partridges and other species inhabiting olive groves (Rodríguez-Estival et al. 2010, Mougeot et al. 2019; see Chap. "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes").

It has been suggested that the olive grove is a suitable agricultural environment for the partridge (Borralho et al. 1999), but this ecosystem can be considered acceptable as long as its natural structure does not suffer alterations. However, the intensive agricultural management, increasingly carried out in olive groves, is modifying their structure creating ecological traps and situations that can endanger the survival of partridge's populations.

The lack of vegetation, especially herbaceous cover during most of the year forces the partridge to seek food in their boundaries with other adjacent environments. This involves many daily journeys through a territory lacking coverage and shelter (Duarte et al. 2014a) that can potentially increase the risk of predation. Such risk is even higher for chicks, due to their high necessity to search for food, which might force them to explore the bare ground, making them more vulnerable.

Olive groves have natural vegetation during autumn, winter and early spring. When red-legged partridges select the nesting sites, they always do it in an environment that supposedly remains unchanged. Nevertheless, during laying and incubation, the environment suffers changes, caused by farming and agricultural works, which reduce the vegetation to the minimum, so these changes can cause severe nest failure rates as well as can increase the risk of predation (Castro-Caro et al. 2014), so this agricultural habitat might be considered as an ecological trap (Battin 2004).

The intense human activity in the crop implies that the main nest predators are generalist species related to human-modified environments (Duarte and Vargas 2001). Therefore, there is a direct impact on the nests (losses due to agricultural works) as well as an indirect impact (alteration of nesting microhabitats). The failure rate of partridge nests in olive groves is estimated at 45% (Duarte 2012). Hence, the management of the crop greatly influences the reproductive success of the species.

Other distinguishing feature of the ecology of red-legged partridges in olive groves is related to nest location. While on the arable crops and open environments the nests are generally found on the boundaries (see Sect. "Nesting Habitat Use and Selection"), in olive groves they are mainly found inside the crop. More than 75% of the nests are found 50 m away from field boundaries (Duarte 2012), which is related to the structure of the crop. Nests are typically built near the trunk of the trees and in the "ruedos", the main redoubt of natural vegetation during spring and summer (Duarte 2012). The trunks of old trees also have a complex structure that determines the existence of gaps and spaces where, sometimes surprisingly, the partridge manages to place its nest (Duarte and Vargas 1998; Duarte 2012).

Olive grove management schemes have evolved continuously during the last decades. The high rates of erosion caused by intensive management, promoting large areas of bare ground over half a year, have encouraged the implantation of herbaceous cover systems and related soil conservation techniques to try to stop high rates of soil loss. The existence of a cruciferous cover species is encouraged, and legumes or grasses are either chemically or mechanically mowed though maintaining the stubble during summer (Saavedra and Pastor 2002). The development of integrated production and organic farming in addition to the need for a herbaceous cover in some of the subsidies available for farming have enabled these systems to increase their cultivated area over the years. Both the presence of stubble and the use of a mechanical mowing (Duarte et al. 2014b) allow the potential existence of cover and nourishment for the red-legged partridge. However, the real effects of these farming systems on partridges are still poorly studied.

Red-Legged Partridge Habitat Requirements in Italy

Historical Range

In its historical Italian range, red-legged partridge was linked to patchy landscapes consisting of traditional rotational crops (mainly alfalfa and winter wheat) mixed with vineyards and orchards and interspersed to scrublands, small oak (*Quercus pubescens*) woods, landslides and calanques (hillsides eroded by rainwater runoff and covered by scarce xerophilous vegetation, Fig. 2), mainly on clay soils. This habitat is typical of the northern Apennines between 300 and 700 m a.s.l. (Meriggi 1992; Spanò 2010). The first ecological research on the habitat requirements of

Fig. 2 Typical calanques in the northern Apennines (Italy)

red-legged partridge in Italy showed a strong selection for uncultivated lands in autumn-winter and hedgerows in spring and summer, whereas the woods were avoided, and crops used as available; nests were preferentially built in the middle of vineyard plots and uncultivated lands (Meriggi et al. 1991). The habitat variables with a positive effect on pair density and brood presence were scrublands, calanques, tree rows and landscape diversity, whereas woodlands showed a negative effect, and uncultivated lands showed a positive effect on the brood production rate (i.e. the percentage of successfully reproduced pairs) (Meriggi et al. 1992).

Some differences in habitat requirements are shown by the red-legged partridge population of Elba Island (Tuscan Archipelago, central Italy) where the presence of the species is confirmed by the early 1800s (Thiebaut De Berneaud 1808). This population is the only living in a typical Mediterranean habitat in Italy, and it dramatically declined (current density 1.8 pairs per km^2) because of the habitat losses due to pasture abandonment and the increase of anthropization, with the consequent encroachment of Mediterranean maquis. A study carried out in recent times showed a positive effect of altitude, garrigues and perennial meadows on the breeding pair presence and a negative effect of woods; besides, the highest pair densities were recorded in mosaic habitats over 364 m a.s.l. in which garrigues are at least 21% and meadows 10% (Chiatante et al. 2013).

Reintroduced Populations

In the first years after reintroductions, populations are usually at low density, and in this situation, habitat requirement analysis can reveal patterns of habitat use and selection partially different from those recorded in stable and denser populations. This is because the best habitats are occupied firstly, and only when density increases, secondary habitats are also used. During a large-scale reintroduction of red-legged partridge in Siena province (Tuscany, central Italy), carried out from 1995 to 2005, a positive effect of hedgerow length on pair presence probability and negative effects of strip farming and spring crops were recorded. Moreover, hedgerow length and pastures with bushes enhanced the presence probability of broods, while vineyards decreased it (Meriggi et al. 2007). Quantitative models of habitat suitability showed that pair density increases as pastures with bushes and the number of woodlots (i.e. the wood fragmentation) increase (Meriggi et al. 2007).

Lowland Populations

The red-legged partridge recently colonized the dry crop lowlands of the Po plain at the foot of the northern Apennines hills. These areas are characterized by rotational crops (maize, alfalfa, winter wheat, barley, soybean and rape) and by wide pebbly shores of streams with sparse bushy vegetation. A study on red-legged partridge habitat requirements was carried out in 2015 and 2016 in three protected areas of the Piacenza province by modelling the presence probability (Binary Logistic Regression Analysis, BLRA) and density (Multiple Regression Analysis, MRA) of pairs by habitat variables measured in sample plots of 300 m radius around the listening points used to survey the populations. The average density varied from 2.1 (SE = 0.42) to 3.2 (SE = 0.39) partridges/km^2 in 2015 and from 2.9 (SE = 0.63) to 3.7 (SE = 0.88) partridges/km^2 in 2016 without significant differences between years and study areas. Fifteen habitat variables were found significant differences between presence and control points (Mann-Whitney U test, $P < 0.05$); in particular winter cereals, pebbly shores, hedgerow density, Shannon diversity index, the patch number, edge density and mean perimeter area ratio had greater values in presence points. Three habitat variables (winter cereals, pebbly shores and habitat diversity) entered the best logistic model with a positive effect on the presence probability of red-legged partridge. The model explained 37.0% of the variance and correctly classified 71.2% of the original cases (presence, 77.8%; controls, 64.9%); ROC analysis showed a good performance of the model (AUC = 0.82, SE = 0.048, $P < 0.0001$) (Table 2). Significant positive correlations between partridge density and percentage of unpaved roads (study areas pooled $r = 0.442$, $n = 39$, $P = 0.005$), hedgerows (Trebbia study area $r = 0.661$, $n = 16$, $P = 0.005$), hay fields (Trebbia $r = 0.601$, $n = 16$, $P = 0.013$) and patch size (Nure; $r = 0.648$, $n = 13$, $P = 0.017$) were found. Considering the study areas pooled, the best regression model explained

Table 2 Results of the Binary Logistic Regression Analysis (BLRA) for modelling the presence probability of red-legged partridges

Habitat variables	*B*	SE	Wald	*P*	Exp(B)	VIF
Winter cereals (%)	0.03	0.02	4.27	0.039	1.03	1.08
Pebbly shores (%)	0.04	0.02	5.89	0.015	1.04	1.08
Shannon index	3. 4	1.03	10.71	0.001	29.49	1.07
Intercept = −5.7 SE = 1.69						

Table 3 Results of the Multiple Regression Analysis (MRA) for modelling the density of red-legged partridge by habitats

Habitat variables	*B*	SE	*t*	*P*	VIF
Roads (%)	0.7	0.22	3.38	0.002	1.09
Patch number	−0.1	0.05	2.63	0.013	1.64
Edge density	1338.0	620.43	2.16	0.038	1.76
Maize (%)	4.4	0.02	1.40	0.169	1.04
Intercept = 4.4 SE = 1.25 $R^2 = 0.318$ SEE = 2.20 $F_{4,34} = 5.42$ $P = 0.002$					

31.8% of the variance in partridge density by the inclusion of three habitat variables of which the percentage of unpaved roads and the edge density had significant positive effects, and the patch number a negative one (Table 3), predicted and observed density values were highly correlated ($r = 0.624$, $n = 39$, $P < 0.001$).

Anthropogenic Factors Affecting Red-Legged Partridge Distribution and Abundance at a Large Scale

The main anthropogenic factors that have modelled the distribution and the abundance of red-legged partridge in Italy from the early 1960s onwards are:

1. Abandonment of mountain areas. Until the late 1950s and the early 1960s, the mountain areas of northern Apennines were widely exploited for livestock breeding and agriculture. Cereals were grown up to 1000 m a.s.l. and beyond, and meadows were regularly cut for hay production. From the 1960s the abandonment of mountain areas caused a dramatic decrease of traditional agricultural and husbandry practices with an important recovery of wooded areas, reducing the habitat suitability for red-legged partridge, causing local extinctions and a marked fragmentation of populations in the whole historical range.
2. Changes in land use in medium-altitude hills. Also in the hills between 400 and 700 m a.s.l., several important habitat changes occurred from the 1970s onwards. In particular the traditional rotation between cereal crops and alfalfa was abandoned with a consequent marked reduction of winter wheat and barley cultivations. This caused the loss of the typical habitat of red-legged partridge and the

population decline further exacerbated by a high hunting pressure and by releases of hybrid *A. rufa* x *A. chukar* (Meriggi 1992; Spanò 2010; Díaz-Fernández et al. 2013; Casas et al. 2016; Guzmán et al. 2020, see Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing" for further details about the effect of farm-reared partridge releases).

3. Agricultural intensification and specialization in low-altitude hills. In the hills below 400 m a. s. l. in the last 20 years, vineyards and orchards increased markedly at the expense of rotational crops, thus reducing habitat diversity and consequently the habitat suitability for red-legged partridge.
4. Releases outside the historical range. In the last 10 years, hunting districts carried out releases of red-legged partridges from game farms in several areas of the Po plain outside the historical range of the species creating new and stable populations. In these areas the traditional rotation between cereals and forage is still a common practice, but maize, soybean and rape are increasing, and the field size is greater than in the hills so populations are at low densities (<5 pairs/km^2).

Habitat Improvement

In 2005 a pilot study to verify the effects of habitat improvement actions on red-legged partridges in two protected areas of the Siena province was carried out (Tuscany, central Italy). Habitat improvements consisted of 6-m-wide strips at the edges of cereal crops (winter wheat and barley) where cereals were not harvested. The first area (22.6 km^2) was mainly cultivated (72.6%) with little natural vegetation, whereas in the second study area (33.7 km^2), crops covered 36.5% and natural vegetation 34.3%. Habitat improvements were 1.6 and 1.7%, respectively. Partridge pairs and broods were surveyed, by mapping birds in spring and summer. Moreover, land use by direct surveys and aerial photographs at a 1:10.000 scale was also mapped. For each study area, it was delineated by kernel analysis at 99% belts of increasing density, and percentages of land use types were calculated. Multiple Regression Analyses (stepwise method) of pair and brood densities vs. land use classes and landscape metrics were carried out.

Habitat improvements entered the models both for pair and brood density as the most important variable, showing the importance of these interventions to enhance population density and breeding success (Tables 4 and 5).

Table 4 Results of Multiple Regression Analysis of pair density vs. habitat variables (study areas pooled)

Habitat variables	Regression coefficients (SE)	β	t	P	Partial R^2
Habitat improvements	0.6 (0.04)	0.90	13.71	<0.001	0.65
Study area 1	−2.2 (0.40)	−0.40	5.94	<0.001	0.04
Vineyards	1.1 (0.24)	0.35	4.30	<0.001	0.04
Buildings	−0.6 (0.13)	−0.32	4.70	<0.001	0.03
Dirt roads	1.9 (0.45)	0.28	4.26	<0.001	0.02
Paved roads	1.1 (0.37)	0.17	3.00	0.004	0.01
Woods	−0.2 (0.05)	−0.11	2.20	0.032	0.03
Olive groves	−0.1 (0.05)	−0.18	2.15	0.036	0.02
Intercept = 0.64 $R^2 = 0.82$ $F_{8,62} = 65.66$ $P < 0.001$					

Table 5 Results of Multiple Regression Analysis of brood density vs. habitat variables (study areas pooled)

Habitat variables	Regression coefficients (SE)	β	t	P	Partial R^2
Habitat improvements	0.4 (0.05)	0.67	7.85	<0.001	0.38
Uncultivated lands	0.1 (0.03)	0.24	2.77	0.007	0.09
Dirt roads	0.9 (0.32)	0.24	2.65	0.010	0.05
Intercept = −0.83 $R^2 = 0.50$ $F_{3,68} = 24.77$ $P < 0.001$					

Red-Legged Partridge Habitat Requirements in France

Habitat Selection

Red-legged partridges can be found in very different habitats at regions in France: undulated areas in mixed farming with cereal, grasslands interspersed with fallow, hedges or bushes in Dordogne, hedges and ploughed fields during autumn in Champagne Berry (Berger and Marchandeau 1988) and vineyards, olive groves near fallow, hedges, bushes or ecotones between cultures and scrubland in the Mediterranean, saline scrub in the Camargue. However, red-legged partridges avoid woody and dense scrubland and irrigated areas (e.g. wet meadows in Crau and rice fields in Camargue), and its occurrence is exceptional above 1500 m a.s.l. in France (Ponce-Boutin et al. 2003; Ponce-Boutin 2009).

Impact of Human Activities on Distribution and Abundance

The remarkable increase in productivity of French agriculture and its intensification have degraded many habitats for the red-legged partridge. Moreover, the abandonment of unproductive lands has had a significant impact on the Mediterranean area as well: the gradual abandonment of crops (such as vines or orchards), grazing or gathering in bush areas and the significant increase in the construction of country houses have gradually transformed the Mediterranean French landscape, increasing the landscape homogenization. Garrigues, scrublands, woods and wastelands are spreading, reducing the habitats favourable to species associated with open lands or ecotones such as red-legged partridges. Moreover, agricultural intensification was followed by the use of pesticides, reducing arthropods and weeds in vineyards and orchards, as well as the aggregation of parcels in larger fields, which since 1950, reduced field boundary surface (from 3 million km in 1930 to 1 million km in 1980). These deep modifications of its habitat constitute certainly one of the causes of its decline (Aebischer and Potts 1994; Ponce-Boutin et al. 2003).

Red-Legged Partridge Habitat Requirements in Mainland Portugal

Habitat Selection

The red-legged partridge inhabits a wide variety of habitats and landscapes across mainland Portugal. It is more common inland and in areas with a stronger influence of Mediterranean climate, mainly south of the Tagus river (Equipa Atlas 2008, 2018). Though it can adapt to a larger set of relatively diversified (semi)-open habitats, it can be absent from very transformed and intensively used habitats, as irrigated fields, but also from wetlands. It also avoids extensively forested habitats or other closed habitats (dense and closed shrubby areas), mainly in the centre and northern coastal areas, whereas it can be quite rare or absent (Equipa Atlas 2008, 2018). However, it may occur in urban areas, as in Lisbon (Catry et al. 2010). Though it clearly prefers sunny locations at low or relatively median altitudes, it may occur well above the 1000 m a.s.l, as in the north-east of the territory, including in winter (Reino 1994; Ramalho and Fontoura 1996; Equipa Atlas 2018). In the Central System (Serra da Estrela), it breeds up to 1900 m a.s.l., but in winter it does not occur above 1600 m a.s.l. (José Conde, pers. comm.).

In general, it prefers diversified environments dominated by open areas with sparse vegetation and small open woods but also open-Mediterranean woodlands as “montados” of cork and holm oak woods (*Quercus suber* and *Q. rotundifolia*, respectively) (Borralho et al. 2000; Reino et al. 2016). It may also inhabit extensive shrubby areas with some scattered trees and open spaces, dominated by either cereal or fallow/pastures fields. In more intensive areas, it may occur in other crops (e.g. vineyards), though its presence should be dependent on small patches of other habitats for shelter and protection.

In summer, the distribution of red-legged partridges in the Mediterranean region (Alto Alentejo, southern Portugal) is determined by the availability of surface water (see Sect. “Habitat Requirements”), land use and distance to field boundaries being the other important factors (Borralho et al. 1998). In the same region, in an area of mixed farmland, rotational set aside (equivalent to 1-year fallow) seems preferable for red-legged partridge breeding (Borralho et al. 1999). In areas of agricultural abandonment, such as those in Mediterranean woodlands, management for partridges would benefit from the introduction of leguminous game crops and water provision (Reino et al. 2016). In central Portugal (Santarém), Tavares et al. (2001) observed variation in habitat use along the annual cycle, with the highest use of cereal fields in winter-spring and vineyards in spring-summer.

Impact of Human Activities on Distribution and Abundance

The red-legged partridge is one of the species whose abundance is very dependent not only on habitat but also on direct or indirect management actions. The fact that it is a species with high hunting value, the type of game management developed is a key factor for variation in abundance, mainly at the local level (Ramalho and Fontoura 1996; Borralho et al. 1997, 2000). Therefore, it is expected that in areas with a more focused management for this or other game species, it may favour the abundance of partridges. These actions include not only a limitation and control of hunting activity but also actions to improve habitat and increase the availability of food and water points, mainly in spring and summer (Borralho et al. 2000; Reino et al. 2016).

Is Habitat Management the Key for Restoring Red-Legged Partridge Populations?

The origin of red-legged partridges is situated in the Mediterranean basin (Chap. "Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"), and it has been suggested that their primary habitat was a mix of short scrublands and open-grassland areas, which would provide the food and shelter needed to fulfil their vital requirements (Potts 2012). Climate fluctuation over the past 3 million years has shaped markedly the distributions of most living organisms, influencing the phylogeography, genetic structure and demographic history of the red-legged partridge (Ferrero et al. 2011). More recently (geologically speaking), habitats have changed several times and in different ways due to climate and human actions (mostly by the development of agriculture and livestock). Simplifying these events in just two great periods, open-land species as the red-legged partridge were favoured by habitat changes (deforestation and expansion of open agricultural landscapes) from the first human settlements in Europe (~8000 years ago) to the onset of agricultural intensification (50's in the twentieth century; Pain and Pienkowski 1997; Bota et al. 2005), while a marked intensification of the agriculture over the last 60–70 years has led to a decrease of habitat quality and quantity, leading to a widespread decline of open-land species populations (Green et al. 2005; Butler et al. 2010; Reino et al. 2010; Santana et al. 2017). Specifically, the effects of this last period in farmland wildlife have been different in every country, according to the timing and degree of agriculture intensification, so northern and central European countries suffered the effects earlier than in southern countries (Sánchez-García and Casas 2018). Later arrival of agricultural intensification to southern countries, such as Spain and Portugal, has caused that current European populations of several open-farmland species are mainly concentrated in these countries, which imply a strong responsibility for their conservation.

Red-legged partridge wild populations have not been an exception, and they have suffered a marked decrease during the last three to four decades throughout their range, including Spain, their main stronghold in Europe (see Chap. "Red-Legged Partridge Monitoring and Population Trends"). Many factors are behind this decline and have been explained in detail in other chapters of this book, like farm-reared partridge releases and their associated problems (Chaps. "Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization", "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing" and "Health Monitoring and Disease Control in Red-Legged Partridges"), predation (Chap. "Is Predation the Key Factor of Partridge Ecology and Management?") and overhunting (Chap. "The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting"). Nevertheless, this long-term decline in red-legged partridge populations seems to be mainly associated with changes in agricultural practices and habitat use by man (Guzmán et al. 2020; see Chap. "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes"). Among these changes, homogenization, the decreasing of field boundaries and herbaceous non-cropped habitat surface (e.g. fallows), the development of more efficient machinery and increasing input of agrochemicals (pesticides and fertilizers) have improved yields significantly but have had direct and indirect effects on wildlife abundance and diversity. This has re-shaped farmland ecosystems over recent decades, severely impoverishing landscape suitable for red-legged partridges (Delibes-Mateos et al. 2012).

It is well established that agrarian ecosystems hold preferred habitats for red-legged partridges along their actual range, so that habitat diversity and heterogeneity (areas dominated by a mosaic of cropped and non-cropped habitats and interspersed patches of short Mediterranean shrubland), along with longer surface availability of field boundaries, define habitat quality for this species (Ricci 1985; Rands 1986a; Lucio and Purroy 1992; Aebischer and Lucio 1997; Fortuna 2002; Ponce-Boutin et al. 2006; Vargas et al. 2006; Buenestado et al. 2008; Casas and Viñuela 2010), and this habitat quality definition also applies to many other bird species that inhabit farmland ecosystems, so that partridges would be considered as bioindicators of the conservation state and quality of farmland ecosystems and their species.

The availability of favoured habitat may affect breeding density and success, survival or food availability, which are also greatly influenced by agricultural or game management. Therefore, the implication of farmers, hunters and game managers is key to improve habitat quality, favouring food and shelter availability, acting over agricultural practices (e.g. avoiding or reducing the use of pesticides, increasing the availability of field boundaries and fallows or slightly delaying cereal harvesting; see also Chap. "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes") and hunting management practices (e.g. controlling hunting quotas; Caro et al. 2015). This is something that is very well known in select large private hunting estates that can manage agricultural and hunting resources at the same time and place, acting as true refuges for wild partridges. Sadly, this is a drop in the ocean, and in most of the red-legged partridge's range, agricultural and hunting practices are dissociated and applied by different people with different goals. For example, in agricultural landscapes the use of habitat by partridges and the way farmers manage their crops will determine the degree of exposure to pesticides in partridges (see Chap. "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes" for further details) and also for other co-occurring species. Therefore, it is urgent to act over habitat conservation and management, applying measures along the farmland ecosystems. In that way, it seems that an "eco-friendly" (bird- and insect-friendly) CAP (Common Agrarian Policy), acting over arable lands and agricultural practices that would favour partridges and diversity in farmland ecosystems, introducing new commitments and incentives for beneficiaries can be essential, and it should be considered a priority to maintain and improve biodiversity and the use of natural resources by humans in agrarian ecosystems. As we have mentioned several times throughout this chapter, one of the most relevant measures would be the maintenance and increase of field boundary surface in arable ecosystems, which has been pointed out as a key habitat for partridges (e.g. Aebischer and Potts 1994; Duarte 2012; Potts 2012), and many other species sharing this ecosystem. Areas with high-density field boundaries achieved higher yields, and where pollinators and pest-controlling insects reached the highest abundances, suggesting that increasing field boundary availability in European agroecosystems can promote functional biodiversity and enhance ecosystem services (Martin et al. 2019). Habitat improvements like favouring grass margins, beetle banks and mixes for game and other wildlife have shown to be positive in several locations for red-legged partridges (Italy, see Sect. "Habitat Improvement"; France, Ponce-Boutin et al. 2006; or the United Kingdom, Buner et al. 2019).

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Is Predation the Key Factor of Partridge Ecology and Management?

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_4

Introduction

The effect of predators on prey populations has long been a topic of much discussion (Holt et al. 2008). For some time, it was argued that the impact of vertebrate predators on prey was trivial since they took only diseased, weak or low-quality individuals, the so-called doomed surplus (Errington 1946). Increasing information indicate that under certain circumstances predators can indeed limit prey numbers. In birds, predation is currently perceived to be a crucial factor in determining prey population dynamics (Newton 1998; Roos et al. 2018; McMahon et al. 2020).

Although bird mortality due to predation is unlikely to always be compensatory, in the case of territorial species, birds lost to predation are frequently replaced from a reservoir of non-breeders (Newton 1998). Field experiments with gamebirds, waterfowl and waders, in which predators have been experimentally removed, indicate that these ground-nesting species can in fact be limited by predators (Newton 1993; Fletcher et al. 2010).

Despite the fact that a number of raptors are known to take relatively high proportions of European gamebirds, only under certain situations does this predation limit their populations and reduce hunting bags (Valkama et al. 2005). In Spain, evidence from hunting bag records indicate that the red-legged partridge (*Alectoris rufa*) has significantly declined in recent decades (Blanco-Aguiar et al. 2003). Hunters and game managers persistently suggest that predators have been the main cause of the scarcity of the species and of other small games (Delibes-Mateos et al. 2013; see Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). Given the complexity of factors affecting prey, *A. rufa* population changes are most likely due to a combination of factors, with predation being one of them (Blanco-Aguiar et al. 2003).

As most members of the pheasant family, Phasianidae (order Galliformes), red-legged partridges are prey to a wide variety of predators and have thus evolved *r*-selected life-history strategies to cope with high losses (Calderón 1977; Yanes et al. 1998; Valkama et al. 2005). As a consequence, red-legged partridges lay large egg clutches and have precocial young (Potts 1986; Ricci et al. 1990). This species also produces replacement clutches if first nests are lost (Casas et al. 2009). During favourable years red-legged partridges can produce two nests (double-nesting), one incubated by the laying female and the other by her mate (Casas et al. 2009). Additionally, as a means of diluting the effect of predation (Petrie and Moller 1991), intraspecific nest parasitism appears to be common among Galliformes (Yom-Tov 2001), including the red-legged partridge (Casas et al. 2006). Moreover, predation has also influenced other behavioural traits such as those affecting habitat selection (Partridge 1978) and even demographic tactics, with lower reproduction rates in areas with lower predation pressure (Souchay et al. 2018). Hence, anti-predator strategies may compensate for the effect of predation pressure up to a certain point. For a given breeding density, this threshold will depend not only on the nature of the anti-predator strategy but also on the interaction between habitat structure, vegetation characteristics and predator abundance (Ricci et al. 1990; Herranz et al. 2000).

In this chapter, we review the available scientific evidence of the incidence of predation, as well as the factors affecting this and other causes of mortality on red-legged partridge populations.

Predation and Other Mortality Causes in Red-Legged Partridges

The main mortality causes of red-legged partridges are predation, hunting, diseases and agriculture activities. The relative importance of these mortality factors depends on the land management practices predominant in an area (Villanúa et al. 2008; Buenestado et al. 2009; Casas and Viñuela 2010; Díaz-Sánchez et al. 2012). Natural predation can be the main cause of losses in non-hunted partridge populations such as in protected areas; average monthly bird survival can be as high as 92.6% compared to 85.8–87.1% in hunted populations (Buenestado et al. 2009). Mortality during a hunting season can be 52–54% compared to 0–10% predation in non-hunted areas (Buenestado et al. 2009). Nonetheless, in areas intensively managed for agriculture or hunting, where partridges can reach high densities, disease may account for an even larger mortality rate than that due to predation and hunting (Buenestado et al. 2009).

Predators of Red-Legged Partridges

Determining the species responsible for red-legged partridge predation is as important as knowing their impact. This is so because not all predators play the same role in an ecosystem, suffer the same level of threat or have the same ecological value. The relative abundance and ecological strategy of each predator can determine the impact on partridge populations as much as how frequent the prey appears in its diet. However, predation impact does not entirely depend on the predator since the population status of the prey and the phenological period of the cycle in which predation occurs can also be critical. Hence, a thorough examination of predation is required to determine its correct management; otherwise predators may suffer detrimental effects from unwarranted persecution (Herranz 2000; Arroyo et al. 2013).

Red-legged partridges are relatively uncommon in the diets of birds other than raptors such as the booted eagle (*Aquila pennata*), the golden eagle (*Aquila chrysaetos*) and the Bonelli's eagle (*Aquila fasciata*). However, the impact of these predators on partridge populations can be limited because (1) these predators usually occur in relatively low population densities; (2) partridge captures occur infrequently, i.e. not daily; and (3) alternative prey is often available (Ontiveros et al. 2005). In the case of mammalian predators, red-legged partridge remains in their diets have been reported to be less than 15%. For example, despite being considered one of the main predators of the species, partridge remains in the diets of the red fox (*Vulpes vulpes*) rarely exceed 5% (Díaz-Ruiz et al. 2013), though Herranz (2000) reported 12% in one locality.

Predators influence partridge populations during two different periods of the species' life cycle by preying on adult and subadult birds during autumn-winter or upon eggs, chicks or even breeding adults in the breeding season (Reynolds et al. 1992). However, the importance of predation and of the identity of predators during the breeding period is relatively well known, but data for the autumn and winter is often limited to studies of predator diets.

Predators During Spring-Summer (Breeding Season)

The main known bird predators of partridge chicks are the marsh and Montagu's harriers (*Circus aeruginosus* and *C. pygargus*), the booted eagle and some members of the crow family. Among the latter group, common magpies (*Pica pica*) are known to be one of the main predators of dummy partridge nests (Herranz 2000; Mateo-Moriones 2021), but most studies agree that partridge eggs make up only a small proportion of this corvid's diet (Martínez et al. 1992; Herranz 2000; Díaz-Ruiz et al. 2015).

Among mammalian predators, the Egyptian mongoose (*Herpestes ichneumon*) and some mustelids are known to impact local partridge populations by predating nests (Carpio et al. 2015). Rodents and some insectivores such as the European hedgehog (*Erinaceus europaeus*) also take partridge eggs (Yanes et al. 1998). However, the main partridge mammalian predators are those associated with humanized environments, e.g. free-roaming dogs and feral cats, important nest predators in farmlands (Duarte and Vargas 2001). The wild boar (*Sus scrofa*) can also play a role as a nest predator especially in forests and mixed Mediterranean scrublands (García and Vargas 2000; Carpio et al. 2014).

Reptiles are also known to take partridge eggs during the breeding period (Duarte 2012; Table 1). In the case of the ocellated lizard (*Timon lepidus*), its impact can be locally high (J. Duarte unpublished results), although Martínez de Castilla (1989) reported low egg predation by lizards in an area of high partridge density.

Predators During Autumn-Winter

Autumn-winter partridge predation is less common than during the breeding period. Despite the relative high number of predators that feed on red-legged partridges during this period, predation rates are generally low (Buenestado et al. 2009).

Table 1 Predators of red-legged partridges[a]. Percentages (%) show partridge occurrence in the predator diet

	Percentage (%)	
Predator	Autumn-winter	Breeding period
Raptors and other birds		
Iberian magpie (*Cyanopica cooki*)	–	<1% (E, C)
Bearded vulture (*Gypaetus barbatus*)[b]	<5%	–
Black kite (*Milvus migrans*)[b]	<5%	–
Black vulture (*Aegypius monachus*)[b]	<1%	–
Bonelli's eagle (*Aquila fasciata*)	<35%	–
Booted eagle (*Aquila pennata*)	<35%	<35% (C)
Carrion crown (*Corvus corone*)	–	<5% (E, C)
Common buzzard (*Buteo buteo*)	<10%	<10% (C)
Eagle-owl (*Bubo bubo*)	<10%	–
Egyptian vulture (*Neophron percnopterus*)[b]	<10%	–
Golden eagle (*Aquila chrysaetos*)	<35%	–
Northern goshawk (*Accipiter gentilis*)	<10%	–
Hen harrier (*Circus cyaneus*)	–	<15% (C)
Eurasian jay (*Garrulus glandarius*)	–	ND (C)
Little owl (*Athene noctua*)	<1%	<1% (C)
Common magpie (*Pica pica*)	–	<5% (E, C)
Marsh harrier (*Circus aeruginosus*)	–	<10% (C)
Montagu's harrier (*Circus pygargus*)	–	<5% (E, C)
Peregrine falcon (*Falco peregrinus*)	<10%	–
Raven (*Corvus corax*)	–	<5% (E, C)
Red kite (*Milvus milvus*)[b]	<1%	–
Short-toed eagle (*Circaetus gallicus*)	–	<5% (C)
Spanish imperial eagle (*Aquila adalberti*)	<10%	–
Eurasian sparrowhawk (*Accipiter nisus*)	–	<10% (C)
Tawny owl (*Strix aluco*)	–	<1% (C)
Mammals		
Common genet (*Genetta genetta*)	ND	ND (C)
Egyptian mongoose (*Herpestes ichneumon*)	<10%	<10% (E, C)
Feral cats (*Felis catus*)	–	ND (E)
Free-roaming dogs (*Canis lupus familiaris*)	–	ND (E)
Garden dormouse (*Eliomys quercinus*)	–	ND (E)
Hedgehog (*Erinaceus europaeus*)	–	ND (E)
Iberian lynx (*Lynx pardinus*)	<5%	–
Pine marten (*Martes martes*)	<5%	–
Polecat (*Mustela putorius*)	<15%	<15% (E, C)
Red fox (*Vulpes vulpes*)	<5%	<5% (E, C)
Rodents[b]	ND	ND (E, C)
Stone marten (*Martes foina*)	<5%	<5% (E, C)
Weasel (*Mustela nivalis*)	<10%	<10% (E, C)
Wild boar (*Sus scrofa*)	<5%	ND (E, C)

(continued)

Table 1 (continued)

Predator	Percentage (%)	
	Autumn-winter	Breeding period
Wildcat (*Felis silvestris*)	<5%	–
Reptiles		
Ladder snake (*Rhinechis scalaris*)	–	<5% (E, C)
Montpellier snake (*Malpolon monspessulanus*)	–	<10% (E, C)
Ocellated lizard (*Timon lepidus*)	–	<15% (E, C)

[a] Data from Valverde (1967), Calderón (1977), Donázar and Castién (1989), Palomares and Delibes (1991), Gil-Sánchez et al. (1994), Gil-Sánchez (1998), Herranz (2000), Duarte and Vargas (2001), López-Martín (2003), Duarte (2012), Díaz-Ruiz et al. (2013, 2015)

[b] Consumption also as carrion

ND, not determined; E, eggs; C, chicks

Almost any raptor or carnivore species can capture a partridge during this period as indicated by the large number of predator species reported (Table 1).

Despite the data presented here, quantification and assessment of predation rates on red-legged partridge remain poorly known. Even for the case of the more generalist predators, wrong conclusions can be easily drawn due to the variety of confounding factors involved. For example, there may be geographical differences in the predators' diet due to disparities in prey species composition (Díaz-Ruiz et al. 2013), contrasts in prey abundance cycles (Donázar and Castién 1989), habitat types inhabited by the predator as well as the influence of the age and gender of the predator itself (Whittingham and Evans 2004).

Causes of Mortality and Factors Affecting the Incidence of Predation at Each Life-History Stage

Understanding the causes of death and determining mortality rates during each life cycle stage of the red-legged partridges is an important first step in reversing population declines. However, causes of mortality are not always easy to identify, and the different study methods used for this often make comparisons difficult.

Incidence and causes of mortality vary in the different biological stages of the red-legged partridge (Table 2). For instance, agricultural activities are a negligible source of mortality for adult birds, but they can be the main cause of nest loss in some areas (Casas and Viñuela 2010). Moreover, mortality rates and causes of death of adults and young vary throughout the year, according to changes in the species' behaviour and the influence of external factors (Duarte et al. 2008; Buenestado et al. 2009; Mateo-Moriones 2021). For example, predation suffered by the adults during the reproductive period is usually higher than during winter months since partridges are more exposed to predators during this period but are less vulnerable when gathered in wintering groups. On the other hand, mortality in hunted populations

Table 2 Survival rates and proportion of deaths due to predation in each life stage of the red-legged partridge according to available studies

Stage	Area	Sample size (n)	Method	Survival	Period	% Deaths due to predation[a]	Main predators	References
Nests	S England	63	Nest monitoring	59%	Nesting	–	Not mentioned	Rands (1988)
	S France	63	Radio-tracking	38%	Nesting	59%	Carnivores	Ricci et al. (1990)
	Central France	39	Radio-tracking	41%	Nesting	–	Carnivores	Léonard and Reitz (1998)
	NE Spain	51	Radio-tracking	37%	Nesting	66%	Carnivores, raptors	Mateo-Moriones (2021)
	Central Spain	97	Radio-tracking + nest monitoring	36%	Nesting	21%	Not mentioned	Casas and Viñuela (2010)
	S Spain	165	Nest monitoring	79%	Nesting	100%	Carnivores, reptiles	Duarte and Vargas (2001)
Hatchlings	NE Spain	61	Radio-tracking	66%	14 days	>48%	Raptors, carnivores	Mateo-Moriones (2021)
	S Spain	11	Radio-tracking	9%	10 days	–	Corvids	Duarte and Vargas (2004)
Young	S Spain	152	Brood monitoring	56%	4 months	–	Raptors	Duarte (1998)
	NE Spain	49	Radio-tracking	51%	4 months	>53%	Carnivores, raptors	Mateo-Moriones (2021)
Subadult	Central-S Spain	45	Radio-tracking	79–90%	1 month	15–65%	Carnivores, raptors	Buenestado et al. (2009)
Adult	Central France	99	Radio-tracking	91%	1 month	–	Carnivores, raptors	Léonard and Reitz (1998)
	Central Spain	89	Radio-tracking	89%	1 month	74%	Carnivores, raptors	Casas et al. (2012)
	NE Spain	167	Radio-tracking	84–95%	1 month	>88%	Carnivores, raptors	Mateo-Moriones (2021)

(continued)

Table 2 (continued)

Stage	Area	Sample size (*n*)	Method	Survival	Period	% Deaths due to predation[a]	Main predators	References
	Central-S Spain	106	Radio-tracking	86–94%	1 month	15–65%	Carnivores, raptors	Buenestado et al. (2009)

[a] % of deaths due to predation from the total number of dead animals

is restricted to the autumn-winter hunting season (Duarte et al. 2008; Buenestado et al. 2009; Mateo-Moriones 2021).

Mortality During Nesting

Predation is a key factor affecting the success of red-legged partridge nests in many parts of the species' range (Fig. 1). Duarte and Vargas (2001, Table 2) reported a predation rate of 20%, mostly by mammals in Andalusian olive groves (S Spain). Contrastingly, Mateo-Moriones (2021) showed that 63% of nests in a study in Navarra (NE Spain) did not hatch; predation accounted for 66% of the losses, including 20% due to predation of the incubating parent (Fig. 2). Similar high nest failure rates (64%) have been reported by Casas and Viñuela (2010) in agrarian pseudo-steppes in central Spain, though most losses here were caused by agricultural practices (56%) rather than by predators (Fig. 3). These authors found a direct relationship between habitat simplification and nest failure and between more complex habitats and nest predation. The authors' explanation was that the lack of optimal nesting habitat might force partridges to select suboptimal areas, therefore increasing nest vulnerability.

Fig. 1 Red-legged partridge nest partially predated and abandoned by the incubating partridge

Fig. 2 Nest remains and plucked feathers from the incubating adult, killed by a carnivore

Habitat structure can be linked to nest and chick predation (Calderón 1977; Rands 1988; Herranz 2000; Duarte et al. 2008). For example, ground vegetation height and cover around nests have been described to be the main factors affecting nesting success of red-legged partridges in various countries (Rands 1988; Ricci et al. 1990). In France and the UK, hedgerows and other permanent field boundaries are important nesting habitats for this species. In spite of this, the reproductive success of partridges nesting close to the edge of cereal fields is negatively affected by higher predation associated with linear habitats (e.g. Ricci et al. 1990). However, in the Iberian Peninsula, hedgerows are scarce, and field boundaries are instead created by linear annual vegetation strips, known as *lindes* (Fig. 4). Often, the highest arthropod and floral diversity can be found just along the field boundaries (Thomas and Marshall 1999), so partridges obtain a clear benefit from living close to these edges. In the agrarian pseudo-steppes of central Spain, nests located on these *lindes* are more successful than nests in cereal fields, perhaps because agricultural practices (mainly harvesting) can cause high nest failure (Casas and Viñuela 2010). The high nesting success associated with *lindes* may explain the higher partridge numbers in landscapes containing abundant and well-preserved *lindes*, as well as the much lower numbers in intensively farmed areas (Casas and Viñuela 2010).

At a landscape scale, the red-legged partridge will select breeding areas of higher food availability such as cultivated areas. However, reproductive success here is comparatively lower than within scrublands (Carvalho and Borralho 1998). Not

Fig. 3 Adult partridge killed by machinery while incubating a nest during ploughing

surprisingly, one common management system to improve partridge productivity in open areas is to increase cover to diminish intraspecific competition for shelter and especially reduce nest and chick predation (Ricci et al. 1990; Carvalho and Borralho 1998).

Predation rates of nests and incubating females vary among red-legged partridge populations (e.g. 3–80%; 12–50%, respectively) due to differences in habitat structure, predator abundance and diversity (Potts 1980; Tapper et al. 1982; Rands 1988; Ricci et al. 1990; Herranz 2000; Casas and Viñuela 2010; Mateo-Moriones 2021). Therefore, the type and quality of the habitat that may be used as shelter among the feeding areas may be critical for the future of the species, inevitably associated with humanized landscapes.

Mortality of Hatchlings and Early Chicks

Chick mortality is highest during the first days after hatching but drops as chicks grow (Potts 1980; Mateo-Moriones et al. 2012a; Table 2). Because hatchlings are especially vulnerable to predation, this stage represents a critical bottleneck for red-legged partridge populations (Duarte and Vargas 2002; Duarte et al. 2008;

Fig. 4 Linear annual herbaceous vegetation strips among cultivated plots (*lindes*) are the preferred nesting habitat for breeding partridges in agricultural areas. Where these patches are too small or narrow, nest and chick predation can be a limiting factor for the birds

Mateo-Moriones 2021). Identifying causes of death at this stage is critical to understand population trends.

In one study, Herranz et al. (2000) found a significant negative relation between brood size and the abundance of canid predators (foxes and dogs) and carrion crows (*Corvus corone*). Information on hatchling mortality remains scarce due to methodological difficulties. Two main methods are usually employed: (1) direct brood observations over time and (2) radio-tracking of hatchlings (Fig. 5). Hatchling losses, estimated from brood observations in olive groves during the summer, ranged between 28% and 43% (Duarte 1998). Radio-tracking of hatchlings, although not exempt from methodological challenges (Mateo-Moriones et al. 2012a), permits the estimation of mortality rates and in some cases also the causes of death. Using this method, chick survival rate ($n = 11$ chicks) during the first 10 days after hatching was estimated as 9% in a Mediterranean landscape of southern Spain (Duarte and Vargas 2004). In Navarra (NE Spain), 66% of 61 radio-tagged hatchlings survived to 2 weeks of age (Mateo-Moriones 2021). Predation, with at least 22% of deaths, was the main identified cause of death, although this value could be underestimated because of signal loss of 20% of transmitters (Mateo-Moriones 2021; Table 2).

Explanations for the increased predation of chicks are largely linked to lack of vegetation cover, such as in homogenous croplands. Less cover limits the availability of refuge areas for chicks to hide allowing aerial predators to find them more

Fig. 5 Radio-tracking of red-legged partridge hatchlings is a useful method for estimating rates and causes of mortality during the first weeks of age, a critical stage of red-legged partridges

easily (Duarte and Vargas 2002). Furthermore, more open environments force chicks to have to travel further in search of food and water, thereby weakening their physical condition. In these habitats, arthropod abundance is scarce due to the use of pesticides (Potts 1980). Some pesticides reduce partridge egg size and chick body condition at hatching (Lopez-Antia et al. 2013), which can have a large influence on chick survival in the wild, where animals may suffer from food limitation and predation risk. Moreover, adverse effects of pesticide exposure on chick growth rate and cellular immune response have been detected (Lopez-Antia et al. 2015), and this could indirectly increase their predation risk.

Mortality of Late Chicks

Partridge chicks become less vulnerable to predators when they are able to fly around 1 month old. At this point, chicks are also less likely to be affected by agricultural activities, such as harvesting, since this will have finished by then. However, chicks are still at risk from several other factors (Potts 1980; Mateo-Moriones 2021). The simplified landscape resulting from agricultural intensification increases exposure of chicks to predation due to the reduction in food and shelter. During summer, mortality of 2–5-month old partridges can be as high as >50% due to predation, starvation or dehydration (Duarte and Vargas 2002; Guzmán et al. 2020). However, significant differences among estates with contrasting landscape and management characteristics have been described (Buenestado et al. 2009; Mateo-Moriones 2021; Table 2). For instance, Mateo-Moriones (2021) reported that the main cause of mortality of young partridges in Navarra (NE Spain) was predation by carnivores and raptors, affecting 13% of tagged birds (Table 2), though the effect of hunting could not be estimated in this study because radio-tracking ended before the hunting season. By monitoring covey size and young/adult ratio along the breeding period, Guzmán et al. (2020) estimated 50% chick mortality between hatching and fledging in Andalucía and Castilla-La Mancha (southern and central Spain), with marked effects of weather, year and land use.

Adult Mortality

Mortality of adult partridges is better known than for chicks. The relative incidence of predation and other causes of mortality depend chiefly on land management and vary along the year (Duarte et al. 2008; Buenestado et al. 2009; Souchay et al. 2018; Mateo-Moriones 2021). Predation is the primary cause of partridge mortality in less managed areas, such as unhunted areas. In central-southern Spain, mortality due to predation was positively related to predator richness (Buenestado et al. 2009). In Navarra (NE Spain) adult partridges suffered the highest mortality rates during the mating and incubation periods, while the lowest number of deaths occurred in winter (Mateo-Moriones 2021). Predation was the main cause of mortality throughout the year, affecting over 35% of radio-tagged partridges, mainly during mating and incubation. However, in this study, radio-tracking did not include the hunting season, when losses due to humans can outnumber those due to natural predation (Buenestado et al. 2009; Souchay et al. 2018). Indeed, hunting is an important cause of death of subadult and adult partridges in autumn-winter, with lower monthly survival in intensive hunting estates (75%) compared to non-intensive estates (80–90%) or non-hunted areas (93%, Buenestado et al. 2009). Females seem more affected by mortality due to hunting than males (Souchay et al. 2018), probably due to a poorer body condition, lighter muscles and less power to flee away (Nadal et al. 2018). Compensation may occur between predation and hunting mortality, as suggested by similar survival rates in several sites of France with different mortality sources (Souchay et al. 2018), although this point would require a stronger assessment.

The relationships between physical condition, habitat characteristics and survival of adult red-legged partridges have been analysed in four different areas of Spain (Buenestado et al. 2009). Higher survival rates were typical of partridges with better body condition, especially those in areas with more diverse vegetation and a higher proportion of habitat edges. These habitat features were also negatively associated with mortality due to predation and disease, indicating that body condition is a critical factor for the species. Since food availability did not clearly affect the spatial behaviour within the home range, predation risk was the most important factor related to space use within home ranges (Buenestado et al. 2008). At the landscape scale, partridges in agricultural areas avoided both low cover and woody patches, while in wilder habitats, the species was associated with high cover with some crops or natural grassland. Hunting mortality decreased with the proportion of scrubland and increased with the proportion of agricultural land (Buenestado et al. 2009). Thus intimidation or perceived risk effects can be more significant than direct effects and directly result in a lower body condition for birds, making them more vulnerable to predators, hunting, parasites or diseases (Buenestado et al. 2008, 2009). In NE Spain, partridge survival was higher in areas with a lower proportion of croplands and with patchier habitat, corresponding to higher availability of refuge against predators (Mateo-Moriones 2021).

Hunting and predation are usually the main causes of mortality in unmanaged areas, whereas diseases are an important cause of mortality in intensely managed areas (Buenestado et al. 2009; Millán 2009). The latter may become an important mortality factor when aggregation of partridges occurs because refuge or good quality patches are scarce and/or managers provide water and food suppliers, which increase contact rates and therefore parasite transmission and disease outbreaks (Millán 2009; see Chap. "Health Monitoring and Disease Control in Red-Legged Partridges"). In such situations, partridge aggregation increases but also disease and/or parasites, in turn making gamebirds also more vulnerable to predators (Hudson et al. 1992; Millán et al. 2002).

Behavioural responses of prey to predation risk (e.g. movement patterns and habitat use) increase the cost for the individual in terms of lower survival, slower growth rate and lower reproduction success. As a result, these responses may have an even more important effect on population dynamics than predation itself (Preisser et al. 2005). Nonetheless, the level of intimidation induced by predators will depend on the structure and type of habitat. Contemporary land use patterns have transformed continuous habitats into a diversity of habitat mosaics where patches vary in size, quality and suitability (e.g. Dunning et al. 1992). This variation in habitat quality will affect the survival of birds that are sequestered in remnant patches of favourable habitat, which also differ in their capacity to offer shelter against predators.

Although the direct effect of predators is often considered as the only important element affecting partridge populations, predation risk as perceived by the prey species is often overlooked. This effect can be even more important than the removal of animals. Unconsciously, gamekeepers have traditionally used predation risk as a valuable tool for partridge management. For example, areas traditionally considered as the most favourable for red-legged partridges are those characterized by undulations or small hills where partridges can easily take flight (Potts 1980). This is related to the observation that habitat quality and structure are major factors determining the distribution and density of gamebirds (Nösel 1992). More specifically, habitat heterogeneity, habitat diversity and connectivity between fields influence the abundance of red-legged partridges in Europe (Potts 1980; Lucio and Purroy 1992; Vargas et al. 2006; Buenestado et al. 2008; see Chap. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?")

affecting the survival of the species (Buenestado et al. 2009). Food abundance and risk of predation determine the persistence of partridges in these sites. Although the effects of food availability and predation risk are difficult to disentangle, food availability has an obvious influence on physical condition, which in turn may determine behaviours and habitat use that expose an individual to predators (Lima and Dill 1990).

Partridge Restocking and Predation

Restocking is widely used as a management tool for recovery of partridge populations (see Chap. “Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing”). However, high mortality due to predation is considered the main cause for the elevated failure of restocking programmes (Gortázar et al. 2000). A number of release techniques such as liberating birds of different ages, acclimatization in pens, direct releases, habitat improvements, water and food supplementation, varying release periods, captive breeding programmes or even anti-predator training have been tested for their relative efficacy (Gortázar et al. 2000; Millán et al. 2003; Pérez et al. 2004, 2015; Alonso et al. 2005; Duarte et al. 2010; Gaudioso et al. 2011a, b). None of these techniques have reduced the recorded high mortality rates.

Predation follows a common pattern in most of restocking experiences: high mortality as well as multiple predation occurs during the first few weeks, or even days, after release (Gortázar et al. 2000; Souchay et al. 2018). The identity of predators depends on the habitat where the release takes place. In most cases, raptors and carnivores contribute similarly to partridge deaths (Gortázar et al. 2000; Duarte et al. 2010; Pérez et al. 2015). Although the red fox appears to be the main predator, other species such as the common genet (*Genetta genetta*), the Eurasian badger (*Meles meles*), the stone marten (*Martes foina*), the northern goshawk (*Accipiter gentilis*), the golden eagle or the Bonelli’s eagle can be locally important (Duarte et al. 2010).

The release habitat as well as the partridges’ capacity to adapt to the new conditions may play a key role in the outcome of releases. Birds raised in captivity are more vulnerable to predation since they generally have reduced anatomic and physiologic skills (Millán et al. 2001, 2003; Pérez et al. 2010, 2015), have greater parasite loads (Millán et al. 2004) and are more vulnerable to diseases (Villanúa et al. 2008), which increase their vulnerability. More significantly, released birds are raised in farms, where red-legged partridges are usually hybridized with other partridge species (mostly *A. chukar*) in order to increase their productivity (Casas et al. 2013). Such hybridization may determine the expression of maladaptive phenotypes which suffer higher predation than pure wild partridges (Casas et al. 2012). Furthermore, captive-bred partridges spend less time vigilant and more time feeding than wild ones (Rantanen et al. 2010b). Contrarily, Martínez de Castilla and Pastor (2002) found similar anti-predator behavioural responses of wild and farm-raised partridge chicks when challenged with simulated aerial and terrestrial predators in captivity tests. In addition, hybrid partridges generally used in restocking (Blanco-Aguiar et al. 2008; see Chap. "Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization") have lower levels of induced tonic immobility, a passive anti-predator behavioural trait, than pure red-legged partridges (Campo et al. 2015).

The presence of water dispensers and feeders, commonly used during repopulations, attracts both released birds and predators (Sánchez-García et al. 2015). Something similar seems to happen with habitat management; non-selective clearings and extensive sowing patches may attract the birds during the days after release, but they also attract predators. These facts increase the risks of predation and disease transmission of released partridges.

Studies regarding habitat selection and predation of released partridges during repopulations are still scarce. Birds tend to avoid forests and dense scrublands, selecting clearings, roadsides, firebreaks, boundaries and croplands (Duarte and Fa unpublished results). However, most dead birds are found within patches of the avoided habitats (Duarte et al. 2010), probably because predators carry them away from selected habitats and releasing points after capture. This occurs in cases of multiple predation caused by foxes, which cache surplus-killed prey, and when raptors carry their prey to perching points away from the capture point.

Predation by raptors usually occurs in open areas, whereas carnivore mammals mainly prey in denser or covered areas or in boundaries (Villafuerte and Moreno 1997). These patterns create a considerable challenge for the released birds. It is likely that the low fitness of these birds (Casas et al. 2012) results in an additive factor to the habitat unsuitability increasing mortality.

The high mortality of released birds during the first days after release is also related to their spatial behaviour. During this period, birds explore different habitats surrounding the release point, including the scrublands where predation risk by carnivores is high (Duarte and Fa, unpublished results). This pattern agrees with the high rate of mortality in all the release experiences. In addition, partridges are not used to the place of release, and finding food is difficult for them. Since partridge survival decreases after short periods of starvation (Rodríguez et al. 2005), this contributes to the low success of restocking. After the second or third week, the surviving birds increase their foraging areas and use more suitable habitats, not returning to the releasing point (Gortázar et al. 2000).

Restocking is a highly questionable management tool for recovering red-legged partridge populations due to its little success (see Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"), the use of farm-bred birds with an uncertain genetic pool, the associated high predation and the likely impact on wild populations (Casas et al. 2016). The effects of habitat management are still poorly understood. Recent experiences have shown conflicting results, probably because of scale dependence of management and predation associated with the habitat that is being managed (Bro et al. 2004). Consequently, the habitat where the repopulation is being carried out might turn into an ecologic trap (Rantanen et al. 2010a), producing the typical high mortality associated with this management measure.

The Role of Other Preys: Is Red-Legged Partridge Affected by Hyperpredation Processes?

Holt (1977) coined the term "apparent competition" to describe the indirect ecological interaction between two prey species and a shared predator. Hyperpredation may be considered a special case of apparent competition which results from an enhanced predation pressure on a secondary prey due to either an increase in the abundance of the predator population caused by an abrupt increase in the abundance of its main prey or a sudden drop in the abundance of the main prey (Courchamp et al. 2000).

The wild rabbit (*Oryctolagus cuniculus*) and the red-legged partridge have similar habitat preferences and ground-dwelling behaviour; therefore they occur in sympatry in most of the Iberian Peninsula. Although there is no evidence of direct competition between these two species, they share a large proportion of predators (Moleón et al. 2008). In addition, both are highly appreciated as game species, with hunters being probably the main "predator" of both wild rabbit and red-legged partridge in Spain. In addition, the rabbit is usually the staple prey of most Iberian vertebrate predators, whereas the red-legged partridge is a secondary prey. This suggests that the population dynamics of these species could be shaped by the interaction between both prey and predators, which might generate apparent competition between rabbits and partridges in a case of hyperpredation.

The sharp decline in rabbit populations after the arrival of the rabbit hemorrhagic disease (RHD) could have produced a change in predator pressure towards secondary prey species such as the red-legged partridge. Moleón et al. (2008, 2013) suggested that the RHD outbreak could have caused synchronized dynamics in the abundance of rabbit and the hyperpredated species (partridge) and predicted three dynamic phases; pre-outbreak, post-outbreak and post-immunization. These authors supported their hypothesis on national hunting bag records and local studies of variation in the predation rate before and after the arrival of RHD. They reported cross-species correlation in the abundance of both prey and abrupt changes in the rabbit and partridge time series simultaneous with RHD emergence, suggesting synchronized prey population dynamics at a large spatio-temporal scale. They described an increase of partridge predation rate after RHD emergence in three raptor species: the Bonelli's eagle, the northern goshawk and the golden eagle in four local study areas. This suggests a disruption of raptor-prey interaction, favouring a nationwide population decline of red-legged partridges.

The underlying limitations of hunting bag records used and some interpretations may not be robust enough to assert that raptors have caused the decline of partridge populations in the Iberian Peninsula (Blanco-Aguiar et al. 2012). The increase of massive releases of red-legged partridges in the mid-1990s could have magnified the

Spanish hunting bag records (Blanco-Aguiar et al. 2008; Caro et al. 2014), leading to an apparent partridge population recovery that mimics the post-immunization phase. The number of partridges released in Spain, estimated in 4–5 million per year (Arroyo and Beja 2002; Caro et al. 2014), is higher than the size of the wild breeding population, estimated in 1.7–3.7 million pairs (Blanco-Aguiar et al. 2004), and the mean return on harvest of released partridges in intensive estates is estimated around 45% (Díaz-Fernández et al. 2012). This means that national bag records might be highly affected by game releases (but see Moleón et al. 2013). In addition, independent data of rabbit and partridge trends contradict the trends of Spanish bag records. For instance, the Spanish bird monitoring programme (SACRE, SEO-BirdLife 2013) shows a negative trend for the red-legged partridge during the period 1998–2003 (overlap range with bag records), whereas bag records show a positive pattern for the same period, a difference likely due to released birds. In a similar way, rabbit population trends in the Iberian area of the greatest rabbit abundance point to an overall reduction of rabbit populations (Delibes-Mateos et al. 2009).

The same pattern observed for both species at a national scale should be expected at regional scales, although with a higher heterogeneity in bag record trends (Moleón et al. 2013). However, results did not follow the predicted epidemiological phases in those provinces where predation studies were performed. For instance, the partridge population increased in Catalonia (NE Spain), contrarily to the epidemiological model expectations (Blanco-Aguiar et al. 2012). In Navarra (NE Spain), where the pattern was similar to national bag record trends, there was no evidence of an increase of predation rate by Bonelli's eagle after RHD emergence (Blanco-Aguiar et al. 2012). On the other hand, feeding data are not strong enough to conclude that the cause of the observed pattern is produced by a changing predation pressure of raptors (Blanco-Aguiar et al. 2012). In this sense, Herranz et al. (2000) did not find a significant relationship between raptor abundance and partridge density or average covey size in 30 estates of central Spain. Only two of the four raptor diet studies provided support to the expectation of an increased consumption of red-legged partridge after the RHD arrival. However, this increase is not enough to produce a negative effect on partridge densities (Valkama et al. 2005), which would require that predation rate exceeds production rate (Newton 1998). Large-scale studies of diet variation on Bonelli's eagle did not detect any increase of red-legged partridge predation (Moleón et al. 2009). Results from another detailed study indicate that Bonelli's eagle responded functionally but not numerically to changes in rabbit and partridge density (Moleón et al. 2012). In the absence of a numerical response, raptors' role as a regulating factor of rabbit and partridge populations should be weak, and such a regulation has not been demonstrated in the case of the red-legged partridge and raptors. Therefore, it seems unlikely that raptors may have a regulatory effect on red-legged partridge populations, and this could be also reflected at the national level. Although Moleón et al. (2013) only explored hyperpredation by shared raptors, they do not rule out that other predators such as mammalian carnivores could be also involved in hyperpredation processes. This would open the door to suggest that hunters, with a wide range distribution and potentially stronger extractive pressure, could also be the direct cause of these processes, but this will require further research.

How to Reduce Red-Legged Partridge Mortality to Predators?

Predator control is known to be effective for the conservation of vulnerable bird populations (Smith et al. 2010) and for increasing the number of some gamebird species when performed intensively (Tapper et al. 1996). However, its effect in ground-nesting birds is smaller than for other birds (Smith et al. 2010). Although predator control can produce short-term results, such as an improvement of breeding success, its effectiveness in the long-term seems limited, especially for ground-nesting birds (Nordström 2003).

Predator control is a widespread game management practice for the red-legged partridge; it is employed in 90% of small game estates in central Spain (Delibes-Mateos et al. 2013). Nevertheless, its effects on red-legged partridge populations are not clear (Díaz-Fernández et al. 2013), according to several studies performed in both its natural range (Ricci et al. 1990; Herranz 2000; Herranz et al. 2002; Mateo-Moriones et al. 2012b) and other areas where the species has been introduced (Potts 1980; Rands 1988). For instance, the effect of controlling predators on red-legged partridge nesting success was experimentally studied in France (Ricci et al. 1990). The rate of predation on nests was significantly lower (41%) in areas where gamekeepers controlled predators than in areas without predator control (79%; Ricci et al. 1990). In England, Potts (1980) found that brood production rate of red-legged partridge was higher (0.53) in estates with predator control than in estates without this management (0.33). In contrast, high losses of red-legged partridges have been found in other areas with predator control. For instance, Rands (1988) estimated that about 39% of red-legged partridges nests were destroyed by predators in areas of southern England where red foxes were controlled.

The effects of experimental common magpie control on partridge nesting success were studied in central Spain using artificial nests (Herranz 2000; Herranz et al. 2002). As expected, nest predation was lower in the magpie control area (47%) than in the area without magpie control (75%). However, the lower predation by magpies in the area where magpies were controlled was partially compensated by a higher incidence of canids. Brood size and number of chicks per adult were also higher (although not significantly) in the area where magpies were controlled (Herranz 2000; Herranz et al. 2002).

The effectiveness of generalist predator control on the survival of red-legged partridges was also experimentally assessed in NE Spain (Mateo-Moriones et al. 2012b). Adult partridges and their chicks were radio-tracked, and their nests were monitored on two hunting estates over 2 years. Generalist predators (mainly foxes but also magpies) were selectively controlled on half of each estate the first year, and the treatment was reversed the second year. Predator control did not significantly improve the survival of adult partridges and nests, but chick survival was significantly improved in the areas with predator control (Mateo-Moriones et al. 2012b).

The effects of intensive predator control found in some experimental situations (Tapper et al. 1996; Fletcher et al. 2010) contrast with the limited effect often reported in real-life management situations (Arroyo and Beja 2002; Delibes-Mateos et al. 2013). For instance, in a study based on questionnaires and field bird surveys in 48 hunting estates in central Spain, Díaz-Fernández et al. (2013) assessed the relationships between different management tools and red-legged partridge abundance and productivity. While addition of feeders and water points were positively related to partridge abundance and productivity, fox and magpie control intensities were not related to these parameters. Moreover, magpie control intensity was negatively related to partridge productivity, and fox control was negatively related to partridge abundance, although these variables had a relatively low importance compared with other factors such as habitat management or other management tools. A possible explanation of this lack of effect is an interaction between predator control effectiveness and other variables, such as the habitat.

Some measures indirectly affecting the effects of predation could be employed as alternative to predator control. For instance, the incidence of predation can be regulated through habitat management, taking into account what is known about the habitat features associated with lower predation (Rands 1988; Ricci et al. 1990). Moreover, habitat management can be used as a tool for improving hen condition and hence breeding success (Buenestado et al. 2009). A protocol for choosing among measures to reduce nest predation of red-legged partridge in Mediterranean farmlands of France was proposed by Ricci et al. (1990). The aim was reducing nest vulnerability to predation by improving the quality of nesting habitats. Ricci et al. (1990) recommended increasing the percent cover and augmenting the number of openings. They also recommended against strip grasslands, as they found a negative effect on nesting success. However, these recommendations suggested for improving nest success in France are not supported by results of recent studies on red-legged partridge in the Iberian Peninsula. There, *lindes* are an optimal nesting habitat, and nest predation is much lower there than in open cereal fields (Casas and Viñuela 2010). Therefore, *lindes* recovery could be an effective alternative measure to predator control for reducing nest predation in agrarian pseudo-steppes, the main habitat of the red-legged partridge in the Iberian Peninsula. Moreover, food for partridge chicks, mainly insects and weed seeds, is abundant in these *lindes* and favours chick survival. On the other hand, habitat management aimed at increasing landscape diversity and reducing plot size could be a measure for improving adult partridge body condition resulting in an alternative to predator control for reducing predation on adult partridges (Buenestado et al. 2009). Managers are usually reluctant to use these indirect ways for reducing predation because of their immediate high cost compared to traditional predator control. However, habitat management has the great advantage of being a long-lasting measure, whereas traditional predator control measures need to be repeated year after year if their effects have to be maintained over time. Habitat management is often beyond the reach of hunters and game managers since they do not usually own the land. Therefore, despite that habitat management is a preferable way to reduce partridge predation over predator control in the long term, socio-cultural aspects of partridge management are often behind its rare implementation (see Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain").

The effectiveness of modifying predator behaviour for reducing predation on partridge nests without the need of reducing predator abundance has been recently tested. Tobajas et al. (2020) proved that conditioned food aversion (CFA) can reduce red-legged partridge nest predation by red foxes in central Spain, by using a before-after control-impact design and artificial nests treated with thiram as a conditioning aversive and GPS-tagged red foxes. CFA decreased artificial nest predation by foxes, although some compensation by other predators occurred. Most (78%) of treated foxes stopped nest predation after treatment. Partridge productivity was higher in thiram-treated areas than in control areas, and partridge density after treatment increased more in thiram-treated areas (193–292%) than in control areas (1.8–99%). This study shows that CFA is a potential non-lethal tool for improving red-legged partridge populations by reducing the effect of predation on their nests, although larger-scale studies are required before its application in real management situations.

The Role of Predation on Population Dynamics of Red-Legged Partridge

The effect of predation on partridge population dynamics varies with the stage of the partridge life cycle. The role of predation on population dynamics can be approached through demographic models. Such a model for the red-legged partridge was built using demographic parameters estimated in Navarra (NE Spain; Mateo-Moriones 2021). According to this model, the highest sensitivity of the population rate of increase corresponds to predation on adults during the pre-reproductive and incubation periods, and the highest elasticity corresponds to rates of nest loss and to predation of chicks under a month of age (Mateo-Moriones 2021). Provided the high elasticity of the population rate of increase to rates of nest loss and predation of chicks under a month of age and the high values of these parameters estimated in the field, they have a high potential for being improved in order to recover partridge populations. Accordingly, chick survival rate was the demographic parameter best explaining annual record fluctuations of grey partridge (*Perdix perdix*) populations during 200 years (Potts and Aebischer 1995). Therefore, chick survival seems to be a key parameter for population dynamics for this close species. Nest predation rate is also an influencing parameter on grey partridge dynamics. Simulation modelling for this species showed that a reduction in chick survival rate from 49% to 32% had a little effect on spring stocks as long as nest predation was controlled but that stocks collapsed when nest predation control was relaxed (Potts and Aebischer 1995).

Table 3 Finite rate of increase (λ) of red-legged partridge populations according to simulation models under different scenarios of predation: the current scenario of average demographic parameters estimated in NE Spain (λ_0) and two hypothetical scenarios resulting from partial (λ_1) and high (λ_2) reduced predation expected as consequence of habitat management. Three hunting scenarios have been considered: no hunting (0%), the average hunting pressure estimated in NE Spain (23% of autumn population) and increased hunting pressure (40%). Values corresponding to positive population growth are shown in bold

	Scenarios of predation		
	Current	Partial reduction	High reduction
Hunting level	λ_0	λ_1	λ_2
No hunting (0%)	0.846	**1.172**	**1.605**
Estimated (23%)	0.656	0.910	**1.257**
Increased (40%)	0.518	0.722	0.994

According to the mentioned demographic model for the red-legged partridge, the rate of nest loss was the only parameter which its isolated improvement would allow the population to increase, even keeping the remaining demographic parameters unchanged (Mateo-Moriones 2021). Nesting success has been identified by previous studies as a key factor of partridge population dynamics (Potts 1980; Rands 1986). Nest success, estimated as 47% as average in Navarra (range 32%–68%), could be improved by reducing losses due to predation and agriculture, the main causes of nest failure (Duarte and Vargas 2001; Casas and Viñuela 2010; Mateo-Moriones 2021). Reducing hatchling mortality would also allow population stability, although this would require mortality values close to zero, a highly unlikely scenario. Positive rates of population growth could be also achieved by simultaneously improving survival of adults, chicks and nests, reaching parameter values within the ranges estimated in the field, even allowing some hunting activity within the range of yields currently estimated in Navarra (Table 3). This mortality reduction of adults, nests and chicks could be attained through management measures tending to lower predation risk, such as recovery of *lindes* (field edges), nesting cover and refuge for chicks and adults (Casas and Viñuela 2010; Buenestado et al. 2009; Mateo-Moriones 2021), with no necessary resort to predator control measures. Taking into account the relationships between the risk of predation and habitat features (see above), some habitat management, such as the increase of *lindes*, habitat diversity and patchiness, could reduce the levels of predation necessary to revert current negative trends of red-legged partridge to positive population growth, even allowing some level of hunting activity (Table 3).

Predation and the Future of Red-Legged Partridge Populations

Most studies agree on the importance of habitat heterogeneity for the survival of red-legged partridges (see Chap. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?"). However, the global tendency in the last decades is the growth of extensive cultivated areas, with an evident decrease of small patches and reduction of *lindes* between cultivated lands as a result of more powerful ploughing machinery, making the landscape of the red-legged partridge range more homogeneous. Unfortunately, it seems that this reduction in environmental heterogeneity will persist in the future, suggesting that the current decline of red-legged partridge populations will also continue (Blanco-Aguiar et al. 2004). On the other hand, it is clear that habitat quality indirectly affects the vulnerability of gamebirds to predation (Hudson and Rands 1988; Buenestado et al. 2009). In this situation, the shrinking linear *lindes* will be the selected areas for nesting, becoming an ecological trap (Herranz 2000; Battin 2004) because of an excessive predation on nests and chicks. Even if predators are controlled, the high-perceived risk of predation in the remaining simpler habitats will accelerate the decline of the species. Such decline might be reversed by recovering mosaic landscapes or increasing safe areas (Buenestado et al. 2009; Casas and Viñuela 2010), reducing partridge vulnerability to hunters, predators, parasites and diseases. Maximizing the value of habitats for foraging birds has largely focused on practical measures to increase food abundance, but food accessibility, predation and perceived predation risk might play more important roles. This supports the hypothesis that habitat management may be an effective tool for reducing the negative influence of predation on partridge population dynamics (Arroyo and Beja 2002). Additionally, the effect of habitat management during breeding is double: increasing hen and chick condition and reducing risk of predation. Under this scenario, predator control, the most often applied measure for reducing the predation impact on red-legged partridge populations, seems not to be the most appropriate management methodology due to its reduced long-term effects and high cost/benefit ratio. Instead, alternative measures tending to reduce the predation risk other than predator control (such as CFA or habitat management) appear to be most recommendable in the long term. However, there is still little scientific knowledge on the factors determining the incidence of predation other than the abundance of predators, for instance, which landscape features increase the risk of predation, either directly or indirectly, through food availability which determines large movements and poor body condition. New research is required on the specific habitat management measures which would improve partridge body condition and how this translates into improved adult survival (i.e. low predation risk), higher production rate, nesting success and chick survival. In agricultural pseudo-steppes constituting most of the range of the red-legged partridge, simple measures such as favouring *lindes* and reducing field size would highly help reduce the incidence of predation on partridge populations. Due to the high cost of these measures in the short term and because they involve the interests of other land managers, their implementation would require the cooperation with stakeholders such as farmers. This will be only possible if a change of paradigm, from predator control to the management of predation, is produced in the mind of game and land managers. In this sense, studies on the application of promising tools for reducing the effect of predation such as conditioned food aversion to real-world management situations are necessary to incorporate them as complementary measures for the management of predation.

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The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future

Carlos Sánchez-García, Julie Ann Ewald, Nicholas J. Aebischer, Neville Kingdon, and G. R. Potts

> If a Frenchman had been asked in 1769 (the year before the successful release in Suffolk), whether red-legged partridges would have had any chance of breeding and establishing themselves in England, he would have certainly replied that as their natural range did not extend much beyond the Loire, how then could they thrive over 300 miles further north?—Charles Coles (*The Complete Book of Game Conservation*, 1971)

What Is the Origin of British Red-Legged Partridges?

As is the case with other gamebirds around the world, humans have moved red-legged partridges (*Alectoris rufa*) to areas outside their natural range because of their value as a quarry species. The first translocations documented in Iberia were conducted in the thirteenth century (from the Peninsula to the Balearic Islands), and the species has been taken to countries outside its native range since then (González-Redondo 2004).

Red-legged partridges were first introduced to Britain in 1673, during the reign of Charles II, who ordered the first birds from France, probably from Chambord (Potts 2012). These introductions occurred near Windsor (Berkshire), though the birds did

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_5

not survive long. Other reintroduction attempts in Essex, Surrey and Sussex also failed (Sharrock 1976). The first successful introductions were achieved between 1770 and 1777 by the Marquess of Hertford, in Orford, Suffolk. These may have been supported by other introductions at the same area by Lord Rendlesham (Coles 1968).

In all it took over a century to establish red-legged partridges in Britain successfully, probably because the first attempts were hard releases that were not accompanied by targeted management. Successful introductions involved the incubation of eggs under broody bantams *Gallus gallus domesticus* (Sharrock 1976), similar to recent work on the re-establishment of native grey partridge *Perdix perdix* (Browne et al. 2009). Local red-legged partridge introductions continued from 1830 to 1958 in Wales, Scotland and Ireland (Sharrock 1976).

As the earliest birds were brought from France, the British population of red-legged partridges was considered to be *Alectoris rufa rufa*. In a study using birds from estates in East Anglia (with no modern history of releasing), Barbanera et al. (2015) compared the genomics of modern and ancient birds (1824–1934) using mitochondrial DNA. Although history would suggest that genomics of the first red-legs translocated into Britain were *A. r. rufa*, this recent work indicated that modern birds were *A. rufa* x *A. chukar* hybrids. This is explained by the large number of red-legged partridges released in Britain over the past three decades (see Sect. 'Harvesting of Red-Legged Partridges in Britain'), including releases of chukar partridges and chukar x red-legged partridge hybrids in the 1970s (Potts 1994).

Chukar partridge releasing was formally banned in Britain in 1992. At least for some well-studied red-legged partridge populations of southern England, it is possible to note phenotypic consequences of chukar partridge introgression (Potts, personal comm.), although it seems that there are no long-term detrimental effects (Potts 2012). It is clear that the British population of 'French partridges' (as they are called in Britain and the United States) has lost its genomic integrity owing to the constant supplementation by reared birds of mixed parentage.

Distribution, Population Estimates, Density and Trends

When looking at the historical data from the late nineteenth century to the 1930s, red-legged partridges occurred mainly in East Anglia (Norfolk and Suffolk) but also in Lincolnshire, Yorkshire and the Home counties, with a scattering in Wales (Holloway 1996). The red-legged partridge range expanded to central and southern England, with breeding confirmed in 44 counties by the end of the nineteenth century (Holloway 1996).

In the 1930s, red-legged partridges may have been present in 800–900 10-km grid squares in Britain, around 30% of total area (data derived from Holloway (1996) and Sharrock (1976)). From 1930 to 1959, a slight contraction of range was observed, probably because red-legged partridges were heavily shot together with the once common grey partridge (Potts 1980) and because some areas tried to eliminate them owing to their perceived poor sport compared to grey partridges (Sharrock 1976).

Middleton and Huband (1965) recorded a three to four times increase in the breeding stock and subsequent autumn populations of East Anglia from 1960 to 1965 compared to 1953–1955, probably because of the high survival of young red-legged partridges in the summers of 1959–1960, together with low winter mortality and reduced shooting from 1962 to 1965.

The turning point in the expansion of red-legged partridge distribution occurred during the 1960s, after releasing for 'put-and-take' shooting started in 1963. In 1961 only 19% of shoots that reported bags of red-legged partridges to the *Game & Wildlife Conservation Trust's* (GWCT) *National Gamebag Census* were releasing red-legged partridges and the numbers were low; the numbers released have increased exponentially since then (Aebischer 2013, 2019).

In 1968–1972, red-legged partridges occurred in 919 10-km grid squares, and in 1998–91 they were present in 1226 10-km grid squares (including 12 in Ireland), which represented a 32% increase (Potts 1994). According to the 2013 *British Trust of Ornithology* (BTO) *Atlas*, the current winter range size is 1591 10-km squares for Britain and 20 10-km grid squares for Ireland, with a confirmed breeding range size of 697 10-km grid squares in Britain, which represents a 78% increase when compared to 1988–1991 (Balmer et al. 2013). Red-legged partridges occur in the majority of England, eastern Wales and eastern Scotland, with a scattering in Ireland and in other isolated locations of the British Isles. The species was observed for the first time during the last decade in the Channel Islands (Fig. 1).

The latest estimate from the BTO suggests that there are around 72,500 pairs of wild red-legged partridges in Britain (Woodward et al. 2020). The areas that historically have held the highest red-legged partridge densities are East Anglia, Cambridgeshire, Essex and Lincolnshire (Potts 1994; Holloway 1996; Gillings et al. 2013). Such areas provide a combination of suitable farmland habitat and continental climate, with low rainfall and sandy ground, which is ideal for red-legged partridges (Howells 1963).

As with grey partridges, higher spring pair densities of wild red-legged partridges are recorded on farms conducting targeted management than elsewhere. On an estate in Sussex where a management package for game and other wildlife was put into practice, densities over 10 spring pairs/km^2 were achieved, with peaks of 25 spring pairs/km^2 (Potts 2012). On a demonstration area in Royston, Hertfordshire, following similar management, the spring pair density went from 4.9 pairs/km^2 to a high of 18.9 pairs/km^2 (Aebischer and Ewald 2010). On both areas there was sustainable shooting of red-legged partridges following management.

National monitoring undertaken by the BTO in the *Breeding Bird Survey* indicates that the breeding density across the country has declined by 19% from 1967 to 2010 (Gillings et al. 2013). Although the trend is negative, it is not as sharp as the decline observed for the grey partridge, whose numbers have dropped by 80% in 40 years to an estimated UK population of 37,000 pairs (Woodward et al. 2020).

In addition to the information collected through the Breeding Bird Survey, counts of partridges are undertaken by members of the GWCT's *Partridge Count Scheme* (Ewald et al. 2009). This free and voluntary scheme collects information on the annual breeding abundance (spring counts) and breeding success (autumn counts) of

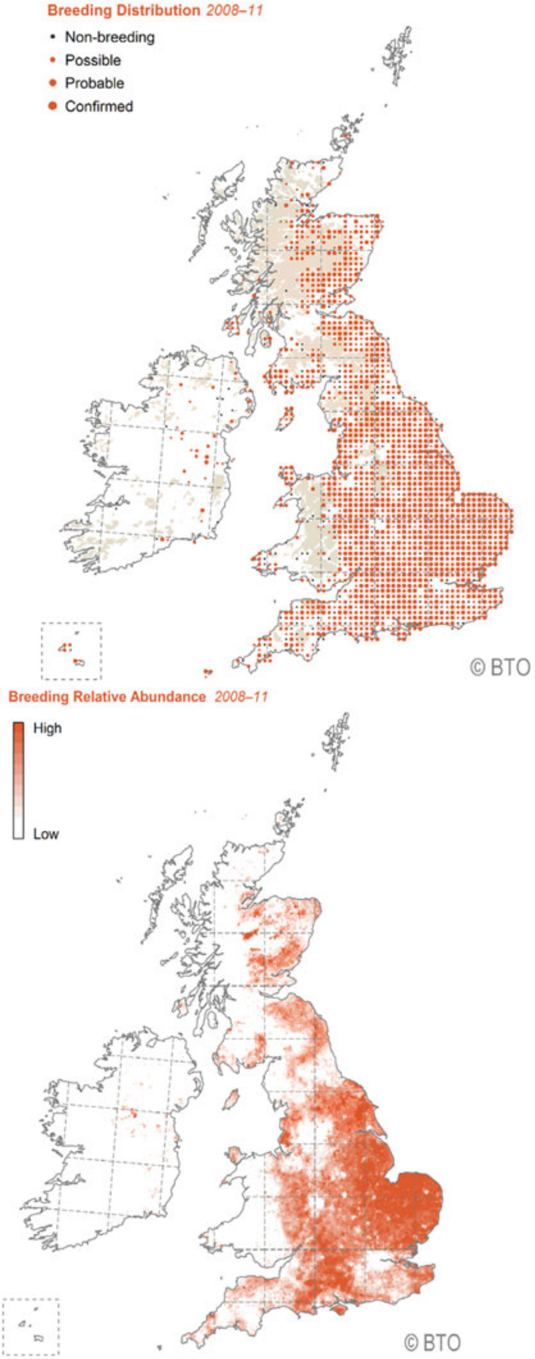

Fig. 1 Breeding distribution (above) and breeding relative abundance (below) of red-legged partridge (2008–2011). Maps reproduced with permission from BTO and taken from *Bird Atlas* (2007–2011) (Balmer et al. 2013), which was a joint project between BTO, BirdWatch Ireland and the Scottish Ornithologists' Club

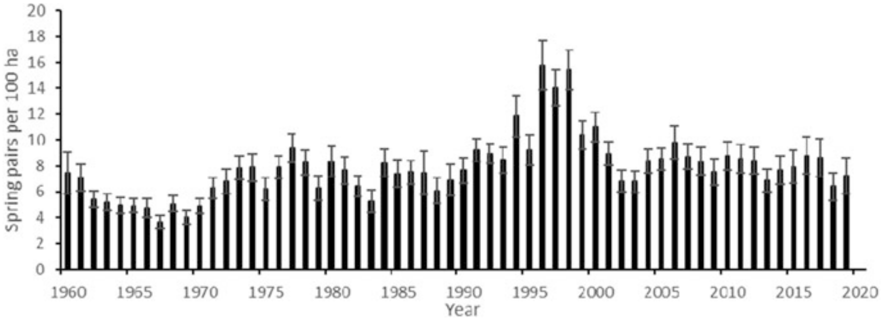

Fig. 2 Long-term trends in the breeding abundance (pairs/100 ha, ± standard error) of red-legged partridges on 338 farms managed by long-term Partridge Count Scheme members

grey partridges and provides members with current information on grey partridge conservation. Partridge Count Scheme contributors are also asked to collect information about red-legged partridges, as both species often occur together.

Owing to their interest in partridge conservation, these contributors are not considered to represent the 'average' farm. For instance, they make greater use of agri-environment options known to be useful for grey partridges than farmers who were not involved in the scheme (Ewald et al. 2010). We used the counts from long-term members (members before the scheme's expansion in 1999; Aebischer 2009) to examine the trend in red-legged partridge breeding abundance from 1960 to 2019. We included information only from members who had counted partridges on at least 100 hectares.

Information on red-legged partridge density was available on a total of 338 farms over this time frame, although not all sites recorded information in all years. Average red-legged partridge breeding density has fluctuated on the ground managed by Partridge Count Scheme members over the past 60 years, with peaks in the mid- to late 1970s and in the late 1990s and troughs in the late 1960s, early 1980s, early 2000s and late 2010s (Fig. 2). These changes should be viewed with care as the series is composed of information contributed by members. As the Partridge Count Scheme is a voluntary scheme, sampling intensity will change from year to year.

In conclusion, the current distribution and abundance of red-legged partridges in Britain are predominantly a result of releasing rather than natural expansion, with many areas supporting high densities of reared birds during the shooting season but fewer breeding birds (Balmer et al. 2013). Although releasing obscures our understanding of the status of red-legged partridges in Britain (Potts 2012), breeding abundance from long-term members of the GWCT's Partridge Count Scheme has remained fairly stable (with some variations) in contrast to the declines seen in the abundance of grey partridges (Ewald et al. 2009; Balmer et al. 2013).

Harvesting of Red-Legged Partridges in Britain

The GWCT's *National Gamebag Census* has collated information on the number of quarry species shot (the 'bag') from over 1000 contributing estates across the UK since 1961. It also accepts and collates heritage bag records prior to 1961; the earliest bag records date back to 1789. These records provide a historical perspective that documents the changes that have taken place in shooting. We summarise here the changes that have taken place for the red-legged partridges as a quarry species.

Until around 1970, the shooting of red-legged partridges relied on the productivity of wild birds. This meant considerable variation in the number of birds shot from 1 year to another. In East Anglia, the UK stronghold for wild red-legged partridges, the average bag was 7–8 birds per 100 ha in the 1960s but locally could exceed 30 birds shot per 100 ha in years of good breeding success while dropping below 3 birds shot per 100 ha in poor years. Bag sizes were smaller away from East Anglia, averaging 4 birds shot per 100 ha in the East Midlands, 2 birds shot per 100 ha in southern England and 1 bird shot per 100 ha in north-eastern England.

Since then, the number of red-legged partridges released for shooting began to increase, initially in south-east England, then by the 1980s across most of the UK, which includes Scotland and Northern Ireland (Fig. 3). Nowadays over two-thirds of *National Gamebag Census* estates that shoot red-legs do so on the basis of releasing birds for shooting. Although some released birds are hatched from eggs and reared on the release sites, the majority are purchased from game farms as poults. The UK's

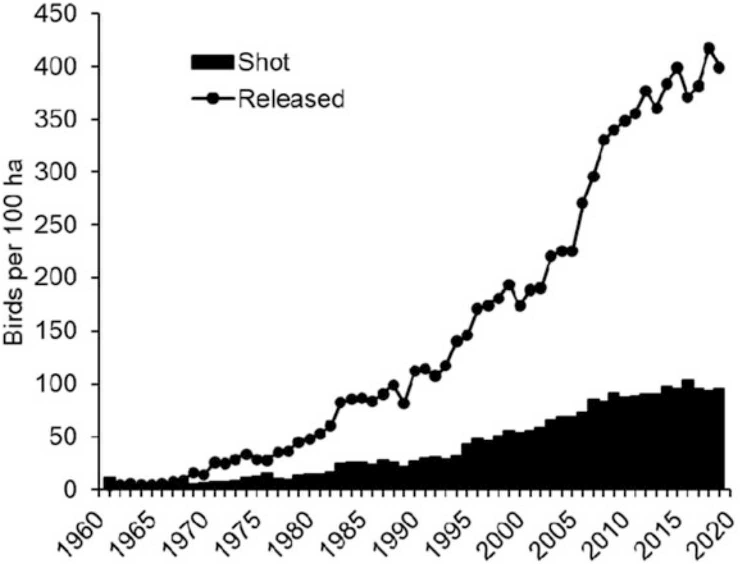

Fig. 3 Mean number of red-legged partridges released per 100 ha and mean number shot per 100 ha, on shoots across the UK annually from 1961 to 2019 (source: GWCT *National Gamebag Census*)

Code of Good Shooting Practice (http://www.codeofgoodshootingpractice.org.uk/) specifies that birds should be released into the wild at least 2 months before shooting begins, so that they have time to adjust to the environment. Over the last 5 years, the average density of birds released has been 370–420 birds per 100 ha. The number of birds shot has risen accordingly, and for shoots where releasing is practised, the number of birds shot currently averages 145 birds per 100 ha, giving a return on releasing of 35–40%. On all shoots combined (with and without releasing), around 95 birds are currently shot per 100 ha (Fig. 3).

Similarities and Differences Between British and Continental Populations

Habitat

From a 'Mediterranean point of view', Britain may be suboptimal for red-legged partridges, but East Anglia, where red-legged partridges were successfully introduced for the first time and now occur at high densities, is dominated by arable agriculture and has an annual rainfall below 600 mm and a mean July temperature above 19 °C, relatively similar to other areas of the continent where red-legged partridges occur.

Red-legged partridges can be found in a range of climates and habitats, from the dry and hot farmland and 'dehesas' of Central Spain (where the highest densities have been recorded, Potts 2012) to the cold and wet uplands where their densities are much lower (Lucio and Purroy 1992). Hence, it seems that in both Britain and the continent, red-legged partridges are able to breed in different habitats, so long as summer temperatures are high enough. Red-legged partridges are more abundant in non-intensive agricultural countryside offering a combination of open landscapes and patches with nesting and wintering cover (Lucio and Purroy 1987; Buenestado et al. 2008).

Food and Water

The food eaten by adult red-legged partridges is dominated by grain in Britain and the continent (wheat, barley, oats, maize), although in Iberia red-legged partridges tend to eat more bulbous and tuberous roots and grasshoppers (*Caelifera*) probably to gain moisture during summer, when water is lacking (Middleton and Chitty 1937; Vizeu 1977; Jiménez et al. 1991; Tavares et al. 1996; Potts 2012).

With regard to the chicks, Green et al. (1987) and Potts (2012) found that insects comprised 50% (at 3 days) and 28% (in the first week) of their diets, whereas studies of the first-week diet from Spain (Rueda et al. 1993) and Portugal (Potts 2012) showed percentages of 56% and 81%. These studies showed that chicks eat a wide range of insects, mainly plant bugs in Spain, aphids and tortoise beetles (*Cassida*) in Portugal and aphids in Britain. In Mediterranean areas insects provide food but also water, especially in dry summers when vegetation is desiccated (Potts 2013), so chick survival in these areas may be reduced when plant-eating insects are lacking, which does not happen in northerly locations.

One of the main climate differences between Britain and the continent is humidity. In Britain, red-legged partridges may find surface water all year round, and during dry periods, they may be able to take water from food or dew. This is not the case in other areas of the continent, which are often subject to extended drought periods. It is known that red-legged partridges need a reliable supply of drinking water in Iberia during the dry months (Lacasa et al. 2010) and so stay close to water sources (Borralho et al. 1998). Water troughs are a common management tool to reduce detrimental effects of drought periods on red-legged partridge productivity (Sánchez-García et al. 2012). In contrast, water troughs are not widely used for wild partridge management in Britain.

Nesting

In British farmland, red-legged partridges select hedgerows with nettles and tall vegetative cover for nesting (Rands 1988), while in southern France, Ricci et al. (1990) found that red-legged partridges selected hedgerows and also uncultivated habitats as long as they were weedy. In Central Spain, Casas and Viñuela (2010) found that the majority of nests occurred in cereal grain fields, though *lindes* (herbaceous strips among fields) were used more than expected by chance. Despite methodological differences among studies, regardless of location or country, red-legged partridges choose to nest in places with enough cover to avoid nest predation, as they do not cover their clutch with dead grass as grey partridges do when they leave the nest (Potts 1986).

Double Brooding

The first studies investigating the double-brooding behaviour of red-legged partridges were conducted by Jenkins (1957) and Green (1984) in Britain, and two decades later Dr. Fabián Casas and his team started a 4-year study in Ciudad Real (Spain). Although Casas et al. (2009) estimated the male incubation rate relative to the total number of males that were radio-tagged rather than the number of nests as per Green (1984), both authors found a similar pattern of double brooding: a high proportion of males incubating a second clutch and 'delayed' and 'undelayed' nests, with values of 1.33 clutches incubated per pair per year in Britain and 1.38 clutches incubated per pair per year in Spain.

Predation

The studies of Coles (1979), Ricci et al. (1990), Otero (1999), Duarte et al. (2008) and Buenestado et al. (2009) showed that in Iberia and France the main nest and chick predators are canids (red fox *Vulpes vulpes*, feral dog *Canis familiaris*), rodents (mainly brown rat *Rattus norvegicus*), mustelids, corvids, reptiles and wild boar *Sus scrofa*, whereas adults are mainly predated by canids and a wide range of raptors (see Chap. 'Is Predation the Key Factor of Partridge Ecology and Management?'). Our knowledge about red-legged partridge predators in Britain is more limited, but it is likely that they are similar to the ones predating grey partridges. The review conducted by Potts (2012) of grey partridges showed that around 50% of nests may be predated by corvids and foxes, with minor proportions attributed to badgers and small carnivores. The sparrowhawk (*Accipiter nisus*) is the main raptor species that preys on adult grey partridges and possibly red-legged partridges in Britain (Watson et al. 2007).

Though much more research is needed in this field, it seems that there are few differences in nest predators between Britain and the continent, whereas adult red-legged partridges on the continent are predated by large raptor species that are absent across the majority of Britain.

Conclusion

Despite the knowledge gaps, it seems that there are no notable differences between the British and continental red-legged partridges as they are found in a variety of habitats within their native range and show the same behavioural and reproductive patterns. Red-legged partridges in Britain illustrate the ability of the species to adapt to differences in the environment (such as diet), which is not surprising as red-legged partridges occupy different types of habitats within their native range.

Effects of Targeted Management for Wild Red-Legged Partridges in Britain

One of the best documented examples of red-legged partridge management in Britain was the 'Royston Grey Partridge Recovery Project' that was undertaken by the GWCT from 2002 to 2010 on multiple contiguous farms near Royston, Hertfordshire (Aebischer and Ewald 2010). The project aimed to demonstrate to land managers that it is possible to restore the number of wild grey partridges in a profitable farming environment. As wild red-legged partridges have similar needs to grey partridges, they also were monitored to evaluate their response to targeted management.

Fig. 4 Targeted management for red-legged partridge conducted in Britain: (**a**) a road sign in Norfolk warning of partridges crossing; (**b**) covey of red-legged partridges on a non-sprayed stubble, with plenty of food and cover in September; (**c**) unharvested cereal headland, hedgerow cover and feeder in Sussex, England; (**d**) red-legged partridges using a feeder (while the grey partridge on the left waits); (**e**) an English gamekeeper setting a tunnel trap to reduce the number of rats and mustelids in spring; and (**f**) a bag of red-legged and grey partridges (Photo credits C. Sánchez-García, P. Thompson and F.D. Buner)

The demonstration area covered 996 ha (six farm holdings), whereas an adjacent area of 1311 ha (seven holdings) was used as the reference area for comparison. Three key measures were deployed in the demonstration area from January 2002 (Sotherton et al. 2013; see Fig. 4):

(a) *Predator removal,* which was conducted by a full-time gamekeeper employed by GWCT. The legal control targeted predators that kill adult partridges (red foxes, stoats *Mustela erminea* and weasels *Mustela nivalis*) or destroy nests (carrion crows *Corvus corone*, rooks *Corvus frugilegus*, jackdaws *Corvus monedula* and common magpies *Pica pica*). The aim of predator removal was to reduce predation during the breeding season (late winter to early summer), especially while partridges were nesting and rearing young chicks. None of the predator species was eradicated, as all of them were replenished by the following season from the local area. Foxes were controlled through lamping and snaring, mustelids were tunnel-trapped, and corvids were trapped using live cage traps.

(b) *Habitat improvement*. The farmers were encouraged to provide nesting, brood-rearing and winter cover through the existing options of the government agri-environment schemes, as well as set-aside. At the beginning of the project, across the whole of England set-aside peaked at 13% of farmland, but it was set to zero in 2008. The area of land providing nesting cover varied across the years of the project, with between 6% and 9% of the demonstration area providing nesting cover. One-third of this was provided by set-aside, with beetle banks and hedgerows also important. Insect-rich brood-rearing habitat (game cover crops, wildlife mixes and set-aside) covered 17.5% of the demonstration area in 2003 but declined to 8% of the area by 2008 (Aebischer and Ewald 2010).

(c) *Supplementary feeding*. The gamekeeper provided wheat through feeders placed along hedgerow cover and field margins from September to March. Feeders were installed at a density of 14 per km^2, targeting grey partridge coveys in autumn-early winter and territorial pairs in winter-late spring. Feeding for gamebirds and songbirds is a widespread management tool on British shoots, with virtually all shoots providing food through feeders or by scattering it on the ground during the shooting season (Steel and Draycott 2014). Partridges use feeders regularly, though the effects on survival and reproduction remain unknown (Sánchez-García et al. 2015). Practitioners believe that using feeders reduces grey partridge pair dispersal.

(d) *Shooting*. Red-legged partridges and common pheasants *Phasianus colchicus* were shot during the project's lifetime. The number of days of shooting and drives per day were carefully planned, aiming to shoot one-third of the red-legged partridges counted in autumn (early September) and as many pheasants as possible. Shooters were told not to shoot grey partridges, with care taken to avoid including them in drives and warnings given to shooters.

(e) *Releasing*. No partridges were released for conservation purposes on the demonstration and reference areas, but several neighbouring farms released red-legged partridges for shooting (possibly 20,000 birds/season). The GWCT gamekeeper occasionally observed red-legged partridges coming from the neighbouring farms from October.

Partridges were counted in March (spring pair counts) and after crop harvesting (autumn covey counts) in the demonstration and reference areas. The gamekeeper recorded the number of partridges, number and size of the broods and distinguished males, females and young.

The red-legged partridge density in 2002 was 4.9 spring pairs/km^2 in the demonstration area and 5.6 spring pairs/km^2 in the reference area. After just 3 years of targeted management, the spring red-legged partridge pair density increased nearly fourfold (from 4.9 to 18.9 pairs/km^2, Fig. 5). The numerical response of red-legged partridges to the management was quite similar to the one experienced by grey partridges, whose densities increased sixfold in 5 years (Aebischer and Ewald 2010).

The density of red-legged partridge broods (coveys that contain young birds) on the demonstration and reference area in autumn 2001 was 0.7 broods/km^2. Under the targeted management, brood density increased on the demonstration area, with the

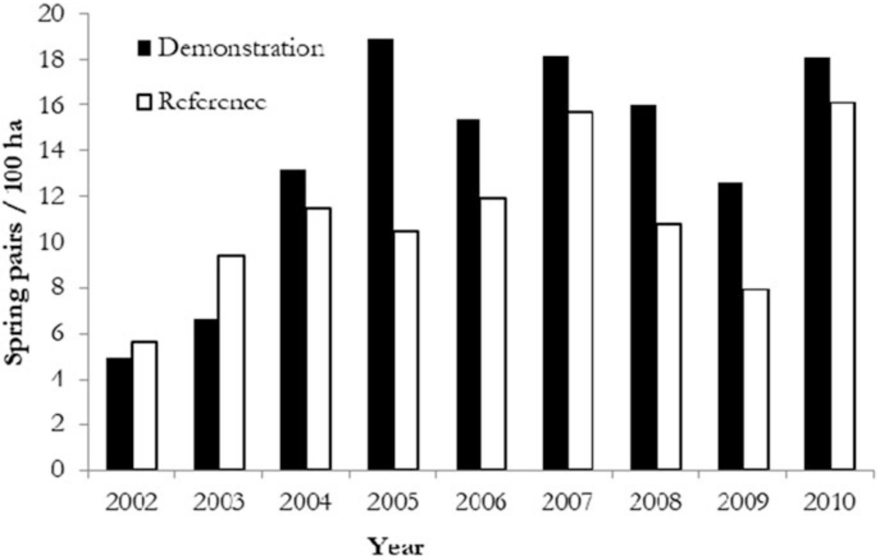

Fig. 5 Red-legged partridge spring pair density on the Royston demonstration project, with the breeding density on the demonstration area in black and that of the reference area in white

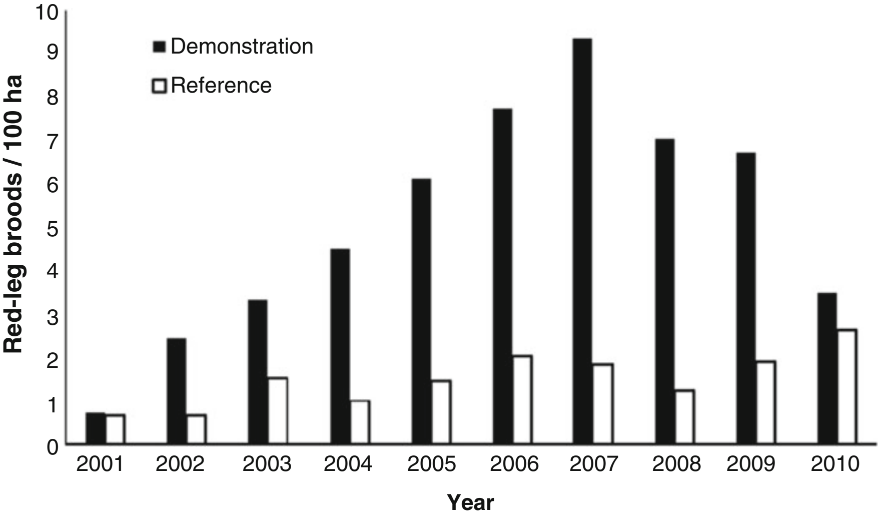

Fig. 6 Red-legged partridge brood density on the Royston demonstration project, with the density on the demonstration area in black and that of the reference area in white

highest brood density on the demonstration area (9.4 broods/km^2) seen in 2007 (Fig. 6). On the reference area, over the course of the project, red-legged partridge brood density averaged 1.5 broods/km^2. The increase in red-legged partridge density

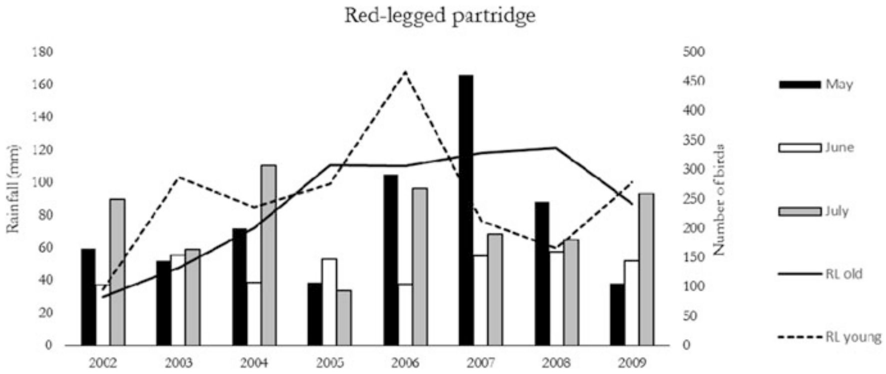

Fig. 7 Cumulative rainfall in May, June and July and the number of young and adult red-legged partridges counted in summer on the demonstration area

on the demonstration area reflects the increases seen in the number of red-legged partridge broods produced.

The number of young red-legged partridges counted in summer seemed not to be affected by the cumulative rainfall from May to July, though we observed a marked decline in the number of young counted after 2007, the year with the highest cumulative recorded rainfall (Fig. 7). It seems that significant weather events may affect red-legged partridge reproduction more than small year-to-year variations in rainfall.

Regarding shooting, on average 60% of the red-legged partridges counted in autumn were shot from 2004 onwards. This apparent high rate of shooting could be explained by undercounting the numbers present at the end of the summer coupled with immigration from the large-scale releasing at some neighbouring farms. Only a small percentage of the grey partridges counted in autumn were shot by accident during red-legged partridge shoots (average of 3%), which did not compromise grey partridge recovery.

One of the highlights of the project was that the targeted management increased the value of the gamebird shooting on the demonstration area. For example, in the 2006–2007 season, 578 heads of game were shot over 4 days (Table 1), which represented a value of £17,340–23,120 (£30–40/bird). The potential value of brown hare *Lepus europaeus* (£10/hare, £3430 in total), deer, wild rabbit *Oryctolagus cuniculus* and wood pigeon *Columba palumbus* shooting, together with the environmental value of farmland birds breeding at the demonstration area (such as Eurasian Lapwing *Vanellus vanellus*), should be added. Today the value of shooting one wild grey partridge is around £100 and one red-legged partridge or common pheasant is £40. Hence, wild gamebird shooting is able to generate enough funds to pay for gamekeeping and support other wildlife (including red-listed species).

In conclusion, the combination of predator removal, habitat management and supplementary feeding worked well for wild red-legged partridges, as their density increased significantly together with that of the red-listed Grey Partridge. It also

Table 1 Autumn counts and value of shooting for the 2006–2007 season (data from M. Brockless)

Autumn counts	Old	Young	Total
Grey partridge	245	631	876
Red-legged partridge	306	467	773
Common pheasant	158	364	522
Shooting		Value range (£)	
Number of days	4		
Number of guns	47		
Bag			
Common pheasant ♂	88	2640–3520	
Common pheasant ♀	144	4320–5760	
Red-legged partridge	320	9600–12,800	
Grey partridge	26	780–1040	
Total	578	17,340–23,120	
Brown hare	343	3430	
Total	921	20,770–26,550	

demonstrated that wild gamebird shooting can be cost-neutral, with the added advantage of supporting other wildlife. These results are similar to studies from Portugal (Borralho et al. 1997), France (Ponce-Boutin et al. 2006) and Spain (Sánchez-García et al. 2017), which showed positive responses to targeted management.

The Future of Red-Legged Partridges in Britain: Conservation Actions and Research Gaps

During recent decades, the lack of wild grey partridges for driven shooting in Britain has resulted in a marked increase in the scale of releasing of red-legged partridges to provide hunting opportunities in open low ground. Thus, the management regime of red-legged partridges in Britain is mainly based on 'put-and-take' releasing (over 6 million birds released per season; see Chap. 'Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing'). The current wild UK red-legged partridge population size (72,500 pairs) is far from the conservation target that the GWCT suggests habitat and management could support (335,000 pairs; Tapper 1999), so the following conservation actions are needed to prevent a serious deterioration of the species' conservation status:

(a) *Increase in wild partridge management.* Red-legged partridges have similar needs to grey partridges, so the efforts to conserve the latter can benefit both species. As shown in the 'Royston Grey Partridge Recovery Project', it is possible to increase densities of red-legged partridges through targeted grey partridge management and provide enough birds for shooting, allowing wild grey partridges to increase in number.

(b) *Recognition of wild partridge shoots*. As in other countries such as Spain, it is not always easy to distinguish between wild and reared shoots in Britain (Martinez-Padilla et al. 2002) as shoots producing wild game are not recognized or labelled as 'wild'. This recognition may help increase the value (monetary and perception) of wild gamebirds as there are hunters demanding this type of shooting and who are willing to pay for it.

(c) *Pheasant releasing to help wild partridges*. An alternative to large-scale red-legged partridge releasing may be pheasant releasing. When pheasants are released at low densities and under careful planning, this may help the recovery of both grey and red-legged partridges as the risk of shooting a partridge instead of a pheasant is very low, if the shooting is well managed (Buner et al. 2014).

(d) *Genetic screening*. Any egg, poult or adult red-legged partridge either hatched or released in Britain should be *A. rufa rufa.* Birds brought from abroad should be genetically screened to avoid further genetic chukar partridge introgressions (Barbanera et al. 2015).

During the last century, our knowledge of red-legged partridges has increased considerably, mainly driven by shooting interests and declines in the wild population. The ecology of red-legged partridges is relatively well understood in Britain, but there are still many gaps when compared to grey partridge, the galliform on which more research has been undertaken than on any other gamebird in the world. More research is needed to improve our knowledge of predators of wild red-legged partridges, especially raptors, the effects of large-scale releasing on wild population and the effects of different management measures (Tapper 1999).

Acknowledgments We thank the British Trust for Ornithology for their permission to reproduce distribution and abundance maps. We are grateful to contributors to the *GWCT's Partridge Count Scheme* and *National Gamebag Census* for their ongoing commitment to the surveys. Special thanks are given to Malcolm Brockless, who gave data and practical information about the 'Royston Recovery Project'. Prof. N. W. Sotherton and Prof. L. Powell gave crucial comments.

This chapter is dedicated to the memory of our great colleague and co-author, Dr. G.R. Potts, who sadly passed away on 30 March 2017 before its publication.

Dr. G. Richard (Dick) Potts (1939–2017). Your legacy will live on (Photograph, Charlie Pye-Smith).

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Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization

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Genus *Alectoris*: Origin and Diversification

Alectoris is a genus of seven extant species with a South Palearctic distribution, with two species breeding in the South of the Arabian Peninsula. The two Arabian species, *A. melanocephala* and *A. philbyi*, have partially overlapping ranges, and this is the only case of current sympatry in the genus. The rest of species are mostly allopatric, although there are three narrow areas of parapatry between pairs of species (Fig. 1). Eastwards, these three small zones occur between the pairs *A. rufa*-*A. graeca*-*A. chukar*-*A. magna*. There is a narrow contact zone along the border of the French Southern Alps where *A. rufa* and *A. graeca* meet and hybridize, setting a stable hybrid zone (Bernard-Laurent 1984; Randi and Bernard-Laurent 1999). There is a contact zone between *A. graeca* and *A. chukar* in the Southern Rhodope Mountains where both species may hybridize (Dragoev 1974), and, thirdly, *A. chukar* and *A. magna* contact and hybridize in the Liupan Mountain Region in Northwestern China (Chen et al. 1999; Liu et al. 2006; Huang et al. 2009). The seventh species of the genus, *A. barbara*, currently lives in complete allopatry in North Africa, but fossils documented that its distribution range reached as far north as South France in the Middle Pleistocene (Mourer-Chauvirè 1975) and the

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_6

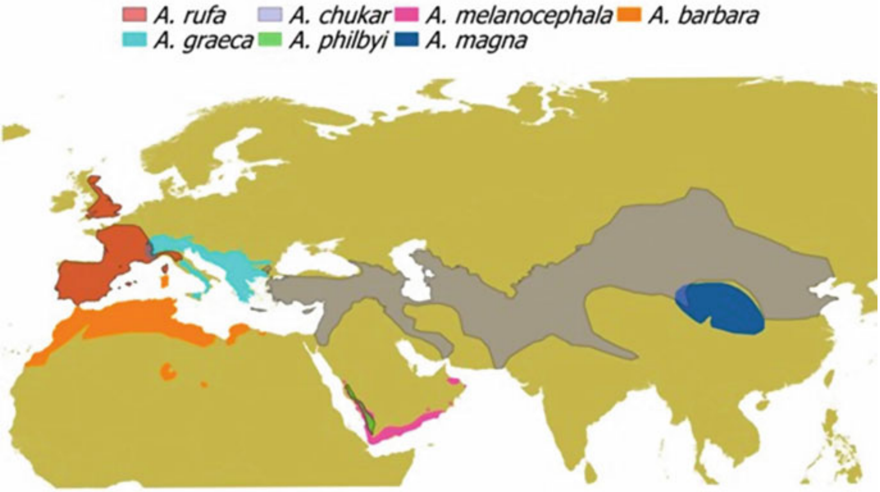

Fig. 1 Current distribution range of seven *Alectoris* species

Mediterranean side of the Iberian Peninsula in the Lower Pleistocene (Villalta 1964; Vilette 1983; García 1995). The biogeographic pattern of *Alectoris* consisting in sibling species with close or parapatric ranges with little or no hybridization is commonplace among young closely related species that featured geographic isolation and differentiation and recontacts until they became different species with no or limited gene flow and that are kept apart in contact zones by ecological divergence and competitive exclusion (Newton 2003).

Genetic divergence and phylogenetic relationships of *Alectoris* have been studied in detail using allozyme markers and nucleotide sequences (Randi et al. 1992; Randi 1996; Randi and Lucchini 1998). The genus diverged through the Pliocene, between 6 and 2 million years ago, in three ways of speciation. The most basal members are *A. barbara* and *A. melanocephala*; a second cluster comprises *A. rufa* and *A. graeca*, speciated 2.4–3.8 million years ago; and there is a third group that includes the species of most recent origin, *A. chukar*, *A. magna* and *A. philbyi*, that radiated about 2 million years ago. The sequence of known fossil deposits is roughly in agreement with phylogenetic reconstruction and calibrated rates of molecular evolution, notwithstanding the uncertainty about molecular chronologies based on canonical mutation rates and the scantiness of the avian fossil record. The oldest occurrence of *Alectoris* corresponds to *A. donnezani*, an extinct species that appeared for the first time in the Miocene-Pliocene boundary and was widespread and abundant in European deposits until the Early Pleistocene. *A. graeca* and *A. rufa* started to appear in the West European Upper Pleistocene deposits, being the former more abundant at first, while *A. chukar* fossils do not appear until the Lower Pleistocene in Asia and the Near East (Tyberg 1998, 2008; Mlíkowský 2001; Sánchez-Marco 2004, 2009).

Man has introduced several species of *Alectoris* partridges outside their natural ranges at least from ancient history and still does (Chaps. “The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting”, “The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future” and “Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing”). *A. chukar* was first introduced in North America in 1834 with birds from Karachi, India (Cottam et al. 1940), and since then feral populations have also been established in South America, the Hawaiian Islands, New Zealand and South Africa (del Hoyo et al. 1994). *A. rufa* was introduced in Atlantic and Mediterranean islands. The King Sancho I of Mallorca introduced the species in the Balearic Islands by the end of the thirteenth century (Alonso 1994). The red-legged partridge was introduced in Madeira by the early settlers in the fifteenth century (Bernström 1951) and in Azores in 1561 (Frutuoso 1998). It arrived to the Canary Islands in the sixteenth century (Núñez de la Peña and Allen 1994), although currently it only remains in Gran Canaria, and it was first introduced in Britain by the King Charles II in the seventh century (see Chap. “The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future”). *A. barbara* was taken to the Canary Islands in the nineteenth century and now is present in all the islands but Gran Canaria (Martín and Lorenzo 2001); meanwhile it was introduced in Gibraltar (Hagemeijer and Blair 1997). The history of *Alectoris* introductions in Mediterranean islands much predates the above-mentioned cases. Ancient Greeks and Romans ate and hunted partridges, kept them as pets and considered them as symbols of fertility that were offered to Aphrodite/Venus (Pollard 1977); thus *Alectoris* bones are frequent in archaeological sites. The four partridges of the Mediterranean Basin, *A. barbara*, *A. rufa*, *A. graeca* and *A. chukar*, have been introduced in Mediterranean islands several times, often releasing different species in the same islands. Interestingly, at present only one species of *Alectoris* lives in each island, which is that living on the nearest similar landscape in mainland (Blondel 2008). The outcome of only one species per island may be the result, again, of ecological divergence and competitive exclusion.

Phylogeography and Genetic Structure of *Alectoris rufa*

Three *A. rufa* subspecies have been recognized: *A. r. rufa* (Linnaeus, 1758) distributed throughout France, NW Italy, Elba and Corsica; *A. r. hispanica* (Seoane 1894) in the N&W portions of the Iberian Peninsula; and *A. r. intercedens* (A. E. Brehm, 1857) in the E&S parts of the Iberian Peninsula and Balearic Islands (Cramp and Simmons 1980). A fourth subspecies, *A. r. laubmanni*, from the Balearic Islands, was described by Jordans (1928), and even a fifth subspecies, *A. r. corsa* (Parrot 1910), was identified in Corsica. Subspecies in red-legged partridges have been delimited by subtle geographical differences in plumage colour (Seoane 1894; Cramp and Simmons 1980; Villafuerte and Negro 1998).

Intense game management makes phylogeographic studies in *A. rufa* challenging because massive releases of farmed birds of unknown origin modify the genetic structure of the species (e.g. Chap. "The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future"). Whereas some authors have not detected geographic genetic structure in the red-legged partridge populations, others disclosed some signs of intraspecific structure. Martínez-Fresno et al. (2008) studied Spanish partridge localities with different restocking pressures using *D-loop* sequences from the mitochondrial DNA (mtDNA) and found a Northern Spanish population (Palencia) with clear genetic differentiation from the rest of the Iberian-studied populations. This population was in a wildlife reservation, with no introduction of foreign partridges, and was the first evidence of any presumable genetic structure in the Iberian Peninsula. However, it is possible that widespread partridge restocking in other areas blurred any additional structure.

Other studies employed ancient vs. current sampled partridges, as in Barbanera et al. (2010, 2015), to assess genetic structure. These authors combined different analytical approaches for evaluating spatial and temporal trends of *A. rufa* genetic diversity mainly by sequencing a fragment of mtDNA of both modern and ancient specimens sampled throughout the entire species' range. They did not detect any genetic structure in current sample analysis, but they did find it in ancient samples. They also found significant changes in the haplotype profile of current vs. ancient *A. rufa*, suggesting a genetic homogenization process as a consequence of intense management in this species. Barbanera et al. (2011) also investigated genetic relationships between Corsican and continental *A. rufa* populations by sequencing the mtDNA *cytochrome b* gene. They did not find phylogeographic structure in continental populations all across the entire range of the species, but grouped Corsican samples apart in a reliable and diverging mtDNA clade with high statistical support.

As a consequence of widespread partridge releases, Ferrero et al. (2011) used a different approach removing partridge localities, not only individuals, with introgression signal, and they did a phylogeographic, population genetic and demographic study using mtDNA control region sequences and nuclear microsatellite loci across the red-legged partridge distribution. These authors inferred five genetic clusters using samples from localities with restocking signal excluded. The pattern and genetic differentiation were more striking for mtDNA than for nuclear markers. Underlying this pattern of population differentiation was one of isolation by distance. Authors suggested that the current populations resulted from post-glacial expansion events and subsequent differentiation, which is compatible with isolation within the main glacial refugee the Iberian Peninsula was.

Rodríguez-García and Galián (2014) suggested a similar conclusion, that is, the continuous release of partridges is affecting the weak genetic structure in the red-legged partridge species, highlighting the lack of current genetic structuring employing contemporary samples from wild, released and farm populations. Their results manifested signals of genetic structure, as specific haplotypes in some regions. They proposed seven genetic clusters as the more probable structure that were similar than the five genetic clusters described by Ferrero et al. (2011). In fact, four of them, Corsica-France-Italy, Balearic, Cadiz and Nortwestern clusters, were the same than described by Ferrero et al. (2011). One of the additional clusters proposed by Rodríguez-García and Galián (2014) was composed of partridges from wild, released and farm localities (probably with haplotypes not associated with geographic locations), and the other two groups were a split from the central-eastern cluster described by Ferrero et al. (2011). This split could have occurred as a consequence of incorporate additional sequences from localities highly affected by releases. A recent study used over 168,000 unlinked markers throughout the *A. rufa* range, obtaining a more accurate picture of the spatial genetic structure of the species (Forcina et al. 2021). These authors found a homogenization of the native genetic structure of *A. rufa*, but, nevertheless, an evident intraspecific structure remains, being *A. r. hispanica* in northwestern Spain and *A. r. rufa* in Corsica, the most genomically distinctive subspecies.

Otherwise, Ferrero et al. (2016) assessed if genetic variability in the Iberian Peninsula could be explained by geographic and/or climatic gradients. Although they did not detect any clear genetic-environmental association for nuclear markers, they found that both mitochondrial genetic differentiation and genetic diversity were associated with thermal gradients and highlighted the role of temperature on shaping partridge spatial genetic pattern in the Iberian Peninsula, suggesting that the genetic patterns of diversity could be related to natural processes. Following this focus, Chattopadhyay et al. (2021) produced a high-quality de novo genome assembly of the red-legged partridge *A. rufa* reconstructing the demographic history of the red-legged partridge using the pairwise sequentially Markovian coalescent model to estimate changes in effective population size inferring a major demographic decline in the context of palaeoclimatic events. This decline was dated ~140,000 years ago, consistent with forest expansion and reduction of open habitats during the Eemian interglacial. So, present-day populations exhibit the historically lowest genetic diversity, which could have consequences in the availability to respond to current climatic changes.

Determination of Hybridization

To determine hybridization it is necessary to look at genetic markers. A genetic marker is any phenotypic or sequence variant able to tell apart two different genotypes. The first genetic markers were physical differences, and the pure foundation of genetics relies on morphological markers (Mendel 1866). The first note on the existence of a parapatric boundary between two *Alectoris* partridges was due to Aristotle on the basis of the different calls of *A. graeca* and *A. chukar*, a phenotype directly perceived by the naked senses, and Theophrastus claimed this boundary was between Boeotia and Attica. The chukar partridge sang “kakkabi” and the rock partridge “tri-tri-tri” for Aristotle and “tittybi” for Theophrastus. If we trust in this ancient report, we have to conclude that range limits at the border of both partridges have changed in the last two millennia (Arnott 1977). Further on the road, differences in plumage patterns among *A. rufa*, *A. graeca* and their hybrids were the genetic markers used to describe for the first time an *Alectoris* hybrid zone (Bernard-Laurent 1984). Morphological markers have been very useful in times when there was no other genetic marker system at hand, but they have limitations. Usually there is just a little number of morphological markers to distinguish species and their hybrids, and that is especially true among species that mostly look the same, as it happens in *Alectoris*. Besides, there is not a direct correspondence between genotype and phenotype in traits like plumage that depend of an unknown number of genes acting in concert that can interact in epistasis and may have differentiated norms of reaction (Danforth 1950). A major drawback to describe introgressive hybridization among *Alectoris* using morphological markers is that the earlier backcrosses are morphologically indistinguishable from the parental species.

The first molecular genetic markers were different forms of the same enzyme, called allozymes, that have different motilities in slab-gel electrophoresis and are revealed by a histochemical stain. The direct relationship between genes and their protein products allows to measure genetic differences between closely related taxa and to detail the distribution of genotypes at polymorphic loci. Allozyme techniques were developed in the 1960s (Hubby and Lewontin 1966) and were lavishly employed for the three decades onwards. These genetic markers were used to describe in more detail the hybrid zone between *A. rufa* and *A. graeca* that was previously studied attending to plumage patterns (Randi and Bernard-Laurent 1998, 1999). Nevertheless, allozyme markers have drawbacks. Differences in electrophoretic mobility do not inform about the evolutionary relationships of allozyme alleles at a locus. Also, both the number of polymorphic loci and the number of alleles per locus sometimes are too low to ascertain a question with confidence (Parker et al. 1998; Triest 2008). In addition, all synonymous and sometimes non-synonymous mutations do not change electrophoretic mobility and yield the same molecular phenotypes when they actually come from different alleles. Importantly, allozymes are a destructive marker system that most of the times requires lethal sampling. The first molecular markers based on polymorphisms in the DNA sequence were restriction fragment length polymorphisms (RFLPs) (Botstein et al. 1980), which have several limitations too, so the need for new systems of genetic markers remained. The advent of PCR (Mullis et al. 1986) accelerated the development of new molecular marker systems that overcame the limitations of the previous ones. Chiefly, PCR-based markers were faster and cheaper, and PCR is so versatile that spur the development of numerous molecular marker systems that greatly broadened the number and types of tools available.

Genetic marker systems can be classified in several different ways as we look to inheritance (dominant and codominant markers and biparental, paternal or maternal inherited markers), copy number in the genome, number of resolved loci per assay (single locus, multilocus or multiplex techniques) and nature of the polymorphisms (variations in the number of tandem DNA motive repeats, single nucleotide polymorphisms (SNPs), indels), but they used to be sorted either attending to the genomic basis of variation (i.e. microsatellites and SNPs) or the technique used to reveal variation (i.e. PCR-RFLP and RAPDs). All molecular marker systems are not equally suitable for the same genetic questions at hand, and it has frequently been highlighted that in choosing a suite of genetic markers many issues have to be considered in a trade-off between precision and convenience, which is to say that each genetic research group does the best it can. Several molecular markers have been used to study introgressive hybridization among *Alectoris*, and all of them worked fairly well to describe introgressed populations.

From the point of view of the quantity and quality of the information yield by molecular markers with regard to introgression, a good start might be to classify them apart between those that are fixed differences between or among taxa and those that are not. Markers that do not rely on fixed differences are probabilistic and have been employed to study introgression using assignment tests (Manel et al. 2005) or principal component analysis (Menozzi et al. 1978). However, since the software Structure appeared (Pritchard et al. 2000), introgression has been studied using non-diagnostic markers mostly by means of Bayesian clustering based on an interpretable population genetic model. Bayesian clustering algorithms assign individuals or a fraction of their genomes to a predefined number of populations or taxa making hybrid identification and population membership reliant on the allele frequencies at several loci and use to need Markov chain Monte Carlo methods. Microsatellites have been the main probabilistic marker system chosen to study introgression among *Alectoris* so far. On the other hand, markers that consist in fixed differences are diagnostic and unambiguously detect introgression. Species-specific diagnostic alleles are discriminatory and more able than quantitative probabilistic markers to detect introgression and to assign later generation hybrids to hybrid classes (Hohenlohe et al. 2011; Amador et al. 2012). Introgressive hybridization in *Alectoris* has also been studied by means of private SNP, microsatellite and RAPD alleles.

We may consider introgression either at the population level or at the individual level, depending on our purpose. It is desirable to measure individual introgression when the aim is to study individual fitness, to identify genes under selection, to remove hybrids from wild populations, for linkage mapping and probably other applications. The problem here is that a large number of genetic markers are necessary to describe or even detect hybridization in individuals with relatively low levels of introgression, as advanced backcrosses (Boecklen and Howard 1997; Vähaä and Primmer 2006; Sovic et al. 2014). Those estimates of the number of dominant or codominant markers required for a given degree of resolution have been done either considering diagnostic and non-diagnostic markers or assuming several simplifications not always explicit but simply assumed, as being the markers unlinked and autosomal with equal rates of recombination along the genome and no selection and, sometimes, not allowing all hybrid classes in the model. The real world is, to some extent, out of the assumed simplifications in a model, and there can be nonrandom patterns of introgression; thus the power of a given number of markers to detect introgression can be different than the theoretical expectation. While the number of markers required for an individual-based study of introgression is large and sometimes impracticable, approximate estimates of hybridization at the population level only need a handful of diagnostic markers such that description of population-level admixture using less than ten diagnostic markers is consistent with the estimates from thousands (Hohenlohe et al. 2013). Accuracy can be improved to levels similar to that of thousands of diagnostic markers using 50–100 independent diagnostic loci (Amish et al. 2012). When the aim is the conservation of natural populations and the monitoring of the artificial ones (farms), the object of study is not the individual but the population. The number of diagnostic markers currently used to study introgression in *Alectoris* is insufficient to distinguish pure individuals from advanced backcrosses with low error but is more than enough to describe introgression in populations. The probability P to detect the presence of introgressed alleles in a population can be calculated as

$$P = 1 - (1 - q)^{2nx},$$

where q is the frequency of alien alleles to be detected (i.e. proportion of hybridization), n is the number of individuals sampled and x is the number of diagnostic markers (Kanda et al. 2002). The power to detect hybridization in a population increases exponentially with the number of samples and the number of diagnostic markers, so the above equation can be employed to have a baseline estimate of the sampling effort for a given number of diagnostic markers.

With the number of molecular markers already in use in *Alectoris*, it is possible to find non-hybridized populations, to reveal the farms that breed hybrids and to study the fate of anthropogenic introgression in natural populations, which are mandatory issues in the management and conservation of partridges. Nonetheless, several additional markers would be welcome for population-based studies, and several thousands more are necessary to study individual-level admixture. The arrival of new genomic tools, particularly next-generation sequencing (NGS) technologies (Metzker 2010; Goodwin et al. 2016), enables to quickly discover and genotype many thousands of SNP markers distributed across the genome allowing genetic analysis at scales not previously conceivable. These new methods are applicable not only to model species with a sequenced and assembled reference genome but also to non-model organisms with little or no genomic information available. Among the new-generation techniques that sequence a reduced subset of the genome, restriction site-associated DNA sequencing (Baird et al. 2008) is being the most widely used in genetic studies on wildlife. NGS is a sort of revolution, as PCR was and, despite not being a magic bullet, is as good as it promised. NGS not only permits marker discovery but also genotyping. If more *Alectoris* markers were needed, NGS could be used to obtain thousands of them. Fortunately, there is already a genome-wide study using NGS (Forcina et al. 2021), and a reference genome assembly of the red-legged partridge (Chattopadhyay et al. 2021).

Finally, it is important to sound a cautionary note about ascertainment bias when diagnostic markers are discovered from a small number of individuals that do not represent the actual polymorphism of the species. Validating diagnostic markers requires re-genotyping many pure partridges from across the distribution range, which is a difficult task nowadays since it is challenging to find non-admixed populations after decades of hybrid releases. Fortunately for the red-leg, hardly other birds have been more stuffed, and samples to extract ancient DNA are not in short supply.

Status of Anthropogenic Hybridization

Alectoris species are naturally reluctant to hybridize. They do not do it in their natural ranges, apart from three narrow hybrid zones (Fig. 1). When different species have been introduced in the same island, the result never was a hybrid swarm. However, the independence of the *Alectoris* genomes is being broken down at an industrial scale since the second half of the twentieth century. Because nature does not yield enough partridges for current hunting demand, *A. chukar* hybrids are mostly bred in farms and sold to be released by its millions yearly (Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"). For some reason, *A. chukar*, or a sort of *A. chukar* is far more prolific than the other *Alectoris* when bred in captivity; thus it has been crossed and backcrossed with *A. graeca* and *A. rufa*, independently, to get selected hybrid lines that are equally prolific and fitted to be raised in farms (Barbanera et al. 2015). Backcrossed prolific-in-farm *A. rufa* x *A. chukar* hybrids are massively released in the distribution range of *A. rufa*, and *A. graeca* x *A. chukar* hybrids are released in the distribution range of *A. graeca*. Released hybrids survive in the wild and have offspring. This anthropogenic hybridization is a serious threat to *A. rufa* and *A. graeca* that might become extinct either by hybridization and by the breakdown of genomes so in tune adapted to particular ecological demands. Indeed, hybridization has been found in the complete distribution range of the red-legged partridge where it has been searched for (Baratti et al. 2004; Barbanera et al. 2005, 2009, 2015; García and Arruga 2006; Tejedor et al. 2007; Barilani et al. 2007; Blanco-Aguiar et al. 2008; Martínez-Fresno et al. 2008; Barbanera et al. 2010; Casas et al. 2012; Negri et al. 2013; Forcina et al. 2021). Phylogenetic analysis of *A. chukar* mitochondrial haplotypes found in mitochondrial introgressed *A. rufa* and *A. graeca* compared with mtDNA sequences of wild *A. chukar* sampled throughout the chukar's range assigned East Asia as the geographic origin of the chukar partridges polluting the genome of native Mediterranean *A. rufa* and *A. graeca* (Martínez-Fresno et al. 2008; Barbanera et al. 2009). However, the addition to the analysis of mtDNA haplotypes from domestic *A. chukar* lines raised for meat production grouped the introgressed mtDNA with them too (Marín et al. 2015; Rodríguez 2016).

Fitness Consequences of Hybridization and Domestication

When two populations have been isolated for a long time and come into contact again, different situations are possible. Firstly, when genomes of two populations recombine, there is a release of genetic and phenotype variability that makes adaptive change possible (Arnold and Martin 2010). The increase of genetic variability originated for this admixing may have benefices on fitness. In fact, heterosis or hybrid vigour has rescued some populations with low genetic variability, increasing their viability and/or reproduction success reversing inbreeding depression (Edmands 2007). Secondly, hybrids with different characteristics from parental populations can take advantage in new colonizing areas or have elevated fitness under particular environmental conditions (Arnold and Martin 2010; Rius and Darling 2014). Third, it is possible that these isolated populations develop local adaptations or simply accumulate a set of neutral or beneficial mutations, but when these populations are hybridized, these mutations may be incompatible or deleterious, causing adverse effects in the fitness of these hybrid populations (Arnold and Martin 2010; Rius and Darling 2014). In the Bateson-Dobzhansky-Muller (BDM) model, it is suggested that in the hybridization of individuals from divergent populations it is possible the disruption of intrinsic interactions between genes or the disruption of extrinsic interactions between genes and the environment, which promotes outbreeding depression through fertility or viability (Bateson 1909; Dobzhansky 1936; Muller 1942). This is supported by the Haldane rule that states that F1 hybrid sterility or inviability usually manifests in the heterogametic sex first (i.e. Haldane's rule; Haldane 1922; Coyne and Orr 2004), probably explained by the exposure of epistatic interactions between recessive sex-linked and dominant autosomal BDM incompatibilities in the heterogametic sex (Johnson and Lachance 2012).

In addition to hybridization, the species under captive breeding tend to be subjected to very different selective pressures from those existing in the natural environment. Usually a relaxation of the selective pressures (i.e. predation or starvation) and a conscious or unconscious selection of certain characters (i.e. docility, productivity, expansion of reproductive period, etc.) are desirable for captive breeding that might not be suitable for the survivability of these species in wildlife. Furthermore, as a result of epistatic interactions, artificial selection of many of these characters can indirectly drag other unselected characters favouring certain genotypes that are disadvantageous in the wild through correlational selection. For instance, the poultry breeds are domesticated genotypes of the red junglefowl, *Gallus gallus*, which lives in Southeast Asia and was domesticated approximately 8000 years ago (Jensen 2006). During the process of domestication, they have encouraged some behavioural characters unsuited to live in wildlife, for example, reduced foraging and exploratory behaviour, less social interaction or less intense antipredator behaviour (Jensen 2006). Several of the selective sweeps detected in broilers overlapped genes associated with growth, appetite and metabolic regulation. One of the most striking selective sweeps found in all domestic chickens occurred at

Fig. 2 Artistic representation of *Alectoris* partridges: (**a**) Mosaic of Delfos' sanctuary (4th BC, Greece) and (**b**) late-Roman sanctuary (third century) in Santa Eulalia de la Bóveda (Lugo, Spain). Image by JA Blanco-Aguiar

the locus for the thyroid-stimulating hormone receptor (*TSHR*), which has a pivotal role in metabolic regulation and in the photoperiod control of reproduction in vertebrates (Rubin et al. 2010). In this species, it has been observed that some characters are associated with pleiotropy, for example, selection on egg size or growth is associated with behavioural traits such as tonic immobility, a trait related to antipredator behaviour (Jensen 2006; Shea et al. 2007). Contrary to a popular belief, there are some evidences that an overly long period of time is not necessary to observe these effects. In this regard, it is paradigmatic the case of the silver fox where the selection of characters associated with docility (lack of fear to humans) over only 10 to 20 generations favoured the emergence of other behavioural and morphological characters (growth, colour, cranial neoteny, vocalizations) that a priori had not been prioritized during this selection process (Belyaev et al. 1984; Vasilyeva 1995).

In the case of the red-legged partridge, both processes of domestication and hybridization with the chukar partridge can be involved in the change of the gene pool and quality of this species. There is historical evidence that already in ancient time, Roman, Greeks and/or Phoenicians used *Alectoris* partridges as ornamental or in religious rituals (Fig. 2). So, different *Alectoris* species could be transported between different regions, favouring domestication and hybridization between species. However, the intensive breeding of *Alectoris* partridges is fairly recent and especially has had its boom in the production of meat, mainly focused on *A. chukar*, and later for hunting-release purposes (Barbanera et al. 2009; Gonzalez-Redondo 2004). This could make us think that despite the introduction of these mechanisms of genetic variation which is relatively recent, this does not mean that the genetic impact it has had is little.

Although different methodological approaches have been used to study the influence of hybridization on different parameters in the biology of the red-legged partridge, the results are still limited and far from conclusive. Some of these studies showed conflicting results, so it is difficult to assess the role of hybridization on partridge fitness. In addition, the methodological constraints complicate to discern whether the observed effects are really due to mechanisms associated with hybridization and domestication or even that these differences were due to the origin (released vs. wild) of the partridges studied. Although molecular markers are a good tool to identify partridge populations with introgression, they may not be so appropriate to identify pure partridge individuals, and this can skew the information that can be obtained from these studies, as we have discussed previously. So, to avoid confusion in this section, we will distinguish between hybrid partridges, when genetic markers detect hybridization, and non-hybrid partridges, when markers do not detect hybridization, but we cannot ensure if they are pure, and pure partridges, being those where it is certain that there is not introgression.

In farms, red-legged partridges have been artificially hybridized with chukar partridges. Although very similar, these two species have different phenotype characteristics, so it is expected that the hybrids may be different from the parental species. For example, chukar partridge is a species with a wide range of distribution and a size slightly larger than the red-legged partridge, and some authors have suggested a more promiscuous behaviour in the former (Vidal and Colominas 2007, but see Casas et al. 2009). Different parental phenotype characteristics might have an influence on life history parameters of hybrids. So, those parameters associated with reproduction and mortality should be important to assess the role of introgression on population dynamics. What do we know about the reproductive differences between hybrid and "pure" partridges? Potts (1989) suggested that red-legged partridges have been artificially hybridized with chukar partridges to increase egg laying period and to produce tamer birds than red-legged partridges. Curiously, these parameters are characteristic of those species that have been subjected to intensive industrial production. However, farm and wild conditions are not comparable, and selection on traits useful in captivity could not be useful for the wild. The chukar partridge has been bred in captivity for a long time as a hunting species but also as a source of meat production (Woodard 1982), so artificial selection could have favoured these "domestic" phenotypes.

What does it happen with these hybrid partridges on the wild? Despite the low survival of released partridges (see Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"), there is evidence that the hybrid partridges can breed in the wild (Potts 1989; Casas et al. 2012; Ferrero 2016). In a study in different British populations, Potts (1989) assured that hybrid and chukar partridges had lower productivity than red-legged partridges; however this study was based on observational discriminations of partridges and did not used any molecular marker to verify the genotype of these partridges. In Ciudad Real (Central Spain), Casas et al. (2012) studying radio-marked wild partridges characterized by molecular tools not only observed that the hybrid partridges were able to breed in the wild but also that the breeding probability was similar between hybrid and non-hybrid partridges. In addition, their clutch size from hybrid partridges was greater than that of non-hybrid partridges, although hatching success was similar suggesting that there was no reproductive advantage between the two types of partridges. Blanco-Aguiar (2007) and Casas et al. (2013) also noted a better body mass index of female hybrid partridges than non-hybrid partridges, and Casas et al. (2013) suggested that the better body mass index could be associated with higher reproductive success observed in female hybrid partridges. These authors suggested that this difference could be also associated with domestication and could be caused by the artificial selection of farm partridges having a larger clutch size or body condition. However hybrid females had significantly lower plasma carotenoid concentrations than non-hybrid females, and authors argued that this could be associated with lower body condition associated with hybrid parasitism or reduced capacity to ingest and/or absorb carotenoids. Blanco-Aguiar (2007) showed that cestode richness was negatively associated with condition and hybrid partridges with more intestinal parasites use to have larger spleen, an organ associated with immune response, than non-hybrid partridges.

In relation to male partridges, bird size could play an important role on sexual selection, male-male interaction and in territory defence. Campo et al. (2015) comparing partridges from a hybrid farm with partridges from other farms without hybridization showed that the mass of male hybrid partridges is greater than the one of non-hybrid partridges. However, in wild studies on hybrid partridges, Casas et al. (2013) showed that hybrid partridges have a smaller size (based on longitudinal measurements) than the partridges without hybridization. So there is no consensus among studies of how introgression affects the size of hybrid partridges.

In the wild, male hybrid partridges had similar breeding probability than non-hybrid partridges (Casas et al. 2012) and had similar carotenoid levels (Casas et al. 2013), and no differences in testosterone concentration plasma levels were observed in captivity (Santiago-Moreno et al. 2015). Casas et al. (2012) did not find differences between the two types of partridges in relation to the date of egg laying, but Santiago-Moreno et al. (2015) suggested an earlier onset of reproduction in hybrid partridges with respect to non-hybrid partridge stocks. This study also suggests that genetic introgression may influence the sperm phenotype variables of the red-legged partridge. While the partridges from non-hybrid stock have a higher percentage of motile sperm than partridges from hybrid stock, the sperm concentration and the parameters associated with sperm motility (speed, linearity, etc.) or sperm morphology (head size) that may be associated with potential fertilization looked better for hybrid partridge stock.

Other important parameters in population dynamics are those associated with mortality. The only study conducted so far on wild populations (Casas et al. 2012) indicated that mortality was higher in hybrid partridges than in non-hybrids. This increased mortality in hybrid partridges was caused primarily by predation and also was higher in males than in females. Interestingly, different types of predators were involved in non-hybrid partridge predation, while carnivores were the main predator of hybrid partridges. In this line, Campo et al. (2015) comparing the behaviour of tonic immobility, an indirect indicator of fearful, observed that the stock with no hybridization had a longer duration of tonic immobility, suggesting more fearful than partridges from the hybrid stock. These results could suggest a differential impact of hybridization on partridge predation.

However, when other indirect indicators of stress were used, the results were not so intuitive. Fluctuating asymmetry (FA) is a non-directional variation of bilateral characters produced during early development and caused by genetic or environmental stress or the interaction of both factors (Leary and Allendorf 1989). Regarding the role of hybridization on FA, two main hypotheses have been proposed: the heterozygosity hypothesis, in which fluctuating asymmetry decreases when biological efficiency is increased, and the genomic coadaptation hypothesis in which developmental stability decreases when coadapted genes are disrupted (Pertoldi et al. 2006). Campo et al. (2015) observed that partridges from the hybrid stock are less asymmetric than partridges from the non-hybrid stock, and if hybridization could have any negative influence on hybrid partridges, we should expect an inverse pattern. One of the major problems of this approach is to distinguish between genetic and environmental sources that modify the FA level (Pertoldi et al. 2006). In our opinion, it is possible that the observed differences could be rather due to environmental or genetic factors associated with stock management (e.g. different genetic variabilities between stocks or domestication selection) than to hybridization. Perhaps these results could be an indicator of the worst acclimatization to captivity attributed to pure partridges, which indirectly affects their productivity or stress susceptibility. This pattern is reinforced by another parameter used in this study, and that is the heterophile-lymphocyte ratio, another indicator of stress also higher in the non-hybrid partridges than in the hybrid partridges (Campo et al. 2015). This raises the question of whether the tonic immobility previously highlighted as a behaviour affected by hybridization could be a response to different stress levels. Similarly, the sperm parameters might be affected more by the stress than by hybridization, so we cannot rule out that the best sperm quality parameters observed in hybrid partridge stock (Santiago-Moreno et al. 2015) may be also due to the lower captive-stress impact or higher domestication level of this stock.

However, it is important to clarify some details in all these studies. Hybrid partridges used in these studies are first, second or more advanced backcrosses. Unfortunately, as we explained above, the power of these molecular tests (8–20 markers depending of each study) is not high enough to ensure that those animals in which hybridization has not been detected are really pure individuals. Given the production system in partridge farms prioritizing in maximizing productivity and assuming the higher productivity in captivity of hybrid than pure partridges, once the hybrid partridges enter within a farm system, in a few generations, all the stock could be homogenized forming what is called a hybrid swarm. With low hybrid detection power, only a few percentage of hybrid partridges are detected, although probably all individuals in that farm are hybrids. In fact, some of these studies (Campo et al. 2015; Santiago-Moreno et al. 2015) used partridges from a "pure" farm that was initially formed by a hybrid swarm stock. Farm managers attempted to eliminate those hybrid animals to achieve a genetic cleansing using this small set of markers, but the remaining individuals in those "clean farms" probably remain hybrid, and only they cannot be detected with the same set of markers. In addition, the potential genetic traits selected as consequence of domestication remain in these farms. A representative number of pure and hybrid lines will be necessary to discern whether the observed differences between "pure" and introgressed partridges could be due to hybridization or differences in domestication breeding lines (heterozygosity, captivity selection) or even other environmental conditions (e.g. latitude, management stress). Those studies analysing wild partridge populations (Blanco-Aguiar 2007; Casas et al. 2012, 2013) could suffer the same difficulty, but probably in these cases, the likelihood that some of the non-hybrids genetically identified were pure partridges increases. The assumption that it is possible to find pure partridges in wild popuations has the drawback that hybrid individuals (genetically identified) could come from unrecorded partridge releases, which blurs whether the observed fitness differences are due to hybridization-domestication processes or are single differences between wild and released partridges misfit to live in the wild, but not associated to genetics changes.

Despite important constraints, these studies are providing the first signals that the hybridization-domestication-release strategies of management in red-legged partridges may have effects on the ability to adapt and survive in the wild and should be taken into consideration. Probably, the main signal of a hybrid fitness breakdown we have comes from an indirect evidence: after many decades of massive red-legged partridge releases—more than 5 million yearly being hybrids (see Ferrero et al. 2016)—we have no signal of wild partridge population recovery. So, the fitness breakdown would result in a constant and slow tendency to the recovery of wild populations if massive releases cease to erode the genetic quality of wild populations. The availability of new genetic tools would be useful to deepen this approach and to assess the role of hybridization and/or domestication in the red-legged partridge.

Concluding Remarks

All the knowledge on partridge hybridization is useless for practical matters. There is a gap between scientific research and applicable sound solutions for the management and conservation of populations (Shafer et al. 2014). Releasing hybrid partridges is banned in all EU European countries by laws that ultimately hang from the Directive 79/409/EEC, unanimously adopted by member states and one of the oldest pieces of EU legislation on the environment. Amended in 2009, it became the Directive 2009/147/EC, also known as "The Bird Directive". The release of hybrids to the wild is also forbidden by the "Habitat Directive" 92/43/EEC. There is a manifest public interest about the problems of anthropogenic hybridization of the red-legged partridge for the fate of the species. However, there is neither a sole formal strategy nor a formal plan to face this problem. Current guidelines to control artificial hybridization in red-legged partridge warrant our attention because those are actually being implemented and appear to be an example of a genetic misconception assumed by many lawgivers, game managers and end-users. Basically, the guidelines in use oblige the use of a set of about 22 diagnostic markers to detect chukar introgression into individual red-legged partridges. Farmed birds are being genotyped one by one with that set of markers, and every partridge in which there is evidence of hybridization is removed, while partridges in which those 22 markers do not detect introgression are considered "pure" and obtain an official certificate that allows them to be sold for releasing. Knowing the limited resolving power of 22 diagnostic markers, the pretended "pure" farmed partridges are actually hybrids too but now legal. Screening the pretended pure partridges with additional markers would evidence introgression, although additional markers are not allowed by the guidelines to test admixture. Farms are actually hybrid swarms. It is hard to believe that hybrids and pure red-legged partridges as unnaturally productive as the hybrids are bred separately in the same farm, as the draft guidelines assume. Nowadays, the conflicts between economic development and nature conservation are immense. Raising hybrids for rearing is a profitable business banned by law. Not without irony, perhaps an easier solution for law makers would be to determine both species as conspecific due to the extensive hybridization between chukar and red-legged partridges, preventing further genetic considerations, as it happened in the United States with the largely admixed Mexican duck (*Anas diazi*) when it was determined as conspecific with the mallard (*A. platyrhynchos*) (AOU 1983), exempting its listing as endangered. Unfortunately, for many species, "conservation" means "management", and the red-legged partridge is not an exception. In this regard, it is discouraging to see that we are not beyond of the Aristotle's tri-tri-tri- and Theophrastus' tittybi.

Acknowledgements We would like to thank João Queirós for his help in referring to the introduction of partridges in the Portuguese islands and to many anonymous hunters who provided us with samples and valuable information.

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Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing

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Why Do We Rear and Release Red-Legged Partridges?

A Brief History of the Gamebird Rearing 'Industry'

It is not known when partridges were first reared in captivity, though there is evidence that the Romans kept them as ornamental birds (second century, Manley 2013). Translocations for hunting purposes have been conducted since the thirteenth century (González-Redondo 2004). What we know for sure is that in the nineteenth century, British gamekeepers reared several gamebird species with broody bantams

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F. Casas, J. T. Garcia (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_7

Gallus gallus domesticus (Browne et al. 2009), a technique also documented in Spain for red-legged partridges *Alectoris rufa* in the twentieth century (José Lara, *pers. comm.*).

The turning point for gamebird rearing in Europe occurred after the Second World War, when farmland birds started a long-term decline caused by agriculture intensification (Donald et al. 2001). During the 1940s and 1950s, rearing gamebirds was costly, but with the onset of artificial incubation and the development of poultry-rearing technologies, producing gamebirds became relatively cheap and easy. In the early days, red-legged partridge rearing was aimed at re-establishing wild populations and was mainly conducted by public agencies, such as the *Office National de la Chasse (later "et de la Faune Sauvage")* in France (e.g. Farthouat 1983; Jullian 1984; Bounineau and Aubineau 1985; Berger 1989; Brun and Aubineau 1989; Niot et al. 1989) and *Servicio Nacional de Pesca Fluvial y Caza* in Spain (and later on *ICONA*). However, as time progressed and reinforcements were not always successful to restore wild populations, also degrading habitats (Bro and Mayot 2006; Péroux et al. 2006; Meriggi et al. 2007), rearing became increasingly popular for put-and-take shooting rather than for re-establishing wild populations. Today gamebird rearing is a well-developed poultry subsector run mainly by private companies, and releases for hunting purposes are a common practice (Reitz 2003; Ponce-Boutin et al. 2006b, 2012; Sánchez-García et al. 2009; González-Redondo et al. 2010).

What Do Hunters Prefer to Shoot?

Hunters were one of the first groups to recognize the degradation of the natural environment and also the first who fought against this degradation (Tori et al. 2002). The paradox is that game management can have both a positive or negative impact on the conservation of game and other wildlife. Hunters or game managers may undertake significant conservation efforts to encourage wild shoots or, at the opposite side, choose a quick way of satisfying a given hunting demand by rearing and releasing game. Those interested only in put-and-take do not seem to develop a connection between man and nature. For example, hunters in Ohio, who argued that releasing was the solution for the satisfaction of hunting demands, had not read books about wildlife and were not members of environmental organizations, and their hunting satisfaction depended on the size of the game bag (Peterle 1967). This new attitude towards a fully artificial hunting and large bags may be related to the increasingly number/proportion of urban hunters in countries such as Spain and France (over 50%; see Martinez-Padilla et al. 2002) which may have no regular access to a hunting ground as not all of them have connection with the countryside.

On the other hand, the size of the game bag should not be considered that important; it is the way in which the game is harvested that really matters. What truly satisfies the hunter is not only the harvested quarry but also the process and the efforts made. Put-and-take makes hunting more predictable, as release locations, numbers and species to be released are known beforehand.

There are hunters who consider shooting as a way of life, which can play a decisive role in the environmental and pedagogic dimension of hunting. In Spain, older hunters (who are often more connected to the countryside than young ones) understand hunting as a way to interact with nature, and regular and experienced partridge hunters value the difference between good- and poor-quality hunting (Delibes-Mateos et al. 2014). In Greece, hunters who consider hunting as a sport mainly support strategies that involve game releasing, whereas those who considered hunting as a way of life believe that habitat improvements and predator control are the best way to increase game (Sokos et al. 2009). In France, similar profiles of hunters have been described the "traditional hunter" for whom hunting is part of his identity; it is an "art of living" vs. the "modern hunter" for whom hunting is leisure. While some of the latter want to receive a benefit from the money spent, others do not pay attention to the bag and appreciate as much to observe game animals. For the ancient Greeks, hunting offered the opportunity to acquire discipline, test skills and enjoy the feeling of freedom (Sokos et al. 2014).

Existing literature from Spain suggests that the majority of hunters may prefer shooting wild red-legged partridges (Delibes-Mateos et al. 2014), and game managers are aware of the negative consequences of releasing (Delibes-Mateos et al. 2015). However, even if wild red-legged partridges are preferred, the reality is that not all the people can afford the management cost (e.g. BIPE 2015). During the last century, the sociological profile of hunters in Europe has changed dramatically, together with the habitat where red-legged partridges were once abundant. The majority of red-legged partridge hunters do not live in rural areas anymore; they cannot take management decisions, and the money spent in hunting is limited, though in countries such as the UK and France the average hunter's budget per season is 2–3 higher (around 2,000€) compared to Spain and Portugal (Martinez-Padilla et al. 2002). A more recent study conducted in 2016 in Spain, showed that the average expenditure per hunter was €9694 per year (Sánchez-García et al. 2021). Hence, for many hunters and managers, the only way to maximize the available money is through releasing, though releasing for conservation purposes with shooting restrain during restocking may be an alternative.

What Kind of Shooting Are Managers Offering?

The few studies conducted on this topic suggest that the majority of commercial shooting estates rely on reared birds (PACEC 2006; Díaz-Fernández et al. 2013b). A detailed study from Central Spain (Díaz-Fernández et al. 2013b) found a lower offer of wild red-legged partridges hunts when compared to commercial for both driven (3 of 29 sellers) and walking-up shooting (15 of 31 sellers). Surprisingly, the same study found no significant price differences between wild and reared shoots, though producing wild game is more expensive than reared. In Britain, only 10% of shooting providers declare not to release game (PACEC 2006). In France, hunting releases are performed in the great majority of communalities where the red-legged partridge is historically present (Ponce-Boutin et al. 2012). This is not surprising, as put-and-take shooting allows for a large number of shooting days per season, together with large bags.

As with other gamebirds, there are several ways to sell red-legged partridge hunts: a whole shooting season, a single day shooting or full ‘shooting packages’, which include transport, food, gun hire and accommodation. In some cases the hunter pays depending on the number of red-legged partridge shot, whereas in other cases, the bag limit is fixed in advance. Available data from advertisements shows that the prize of red-legged partridge shooting varies significantly among countries and types of shoots. In commercial estates, the cost of one red-legged partridge shot varies between 6 and 30€, while in non-commercial estates, it is 50–90€, though this prize may apply to both reared and wild red-legged partridges (Martinez-Padilla et al. 2002). In Central Spain, the average cost of red-legged partridge-driven shooting per gun and day is around 2700€ (being the bag limit 100 birds), while walked-up shooting per gun and day is around 200–300€ (bag limit of 3 birds, Díaz-Fernández et al. 2013b). In France, it is an average of 15€–25€/released bird (6–10 birds/day) (e.g. see shooting packages available in www.planetachasse.com, “CHASSES À LA JOURNÉE”).

To date, in some countries it is still not possible to know for sure whether red-legged partridge hunts are truly wild, especially on shooting estates selling a limited number of days or offering smaller bags, where non-declared releasing cannot be ruled out (Caro et al. 2014). Typically, wild red-legged partridge shoots are sold or offered by word-of-mouth or close connections. As suggested by other authors, promoting ways to certificate wild shoots where sustainable wildlife management is conducted will help increase the value of truly wild shoots (Díaz-Fernández et al. 2013b; Delibes-Mateos et al. 2014). However, it is important to note that in countries such as Spain, there are commercial shooting estates that do not ‘hide’ the origin of their birds and have developed a professional put-and-take system, complying with strict regulations.

The Scale of Red-Legged Partridge Releasing and Legal Framework in Europe

How Many Red-Legged Partridges Are Reared and Released in Europe?

For decades, researchers have tried to assess how many gamebirds are reared and released in Europe, but it is still difficult to get accurate data when compared to other livestock sectors. In our opinion, this can be explained by the fact that gamebirds are released to the wild (so they do not go to the slaughter house); not all countries have accurate game bag recording systems, and information about international gamebird trade is lacking. Perhaps data exist, but it is neither computerized nor analysed.

Table 1 Estimation of the number of red-legged partridges reared and released in Europe. [a]Data from regional game and wildlife plans from Tuscany, Piedmont, Liguria and Emilia Romagna. [b]It has been estimated that fewer than 100,000 grey partridges are released in the UK (Aebischer 1997, 2013)

Country	Species	Year	*n*	Data source
France	*A. rufa*	1995	2,504,320	Tupigny (1996)
	A. rufa and *P. perdix*	2011	5,000,000	French Association of Game Farmers
Italy	*A. rufa*	2015	55,000–60,000	F. Santilli (*pers. comm.*)[a]
Portugal	*A. rufa*	2009	100,000–200,000	Extrapolated from Beja et al. (2009)
Spain	*A. rufa*	2015	4,717,317	Spanish Ministry Rural Affairs
	A. rufa	2007	5,153,618	Spanish Ministry Rural Affairs
United Kingdom	*A. rufa* and *P. perdix*	2004	6,500,000	PACEC (2006)[b]
Total	*A. rufa*		c 14,000,000	

A conservative estimate suggests that around 14 million red-legged partridges are reared for shooting in Europe annually (Table 1). These figures have to be treated with caution, because in some countries red-legged and grey partridges *Perdix perdix* are pooled together in the statistics (making it impossible to get numbers for each species), and we have not been able to get exact data from Portugal, where it is likely that at least 100,000–200,000 birds are released per season (a mean release density of 410 birds/km^2 was calculated by Beja et al. (2009) from 24 Portuguese estates).

Spain and France produce the majority of eggs and poults, also providing birds for Italy, Portugal and the UK. The French Association of Game Producers declares that over 10 million gamebird eggs are sold mainly to Spain and the UK every year (http://www.snpgc.fr), and it is known that in the UK, 278,638 live partridges (red-legged and grey partridges) were imported in 2015 (http://www.parliament.uk).

In Spain, public game farms reared and released annually around 2,000–3,000 red-legged partridges in the 1960s, whereas nowadays this figure may be around 3–4 million (Sánchez-García et al. 2009), and in the UK, the numbers of red-legged partridge released compared to 1985 are fivefold higher (*National Gamebag Census*, Aebischer 2013).

There are around 300 gamebird farms in the UK (http://www.gfa.org.uk), 400 farms of red-legged partridges in Spain and 1,500 gamebird farms in France, with at least 11,000 employees working at these farms. In the UK, some gamekeepers rear their own stock (Game Conservancy Trust 1994), which is not a common practice in other countries. Considering only the market value of the birds (4.5€/bird), an income of 60€ million is generated each year in Europe. As rearing and releasing supports commercial shooting of red-legged partridges, its socioeconomic value is high in regions where shooting is one of the only economic activities.

In Spain, the market value of red-legged partridge shooting in 2011 was calculated to be €306 million (Garrido 2012), with Castilla-La Mancha being the 'hot spot' (Bernabéu 2002). A study conducted in Spain estimated that the total expenditure of hunting providers (including commercial estates specialized in driven partridge hunting) when calculated nationally was €781 million (Sánchez-García et al. 2021). In Britain, €1 billion was spent directly with shooting providers or on site in 2012–2013 (PACEC 2014), so it is likely that the contribution of reared red-legged partridge to this figure is significant. Similarly, in France, the global economic weight of hunting (all species and sectors combined) is estimated to 2.1 billion euros in 2013–2014 (BIPE 2015), but the specific part related to each game species is not known.

Despite the negative views of some game managers towards releasing (Delibes-Mateos et al. 2015) and both positive and negative effects of releasing on wild counterparts and other wildlife (to be discussed later in this chapter), it is likely that reared birds will continue to be used as the main supply for shooting, unless the shooting community and policy makers decide to turn research into practice to increase the number of wild birds, as has been demonstrated in grey partridges (Sotherton et al. 2013).

Legislative Framework of Releasing

In Spain, Italy and Greece, estates must have a releasing plan approved by the Forest Service indicating the number of gamebirds to be released. In Italy, releasing is not allowed after the 30th of August in non-commercial estates, and in Greece it depends on the aim of release: releasing for re-introduction is allowed all year round, while for hunting purposes, it should be conducted until 1 month before the opening of the hunting season. In Spain, each County Forest Office decides releasing depending on the type of estate (commercial and non-commercial) and the aim of releasing, and it is needed to submit the date of releasing, number of birds released and shooting bag after the hunt. In recent years the legislative framework has been enforced, as the genetic integrity of game farms is mandatory and releasing in non-commercial hunting grounds is discouraged by the authorities. For none of the above countries, it is needed to be licensed to handle or release gamebirds (with the exception of people transporting birds).

In the UK, there are no official releasing plans, though this country has developed 'The Code of Good Shooting Practice' (www.codeofgoodshootingpractice.org.uk), which indicates that under normal circumstances, (1) all birds should be released before the start of their shooting season, (2) shooting must not commence until the birds are mature and fully adapted to the wild—a minimum of 1 month from release, (3) birds must never be released to replenish or replace any birds already released and shot in that season and (4) partridge release pens should be removed before shooting begins. This code is not mandatory, but it seems that there is good widespread adherence to it. Similar recommendations exist in other countries, but to our knowledge, there are no compulsory codes.

In France, the red-legged partridge can be released anywhere except if local rules forbid or restrict it to specific areas or conditions (habitat management, predator control, genetic profile, numbers, etc.) (Charlez 2010). These local rules are defined by the *Schema Départemental de Gestion Cynégétique* developed by the local hunting association. This scheme is validated by the Prefect and is mandatory. If releasing is allowed, no prior administrative approval is required to release red-legged partridges (Article L 424-11 of the French *Code of Environment*). A request to make any release subject to an authorisation has been recently rejected. However, sanitary issues such as those related to bird flu will perhaps make this rule change in the near future. However, game farmers are required to record any sales.

How Rearing and Releasing Work?

Description of Rearing Systems

Generally speaking, there are two main types of gamebird rearing: commercial and non-commercial. Rearing techniques are similar among gamebird species, though we will refer specifically to red-legged partridges.

Commercial rearing is based on the following stages: (1) production of eggs for incubation, (2) incubation and hatching and (3) rearing in brooder houses during the first weeks and flight pens before release. Farms can conduct a ‘complete cycle’ when all stages take place at the same farm, though farms conducting only one or two stages are becoming more popular (González-Redondo et al. 2010).

To produce fertile eggs for incubation, breeding pairs are kept in laying cages for the whole year (Fig. 1), or the sexes are kept separate outside the reproductive period (autumn and early winter). Forced pairing is a common practice, but welfare problems such as feather pecking have been identified (Prieto et al. 2012). Depending on the latitude and the artificial manipulation of photoperiod, egg laying starts in January–February and lasts for 14–16 weeks. Hens selected for laying may produce over 50 eggs per season, attaining the highest values of clutch size and fertility at the second reproductive year (Mourão et al. 2010). The eggs are collected daily, and intact eggs are stored in large batches (temperature 14–15 °C, relative humidity 70–80%), before the start of artificial incubation which lasts 23–24 days (37.6–37.7 °C, 50–55%). Egg storage and incubation are the most technical phases, as temperature, humidity and ventilation must be controlled at all times to avoid loss of hatchability and disease (Sánchez-García et al. 2013).

After hatching, chicks aged 0–1 days are brought to brooder houses, where the room temperature is kept from 30 °C to 35 °C during the first 4 weeks using infra-red lamps or gas heating. Chick densities in brooder houses should not go over 20–25 birds/m^2 during the first 4 weeks of life. Feed for chicks from 1 to 7 weeks of life must provide 26–27% of crude protein and a balance amount of vitamins, amino

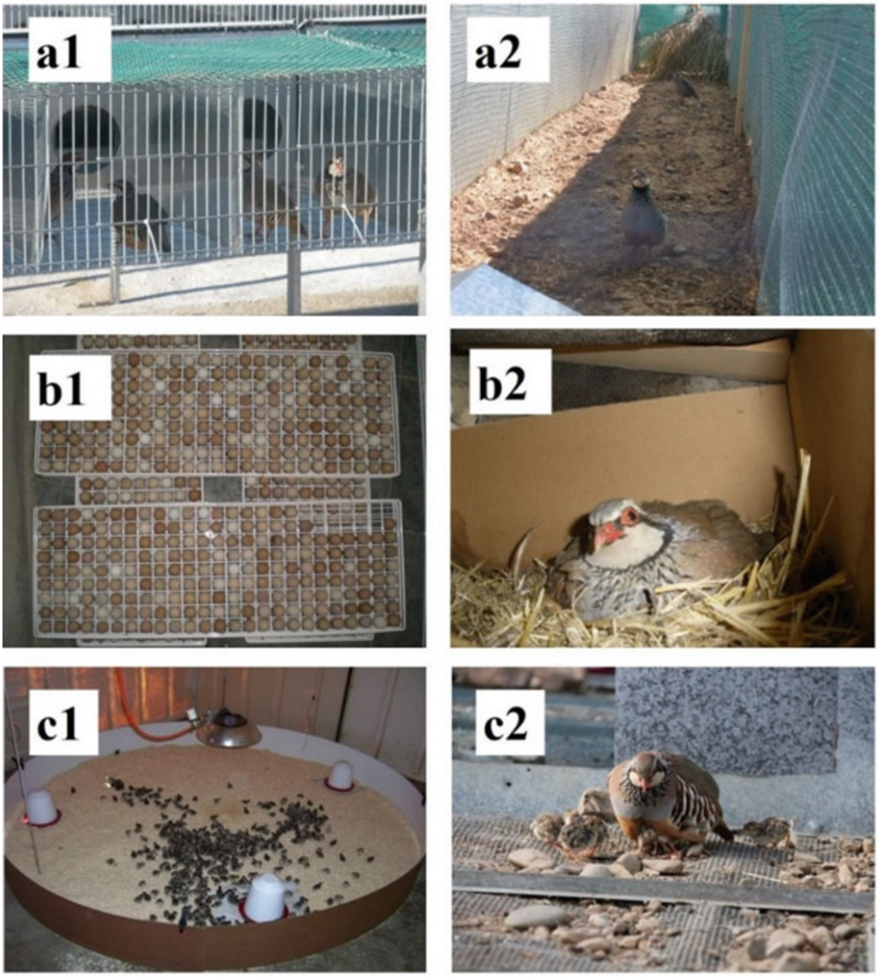

Fig. 1 Comparison of the commercial (left side) and non-commercial (right side) rearing systems: (**a1**) pairs kept in laying cages with wire mesh of 0.45 m^2, (**a2**) a pair kept in a pen of 8 m^2 on the ground, (**b1**) a batch of eggs ready to be incubated, (**b2**) a male incubating the clutch, (**c1**) a group of 250 chicks in a brooder house and (**c2**) the same male brooding his chicks (Photo credit by C. Sánchez-García and NANTA, SA)

acids and minerals (calcium, phosphorus, selenium). Food and water are provided ad libitum, and dry litter should be in place at all times to reduce disease transmission. Depending on how well the chicks are growing and the prevailing weather, they may be allowed to leave the brooder houses and enter into the flight pens from an age of 3–5 weeks. Flight pens should give enough space for running and flying and simulate natural conditions, though natural food and shelter (i.e. herbaceous and bushy plants) and visual contact with natural predators are typically not provided. It is recommended not to go over densities of 2 birds/m^2 in the flight pens and, together with feed provided through feeders, spread cereals and legumes regularly on the ground to favour foraging behaviour. Although the size of the flight pens depends on the density of birds, a minimum size of 75 m length × 50 m width × 2.5 m height is recommended to ensure that birds can exercise properly.

Red-legged partridges are often subject to antimicrobial and anti-parasite treatments before and after release. Birds are normally sold from the age of 3–4 months, with a price range in Spain of 3–6€/bird and up to 17€/bird of 3–4 months old (20–30 €/pair). Some farms specialize in selling eggs for incubation and 1-day-old chicks.

The main characteristic of non-commercial rearing is that eggs and chicks are incubated, nurtured or both by natural or foster parents. Rearing systems imitate the wild, including natural food and shelter, large flight pens, and contact with natural or simulated predators (Sokos et al. 2008). Compared to other species such as grey partridges and common pheasants *Phasianus colchicus*, non-commercial rearing of red-legged partridges is anecdotal in Europe, though there is evidence that parent-rearing and fostering can be conducted in captivity (Sánchez-García et al. 2011; Pérez et al. 2015). Given the low productivity of red-legged partridges under non-commercial rearing, it is estimated that producing one bird costs around 30€.

As for any other poultry reared for meat and eggs, gamebird farmers, whether they are commercial businesses or private stakeholders, must follow good veterinary practice and comply with animal health laws, asking for veterinary advice when needed. There are codes of good practice for gamebird rearing in France (www.snpgc.fr) and the UK (www.gov.uk), though the European Union has not produced welfare requirements yet. However, current rules are by no means as strict as for domestic poultry farms.

Releasing Strategies

In gamebirds, three main releasing strategies have been described: put-and-take release (i), releasing after the hunting season (ii) and releasing for re-establishment purposes (iii) (Sokos et al. 2008).

(i) *Put-and-Take Release*

Put-and-take consists of releasing birds before and during the hunting season and is now a common practice in Europe and North America (Reitz 2003; Ponce-Boutin et al. 2012; Delibes-Mateos et al. 2014). In the UK, red-legged partridges are released a minimum of 1 month before the start of the shooting season, In France, red-legged partridges are released in July–August (i.e. 1 or 2 months before the opening of the hunting season), in order to hunt more acclimatised birds (Ponce-Boutin et al. 2006a). The former represent ca. 35% of releases in southern France, the latter ca. 30% (Ponce-Boutin et al. 2006a). In the second half of the twentieth century, eggs of rescued clutches were collected and artificially incubated, and the young were released locally. This rescue plan covered tens of thousands of eggs (Berger 1987).

Put-and-take provides birds for shooting in areas with relatively dense human populations, small areas of public lands and limited hunting opportunity (Greene 1970), but for red-legged partridges, it is mainly related to the high demand of birds needed to satisfy bag demands (Sánchez-García et al. 2009). This type of releases is generally not associated with land management (game cover, predator control, artificial feeding and water provision) compared to other types of releases. In Central Spain, the mean number of red-legged partridges released in traditional shooting partridge estates is 8,465 birds per season, though in intensive estates the mean is 21,408 birds, with some estates releasing up to 90,000 birds (Caro et al. 2014). In the same area, commercial estates may release up to 6,000 birds/km^2, while non-commercial estates may release <50 birds/km^2. It is likely that similar densities are released in countries where driven shooting is conducted (France; Ponce-Boutin et al. 2012 and unpublished data from the UK), while lower densities may occur when walking-up shooting is common (300 birds/km^2 in Italy; F. Santilli, *pers. comm.*). More research is needed in this topic.

Commercially reared birds are normally chosen for put-and-take to reduce costs, though only a proportion of them will be shot. In reared red-legged partridges, the shooting return rates may vary between sites (from 15% to 50%; Mauvy et al. 1992; Bro et al. 2006; Draycott et al. 2012b), and in other gamebirds, the best return rates are around 40–50%, with the majority of birds (80%) harvested during the first week after the release (Mauvy et al. 1992; Ponce-Boutin et al. 2006b; Sokos et al. 2008). Hence, the cost for each released bird is not always that cheap; for example, the cost of shooting one chukar partridge *Alectoris chukar* or pheasant in Greece ranges from 20.8 to 143€ depending on the date and location of release (Sokos et al. 2016).

Put-and-take is mainly used on private and commercial shooting estates but also by non-commercial ones (Ponce-Boutin et al. 2009; Arroyo et al. 2012). In Europe there are some farms belonging to associations of hunters, but it cannot be considered a subsidized activity. However, for other species and countries such as Cyprus, Greece, Italy and some North American States, put-and-take takes place on public land supported by public funds (Sokos et al. 2008). In recent years, put-and-take shooting and large-scale releases of gamebirds in Europe, including red-legged partridges, have been increasingly questioned by the general public and conservation organizations owing to ethical reasons and potential negative effects for wild gamebirds and other wildlife. This has encouraged the development of Codes of Practice by the shooting industry, and in countries such as Spain and the UK, some commercial estates are improving put-and-take systems to reduce detrimental effects on the ecosystem (R. Draycott *pers. comm.*).

(ii) *Releasing Commercially Reared Birds After the Hunting Season*

This type of releasing aims to replace hunting losses and to increase the breeding stock in the short term to ensure the bag the next hunting season. In Spain and France (where such releases represent ca. 20% of releases in southern France; Ponce-Boutin et al. 2006b), releasing normally takes place in late winter and early spring, and available studies for the success of this practice using radio-tracked birds repeatedly show poor results owing to low survival and reproduction rates, even when habitat is improved and predators are controlled (see Box 2).

Several studies based on economic criteria have shown that releases of commercially reared pheasants after the hunting season are not justified as the number of young produced by reared hens is low (Sokos et al. 2008). A different option may be the translocation of wild birds, though no data is available for red-legged partridges. Santilli and Bagliacca (2008) found that translocating wild pheasants increases the bag the following hunting season, though the cost of one pheasant shot (50–60€/wild pheasant shot; F. Santilli, *pers. comm.*) is more expensive than one put-and-take (around 14–18€/reared pheasant shot).

(iii) *Releasing for Re-establishment Purposes*

Releasing for re-establishment purposes, including for threatened populations, aims to create a self-sustainable breeding population. In recent years several guidelines have been produced specifically for gamebirds (Buner and Aebischer 2008; WPA/IUCN 2009). This strategy is conducted when gamebirds have disappeared or are on the verge of extinction, so releasing should be only considered when it is not possible to recover wild populations through targeted management.

The success of releasing grey and red-legged partridges for re-establishment purposes has been evaluated at a large scale. Bro and Mayot (2006) found that the success of commercially reared birds released to increase partridge densities in France was high in the short term (i.e. first years after the end of the releases) but moderate in the medium and long term and highlighted the need of careful planning, monitoring and commitment from hunters to achieve results (see Text Box 2). In the French Auvergne-Limousin region, Péroux et al. (2006) found different types of population trends after red-legged partridge releasing, with mixed results depending on the release site but with an overall few number of successful attempts. Péroux et al. (2006) stressed the effects of suitable habitat and weather on partridges (as inter-annual differences affect population demographics) and discussed the importance of the ‘human factor’ for the success of re-establishment (motivations and perceptions from hunters): ‘when all the necessary conditions, biological and human, are met, the recovery of a wild partridge population is not a utopia’.

In Central Italy, where the red-legged partridge became extinct in the first decades of the twentieth century, Meriggi and Mazzoni (2004) and Meriggi et al. (2007) evaluated the success of releasing commercially reared red-legged partridge in areas where predator removal was conducted and hunting was stopped. Birds were released in coveys of 20–30 individuals at an approximate density of 3–5 birds/100 ha during 3 years. Although authors did not consider these attempts ‘fully successful’, red-legged partridge reached breeding densities and reproductive parameters comparable to other wild red-legged partridge populations, so a certain degree of success can be achieved.

Failures in re-establishment releases are attributed to a series of factors, including maladaptations of reared birds. Tests performed with rescued eggs did not provide better results than with farmed birds (Novoa 1982). It seems then that using wild gamebirds is the most suitable way to establish or augment a threatened population

(Buner and Aebischer 2008; Sokos et al. 2008). In Spain, translocations of red-legged partridges were conducted in the past with a certain degree of success (Silos 1953), but no scientific data are available. Some examples for other gamebirds have shown that translocation may work. In grey partridges, a translocation of nine pairs to a well-managed estate in Southern England helped increase a starting population of 11 pairs to 375 pairs in 8 years (Potts 2012), but failures in this species have been recorded in several attempts around the world (Browne et al. 2009). Owing to environmental factors, the stress that birds may suffer during transport and release and behavioural difficulties, translocation may not be always advisable (Letty and Marchandeau 2007). Moreover, translocation may be detrimental for the conservation of the donor populations (WPSA and IUCN 2009).

When translocation is not possible and the only option is releasing reared birds, better results are achieved with non-commercially reared, though there is evidence that using commercially reared birds together with tailored management may work to some extent for red-legged partridges (Brun and Aubineau 1989; Carvalho et al. 1998; Bro and Mayot 2006; Péroux et al. 2006). Buner et al. (2011), who conducted an extensive re-establishment study of grey partridges in England comparing different release methods, suggested that the best methods were fostering juveniles to wild failed breeders together with the releasing of autumn coveys. Although there are no extensive studies to confirm the effectiveness of releasing parent-reared red-legged partridges, two studies suggest that they have much better survival than commercially reared birds (Santilli et al. 2012; Pérez et al. 2015).

In conclusion, when releasing is targeting re-establishment, it is then crucial to choose the right technique. Releasing of commercially reared birds should be replaced by releases of birds more capable of surviving, even if they are fewer in number. This could be achieved by replacing commercial rearing with non-commercial rearing, following the guidelines at the end of this chapter.

What Are the Consequences of Rearing and Releasing?

Effects of Line Selection, Hybridization and Commercial Rearing Systems on Partridges

The majority of released red-legged partridges are reared under commercial systems, which affects their survival and breeding success because of genetic, behavioural, physiological and sanitary problems.

1. *Genetics*

Red-legged partridges have been historically hybridized with chukar partridges (see Chap. "Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization" for further details). Because the two species do not have overlapping distributions, this hybridization is purely anthropogenic. Hybridization aims to increase productivity of red-legged partridges, as chukar partridges and hybrids with red-legged partridges are more productive (Potts 1989). In Spain, 63% of a sample of game farm red-legged partridges and 45% of a sample of wild ones showed mitochondrial introgression with chukar partridges (Blanco-Aguiar et al. 2008), and hybridization between chukar partridges and other *Alectoris* has been also documented in France and Italy (Barilani et al. 2007; Vallance et al. 2007). However, hybridization may cause outbreeding depression, which is a fitness reduction observed in hybrids suffering from underdominance (heterozygosity disadvantage), the disruption of beneficial interaction (e.g. between genes and the environment) or intrinsically coadapted gene complexes (Frankham 1999; Laikre et al. 2012). Casas et al. (2013) found that male hybrid red-legged partridges were smaller than pure ones, suggesting that hybrids have poorer competitive capacity. In contrast, female hybrids showed better body condition and laid larger clutches (not showing differences in hatching success) but had lower carotenoid levels in blood plasma compared to wild ones. This may be a limitation for reproduction, though it is known that hybrids breed successfully in the wild (Casas et al. 2012). In Spain, a partnership between the hunters' federation, several research bodies and laboratories promoted a project to develop a genetic certification of reared red-legged partridges (Garrido 2011) to be implemented nationally. Unfortunately, not all regional governments have implemented yet this certification in current regulations.

Box 1 Results of Eight Studies Using Radio-Tracked Red-Legged Partridges in Spain

Type	Commercially reared	Commercially reared	Commercially reared	Commercially reared	Commercially reared but trained	Parent-reared	Wild	Wild
Location	Zaragoza	Málaga	Valladolid	Valladolid	León	Valladolid	Cádiz and Ciudad Real	Valladolid
Habitat	Mainly farmland	Mediterranean woodland and shrubland	Farmland and Mediterranean shrubland	Farmland and Mediterranean shrubland	Farmland	Farmland and Mediterranean shrubland	Farmland, Mediterranean woodland and shrubland	Farmland and Mediterranean shrubland
Targeted management	Not specified	Not specified	Game crops, control of predators, water troughs and feeders	Game crops, control of predators, water troughs and feeders	Control of predators, water troughs and feeders	Game crops, control of predators, water troughs and feeders	Varied among sites	Game crops, control of predators, water troughs and feeders
Season of release	Autumn	Spring-summer	Summer	Late winter-spring	Late winter and autumn	Late winter-spring	All year round	Late winter-spring
Age of release	4 months	9–10 months	2–3 months	10 months	3–4 months and 9–10 months	9–10 months	Adults and juveniles	>9 months
Number	62	20	54	68	44	31	170 (151 survival studies)	35
Survival	25–34% dead within 72 h after release. 120 days after release 25% survived	68 days after release 20.6% survived, with a mortality peak during the first 10 days	77 days after release 0% survived	45 days after release less than 10% survived	Mean of 105 days in late winter and 46 days in autumn (300 days studied)	Mean of 108 days (300 days studied)	270 days after tagging survived between 16–23%, varying among estates	Mean of 160 days (300 days studied)

(continued)

Causes of mortality[a]	Terrestrial predators (51%) and raptors (44%)	Raptors (60%) and terrestrial predators (40%)	Raptors (42%) and terrestrial predators (37%)	Raptors (49%) and terrestrial predators (36%)	Terrestrial predators (36.6%), raptors (18.2%) and hunting (11%)	Terrestrial predators (52%) and raptors (30%)	High impact of hunting (50%), followed by diseases	Raptors (52%) and terrestrial predators (17%)
Dispersion	The majority <500 m	Mean 830 m	Mean 400 m	Ranged 240–600 m	Mean 550 m	Not specified	Not specified	Not specified
Home range size	Not specified	Mean 15–16 ha	Mean 10 ha	Mean 7 ha	Mean 13 ha	Mean 23 ha	Mean of 52 ha, higher values in spring-summer compared to autumn and winter	Mean 27 ha

[a] Only known causes of mortality are given. Similar data from non-radio-tracked birds are also available for different regions of France

Box 2 Key Findings of Partridge Releasing Success in France (Bro and Mayot 2006)

Success of partridge releasing in France: key findings (from Bro and Mayot 2006)

Methodology

- The authors evaluated the success of 105 releases conducted from 1970s to 2000s, including 20 releases of red-legged partridge, 36 releases of grey partridges and 49 of both species.
- A total number of 237,000 partridges were released in 790,000 has.
- Releases used mainly commercially reared birds (86%) and were conducted in different habitats (including arable farmland, mixed farmland, vineyards and grasslands). Releases generally lasted for 2–3 years.
- Releases were conducted mainly at farms where partridge densities were low (<5 pairs/100 ha, 61.5% of the farms) but also at farms where the species was extinct (3.8% of the farms).
- Hunting was stopped in 78% of the sites and lasted for 3 years on average.
- The authors considered a release as 'successful' when the number of partridges increased after releasing and 'unsuccessful' when it was the same or decreased.
- The success was evaluated in the short term (at the end of releasing), medium term (5–10 years after the end of releasing) and long term (10 years after releasing).

Results

- From the sites where data was available after releasing ($n = 65$), 88% of releases were successful in the short term, 43.7% in the medium term and 26.7% in the long term.
- Both successful and unsuccessful releases were observed on small and large hunting estates.
- Releasing density in successful releases was lower (26 birds/100 ha) compared to unsuccessful ones (40 birds/100 ha).
- Density of feeders had no effect on the success of releasing.
- It seems that in the medium-term grey partridges were more successful than red-legged partridge (Péroux et al. 2006).
- The cost of increasing the partridge density by two pairs/100 ha through releasing in the previous summer was at least 1,200€.

2. *Behavioural Patterns*

Inadequate anti-predator, spatial and reproductive behaviours of reared red-legged partridges are the main problems associated with captive rearing. Historically, tame red-legged partridges have been selected in the farms to reduce mortality. Anti-predator behaviour is inherited, but it needs to be learnt from experienced conspecifics or foster parents to become properly developed (Putaala 1997). For example, parent-reared grey partridges show more appropriate anti-predator responses compared to partridges fostered by broody bantams and commercially reared (Dowell 1990) and commercially reared, but trained chicks show better responses than untrained chicks (Sánchez-García et al. 2016). In the same way, wild and parent-reared red-legged partridges have shorter reaction time than reared ones, the latter escaping by walking rather than flying (Pérez et al. 2010, 2015). On the other hand, the lack of contact with natural predators hampers the development of appropriate fear responses, as reared birds cannot identify which are the predators they may encounter after release, becoming habituated to humans (Csermely et al. 1983; Gaudioso et al. 2011a).

Young pheasants reared with a foster mother showed a lower stress level and a higher response to a simulated aerial predator compared to artificially reared pheasants (Santilli and Bagliacca 2019). The presence of the parents promotes behavioural cohesion and can also reduce the development of behaviours that directly relate to stress, fear and injury (Madden et al. 2020).

Birds fed an artificial diet may have difficulty recognizing natural foods once released into the natural environment. Post-release survival was improved in pheasant with exposure to more naturalistic diets prior to release (1% of live mealworm and 5% mixed seed and fruit). Birds reared with more naturalistic diets foraged for less time, had a higher likelihood of performing vigilance behaviours and were quicker at handling live prey items reducing the risk of predation (Whiteside et al. 2015).

Hybridization also changes behaviour, as hybrids show a decreased anti-predator response when compared to genetically pure birds (Campo et al. 2015), which may explain the low survival rates of hybrids after release (Casas et al. 2012). However, fitness differences between hybrids and pure red-legged partridges may be also attributed to domestication rather than genetic introgression (Casas et al. 2012), as traits selected in captivity may be not advantageous in the wild (Ford 2002). Finally, genetic variability may be reduced in captivity owing to the limited number of birds used as breeding stock, though Tejedor et al. (2008) found that reared red-legged partridges were not genetically more related than expected under random mating.

Despite the effects on behaviour, reared red-legged partridges are in general well adapted for hunting, which is the most important aim of releasing in current days. In certain commercial estates, hunters may struggle to distinguish between reared and wild red-legged partridges, possibly because birds are ‘trained’ through mock-driven hunting before the beginning of the season, improving their escape and flying behaviour. More research should be conducted in this field.

3. *Physiology*

Rearing conditions affect red-legged partridge anatomy and physiology. Commercial feed enables optimal growth but may be inadequate to prepare birds for natural food. These low-fibre-content, energy-rich diets are associated with shorter intestines and lighter gizzards when compared to wild birds and captive birds fed with natural food (Liukkonen-Anttila et al. 1999; Millán et al. 2001). The sudden shift from commercial to natural food is assumed to be one of the causes of the low success of gamebird releasing. Higher fibre content in diets not only affects gut size but also other physiological parameters such as the immune organ size, blood chemistry and muscle size (Millán et al. 2003a). In rock partridges *Alectoris graeca*, larger intestines obtained with a higher-fibre diet (17%) improved survival after release (Paganin et al. 1993).

Commercial feed also lacks carotenoids, and hence reared red-legged partridges are not 'as red' as wild ones (García de Blas et al. 2013). Ornaments are honest signals of bird quality in sexual selection, and better ornaments are related to better body condition and immune capacity (see Chap. "The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting"). Higher amounts of lipids in the natural diet may favour higher absorption of carotenoid pigments (Surai 2002), and antioxidants as polyunsaturated fatty acids (PUFA) play a role in brain development and cognitive capacity of red-legged partridge chicks (Fronte et al. 2008). It is important to note, however, that reared red-legged partridges have higher intestinal parasite burdens than wild conspecifics, which is known to decrease both carotenoid absorption and deposition in ornaments (Mougeot et al. 2009). Undoubtedly, reared birds have lower rates of physical exercise, resulting in metabolic and endocrine differences. Although strenuous exercise may increase oxidative stress, moderate physical activity seems to reduce free radical production and strengthen the antioxidant system (Metcalfe and Alonso-Álvarez 2010), conferring greater protection against carotenoid bleaching in wild birds. Owing to these problems, the animal feed industry has developed specific feed for red-legged partridges, adapted to the different life stages (Sánchez-García et al. 2013).

4. *Disease*

As with any other poultry, farm-reared red-legged partridges are often kept at high densities (>5 full-grown birds/m^2; Sánchez-García et al. 2013) and are not subject to natural selection, which favours the transmission of pathogens among birds (see Chap. "Health Monitoring and Disease Control in Red-Legged Partridges" for further details). Reared red-legged partridges show a higher prevalence of parasites (Millán et al. 2004a, b; Villanúa et al. 2008; Santilli and Bagliacca 2012; Máca and Pavlásek 2020) and other pathogens (Díaz-Sánchez et al. 2012), some of them not common in wild ones.

Despite the long list of detrimental effects mentioned above, commercial rearing has been able to provide birds suitable for short-term shooting. These birds will fly well in front of the guns, and a small proportion may breed if given the chance.

Survival and Breeding Success After Release

Commercially reared red-legged partridges have lower values of home range sizes and survival rates compared to wild ones. After releasing, birds tend to aggregate around releasing areas and are easily killed during the first weeks, even when control of predators is conducted (Gortázar et al. 2002; Duarte and Vargas 2004; Pérez et al. 2004; Alonso et al. 2005; Duarte et al. 2011; see Box 1 for further details). As the rate of success of soft releases in the medium and long term is limited (Bro and Mayot 2006), commercial rearing and environmental conditions would be the main factors driving the poor survival and breeding success. This has been also observed in other gamebirds (Sokos et al. 2008), suggesting that reared gamebirds are more prone to predation owing to poor anti-predator behaviour (Dowell 1990), which would also be partly a result from other maladaptive traits (Rantanen et al. 2010).

Commercially reared red-legged partridges struggle to pair with wild ones (Pérez 2006), which may be attributed to marked behavioural and ornamental differences (Alonso et al. 2008), resulting in red-legged partridges 'not attractive' enough for wild counterparts. Once paired, a few data from radio-tracking studies suggest that birds are unable to nest and rear the chicks as well as their wild counterparts (Duarte and Vargas 2004; Duarte et al. 2011). For released grey partridges, we know that the proportion of females producing their own chicks is a third lower than for wild hens (Buner et al. 2011), whereas wild pheasant hens are from 3 to 23 times more productive than reared ones (Brittas et al. 1992; Musil 2004).

These negative results contrast with parent-reared red-legged partridges: Santilli et al. (2012) found that the survival of parent-reared red-legged partridges was double than that of commercially reared ones in a 6-month period, and Pérez et al. (2015) found no significant differences in survival or breeding success between parent-reared and wild birds in a 10-month period. For grey partridges, different releasing techniques have been tested in different countries, and the best survival is achieved through fostering juveniles to wild failed breeders, being the survival after 1 year double than other rearing methods (Buner et al. 2011), with 90% of commercially reared birds failing to survive at the beginning of the second breeding season (Buner and Schaub 2008).

There is evidence that the post-release survival of commercially reared red-legged partridges can be improved by anti-predator training (using adult red-legged partridges as experienced demonstrators and an aerial predator model; see Gaudioso et al. 2011b) or by exposing chicks to dog and hawk models (Slaugh et al. 1992). Whiteside et al. (2015) showed that simple improvements in husbandry and diet improved gut physiology, behaviour, cognition and perching strength in captive-reared pheasants.

Effects on Wild Counterparts

Releasing may compromise the fitness and breeding success of wild birds. As described earlier, the physiology and behaviour of reared birds are heavily altered by rearing systems, resulting in birds looking wild but having 'poultry' adaptations. Even when genetics and health status are guaranteed, interbreeding between reared and wild (Duarte and Vargas 2004) may lead to the disruption of local adaptations

(Champagnon et al. 2012). The effects of releases on the wild breeding population have not been well studied for red-legged partridges, but for pheasants, Robertson and Hill (1992) found that an increase in the number of released birds resulted in a steady decrease in general breeding productivity, reaching a lower equilibrium point than that attained in the absence of released birds.

Guzmán et al. (2020) detected a lower young-to-old ratio in areas with high release intensity of red-legged partridges, which suggests that releases may be contributing to the decline of wild populations. The combined effect of overhunting and releasing farm-reared birds can compromise the conservation of wild populations.

When releasing is aimed at put-and-take, the young-to-old ratio of red-legged partridges in summer is negatively affected, even when conducted at low densities (Arroyo et al. 2012; Díaz-Fernández et al. 2013a). Mauvy et al. (1992) and Ponce-Boutin et al. (2006b) found that partridge releases are not a tool to protect wild populations if shooting is not restrained, and it has been demonstrated that the mortality of wild radio-tracked red-legged partridges in estates conducting put-and-take is much higher than on estates without releasing (Casas et al. 2016).

Releasing may also attract predators to the release sites (Robertson 1988), as reared birds are easier prey than wild ones owing to poor anti-predator behaviour (Parish and Sotherton 2007). Several studies suggest that surplus killing of reared red-legged partridges may occur (Pérez et al. 2004; Alonso et al. 2005), as it has been observed that canids kill and bury radio-tracked birds briefly after release (Pérez, *pers. comm.*).

As will be explained in Chap. “Health Monitoring and Disease Control in Red-Legged Partridges”, reared red-legged partridges are often subject to inefficient preventive treatments (Villanúa et al. 2007b), which together with the stress of releasing favours the spread of new pathogens into the wild (Millán et al. 2004a; Villanúa et al. 2008).

Specific concerns have been raised with (intensive) supplementary feeding. Such practice may induce some anatomical changes in wild birds on hunting estates where wheat is supplied (Millán et al. 2003b). However, the suspected risk of intoxication due to aflatoxin is not demonstrated.

On the other hand, releasing may have positive effects for wild red-legged partridges where releasing aims at the conservation of the species. In France, releases for shooting purposes in later summer (around 1–2 months before the opening of the hunting season), accompanied by habitat management, predator removal and shooting restrain, can overall benefit the species (Ponce-Boutin et al. 2006b, 2007).

Effects on Other Wildlife

1. *Shooting and Disturbance*

In the UK, it has been demonstrated that driven shooting of released common pheasants and red-legged partridges can be detrimental for the conservation of wild grey partridges due to unfortunate shots when no warning systems are in place (such as whistles) (Watson et al. 2007; Aebischer and Ewald 2010). However, when common pheasant releasing is carefully planned and conducted in low densities, it may help on the recovery of both grey and red-legged partridges, as common pheasants are alternative feathered game until partridge numbers are enough for shooting (Buner et al. 2014). In Spain, Tarjuelo et al. (2015) found that the little bustard *Tetrax tetrax* can be negatively affected by shooting disturbance. Interestingly enough, in a study conducted at the same region, Cabodevilla et al. (2020) found that the only hunting estates where little bustards did not decrease were those with higher release intensity, which may be a consequence of management measures or other factors that benefit bustards, such as game crop provision, predator control or habitat quality.

2. *Increased Predation Risk*

In the UK, it is known that foxes are attracted to pheasant release pens owing to the very high prey density (Robertson 1988), and common buzzards *Buteo buteo* may attack pheasant poults depending on the measures taken at the release pens, not discarding that some individuals may specialize in predating pheasants (Parrott 2015). In Iberia, the control of predators on commercial shooting estates is more intensive than on non-commercial ones (Arroyo et al. 2012), and in France predator control is more frequent/intensive on hunting estates that release red-legged partridges (Ponce-Boutin et al. 2006b). Thus, it cannot be rule out that in some cases releasing areas may be 'population sinks' for predators, including protected species (Beja et al. 2009). The real impact of releasing on predators is still to be understood, but it is likely that both opportunistic and specialist predators may be influenced by the presence of a large number of preys.

3. *Habitat Management and Disease*

In some cases, releasing is an economic motivation for landowners to improve habitat, and this can have benefits for local biodiversity (Ponce-Boutin et al. 2004; Arroyo et al. 2012). In Spain, some management traits associated with releasing (such as feeders and control of predators) may favour steppe birds of conservation concern (such as little bustard and great bustard *Otis tarda*), but indirect effects of releasing (competition for food and disturbance) may also be detrimental (Estrada et al. 2015). In the UK, winter game crops and brood-rearing cover for common pheasants have been shown to be good for farmland birds (Parish and Sotherton 2004; Sage et al. 2005b). Draycott et al. (2008) found higher bird densities (tits, finches, warblers and pigeons) in woods managed for released pheasants, though the same authors found no strong evidence that managed hedgerows for pheasants had beneficial effects for bird species (Draycott et al. 2012a). In southern France, fire or fire associated with grazing as habitat opening measures in areas suffer from land abandonment generally benefit the red-legged partridge as well as an array of songbirds listed on amber or red lists of conservation status (Ponce-Boutin et al. 2004).

Sánchez-García et al. (2015) found that gamebird feeders at English estates where common pheasant releasing was conducted also benefited songbirds, including species of conservation concern. This study also suggested that when feeders are not managed properly, they can be detrimental for targeted species owing to the use by potential predators, and the same applies for water troughs though there is not strong evidence (Simpson et al. 2011).

In the little bustard, an uncommon nematode was found, probably spread by reared red-legged partridges (Villanúa et al. 2007a). Interestingly enough, it was demonstrated that red-legged partridge had little or no role in the transmission of *Heterakis gallinarum* to grey partridges in the UK, being then common pheasants the sole responsible species (Tompkins et al. 2002).

Overall, demonstration projects in France and the UK combining habitat management and predator removal have improved the diversity of non-gamebird species (Stoate and Szczur 2001; Ponce-Boutin et al. 2004; Buner et al. 2013).

4. *Impact of Released Birds on Their Prey Items*

As invertebrates are preys of gamebirds, some studies have evaluated the impact of releasing on their communities at releasing sites. Neumann et al. (2015) found no significant change on the *Carabidae* or *Staphylinidae* richness in English woodlands managed for common pheasant releasing, but the species composition of *Carabidae* was changed, with shifts towards species typical of arable fields and grassland. In the same habitat, Robertson et al. (1988) found that woodland management benefited declining butterfly species owing to the sunny and open woods. In chalk grasslands of Southern England, Callegari et al. (2014) observed a negative but not strong effect between red-legged partridge large-scale releasing and adult butterfly (*Polyommatus bellargus*) emergence.

Anecdotal reports suggest that British reptile species may be vulnerable to predation by common pheasants, as reptiles may be exposed to common pheasants before hibernation in autumn. However, in the UK released common pheasants tend to occupy woodlands, while reptiles are in more open habitats, so spatial overlap may not commonly occur. Sage et al. (2005a) found that ground flora at the releasing pens can be altered by high common pheasant densities and recommended not to release more than 1000 pheasants per ha of release pen to avoid detrimental effects. The effects of high red-legged partridge densities at releasing sites remain unknown, so more research is needed.

5. *Hybridization with Rock Partridge*

In areas in France where both the red-legged and rock partridges are sympatric, natural hybridization occurs, resulting to fertile hybrids, the “perdrix rochassière” (*A. graeca saxatilis*), that share traits with both species (Bernard-Laurent 1990;

Randi and Bernard-Laurent 1999; Chap. "Molecular DNA Studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"). Therefore releasing of red-legged partridges on areas near the range of the rock partridge has the potential to endanger the integrity of the latter species (Barilani et al. 2007).

6. *Effects on Endangered Predators*

Red-legged partridges are important preys for the endangered Bonelli's eagle *Aquila fasciata* (Martínez et al. 1994), species that benefit from a LIFE program in the Mediterranean area. Releases of red-legged partridges may have a positive effect through the provision of food resource (winter/spring releases), as well as a negative impact if land management is neglected as a consequence of put-and-take releases. However, these aspects should need to be documented on the field.

Conclusion
Gamebird management can benefit habitats and wildlife using those habitats, but it is the presence of the released birds themselves (especially at high densities) that is usually detrimental (Sage et al. 2020).

How Can We Make Rearing and Releasing Sustainable?

Wild Red-Legged Partridges Come First

Not many estates in Europe aim to produce wild red-legged partridges owing to the lack of profitability, as they simply cannot compete with 'intensive' estates. We suggest the development of practical research to improve habitat management, predation control and shooting decisions, as done for grey partridges, to help sustain wild estates (Sotherton et al. 2013). This may need public or private funds to subsidize certain practices (that may benefit other wildlife) and the creation of quality labels to certify those estates producing wild red-legged partridges and perhaps justify a premium price.

There is a true conflict between those in favour and those against red-legged partridge releasing, though in Spain managers and hunters with different views may agree on the need to tag reared birds (Delibes-Mateos et al. 2014, 2015). This is a first step towards the change from large-scale releasing for shooting into releasing for conservation, though more research is needed to increase the shooting return rates of released red-legged partridges, which would reduce the number of birds released and their negative effects on wild counterparts and other wildlife.

It is true, however, that commercial shooting estates conducting large-scale releasing in some countries are crucial for the economy of some depopulated areas (which is the case of Central Spain). Some of these estates, which cover a small proportion of the land compared to non-commercial ones, have been able to develop a professional put-and-take system which may benefit non-game species (including endangered predators and pseudo-steppe birds) and may provide hunting opportunities, which otherwise would be inexistent. In our opinion, more research should be conducted to understand the contribution of these estates and ensure that detrimental effects are diminished.

In France, it has been demonstrated on a pilot site that it was possible to conciliate population management of wild red-legged partridges and shooting bags (Ponce-Boutin et al. 2006b). Ringed red-legged partridges are released every year (200–300 birds on 600 ha), and a hunting quota calculated for the wild population is simultaneously applied to manage the wild population. These measures appear to be suitable, but they restrict hunting and are technically and administratively unwieldy, which limit their practical application.

During the last 40 years, red-legged partridge shooting in Europe has been sustained by releasing, which simply produces the type of bird required by hunters and managers. If the demand was changed into quality birds, gamebird rearing may go back to its origin: conservation for sustainable shooting. Education of hunters, especially of young ones, may contribute to this.

Guidelines for Red-Legged Partridge Re-establishment

Releases of individuals to supplement decreasing wild stock, or into areas where they have occurred previously (re-introductions), have become an increasingly popular conservation method to restore declining or locally extinct species. In an attempt to impose some order into what could become chaos, the World Conservation Union (IUCN) devised a set of 'Guidelines for Reintroductions and other Conservation Translocations' in 1995 which were revised in 2013. We strongly recommend reading these Guidelines together with the 'Guidelines for the Re-introduction of Galliformes for Conservation Purposes' (WPA/IUCN 2009), the review of partridge releasing written by Bro and Mayot (2006), and the 'Guidelines for Re-establishing Grey Partridges Through Releasing' (Buner and Aebischer 2008) which must guide any re-introduction, re-stocking or release programmes for red-legged partridges. The successful re-establishment of any species through releasing is a serious affair. Red-legged partridge re-establishment efforts are labour-intensive, lengthy and expensive operations with very little guarantee of success if Guidelines are not followed in full.

Reasoning

Before any red-legged partridges are released, it is crucial to define the main aim of the project. There are three main reasons why red-legged partridges are released: (1) for shooting (put-and-take), (2) for conservation or (3) for shooting and conservation. In terms of achieving self-sustainable populations of red-legged partridges together with yielding maximum benefits for biodiversity in the project area, the least successful approach is the one that is solely based on a put-and-take strategy. The release for shooting purposes only is therefore the least favourable. On the other hand, the most successful outcomes have been achieved when the aim is to produce sustainable harvestable numbers of wild stock, and hence, approaches that combine shooting and conservation interests are the most recommended. Defining the main aim right from the start allows setting realistic project goals and defines the release strategy that needs to be used.

When Is Releasing Appropriate?

1. How to proceed where the species still exists above self-sustainable numbers.

   The first step towards re-establishing red-legged partridges on a piece of land must be a systematic count to determine the number present and hence the density. Where wild red-legged partridges persist above self-sustainable levels, releasing of reared stock is inappropriate and therefore not recommended. From the existing literature, we know that from a starting density of 3 pairs/km^2, it is possible to exceed 10 pairs/km^2 in 5 years with the correct management (Borralho et al. 1997; Sánchez-García et al. 2017). Recovery should be based on habitat improvements, supplemental feeding and water, legal predator removal and shooting restrain (Bro and Mayot 2006; Pérez 2006). Shooting restrain and hunting management are crucial to achieve results (Ponce-Boutin et al. 2006b). Once the full management package has been implemented, it may be necessary to translocate a few wild red-legged partridge pairs (typically 1–2 per km^2) to boost the genetic variability of the local wild population, though there are no scientific studies on the effectiveness of this practice. Donor stock must be chosen carefully in order not to damage the viability of the source population.

2. How to proceed where the species is extinct or persists below self-sustainable numbers.

   Where red-legged partridges have disappeared completely or where they persist below self-sustainable numbers in an area of appropriate size (a threshold for self-sustainability may be as low as 1–2 pairs per 1 km^2 ha within an area of 4 km^2 ha), the reasons for their local extinction or decline need to be fully understood, and all factors that are responsible for their decline must be addressed prior to any release. In red-legged partridges, at least five factors need to be addressed simultaneously before a re-introduction can start: (1) the habitat needs to be restored to provide suitable all-year habitat (possibly 5–7% of the total area) such as nesting and chick foraging cover in summer and holding and predator escape cover during winter and into early spring; (2) fresh water needs to be available throughout the project area (where natural water is a limiting factor, water troughs can provide significant improvements); (3) where winter food availability has diminished as a result of intensive agriculture, additional winter feeding should take place (Sánchez-García and Buner 2017); (4) legal predator control must be carried out, especially during the breeding season (April–July); and (5) a suitable shooting management plan needs to be implemented to limit bags during the recovery years (or provide alternative quarry) and to prevent over-harvest. It cannot be over-stressed that attempts to re-establish birds in areas with unsuitable conditions contravene IUCN guidelines will fail and will discredit the practice.

What Release Stock to Use

For the reasons previously addressed in this chapter, conventional commercially reared red-legged partridges should never be used for re-introduction and re-establishment programmes. Therefore, only non-hybridised release stock with appropriate natural behaviour must be used in the future in order to have any chance of success. Where shooting is the sole purpose, high-quality birds should become standard in order to improve shooting standards, pleasure and public opinion while minimising negative impacts on wild stock. Highest-quality reared stock are parent-reared birds of pure wild origin, kept under non-commercial systems. It is recommended to refresh the bloodline of captive birds via wild eggs every 3–4 years.

How to Release

Red-legged partridges should be released in family groups in summer/autumn or in well-established groups (2–3 well-bonded family groups together) not exceeding more than 20–25 birds. The number of total birds released should not exceed more than 20–30/km^2. Birds should be transported in soft cardboard boxes to minimise injury (Fig. 2). Only healthy birds should be released, while unhealthy individuals must be removed from the breeding programme. All captive-reared birds should be marked with an identifiable leg ring. At the release site, each group should be kept in mobile release pens of at least 3x3 m in size, located in suitable natural cover. All pens should be within hearing distance of the captive partridges but at least 200 m apart. This will reduce post-release dispersal. Neighbouring groups at the release site should not be from neighbouring pens at the rearing station to prevent post-release merging into larger troops. After a maximum of 5 days, each group should be released at once, allowing them to exit the pen freely without being forced. Natural food such as wheat should be provided at least 3 weeks before release to allow the development of a natural digestive system. The same type of natural food must be provided in the release area using the same feeders as in the release pens. Translocated wild birds must be released into suitable cover in pairs directly from their transport boxes.

Post-Release Activities

Any release project should follow an adaptive management approach, whereby the project is evaluated and adjusted where necessary on a yearly basis at minimum. In order to be able to make informed decisions, a standardised monitoring programme needs to be in place, counting spring pair numbers and brood production in summer and autumn. Additionally, all other management interventions such as the amount and quality of habitat created and managed, number of water troughs maintained, number of traps run, etc. should be well documented and reported upon. Finally, a public awareness campaign running alongside the project is highly recommended.

Fig. 2 Some key points on red-legged partridge re-establishment: (**a**) choose quality farms and birds, (**b**) check their genetics and health status, (**c**) transport to release sites, (**d**) improve habitat and control predators, (**e**) monitor and (**f**) you may succeed

Acknowledgements We are indebted to Nick Sotherton for his comments and suggestions on early versions and Nicholas Aebischer, who gave data of partridge releasing and improved the final draft. Special thanks are given to Jasmine E. Clark for her help with French translations. We are grateful to the editors for their invitation to participate in this book.

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Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes

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Introduction

Wild birds are exposed to various types of environmental pollutants and toxic substances throughout their lives depending on their trophic level and on the environment in which they live. For example, birds of prey tend to accumulate significant amounts of persistent organic pollutants (POPs), such as organochlorine (OC) pesticides (used in the second half of the twentieth century), polychlorinated biphenyls and polybrominated diphenyl ethers, because these POPs are bioaccumulative and tend to biomagnify along food chains. On the other hand, herbivorous and granivorous birds, such as the Red-legged Partridge (*Alectoris rufa*), have a higher risk of being exposed to pesticides, because these farmland

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_8

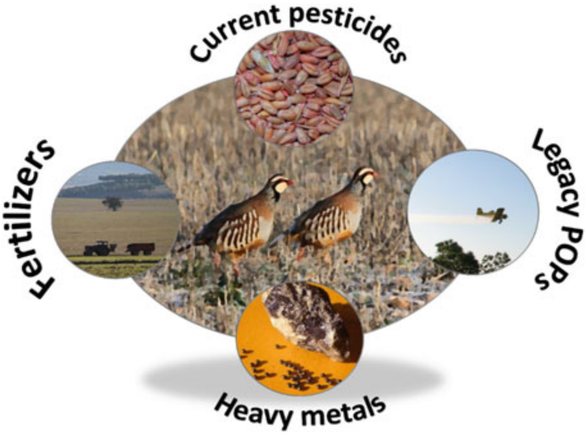

Fig. 1 Four types of toxic substances that are particularly relevant for the Red-legged Partridge, either because of their adverse effects on birds, or because of risks to game meat consumers (from a human food safety point of view)

birds can be directly exposed through treated seeds, plants and insects. Moreover, focal sources of pollution can also threaten animal populations. This is the case, for example, where soil is contaminated with heavy metals resulting from mining activities, or due to the accumulation of lead shot pellets in areas with intense hunting activity. In this chapter, we will give an overview of the varying toxic threats faced by the Red-legged Partridge and other upland gamebirds of the order Galliformes. Many of these species are key resources for predators and hunters, and the effects of pollutants can resonate in a bottom-up way to the rest of the food web. Here, we discuss the implications that some of these pollutants and toxic substances can have on the conservation of these species, as well as on their value as hunted species and as game meat for human consumers. According to habitat use, diet, trophic level and other behavioural traits of Red-legged Partridge, we consider four groups of toxic substances that can represent a risk for this species under certain circumstances. With important differences in their toxicological relevance and the information available in the literature, these are (1) heavy metals (especially lead ammunition and polluted soils), (2) currently used pesticides, (3) fertilizers (e.g., when used in water through fertigation) and (4) legacy POPs (e.g., organochlorine pesticides; Fig. 1).

Heavy Metals

Soils polluted as a consequence of human activities like mining and metal smelting are one of the main sources of exposure for terrestrial birds to heavy metals (Beyer et al. 2008; Martinez-Haro et al. 2013). This type of contamination can affect large geographical areas where there is a dispersion of metals through the air or water. Moreover, the immediate environment around mines, where there are often mine tailings or rivers receiving water used for ore washing may be highly polluted. The Red-legged Partridge is a granivorous species that requires grit for the proper functioning of the gizzard (Ferrandis et al. 2008). Therefore, grit ingestion from polluted soils can be a significant source of heavy metal intake that adds to diet itself (Bendell-Young and Bendell 1999). The Red-legged Partridge is a good bioindicator species of metal pollution in sites contaminated by mining activities and their feathers can be used as non-destructive samples for monitoring studies (Gil-Jiménez et al. 2020).

Mercury (Hg) is a heavy metal with a global distribution because of the capacity of some bacteria to form methylmercury, which is highly bioaccumulative and biomagnifiable along food chains. Sources of mercury are diverse, but among the anthropogenic ones, coal burning in power generation plants is one of the most important. In studies carried out in Portugal, levels of mercury measured in feathers of Red-legged Partridge (0.04–0.071 μg/g) and Rock Dove (*Columba livia*) (0.079 μg/g) were much lower than in their potential predators like Bonelli's Eagle (*Aquila bonelli*) (1.31 μg/g) or Eagle Owl (*Bubo bubo*) (1.29 μg/g), which highlights the potential for biomagnification of this metal (Figueira et al. 2009; Lourenço et al. 2011).

Contamination by heavy metals in soils can simply be a consequence of the underlying geology of an area, even in the absence of mining or smelting operations. This diffuse pollution determines the basal levels of metals in a given population, which in many cases have no impact on the health of individuals, although in some cases it can cause chronic adverse effects on birds (e.g., cadmium (Cd), Larison et al. 2000). Any additional input of heavy metals and metalloids, such as sewage sludge used as fertilizer in agricultural fields, can result in burdens above these basal levels, with the consequent long-term risk of adverse effects to animals (Stoewsand et al. 1984).

Among heavy metals, lead (Pb) is one of the most toxic and most frequently involved in animal poisoning. As with cadmium, soil pollution is an important source of metal contamination for animals, but lead ammunition constitutes the most toxicologically relevant source of lead for wild birds in terms of epidemiology and severity of adverse effects.

Lead Exposure of Red-Legged Partridge and Other Galliformes in the Field

Partridges, as well as other upland gamebirds and waterfowl species, have a particularly well-developed muscular stomach (gizzard; see Box 1) because they usually feed on hard food items like plant material, seeds or animals with hard shells. These species commonly need to ingest and maintain sand or gravel (gastroliths or grit; Fig. 2) to break and grind such food down in their powerful gizzards (Bialas et al. 1996; Gionfriddo and Best 1999). Hunting areas, where lead shot pellets accumulate over time, are especially risky environments for these species, which confuse shot pellets with particles of grain or grit (Fig. 2) (Trost 1981; Pain 1990; Moore et al.

Fig. 2 Open gizzard of Red-legged Partridge with several ingested particles of grit and lead shot pellets (Author: Elisa Pérez)

1998; Mateo and Guitart 2000; Mateo et al. 2000). In general, exposure to lead shot is greatest when four basic conditions are met: (i) high shot densities exist in the habitat used by birds, (ii) environmental conditions result in the shot being available to birds, (iii) feeding habits result in shot ingestion, and (iv) there is a shortage or absence of grit (Pain 1992; Mateo 2009).

Box 1 Avian Gizzard

The avian stomach consists of two chambers, the proventriculus (*pars glandularis*) and the gizzard (pars muscularis), with the former being the mammalian counterpart. The proventriculus or glandular stomach is located oral to the gizzard or muscular stomach. The proventriculus is the site where gastric juices are secreted (hydrochloric acid, pepsin and mucous at approximately pH 2.6), whereas the gizzard aids mechanical digestion and is the site of gastric proteolysis. The gastric anatomy of partridges, upland gamebirds and waterfowl species, constitutes one of the two extreme typologies recognized in birds. The first type, characteristic of carnivorous and piscivorous species, is adapted for storage and digestion of a relatively soft diet, while the second type, characteristic of omnivores, insectivores, herbivores, and

(continued)

Box 1 (continued)
granivores, is adapted for very hard diets. This type of gizzard is large and powerful, and consists of two pairs of opposing muscles termed thick and thin pairs, which are composed of circular muscle. The interior surface of the gizzard is lined with a cuticle, which protects the gizzard from the acid and proteolytic enzymes secreted by the proventriculus and from injury during grinding of hard food items (Denbow 2000).

Once ingested, lead shot can remain in the avian gizzard for 18–44 days before being expelled (regurgitated or excreted via the intestine) (Clemens et al. 1975; Roscoe et al. 1979; Sanderson and Bellrose 1986). During this time, retained lead shot pellets are eroded by digestive acids and the friction produced by muscular action (Clemens et al. 1975). Dissolved lead may then be absorbed through the intestine wall into the blood stream, becoming deposited in soft tissues such as the liver or kidneys, and ultimately in bones. Residual, unabsorbed lead is excreted in the faeces (Sanderson and Irwin 1976). Up to 88–100% of lead dissolved in the gizzard from lead shot is excreted in faeces by birds on an adequate diet (Irwin 1977), but this can, for example, decrease to 30% when birds feed on a corn-based diet (Coburn et al. 1951; Sanderson and Irwin 1976).

Lead is a non-essential metal for living organisms, known for its toxicity since ancient times (Orfila 1817; Waldron 1973; Nriagu 1983). Lead acts as a non-specific toxicant and competes with calcium at the plasma membrane for transport systems, disrupting intracellular calcium homeostasis, which has important effects on nervous system function (Simons 1993). In the bloodstream, lead has a high affinity for the sulfhydryl (SH) group and extremely low concentrations are able to inhibit enzymes with this functional group (Gurer and Ercal 2000; Martinez-Haro et al. 2011). Additionally, lead has antagonistic activity with some essential metals needed for antioxidant enzyme function (Gurer and Ercal 2000). These features make lead able to inactivate enzymes involved in major metabolic pathways affecting many body systems, including, among others, the cardiovascular, muscular, digestive, nervous, and reproductive systems (Locke and Thomas 1996; Goyer and Clarkson 2001).

Acute lead poisoning in birds is usually due to the ingestion of a large number of lead shot pellets. In these cases, birds usually die within several days of exposure. However, the commonest cause of death through lead poisoning is due to subchronic exposure. In these cases, birds die within 2 or 3 weeks after the ingestion of a small number of lead shot pellets, often exhibiting signs of lead poisoning (Table 1). Lead poisoned birds usually die of starvation due to paralysis of the intestinal muscles. During this time, affected birds lose mobility, tend to avoid other birds, and become increasingly susceptible to predation and other causes of mortality. High susceptibility of lead intoxicated animals to predation, alongside rapid consumption of their carcasses by scavengers, have also been suggested as key reasons why lead poisoning incidents in wildlife frequently go unnoticed by game and wildlife managers (Mudge 1983; Pain 1991; Friend 1999b).

Table 1 Clinical and pathological signs described in lead poisoned birds (Jordan and Bellrose 1951; Locke and Friend 1992; Friend 1999b; Franson 1996)

Clinical signs
Inability to hold up the wings or tail
Roof-shaped wings
Weakness
Inability to fly
Tendency to seek shelter
Emaciation—loss of condition—severe weight loss
Prominent sternal keel—Hatchet-breast
Bright green-coloured faeces
Bright green staining of the vent area
Puffy or swollen head
Change in phonation
Blindness
Pathological signs/post-mortem signs of lead poisoning
Lead shot in gizzard
Absent of fat
Impactation (stasis) of oesophagus and proventriculus
Atrophy of pectoral muscle—loss of muscle mass
Liver atrophy
Distended gallbladder
Bright green bile
Flaccid heart muscles
Hydropericardium and fibrinoid necrosis of arterial walls

Galliformes found dead with several lead shot in the gizzard and/or liver lead levels higher than 15 μg/g wet weight are considered as lead poisoned individuals. Kidney levels in lead poisoned birds are usually higher than liver levels, and bone lead levels up to 10 μg/g can be considered as background values. In live birds, blood lead levels above 5 μg/g are considered compatible with clinical toxicity, but adverse effects on sensitive biomarkers can be observed at 0.2 μg/g (Fig. 3).

Overall, lead shot ingestion and associated lead poisoning have been shown to be a significant cause of mortality for many avian species in numerous scenarios worldwide (Sanderson and Bellrose 1986; Friend et al. 2009; Mateo 2009; Pain et al. 2009; Scheuhammer 2009). This is especially significant for waterfowl, with 1.6–2.4 million deaths per year estimated in North America and almost 1 million per wintering season estimated for Europe. This represents annual mortalities of 2–3% and 8.7% of wintering populations, respectively (Bellrose 1959; Mateo 2009). The high prevalence of lead shot ingestion in waterfowl is largely related to the high lead shot densities that often occur in wetlands (for complete reviews, see: Mateo 2009; Pain et al. 2009; Franson and Pain 2011). Densities higher than 100 shot/m^2 have frequently been detected in the upper centimetres of sediments from heavily hunted wetlands worldwide (Mateo 2009). These high densities occur because waterfowl

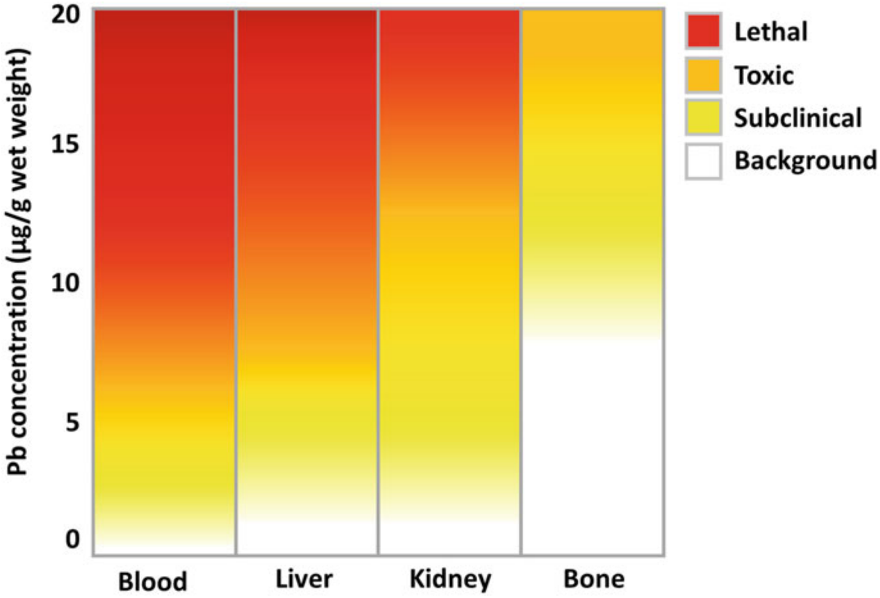

Fig. 3 Guidelines for interpretation of tissue lead concentrations (µg/g wet weight) in Galliformes according to the threshold values given by Franson (1996)

hunting is usually carried out on wetlands from permanent blinds distributed along the wetland edges. In an arc around these blinds, lead shot pellets that miss targets are deposited onto sediments and then remain available for waterbirds for many years. Additionally, some studies have reported densities of lead shot pellets above 1000 shot/m^2 associated with shooting ranges (Petersen and Meltofte 1979; Bonet et al. 2004) and clay pigeon shooting sites located in wetlands (Smit et al. 1988; O'Halloran et al. 1988).

The scenario described for wetlands contrasts with that found in upland habitats where small game hunting is less frequently performed from permanent hunting blinds. In this case, lead shot pellets are dispersed across much larger areas, and therefore, the lead shot densities in upland habitats are in general much lower than those reported in wetlands (Table 2). Studies describing lead shot densities in upland habitats have been conducted in Canada, Denmark, the Netherlands, Hungary, Ireland, Spain and from 10 different states of the USA (Table 2). Only one study from Central Spain has addressed lead shot densities present on a private upland small-game hunting estate where Red-legged Partridge has been hunted by driven shooting since the 1950s. In that work, the spatial distribution of lead shot was studied in relation to the fixed shooting stations. An average of 7.4 shot/m^2 was reported, with up to 120 shot/m^2 in front of the shooting lines (Ferrandis et al. 2008). Additionally, this work reported a prevalence of lead shot ingestion in hunted Red-legged Partridge of 3.9% ($n = 66$) during the sampling period of 2004–2006 (Table 3). Two additional studies have quantified the prevalence of lead shot

Table 2 Lead shot densities reported in upland habitats

Country	Site description	Mean shot/ m^2	Max. shot/ m^2	Depth (cm)	References
Canada	Hunting field never tilled	27	56		Holdner et al. (2004)
Canada	Hunting field tilled	8	32		Holdner et al. (2004)
Canada	Hunting field not tilled in 2 years	3	12		Holdner et al. (2004)
Hungary	Pheasant hunting area	0.46	1.09	5.00	Akoshegyi (2000)
Spain	Driven shooting estate for Red-legged Partridge	7.4	120		Ferrandis et al. (2008)
USA-New Mexico	Dove shooting range—post hunt	86	1.30		Best et al. (1992a)
USA-Florida	Bobwhite hunting area—low intensity		0.78		Keel et al. (2002)
USA-Illinois	Mourning dove hunting area—sunflower heavily hunted		18.08	1.30	Anderson and Havera (1989)
USA-Illinois	Management Pheasant hunting—fence/corn stubble		13.61	2.50	Anderson and Havera (1989)
USA-Illinois	Mourning Dove hunting area—sunflower		8.18	1.30	Anderson and Havera (1989)
USA-Illinois	Management Pheasant hunting—cultivated field		5.1	2.50	Anderson and Havera (1989)
USA-Illinois	Dove fields		18.07	1.30	Anderson (1986)
USA-Illinois	Northern Bobwhite fields		14.80	2.50	Anderson (1986)
USA-Illinois	Pheasant hunting area		13.61	2.50	Anderson (1986)
USA-Illinois	Dove field-post hunting		34.87		Buck (1998)
USA-Illinois	Cultivated shooting field		33.36	2.50	Semel et al. (1987)
USA-Indiana	Dove shooting range-post hunt	2.75	8.40	1.30	Castrale (1989)
USA-Indiana	Dove shooting range-pre hunt	0.32	0.86	1.30	Castrale (1989)
USA-Missouri	Mourning Doves hunting area—intensive		0.63	5.00	Schulz et al. (2002)
USA-Nevada	Field managed for dove		86		Gerstenberger and Divine (2006)
USA-North Carolina	Publicly managed Mourning Dove fields	6.78		1.30	Douglass (2011)
USA-South Dakota	Upland—National Wildlife Refuge	0.18			Pelizza (2004)
USA-South Dakota	Pheasant hunting area 3	62.5	1.30		Runia and Solem (2014)
USA-South Dakota	Pheasant hunting area 1	16.62	1.30		Runia and Solem (2014)

(continued)

Table 2 (continued)

Country	Site description	Mean shot/ m^2	Max. shot/ m^2	Depth (cm)	References
USA-South Dakota	Pheasant hunting area 2	1.1	1.30		Runia and Solem (2014)
USA-Tennessee	Managed public dove shooting—post hunt		10.76	0.95	Lewis and Legler (1968)
USA-Tennessee	Managed public dove shooting—pre-hunt		2.69	0.95	Lewis and Legler (1968)

ingestion in Red-legged Partridge (Table 3). In Spain, Soler Rodríguez et al. (2004) examined seven individuals hunted in 2000, and found one of them to have 14 lead shot pellets in the gizzard and 35.6 μg/g of lead in wet weight of liver. Recently, Romero et al. (2020) have detected 14 Red-legged Partridges (7.25%) out of 193 individuals hunted in Spain having ingested Pb shot (Table 3). In some hunting states devoted to driven hunting of Red-legged Partridge in Ciudad Real (Spain), the prevalence of lead shot ingestion in this species was up to 29.2% (Romero et al. 2020). In the UK, Butler et al. (2005) found just one hunted Red-legged Partridge having ingested lead shot (0.16%) out of 637 individuals collected between 1955 and 1992, and two out of 144 partridges (1.4%) hunted in the 2001/2002 season (Table 3).

Several studies have reported cases of lead shot ingestion and poisoning in other species of Galliformes (Table 3). The first report regarding the ingestion of lead shot by Common Pheasants (*Phasianus colchicus*) was among the earliest published on this topic (Calvert 1876). Since that first description in the UK, more cases have been described in Phasianidae species from numerous countries including Denmark, Hungary, Spain, Canada, and in 12 different states of the USA (Table 3). Although still lower than in waterfowl, prevalence of lead shot ingestion above 10% has been observed in upland birds like common pheasants hunted in Canada, Hungary and North Carolina, and Chukar Partridges (*Alectoris chukar*) hunted in Utah (Table 3). Reported lead poisoning cases among Phasianidae include Grey Partridges (*Perdix perdix*) from the UK, common pheasants from UK and California, Northern Bobwhite (*Colinus virginianus*) from Georgia and Illinois, and Wild Turkey (*Meleagris gallopavo*) from New York (Table 3). At the population level effect, Meyer et al. (2016) estimated that lead shot ingestion at a mortality rate of 4% may reduce population size of Grey Partridges in Europe by 10%.

Sublethal Effects of Lead Exposure in Galliformes

Some experimental and field studies have been conducted on the Red-legged Partridge as a model species to understand the sublethal effects of lead in birds.

Table 3 Prevalence of lead shot ingestion or abnormal Pb exposure in the Red-legged Partridge and other upland Galliformes species

Country	Species	Sampling method	Sampling year	*N*	*N* with Pb shot^a	Prevalence (%)	N° Pb shot	References
	Red-legged Partridge							
Spain	*Alectoris rufa*	Hunted	2000	7	1	14.3	14	Soler Rodríguez et al. (2004)
Spain—Albacete	*Alectoris rufa*	Hunted	2004	10	2	20.0	1	Ferrandis et al. (2008)
Spain—Albacete	*Alectoris rufa*	Hunted	2006	66	1	1.5	1	Ferrandis et al. (2008)
Spain—Valencia	*Alectoris rufa*	Hunted	2016–2018	30	0	0.0		Romero et al. (2020)
Spain—Alicante	*Alectoris rufa*	Hunted	2016–2018	36	3	8.3		Romero et al. (2020)
Spain—Ciudad Real	*Alectoris rufa*	Hunted	2016–2018	97	10	10.3	1–11	Romero et al. (2020)
Spain—Zamora	*Alectoris rufa*	Hunted	2016–2018	30	1	3.3		Romero et al. (2020)
UK	*Alectoris rufa*	Hunted	1955–1992	637	1	0.16		Butler (2005)
UK	*Alectoris rufa*	Hunted	2001–2002	144	2	1.4		Butler (2005)
	Other Galliformes							
Spain—Canary Islands	*Alectoris barbara*	Hunted	2016–2018	13	1	7.7		Romero et al. (2020)
USA—Utah	*Alectoris chukar*	Hunted	2003–2011	461	43	9.3 (0–21.3)	1	Bingham et al. (2015)
USA—Utah	*Alectoris chukar*	Hunted	2003–2011	121	10 (liver)	8.3 (0–21.4)		Bingham et al. (2015)
USA—Oregon	*Alectoris chukar*	Hunted	1995–1998	140	10	7.1		Walter and Reese (2003)
USA—Utah	*Alectoris chukar*	Hunted	2003–2004	106	2	1.9	1	Larsen et al. (2007)
USA—Utah	*Alectoris chukar*	Hunted	2003–2004	75	8	10.7	1	Larsen et al. (2007)

USA—Utah	*Alectoris chukar*	Hunted		286	25	8.74		Bingham et al. (2009)
Canada	*Alectoris chukar*	Hunted	2000	76	6	8	1–2	Kreager et al. (2008)
USA—Oregon	*Alectoris chukar*	Hunted	1995–1998	123	7	5.7	1–2	Walter and Reese (2003)
Canada	*Bonasa umbellus*	Hunted	1996–1998	155	2	1.2	1	Rodrigue et al. (2005)
USA—N. Mexico	*Callipepla squamata*	Hunted	1985–1987	226	1	0.4	1	Best et al. (1992b)
USA—N. Mexico	*Callipepla squamata*	Found dead	1948	1	1		13	Campbell (1950)
USA—N. Mexico	*Colinus virginianus*	Hunted	1985–1987	111	2	1.8	1–2	Best et al. (1992b)
USA—Florida	*Colinus virginianus*	Hunted	1989–1992	241	3	1.3	1–3	Keel et al. (2002)
USA—Georgia	*Colinus virginianus*	Found dead	1997	1	1		2	Lewis and Schweitzer (2000)
USA—Illinois	*Colinus virginianus*	Found dead	1964	1	1		4	Westermeier (1966)
USA—Florida	*Colinus virginianus*	Ailing	1925	1	1		2	Stoddard (1931)
USA—Georgia	*Colinus virginianus*	Found dead-chick	1926				≥1	Stoddard (1931)
USA—Texas-Oklahoma	*Colinus virginianus* & *Callipepla squamata*	Captured	2011–2012	282	9 (bone)	3.2		Baxter et al. (2015)
Canada	*Dendragapus canadensis*	Hunted	1996–1998	22	0	0		Rodrigue et al. (2005)
Canada	*Dendragapus canadensis*	Hunted	1990–1996	6	0			Tsuji et al. (1998)
Canada	*Lagopus lagopus*	Hunted	1996–1998	46	0	0		Rodrigue et al. (2005)
UK	*Lagopus lagopus scotica*	Hunted	2003	234	34 (bone)	14.5		Thomas et al. (2009)
Canada	*Lagopus mutus*	Hunted	1996–1998	33	0	0		

(continued)

Table 3 (continued)

Country	Species	Sampling method	Sampling year	N	N with Pb shot[a]	Prevalence (%)	N° Pb shot	References
								Rodrigue et al. (2005)
Canada	*Meleagris gallopavo*	Hunted	2000	1	1			Kreager et al. (2008)
USA—New York	*Meleagris gallopavo*	Found dead	1975	1	1		4	Stone and Butkas (1978)
Canada	*Perdix perdix*		2001	169	19 (bone)	11		Scheuhammer (2009)
UK	*Perdix perdix*	Captured (chicks)	1968–1978	29	2	6.9	13–14	Potts (2005)
UK	*Perdix perdix*	Found dead	1963–1969	224	12	5.3	1–26	Potts (2005)
UK	*Perdix perdix*	Found dead	1963–1992	446	20	4.5	1–26	Potts (2005)
UK	*Perdix perdix*	Found dead	1970–1992	222	5	2.2	1–26	Potts (2005)
Denmark	*Perdix perdix*	Found dead	1971–1977	62	1	1.6	34	Clausen and Wolstrup (1979)
UK	*Perdix perdix*	Found dead	1947–1992	1318	18	1.4	1–26	Potts (2005)
UK	*Perdix perdix*	Found dead	1947–1958	872	2	0.2	1–26	Potts (2005)
UK	*Perdix perdix*	Ailing	1984	1	1			Keymer and Stebbings (1987)
UK	*Perdix perdix*	Found dead	1954–1957	1	1			Keymer (1958)
Hungary	*Phasianus colchicus*	Hunted		947	45	0–23.1 (4.75)	1–8	Akoshegyi (2000)
Canada	*Phasianus colchicus*	Hunted	2000	47	16	34	1–66 (5% >10)	Kreager et al. (2008)
USA—N. Carolina	*Phasianus colchicus*	Hunted	1994–1998	30	5	16.7		Dutton and Bolen (2000)
USA—S. Dakota	*Phasianus colchicus*	Hunted	2011	123	8	6.5	1–9	

								Runia and Solem (2014)
USA—S. Dakota	*Phasianus colchicus*	Hunted	2012	167	9	5.4	1–4	Runia and Solem (2014)
UK	*Phasianus colchicus*	Hunted	1996	111	5	4.5	1–3	Butler et al. (2005)
USA—S. Dakota	*Phasianus colchicus*	Hunted	2013	493	17	3.4	1–13	Runia and Solem (2014)
UK	*Phasianus colchicus*	Hunted	1996–2002	437	13	3	1–3	Butler et al. (2005)
UK	*Phasianus colchicus*	Hunted	1999–2000	105	3	2.9	1–2	Butler et al. (2005)
UK	*Phasianus colchicus*	Hunted	2001–2002	120	3	2.5	1–2	Butler et al. (2005)
UK	*Phasianus colchicus*	Hunted	1997	101	2	2	1	Butler et al. (2005)
USA—S. Dakota	*Phasianus colchicus*	Hunted	2013	1301	10	0.77	1–11	Runia and Solem (2014)
Denmark	*Phasianus colchicus*	Found dead	1971–1977	199	0	0		Clausen and Wolstrup (1979)
UK	*Phasianus colchicus*	Ailing	1876	2	2		4–13	Calvert (1876)
UK	*Phasianus colchicus*	Poisoned	1875–1876	1	1			Tegetmeier (1881)
UK	*Phasianus colchicus*	Found dead	1882	1	1		8 (n°5)	Holland (1882)
USA—California	*Phasianus colchicus*	Found dead	1963	1	1		29	Hunter and Rosen (1965)
USA—California	*Phasianus colchicus*	Poisoned						Tegetmeier (1881)
Canada	*Tympanuchus phasianellus*	Hunted	1994–1996	118	0	0		Tsuji et al. (1998)
Canada	*Tympanuchus phasianellus*		2001	79	4 (bone)	5.0		Scheuhammer (2009)

[a] Prevalence of abnormal exposure to Pb was obtained in the specified studies by bone or liver analysis

Here, we complement the information acquired from these studies with that obtained from other birds of the order Galliformes.

Effects of Lead on Bone Mineralization

Early experimental studies on the effects of sublethal doses of lead in Galliformes date from the late 80s. These studies elucidated the interaction between lead exposure and dietary calcium levels, and their relationship with the metabolism of vitamin D in Japanese Quails (*Coturnix coturnix japonica;* Baksi and Kenny 1978, 1979). This modification of vitamin D homeostasis can be linked to altered bone remodelling and may cause skeletal defects (Rodríguez-Estival et al. 2013), as observed in wild Red-legged Partridges environmentally exposed to lead through shot ingestion, in which increasing levels of bone lead were associated with reduced mineralization and increased apatite crystal size (Álvarez-Lloret et al. 2014).

Effects of Lead on Reproduction

During the breeding season, laying female birds show higher lead accumulation in bones than males or non-laying females (Kendall and Scanlon 1981). This can be explained by the increased turnover, requirement and therefore absorption of calcium for eggshell formation and the similarity between calcium and lead (Tejedor and Gonzalez 1992), which makes females especially vulnerable to lead toxicity during the pre-breeding period. Both female and male birds also tend to accumulate lead in reproductive tissues; Rain Quails (*Coturnix coromandelica*) treated with lead acetate for 21 days accumulated lead in ovaries and testes to a lesser extent than in other organs such as liver or kidneys (Mehrotra et al. 2008). The oral administration of 2 to 6 lead shot pellets per week during 10 weeks to common pheasants resulted in lead accumulation in ovaries leading to reproductive effects at the highest dose, such as reduced egg mass and hatching rate, and, to a dose-dependent reduction of fertilization rate (Gasparik et al. 2012). Reduction of hatching rates could in part be explained by the maternal transfer of lead into the eggs (Vallverdú-Coll et al. 2015a), which might consequently affect embryos during the particularly sensitive initial stages of their development (Lee et al. 2001).

In Red-legged Partridge, females experimentally exposed with 0, 1 or 3 Pb shot pellets (No. 6 pellets; 2.8 mm in diameter, mean mass ± SD: 109 ± 7.97 mg) laid eggs with increasing eggshell Pb concentrations (Vallverdú-Coll, unpublished data; Table 4). These lead levels were highest immediately after treatment administration, decreased as the laying period progressed, and were greater than those observed in eggs from wild waterfowl populations environmentally exposed to lead (Table 4). The exposure of Red-legged Partridges to a single lead shot resulted in the laying of larger and heavier eggs during the first 20 days after exposure when compared to unexposed animals (Vallverdú-Coll et al. 2016), which in precocial birds is associated with larger yolks and higher lipid storage to favour energetic resource

Table 4 Mean (± SE) eggshell lead concentration in hatched Mallard (*Anas platyrhynchos*) eggs collected in the Ebro Delta[a] and in eggs laid by Red-legged Partridges[b] experimentally exposed to 0, 1 or 3 lead shot pellets (109 mg of lead/shot)

Species	Study type	Eggshell lead concentration (ng/g)	References
Mallard[a]	Field study (2008)	150 ± 24	Vallverdú-Coll et al. (2015a)
Mallard[a]	Field study (2009)	248 ± 16	Vallverdú-Coll et al. (2015a)
Red-legged Partridge[b]	Experimental study	224 ± 20 (unexposed females)	Vallverdú-Coll, unpublished data
		918 ± 62 (females exposed to 1 lead shot)	
		2,103 ± 149 (females exposed to 3 lead shot)	

availability in hatchlings (Østnes et al. 1997). This effect is consistent with chicks produced by these female partridges (exposed to one lead shot) presenting higher weight at birth than chicks hatched from unexposed females. In the same experiment (Vallverdú-Coll et al. 2016), female Red-legged Partridges exposed to three lead shot laid larger and heavier eggs during the period from 20 to 40 days after exposure, but these eggs did not result in heavier chicks, and presented a reduced hatching rate (62%) compared to control females (80.5%).

Exposure to lead during the breeding season also affects male reproductive parameters. Several studies have reported male infertility associated with lead exposure in humans (Hernández-Ochoa et al. 2005) and other mammals (Batra et al. 2004; Castellanos et al. 2015). However, this issue has been little studied in birds. To our knowledge, only two studies on the effects of lead on avian sperm have been conducted. The first one is a field study that reports a reduced number of spermatozoa on the periviteline layer of eggs from a heavy metal polluted area in Blue Tits (*Cyanistes caeruleus*; Dauwe et al. 2004). The second one (Vallverdú-Coll et al. 2016) reports, in male Red-legged Partridges exposed to lead shot, an increase in parameters related to sperm vigour that did not result in changes in sperm progressiveness. This enhanced sperm vigour can be explained by the well-known interaction of lead with physiological mechanisms mediated by calcium to produce the capacitating process of spermatozoa (Castellanos et al. 2016; Suarez 2008).

The results of Vallverdú-Coll et al. (2016) regarding lead effects on Red-legged Partridge reproductive parameters suggest that females exposed to low doses (i.e., one shot) increase reproductive investment, leading to improved reproductive output features such as production of heavier eggs and chicks as possible mechanisms of compensation (Gowaty et al. 2007). However, exposure to higher but still sublethal doses of lead (i.e., three shots) affects sperm quality (i.e., decreased the acrosome integrity and sperm motility) and reduces hatching rate, which might then have an impact on population trends. Lead exposure during the reproductive period also negatively affected maternal condition in Red-legged Partridges (i.e., decreased body condition and induced changes in the plasma biochemical profile—inducing oxidative stress; Vallverdú-Coll et al. 2015b), which may have negative effects on the development of offspring immune system. Furthermore, direct toxicity on the offspring might also occur through maternal transfer (Vallverdú-Coll et al. 2015a), and may further compromise offspring survival. Developmental exposure to Pb (i.e., in ovo administration) has been shown to affect immunocompetence in galliform species, affecting both the constitutive and induced immune responses in the offspring (Bunn et al. 2000; Fair and Ricklefs 2002; Lee et al. 2001, 2002; Youssef et al. 1996).

Effects of Lead on the Immune System

Another important target relevant to lead exposure in birds is the immune system. Lead has potential immunosuppressive effects on both constitutive and induced immune responses, which in turn can impair resistance to pathogens (Fairbrother et al. 2004; Vallverdú-Coll et al. 2019). One of the most relevant effects of lead exposure on the avian immune system is the induced imbalance between cellular and humoral immune responses (Vallverdú-Coll et al. 2019). Such an imbalance is produced through the shift in T-helper cell differentiation into type 1 (Th1, responsible for cellular responses) or type 2 (Th2, responsible for humoral responses) cell populations. This effect has largely been studied in developmental exposures (e.g., in ovo, after hatching) and has been shown to result in suppressed cytokine production by Th1 cells (Lee et al. 2001, 2002; Lee and Dietert 2003; Hussain et al. 2005). Proliferation of T-lymphocytes after the inoculation of mitogens has been frequently used as an indicator of cellular immune responses in birds. Experimental studies carried out with adult Japanese Quails have, however, not provided consistent results. For instance, Nain and Smits (2011) reported no effects of lead exposure on cellular response, while others found reduced cellular and humoral responses in lead exposed adults of this species (Grasman and Scanlon 1995).

Experimental exposure to lead (shot ingestion) in Red-legged Partridges has been shown to enhance cellular responses and suppress humoral responses (Vallverdú-Coll et al. 2015b). In the specific case of constitutive immunity, lead exposure during the breeding season reduced levels of natural antibodies, whereas in the non-breeding season, it reduced lysozyme levels (an antibacterial protein) and increased blood phagocytic activity (Vallverdú-Coll et al. 2015b). In the same experiment, as an endpoint of immunotoxic effects of lead, exposed Red-legged Partridges showed greater abundance of non-coliform bacteria and lower abundance of coliform Gram-negative bacteria in the gut than non-exposed individuals did. In another experiment, macrophages from lead exposed wild turkey chicks showed a decreased phagocytic activity compared to controls, which was associated with an increased production of eicosanoids (immunomodulatory metabolites) and decreased number of activated macrophages (Knowles and Donaldson 1997). In general, lead exposure has been associated with an increased susceptibility to infections, which may be related to a reduced Th1 capacity, and with the increased production of tumour necrosis factor-α, prostaglandin E2 and reactive oxygen species (ROS) by macrophages that can result in reduced pathogen clearance (Dietert and Piepenbrink 2006).

As mentioned above, Vallverdú-Coll et al. (2015b) found some season-dependent differences in the effects of lead on Red-legged Partridge immunity. In general, effects on the induced immune response remained constant throughout the year. Partridges seemed to compensate for depression of constitutive immunity during the breeding season, but not during the non-breeding season, even when they did not have to invest in reproduction. This suggests a greater immune susceptibility during the non-breeding period. This seasonal variation may be related to different resource allocation priorities, depending on the physiological status of individuals (Vallverdú-Coll et al. 2015b). This is perhaps very similar to the well-known ability of lead to induce oxidative stress in birds (Mateo and Hoffman 2001; Mateo et al. 2003), as well as the proposed trade-off in the use of available antioxidants among different functions (Alonso-Álvarez et al. 2008). Carotenoid-based coloration displayed by the Red-legged Partridge makes this species especially interesting for the study of carotenoids and other antioxidant allocation trade-offs relevant to oxidative balance, reproduction and immunity (Vallverdú-Coll et al. 2015b, 2016). In the next section, we review the effects of lead on the relationships among these functions.

Because the immune system consists of a large number of interrelated components, unexpected positive or negative correlations and feedback loops may be observed when studying the effects of lead on different types of immune response. Trade-offs between cross-regulated mechanisms may occur, each one with different inherent costs (Lee 2006). Hence, the general view is that lead generates an immune disruption in Red-legged Partridges—up-regulating some components and suppressing others—which may then translate into a decreased capacity to combat pathogen attack, or, lower disease resistance.

Antioxidant Allocation Trade-Offs and Ornamental Coloration

Oxidative stress is one of the mechanisms involved in lead toxicity. Oxidative stress results when there is an imbalance between pro-oxidant mechanisms (e.g., the generation of reactive oxygen species) and antioxidant defences (Schrauzer 1987; Bechara 1996; Gurer and Ercal 2000; Gurer-Orhan et al. 2004)—this may result in damage to lipids, DNA and proteins (Dowling and Simmons 2009). Regarding metal-related oxidative stress, avian species may tolerate and eliminate metals and thus defend themselves against ROS more effectively than other species due to their low rate of mitochondrial oxygen radical production (Cohen et al. 2008), and their ability to modulate their enzyme activities and detoxification systems in relation to pollution levels (Fossi et al. 1991; reviewed in Koivula and Eeva 2010).

Once absorbed into the bloodstream, lead accumulates in erythrocytes due to its high affinity for the metallo-enzyme delta-aminolevulinic acid dehydratase (δ-ALAD), displacing zinc at the binding site and thereby inhibiting its activity (Kelada et al. 2001). There is then a consequent accumulation of ALA (Gurer and Ercal 2000), which is directly linked to the generation of pro-oxidant substances

(Bechara 1996). Erythrocyte δ-ALAD inhibition has been considered a specific and highly sensitive biomarker of lead exposure (Goyer and Clarkson 2001), and has been associated with experimental lead shot ingestion in Northern Bobwhites (Kerr et al. 2010, 2011; Holladay et al. 2012) and Red-legged Partridges (Vallverdú-Coll et al. 2015b).

Lead may also inhibit the activity of other enzymes linked to the antioxidant system, such as that of the glutathione reductase. Inhibition then results in decreased levels of glutathione (GSH; the main endogenous antioxidant) (Gurer-Orhan et al. 2004) which renders cells more susceptible to oxidative damage. Furthermore, lead can also bind directly to GSH (Christie and Costa 1984). Blood lead levels have been shown to positively relate to levels of GSH and oxGSH (oxidized glutathione) in Red-legged Partridges treated with lead shot (Vallverdú-Coll et al. 2015b). While increased levels of GSH (Mateo and Hoffman 2001) may result from the induction by lead of enzymes involved in the hepatic synthesis of this antioxidant (Griffith 1999), increased levels of oxGSH are indicative of oxidative stress. Similarly, levels of dietary antioxidants (i.e., vitamins and carotenoids) have been positively associated with levels of lead in this species (Vallverdú-Coll et al. 2015b, 2016), which may be due to a compensation response to cope with the oxidative stress generated by lead poisoning (Martinez-Haro et al. 2011; Matović et al. 2015).

Changes observed in the oxidative balance induced by lead exposure can be used to explain some of the effects on immunity reported in Red-legged Partridges. For instance, cellular immune response has been shown to relate negatively to levels of antioxidants and oxidative stress biomarkers within the first 14 days after lead exposure, while the same relationships were positive when analysed 28 days after lead exposure (Vallverdú-Coll et al. 2015a, b). These results suggest a lead-induced imbalance between Th1 and Th2 responses skewed towards Th1, which could be modulated by levels of GSH (Murata et al. 2002; Townsend et al. 2003) and ROS (Hemdan et al. 2007). The oxidative stress induced by lead appears to promote the use of antioxidants to combat ROS generation (Vallverdú-Coll et al. 2015a, b). Such antioxidants invested in maintaining the oxidative balance are then not available for other functions and this deficit may thus result in impaired immune responses (Hasselquist and Nilsson 2012).

Taking another step in the attempt to link various functions affected by lead, due to their role as immune-stimulants and antioxidants (Pérez-Rodríguez 2009), carotenoids may be key molecules in the physiological trade-off between reproduction (i.e., colouration, egg production, sperm quality) and self-maintenance (i.e., oxidative balance, immunity; Alonso-Álvarez et al. 2008). The ornaments displayed by birds, such carotenoid-based coloured traits, have often been shown to reliably indicate individual quality and are used to optimise mate choice and reproductive decisions (Horváthová et al. 2012). Several experimental studies have demonstrated that carotenoid-based coloration displayed by upland birds can be used as an indicator of parasite infection (Mougeot et al. 2007), immunocompetence (Mougeot 2008) or oxidative stress (Alonso-Álvarez et al. 2008; Pérez-Rodríguez et al. 2010; Mougeot et al. 2010), and that it is modulated by hormonal levels (Mougeot et al. 2009a; Martínez-Padilla et al. 2010). Therefore, coloration is potentially a sensitive but also perhaps a rather poor, non-specific biomarker since it can be altered by numerous factors.

The Red-legged Partridge has been used to study the effects of lead on immune and reproductive functions whilst also considering lead induced oxidative stress and the use of available carotenoids for oxidative balance maintenance, immunity and reproduction (Vallverdú-Coll et al. 2015b, 2016). These holistic studies suggest that lead exposure is mainly (but not exclusively) associated with a decreased carotenoid-based coloration in ornaments (i.e., beak and eye-ring redness) of Red-legged Partridges (Vallverdú-Coll et al. 2015b, 2016). In one study, experimental lead exposure was associated with a reduction in carotenoid-based coloration in both genders during the non-breeding season (Vallverdú-Coll et al. 2015b). Moreover, a trade-off between constitutive immunity and carotenoid-based coloration was found. The results of this experiment suggest that during the non-breeding season both genders prioritise circulating carotenoid levels to fight oxidative stress at the expense of coloration (Alonso-Álvarez et al. 2008). Such reduced coloration in lead exposed males during the non-breeding season (Vallverdú-Coll et al. 2015b) remained until the next breeding season (6 months after lead exposure; Vallverdú-Coll et al. 2016), which may decrease their opportunities to mate (Omland 1996; Perez-Rodriguez et al. 2013). Furthermore, colourful males seem to have greater sperm motility and velocity (Vallverdú-Coll et al. 2016). In females, a repeated lead exposure in the following breeding season (Vallverdú-Coll et al. 2016) reduced the allocation of carotenoids to coloration. This may be because females are more vulnerable to oxidative stress than males (Vallverdú-Coll et al. 2016) and because allocation of carotenoids to the egg yolk occurred in order to protect the embryo from oxidative stress (Pérez-Rodríguez 2008). This would tend to increase offspring survival prospects at the expense of the female´s own oxidative balance (Velando et al. 2014). Although lead exposure has been predominantly associated with less coloured birds in these studies, in some scenarios carotenoid-based coloration has increased rather than decreased after lead exposure. Transformation of dietary carotenoids into ketocarotenoids (responsible for the red colouration of partridges) may be favoured by low intensity oxidative stress (García-de Blas et al. 2014, 2016). For instance, exposed male Red-legged Partridges showed greater coloration than controls after their first exposure to lead shot ingestion during the breeding season (Vallverdú-Coll et al. 2015b), which could be related to the lead induced oxidative stress reported in these individuals. This increased coloration may also be indicative of an increased investment in current reproduction, possibly at the expense of survival and future reproduction events (Bell 1980).

Risks of Agrochemicals to Red-Legged Partridges

The use of pesticides constitutes one of the most relevant pathways by which wildlife in general, and partridges, in particular, may become intoxicated. Agricultural land occupies 38.5% of the world’s emerged surface area (FAOSTAT 2015). The large area occupied by cultivation, together with the particularities of these anthropogenic systems, make them a unique type of ecosystem. Agricultural land harbours and supports typical farmland communities and species like the Red-legged Partridge can do well in such areas. In fact, agricultural land is the preferred habitat for Red-legged Partridge across its entire distribution area (Lucio and Purroy 1992; Aebischer and Lucio 1997; Suárez et al. 1997; Blanco-Aguiar et al. 2004; Vargas et al. 2006). Farmland species are also those that can potentially suffer most due to the impact (intentional or non-target) of pesticides. Every year, more than 300,000 metric tons of pesticide active ingredients are sold in the European Union (EUROSTAT 2013).

Exposure of Partridges to Pesticides and Fertilizers

An important consideration when determining the exposure of partridges to pesticides is: how do they use agricultural habitat? In this context, it is worth noting that the area of potential exposure is not necessarily limited to the fields where pesticides are applied. Depending on the type of application, there will also be an area surrounding the treated field that may receive pesticide dosage via aerial drift. To become exposed, animals must come into contact with pesticides, either during their application, or subsequently as they persist in the treated area. Therefore, understanding the frequency and timing of occurrence of Red-legged Partridges in fields (or in the drift area) is crucial in order to characterise their risk of exposure to pesticides.

Within farmland, Red-legged Partridges seem to benefit from landscape diversity (Lucio and Purroy 1992) and from the presence of natural vegetation patches (Buenestado et al. 2009; Casas and Viñuela 2010), showing preference for hedgerows and habitat edges (Rands 1987a, b, 1988; Buenestado et al. 2008) and for uncultivated land in general (Meriggi et al. 1991). This preference tends to limit their presence in open monoculture-based treated fields, although hedgerows can also be located within drift areas.

Seasonality in habitat use also plays an important role in this exposure scenario, as pesticide applications are dependent on the seasonal management of crops. In summer, when food availability decreases in dry regions (like central or southern Iberia), Red-legged Partridges are more attracted to areas of natural vegetation where the resources, especially invertebrates to feed chicks, are more abundant (Ricci 1985; Buenestado et al. 2008; Duarte et al. 2014). In autumn and winter, the homogeneity in resource availability and the lack of necessity for invertebrate prey for chicks means this preference for certain habitat patches disappears (Buenestado et al. 2008; Duarte et al. 2014). However, the presence of sown cereal seeds can, as discussed below, attract partridges into fields.

Apart from co-occurring with pesticides in a field, the potential for Red-legged Partridges to become exposed to pesticides also depends on the way that these products are applied. Formulated pesticides can occur as water-soluble liquids or powders that are then sprayed (in solution) on bare soils (e.g., pre-emergence herbicides) or crop plants (e.g., foliar fungicide and insecticide treatments). They can also occur as granules, or as liquid products specifically used for seed coating. Ingestion of treated material is the key route for pesticide exposure not only for Red-legged Partridges, but also for birds in general (EFSA 2009). Animals may ingest plants, invertebrates, grain, seeds and granules sprayed or treated directly with pesticides either within crop fields or within the drift zone. Information on the relative importance of different food items in determining pesticide uptake by partridges is lacking, and only one study (Lopez-Antia et al. 2016) has related the amount of pesticide found in the digestive tract of hunted partridges to the composition of their ingested food. In that study, a positive association was found between pesticide concentrations in crop and gizzard contents and the percentage of cereal seed ingestion by Red-legged Partridges. This was supported by a second positive association between pesticide levels in the gastric content of partridges and the percentage of surface area occupied by cereal fields in the locations of origin of each animal. However, exposure to pesticides does not always occur through ingestion. For example, Bro et al. (2016) found that in 46.2% wild Grey Partridge eggs analysed in cereal ecosystems in France contained detectable levels of 15 pesticides. Ortiz-Santaliestra et al. (2020) have recently observed that egg overspray is a significant source of exposure with adverse effects on the embryo development. In particular, overspray of eggs with tebuconazole and 2,4-D, two commonly used pesticides for foliar treatment of cereal crops in spring, increased chick mortality in 26% and 24% relative to controls, respectively.

Exposure to Pesticide-Coated Seeds

The ingestion of cereal seeds, previously treated with pesticides, is one of the main routes of pesticide exposure in partridges (and many other birds). The practice of coating seeds with pesticides before sowing is widely used. For example, 89% of arable crops in Great Britain were sown or planted with pesticide coated seeds between 1992 and 2002 (Garthwaite et al. 2003). Seed coating has the advantage of eliminating the need for spraying, thus reducing exposure risks for humans (farmers, etc.), and reducing the amount of pesticide added to the wider environment by placing active ingredients exactly where they are needed (Dewar and Asher 1994; Hart and Clook 1994). However, seeds that remain available often attract granivorous wildlife species who can then ingest high amounts of pesticide in a short time. Coated seeds are responsible for up to 50% of incidents involving wildlife affected by the approved use of pesticides (de Snoo et al. 1999). The history of adverse effects due to coated seeds on granivorous birds goes back to the early twentieth century, when methylmercury and other organomercurial products were used to treat seeds (Stanley and Bunyan 1979; López-Antía et al. 2011). Organochlorine insecticides, especially the highly toxic cyclodienes had extreme negative impacts on many bird species until their replacement with anticholinesterasic (anti-ChE) insecticides (Stanley and Bunyan 1979; Blus et al. 1984) in the 1970s and 80s. However,

Fig. 4 Pesticide treated seeds available for birds in a recently sown field (Author: Rafael Mateo)

the appearance and widespread use of anti-ChE insecticides like organophosphates (during the 1970s and 1980s) also resulted in scenarios in which, because of the high acute toxicity of these products, a lethal dose for a bird feeding on coated seeds could be reached in less than a day (Hart 1990). Over the last two decades, the development of systemic pesticides like neonicotinoid insecticides, has brought a new battery of substances into play that can be used for seed treatment. However, potential lethality to farmland birds associated with the ingestion of seeds treated with neonicotinoid insecticides like imidacloprid has also now been reported (Goulson and Kleijn 2013; Mineau and Palmer 2013; Lopez-Antia et al. 2013, 2015a). Likewise, significant concerns remain regarding these compounds and their impacts on invertebrate communities, especially pollinators (Goulson and Kleijn 2013).

During the sowing season, spilled and unburied seeds constitute an abundant resource easily accessible for Red-legged Partridges and other granivorous farmland birds (Lopez-Antia et al. 2016). Goulson and Kleijn (2013) noted that the United States Environmental Protection Agency (USEPA) estimated that, without considering spillages, about 1% of drilled seeds remain accessible to granivorous vertebrates (Fig. 4). De Snoo and Luttik (2004) refined this calculation depending on sowing technique and season, and proposed that for risk assessment purposes, 0.5% of seeds were likely to remain available in fields where precision drilling is used, rising to 3.3% with standard drilling during spring, and 9.2% with standard drilling during autumn. Another factor that determines seed availability is location within the field. Surface seed density is commonly between 3 and 4 times higher on the headland than in the field centre (Tamis et al. 1994; Pascual et al. 1999a; de Snoo and Luttik 2004; Lopez-Antia et al. 2016). For instance, Lopez-Antia et al. (2016) reported surface seed densities in cereal fields from central Spain of 11.3 seeds/m^2 in the field centre and 43.4 seeds/m^2 on the headland. Considering this seed availability, the authors estimated that a Red-legged Partridge could reach a lethal dose of an acutely toxic pesticide (i.e., imidacloprid or fipronil) by consuming the seeds available in an area of 6 to 20 m^2 of headland or 24 to 50 m^2 at the field centre. Higher seed availability on the headland, which may be due to poorer soil conditions (i.e., compaction due to increased traffic), double drilling or spillages when tractors turn (Tamis et al. 1994; Pascual et al. 1999a; de Snoo and Luttik 2004), is particularly important as headlands are the field sections most commonly used by Red-legged Partridges (Duarte et al. 2014). Prosser and Hart (2005) confirmed the likelihood of ingestion of different types of seeds (i.e., barley, maize, oilseed rapeseed and pea) treated with pesticides by Red-legged Partridges. In Spain, the presence of cereal seeds in autumn was detected in 53.4% of analysed Red-legged Partridge digestive tract contents, and the presence of pesticides was confirmed in 32.3% of them (range 0–56.7%, depending on locality). That study also reported that, out of nine active substances analysed in partridge digestive contents, tebuconazole was the most prevalent (19.1%; Lopez-Antia et al. 2016). Lennon et al. (2020) recently showed that the prevalence of exposure to clothianidin, a neonicotinoid insecticide used for cereal seed treatment, which was recently banned in the EU, rose from 6% pre-sowing to 89% post-sowing in liver and plasma samples of hunted gamebirds, mostly Red-legged Partridge, from the UK.

The risks posed by coated seeds could be minimized if exposure to seeds was reduced. In this context, avoidance of coated seeds has been investigated as a mitigation factor in risk assessment. In the only experimental study conducted in this context with Red-legged Partridges, Lopez-Antia et al. (2014) confirmed avoidance of four different pesticides coated on seeds when alternative untreated seeds were offered; imidacloprid and thiram were both rejected even when no alternative was available. Avoidance of treated seeds may occur because of a neophobic effect motivated by seed treatment colour or smell (Avery et al. 1998, 1999), or, conditioned aversion may occur due to adverse effects felt after exposure to treated seeds (Pascual and Hart 1997; Prosser et al. 2006). Whether the experimental scenarios used for testing avoidance are representative of field conditions remains, however, unclear. McKay et al. (1999) observed that Common Wood Pigeons (*Columba palumbus*) used fields recently sown with coated seeds less frequently than untreated fields. However, in an attempt to simulate field conditions, Lopez-Antia et al. (2014) observed that the avoidance of imidacloprid-treated seeds by Red-legged Partridges decreased when they were forced to increase food search efforts. In the field, animals may often face food shortage situations, which could compromise the efficacy of avoidance behaviour. It has been shown that under food stress conditions avoidance of pesticide coated seeds by birds is reduced (Pascual et al. 1999b), and, that the rejection of some seed treatments initially avoided declines over time if no alternative food sources are provided. This was also seen for Red-legged Partridges exposed to thiram-treated seeds (Lopez-Antia et al. 2014).

Exposure Through Drinking Water: Fertilizers

Oral uptake of agrochemical substances by partridges is not solely limited to ingestion of food items, contamination of drinking water can also provide a route of exposure. Some puddles and dew within crop fields may be contaminated with pesticides immediately after application. Another potential exposure scenario for partridges via drinking water is through fertigation water (i.e., irrigation water to which chemical fertilizers are added). In arid Mediterranean environments, where Red-legged Partridges are common, drip irrigation systems are also used to save water. These may constitute one of the few water supplies available for wildlife during dry months (Rito and Borralho 1997). Red-legged Partridges may be attracted to water used for fertigation (Duarte et al. 2014; Cabodevilla et al. 2021) and thus drink water with elevated nitrate concentrations. Rodríguez-Estival et al. (2010) found that Red-legged Partridges experimentally exposed to drinking water with nitrate concentrations potentially present in fertigation water (100 mg nitrate/L) showed elevated methemoglobin levels along with signs of oxidative stress (increased lipid peroxidation, glutathione oxidation and lymphocyte DNA damage).

Dermal and Inhalation Exposure

Besides ingestion of contaminated material there are other generally overlooked exposure pathways for partridges to pesticides, such as dermal exposure or inhalation. Those chemicals with potential for adsorption onto soil or plant surfaces, or systemic products that are distributed via vascular systems to all plant surfaces, can in turn be absorbed by Red-legged Partridges via dermal contact. Exposure through dermal contact will depend on the surface area of the animal in contact with the treated surface, which in birds is generally considered to be low. For example, the model used by the USEPA to estimate terrestrial exposure of birds to pesticides uses a standard value of 7.9% to determine the percentage body surface in contact with treated plants (USEPA 1993). However, the importance of dermal exposure should not be neglected, especially when it adds to dietary sources of pesticide uptake (Mineau 2012). A particularly risky dermal exposure route is via overspray (i.e., where animals are directly "oversprayed" during pesticide applications). However, this scenario is usually disregarded in most avian risk assessments because the presence of humans and machinery would tend to make Red-legged Partridges and other birds move away from crop fields during pesticide application. However, overspray could be important for egg exposure; Meriggi et al. (1991) found 10 out of 17 Red-legged Partridge nests studied in a region of Italy were laid inside cultivated fields. Given that the partridge breeding season overlaps with the foliar development time of many crops (e.g., vineyards or cereals), pesticide applications may well happen at the same time as egg incubation; with the potential risk for overspray and pesticide diffusion through the eggshell. By comparing pesticide application times with incubation periods in Grey Partridge populations across France, Bro et al. (2015) estimated that 71.4% of clutches in populations inhabiting agricultural areas were exposed to at least one pesticide.

Pesticides can also enter organisms through inhalation. As with overspray, because of avoidance behaviour during application, the inhalation of droplets during pesticide application is limited. Inhalation might happen through vapours emanating from treated surfaces, but no characterization of this exposure route has been made with partridges. Driver et al. (1991) compared experimentally, in a simulated spray application scenario, the relative toxicity of methyl-parathion (measured as cholinesterase inhibition) on bobwhite quails exposed through different routes. They found that, although inhalation was the least relevant exposure route overall, during the first hour following application this route was the one that led to the highest cholinesterase inhibition.

Effects of Pesticides on Red-Legged Partridges

Although the contribution that pesticides have played in the decline of Red-legged Partridge and other farmland birds is difficult to quantify precisely, it is highly likely to be an important factor (Pimentel et al. 1992; Delibes-Mateos et al. 2012; Mineau and Whiteside 2013; Lopez-Antia et al. 2016). The exposure of an individual to a pesticide could be lethal or sublethal, which, depending on the target system and the degree of severity, can ultimately affect survival, reproduction, and therefore, affect population dynamics.

Acute intoxication of birds with pesticides can occur due to legal use (i.e., accidental non-target intoxication), or due to deliberate illegal use (poisoning) of the pesticide. Although in Europe most registered incidents are due to illegal use of pesticides (e.g., de Snoo et al. 1999; Martinez-Haro et al. 2008; Guitart et al. 2010), in this chapter we will focus on those pesticides whose legal use poses a risk of lethal intoxication to birds.

Insecticides and rodenticides are the pesticide classes most commonly involved in accidental acute intoxication of wildlife in Europe (Berny 2007; de Snoo et al. 1999; Martinez-Haro et al. 2008), and as mentioned above, seed treatment is the agricultural practice, which causes the highest number of deaths. Farmland birds most commonly affected by intoxication are pigeons, pheasants, partridges and ducks (de Snoo et al. 1999). Unfortunately, this information comes from just a few countries that have established national wildlife poisoning surveillance programs and where incidents are systematically registered (Berny 2007; Köhler and Triebskorn 2013). Data from other countries, like Spain, are restricted to regional wildlife poisoning surveillance programs or opportunistic/scattered observations.

In the 1970s, organophosphate and carbamate insecticides emerged within agriculture as an alternative to organochlorine insecticides. In contrast to the high persistence of their predecessors, these insecticide types showed little environmental persistence and their mechanism of action was dependent on their acute toxicity. Organophosphates and carbamates inhibit the acetylcholinesterase, the enzyme responsible for inhibition of acetylcholine, a neurotransmitter shared by invertebrates and vertebrates. Thus, these pesticides are potent, nonspecific neurotoxicants that affect a very wide range of animals (Friend 1999a). Around the world, incidents of accidental intoxication with organophosphate and carbamate pesticides have been reported in a diversity of wild birds including raptors, waterfowl, galliforms, pigeons and passerines (Hamilton et al. 1976; Stone and Gradoni 1985; de Snoo et al. 1999; Mineau et al. 1999; Lelievre et al. 2001; Fleischli et al. 2004; Martinez-Haro et al. 2007). While incidents involving raptors and insectivorous birds are related to secondary poisoning, i.e., the ingestion of poisoned prey by raptors or the ingestion of contaminated invertebrates by insectivores (Mineau et al. 1999), most incidents involve granivorous birds ingesting treated seeds (Hamilton et al. 1976; Stone and Gradoni 1985; de Snoo et al. 1999; Lelievre et al. 2001).

Since the early 1980s, the most toxic organophosphates and carbamates have been progressively replaced by less toxic alternatives, which were also supposedly safer for non-target organisms. This new generation of insecticides includes pyrethroids, neonicotinoids or phenylpyrazoles. However, evidence regarding the risks posed by some of these products has led the European Union to ban the marketing and application of the most commonly used phenylpyrazole (i.e., fipronil; Regulation 781/2013) and to restrict the use of three neonicotinoids (i.e., imidacloprid, thiamethoxam and clothianidin; Regulation 485/2013) due to their toxicity to pollinators (Goulson and Kleijn 2013). Moreover, recent studies have shown that some of these compounds pose a risk of lethal poisoning to birds (Mineau and Palmer 2013; Lopez-Antia et al. 2015a, 2016), especially when they are used as seed treatment. For example, Grey Partridge mortality in France has been linked to the ingestion of sown seeds treated with imidacloprid in farmland populations (Millot et al. 2015a; Millot et al. 2017), while other pesticides did not appear to be a major cause of direct mortality (Millot et al. 2015b). In addition, some cases of Red-legged Partridge mortality associated with detectable body residues of imidacloprid have been reported in France (Millot et al. 2017). In the United Kingdom, the decline of farmland birds has not been clearly associated with the exposure to neonicotinoids, but significant negative estimates of population trends of some species, such as the Red-legged Partridge, may warrant further research (Lennon et al. 2019). Furthermore, experimental studies with captive Red-legged Partridges showed that exposure to seeds treated with imidacloprid at recommended application rates resulted in lethality, with females dying more rapidly than males (Lopez-Antia et al. 2013, 2015a). Ingestion of seeds treated with other pesticides, such as thiram, difenoconazole or fipronil did not cause similar mortality in Red-legged Partridges (Lopez-Antia et al. 2013, 2015b, c).

Direct Effects on Reproduction

Experimental studies on captive Red-legged Partridges have shown the potential for pesticide exposure to reduce female condition during breeding and to reduce breeding performance. For example, females exposed to seeds treated with thiram laid fewer and smaller eggs, with a reduced shell thickness and lower fertile egg rate, and produced smaller broods (Lopez-Antia et al. 2013, 2015b). Females exposed to seeds treated with fipronil also tended to lay fewer eggs and had reduced fertile egg rate (Lopez-Antia et al. 2015c). In addition, triazole fungicides used for seed treatment are suggested to act as endocrine disruptors, altering the synthesis of reproductive hormones and thereby reducing the reproductive capacity of partridges (Fernández-Vizcaíno et al. 2020; Lopez-Antia et al. 2021). In Red-legged Partridges feeding on flutriafol, tebuconazole and prothioconazole treated seeds, an overexpression of genes encoding for enzymes involved in the biosynthesis of sterols and steroid hormones was observed. This effect was accompanied by a reduction of plasma levels of oestradiol in partridges exposed to tebuconazole and a 14-day delay in the laying onset of partridges that had been exposed to flutriafol (Fernández-Vizcaíno et al. 2020). This may explain the delayed reproductive effects (i.e. effects occurred several months after the exposure) found after feeding couples of Red-legged Partridges with tebuconazole (Lopez-Antia et al. 2021) and flutriafol (Lopez-Antia et al. 2018) treated seeds; while tebuconazole produced a significant reduction of hatching success (i.e. a increased embryonic mortality), flutriafol reduced clutch and brood sizes by half, even when it was applied at doses far below the recommended application rate (Lopez-Antia et al. 2018). Both compounds produced a reduction in plasma cholesterol and triglyceride levels (Lopez-Antia et al. 2018, 2021). In addition to reducing breeding input (number of eggs and egg quality), the exposure of breeding females to treated seeds can negatively affect their offspring, which may have a reduced survival rate (Lopez-Antia et al. 2013), or a reduced cell-mediated immune responsiveness (Lopez-Antia et al. 2015b, c). Carotenoid-based coloration is known to play an important role in social and sexual signalling (pairing, mate choice, etc.) and to reflect reproductive investment and allocation priorities (Alonso-Álvarez et al. 2012). Many birds display bright yellow-red ornaments (coloured feathers, eye-rings, legs or beak) that are pigmented by carotenoids sensitive to oxidative stress. Although animals cannot synthesize carotenoids, they accumulate them in exposed parts of the body for communication purposes: coloured ornaments can advertise an individual's superior foraging ability, condition or health (Perez-Rodriguez et al. 2013). Carotenoids also have key physiological roles in the organism. Specifically, as mentioned above, they are hypothesized to be significant antioxidants and immuno-stimulants, and are therefore intimately linked to oxidative stress and immunity (Perez-Rodriguez et al. 2013). Carotenoid-based ornaments have therefore been suggested to signal an individual's immuno-competence or ability to resist oxidative stress. The Red-legged Partridge displays bright red legs, beak and eye rings that are pigmented by carotenoids (Garcia-de Blas et al. 2013; Perez-Rodriguez et al. 2013). Eye-ring and beak coloration have been shown to differ between sexes (with males being more coloured than females), to be condition-dependent, to be negatively affected by parasites, and to be linked with immunity and oxidative stress (Mougeot et al. 2009b; Pérez-Rodríguez et al. 2010, 2013). Pesticides and contaminants have also been shown to affect carotenoid-based coloration, but these effects are complex and depend on the type of pesticide, the exposure dose, as well as season and sex (Lopez-Antia et al. 2013, 2015b, c; García-de Blas et al. 2016). Experimental exposure to treated seeds has shown that high doses of thiram, imidacloprid or difenoconazole can reduce carotenoid-based eye ring pigmentation in Red-legged Partridges (Lopez-Antia et al. 2013, 2015a). A similar effect was found with fipronil (Lopez-Antia et al. 2015c) and flutriafol exposures (Lopez-Antia et al. 2018), consistent with the idea that pesticide exposure can be associated with reduced breeding resources and investment. However, at low doses, thiram exposure increased rather than decreased carotenoid based-coloration (specifically, beak redness; Lopez-Antia et al. 2015b). This effect has also been observed in Red-legged Partridges exposed to low doses of the herbicide diquat (García-de Blas et al. 2016). Such an increase in coloration may occur because mild oxidative stress could favour the oxidation steps that transform zeaxanthin and lutein (acquired from the diet by partridges) into the ketocarotenoids astaxanthin and papilioerythrinone responsible for colouration (García-de Blas et al. 2016). Alternatively, this increased colouration may reflect an increased investment in reproduction as a "terminal investment" that occurs when a bird's health or survival prospects are compromised (Cote et al. 2010).

Other Sublethal Effects

Besides lethal and reproductive effects, the exposure of a bird to a pesticide can produce many other types of sublethal effect that can ultimately affect survival and/or reproduction. One of the most common sublethal effects of the ingestion of pesticides is the loss of body condition, which is normally due to a reduction in food ingestion because of the adverse effects caused by the pesticide (EFSA 2009). This reduction in body condition has been registered in Red-legged Partridges after the ingestion of small amounts of imidacloprid and fipronil (Lopez-Antia et al. 2015a, c). Furthermore, in the case of fipronil, this reduction in body condition came with a reduction in the cellular immune response and levels of sexual steroid hormones of exposed partridges, which could have important implications for partridge survival and reproduction (Lopez-Antia et al. 2015c).

An imbalance in antioxidant status is another common sublethal effect caused by many pesticides. Detoxification of pesticides produces free radicals that need to be neutralized by the antioxidant system to avoid cellular damage (oxidative damage). As discussed above (in the section on lead toxicity), both the immune system and spermatozoa are vulnerable targets to oxidative damage. Furthermore, the organism may need to use up dietary antioxidants (carotenoids and vitamins) to deal with oxidative stress—which in turn, may cause an imbalance in the allocation of these substances among different physiological functions (e.g., reproduction, sexual signalling). The extent and the consequences of the antioxidant response depend on multiple factors, i.e., the kind of pesticide, dose, sex and age of the animal, or level of previous exposure to the pesticide. In Red-legged Partridges, exposure to a small dose of imidacloprid (ingestion of seeds treated with 20% of the recommended application rate for 20 days) produced an increase in superoxide dismutase (SOD) activity (the first line of antioxidant defence) without further changes in other antioxidant parameters (Lopez-Antia et al. 2015a). However, an equivalent exposure to thiram (a fungicide that has been used in agriculture for more than 60 years), produced not only an increase in SOD activity but also in circulating plasma levels of dietary antioxidants (Lopez-Antia et al. 2015b). At this low dose, the increase in antioxidant defences was enough to prevent oxidative damage. However, at a higher dose (i.e., ingestion of seeds treated with the full recommended application rate for 20 days), Red-legged Partridges exposed to thiram exhibited increased lipid peroxidation levels (a measure of damage caused by free radicals to cell membranes). Lipid peroxidation could therefore explain some of the observed effects of thiram on fertility of partridges, as reported above (Lopez-Antia et al. 2015b). Contrary to what was observed for imidacloprid and thiram, exposure of Red-legged Partridges to fipronil resulted in decreased plasma levels of carotenoids, but this effect was only detected in males. The lack of effect in females could be offset by a lowered investment in reproduction (see "*direct effects on reproduction*" section above; Lopez-Antia et al. 2015c). Moreau et al. (2021) have observed differences in carotenoid-based ornaments, immune function, physiological stress, behaviour, and breeding investment between Grey Partridges fed with organic or conventional cereal grain, despite residue levels of the detected pesticides in conventional grains were very low and below maximum levels allowed by food safety regulations in Europe. The use of gas chromatography instead of liquid chromatography to analyse pesticide residues in the grains might have limited the capacity to detect some of the pesticides eventually present in conventional grain.

Indirect Effects

Pesticides can also negatively affect partridges through indirect effects on food availability or habitat characteristics. Invertebrates, including insects, are important food resources for partridges during breeding, and in particular for chicks, as documented in the Grey Partridge (Potts 1986; Henderson et al. 2009). Where pesticides are not applied to field margins, the abundance of invertebrates is greater, as is the breeding success of partridges (Rands 1985; Aebischer 1990). Herbicides can also kill essential weeds and thereby indirectly reduce insect numbers (Taylor et al. 2006). In addition, insecticide applications can kill the chick food insects directly. The net result is a diminution in the supply of insect food for partridge chicks (Rands 1985). Pesticide use has also already been shown to indirectly affect the breeding success of Red-legged Partridge (Green 1984) as well as other gamebird species (Hill 1985). Herbicides can alter habitat characteristics, makings these less suitable for breeding partridges or foraging broods in terms of both vegetation characteristics (cover and protection from predators) and food abundance. As mentioned, the Red-legged Partridge is particularly abundant in agrarian pseudo-steppes characterized by a high diversity of crops intermixed with natural vegetation. Many studies have shown that field margins or edges are key habitats for them and are preferentially used by partridges (Rands 1986; Ricci et al. 1990; Casas and Viñuela 2010; Villanúa et al. 2011). Partridge abundance increases with habitat quality and heterogeneity, and the presence of field margins is a key factor for adult survival as well as productivity (Pépin et al. 2008; Casas and Viñuela 2010; Villanúa et al. 2011). In the UK, Grey Partridge chick survival rate was positively related to measures of weed abundance and diversity in cereals, and, to food abundance for chicks. Restrictions on the use of herbicides or insecticides, in particular in field margins, have been shown to be beneficial for the species (Rands 1985; Chiverton 1999; Moreby and Southway 1999; Henderson et al. 2009).

Effects of Pesticide Mixtures

Commonly, pesticide use involves the application of several active ingredients. For instance, coated seeds are sometimes treated with more than one substance (e.g., one insecticide and one fungicide). Lopez-Antia et al. (2016) detected the presence of up to three different active ingredients in the gizzard of the same hunted Red-legged Partridge. Working with Grey Partridges, Bro et al. (2015) estimated that 67.1% of clutches could be exposed to several active substances (up to 22 of these in the most extreme cases). Up to 46.2% wild Grey Partridge eggs analysed in cereal ecosystems in France contained detectable levels of one compound, whereas two compounds were found in 12.5 % of the samples and more complex mixtures (three to five compounds) in 16.7 % of them (Bro et al. 2016). Cocktails of pesticides of this nature are not included in risk assessments, and therefore, the effects of such mixtures on wildlife may well pass unnoticed. Several experimental studies have reported synergistic effects on Red-legged Partridges of pesticide combinations, with toxicity increasing up to 100-fold (Thompson 1996).

Population Impacts

If pesticides reduce survival or reproduction, they are likely to impact population dynamics and cause reduced population growth or population declines. The Red-legged Partridge is a species with high productivity—i.e., large clutch size, combined with a double nesting strategy, with two clutches laid in c. 50% of pairs, one incubated by the female, the other by the male (Green 1984; Casas et al. 2009). Direct adult mortality due to pesticides may be low in natural populations and may have a negligible impact on population growth rates (Millot et al. 2015a). However, given that productivity is a key demographic parameter, all factors that contribute to reduced productivity or offspring survival can have detrimental population effects. A population viability study has highlighted that high productivity is particularly important to maintain a high Red-legged Partridge population density in Spain (Ferreras et al. 2010).

While there are a growing number of studies working at the individual level that relate pesticide exposure to reduced survival or breeding performance, studies or experiments demonstrating pesticide effects on population level dynamics are much scarcer. This is in part due to the need to have long-term data on population abundance or demographic parameters, as well as pesticide exposure levels, or due to the difficulty of conducting replicated experiments at the population level (Henderson et al. 2009). It is therefore not surprising that such information is currently lacking for Red-legged Partridge, but there is relevant information from other closely related species. One of the best-documented cases is that of pesticide use and Grey Partridge population dynamics in the UK (Potts 1986; Kuijper et al. 2009). There, Grey Partridge populations have been declining since the 1940s. On farmland, Grey Partridge broods often forage for insects around field edges where arthropods and weeds are most abundant. Studies have shown that chick survival is related to abundance of insect food and field experiments have shown that herbicides and fungicides used on cereal fields reduce insect abundance as well as chick survival and brood size in Grey Partridges (Rands 1985, 1986; Potts 1986; Sotherton 1998). Weight of evidence also suggests that the indirect effect of using some pesticides on cropland may be a key factor in the decline of many other farmland birds (Donald et al. 2001).

Regulatory Framework and Practices to Reduce Risk of Pesticides to Partridges

The use of pesticides is controlled at the regulatory level with legislation that aims, among other things, to avoid unacceptable risks to wildlife. In the European Union, a common Regulation (1107/2009) establishes the requirements for allowing pesticides onto the market, including the process of ecological risk assessment.

In the initial pesticide risk assessment for birds, acute and long-term toxicity data should be obtained such as the median lethal dose (LD_{50}, the dose required to kill half the members of a tested population; OECD 2010) and the no observed adverse effect level (NOAEL, the maximum level causing no adverse effect using the response variables: body condition, food consumption, clutch size, eggshell thickness, ratio of fertile eggs, viable embryos during the incubation period, hatching rate and chick survival at days 1 and 14 after hatching; OECD 2006). These endpoints are normally retrieved from toxicity assays conducted with common laboratory species such as the Japanese Quail, the Northern Bobwhite, or the Mallard (*Anas platyrhynchos*). Endpoints are then compared to predicted exposure concentrations in worst-case scenarios (i.e., defined for an unreal species that would comprise all ecological and biological traits leading to increased exposure risk). If the toxicity endpoints are more than 10 (for acute exposure) or 5 times (for long-term exposure) above the predicted, worst-case exposure level, the pesticide is considered to be safe to birds (EFSA 2009). However, in the majority of cases, and in particular in the assessment of treated seed ingestion risks, these safety margins are not reached. Hence, refined, more realistic exposure scenarios are used to assess pesticide risks.

At a higher tier risk assessment stage, a range of options are used to refine the risk assessment of pesticide treated seeds in birds: the use of a focal species (a species that actually occurs in the crop when the pesticide is being used) to estimate exposure concentrations, the ratio of treated seeds in the diet (in contrast to a diet consisting of 100% treated seeds, as used in the first tier), the availability of treated and non-treated seeds in the field, or the display of certain behavioural traits such as treated seed avoidance or de-husking. In the last step of the risk assessment all this information is used to characterise risk and to take a decision on the pesticide under review. Among medium-sized birds, Partridges are considered good focal species to assess the exposure to pesticide treated seeds (Bonneris et al. 2019).

One of the main criticisms of this procedure is that it underestimates the differences that exist among species in terms of their sensitivity to toxicants, even with the application of safety factors. It has been demonstrated that sensitive species are under-protected (Mineau et al. 2001; Luttik et al. 2011). This lack of protection can be observed when LD_{50} values are compared with HD_5 values—the acute hazardous dose estimated to lead to 50% mortality in a species in the top 5% of a species sensitivity distribution model (i.e., more sensitive than 95% of other bird species) (Mineau et al. 2001; Table 5). The HD_5 considers interspecific variability and is therefore a more conservative benchmark for assessing the acute risk of different pesticides to birds.

In Europe, future management decisions must be taken under an Integrated Pest Management (IPM) strategy (European Directive 128/2009/EC), which means that the use of pesticides should be minimized and limited to cases in which it is economically justified, and no alternatives exist. In many cases, the use of treated seeds is a prophylactic use and therefore contrary to the principles that rule the IPM; this suggests that the use of these treatments should be limited to those cases that solely fit the IPM principles; and, that products that pose the lowest risk to wildlife should always be selected.

Persistent Organic Pollutants (POPs)

The emergence of synthetic organic pesticides in the second half of the twentieth century marked a milestone in the development of agriculture, but also in the birth of ecotoxicology (Carson 1962). Compounds such as p,p'-DDT and its main metabolite p,p'-DDE would be detected in the tissues of living organisms several decades after being banned for use in most countries. The high persistence of organochlorine pesticides along with their affinity for lipids makes them very bioaccumulative, and therefore, they tend to be biomagnified along food chains. Because of the low trophic

Table 5 Pesticides used in Spain for cereal (excluding rice) seed treatment during the last 10 years, including application rates to these seeds and toxicity levels (LD_{50} and HD_5) for birds

Chemical	Application rate (mg kg_{seed}^{-1})	Species	LD_{50}[a] (mg kg_{bw}^{-1})	Acute HD_5[b] (mg kg_{bw}^{-1})
Copper oxychloride[c]	900	*Coturnix japonica*	176	49.95
Mancozeb[c]	300	*Anas platyrhynchos*	>2000	710.95
Maneb[d]	1400	*Coturnix japonica*	>6400	345.34
Thiram[e]	1750	*Phasianus colchicus*	673	36.81
Metalaxyl-M	1017	*Colinus virginianus*	981	137.03
Fludioxonil	20	*Anas platyrhynchos*	>2000	208.12
Difenoconazole	60	*Coturnix japonica*	>2000	207.13
Flutriafol	62.5	*Alectoris rufa*	616	481.7
Tebuconazole	375	*Colinus virginianus*	1988	347.3
Triticonazole	50	6 species	>2000	232.29
Propiconazole[f]	277	*Anas platyrhynchos*	>1000	296.8
Fluxapyroxad	500	*Colinus virginianus*	>2000	n/a
Prothioconazole	37.5	*Colinus virginianus*	>2000	n/a
Sedaxane	50	*Colinus virginianus*	>1068	n/a
Silthiofam	2500	*Colinus virginianus*	>2250	n/a
Imidacloprid[g]	700	*Coturnix japonica*	31	8.4
Fipronil[h]	1250	*Alectoris rufa*	34	1.47
Thiacloprid	1[i]	*Coturnix japonica*	49	n/a

[a] Data obtained from EFSA pesticide assessment reports (available at http://www.efsa.europa.eu/)
[b] Data from Mineau et al. (2001)
[c] Currently not used for cereal seed treatment in Spain
[d] Banned in the European Union since 2018
[e] Banned in the European Union since 2019
[f] Banned in the European Union since March 2020
[g] Banned in the European Union for cereal seed treatment since 2018
[h] Banned in the European Union for cereal seed treatment since 2014
[i] Application rate in mg/seed unit; applicable to maize only

Table 6 Concentrations of organochlorine compounds detected in tissues of Red-legged Partridge in Spain ($n = 99$) and percentage of samples exceeding maximum residue levels (MRL) established by the European Union for meat for human consumption. Source: Herrera et al. (2000)

Compound	Mean concentration (maximum) in ng/g of extractable lipid		MRL ng/g	% >MRL
	Fat	Muscle		
HCB	8.2 (106)	2.8 (240)	200	1
α-HCH	2.1 (11)	2.2 (42)	100	–
β-HCH	10.7 (252)	8.0 (392)	100	2
γ-HCH	14.5 (17963)	11.6 (6903)	1000	4
Dieldrin	2.1 (172)	2.0 (253)	200	2
p,p'-DDE	29.3 (5004)	14.0 (2788)	1000	3
p,p'-DDT	10.2 (226)	10.4 (243)		

level of the Red-legged Partridge, its exposure to bioaccumulative pollutants is low when compared with other species, such as raptors. However, it has been possible to detect low concentrations of organochlorine pesticides in Red-legged Partridges, especially of pesticides widely used in the past such as p,p'-DDT (and p,p′-DDE) and γ-HCH (lindane) (Herrera et al. 2000) (Table 6).

In Portugal, with a sample of 84 Red-legged Partridges, low concentrations of p,p'-DDT and its metabolites were also observed, and levels >10 ng/g were only detected in 6% of samples for p,p'-DDE, 1% for p,p'-DDD and 6% for p,p'-DDT. Overall, 13% of samples contained residues >10 ng/g for total DDTs (DDE+ DDT +DDD). The highest levels were detected in samples collected in the Alto and Baixo Alentejo, two regions where cork had been extensively treated with p,p'-DDT against lepidopteran (*Tortix viridana*) in the past. Residues of dieldrin and hexachlorobenzene (HCB) were also found in 2.3% and 10.5% of the Red-legged Partridges analysed, respectively (Conte de Barros 1978).

Besides OC pesticides, there are other halogenated persistent organic compounds that could be detected in tissues of Red-legged Partridge and may deserve more attention in studies designed to assess the food security and safety of game meat. Among these compounds are polychlorinated biphenyls (PCBs, used in various industrial applications, i.e., insulation in electrical transformers), polybrominated diphenyl ethers (PBDEs, used as flame retardants) and perfluorinated compounds (PFCs, used as coatings on fabrics and utensils). However, the two studies conducted to date on OC contaminants in Red-legged Partridge in Spain and Portugal did not detect residues of PCBs in tissues (Herrera et al. 2000; Conte de Barros 1978) and there are no published studies on the other groups of persistent organic pollutants listed above.

Food Safety

As a gamebird species, the presence of contaminants in Red-legged Partridges is an issue of interest in terms of human food safety. Wildlife can be exposed to a wide range of pollutants in the natural environment, such as POPs, pesticides or heavy metals, but only some of these may be toxicologically relevant for game meat consumers. Herrera et al. (2000) detected organochlorine pesticide residues in Red-legged Partridges from Spain, but only 4% of those analysed exceeded the maximum residue levels (MRL) established for meat destined for human consumption in the European Union (Table 6). In terms of heavy metals, there are three important routes whereby game meat contamination may occur. The first is via the dietary route where gamebirds are exposed to a wide range of heavy metals and metalloids through the ingestion of food, water, soil or grit containing such elements (Bendell-Young and Bendell 1999; Larison et al. 2000; Braune and Malone 2006). The other two routes are closely related to hunting practices involving lead ammunition. As noted above, gamebirds can ingest lead shot pellets when they confuse these with grit or food and this can produce a significant elevation in lead concentrations in bird tissues, including muscle (Kreager et al. 2008; Mateo et al. 2014). The last contamination route involves the ammunition itself, which is used to kill the birds. After removing lead shot pellets from edible flesh (muscle tissue), Red-legged Partridges hunted with lead ammunition had >0.1 mg/kg w.w. Pb in muscle (the MRL established by the EU for meat—notably, excluding game) in 63% of cases ($n = 26$) in the UK (Pain et al. 2010) and 54.7% of cases ($n = 64$) in Spain (Mateo et al. 2011). There is also the potential for further transfer of lead during cooking from lead shot pellets/fragments embedded in harvested Red-legged Partridges to meat. This transfer can be favoured by the use of acidic recipes like Spanish "escabeche", which uses vinegar to tenderize the meat and to preserve it for longer periods (Mateo et al. 2007). The use of wine also tends to reduce cooking pH and increase lead transfer, although less than vinegar (Mateo et al. 2011). The fragmentation of lead shot pellets on impact can also increase the risk posed by game meat because these tiny fragments are highly unlikely to be removed during meat preparation (before cooking) or while eating (as they will not be felt in the mouth). In an in vitro simulation using a gastrointestinal model, the intestinal bioaccessibility of Pb was higher in meat cooked with vinegar (6.75%) than with wine (4.51%). These values can be transformed into in vivo bioavailabilities (relative to the 50% bioavailability of lead acetate in children) of 23.6% and 15.7% of the lead present in meat after cooking, respectively (Mateo et al. 2011). A risk assessment recently performed in Spain has shown that moderate or low consumption of Red-legged Partridge meat may not represent a significant public health risk in the general population, but a high consumption can pose a greater health risk, especially to hunters and their families (Sevillano-Morales et al. 2021).

Red Legged Partridge as a Model Species for Experimental Studies in Toxicology

The use of Red-legged Partridge as an experimental model species in ecotoxicological studies has increased in recent years. As reported here, several experimental studies have used this species to investigate the effects of different chemicals. The effects of exposure of partridges to pesticides have been assessed through the study of biomarkers, i.e., considering the induction of liver enzymes (Walker et al. 1993), or the inhibition of cholinesterase activity in the case of anti-ChE insecticides (Johnston et al. 1989). In this latter case, Red-legged Partridges are now considered one of the most sensitive avian species tested to date (Johnston et al. 1994; Johnston 1995). The use of other physiological responses, such as alterations in the antioxidant system as a response to pollutant metabolism, or impairment of aspects of immune function, have been validated and applied to ecotoxicological studies with this species (e.g., Rodríguez-Estival et al. 2010; Lopez-Antia et al. 2013). Red-legged Partridges are also interesting model species to investigate trade-offs among different organism functions when challenged by a pollutant. For example, the allocation of carotenoids may have important consequences as these carotenoids play a major role during the mating period, and their allocation to ornaments can be at the expense of other functions, such as the neutralization of pollutant effects at the physiological level (Vallverdú-Coll et al. 2015b). Whilst this is not a measurable response that is exclusive to partridges, the importance of carotenoid-based ornamentation in this species makes it a very relevant ecotoxicological model bird.

Besides experimental use, individuals from the wild have also been used to biomonitor environmental pollution; for example, Red-legged Partridge is an avian species at high risk of lead intoxication due to ingestion of lead shot pellets, and several populations have been monitored in this context (Soler Rodríguez et al. 2004; Álvarez-Lloret et al. 2014). In addition, Red-legged Partridges have been monitored with regard to persistent organochlorine compounds (Herrera et al. 2000).

Because of their importance as a game species, Red-legged Partridges are commonly bred and grown on farms for subsequent release onto hunting estates. This practice has turned the husbandry and maintenance of these animals in captivity into an important economic activity in itself. This has facilitated the acquisition of knowledge regarding farming/rearing techniques and provides an opportunity for greater use of this species as a model in ecotoxicological research. In addition, as a game resource, it remains important that Red-legged Partridge meat is considered (alongside other popular game meat) within a food safety context (Herrera et al. 2000; Pain et al. 2010; Mateo et al. 2011; Silva et al. 2011).

The suitability of Red-legged Partridge as a model species for ecotoxicological studies may be especially pertinent when evaluating the risks related to pesticide treated seeds. The medium size of Red-legged Partridges among steppe birds means that it is likely to feed on many different types/sizes of seed (Prosser and Hart 2005). This is likely to increase their exposure risk relative to other, more selective species. Furthermore, behavioural traits that contribute to reduced exposure, such as de-husking, have not been observed in this species. Avoidance behaviour that does lead to reduced pesticide ingestion can be readily studied in experimental/observational work (Lopez-Antia et al. 2014). One of the most commonly used avian model species in ecotoxicology is the Northern Bobwhite, another galliform species native to North America, which shares many of the preferences of Red-legged Partridge for cropland habitats. However, this model species does not seem as suitable as Red-legged Partridge for specific ecotoxicological assessment of treated seeds. A recent study found a complete absence of treated seed in the crop contents of Northern Bobwhite captured from the Rolling Plains in Texas and Oklahoma (Turaga et al. 2016). By contrast, Lopez-Antia et al. (2016) observed Red-legged Partridges feeding on cereal fields that had recently been sown with treated seeds. The analysis of digestive contents in this species revealed that 32% of the Red-legged Partridges had ingested pesticides used for seed treatment.

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Health Monitoring and Disease Control in Red-Legged Partridges

Sandra Díaz-Sánchez, Ursula Höfle, Diego Villanúa, and Christian Gortázar

Introduction

Pathogens are key components of all ecosystems. They depend on their host's life cycles and contribute to modulate fitness, abundance, and distribution. In farm-reared game birds, viral and bacterial infections can cause significant losses (Butcher and Banigrahy 1985; Wünschmann and Ziegler 2006). Parasites do also influence the fitness and survival of free-living game birds, such as Red Grouse (*Lagopus lagopus scoticus*), in which dramatic population fluctuations take place (Dobson and Hudson 1995; Hudson et al. 1998).

Host-pathogen interactions are extremely complex and go far beyond the simple outcomes of disease and mortality, for instance, interacting with many other life-history traits such as ornamentation or immune responsiveness (Mougeot et al. 2009). As a gamebird, the Red-legged Partridge (*Alectoris rufa*) represents an interesting model species for the study of disease dynamics and host-pathogen evolution, since populations range from natural ones, through those managed for

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_9

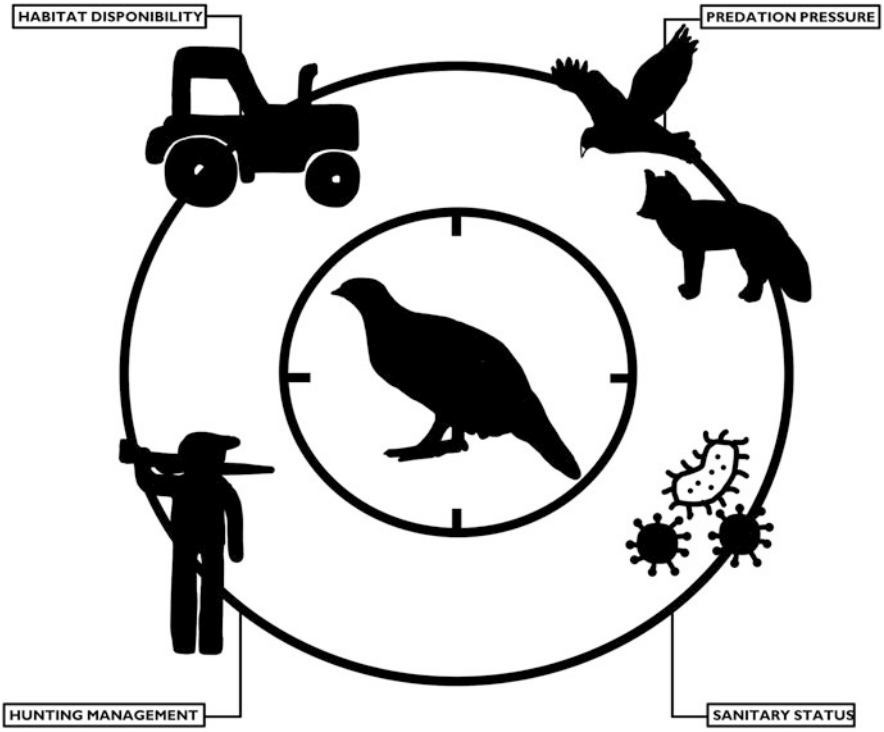

Fig. 1 Challenges of partridges inhabiting natural ecosystems

maximum hunting yields, up to completely artificial captive-reared ones. This gradient generates opportunities for both comparative and experimental studies, and much has been learned in the last decades.

A few definitions are needed to aid in understanding the sections of this chapter. These are given in Box 1. Exposure to pathogens is just one of many challenges for partridges inhabiting natural (relatively unaltered) ecosystems (Fig. 1). Pathogens are drivers of partridge population dynamics along with predation, game management, and habitat characteristics (Chaps. "The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting", "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?", "Is Predation the Key Factor of Partridge Ecology and Management?", "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing", "Red-Legged Partridge Monitoring and Population Trends", and "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). Indeed, interactions between these components are substantial: predators may prey preferentially on diseased birds; intermediate hosts are often more abundant, and generalist predators often less (Curio 1976; Temple 1987; Genovart et al. 2010), in well-preserved habitats; hunters may release parasites along with farm-reared birds and aggregate birds at feeders,

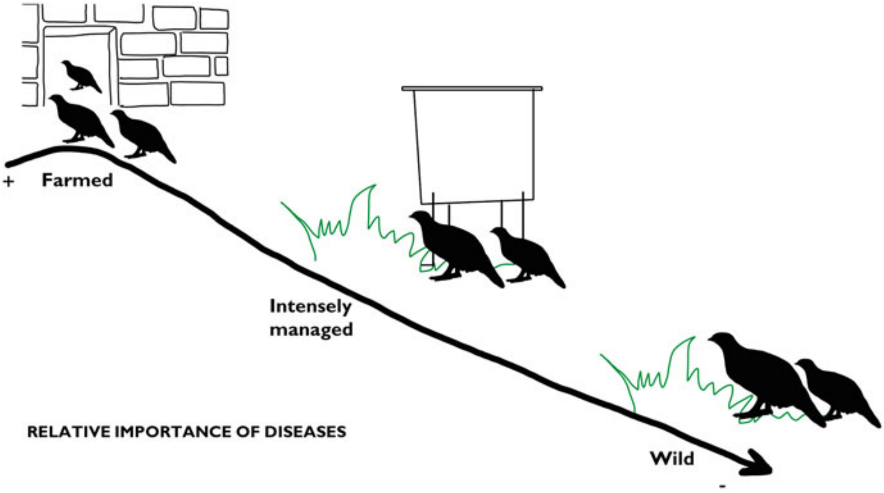

Fig. 2 Scheme of the relative importance of diseases from farmed red-legged partridges to wild ones

increasing their vulnerability to infectious agents and predators (Calvete et al. 2003; Millán et al. 2004b, c; Gortázar et al. 2006; Villanúa et al. 2008). These interactions result in complex networks that need to be explored to understand partridge disease dynamics.

One specific aspect needing attention is the farm-to-field gradient (Fig. 2): diseases are more relevant for partridges in captivity (farmed) than in managed hunting estates (i.e., those with high densities, often due to releases, generally providing supplementary food), and far more than in natural populations, where low densities hamper infection maintenance and predators possibly contribute to disease control acting as sanitary police (Gortázar et al. 2006). As addressed below in Sect. "Disease-Related Mass Mortalities", many of the main pathogens of partridges, such as pathogenic *E. coli*, coccidia, or direct-cycle nematodes, are of great concern for farmed birds but almost irrelevant for wild ones (Millán 2009; Naciri et al. 2011; Díaz-Sánchez et al. 2012a, b, 2013). The situation of intensely managed hunting estates is an intermediate one, since parasites of farm-origin may be introduced through releases or may survive given the higher density and spatial aggregation, for example, at feeders or watering devices (Gortázar et al. 2006).

Because of the above-mentioned gradient and of their susceptibility to a large variety of pathogens, partridges can serve as indicators of ecosystem health. A set of sampled partridges revealing a diversity of heteroxenous parasites (see Box 1), low levels of enterobacterial infection (see Box 2), and possibly no or only low levels of antibiotic resistance in those enterobacteria (see Sect. "Human Health Aspects of Partridge Diseases"), probably, belong to a healthy natural population (Villanúa et al. 2008; Millán 2009; Díaz-Sánchez et al. 2012a, b). By contrast, partridges presenting diarrhea or emaciation (extreme loss of body condition) are likely to carry monoxenous parasites such as coccidia or monoxenous helminths or to be affected by avian pathogenic *E. coli*, characteristic of farm-like environments with higher contamination by pathogens (Villanúa et al. 2008; Millán 2009; Díaz-Sánchez et al. 2011).

Existing knowledge on Red-legged Partridge diseases includes comprehensive literature reviews (Millán 2009; Welchman 2016), as well as several important references on selected partridge pathogens including parasites (Cooper et al. 2004; Höfle et al. 2004a; Villanúa et al. 2008; Naciri et al. 2011, 2014; Stockdale et al. 2015; Bolognesi et al. 2016; Gerhold et al. 2016), bacteria (Butcher and Banigrahy 1985; Millán et al. 2004c; La Ragione et al. 2004, Díaz-Sánchez et al. 2012a, b, 2013), fungi (Lanteri et al. 2012), and viruses (Gortázar et al. 2002a; Buenestado et al. 2004; Agüero et al. 2011; Sotelo et al. 2011; Gamino et al. 2012, 2016).

This chapter to synthesizse the current knowledge without repeating this literature. Rather, we focus on those aspects of relevance for game biologists, wildlife managers, and in general, those interested in the role of pathogens and diseases in Red-legged Partridge ecology, management, and conservation. The first section addresses diseases causing mass mortality, since these are of obvious concern. The second section focuses on sporadic mortality and sublethal infections, which are equally relevant and much more frequent, but far less conspicuous. The third section deals with human health aspects of partridge diseases, including transmissible (zoonotic) infections, antibiotics use, and antibiotic resistance. Finally, the fourth section comments on aspects of gamebird health monitoring and disease control options in partridge farms, managed populations, and natural populations.

Disease-Related Mass Mortalities

Avian mortality or mass mortality can be defined as those events in which five or more wild birds of the same or different species are found dead at the same time or over a short period in the same location (Animal and Plant Health Agency Department for Environment, Food, and Rural Affairs 2014). Mass mortalities associated with *Alectoris rufa* can be associated with viral infections (Box 5) (i.e., Bagaza virus, Avian pox), enterobacteria outbreaks, and certain parasites including coccidia and flagellates. Occasionally, the causes of mass mortalities can also be multifactorial. All these examples are described in the following pages.

Bagaza Virus

In August 2010, a mass mortality of Red-legged Partridges occurred in natural and highly managed partridge populations in Cádiz, southern Spain, caused by a hitherto undetected mosquito-borne Flavivirus called Bagaza virus (BAGV) (Agüero et al. 2011). Locally, the infection led to a population reduction of Red-legged Partridges of close to 90%, while Ring-necked Pheasants (*Phasianus colchicus*) present in the same region were affected to a much lesser extent, and other species such as Wood Pigeons (*Columba palumbus*) only sporadically (Agüero et al. 2011). The lethal effect of the virus on partridges was mainly due to severe hemolysis, encephalitis, and myocarditis, whereas in the pheasants and pigeons, the virus affected primarily the central nervous system (Gamino et al. 2012). An experimental infection has shown that in addition to mosquitoes, direct transmission of the virus occurs between Red-legged Partridges (Llorente et al. 2015), which may have been an additional factor for the rapid expansion of the outbreak in areas with high densities of partridges and management using feeders that promote aggregation, especially of diseased, less mobile individuals. BAGV has since been shown to be endemic in the region (Llorente et al. 2015). A more recent (2019), less severe mortality event in partridges in the same region was due to the coinfection of the birds with BAGV and the avian malaria parasite *Plasmodium* (P.) *relictum* (Cardona-Cabrera et al. 2021).

Avian Pox

Lesions due to avipoxvirus infections on the unfeathered parts of the body are frequently found in many avian species including Red-legged Partridges. The virus is transmitted by mosquitoes and the wart-like lesions can appear on the legs, eyelids, beak commissures, and ceres. Lesions are mostly found in juvenile birds, and pox is generally considered a self-limiting process (Cunningham 1978). However, the occurrence of an Avian pox infection outbreak in a Red-legged Partridge population in Southern Spain that was subject to a telemetry study showed that Avian pox virus–affected juvenile birds were in worse body condition and less likely to survive until the hunting season (Gortázar et al. 2002a). The outbreak peaked in July–August and affected primarily chicks. Pox-affected partridges (41–75% of the total juveniles) had a summer survival of just 31% (Buenestado et al. 2004). This mass mortality due to avian pox was potentially mediated by an especially rainy spring and might contribute to explain the poor productivity of natural partridge populations in years with rainy springs.

Enterobacteria Outbreaks (See Box 2)

Avian colibacillosis associated with Avian Pathogenic *E. coli* (APEC) infections is responsible for frequent mortalities within farms or immediately after the release of farm-bred partridges (Díaz-Sánchez et al. 2012b, 2013). However, producers hardly identify the causative agent of the process, and erroneous treatments together with scarce biosecurity measures jeopardize proper APEC control (Díaz-Sánchez et al. 2012b, 2013). La Ragione et al. (2004) were the first to describe an APEC outbreak in hand-reared partridges. Two episodes of enteritis with high morbidity and mortality occurred in outdoor aviaries. Microbiological investigations suspected coinfection with an attaching and effacing *E. coli* strain of serotype O103:K+:H- together with *Salmonella binza* as the causative agent of the outbreak. In Spain, Díaz-Sánchez et al. (2013) reported an outbreak that occurred in 1-day-old Red-legged Partridges. Diseased birds showed weight loss and yellowish diarrhea or died suddenly in absence of clinical signs. Bacteriological analysis was carried out, and APEC strains were detected by PCR from tissues. Further analysis of the isolates revealed indistinguishable profiles, suggesting a common source. Predisposing factors such as high temperatures, eggs belonging to the last batch of the breeding season, and lack of efficient hygienic measures in the hatchery may have contributed to the outbreak. *Salmonella* spp. has also originated disease in partridges (Francis 1963). *Salmonella* outbreaks are very likely to occur in captive gamebirds but not in their wild counterparts. Nevertheless, sporadic mortality events have been reported in restocked Red-legged Partridges, mainly associated with aggregation at feeders (Lucientes 1998).

Parasitic Diseases Causing Significant Mortality

(a) *Coccidiosis*

The primary causes of chick and juvenile bird mortality in partridge farms are probably coccidida of the genus *Eimeria* (Romero Rodríguez and Lizcano 1974; Naciri et al. 2011, 2014; Bolognesi et al. 2016; Gerhold et al. 2016). In rainy seasons, mortalities can also take place in natural populations. Juvenile birds acquire sporulated *Eimeria* oocysts rapidly from contaminated soil and litter. As a consequence, coccidiostat treatments and management of the soil of flight cages between production cycles is common practice in most Red-legged Partridge farms (Cordero del Campillo and Pla Hernández 1966; Gerhold et al. 2016). However, important postrelease losses in restocked partridges can occur even after administration of coccidiostats at prerelease stages (Millán et al. 2003; Millán 2009). Another important genus of coccidia in farmed partridges is *Cryptosporidium*, which can cause significant outbreaks of diarrhea with mortalities of up to 50% in specimens that are a few days old (Pagès-Manté et al. 2007).

(b) *Flagellated protozoa*

In farm-reared juvenile partridges, protozoa of the genera *Hexamita* and *Trichomonas* can lead to high mortalities with sudden onset and significant losses (Cooper et al. 2004; Stockdale et al. 2015). Both parasites are acquired via contaminated food or water (fecal-oral cycle) and affect the large intestine and, eventually, the liver, causing severe diarrhea that is liquid and often blood-tinged in *Hexamita* infections and frequently contains white foam when caused by *Trichomonas* (Cooper et al. 2004; Lloyd and Gibson 2006; Amin et al. 2014). The parasites can be readily differentiated under the microscope, and both are often shed by adult birds acting as chronic, clinically unaffected, carriers.

(c) *Helminths*

Helminth parasites are largely part of the intestinal flora of Red-legged Partridges, and the helminth parasite community in natural Red-legged Partridge populations across the Iberian Peninsula under natural conditions is influenced primarily by the latitude, annual mean temperature, and relative humidity in the area (Calvete et al. 2003) as well as sex and age of the partridges (Millán et al. 2004a). However, farming and intense management exposes Red-legged Partridges to very different environmental conditions. This is the reason why farm-reared partridges are mostly affected by parasites with a direct (monoxenous) cycle in contrast to partridges from natural populations that mostly carry parasites with a heteroxenous life-cycle (Millán et al. 2004b). This is mediated by the direct contact with contaminated soil and the lack of intermediate invertebrate hosts under farm conditions. Severe infestations with nematodes such as *Heterakis* or *Ascaridia* can lead to significant losses for farms and after the release of farm-reared partridges. Certain cestodes, despite being heteroxenous, can also lead to mass mortality, both in farms and in managed populations (Millán et al. 2004a; Millán 2009).

(d) *Summer mortalities*

Summer mortalities of juvenile partridges occur during summer in intensively managed small game estates in central and southern Iberia. They are an example of a noninfectious disease due to multiple causes including partridge overabundance with depletion of natural protein sources (invertebrates), diet imbalance toward the carbohydrate-rich grain, and high ambient temperatures, among other factors (Gortázar et al. 2002b; Höfle et al. 2004b; Panek 1992).

Sporadic Mortality and Sublethal Infections

Sporadic mortality cases are those not matching the definition of mass mortality. Most disease agents do rarely cause mortality but do have adverse effects on the bird's body condition or fitness, eventually including key aspects such as reproductive success. The following pages review selected sublethal infections, some of them causing sporadic mortality.

Viral Diseases

Agents such as West Nile virus, Avian influenza virus, and avian-Paramyxovirus can cause sporadic mortality and sublethal infections in Red-legged Partridges. Red-legged Partridges have been shown experimentally to be susceptible to West Nile Virus (WNV) infection (Sotelo et al. 2011; Gamino et al. 2016). Under experimental conditions and depending on the infecting strain, mortality in juvenile Red-legged Partridges ranged from 21% to 70%. However, in contrast to the mass mortality caused by Bagaza virus (BAGV) (Gamino et al. 2012; Llorente et al. 2015), no WNV-related mass mortalities associated with Red-legged Partridge have yet been reported in the field or on farms. An interesting case was described in 2012 in California, a WNV-*Salmonella typhimurium* coinfection in a Chukar Partridge (*Alectoris chukar*) farm (Eckstrand et al. 2015).

Similarly, partridges have been shown experimentally to be very susceptible to infection with Highly Pathogenic Influenza Virus H7N1 (HPAIV), suffering 100% mortality (Bertran et al. 2011), but outbreaks due to any HPAIV have luckily not yet been recorded. This may be due to a lack of exposure by contact with waterfowl on farms and in the field. However, it is important to notice that HPAIV-infected partridges do shed virus in their feces for 2 days before showing clinical signs (Bertran et al. 2011).

In contrast, the detection of antibodies confirms exposure of Red-legged Partridges to avian Avula virus (aAv-1, formerly Paramyxovirus- 1 aPMV-)-1, the cause of Newcastle Disease and repetitive epornitics among Columbiformes (Höfle et al. 2002). However, the absence of mortality suggests resistance and subclinical infection in Red-legged Partridges. Probably because of a direct fecal-oral transmission route and close contact between individuals, exposure is much more frequent on farms and among restocked birds, as compared to natural populations (Villanúa et al. 2008; Millán 2009).

Bacterial Infections

Significant mortality of Red-legged Partridges due to *Clostridium perfringens* can occasionally occur on farms and in dense natural populations (Millán 2009; Lucientes 1998). This large anaerobic bacterial rod is acquired from contaminated water sources. The infection causes severe necrotizing enteritis and may cause local mortality events, particularly during hot summers. Red-legged Partridges may also occasionally succumb to botulism, a progressively paralytic condition caused by the neurotoxins produced by some *Clostridium botulinum* strains in the water and mud of eutrophic wetlands under extreme conditions in summer (temperature above 35 °C, decaying organic matter) (Anza et al. 2014). Isolated cases of fatal *Mycobacterium avium* infection in Red-legged Partridges from intensively managed free-living populations have been described and were thought to be related to aggregation of Red-legged Partridges and other game birds around feeders and water points (Millán et al. 2004c). Additionally, rare cases of bacterial infection should also be considered in partridge flocks, for example, encephalitic listeriosis caused by *Listeria monocytogenes* (Jeckel et al. 2015).

Parasites

Carriage of the esophageal nematode *Eucoleus contortus* and gizzard worms (*Cheilospirura gruvei*) is able to negatively affect body condition in free-living partridges (Calvete et al. 2003; Millán et al. 2004a, b). Villanúa et al. (2008) demonstrated that parasite species related to farm environments such as *Aonchoteca caudinflata*, *Eucoleus contortus*, and *Skryabinia bolivari* can be found in wild partridges from hunting areas where the release of farm-reared partridges is common practice. Prerelease anthelminthic treatments of farm-reared Red-legged Partridges reduced excretion of parasite propagules and improved body condition in the partridges but failed in significantly reducing the burden of adult parasites. Hence, reactivation of excretion after release and removal of treatment pressure could lead to increased contamination of the environment, mitigated only by the short post-release survival of restocked partridges (Villanúa et al. 2007).

In farm settings, the transmission of the protozoan *Histomonas meleagridis* by *H. gallinarum* or earthworms has led to outbreaks of histomoniasis (blackhead). This disease that causes severe typhlitis and characteristic concentric hepatic lesions can affect both juvenile and adult birds (Revilla et al. 2006). In addition to *H. meleagridis*, *Tetratrichomonas gallinarum* can induce typhlohepatitis as reported by Liebhart et al. (2014) in Great Britain.

Molin et al. (2020) described a case of Trombiculosis caused by *Neoschoengastia simonovichi* in a juvenile Red-legged Partridge. Although this parasitation is not lethal, granulomatous dermatitis associated with it causes significant pruritus and can alter the behavior of birds and condition their survival (Dietsch 2007).

Regarding blood parasites, the studies carried out to date are very scarce (Millán 2009) and are limited to the description of *Haemoproteus* parasitizing wild partridges without apparent symptoms and in low prevalence (Millán et al. 2002; Tizzani et al. 2020). In a recent limited mortality event, a coinfection with *P. relictum* and BAGV was reported (Cardona-Cabrera et al. 2021).

Fungal Infections

Very likely, *Candida* yeasts are commensals of the upper digestive tract mucosal flora of Red-legged Partridges. However, under farm settings crop, candidiasis due to *Candida spp.* is frequent and may lead to retarded growth and death from cachexia as the lesions cause the birds to drastically reduce food intake (Hermoso de Mendoza et al. 1986; Lanteri et al. 2012). The condition is frequently due to lowered defenses after prolonged antibiotic treatments, poor husbandry, vitamin deficiency, and benefits from increased hygiene and ameliorated husbandry. Poor husbandry and/or extreme ambient conditions (high humidity or lack thereof and high or very low temperatures) can also lead to *Aspergillus fumigatus* infections, especially in juvenile birds. In these cases, the invasion of the air sacs and lungs by hyphae of this facultative pathogenic fungus can cause significant mortality. This disease is rarely seen in free-living individuals, and if so as a chronic, subclinical process leading to granuloma formation in pulmonary tissue.

Human Health Aspects of Partridge Diseases

Zoonoses *(See Box 3)*

Human exposure to zoonotic pathogens carried by gamebirds is unlikely. However, accidental ingestion, handling, or consumption of contaminated meat might be the origin of sporadic cases. In general, the processing and consumption of game meat are less controlled than for meat derived from domestic species and several factors exist on the route from field to table that alters the microbiological condition of the meat and therefore its hygienic condition. As an example, the locations of the shot within the carcass or dressing of carcasses in the field are some of the multiple factors that are prone to cause contamination and proliferation of pathogens on the muscle surface (Coburn et al. 2003). The Food Standards Agency (FSA) proposed the assessment of the risks to human health derived from the handling and consumption of wild game meat (Coburn et al. 2003). However, European Community regulations were focused on controlling hazards in game meat plants rather than determining risks from handling and self-consumption of gamebirds. The training of hunters in these aspects is regarded as the alternative.

Cross-contamination from feces to carcasses can occur when shots puncture the intestinal wall or during the evisceration of birds (El-Ghareeb et al. 2009). Pathogenic bacteria like *Campylobacter*, *Salmonella*, and *E. coli* disseminate from guts to the muscle and might overgrow under favorable conditions. It is hard to know the real incidence of human disease associated with the consumption of game meat, because the great majority of the sporadic cases are not reported. In 2002, the Animal and Plant Health Agency in Great Britain (AHVLA) listed at least 18 pathogens responsible for human disease associated with small gamebirds.

Within this list, *Campylobacter* sp., pathogenic *E. coli* strains including VTEC, *E. coli* with Extended Spectrum Beta Lactams (ESBL), *Enterococcus*, *Salmonella* and *Listeria monocytogenes*, and the protozoan *Toxoplasma* (*T.*) *gondii* are considered as potential zoonotic agents likely transmitted by gamebirds (Martínez-Carrasco et al. 2005; Silva et al. 2011; Jeckel et al. 2015). Although there are no outbreaks or cases reported linking these pathogens and gamebird meat consumption, all of them have been eventually isolated from bird carcasses or do frequently cause infection in humans through other food sources (El-Ghareeb et al. 2009; Dubey 2010; Horigan et al. 2014). *Toxoplasma gondii* and *Campylobacte*r spp. were identified as the pathogens with a higher risk of infection for humans, in both eviscerated and uneviscerated Red-legged Partridges (Horigan et al. 2014). In human beings, doses as low as 500 colony-forming units (cfu) of pathogenic strains are enough to cause *Campylobacter* disease (Newell 2002). The risk of human infection from resistant *E. coli* strains is more likely to occur from cross-contamination in the kitchen environment rather than from the consumption of the cooked bird itself (Depoorter et al. 2012). Furthermore, recently, the AHVLA (2002) has recommended the inclusion of *Chlamydia psittacci* in the list of gamebird zoonotic pathogens. *C. psittaci* is not currently known to be infectious via ingestion. However, the human infection (called chlamydiosis) may occur via inhalation depending on the initial concentration and prevalence of infection in the birds. Therefore, plucking and evisceration may expose consumers, hunters, and abattoir workers to the bacteria.

Antibiotic Usage in Gamebirds (See Box 6)

Disease problems within farms are difficult to control, especially signs associated with helminth infestation and diarrhea outbreaks. The preventive use of antimicrobials and coccidiostatics is a common practice in game bird farms, even immediately before restocking in the wild. Occasionally, antibiotics and antiparasitic treatments are also used in the field, in intensely managed hunting estates. Since almost no controls are enforced upon restocked or hunter-harvested partridges, these practices can lead to an increase in disease transmission and the spread of resistant pathogenic bacteria to the environment (Slota et al. 2011). The Game Farmers Association in UK (GFA 2013) estimated that 80% of the hunted gamebirds have probably been exposed to antibiotics directly or via their parents.

In Sweden, interviewed farmers reported that at least 25% of pheasants and Grey Partridges (*Perdix perdix*) are treated with antibiotics. Tetracycline, a wide-spectrum antibiotic and one of the most popular antimicrobials used in gamebird farms, has a high risk to elicit resistance among bacteria (Wiberg and Gunnarssson 2009). Few data report the antimicrobial-resistant bacteria incidence in farmed Red-legged Partridges. A study screening antimicrobial resistance against *E. coli* strains in farmed and restocked Red-legged Partridges revealed significant resistance profiles against enrofloxacin and gentamicin in both groups (Díaz-Sánchez et al. 2012b). And recent studies have reported vancomycin-resistant enterococci isolates from wild Red-legged Partridge (Silva et al. 2017; Lozano et al. 2016).

Gamebird roaring may be a challenge and a risk factor for spreading multi-resistant bacteria into the food chain and the environment. In intensively managed areas where massive numbers of partridges are released, or where densities are kept above the natural carrying capacity, feeders and water points might account as important spreaders of pathogenic and resistant strains. Moreover, food and water are often supplemented with medication to boost the fitness of the released partridges, leading to residual and antimicrobial resistance dissemination into the wild (Höfle et al. 2004a). Wild birds have only occasional contact with antimicrobial agents but bird aggregation areas shared by wild and restocked partridges increase the chances of resistant bacteria transmission (Díaz-Sánchez et al. 2011, 2012b).

The acquisition of pathogenic bacteria carrying resistance genes by wild birds can cause these to act later as reservoirs for resistant bacteria and genetic determinants of antimicrobial resistance (Guenther et al. 2011). The Red-legged Partridge is a key prey species in Mediterranean ecosystems and could, thus, be a significant source of antimicrobial-resistant bacteria for numerous avian predators (see Chap. “Is Predation the Key Factor of Partridge Ecology and Management?”) including the endangered Spanish Imperial Eagle (*Aquila adalberti*). The joint use of feeders and watering points provided for farm-bred released partridges can also lead to transmission of antimicrobial resistance or bacteria such as avian pathogenic *E.coli* (APEC) from farm-bred birds to sympatric wild birds (Camacho et al. 2019).

Health Monitoring and Disease Control

As shown in Fig. 2, diseases are proportionally more relevant in farms, do also have an impact on managed populations, and are generally less evident in natural populations. In compensation, intervention is easier to implement on farms, or at least in managed populations (e.g., via feed), than in wild ones.

Monitoring

In a disease control context, wildlife monitoring has three components: (1) population monitoring including regular surveying to identify trends in host abundance, and tracking of wellness physiological indicators (i.e., indices of body condition; antipredator behavioral patterns, reproductive success, etc.); (2) scanning or passive disease detection (i.e., detecting sporadic disease); and (3) active or targeted disease surveillance (i.e., searching for trends in pathogen prevalence). Ideally, each component of an integrated wildlife monitoring scheme (population, scanning, and targeted monitoring) feeds the others. Provided good population data are available, scanning surveillance yields early detection of emerging disease events or syndromes, while targeted surveillance produces appropriate numerator data to assess prevalence trends. Monitoring is needed to enable the wildlife manager to assess the effect of diseases and of any intervention to control them. However, monitoring efforts need to be adapted to the specific environment, from farms to natural populations.

Farms

In farms, population monitoring is granted, while sporadic mortality events or individual sick birds should be immediately diagnosed. Based on the findings of this scanning surveillance, and on regular microbiological and parasitological analyses, a proper surveillance scheme and disease control program should be set up, improving it through time as new insight is gained. Continuous monitoring of flock health can help to prevent disease emergence and reduce the need for treatment.

Farm rearing and releasing farm-bred Red-legged Partridges is widespread (e.g., Chaps. “Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization” and “Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing”). Hence, the first and most important area for action against disease emergence and spread is in the farm settings. Healthy farmed partridges will perform better in terms of fitness and on-farm and after-release survival and will represent a lower risk of introducing and spreading pathogens into the release sites (Villanúa et al. 2008; Díaz-Sánchez et al. 2012a). The two major fields of action are (1) implementing strict biosecurity measures and (2) setting up husbandry and feeding options to reduce the use of antibiotics and antiparasitic.

Biosecurity Typical gamebird farms hardly accomplish the appropriate biosecurity measures required, which, for example, jeopardize the control of enteropathogens within the farm (Díaz-Sánchez et al. 2012a). Work to implement better biosecurity strategies might be undertaken to minimize the risk of pathogen dissemination. Resources spent on preventive treatments could potentially be reduced by enforcing biosecurity measures on the farm to reduce the chances of partridges becoming infected with different pathogens. The implementation of proper rodent and insect control programs is crucial, as they are significant vectors of many of the pathogens affecting these birds (Lyngstad et al. 2008). Bates et al. (2004) reported isolating *Campylobacter* from beetles and flies on poultry farms. Reducing direct and indirect (via feeders) contact with other wild birds providing complete isolation of the aviaries is another effective method (Huneau-Salaun et al. 2007). Improved hygiene can effectively reduce the risk of horizontal transmission within the farm. Similarly important are security measures such as restrictions on the number of personnel and fomites and their contact with the birds. Strict surveillance of the sanitary conditions should be a priority to reduce the need for medical treatments during production cycles on farms and before restocking.

Reducing Antimicrobials The traditional approach in aviculture used to be the preventive use of antimicrobials. In the last decade, European legislation has banned the use of antimicrobials both as growth promoters and as a preventive treatment in poultry (EC regulation No. 1831/2003) (see: http://eur-lex.europa.eu/LexUriServ.do?uri=OJ:2003: 268:0029:0043:EN:PDF.). However, antimicrobials are still used for such purposes in many partridge farms, even immediately before the release into the wild (Díaz-Sánchez et al. 2012b). Law enforcement is weak in gamebird farming, and more actions need to be accomplished in terms of improving gamebirds welfare and survival. The progressive barriers to the use of antibiotics in livestock have driven the search for alternatives in livestock production. In poultry, probiotics (see Box 4) have been commonly used (Díaz-Sánchez et al. 2015) because of the desired indirect effect on the increase of weight gain and chicken performance. But at the same time, probiotics have been demonstrated to exert a protective effect against different pathogenic bacteria. Probiotics use has different strategies to reduce pathogen load within the host. Beneficial bacteria, including *Lactobacillus*, thrive in an acidic pH environment and are in an advantageous position compared to acid-sensitive pathogens (Ganguly 2013). Some probiotic strains favor the synthesis of antimicrobial substances and inhibit colonization of zoonotic bacteria by occupying niches or competing for nutrients with other bacteria. Most importantly, probiotic bacteria defend the host from infection including zoonotic bacteria such as *Salmonella* and *Campylobacter* Another approach consists of using natural compounds including herbs, spices, and plant extracts (phytobiotics). Compared with synthetic antibiotics or inorganic chemicals, plant-derived products are natural, relatively less toxic than antibiotics, and typically residue-free: these features make them ideal candidates to be used in partridge farms. Recently, the food industry and animal producers have shown increased interest in the use of essential oils, not only for their anti-oxidative and anti-inflammatory properties, but also for their antimicrobial, coccidiostats, anthelmintic, and antiviral effects (Díaz-Sánchez et al. 2015). For example, Cross et al. (2007) observed a decrease of the caecal coliform population in birds treated with thyme oil after a colisepticemia infection, suggesting a protective effect after its administration. Nevertheless, the susceptibility of each bacteria species is different and also species-dependent.

Current research on alternative antimicrobials for reared gamebirds has been more focused on their performance and productivity improvement capacities than on the antimicrobial effect of these products. For example, the probiotic mix PrimaLac (*Lactobacillus acidophilus, L. casei, Bifidobacterium thermophilum,* and *Enterococcus faecium*) was administrated in reared Chukar Partridge chicks until the following breeding season showing an increase in egg weight and albumen weight (Hashemipou et al. 2011). Biovet, a commercial product that combines the probiotic bacteria *Lactobacillus sporogenes* and *Saccharomyces boulradii* with prebiotic dextran oligosaccharides, seems to exert a beneficial effect on egg quality, fertility, and hatchability in Japanese quail (Swain et al. 2014). Other so-called nutrigenomics products such as Actigen and Bio-Mos have been tested in laying quail with positive effects on production performance (Maldarasanu 2013). More studies are needed in gamebirds to better design alternative antimicrobial strategies. The study and testing of alternative preventive and therapeutic strategies to achieve a Red-legged Partridge of “quality” could be of great interest for the gamebird production sector.

Managed Populations

In most estates with partridge releases and many of those with high-density natural populations, a higher or lower intensive management through feeding and watering, and often through generalist predator control, is common (Díaz-Fernández et al. 2013). With view to disease emergence and impact, the most important risk factors of managed partridge populations are host density and the aggregation of individuals at feeders and water sources (Gortázar et al. 2006).

Monitoring activities needs to combine surveys (including game-bag records) with scanning surveillance for mortality and active surveillance targeting the most relevant pathogens suspected for the geographical region. Active surveillance can be based on noninvasive fecal samples during the breeding season and on hunter-harvested partridges during the hunting season.

Simple and effective strategies for disease prevention and reduction of pathogen spread are the hygienic management of artificial feeding and water provision. This includes regular cleaning using bleach or similar disinfectants, providing food and/or water off-ground, and, where possible, regular changes of the feeding or watering sites to reduce contact of the birds with the contaminated ground.

Regular controls of the surroundings of feeders and water ponds for dead, weak, or sick birds will help to detect any process early, as birds in worse condition will move closer to food and water artificially supplemented but might also be easier prey.

Natural Populations

As in managed populations, monitoring activities in natural partridge populations should ideally combine surveys (at least game-bag records) with scanning surveillance for mortality and active surveillance targeting the most relevant pathogens. Where natural populations exist (i.e., those not maintained through releases and not supplementary provided with food and water), prevention should mainly focus on avoiding releases and thus limiting the likelihood of introducing new pathogens. Not only in areas with natural populations but the whole partridge range the maintenance of appropriate habitat conditions (mosaic landscape, untreated banks of roads and fields, etc.) providing the necessary variety and quantity of food also help in reducing exposure to certain pathogens (Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"). Lack of appropriate food can lead to exploitation of alternative resources such as food laid out for other species and to the interspecies transmission of new or virulent pathogens. As an example, a Red-legged Partridge acquired a fatal *Trichomonas gallinae* infection from seeds that had been laid out to bait European Turtle Doves (*Streptopelia turtur*) (Stockdale et al. 2015).

Box 1 Basic Epidemiological Terms

Pathogen: The causal agent of an infection. Most avian pathogens are viruses (depending on the host cells for reproduction), bacteria (procariotic organisms), or parasites (uni- or pluricellular eucariotic organisms). Pathogens may

(continued)

Box 1 (continued)

cause visible disease with or without mortality, or may cause subclinical infection, without obvious signs of disease. Most avian disease agents are multihost pathogens, also called shared pathogens (responsible for shared infections). These are able to infect several wild or domestic host species, eventually including humans.

Disease: If an infection produces clinical signs (such as fever, diarrhea, or weakness), it is causing disease. However, disease is any alteration interfering or modifying normal functions, including the response to environmental factors such as nutrition, toxics or climate, infectious agents, inherited or acquired malformations, as well as their combinations.

Host: The organism where a pathogen spends at least part of its life-cycle. Definitive hosts or end hosts are those where the parasite produces reproductive forms, which are often shed with the feces. Intermediate hosts carry immature stages of the parasite.

Parasite life-cycles: Monoxenous parasites are parasitic organisms that only need one host to complete their life cycle. Monoxenous parasites such as coccidia are transmitted directly generally via contaminated soil or feed and are common in farm settings. Heteroxenous parasites need more than one host to complete their life cycle. Intermediate hosts of avian heteroxenous parasites are generally invertebrates that are absent from farms; thus, these parasites are generally only found in free-living partridges.

Prevalence: The proportion of infected hosts. Antibody prevalence is the proportion of hosts in contact with a pathogen that have mounted an immune response, including infected and recovered hosts.

Mortality: Death rate in a host population caused by a given pathogen or a given lethal disease. Most infections are sublethal, causing difficult-to-assess reductions in host fitness including body condition and reproductive success.

Box 2 Enterobacteria Causing Disease in Farms

Enterobacterial infections: Disorders of the digestive tract and other organ systems produced by a group of bacteria within the Family *Enterobacteriaceae*. Within this taxa avian pathogenic *E. coli* (avian colibacillosis) and *Salmonella* sp (avian salmonellosis) are major causes of disease in captive birds.

Avian salmonellosis: Salmonella infection in birds can occur in either acute or chronic form by one or more members of genus *Salmonella* with a variety of clinical signs, from systemic to typically enteric disease.

(continued)

Box 2 (continued)

Avian colibacillosis: Avian pathogenic *E. coli* is one of the principal causes of disease and mortality in poultry including gamebirds. Disease signs include yolk infection, enteritis, poliserositis, salpingitis, pericarditis, and even acute septicemia. Some infections can be asymptomatic. Typical coligranulomata can be observed in different organs including liver and duodenum.

Box 3 Zoonosis

Zoonosis: EFSA (European Food Safety Authority) defines a zoonosis as any infection or disease that can be transmitted directly or indirectly between animals and humans, for instance, by consuming contaminated foodstuffs o through contact with infected animals.

Campylobacteriosis: It is the most important food-borne illness in humans worldwide. Usual symptoms are fever, diarrhea, and abdominal cramps. Main sources of infection are associated with consumption of undercooked poultry, or contaminated ready-to-eat foods.

Salmonellosis (nontyphoidal): Is the second cause of food-borne zoonosis worldwide. *Salmonella enteritidis* and *Salmonella typhimurium* are the most reported serotypes transmitted from animals to humans. Typical symptoms include fever, diarrhea, and abdominal cramps. Generally acquired through food consumption including eggs and raw meat, dairy and vegetables.

Colibacillosis: It is a food-borne zoonosis associated with *E. coli* strains that are capable to produce toxins, such as STEC/VTEC (shiga toxin or verotoxin-producing *E. coli*) or EHEC (enterohaemorrhagic *E. coli*) and have the potential to cause bloody diarrhea and Hemolytic Uremic Syndrome (HUS). Most of the outbreaks have been associated with the consumption of retailed meat products, sewage contamination, and other environmental sources.

Chlamidiosis: The main agent of disease, *Chlamydia psittaci*, is commonly associated with avian chlamydiosis. However, infected birds might serve as a source of infection for humans. Inhalation or contact with contaminated dust, bird feces, and secretions can cause pneumonia in humans.

Toxoplasmosis: It is the most common parasitic zoonosis in human beings. The causative agent, *Toxoplasma gondii*, is a ubiquitous protozoan with felids as definitive hosts. Ingestion of tissue cysts or tachyzoites present in meat, viscera, or meat-derived products are the main routes of human transmission.

Box 4 Probiotics and Prebiotics

Phytobiotic: It comprises of a wide range of substances with respect to biological origin, formulation, chemical description, and purity; they can be classified into four groups (1) herbs (products from flowering, nonwoody, and nonpersistent plants); (2) botanicals (entire or processed parts of a plant, e.g., roots, leaves, bark); (3) essential oils (EOs) (hydro-distilled extracts of volatile plant compounds); and (4) oleoresins (extracts based on nonaqueous solvents).

Probiotic: It is a "live microorganism" that when administered in adequate amount to the host provides a health benefit.

Prebiotic: It is a selectively fermented ingredient that results in specific changes in the composition and/or activity of the gastrointestinal microbiota, providing benefits for host health.

Box 5 Selected Viral Infections

Flaviviruses: Most viruses of this family originate from Africa. They are generally vector transmitted and several of the viruses belonging to this family have a worldwide distribution. The Flaviviruses detected to date in gamebirds are mosquito transmitted. West Nile Virus (WNV) and Usutu Virus (USUV) have zoonotic potential. In periods of high viral replication and mosquito activity, they can affect equine and human hosts causing unapparent to severe disease including potentially fatal encephalitis.

Avian influenza: Avian influenza viruses (AIV) are influenza A viruses that are maintained in the waterfowl reservoir. According to pathogenicity in the chicken, AIV are classified into Low Pathogenic AIV (LPAIV) and High Pathogenic AIV (HPAIV). Some of the latter, in addition to being highly pathogenic for chicken and waterfowl, have zoonotic and pandemic potential, such as H5N1 HPAIV strains.

Newcastle Disease Virus: This Paramyxovirus 1 subtype was named after the city of its first occurrence in poultry for which it can be highly pathogenic. In poultry, vaccination is compulsory worldwide, but strains highly pathogenic for pigeons exist in columbiforms across Europe and cause seasonal mortality events in Eurasian Collared-doves (*Streptopelia decaocto*) or rock pigeons (*Columba livia*).

Box 6 Antibiotic Resistance Terms

Antibiotic: Strictly defined as chemical substances produced naturally by different microorganisms with the ability to kill or inhibit growth of microbes.

Antimicrobial: Include natural, synthetic, and semisynthetic substances that kill or inhibit growth of all types of micro-organisms including bacteria (antibacterial), viruses (antiviral), fungi (antifungal), and protozoa (antiprotozoal). "All antibiotics are antimicrobials but not all antimicrobials are antibiotics."

Antibiotic Growth Promoters (AGPs): Traditionally known as the antibiotics used in production to improve the health and well-being of animals due to their prophylactic effects against bacterial infections, improved growth rate, and feed conversion efficiency.

Antibiotic resistance: This phenomenon occurs when bacteria do not respond to treatment with traditional antibiotic drugs. Microbes can acquire antimicrobial resistant features as a result of natural genetic changes. However, micro-organisms can accelerate the development of their antibiotic resistance due to exposure to low nonlethal doses of antimicrobials from the overuse and misuse of synthetic antibiotics in animal production and human medicine.

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Red-Legged Partridge Monitoring and Population Trends

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_10

Current Monitoring Used in European Countries

The main parameters assessed to monitor and manage Red-legged Partridges are abundance/density, reproduction/productivity and hunting records.

France

The monitoring of the Red-legged Partridge is mainly conducted by the French Office for Biodiversity (OFB, former National Hunting and Wildlife Agency – ONCFS). Additionally, a national survey is organized annually by the French National Museum of Natural History through the French Breeding Bird Survey program (hereafter FBBS).

(a) *OFB programmes*

An absolute method to estimate Red-legged Partridges density is the mapping method (Blondel 1969; Pépin 1983). However, with the creation of a network of sites (i.e. game management units, communal, or private property) for Red-legged Partridges in 1979 (from 5 in 1979 to ca. 250 sites in 2016, Fig. 1), it has been necessary to have a less costly method for the network monitoring (Farthouat 1983). Several methods were investigated during the eighties (Farthouat 1983; Pépin 1983; Ricci 1989; Bibby et al. 1992), such as blank beat (where a line of beaters spaced 25 m apart walks the sampled unit, and both beaters and observers outside the sampled unit count fleeing birds), pointing dog count (where a hunter uses their dog to detect birds in the sampled area), kilometric abundance index (KAI—sampling of

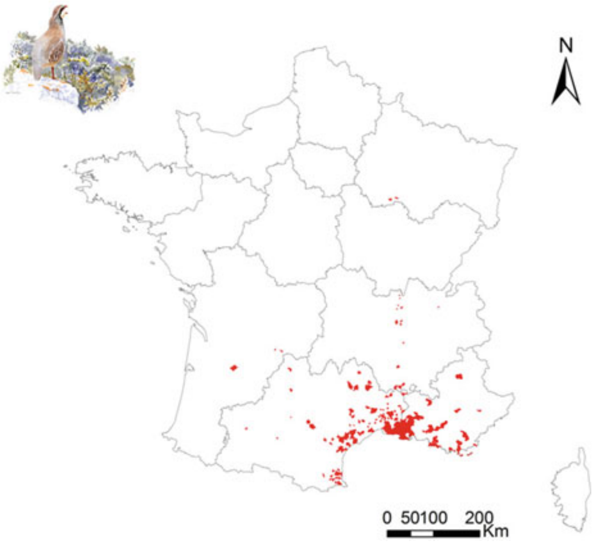

Fig. 1 Map of sites included in the French Red-legged Partridge network. Source of the data: ONCFS. Reproduced with permission

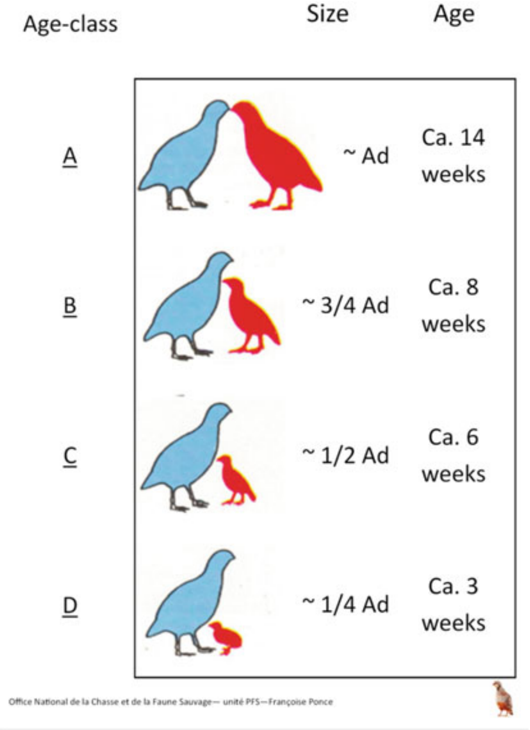

Fig. 2 Age-classes of young Red-legged Partridges ascertained by the relative size of young to adult individuals (red and blue, respectively): (*i*) class A refers to young being the same size as adults (age is ~14 weeks); (*ii*) class B, ¾ of adult size (~8 weeks); (*iii*) class C, ½ of adult size (~6 weeks); and (iv) class D, ¼ of adult size (~3 weeks). Adapted from the French Red-legged Partridge network—OFB/ONCFS available at https://profesionnels.ofb.fr/fr/reseau-perdrix-rouge

a spatial unit from track/routes by car circulating at low speed or by horse), and call-back counts (use of playback calls to detect territorial male birds responding to them during the breeding season). Finally, since the early nineties the call-back census has been implemented on both historical sites and new sites of the Red-legged Partridge network to obtain density estimates, as it is the only method assuming imperfect detection during field work (Jakob et al. 2014). The survey design is based on 1–3 established tracks with five to ten points per track. Each point is chosen as close as possible to the intersection of an 800-m grid superimposed on an aerial photo (500-m grid has to be used as *a minima*). Each track is surveyed three times each spring (late February—late April) by a given observer during the 2 h around sunrise. Given a 1:1 sex-ratio, density of breeding pairs is thus obtained. For areas outside the network or wooded countrysides, KAIs and adapted line transects are used with associated conversion to obtain density estimates (D = car count × 7 for KAIs and $D = 1.45 \times$ index for wooded countrysides, Ricci 1989; Brun et al. 1990; Brun and Aubineau 1995).

Productivity is assessed from group counts obtained in summer, from mid-July to mid-August. Along tracks (3 km long for a 100 ha cell), numbers of young and their respective age-classes (Fig. 2) and adults in each group are recorded. Surveys are done in a 3-h period either from dawn or before dusk and repeated up to six times. The derived age-ratio is then used as a proxy for productivity. Analyses are currently in progress to investigate potential causes of bias when estimating and using age-ratio in Southern France.

In addition, an abundance index is obtained at the national scale within the ACT survey (ONCFS-FDC-FNC network, Roux et al. 2017) and the French Bird Birding Survey, since 2008 and 1989 respectively (Boutin et al. 2003; Eraud et al. 2007; Roux et al. 2017; Jiguet 2016). For the ACT survey, the country is divided into 1065 grids in which 5 points are surveyed twice. Abundance indices are derived from a log-linear Poisson distribution model (ter Braak et al. 1994; van Strien et al. 2004).

Finally, national hunting inquiries have been carried out every 10 years since 1979 (Reitz 2003; Ponce-Boutin et al. 2012). For each municipality, class of abundance and information about hunting (existence of a management plan, quotas, releases, etc.) are requested.

(b) *French breeding bird survey (FBBS)*

The FBBS is the French contribution to the Pan-European Common Bird Monitoring Schemes (PECBMS). The design was proposed by the European Bird Census Council (EBCC). Squares (2 × 2 km) are randomly selected from a national grid (comprising 136,501 possible squares). Each square is monitored twice in the spring, once before and once after the 8th of May. Each observer realizes 10 point-counts within a given square and counts every detected species on each point during 5 min exactly, beginning the survey at dawn and continuing until the 10 counts are done (Jiguet and Julliard 2006).

Italy

For scientific research on Red-legged Partridge different census methods have been used and these have changed over time. The first estimates of the Red-legged Partridge populations were obtained in late seventies and in mid-eighties by inquiries addressed to the hunters and to the owners of private hunting estates (Spanò and Meriggi 1980; Spanò et al. 1986; Meriggi 1992). Afterwards, ecological research was carried out in protected areas to study demography and population dynamics. For these aims partridge density estimates were obtained by the mapping method of breeding pairs in spring and broods in summer (Meriggi and Zacchetti 1989; Meriggi 1992; Meriggi et al. 1992). In more recent times the mapping method was combined with the use of playback to increase pair detectability (Gibbons and Gregory 2006), in studies carried out to assess the success of some reintroductions (Meriggi and Mazzoni della Stella 2004; Meriggi et al. 2007). Currently the main methods used to assess population dynamics and habitat requirements are point transect counts of calling males with playback and car counts of broods (Jakob et al. 2010; Tizzani et al. 2012; Chiatante et al. 2013; Meriggi et al. 2013; Jakob et al. 2014; Mascarino 2015; Veronese 2015). With the mapping method, pair density is estimated by Distance Sampling, whereas with the latter parameters such as breeding success, brood size, chick survival, and age ratio are also calculated.

For hunting management, monitoring of Red-legged Partridge has been mandatory since 1992 (Italian Law #157/92 on wildlife conservation and exercise of hunting). Land has been divided into regions, themselves divided into provinces and finally subdivided into hunting districts (hereafter *HDs*). The HDs, basic spatial units created by law, are responsible for the monitoring activities aimed for harvesting planning under the supervision of the Wildlife Services of the Provinces. The recommended methods for Red-legged Partridge monitoring are spring counts of breeding pairs in March–April and summer counts of broods in August. However, no fixed and standardized survey design is used and it can change markedly among Regions, Provinces, and HDs. For example, neither a minimum number of points per unit area, nor the minimum length of the transects, nor the minimum percentage of land to explore in the case of the counts with pointing dogs (dogs are assumed to locate each bird in the studied area, Bibby et al. 1992) are established. Moreover, several HDs make no counts despite the obligations by law. Finally, surveys are often carried out only in the denser partridge areas, which may lead to biased estimates.

Portugal

Red-legged Partridges in Portugal have been monitored occasionally during the nineties for the purpose of specific studies (Borralho et al. 1996, 1997, 1998, 1999, 2000b; Carvalho et al. 1998; Reino et al. 2016). Borralho et al. (1996) investigated the performance of driven transects and mapping counts, the latter being recognized as an absolute method allowing precise estimate of abundance and density. Subsequent studies thus used either driven transect or mapping methods.

Additionally, the Portuguese Society for the Study of Birds (SPEA) launched the Common Bird Census in continental Portugal and Madeira in 2004 and in the Azores in 2007. Each volunteer conducts counts at a minimum of 20 census points located within a 10 × 10 km UTM grid twice a year (in April and May). 5 min are spent at each of the sequential 20 spots and this should be done in a single day during the 4 h after dawn (should be finished by 11 am in the first visit and 10:30 am in the second visit). The census is carried out each year in the same established sequence of points, recording any changes in the habitats.

There is also another census conducted mainly at the estate level, although a formal report compiling all of the information is still lacking.

Spain

In Spain, monitoring of Red-legged Partridge abundance is conducted at two different levels: by the Spanish Society of Ornithology at the national level and by

Spanish Regional governments at the regional level. Additionally, hunting statistics are collected by Regional Government and compiled at the National Statistics Institute (INE).

(a) *Spanish Society of Ornithology (SEO-Birdlife) programmes*

SEO/Birdlife performs two different bird monitoring programmes that include information about Red-legged Partridge numbers: the Common Bird Census (SACRE), the Spanish part of the PECBMS, that aims to identify trends of breeding birds, and programmes aimed to detect bird trends in winter (SACIN). The SACRE programme began in 1996 and participation has increased particularly since 2006 (with more than 1000 volunteers currently), thus it is able to assess large-scale trends. Like for census carried out in Portugal by SPEA, each volunteer carries out 20 census points located within a 10 × 10 km UTM grid, which are visited twice per spring, the first time between 15 April and 15 May, and the second between 15 May and 15 June (earlier in the Canary Islands and later in the mountains). Five minutes are spent at each census point noting all species (including Red-legged Partridge) detected. It begins at sunrise and ends before midday. The SACIN programme began during winter 2008/2009. The sampling unit is 8 itineraries, located within a 10 × 10 km UTM grid, carried out by foot walking slowly (400–700 m in 15 min). Each quadrat is visited twice a winter: the first time between 1 November and 31 December, and the second time between 1 January and 15 February. It begins 1 h after dawn and ends before mid-day.

(b) *Governmental monitoring*

The Spanish Central Government and the Regional Governments (Autonomous Communities) share legal and legislative responsibilities regarding environment protection, but the regional responsibilities in monitoring and management are higher than those of the Spanish state itself. Many of the Autonomous Communities have implemented monitoring programs for game or protected species, but without a homogeneous structure. This is highlighted by the results of a recent email and phone consultation to governmental hunting services from the different Autonomous Communities seeking information about monitoring programmes implemented in each region to assess partridge populations.

The most detailed programme occurs in Catalonia, where the Catalan Common Bird Survey (SOCC; Seguiment d'Ocells Comuns a Catalunya), a monitoring programme lead jointly by the Catalonian Institute of Ornithology (Institut Català d'Ornitologia) and the environmental service of the Catalonian government ("Departament de Territori i Sostenibilitat de la Generalitat de Catalunya"), aims to quantify abundance and temporal trends of common birds. This programme has been conducted since 2002, and 150–300 transects (each 3 km long) are carried out by volunteers annually. Bird densities in each transect are calculated taking into account detectability and distances to observed birds (Järvinen and Väisänen 1975). This information is integrated in high-resolution distribution maps from the Catalan Breeding Bird Atlas, and is used to estimate partridge population size during the breeding season (http://www.sioc.cat/fitxa.php?sci=0&sp=ALERUF). In other Regions, environmental wardens belonging to the governmental agencies of each Autonomous Community (Navarra, Andalucía, Castilla-La Mancha and Castilla y León) or contracted personnel specialized in wildlife monitoring (La Rioja) make partridge abundance estimates annually, based on transects distributed throughout the region. These programmes started in most areas at the end of the twentieth century, sometimes more recently (e.g. 2011 in Castilla y León and Castilla la Mancha). Estimates are taken twice a year (e.g. Navarra or La Rioja), or four times a year (e.g. Andalucía). This information is compiled as KAI (Castilla y León, La Rioja, Andalucía and Navarra), or density estimates are calculated (e.g. Andalucía and Aragón) using the Kelker's method (Burnham et al. 1980) assuming that all the birds within the transect width are detected (Gortázar et al. 2002; Villanúa 2008). In some other regions, like Castilla-La Mancha, information from transects is mainly aimed at assessing breeding phenology (Arroyo and Guzmán 2016), but has also been analysed to estimate abundance and trends (Arroyo et al. 2019). Following the economic crisis after 2009, some of these programmes have been reduced or even entirely stopped (e.g. Aragón).

Regional Governments regulate the obligation of each hunting estate to carry out a Hunting Technical Plan, which also includes information about game abundance and expected bags. However, these estimates are rarely made in a consistent methodological way. According to interviews and discussion groups with managers of Red-legged Partridge hunting estates from Central Spain, managers usually assess partridge abundance in summer, but they rarely base their estimate on systematic surveys; they use personal observations or qualitative information provided by other people (i.e. game-keepers, farmers, shepherds; Caro et al. 2015). Therefore, systematic quantitative information about partridge abundance at the local level is not gathered in most cases. There are a few exceptions, where certain hunting estates have medium or long-term records of partridge abundance and bags through local monitoring.

(c) *Spanish bag records*

The National Statistics Institute (NSI) of Spain compiled information on bag records of all hunted species since 1973 to 2003 at the provincial, regional and national level. Information available includes the annual number of both hunting licenses and partridges hunted in each of the 50 provinces, including Canary and Balearic Islands (where partridges have been introduced). Since 2005, responsibility for monitoring numbers of animals hunted lies with the Ministry of Agriculture, Fishing, Food and the Environment (MAPAMA in its Spanish acronym), which compiles information provided by the Autonomous Regions. Information about one or a few regions (or provinces within each region) is missing every year, which affects the reliability of national data. In recent years, the achieved annual bags are meant to be submitted annually by hunting estates to Regional Governments, which may be used to produce provincial and regional reports. However, protocols vary among regions and there could be heterogeneous criteria to determine regional hunting bags.

United Kingdom

In United Kingdom, monitoring of Red-legged Partridges is organised separately by the British Trust for Ornithology (BTO) and the Game and Wildlife Conservation Trust (GWCT).

(a) *BTO programmes*

The BTO is responsible for both the Common Birds Census (CBC) and the Breeding Bird Survey (BBS), the latter being organized with the Royal Society for the Protection of Birds (RSPB) and the Joint Nature Conservation Committee (JNCC). The CBC and the BBS aim to monitor change in the breeding bird populations of Great Britain and United Kingdom. However, their survey methods are different. The CBC ran from 1962 to 2000 and used a territory-mapping method with 10 visits to each plot of more than 10 ha (over 100 sites from late March to early July throughout the country) (Marchant et al. 1990). The BBS started in 1994 and used a design common to the PECBMS with two visits, one before and one after mid-May, to a randomly selected 1x1-km square stratified by region (ca 4000 squares throughout GB/UK in 2019, Field and Gregory 1999; Harris et al. 2020). On each visit, birds are recorded on two parallel transects in three distance bands. Red-legged partridges are counted in 6 English regions: East of England, East Midlands, South East, South West, West Midlands and Yorkshire & Humber (Harris et al. 2020). In addition, Red-legged Partridge distribution across the UK is recorded in three atlases of breeding birds, produced following complete coverage of every 10x10-km square in Britain and Ireland (Sharrock 1976; Gibbons et al. 1993; Balmer et al. 2013).

(b) *GWCT programmes*

The GWCT organizes both the Partridge Count Scheme (PCS), a survey of productivity and abundance trends in partridges (Potts 1986; Ewald et al. 2009) and the National Gamebag Census (NGC) to monitor numbers of game species released and shot (Tapper 1992; Aebischer 2019). The PCS first ran from 1933 to 1939, resumed in 1947 and continues to the present day. It relies on counts (number of birds by sex and age) conducted on participating sites by driving along tracks in spring and by quartering stubbles in late summer after harvest. Questionnaires are sent out in February and July to collate counts occurring in March–April and August–September respectively. Collecting information on the number of birds shot each year is done through the NGC via a questionnaire sent out to shoots at the end of the hunting season.

In addition to the gamebag survey by the GWCT, the Public and Corporate Economic Consultants (PACEC) conducted two questionnaire surveys in 2004 and 2012 to estimate economic, environmental and social benefits of shooting sports in the UK, including numbers of quarry species shot and released for shooting (PACEC 2006, 2014).

Population Estimates and Trends in Europe

The Pan-European Common Bird Monitoring Scheme has recorded the result of the CBC for the Red-legged Partridge in France, Portugal and Spain from 1998 to 2015. The CBC allows the calculation of an index to evaluate trends in abundance index. Based on these data (the base index being in 1998), the long-term trend for the Red-legged Partridge at the continental scale is classified as moderate decline, i.e. significant decline, but not significantly more than 5% per year (Fig. 3). The long-term trend is −33% and the 10-year trend is −32% (EBCC http://www.ebcc.info/index.php?ID=587).

France

Information at the national scale is available with the FBBS, the ACT survey and national inquiries. Based on the data of the FBBS, the trend of the Red-legged Partridge abundance over the period 1989–2015 has been classified as stable since 1989 (−3%), moderate decline since 2001 (−14%) and moderate decline over the last 10 years (−38%) in France (Fig. 4, Jiguet 2016).

Based on data of the ACT survey over the period 2008–2017 (Fig. 5), the long-term trend is a decline of ca. 33% (−4.4% per year; Roux et al. 2017) but this result needs to be interpreted with caution owing to a relative low sample size of encounters ($n = 139$). Despite the different datasets, the general trend over the last decade is quite similar between both breeding bird surveys in France (−33% and −38%).

The national inquiry enable the number of breeding pairs for each sampled year to be derived: between 300,000 and 500,000 pairs in 1979, 300,000 in 1998 and 322,000 breeding pairs in 2008 (Reitz 2003; Ponce-Boutin et al. 2012; Olioso 2015). These numbers suggest a stable situation before the last decade.

Regarding hunting, ca. 3.2 millions of individuals are currently released each year for shooting (National Union of Game Producers, available in French at http://www.snpgc.fr/communiques_presse.php). To date, the number of harvested Red-legged Partridges is available for 3 hunting seasons. Inquiries are set up every 15 years. For the Red-legged Partridge, 1.16 millions of individuals were harvested during the hunting season 1983–1984, ca. 1.73 millions in 1998–1999 and 1.27 million in 2013–2014 (Ricci and Biadi 1986; Ponce-Boutin 2000; Aubry et al. 2016). However, no inference from these studies can be done owing to different methods used and potential bias associated with them (Aubry et al. 2016).

Despite some evidence for a decrease in trend of the Red-legged Partridge populations, the breeding pairs seem quite stable; however no recent number is available. Nonetheless, the species is still one of the most hunted species in France (in the top 5 species in estimated total number, Aubry et al. 2016). The situation is thus unclear, probably owing to restocking programmes occurring in several regions

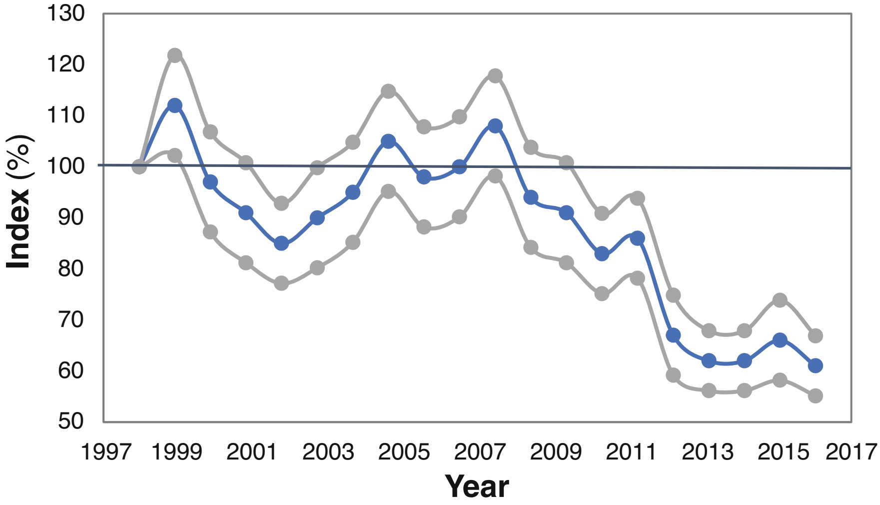

Fig. 3 Temporal change in abundance index of the red-legged partridge at the continental scale (1998–2017). Grey lines indicate lower and upper confidence intervals. Long-term slope = 0.9743 ± 0.002. 10-year slope = 0.9383 ± 0.0036. List of contributing countries: France (2001–2017), Portugal (2004–2017), Spain (1998–2017). Source of the data: https://pecbms.info/trends-of-common-birds-in-europe-2019-update/

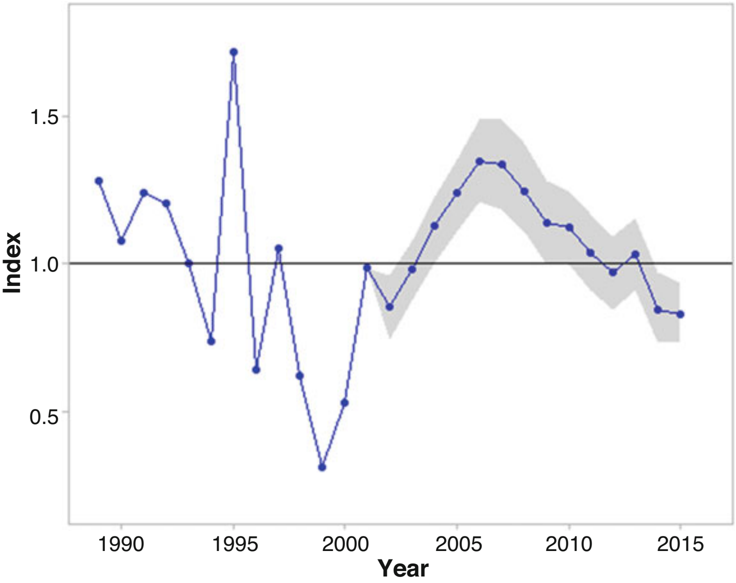

Fig. 4 Temporal evolution of abundance index of the Red-legged Partridge in France based on the French Breeding Bird Survey from 1989 to 2015 (95% confidence intervals are available for 2001–2015). Adapted from Jiguet (2016). Reproduced with permission

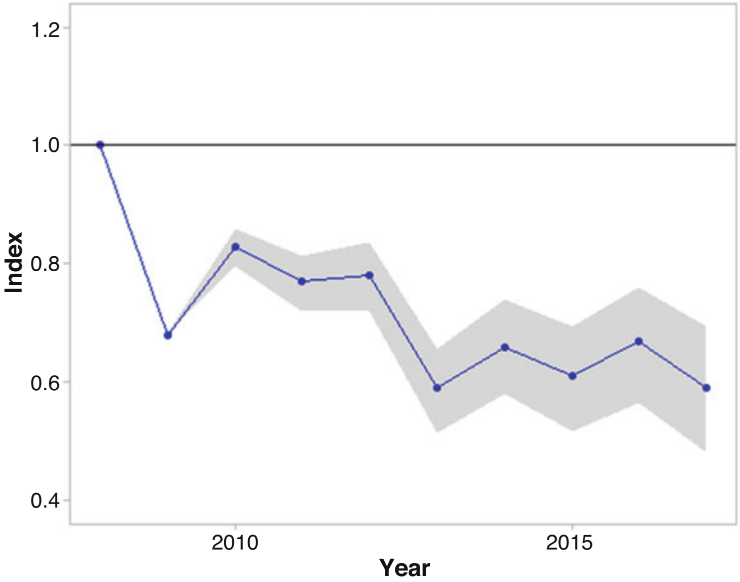

Fig. 5 Temporal evolution of abundance index (blue point) and temporal trend (blue line) of the Red-legged Partridge in France based on OFB/ONCFS-Breeding bird survey, from 2008 to 2017. Adapted from Roux et al. (2017). Source of the data: ONCFS-FNC-FDC

in France but for which neither the number of released birds, nor the effect on the wild population are known.

Italy

To our knowledge, no global index or abundance estimate is available. The Italian population may have slightly increased in recent decades and the global population may be ca. 3000–4000 individuals (Silvio Spanò, personal comment). However, local density estimates are available for different hunting districts and study areas (Tables 1, 2, and 3).

Portugal

From several studies in the nineties, estimates of density are available for some sites (Table 4). The Common Breeding Bird Survey (CAC, 2004–2014) by the SPEA in Portugal allows the estimation of the mean abundance at national and regional scale

Table 1 Population estimates and densities (SD) in some Hunting Districts (HD) in Italy

HD	Surface (ha)	Province	Region	Years	Season	Population estimate	Density (n°/km^2)
CN4	41,398	Cuneo	Piedmont	2010–2011	Summer	193 (7.1)[a]	29.7 (1.1)[a]
PC1	19,318	Piacenza	Emilia-Romagna	2008–2009	Spring		1.7 (1.05)[b]
PC1	19,318	Piacenza	Emilia-Romagna	2014–2015	Spring	107 (17.7)[b]	2.5 (0.42)[b]
PC2	21,544	Piacenza	Emilia-Romagna	2001–2009	Spring		0.7 (0.28)[b]
PC2	21,544	Piacenza	Emilia-Romagna	2014–2015	Spring	202 (7.8)[b]	0.9 (0.28)[b]
PC3	10,341	Piacenza	Emilia-Romagna	2000–2009	Spring		3.0 (1.79)[b]
PC5	3755	Piacenza	Emilia-Romagna	2000–2009	Spring		3.8 (2.15)[b]
PC6	17,614	Piacenza	Emilia-Romagna	2000–2009	Spring		2.3 (1.24)[b]
PC7	19,111	Piacenza	Emilia-Romagna	2000–2009	Spring		4.7 (2.94)[b]
PC8	20,910	Piacenza	Emilia-Romagna	2001–2007	Spring		3.0 (2.73)[b]
PC9	12,337	Piacenza	Emilia-Romagna	2001–2009	Spring		2.9 (1.16)[b]
PC11	14,027	Piacenza	Emilia-Romagna	2001–2009	Spring		1.2 (0.69)[b]
PR4	38,579	Parma	Emilia-Romagna	2003–2015	Summer	348 (97.7)[a]	
MO2	72,082	Modena	Emilia-Romagna	2014–2015	Summer	1528 (130.1)[a]	
FC 1	40,555	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	1806 (91.2)[a]	
FC 2	57,432	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	1359 (23.3)[a]	
FC 3	8630	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	240 (23.3)[a]	
FC 4	21,095	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	542 (4.9)[a]	
FC 5	17,527	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	455 (40.3)[a]	
FC 6	8241	Forlì-Cesena	Emilia-Romagna	2014–2015	Summer	375 (23.3)[a]	

[a] Individuals

[b] Pairs

Table 2 Pair density estimates (pairs per km^2) in some studies carried out in Italy

	Pair density					
Years	Min.	Max.	Province	Region	Habitat	Source
1981–1986	2.4	16.2	Pavia[a]	Lombardy	Hills	Meriggi et al. (1992)
1983–1984	1.9	2.0	Modena	Emilia-Romagna	Hills	Ferri (1985)
1994–1995	6.0	25.0	Livorno[b]	Tuscany	Hills	Gariboldi (2006)
1996–1999	3.5	3.7	Siena[a]	Tuscany	Hills	Meriggi and Mazzoni della Stella (2004)
1996–2002	3.2	8.5	Siena[a]	Tuscany	Hills	Meriggi et al. (2007)
2000	0.3	1.2	Pavia[a]	Lombardy	Hills	Meriggi et al. (2000)
2010–2011	1.5	3.8	Alessandria	Piedmont	Hills	Tizzani et al. (2012)
2010–2011	1.6	2.6	Alessandria	Piedmont	Lowland	Tizzani et al. (2012)
2011	0.6	5.3	Livorno[b]	Tuscany	Hills	Chiatante et al. (2013)
2012	1.0	7.7	Piacenza[a]	Emilia-Romagna	Lowland	Meriggi et al. (2013)
2015	2.1	3.2	Piacenza[a]	Emilia-Romagna	Lowland	Veronese (2015)
2015	–	3.6	Alessandria[a]	Piedmont	Hills	Mascarino (2015)

[a] Protected areas
[b] Elba Island

Table 3 Post-breeding density estimates (individuals per km^2) in some studies carried out in Italy

	Density			Region		
Years	Min.	Max.	Province		Habitat	Source
1980	–	10.6	Alessandria	Piedmont	Hills	Spanò and Meriggi (1980)
1980	–	6.9	Imperia, Savona, Genova, Spezia	Liguria	Hills	Spanò and Meriggi (1980)
1978–1983	1.3	2.7	Pavia	Lombardy	Hills	Meriggi et al. (1992)
1981–1986	8.0	70.8	Pavia[a]	Lombardy	Hills	Meriggi et al. (1992)
1986	–	3.3	Alessandria	Piedmont	Hills	Spanò et al. (1986)
1986	–	6.6	Imperia, Savona, Genova, Spezia	Liguria	Hills	Spanò et al. (1986)
1994–1995	19	186	Livorno[b]	Tuscany	Hills	Gariboldi (2006)
1996–1999	8.2	22.5	Siena[a]	Tuscany	Hills	Meriggi and Mazzoni della Stella (2004)
1996–2002	4.1	24.0	Siena[a]	Tuscany	Hills	Meriggi et al. (2007)

[a] Protected areas
[b] Elba Island

Table 4 Density estimates (± SE if available) of Red-legged Partridges from different study sites

Area	Region	Year	Density (n°/km^2)	Source
Archino	Central	1995—Summer	16.1 ± 2.7^a	Carvalho et al. (1998), Borralho et al. (2000a)
		1996—Spring	16.6^a	
		1996—Summer	53.9^a	
		1997—Spring	29.6^a	
		1997—Summer	50.1^a	
		1998—Spring	17.0^a	
		1998—Summer	11.1^a	
Casebres	Southern	1995—Summer	2.6 ± 0.6^a	Carvalho et al. (1998), Borralho et al. (2000a)
		1996—Spring	10.2^a	
		1996—Summer	25.8^a	
		1997—Spring	9.5^a	
		1997—Summer	21.8^a	
		1998—Spring	9.2^a	
		1998—Summer	19.2^a	
Alentejo	Central	1992	3.7 ± 0.8^b	Borralho et al. (1999)
		1993	6.9 ± 1.4^b	
		1994	8.2 ± 1.4^b	

[a] Number of individuals
[b] Number of pairs

(Fig. 6). The trend seems to indicate a decline in the last years, likely linked to a decline in Southern Portugal.

Spain

Information from trends in bag records suggests that there was a large decline (>60%) in numbers of partridges hunted between 1973 and 1994 (Blanco-Aguiar 2007) (Fig. 7). Bag records at the provincial level were correlated with abundance as

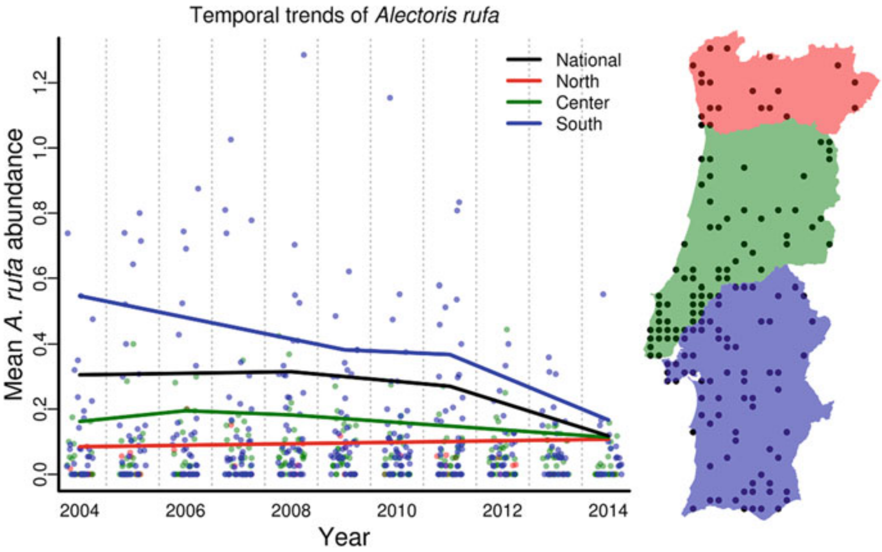

Fig. 6 Variation in mean *Alectoris rufa* abundance per 10 × 10 km UTM square and year, from 2004 to 2014 (left); and location of the sampled UTM squares (right). Each UTM square was sampled, with few exceptions, twice per year (although not all squares were sampled in all years). Dots represent the maximum of the two samples. For each sample, the mean abundance was calculated by averaging the number of counts in the sample, conducted in 20 points per UTM square. Curves were fitted with Additive Quantile Regression for the 95th percentile using a smoothing parameter lambda = 3 (see Koenker 2016 for details), hence represent the expected variation in the 95th percentile of each year's mean abundances. Dots are coloured according to the sector of the country where the center of the UTM square is located (right), and were jittered along the X axis for the sake of clarity. Sectors: North—north of river Douro; Center—between river Douro and river Tagus; South—south of river Tagus. (Reino & Porto, unpublished result). DATA Source: SPEA (Sociedade Portuguesa para o Estudo das Aves)

estimated in the Spanish Atlas of Breeding Birds, carried out in the late 1990s (Blanco-Aguiar 2007). Therefore, the decline in numbers hunted at the end of last century probably reflects a trend in abundance occurred at that time. Subsequently, bag records indicate that captures increased, although not to the levels of the 1970s (Fig. 7). However, at that time releases of farm-reared birds became increasingly frequent, currently reaching numbers similar to overall national bags (Blanco-Aguiar et al. 2008; Caro et al. 2014). Since it is unfeasible to identify whether shot birds are wild or released, bag records are currently useless to monitor trends in wild partridge abundance (Blanco-Aguiar et al. 2012).

On the other hand, both sets of bird census data from SEO/Birdlife Programmes indicate continuing decline of Red-legged Partridges after the mid-1990s (Fig. 8). Population decline assessed in spring was estimated to be around 30% between 1998 and 2018 (Fig. 8), being particularly marked in the Southern Mediterranean region of Spain (SEO/Birdlife 2013a, b), which is the one with higher overall densities. The decline is estimated to be −38% during the period 1998–2019 (Arroyo and Mougeot 2022). This decline have also been documented in winter in the last 10 years

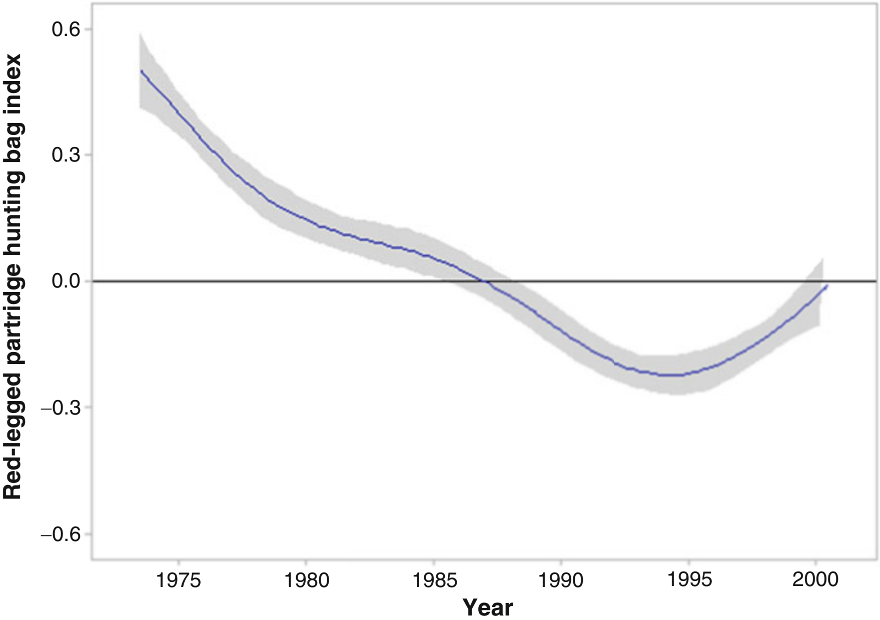

Fig. 7 Temporal trends of Red-legged Partridge harvesting index (hunted partridges per hunting license) obtained using provincial values from TRIM analysis; dotted lines show 95% confidence bands (modified from Blanco-Aguiar 2007)

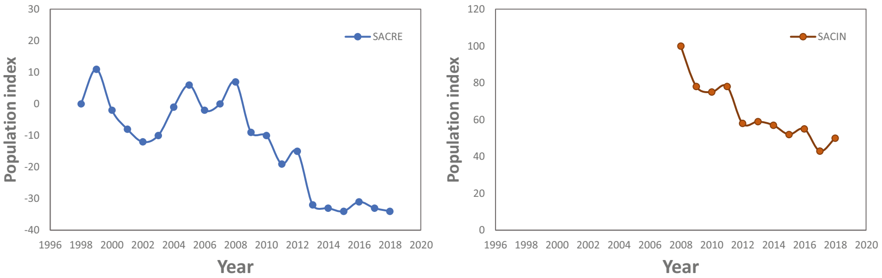

Fig. 8 Population change of the Red-legged Partridge in Spain based on the SACRE (spring monitoring) and SACIN (winter monitoring) Bird Surveys. SACRE data considers 0 the reference value (estimate for 1998) whereas SACIN considers 100 the reference value (2008). Modified from data available at: SEO/Birdlife (2020). https://www.seguimientodeaves.org/ESPECIOS/docs/ESPECIES/1730_RES_SP.pdf and Arroyo and Mougeot (2022)

(SEO/Birdlife 2020). These bird monitoring programmes have received some criticism, mainly when used to estimate national population size, although they have been found to be a reliable index of national population trends (Carrascal 2011; Murgui 2011). However, the spatial distribution of sampled 10 x 10 km UTM quadrats is too sparse in some regions, it is not randomly established and it could be skewed in some strata, so trends estimated at smaller scales from these data could be biased (Carrascal 2011).

The general decline is however confirmed by at least some of the regional monitoring programmes. For example, a continued decline (of ca. 25–30%) has been observed in Catalonia between 2001 and 2018 (Arroyo and Nadal 2021). In Navarra, continuing declines have also been observed in the regional monitoring programmes in the last two decades. A 50% decline has been quantified in Castilla-la Mancha between 2010 and 2017, occurring mostly in 2012–2014 (Cabodevilla et al. 2021).

United Kingdom

The CBC indicates a 20-year decline in abundance from 1978 onwards while the BBS indicates a significant positive change (+16%) in the trend of Red-legged Partridge abundance over the period 1995–2018 at the scale of the United Kingdom, and no significant change (+11%) at the scale of England (Fig. 9, Harris et al. 2020). The breeding distribution covered 57% of Great Britain in the most recent atlas survey (2008–11), representing a 78% increase since the first atlas survey (1968–1972); 96% of that change happened since the second atlas survey (1981–1984), with the expansion thought to be caused mainly by releasing for shooting (Balmer et al. 2013). Because the species was introduced for hunting

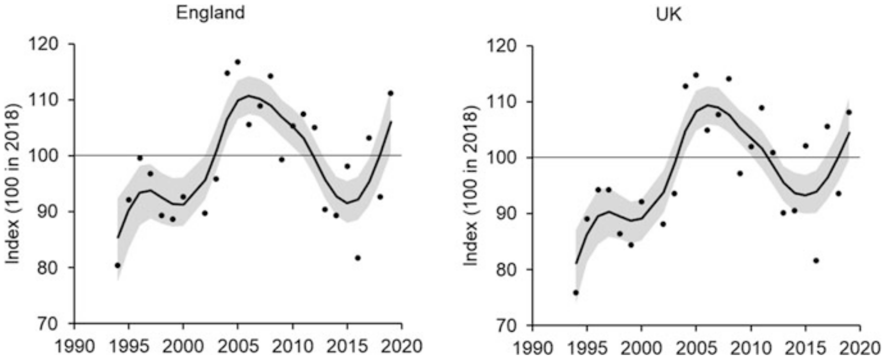

Fig. 9 Smoothed population index for Red-legged Partridge in (left) England and (right) United Kingdom, relative to an arbitrary 100 in 2018, with 85% confidence limits in grey. On each graph, the solid line is the smoothed trend, the dots are the unsmoothed annual indices, and the pale grey area is the upper and lower 85% confidence limits of the smoothed trend. Data from the BTO/JNCC/RSPB Breeding Bird Survey, a partnership jointly funded by the BTO, RSPB and JNCC, with fieldwork conducted by volunteers. Reproduced with permission from Woodward et al. (2020)

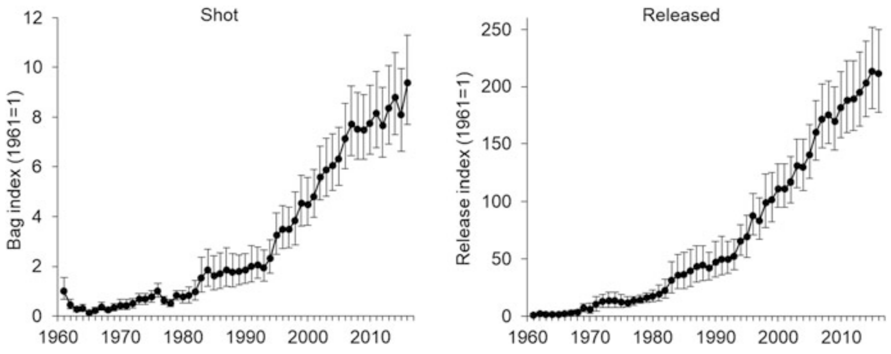

Fig. 10 Bag index (left) and releasing index (right) for Red-legged Partridge in the United Kingdom, relative to 1961 (set to 1), with 95% confidence intervals. Data from the GWCT's National Gamebag Census, based on voluntary returns from up to 900 shoots annually. Reproduced with permission from Aebischer (2019)

purposes, there is no concern over the conservation status of the species (Woodward et al. 2020).

Over the 50-year period 1966–2016, Red-legged Partridge bags in the UK increased by a factor of over 25; the increase was driven by a 65-fold increase in the number of Red-legged Partridges released for shooting (Fig. 10, Aebischer 2019). In terms of absolute bag sizes and numbers released, PACEC (2006, 2014) provided aggregate estimates of 6.5 million partridges[1] released for shooting in 2004 and 2.6 and 4.4 millions of birds shot in 2004 and 2012 respectively. Disaggregating these numbers to species based on NGC composition and using them to calibrate NGC indices, Aebischer (2019) estimated that in 2016 10 million Red-legged Partridges were released for shooting and 4.6 million shot.

What's Next?

The Breeding Bird Survey is the only monitoring programme occurring in each country at the national scale. However, this protocol aims at evaluating trends in abundance index and may not be sufficient on its own for management purposes. Estimates of demographic parameters (population size, vital rates) are more informative than indices and are thus critical.

The mapping method seems to be the most accurate method to estimate abundance or density but may have high sampling costs (Pépin 1983; Borralho et al. 1996; Gibbons and Gregory 2006). Robust, effective and less costly techniques involve transect methods (with play-back calls or not) associated with modelling

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[1] Combined Red-legged and Grey Partridges.

approaches to take into account imperfect detection during observations. Such model-based approaches to estimate abundance and/or densities include a wide range of models from state-space models accounting for error during the observation process (de Valpine and Hastings 2002) to models that explicitly estimate detection probability such as N-mixture models (Royle 2004; Kéry et al. 2005; Jakob et al. 2014) or distance sampling (Buckland et al. 1993, 2004; Borralho et al. 1996) models. However, without a proper spatial sampling regime, extrapolation to larger scales may be not accurate.

Models based on a survey of unmarked individuals such as the N-mixture models for open populations can also provide information about vital rates (survival and recruitment; Dail and Madsen 2011). If capture programmes exist, capture-mark-recapture (CMR) models such as Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965) and all its derived development (e.g. multistate and multievent models: Lebreton et al. 1992, 2009; Pradel 2005; robust design models: Pollock 1982; Kendall and Nichols 1995; Kendall et al. 1997; joint modelling: Kendall et al. 2012; Souchay et al. 2014) can be used to estimate survival, breeding and detection probabilities. Radio-tracking surveys of individuals allow the estimation of survival but also can be used to estimate relative importance of several sources of mortality (Schaub and Pradel 2004; Sanz-Aguilar et al. 2015). Models based on capture-recapture are commonly used to assess survival and breeding performance of wild and released birds (Alonso et al. 2005; Buenestado et al. 2009; Souchay et al. 2018), and they can be also used to evaluate whether the mortality by hunting of wild breeding stock differs between hunting estates where farm-reared partridges are released or not (Casas et al. 2016). Productivity may be obtained by age-ratio computation and group survey. However, data may be biased owing to composition, size of groups surveyed or imperfect detection depending on study sites.

In contrast to the generalized use of transect sampling methods to estimate abundance, capture-recapture methods have not been yet used in all countries. There thus exist an opportunity to create a network around the Red-legged Partridge to share both sampling design and materials to realize it.

A step further could be the implementation of a joint spatial sampling design from Portugal to Italy to provide the opportunity of extrapolation at large scale and proper comparison between demographic rates (density, survival and/or breeding rates).

Another opportunity based on this standardization would be the potential use of integrated population models (IPM) in each region, a promising tool to integrate these different sources of information into a single framework (Abadi et al. 2010; Schaub and Abadi 2011). IPMs can be used to estimate demographic parameters not supported by separate datasets, such as productivity in absence of brood surveys or annual survival without year-round monitoring. Moreover, one can see IPMs as a tool to estimate the importance of released birds for natural populations of Red-legged Partridges via both the estimation of breeding performance of released birds even in absence of brood surveys for these birds and sensitivity analysis. Such topic is currently in progress with data from the French Red-legged Partridge network (G. Souchay, pers. comm.). Finally, as IPMs allow investigation of density-dependence (Abadi et al. 2012; Lebreton and Gimenez 2013), they could be used to assess the link between external covariates and population dynamics. Such covariates could be linked to hunting (harvest rate, restriction/liberalization of practice) or habitat management (links with environmental covariates or implementation of special practices). The next step could be the use of IPMs to evaluate several scenarios, such as hunting and/or habitat management plans (Arnold et al. 2018). Population viability analyses based on IPMs are also worth considering within the context of global climate change.

As we saw in this chapter, important efforts in monitoring for this species are already being done, but methodological diversity makes it difficult to integrate results and reduces their value. Therefore, more efforts need to be implemented to improve local and global monitoring. A first step would be a technical analysis to select the optimal survey methodology in each case taking into account available resources, as well as the costs and the accuracy of data needed to monitor Red-legged Partridge populations in an integrative and informative way. This methodological and viability analysis based on real data would allow the development of a technical agreement, which would lead to precise instructions to the different stakeholders who nowadays monitor Red-legged Partridges with more or less success: Regional Governments, hunting managers and other organizations. A suitable methodological choice, a flexible survey design, an easy and uniform system to store and upload data into PMIs and good analyses of available results are critical ingredients of a successful integrative system with many contributors. This should serve everyone (managers, governments, scientists, etc.) better than the current approach without a great increase of costs, and thus, to explore this path would be desirable.

Acknowledgements LR and MP were funded by the Portuguese Science and Technology Foundation (FCT) through the grant SFRH/BPD/93079/2013 (LR) and SFRH/BPD/97025/2013 (MP) and by public funds available from the POPH/FSE.

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Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain

Beatriz Arroyo, Jesús Caro, and Miguel Delibes-Mateos

Introduction

The Red-legged Partridge (*Alectoris rufa*) is a characteristic species of Spanish ecosystems, associated with farmland and Mediterranean scrub areas, and serves as prey for many predators of conservation concern (Valkama et al. 2005, Chaps. “Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?” and “Is Predation the Key Factor of Partridge Ecology and Management?”). Beyond their ecological roles, Red-legged Partridges also have a relevant role in society as an iconic game species. Available information reveals that the numerical, spatial and socio-economic magnitude of Red-legged Partridge hunting in Spain is large, even if information about game use remains less consistently gathered than for other renewable resources (Apollonio et al. 2010; Martinez-Jauregui et al. 2011; Moreno-Zarate et al. 2021). This species is considered by many Spanish hunters as the “queen” of small game and is thus associated with high emotional value for hunters. Its hunting also generates significant income (Garrido 2012) and attracts good numbers of foreign hunters (Reginfo 2008).

Partridge populations have strongly declined in recent decades in its native range, including Spain (Chap. “Red-Legged Partridge Monitoring and Population Trends”), but demand, together with the economic potential of Red-legged Partridge hunting, has led increasingly to the development of more intensive, potentially more

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_11

profitable management systems, whose legitimacy has been challenged even amongst hunters (Fischer et al. 2013a).

Social-psychological theory has shown that emotions, beliefs and economic interests may influence attitudes, and that these last may influence behaviour (Manfredo and Bright 2008; Hazzah et al. 2009), so decision-making in relation to Red-legged Partridge hunting or management may vary in relation to these aspects.

We review these aspects, focusing on central and southern regions of Spain, the core area for partridge hunting in the country (see below), and where the highest Red-legged Partridge abundances are found (Blanco-Aguiar et al. 2003). First, we detail aspects of Red-legged Partridge hunting and its management. Second, we review information about the economic consequences of different management styles and how hunters and game managers perceive such management systems, and which factors influence management decisions and hunting choices. Finally, we discuss and illustrate that hunting and management of Red-legged Partridges in Spain is currently strongly influenced by hunters' or game managers' beliefs and economic interests, and that the direction that the hunting of this iconic species is currently taking is not necessarily appreciated by hunters themselves.

Red-Legged Partridge Hunting in Spain

Hunting is currently practiced in Spain in approximately 85% of the territory (MAGRAMA 2015). Only in a small part of this surface (<5%) do hunting rights belong to the Spanish administration, and hunting is regulated directly by the local or regional governments. In the remainder, the surface is divided in ca. 33,000 privately managed hunting estates (MAGRAMA 2015). The owner of the hunting rights (the administration, a person, or a legal entity) is legally responsible for making decisions on hunting management (Gálvez Cano 2006), but may not be the owner of the land, and, in fact, in most cases the ownerships are dissociated (Arroyo et al. 2012). In such cases, the owner of the hunting rights may pay a fee to the land owners for the right of access to hunt.

Small game hunting (which, in Spain, involves mainly lagomorphs and game birds) occurs over a large surface overall, and is more widely distributed than big game hunting (involving mainly ungulates), particularly in southern Spain. For example, in ca. 85% of all estates in southern Spain the main use is small game (Farfán 2010; Ríos-Saldaña 2010). Among small game, game birds are numerically more important than mammals, and Red-legged Partridges, besides thrushes (*Turdus* spp.), are the most frequently hunted game bird species (MAGRAMA 2015). Additionally, Red-legged Partridges are particularly prized by hunters. For example, 55% of 109 hunters interviewed in the most important hunting magazine in Spain (TROFEO) identified the Red-legged Partridge as their preferred small game species, whereas no other species or group was highlighted by more than 10% of interviewees (C. Vázquez-Guadarrama and authors, unpublished data). The central and southern part of Spain contains a sizable proportion of the partridge hunting estates and includes what historically and currently are Spain's most productive partridge hunting lands. Red-legged Partridge hunting is practiced in more than 90% of small game hunting estates of this region (Vargas et al. 2006; Ríos-Saldaña 2010). The most widespread method is walked-up hunting (with or without dogs), where hunters shoot partridges as they encounter them, followed by '*reclamo*' (decoy) hunting and driven-shooting (Farfán 2010; Ríos-Saldaña 2010). '*Reclamo*' hunting consists of using a live male Red-legged Partridge inside a cage to attract other partridges (through its calls) to a set place where hunters lie in wait (Vargas et al. 2012). In driven shooting, assistants beat the land to flush partridges and drive them towards a strategically arranged line of hunters.

Hunting seasons are set by each of the Spanish regional governments. The Red-legged Partridge hunting season runs from mid-October to mid-February, with some regional differences, although hunters usually limit the season to a shorter period when the availability of partridges is low and/or decreases sharply during the season (Caro et al. 2015, and see below). One notable exception is the '*reclamo*' hunting season, which runs from mid-January to late February or mid-March, depending on the region.

In socio-economic terms, Spanish private hunting estates can be categorized in two main classes according to their purpose:

(a) *Social or non-commercial estates*, where the stated aim is mainly to provide access to game (frequently to local hunters) without economic profit motives. In southern Spain, these estates are generally oriented towards small game (Arroyo et al. 2012; Macaulay et al. 2013). Local hunters can be involved in the decision-making process that regulates game management and hunting pressure in these estates through participation in local hunting societies, which are the owners of the hunting rights and thus the legal entities that privately manage hunting in the estate.

(b) *Commercial estates*, where the stated aim is to make economic profit from the hunting rights. These estates are managed by either an individual or a company (legal entity), and in certain cases (e.g. for certain large properties), the owner of the hunting rights is also the land owner (Arroyo et al. 2012).

There are no official statistics on the frequency of each type of estate within Spain, but social or non-commercial estates are probably more numerous than commercial estates (e.g. it has been estimated that non-commercial hunting occurs in 70% of the hunting surface in Spain, Sánchez-Roig 2016). Commercial estates are more frequent in central and southern Spain than in the north.

Official statistics estimate that 2–4 million Red-legged Partridges are shot in Spain each year (MAGRAMA 2015). Red-legged Partridge national bag in recent years is 50% lower than that estimated for the 1970s (Blanco-Aguiar 2007, and see Chap. "Red-Legged Partridge Monitoring and Population Trends"); annual values decreased regularly until the mid-1990s, subsequently increasing slightly and stabilizing in the early 2000s (Blanco-Aguiar 2007), until 2008 when there has again occurred a weak decrease (MAGRAMA 2015) (see Figs. 7 and 8 in Chap. "Red-Legged Partridge Monitoring and Population Trends").

To interpret these figures, it is necessary to take into account that partridge population declines and increasing social and commercial interests in the species led to an exponential increase in game farms and the associated release of farm-reared Red-legged Partridges (Blanco-Aguiar et al. 2008; Duarte et al. 2011). The increase in the number of Red-legged Partridges shot since the 1990s thus probably reflects the increasing number of farmed-reared birds released (Blanco-Aguiar et al. 2012). No official data exist on the percentage of harvested partridges that comes from game farms, since released birds do not need to be marked. Nevertheless, Vargas et al. (2006) estimated that in Andalucía (southern Spain) one-third of Red-legged Partridges shot are farmed-reared birds. Official figures estimate that between 1 and 2 million Red-legged Partridges are released annually (MAGRAMA 2015), but it is generally accepted that these figures significantly underestimate the real numbers (Díaz-Fernández et al. 2012; Caro et al. 2014).

For example, a detailed study showed that, only in the province of Ciudad Real (one of the 50 provinces of Spain), almost 1 million Red-legged Partridges were released annually between 2006 and 2012, which represents more than half of the official figures of partridges released in the whole country (Caro et al. 2014). In that province, the study also showed a notable decrease in the number of non-intensive estates that released partridges from 2008 to 2013, coinciding with the economic crisis (Garrido 2012; Cabodevilla et al. 2020). It is likely that this may have also occurred in other regions of Spain, which might explain the recent decrease in Red-legged Partridges hunted nationally (see above). This would support the importance of farm-reared birds in current partridge hunting systems in Spain.

In principle, the release of farm-reared Red-legged Partridges is mainly carried out as part of "population reinforcement" management, and can thus only legally occur outside the hunting season. However, most releases take place in late summer, usually as close as possible to the opening of the hunting season, in order to increase stock in the short term. In addition, since the end of the twentieth century, legislation also allows hunting estates to apply (through the payment of a special fee) for the label "intensive". Intensive hunting estates are defined as those where "*hunting is carried out through the regular release of game raised in game farms, or where there are frequent population reinforcement and intensive food management*" (e.g. BOJA 154:36/9 August 2005). In intensive hunting estates there are no legal temporal or numerical limits throughout the hunting season to release farm-reared animals, and hunting is mainly based on 'put-and-take' (i.e. game released just prior to hunting; Farfán 2010; Díaz-Fernández et al. 2012). Intensive hunting estates are almost always commercial, and represent overall less than 1% of all estates in Spain, although in regions such as Castilla-La Mancha (central Spain) their frequency increases to 4–5% (MAGRAMA 2015). Despite their low numbers, their global contribution to national bags is likely to be higher, given that many more partridges are shot in intensive states than in other estates (Arroyo et al. 2012 and see below).

Economics of Red-Legged Partridge Hunting in Spain

The value of hunting activities for the rural economy has been highlighted in various countries (Fischer et al. 2013b; Arnett and Southwick 2015), including Spain (Garrido 2012; Sánchez-García et al. 2021). In this country, hunting possesses an important economic dimension, although reliable quantitative information of its importance is frequently lacking (Martinez-Jauregui et al. 2014). According to estimates from the hunting sector, partridge hunting provides more than 1 million euros per year, or about 25% of income related to hunting in general (Garrido 2012). These estimates include revenues, among others, from hunting fees, trading of farm-reared Red-legged Partridges (with more than 600 game farms raising Red-legged Partridges in Spain; Sánchez García-Abad et al. 2009, Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing", hunting estate management expenses, rent for the landowners for hunting rights, insurance, and hospitality (e.g. food and drink). Additionally, it has been estimated that partridge hunting produces almost 15,000 jobs (Garrido 2012), including gamekeepers, supplementary staff for hunting days, intermediary suppliers, and other staff.

Management carried out for Red-legged Partridges in Spanish hunting estates involves a variety of tools that include the provision of supplementary food and water, predator control, sowing game crops, regulation of hunting pressure, and, as explained above, release of farm-reared partridges (Díaz-Fernández et al. 2013a). Arroyo et al. (2012) showed that, in central Spain, these management tools were applied in almost all studied hunting estates ($n = 59$) to a certain extent, but that commercial estates had overall more intensive management than social ones, including more and larger partridge releases, higher density of supplementary feeders and more intensive predator control, for which they employed more gamekeepers. More partridges were hunted per km^2 in commercial than social estates. Differences in management intensity, employed game keepers and harvesting were most marked between intensive estates and non-intensive estates (both commercial and non-commercial). For example, the number of released birds was two orders of magnitude higher in intensive estates, being above 4000 partridges/km^2 in some of them. Concomitantly, partridge annual harvest was also two orders of magnitude higher in intensive estates than in other commercial estates (Arroyo et al. 2012).

Given the varying income and expenses, it is conceivable that economic turnover differs among types of hunting estates (social, commercial or intensive). Arroyo et al. (2017) analyzed economic parameters using detailed data provided by 20 Red-legged Partridge hunting estates with different management and economic aims in central Spain. The study showed that staff salaries represented the greatest proportion of expenses in all estates, but that purchase of farm-reared Red-legged Partridges was the second largest expense for those estates that used this management tool. Overall, the economic benefits of intensive estates (i.e. income minus expenses) were on average an order of magnitude higher (20,404 ± 24,413 euro/km^2, $n = 8$) than those of other commercial estates (1713 ± 1280 euro/km^2, $n = 7$).

Non-commercial estates, as expected from their stated aim, just broke even, having almost no benefits ($n = 5$). These results, although based on a relatively small sample size, show that hunting based on put-and-take partridges may produce benefits that are qualitatively larger than what may be obtained by the commercialization of wild Red-legged Partridges. In these studied intensive estates, most income was related to driven-shooting. The higher benefits in intensive estates are thus related to the fact that estates based on continuously releasing farm-reared partridges throughout the hunting season may offer a much higher number of driven-shooting days that estates based on wild partridges (Arroyo et al. 2012; Díaz-Fernández et al. 2012).

The fact that driven-shooting is associated with higher income is also related to the market prices of this method vs. the walked-up hunting offered in the Spanish hunting market. Based on information from 47 estates advertising hunts in magazines and websites, Díaz-Fernández et al. (2013b) showed that hunts varied considerably in price, but that prices were overall much higher for driven-shooting days (between 1100 and 4700 euro) than for walked-up shooting days (between 50 and 450 euro). All but 3 of the 29 estates that provided information on driven-shooting days admitted to using farm-reared partridges. Interestingly, the variation in price for walked-up shooting was not related to whether they restocked or offered wild partridges. Many other factors may influence market prices, including the number of partridges shot (Martinez-Jauregui et al. 2015). However, the lack of relationship in market prices associated with partridge origin in walked-up hunting days contrasts with the results of a choice experiment made on Spanish partridge hunters, which showed that they were willing to pay >20 times more per additional wild partridge in a walked-up hunting day than for an additional farm-reared bird (Delibes-Mateos et al. 2014). These results, combined, could reflect the difficulty of hunters to distinguish between commercial estates using wild Red-legged Partridges and those using farm-reared birds (see also Garrido 2012).

On the other hand, Arroyo et al. (2017) showed that the economic benefits of non-intensive commercial estates using releases were on average lower than those of commercial estates without releases. In fact, the profitability (i.e. income divided by expenses) of commercial estates not using releases was similar to that of intensive estates, because their expenses were also much lower. This indicates that commercialization of hunting wild partridges may indeed be profitable, even if total benefits are much lower than in intensive estates. Furthermore, the results suggest that carrying out small-scale releases (such as those allowed in non-intensive estates) does not render any economic benefit, and rather decreases profitability, as expenses occurred without necessarily increasing total harvest (Díaz-Fernández et al. 2012). It would be important to evaluate more widely, including information from a larger number of estates, the economic information about partridge hunting, and the implications of the use of farm-reared partridges for the economic sustainability of commercial partridge hunting. However, it has been shown that releases of farm-reared partridges are associated with lower productivity in wild Red-legged Partridges (Díaz-Fernández et al. 2013b), so it is also plausible that increasing the rate of releases decreases the likelihood of economic sustainability of commercial hunting based on wild stocks.

Social Aspects of Red-Legged Partridge Hunting: Views Within the Hunting Sector About Farm-Reared Bird Releases

Non-hunters usually associate the release of farm-reared partridges with connotations of illegitimacy and other negative attributes (Díaz et al. 2009; Gamborg and Jensen 2017). Interestingly, criticisms of partridge releases are also frequent among Spanish partridge hunters (Caro et al. 2017), who usually show a clear preference for wild partridges over farm-reared birds. For example, Delibes-Mateos et al. (2014) assessed the values given by partridge hunters to different attributes related to a walked-up hunting day, and they found that the "quality" of the partridges (i.e. wild vs. farm-reared partridges) got the highest score; an average of 8.9 ± 1.5 (mean ± SD) on a 1–10 scale, more so than the "quantity" of partridges shot during the day (score 6.7 ± 2.4), or other variables such as estate habitat or the possibility of hunting other small game.

Spanish game managers also express frequent negative opinions towards the release of farm-reared partridges. In this regard, Delibes-Mateos et al. (2015) observed that about half of 45 interviewed game managers in central Spain expressed purely negative views towards releases, whereas only two of them expressed purely positive views towards this game management tool. Eight managers provided opposing comments about releases, e.g. *releases are ecologically harmful but economically important* (Delibes-Mateos et al. 2015). Negative views towards the release of farm-reared partridges dominated among game managers who had never employed this type of management. These managers never used positive arguments about releases. Interestingly, negative arguments were also expressed by managers who released partridges, and even dominated among those who used this management practice occasionally. Logically, positive and neutral views were more common among managers who had used releases, particularly those who released partridges annually (including those from intensive estates). A similar pattern was also observed when comparing non-commercial, commercial and intensive estates: positive views were most common amongst managers of intensive estates, and least common amongst those of social or non-commercial ones (Delibes-Mateos et al. 2015).

Spanish hunters also say often that partridge hunting based on releases contributes to hunting denaturalization, and that this may contribute to a gloomy future of hunting (Caro et al. 2017). Similarly, a third of the game managers interviewed by Delibes-Mateos et al. (2015) made moral assessments about shooting farm-reared partridges, which was contemptuously referred to as "artificial hunting". References to the artificiality of released partridges arose frequently in focus groups with hunters and game managers (authors, unpubl. data), some of which used very pejorative terms when talking about farm-reared partridges, including *ducks*, *chicken*, *plastic or canned partridges*, etc. This negative valuation of farm-reared partridges was, at times, based on the perceived different behaviour between wild and farm-reared birds, e.g. the former escape earlier and fly longer and faster, in the view of hunters.

However, some hunters, whilst acknowledging such differences, were not too critical of them. For example, one manager said during an interview: "*it is completely different shooting wild partridges than farm-reared ones, but the latter is also enjoyable*" (Delibes-Mateos et al. 2015). Beyond the behaviour or quality of farm-reared partridges, some hunters also say that hunting based on the release of farm-reared partridges is more related to an industrial activity or animal husbandry than to hunting per se (Covisa 2015), which they also link to the denaturalization of hunting. A generational variation may however be present. Caro et al. (2017) showed that older hunters mentioned more frequently than younger hunters their concerns about hunting being denaturalized through the release of farm-reared animals. In agreement with this, older hunters showed a lower willingness to pay for farm-reared partridges (Delibes-Mateos et al. 2014).

Besides moral arguments, the most frequently expressed negative opinions given by hunters towards the release of farm-reared partridges referred to ecological aspects. For example, 64% of the game managers who expressed negative views on partridge releases ($n = 33$) used ecological arguments against this management activity (Delibes-Mateos et al. 2015). There was a widespread belief among hunters that releasing farm-reared partridges damages wild ones. Importantly, some partridge hunters often stated during focus groups that the release of farm-reared partridges has been the main cause of the decline of wild populations. Some hunters even believe that releasing farm-reared birds drives wild partridges towards extinction, and that it is therefore impossible to preserve wild stocks if this type of management is used (Delibes-Mateos et al. 2015). One of the ecological arguments frequently expressed by hunters and game managers is that farm-reared partridges introduce new parasites and diseases, which is indeed supported by scientific knowledge (Villanúa et al. 2008, Díaz-Sánchez et al. 2012; Chap. "Health Monitoring and Disease Control in Red-Legged Partridges"). In addition, many hunters think that released partridges hybridize with wild birds, which is perceived as detrimental for natural populations. This opinion, frequently expressed both in interviews (Delibes-Mateos et al. 2015) and focus groups (authors' unpublished data), is again in agreement with scientific studies (Blanco-Aguiar et al. 2008; Barbanera et al. 2010; Chap. "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"). Interestingly, Delibes-Mateos et al. (2015) showed that almost all managers who considered that releases detrimentally affected wild partridges had never used this management activity, whereas none of those who released partridges annually mentioned these issues. The fact that some scientific studies about the effect of releases on wild partridge populations have been funded by hunting associations (e.g. FEDENCA 2012) also shows the preoccupation that the sector has about this topic, and may have also facilitated the transferability of the results to the hunting sector, thus likely explaining the frequent references of hunters and game managers to these points.

It may then seem puzzling that Red-legged Partridge release is carried out so widely in Spanish hunting estates despite these frequent criticisms by both hunters and game managers. The main reason explaining this apparent paradox lies in the

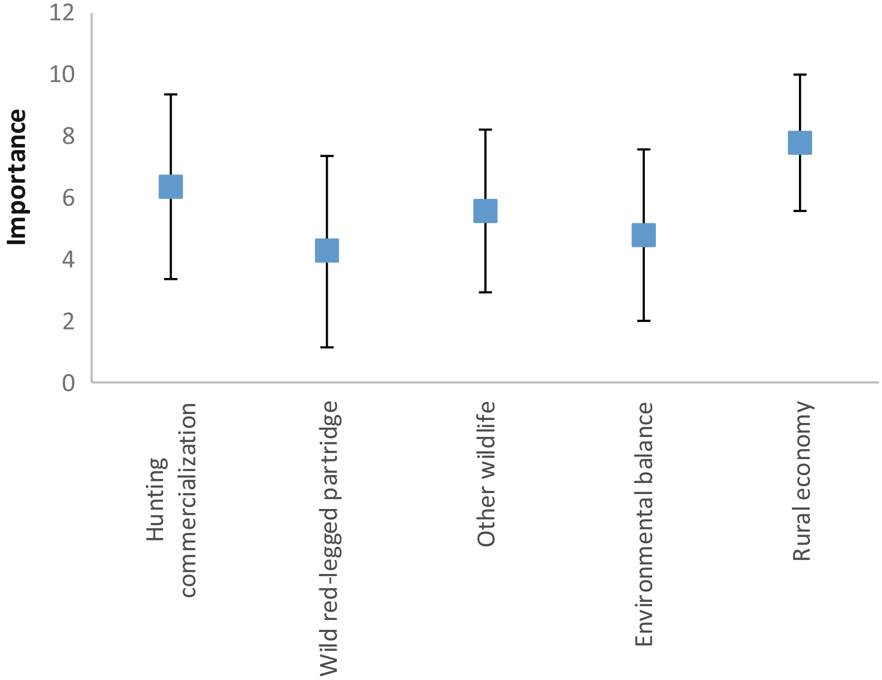

Fig. 1 Importance (on a scale of 1: not important, to 10: extremely important) of partridge releases on different areas according to hunters of Castilla-La Mancha (central Spain, $n = 51$)

perceived economic implications of this management tool together with the decline of wild populations. Interviews and focus groups showed that there was a relatively widespread perception among hunters and game managers alike that partridge releases are economically important. The belief that partridge releases work well to make money and are a profitable business is widespread in the hunting sector (Delibes-Mateos et al. 2015, see also Fig. 1). In addition, some game managers view the release of farm-reared partridges as essential to maintaining commercial hunting in the current context of wild partridge scarcity. On the other hand, abandonment of commercial hunting is viewed as globally negative, beyond the impact on the hunting sector: the argument is that if commercial hunting was unsustainable, hunting estates would be possibly transformed in other land uses less compatible with nature conservation (e.g. intensive agriculture, urbanization, golf courses). In accordance with this idea, a study of 59 partridge hunting estates in central Spain found that agricultural land predominated in all of them, but that commercial estates preserved more natural vegetation within the agricultural matrix (Arroyo et al. 2012). These ideas were expressed more or less equally by managers who had or had not released partridges, although they were particularly praised by managers from intensive estates (Delibes-Mateos et al. 2015). As seen above, intensive hunting estates offer more hunting days for partridge driven-shooting, which are overall more expensive, leading indeed to very high economic benefits (Díaz-Fernández et al. 2013b; Arroyo et al. 2017). On the other hand, the perceived importance of farm-reared partridges for maintaining the economic benefits of commercial partridge hunting may not be substantiated by data from non-intensive estates, as small-scale releases before the hunting season do not lead to higher bags (Díaz-Fernández et al. 2012) and apparently lead to lower profitability (see above).

Beyond the economic or moral aspects of using releases in partridge hunting, or the effects on wild stocks, some hunters also express opinions about the effects of this activity on predators. For example, some game managers, particularly from intensive estates, defended the role of released partridges as prey for predators, including those of conservation concern, such as Spanish Imperial Eagles (*Aguila adalberti*). In this sense, one manager declared in a focus group that, a few days after the release of partridges, all the predators from thousands of hectares around are in his estate because they find abundant food very easily. These ideas are closely linked to the role of stewards of nature that hunters often attribute to themselves (Kaltenborn et al. 2013); i.e. they consider that hunting and its associated management keep some sort of ecological balance, and thus that hunters provide a service to society at large (Treves 2009; Delibes-Mateos et al. 2013). In contrast, other game managers used precisely the same argument (released partridges as the prey of predators) as a negative consequence of restocking: released partridges attract predators, and predation pressure on wild partridges and other species increases (Delibes-Mateos et al. 2015), thus increasing the need to carry out predator control to counteract the increased predator density. Therefore, the same ecological effect (a positive relationship between released partridges and predators) was perceived as positive or negative by different hunters, providing an example of how the relationship between hunters and predators is a complex issue where emotions and beliefs interact with ecological knowledge.

Predator Control for Partridge Hunting: Perceptions, Beliefs and Decision-Making

Traditionally, the relationship between humans and predators has been conflictual: predators cause, or are perceived to cause, damage to human livelihood, and humans often respond killing them (Woodroffe et al. 2005). In particular, hunters usually see predators as competitors for the same resources (i.e. game species), and therefore they frequently employ diverse techniques to control predator species (Reynolds and Tapper 1996). The case of Red-legged Partridge hunters in Spain is no exception (Chap. “Is Predation the Key Factor of Partridge Ecology and Management?”). According to focus groups held in central Spain, there is a widespread belief among hunters that partridge populations have drastically declined over recent years, and that this decline has been mostly caused by predation. For example, game managers often state that where predator control has been abandoned there is "nothing left". It is not surprising therefore that a survey based on interviews showed that most game managers in central Spain believe that predators affect negatively small game species, particularly partridges, within their hunting estates (Delibes-Mateos et al. 2013). Interestingly, some hunters think that predators have switched towards partridges following the sharp decline experienced by European Rabbit (*Oryctolagus cuniculus*) populations in Spain over recent decades (Delibes-Mateos et al. 2009), whereas some researchers have questioned the effect of this potential case of hyperpredation on Spanish Red-legged Partridge populations (Blanco-Aguiar et al. 2012, but see Moleón et al. 2008).

Hunters' perception of the negative effects of predators on partridges is mostly based on their belief that predators are too abundant (Delibes-Mateos et al. 2013). In fact, game managers often complained during the above-mentioned focus groups not only about the (perceived) high number of predators occurring in their game estates, but also about the alleged increase in predator numbers observed over recent decades. For example, hunters mentioned that carnivores such as Feral Cats (*Felis catus*) and raptors such as the Eagle Owl (*Bubo bubo*) have increased their numbers substantially. This is partly attributed by hunters to the increasing development of conservation policies over the past decades. In this sense, some hunters think that predators were formerly less abundant because aggressive control methods such as poisoning were allowed to eradicate them (see also below). In general, hunters acknowledge that they do not conduct any sort of systematic survey to estimate predator abundance (Delibes-Mateos et al. 2013); they mostly rely on sporadic observations and/or the evolution in the number of predators captured between years. A common reasoning expressed by hunters can be summarized in the following statement: "*we are always in the field and see predators, and when you see predators this means that there are too many*." Some game managers state that they do not need to survey predators because their aims do not include knowing how many there are; they just want to remove as many as possible.

Hunters believe that a large number of predator species detrimentally affect partridge populations. The list of species most affecting Red-legged Partridges in the view of hunters according to focus groups and interviews includes carnivores such as the Red Fox (*Vulpes vulpes*), the Common Genet (*Genetta genetta*), the Egyptian Mongoose (*Herpestes ichneumon*), mustelids or feral cats and dogs; raptors such as kites (*Milvus* spp) or harriers (*Circus* spp); owls; corvids such as the Eurasian Magpie (*Pica pica*) or the Eurasian Jay (*Garrulus glandarius*); other large birds such as the White Stork (*Ciconia ciconia*) or the Cattle Egret (*Bubulcus ibis*); small mammals such as the Garden Dormouse (*Eliomys quercinus*); and reptiles such as the Ocellated Lizard (*Timon lepidus*) and snakes. The significant recent expansion of Wild Boar (*Sus scrofa*) in Spain (Acevedo et al. 2011), both in numbers and spatially, is also seen by many hunters as an emergent problem for Red-legged Partridge populations. Many of these species are legally protected, and actually about 80% of the managers ($n = 50$) interviewed by Delibes-Mateos et al. (2013) cited a protected species among those allegedly impacting partridge populations. In the focus groups mentioned above, dialogues between hunters about predator species impacting partridges frequently revolved around foxes and

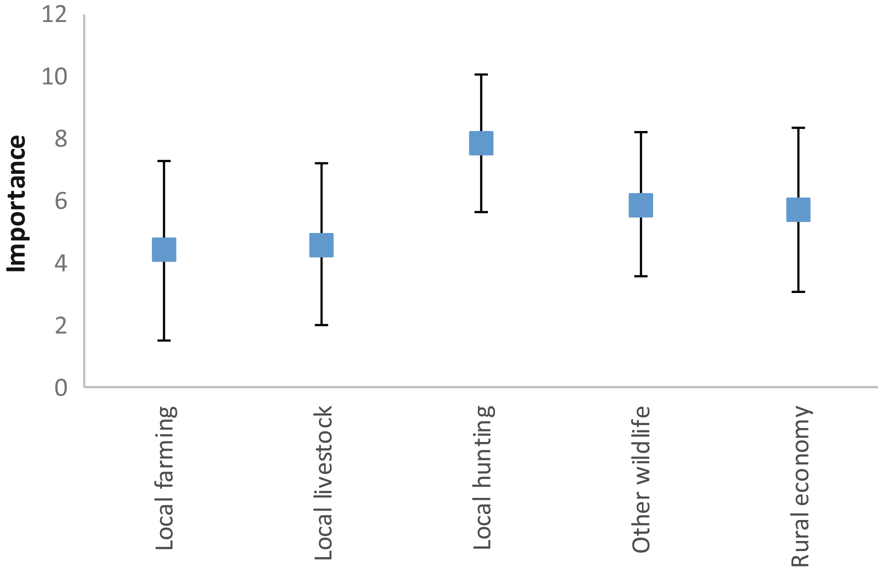

Fig. 2 Importance (in a scale of 1: not important, to 10: extremely important) of predator control on different areas according to hunters in Castilla-La Mancha (central Spain), $n = 51$)

magpies, probably because these are among the most widespread partridge predators in Spain (Díaz-Ruíz et al. 2013, 2015) and also because their control in hunting estates is legally permitted. In general, hunters believe that foxes are more harmful to small game than magpies, because, while the latter prey only on eggs, the former also kill partridges (both adults and chicks). In addition, it is commonly thought that foxes kill as many partridges as they can, even if they cannot eat all of the birds. In contrast with these perceptions, scientific studies have found no relationship between Red Fox control and Red-legged Partridge abundance or adult survival, and the relationship with productivity was contrasted among studies (Mateo-Moriones et al. 2012; Díaz-Fernández et al. 2013b), probably because there exists compensatory predation in areas such as Spain, where the predator community is diverse and rich.

Regardless of the results of the above scientific studies, most managers in central Spain believe that not carrying out legal predator control will lead to smaller hunting bags and that predators interfere with hunting objectives; the most extreme managers consider that hunting would not be possible if predators were not removed (Delibes-Mateos et al. 2013). In agreement with this, a questionnaire survey conducted amongst hunters in central Spain showed that most of them considered that predator control has a very positive effect on small game species and, to a lesser extent, on other species and the rural economy (Fig. 2). In this context, it is not surprising that predator control is performed to some degree in nearly all small game estates (Delibes-Mateos et al. 2013; Díaz-Ruiz and Ferreras 2013). In general, most reasons for negativity among hunters towards predators are based on perceived economic losses (Lindsey et al. 2005). Analysis of focus group discussions indicates that game managers from commercial estates are generally much more intolerant towards predators than those from non-commercial estates (authors, unpubl. data). The former not only focused their discourses about management and hunting mostly on predators, their effects on game, and predator control activities, but also used stronger arguments such as their belief that hunting would be impossible without predator control. Similar findings were obtained in the study based on interviews with game managers conducted by Delibes-Mateos et al. (2013). Importantly, and as mentioned before, predator control is much more intensive in commercial than in non-commercial game estates (Arroyo et al. 2012). In addition, commercial estates more frequently use control methods that are potentially non-selective, such as snares (Delibes-Mateos et al. 2013). All of this indicates that there is a relationship between the intensity of predator control carried out, economic interests, and the strength of game managers' arguments about the effect of predators on hunting (Delibes-Mateos et al. 2013).

In general, game managers consider that predator control is effective in reducing the number of predator populations. However, many of them think that it is effective only in the short term, and that predators recover their original numbers if control is not maintained every year (Delibes-Mateos et al. 2013). Most managers believe that cage-traps constitute an effective way to reduce the number of magpies, whereas perceived efficiency in capturing foxes is much lower (Delibes-Mateos et al. 2013), which agrees with field tests conducted by researchers (Díaz-Ruiz et al. 2010, 2016). There is the common belief among hunters that predator control is not efficient if neighbouring estates do not remove predators. According to the statements given during the focus groups, the argument is that predators (particularly foxes) from the surroundings where they are not sufficiently removed move to unoccupied territories in game estates where predator control is intensive and game species are abundant. In this line, it was frequently pointed out during discussions that the fact that in Spain land property and hunting rights are most of the time dissociated (as explained in the first section of this chapter) constitutes a serious limitation for some game estates to control predators.

Spanish hunters also often believe that the bureaucracy relative to predator control is excessive, and express their discontent towards people in charge of policy, who are usually seen as unfamiliar with hunting activity (Caro et al. 2017). Current game legislation draws intense criticism among hunters and game managers, particularly those from commercial estates. In terms of predator control, hunters often believe that too many predators are protected and that the list of protected species has increased a lot. Some hunters actually argue that there is a need to spread predator control to other protected predators such as mustelids to make it really effective. In addition, there exists the perception among hunters that current legal methods to capture carnivores are inefficient (Delibes-Mateos et al. 2013). In this sense, hunters from central Spain assigned an average score of 5.9 ± 2.3 ($n = 45$) to the efficiency of legal predator control methods (1: non efficient, 10: totally efficient; authors' unpublished data). Similarly, game managers frequently complained during the focus groups because some methods that were used legally in the past have been banned as a consequence of pressure exerted by other sectors of society. This opinion was mostly expressed by managers from commercial estates (authors, unpubl. data).

Overall, therefore, decisions about predator control to benefit partridge populations are framed on perceptions about excessive predator abundance, and influenced by hunters' beliefs about predators' impact on partridge populations and by the economic motivation of hunting activities. Discourses in the focus groups indicated that scientific studies showing a lack of efficiency of predator control as currently implemented in partridge estates were received with disbelief, or with comments indicating that personal experience was more valid for hunters than scientific information: "[. . .] *each person in their estate knows what they need . . . no one knows better than me or better than each [manager] what you have in your estate and whether you need to kill it now or kill it in two months*.". This concurs with the results of a questionnaire survey to 198 game managers (authors, unpublished data) that attributed the highest reliability (8.1 ± 1.7, in a scale 1 to 10) to personal experience, a higher value than that attributed to scientific studies (7.4 ± 2.3). This also stresses the relative importance of different information sources for estate decision-making.

Information Sources and Regulation of Hunting Pressure

Sustainable use of natural resources such as game is possible if rates of use do not exceed rates of regeneration (Lande et al. 1997). Therefore, game management that includes regulatory mechanisms applied to hunting pressure has the potential to avoid overexploitation (Aanes et al. 2002). Although Spanish partridge hunters are concerned about the drastic decline of Red-legged Partridge populations, they do not usually consider over-exploitation to be among the main factors causing such decline; in their discourses, predation and agricultural changes predominate. Nevertheless, partridge hunters often acknowledge that a certain amount of harvest regulation is needed to keep wild populations and hunting viable. For example, most hunters and managers stated during the focus groups that they aimed to leave at the end of the hunting season enough partridges alive to ensure adequate breeding densities the following spring (what they call colloquially "*the mother*").

A critical premise for efficient harvest regulation is to acquire reliable data on population size (Sutherland 2001). In Spain, hunters agree that it is important to know population abundance in order to define regulation strategies, and they usually assess partridge abundance in summer, after partridge reproduction (Caro et al. 2015). However, according to their statements, this assessment is rarely based on systematic surveys (thus repeatable, and where uncertainty may be quantified); rather, it is usually made through qualitative (albeit frequent) observations. For example, hunters usually stroll across the estate in spring or summer, and they "know" whether the year is good for partridges or not, based on their observations; "*if there are partridges, you see them*", said one game manager during the focus groups (Caro et al. 2015). This suggests that hunters' assessment of partridge

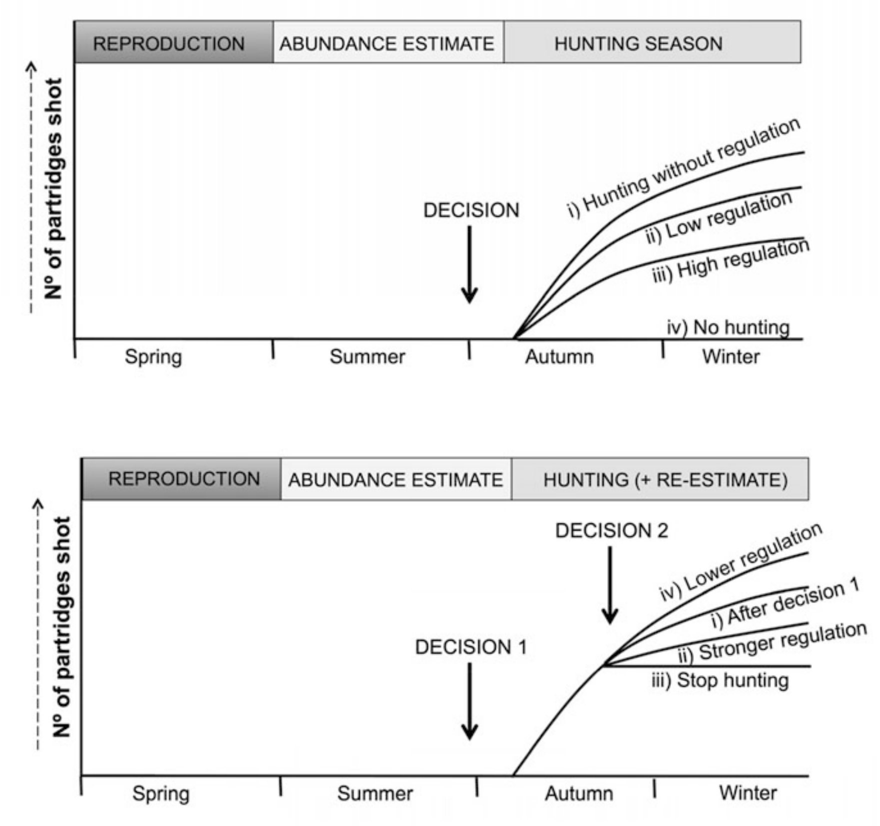

Fig. 3 Decision-making process of Red-legged Partridge hunting pressure. (**a**) First decision taken before the beginning of the hunting season; (**b**) Second decision taken during the hunting season (from Caro et al. 2015, Sustainability Science 10: 479–489)

abundance is based not only on their observations, but also on their experience; hunters usually defend their high knowledge on the functioning of ecosystems, including game population dynamics (Caro et al. 2017). In addition, it is also common that game managers' perceptions of partridge abundance rely on what other people who carry out frequent field activities, such as game-keepers, farmers or shepherds, tell them. However, field surveys show that annual take does not follow closely variations in annual abundance (Díaz-Fernández et al. 2012; Casas et al. 2016), indicating that these qualitative data are not precise enough to adequately adjust hunting pressure, or else that the regulatory mechanisms in place are not sufficiently efficient.

In general, decision-making about partridge hunting pressure takes place before the official start of the hunting season around mid-October (Caro et al. 2015, see Fig. 3). In years of very low partridge abundance (or very poor partridge reproduction), the decision may consist of banning hunting, although this option is rarely chosen, according to game managers (Caro et al. 2015). The opposite situation, that is hunting without any self-regulation, also occurs, but it is also not frequent. Between these two extreme possibilities, there are many different levels of hunting pressure, which depend on a number of varied factors including the type of estate (non-commercial, commercial or intensive estates, see above), the perceptions of the game manager, and the perceived partridge abundance. Game managers often readjust hunting pressure during the course of the hunting season (Caro et al. 2015, see Fig. 3). If hunters perceive during the hunting season that partridge abundance is low, this information is conveyed to the game managers, who can impose additional stronger regulation or even decide to stop hunting. On the other hand, managers may decide to exceptionally add some extra days of hunting, or allow driven shooting rather than walked-up shooting on one particular hunting day, if partridge abundance during the hunting season is perceived as very high. This also suggests that initial partridge abundance estimates, on which the initial decision is based, are normally insufficiently accurate for regulation decisions.

Regulatory mechanisms on partridge hunting pressure in Spain are similar to those used for other game species (e.g. Angulo and Villafuerte 2004; Moreno-Zarate et al. 2021) or in other areas (e.g. Broseth et al. 2012; Wam et al. 2013). These are widely described in Caro et al. (2015), and commonly include limiting the number of hunting days, or imposing a limitation of duration of hunting in a given day. Additionally, as mentioned before, they may include modifying the relative frequency of different hunting types, such as whether or not to allow (or how many days of) driven shooting. In certain estates, regulatory mechanisms also include limiting the number of hunters per day. Setting hunting quotas (limiting the number of partridges to be shot per hunter and day) is another strategy commonly used in Spain to limit partridge hunting pressure. Pressure is sometimes regulated spatially. First, the establishment of free-hunting reserves in each hunting estate (totalling at least 5% of total estate surface) is imposed by law for estates of a certain surface area. However, in most cases these include only the least accessible areas of the estate and where game abundance is low. Some estates also use a "quartering" system, hunting each day a different part of the hunting estate. This rotation mechanism means that some parts of the estate remain non-hunted for several days (until the full rotation is completed).

Overall, therefore, a variety of regulatory mechanisms are implemented in different hunting estates, but whether using one or another is best to achieve the purposes of adjusting harvest to abundance, is rarely evaluated. No study has evaluated the effect of daily quotas on total take, although some hunters question the effectiveness of this mechanism (Caro et al. 2015), as demonstrated for of other small game birds in Spain (Moreno-Zarate et al. 2021). Although the establishment of reserves and hunt-free areas with available food is thought to have a very positive effect in limiting the negative sub-lethal effects of hunting on game and non-game species (Duriez et al. 2005; Tarjuelo et al. 2015), it has not yet been evaluated whether they have an effect on total take and thus their efficiency as regulatory mechanisms of hunting pressure.

Caro et al. (2015) suggested that annual harvest on a given estate was significantly related to the number of driven-shooting days and the density of hunters during walked-up hunting days, but not to the total number of walked-up hunting days or the density of hunters during driven-shooting days. So, modifying the density of hunters during walked-up hunting days is likely to be more efficient (in terms of limiting total take) than limiting the number of hunting days during the hunting season. However, this option may not be acceptable to hunters. For example, during the focus groups some managers said that is not always possible to limit the number of hunters per day, particularly in non-commercial estates. Results from the questionnaire applied to 198 game managers (see above; authors, unpubl. data) showed that personal experience was the most frequently mentioned criterion in deciding what management to apply in a hunting estate (mentioned by 82% of respondents). The second most important was the opinion of members or clients of the hunting estate (mentioned by 58% of managers), suggesting that unpopular regulatory systems would be less likely to be applied.

Overall, then, decisions about the regulation of annual harvest are based, in many cases, on inaccurate information about abundance, and are also influenced by which mechanisms are more traditionally used or are likely to be accepted in particular estates. Sustainability of partridge hunting could be improved if more effort was made to improve the reliability of abundance information, and to assess the most efficient, as well as acceptable, mechanisms to regulate annual take in different contexts (social and commercial estates).

Conclusions

Red-legged Partridge hunting is an important social and economic activity that occurs throughout Spain. Decisions about Red-legged Partridge management (including whether or not to release farm-reared partridges, how much to invest in predator control, and how much to hunt in a particular year or how to organize hunting pressure), are influenced by perceptions (framed in personal experience and tradition), beliefs (sometimes not supported by scientific data) and economic interests. Information used to take those decisions is sometimes inaccurate or imprecise. This implies that partridge hunting in Spain is moving towards a system increasingly based on farm-reared birds, a situation that is resented by an important part of the hunting sector. This shift is viewed by some hunters as necessary to maintain the economic viability of hunting estates, but results in this review show that this is not necessarily the case in all situations, and that improving conditions for wild partridge populations, clearly identifying estates using farm-reared birds, and increasing information quality about population abundance to improve the efficacy of regulatory systems could also help the sustainability of hunting this iconic game species.

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Does the Red-Legged Partridge Have a Future?

Jesús T. García and Fabián Casas

Many decades ago, in the middle of the twentieth century, Miguel Delibes, known as ‘the hunter that writes’, predicted a bleak future for partridges in the Lands of Castilla and also denounced unfair hunting practices and other wildlife abuses, supporting some of the beliefs of José Ortega y Gasset about hunting (see, for example, the prologue by the Spanish philosopher to *Veinte Años de Caza Mayor* [Twenty Years of Big-Game Hunting], by the Count of Yebes, originally published in Madrid in 1943). Delibes subsequently claimed several times that the ‘factory partridges’ could be endless. After reading the chapters of this book, it can be perceived that the predictions of Miguel Delibes have been, or are in the process of being, fulfilled.

The Red-legged Partridge is, primarily, a Mediterranean endemic species linked mainly to agricultural habitats (Chap. “Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?”), and also one of the most socioeconomically valued game species, especially in Spain, the stronghold of the species. The Red-legged Partridge has experienced a severe range-wide contraction and population decline during the past century due to a variety of human-mediated factors (Chap. “The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting”). Loss of suitable habitat due mostly to changes in agricultural practices, overhunting and releases of farm-reared

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F. Casas, J. T. García (eds.), *The Future of the Red-legged Partridge*, Wildlife Research Monographs 6, https://doi.org/10.1007/978-3-030-96341-5_12

specimens were the leading known causes for the current situation facing wild populations of the species (Chaps. “The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting” and “Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?”).

Looking over the past decades, it seems that we aligned our efforts in research on how partridges cope with different human-related activities and how to boost their ever declining numbers (Chaps. “The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting” and “Red-Legged Partridge Monitoring and Population Trends”). The need for immediate knowledge for management has been detrimental to knowledge on basic natural history, ecological and ethological research, which are basic tools and fundamental to a real and whole comprehension of species interaction networks. Some exceptions are recent studies in which the Red-legged Partridge was used to address burning questions in Evolutionary Ecology and that have improved our knowledge of its breeding systems, behaviour, ecology and physiology (Chaps. “Advances in Research on Ecophysiology and Evolutionary Ecology: The Red-Legged Partridge as a Study Model”, “Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?” and “The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future”). This recent attempt to follow the example of the Red Grouse or the Grey Partridge in the United Kingdom as a way to connect basic and applied research on a species is essential to deploy robust and effective – science-guided – management and conservation strategies. Unfortunately and in addition, the Red-legged Partridge tells us a lot about human impacts on the environment, with the scarce wild remnant populations used as good biological models for biomonitoring environmental pollution, such as the impact of pesticides, fertilizers, heavy metals, coated seeds and persistent organochlorine compounds (Chap. “Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes”), or to study the spread of pathogens acquired in farm environments into the wild because releases have the potential to disseminate bacteria, viruses and parasites into new areas and hosts, opening a Pandora’s box of diseases (Chap. “Health Monitoring and Disease Control in Red-Legged Partridges”). However, partridges also possess many of the hallmark traits of good bioindicators, especially to assess the health and quality of an environment and how it changes over time, informing – from a management perspective – our actions as to what is and is not biologically sustainable (Chap. “Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?”).

More recently, the wave of hunting has increasingly invaded the research conducted on Red-legged Partridges, with new fields of research that use approaches to understand and solve the genetic, ecological and sanitary problems of the releases phenomenon, as evidenced in the chapters of this book (see Chaps. “The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting” and “Is Predation the Key Factor of Partridge Ecology and Management?”, “The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future”, “Molecular DNA studies in the Red-Legged Partridge: From

Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization", "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing", "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes", "Health Monitoring and Disease Control in Red-Legged Partridges", and "Red-Legged Partridge Monitoring and Population Trends"). Most of this research tries to make releases compatible with the conservation of wild partridge populations (e.g. Chap. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"), which sometimes involves important conflicts between different stakeholder groups (Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). Undoubtedly, today's biggest issues for Red-legged Partridges are associated with, or exacerbated by, hunting.

Hunting is one of the oldest known recreational activities using wildlife. Hunting has a vital role to play for the sustainable future of the countryside, as it can benefit the development and economy of local communities, thereby promoting the protection of wildlife resources as well as both ecological and economic sustainability. For instance, hunting contributes to regulate the overabundance of certain species caused by anthropogenic disturbances that affect other species or ecosystems, and which may pose health risks or agronomic losses. However, the hunting–antihunting debate is old, still open (clearly defined by Ortega y Gasset in the aforementioned prologue), and it seems to have been reactivated based on moral, social and ecological issues. Many environmental and animal advocates see hunting as morally unacceptable, arguing that unlike natural predation, hunters kill for pleasure. Other people recognize a difference between a morally justifiable hunting (designed to secure the welfare of the target and non-target species and the integrity of its ecosystem) and a non-defensible hunting when it only benefits human beings. The internal debate remains open among hunters with opposing views on the conception – and practice – of hunting (fortunately the contemporary internal diversity is high!; see Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). The division is patent between the defenders of a natural and traditional interaction with nature ("*shooting as a way of life*") and the 'modern' sport hunters (Chaps. "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing" and "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain").

It is also unquestionable that hunting activities often lead to problems that might have negative consequences for wildlife and ecosystem conservation. The strong belief that 'game species were more abundant in the past than they are now' has driven us to manage game species more and more to meet the increasing demand of the hunting sector. However, if we look at history, we see that game species must have always been scarce (by definition, the desired animal is uncommon, neither plentiful nor constant); only now scarcity is exacerbated by other human-related alterations. Not surprisingly, many decisions in the human–partridge conflict have been influenced by perceptions, tradition, beliefs and economic interests, criteria that commonly go beyond the scientific evidence (Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain") and, of course, above the interests of the species itself. A major challenge of modern partridge hunting is how to balance the protection of wild Red-legged Partridge populations with the needs of hunters and local communities, closing the gap between scientific research and applicable sound solutions for the management and conservation of populations (Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). Note that the needs of partridges have not traditionally been fully considered and should now occupy the preponderant position with regard to local people or sectorial needs or demands.

It seems clear that the Red-legged Partridge has had the misfortune that humans noticed and chose her as the 'queen' of the small game (as it is known in Spain). It is a species iconic of the countryside in Western Europe with hundreds of years of active harvest and under active human management for decades. What we find today is a noticeable decline in its wild population and the contraction of its range (Chaps. "The Red-Legged Partridge: A Historical Overview on Distribution, Status, Research and Hunting" and "Red-Legged Partridge Monitoring and Population Trends"). An attempt has been made to counteract the population decline for some, or the scarcity of quarry for others, by restocking with farm-reared birds and intensive predator control programmes (Chaps. "Is Predation the Key Factor of Partridge Ecology and Management?", "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization", and "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"), without much success in both cases so far. However, the spread of restocking with farm-reared partridges to initially reinforce wild populations seems to have become an easy and rapid method to guaranty hunting quotas precisely at the expense of the wild populations themselves, covering the hunting needs but resulting in the loss of biological diversity, genetic integrity and ecological balance (Chaps. "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization" and "Health Monitoring and Disease Control in Red-Legged Partridges"). This is especially evident in intensive game estates (Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"), and maybe also in those game estates that cannot apply habitat management measures for favouring partridge populations (e.g. using beneficial agricultural practices for partridges) because they have no capacity for habitat management (in most of these cases because land property and the right for exploiting it belongs to others). Scientific evidence is unequivocal: massive releasing of farm-reared partridges (mostly *A. rufa* x *A. chukar*) homogenizes the genetic structuring of wild populations and contaminates the gene pool of the Red-legged Partridge with the genome of an exotic partridge (Chaps. "The Introduced Red-Legged Partridge in Britain: Management and Challenges for the Future" and "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"). Despite this, an important part of the hunting sector relies on restocking with farm-reared partridges, so that millions of partridges from farms are released every year in the countryside (Chaps. "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization" and "Enough Reared Red-Legs for Today, but Fewer Wild Ones for Tomorrow? The Dilemma of Gamebird Rearing and Releasing"). This is quite surprising and paradigmatic, as releasing hybrid birds is forbidden in all UE European countries by the Directives 2009/147/EC and 92/43/EEC (Chap. "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"). Partridge farming (rearing and releasing) is, for instance, one of the main challenges in the Red-legged Partridge Agenda for the twenty-first century. The involvement of European and National administrations is essential for the resolution of the partridge conflict, and they must work hard to develop a mature environmental legislation and to ensure compliance of our laws. However, we should not remain anchored to the hunting debate, and a greater involvement of researchers is needed to fill the knowledge gaps existing on partridges and in favour of a much more thoughtful science that guarantees, if possible, the persistence of the species in the face of the inevitable environmental changes that will occur in this new century. Priority should be given to species protection, and preserving or compatibilizing a suitable hunting use of the species should take a back seat to species protection in future research.

We have to think deeply on what traits of humanity have led to this situation. Undoubtedly, a logic based on the principle of endless economic growth so characteristic of capitalism – particularly in its neoliberal form – that have shaped over decades the management of agroecosystems and hunting practices. But also the importation of hunting practices from England early in the twentieth century, such as driven partridge shooting, which led to a considerable increase in the number of partridge losses. Or the vulgarization of hunting and its recent evolution towards recreation, entertainment and social interest, where no prior knowledge of hunting task and/or of the target species is needed (see Chap. "Social and Economic Aspects of Red-Legged Partridge Hunting and Management in Spain"). Another key issue has been the progressive shift from a game dominated by rural hunters, unhurried and little greedy, to an urbanite-hunter model with a greater need for shoots to help alleviate psychosocial stresses. It is probably time to move from our current instrumentalist view of nature, and the concept of ourselves as conquerors of nature, towards a more eco-centric worldview.

To preserve the remaining native Red-legged Partridge populations that are genetically unique, policy and management need to be implemented quickly; therefore, strict regulatory measures to protect wild populations from deliberate and/or accidental hybridization with exotic partridges should be the first step to draw up a species conservation strategy. The adoption of a proper traceability system for partridge releases is very simple and could be implemented at very low cost, also providing crucial data for researchers and managers on success of releases, movements of released birds, or the number and proportion of released vs. wild breeding stock that are harvested.

Research can help in this effort, and it is essential to further the development of science-based, quantitative conservation policies. In the chapters of this book, different authors have highlighted the main factors behind the decline of this species throughout its range, but it seems that acting on releases and habitat management could be the keys to recover wild Red-legged Partridge populations (Chaps. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?", "Is Predation the Key Factor of Partridge Ecology and Management?", and "Ecotoxicology Relevant to the Red-Legged Partridge and Other Galliformes"). On the one hand, today there are a plethora of methods and molecular tools that allow for fast and accurate detection of hybrids (Chap. "Molecular DNA studies in the Red-Legged Partridge: From Population Genetics and Phylogeography to the Risk of Anthropogenic Hybridization"), and adapted statistical methods can be applied to quantify the rates of hybridization in different populations (and therefore, estimate the actual wild stock), so as to advise proper conservation strategies. One of the challenges facing researchers is the need to determine population size measures and threshold levels of hybridization with the aid of population simulation software, to assist in determining the optimal conservation management strategy. The implementation of a hybrid culling policy must be preceded by accurate and strong statistical support after having performed simulations under various scenarios with different hybridization thresholds. However, quantitative evaluation of hybrid management is rarely performed, and molecular data are rarely integrated with management decisions in a quantitative, predictive framework.

In addition, further research is needed to determine and quantify the role of habitat and landscape on the incidence of predation in Red-legged Partridges, which would help to shed some light on the most efficient management and conservation measures (e.g. in cost/benefits for game managers) at long-term to favour Red-legged Partridge populations. Therefore, it is also urgent to determine how to improve habitat quality, favouring food and shelter availability and, therefore, survival and success of the partridges (Chaps. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?" and "Is Predation the Key Factor of Partridge Ecology and Management?"). In that way, it seems that a Common Agricultural Policy (CAP) that reinforces bird- and insect-friendly agricultural practices by introducing new commitments (and incentives) for beneficiaries can be essential (Chap. "Habitat Use and Selection: Is Habitat Management the Key to Restore Red-Legged Partridge Populations?").

Furthermore, researchers should begin to understand quickly the resilience or the ability of partridge populations to withstand both current perturbations and future threats, such as habitat loss, climate change, or changes in the amount and/or structure of predator communities. This knowledge must be considered and incorporated into policy and management to ensure viability of wild Red-legged Partridge populations.

Will we act while we still have time before Miguel Delibes' predictions come true? Or will the next generation of students, hunters and future scholars study the case of the *silent extinction of the Red-legged Partridge*?