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Conflict between grey partridge *Perdix perdix* hunting and hen harrier *Circus cyaneus* protection in France: a review

Elisabeth Bro, Beatriz Arroyo & Pierre Migot

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The recovery of protected predators raises tensions and divisions within society when their prey are of socio-economic value. For instance, conflicts may arise when hunters perceive protected predators as a threat for declining game populations, and cull them. These conflicts can have a strong impact on the status of the affected predator species. In this paper we review a conflict between hunters and raptor protectionists related to grey partridge *Perdix perdix* - hen harrier *Circus cyaneus* relationships in central northern France. We compiled all available information from scientific journals as well as hunting or protectionist journals, in order to present the polarised views of the problem and to analyse the social, political, legal and scientific aspects of the conflict. The results of existing studies suggest that in some circumstances hen harrier predation may have an impact on grey partridge populations. However, these studies also suggest that the problem is currently restricted to certain areas. The impact of hen harrier predation on grey partridge populations is not fully understood. Further research is therefore needed to better understand the ecological basis of the conflict. We also present and discuss potential solutions to alleviate predation that might help to reduce the conflict.

Key words: conflict, diet composition, hunting, predator-prey relationships, protection, socio-economics, solution

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Destruction of many predator species has been a feature of human development for centuries (Reynolds & Tapper 1996). The view of wildlife was dualistic: species were

divided into 'valuable' animals (those which had a commercial value or could be eaten) and 'vermin' (those which threatened human safety or food supply). Destruction of

the latter to local extinction was undertaken, for instance, for self-protection, protection of domestic stock or game and fur. In the last few decades, a new attitude towards wildlife has emerged (Charlez 1993). Protective laws resulting from international conventions and European directives (e.g. Fiers et al. 1997) have been implemented to protect animals and their habitats. As a consequence, the populations of a range of predator species have been recovering (Hagemeijer & Blair 1997, Mitchell-Jones et al. 1999). This recovery raises tensions and divisions within society when their prey are of socio-economic value (domestic animals, harvested or protected species; see Conover 2002). Well known examples of conflicts are those of wolves *Canis lupus* and live-stock producers in France, Spain and Italy (e.g. European Commission 1999), peregrine falcons *Falco peregrinus* and racing-pigeon *Columba livia* fanciers (see Lawton 1998), and fish-eating birds and fish farmers (e.g. Draulens 1987).

Similar tensions arise when hunters perceive protected predators as a threat for game. They are particularly acute when managers of hunting estates actively invest in land management, without the expected results; when hunting is intensive or non-sustainable; or when predators are subjected to illegal or excessive control with the purpose of maximising hunting bags. This is, for example, the case for raptors and released pheasants *Phasianus colchicus* in France, England and Sweden (Mayot et al. 1993, Kenward 1986, Kenward et al. 2001), hen harriers *Circus cyaneus* and red grouse *Lagopus lagopus scoticus* in Scotland (Thirgood et al. 2000a), and red kites *Milvus milvus* and rabbits *Oryctolagus cuniculus* in Spain (Villafuerte et al. 1998). These conflicts may have a strong impact on the status of the affected raptor species. For example, poisoning and shooting have led to major reductions in both geographic range and numbers of red kites in Spain (Villafuerte et al. 1998) and hen harriers in the United Kingdom (Etheridge et al. 1997).

Among these, the hen harrier - red grouse conflict on grouse moors in the UK is the best documented. Predation by raptors, in particular by the hen harrier, when they occur at high density can limit grouse populations (Thirgood et al. 2000b). On the other hand, hen harriers are of particular conservation concern in Britain where illegal control on grouse moors limits their range and abundance (Etheridge et al. 1997). The dilemma is that uncontrolled populations of raptors can destroy the economic viability of grouse moors and thus remove the incentive for landowners to conserve heather moorland which is of international conservation importance, and critical for breeding hen harriers.

Since the early 1960s, the science of damage management suggested a range of methods to try to resolve human-wildlife conflicts (see Conover 2002). A recent European project, 'R.E.G.H.A.B.' (Viñuela & Arroyo 2002), addressed specifically the conflicts involving gamebird hunting and raptor protection. It reached the conclusion that solutions valid for one conflict are unlikely to be applicable to other conflicts, particularly if the socio-economic aspects of hunting vary. Nevertheless, the evaluation of various conflicts may help assess whether general patterns arise, and also give insight into the development of general guidelines for the resolution of such conflicts. Thus, in this paper we review a conflict between hunters and raptor protectionists related to grey partridge *Perdix perdix* hunting and hen harrier protection in central northern France. This conflict has never been thoroughly addressed. We compiled all available information from scientific journals as well as popular journals of hunters and protectionists to analyse the conflict. We report both the social and ecological backgrounds, and the scientific knowledge about the impact of raptor predation on partridge populations. We discuss potential solutions to alleviate predation, referring to previous knowledge and lessons from other conflicts.

Legal background: status of the hen harrier and the grey partridge

France has progressively enacted raptor protection through decrees in the 1960s - early 1970s and laws in 1976 (Charlez 1993). The hen harrier is currently fully protected: it is listed in Annex I of the European Bird Directive, Annex II of the Bern, Bonn and Washington Conventions (Rocamora & Yeatman-Berthelot 1999), and this international legislation has been included in the French regulation (Code de l'Environnement 2000) protecting harriers against destruction, disturbance, capture, transport, detention and trade. The code also protects their breeding and wintering habitat.

In contrast, the grey partridge is listed in annexes II and III of the European Bird Directive and annex III of the Bern Convention (Rocamora & Yeatman-Berthelot 1999), allowing hunting and trade.

Social background: views and perceptions

Grey partridge hunting in France

Grey partridge hunting is a communal activity that occurs in autumn throughout France, by both driven and walk-up hunts (see Birkan & Jacob 1988). The grey partridge is the most highly appreciated small game in French cereal ecosystems (ONCFS 2000), particularly in cen-

tral northern France. In this region, 900,000 grey partridges were harvested by 470,000 hunters during the 1998/99 hunting season (ONCFS 2000).

French hunters are concerned by the decline of partridge populations, and the future of hunting. In the 1970-1980s, releases of hand-reared birds were promoted with the hope of reinforcing, and thus restoring, wild populations (Havet & Biadi 1990). Since then, release of hand-reared birds has been extensive (Table 1). This practice, however, is causing concern because it may have direct adverse effects on wild stocks through sanitary problems or genetic pollution. In addition, it does not encourage hunters to manage wild populations and the habitat. Numerous French hunters therefore reject releases and strive instead to preserve (and thus hunt) wild birds. For this purpose, they have voluntarily restricted their hunting bags since the mid-1980s. Bags may now be limited by a quota, a limited number of hunting days or other local rules (Reitz 2003b). A quota is determined through a hunting plan based on surveys of population density (spring counts) and an estimation of breeding success (covey survey in summer; Reitz 2003a). The quota may be zero when densities and/or reproductive success are too low. Such population management is, however, only undertaken on hunting estates where hunters agree to such limitations to manage their wild population. On other hunting estates, often practising releases, there are no particular rules of shooting limitation.

Hunters also manage their land to preserve wild stocks. They control predators to limit losses of breeding partridges, eggs and chicks, they provide food to laying partridges and to birds during winter, and they manage the habitat to provide nesting sites, refuge cover in summer-winter, and invertebrates for chicks (see Bro et al. 2005 and references therein).

History of the conflict

When laws protecting raptors in France came into force in the 1970s, partridges were abundant, in particular in the Beauce region, where the conflict first arose later on (Garrigues 1981), and harriers were scarce (FIR-UNAO 1984), so no conflict existed.

During the 1980s, hunters from the Beauce region noticed a decline in partridge and an increase in harrier abundance (Lett & Perrot 1990). They complained about harriers killing partridges, whereas protectionists said that harrier numbers were limited to a few tens of pairs in Beauce (FIR-UNAO 1984, FIR 1993, 1995a). In 1986, hunters and protectionists asked for an official assessment of harrier abundance. This demand coincided with the application by hunters for the first partridge hunting quota. Harrier counts were first conducted in Beauce in 1987 and were extended to neighbouring regions during the early 1990s (see Table 1). Both stakeholder groups recognised the presence of hen harriers in areas where partridges were hunted, at densities of 1.5-3 harriers/10 km².

Table 1. Existing data on population range, abundance and trend of hen harriers and grey partridge in France, as assessed through extensive monitoring and specific studies.

	Hen harrier	Grey partridge
National breeding range	<ul style="list-style-type: none">evaluated in 1970-1975 and 1985-1989 \Rightarrow recent colonisation of central northern France by breeding harriers (see Fig. 1; Yeatman-Berthelot & Jarry 1994)evaluated in 2000 (Thiollay & Bretagnolle 2004)	<ul style="list-style-type: none">evaluated in spring 1970-1975 and 1985-1989 (Yeatman-Berthelot & Jarry 1994)presence/absence evaluated in 1979 (unit sampling: farming region; Garrigues 1981)presence, status (wild, release) and abundance evaluated in 1998 (unit sampling: commune; Reitz 2003b) \Rightarrow range contraction (see Fig. 2)
National breeding population size (in pairs)	<ul style="list-style-type: none">France early 1980s: 2,700-3,800 (FIR-UNAO 1984), 2000: 7,800-11,200 (Thiollay & Bretagnolle 2004)Europe (without Russia): 8,332-10,840 (Hagemeijer & Blair 1997)	<ul style="list-style-type: none">France early 1980s: ca 900,000 (Hagemeijer & Blair 1997); 1998: 750,000 (Reitz 2003b) \Rightarrow decrease in numbers by ca 20%Europe (without Russia): 1.7-2.9 million (Hagemeijer & Blair 1997)
Spring abundance of local populations in northern France	<ul style="list-style-type: none">Beauce region, late 1980s - early 1990s : 1.5-3 ind/10 km² (Lett & Perrot 1990, Fossier 1993)Central northern France, 1995-1997: 0.5-4 ind/10 km² (see Fig. 4)Champagne region: early 1990s: 2.5-3 pairs/100 km², late 1990s: 6.5-7 pairs/100 km² (Millon et al. 2002) \Rightarrow 3-fold increase of breeding pairs in a 650 km² study area (such trend not observed on other study sites; Thiollay & Bretagnolle 2004)	From a few pairs/km ² to 80 pairs/km ² depending upon hunting estates (large variability at a small spatial scale and across years; see Fig. 2 and Bro et al. 2005)
National hunting bag		<ul style="list-style-type: none">1983-1984: 2.2 million birds (Birkan 1986) / 1.9 million hunters1998-1999: 1.5 million birds (ONCFS 2000) / 1.5 million hunters <p>The proportion of released partridges is unknown</p>
Release of hand-reared birds		<ul style="list-style-type: none">2 million grey partridges reared in France in 1995 (Tupigny 1996)releases mostly practised in areas where the grey partridge has declined (Reitz 2003b)

In the 1990s, hunters claimed that hen harriers were partly responsible for the low reproductive success of partridges (Anon. 1994a,b,c), and consequently for the small hunting bags. The conflict was particularly acute in 1994-1995. A legal control of harriers by government officials was officially demanded by hunting authorities (see Anon. 1994a,b,c). Hunters attributed the *status quo* to political reasons (to satisfy the 'Ecologist' Party in view of politic alliances for local and presidential elections in 1995; Anon. 1995). Full protection of raptors was perceived by hunting authorities to be an 'anti-hunting strategy' (Anon. 1994c). At the same time, an increasing number of raptors carrying gunshot pellets were sent to recovery centres in late 1994 - early 1995 (FIR 1995b). This was interpreted by protectionists as a political pressure from hunters that constitute an important part of the electorate (FIR 1995b) and have a political party that may be locally important.

A few years later, the question of hen harrier control was addressed by a deputy defending hunting interests to the Ministry in charge of the Environment, who answered that there was no valid reason to regulate harriers (J.O.R.F. 1998).

Hunters and raptor protectionists' views

In areas where the grey partridge has become a rare bird hunters have been releasing hand-reared birds to satisfy shooting interests (see Reitz 2003a). In many other areas, hunters tried to preserve a high abundance of wild grey partridges (see 'Grey partridge hunting in France'). They had to reduce their bags to reach this goal (ONCFS, unpubl. data), and many of them were therefore frustrated. Moreover, they felt that they did not always benefit from their efforts to manage the grey partridge, in the sense that hunting bags either kept on declining, sometimes leading to no hunting, or did not increase as wished. They often attributed this situation to the recovery of the hen harrier, i.e. to a high predation rate on breeding birds and chicks (Anon. 1994a,b, 1995). Hunters perceived hen harriers as competitors because they share a resource, the grey partridge. The most contentious problem is that harriers may feed on partridges before hunters are allowed to hunt them; the hunting season opens in late September in northern France. Hunters generally considered hen harriers to be too abundant (see Tournier 1996). Thus, despite raptors being fully protected in France, some hunters (proportion unknown) culled harriers (e.g. FIR 1994, 1995a, 1997) for one or both of the following reasons. First, they perceived the hen harrier in central northern France as a further threat for the declining grey partridge populations. Second, hunters could not understand why no legal measures were under-

taken in response to their demand for control of hen harriers (Anon. 1995). It is, however, important to note that a moderate opinion was also reported in hunting journals explaining that the problem of the partridge is complex because of its multi-factorial elements, e.g. habitat, farming practices, predation and hunting abuse. To limit raptor predation, habitat management was advocated (Burias 1998).

On the other hand, protectionists considered that the demand of the hunting lobby to control hen harriers had no basis for the following reasons (see FIR 1995a): harriers mainly feed on small mammals and passerines, gamebirds only represent a small part of their diet, and the partridges eaten are likely either to have been weakened by other causes or to already be dead (see Clarke & Tombal 1989, Farcy 1994). Thus, hen harriers have, according to protectionists, no important adverse impact on partridge populations (FIR 1995a, Tombal 1982). Raptor protectionists argued that the grey partridge mostly suffered from simplified habitat and intensive farming practices (FIR 1995a), and that harriers were being made scapegoats for the failure of management to increase partridge populations (FIR 1995a). Moreover, they considered that harrier increase was not as marked as the hunters claimed (FIR 1993, 1995a). Indeed, the hunters' perception of harrier abundance (and thus of the predation rate) is likely to be psychologically biased by the behaviour of this species. First, the species is present throughout the year and is diurnal. Second, its abundance increases in autumn due to immigration of north-eastern birds, and the increase starts in September, before the opening of the hunting season. Third, harriers may congregate semi-colonially in roosts, which makes them highly visible. Fourth, its flapping and gliding hunting flight and the male's black and grey plumage are especially conspicuous and thus attract attention. Fifth, its hunting success is also relatively poor (Madders 2000) so the birds have to spend much time in the air hunting for food [author's comment]. Additionally, raptor protectionists accused hunters of killing raptors indiscriminately. Indeed, culling is conducted through shooting, poisoning and nest destruction (FIR 1994, 1997), and some of these methods are unselective. Protectionists claimed that some poisoning incidents were the result of deliberate abuse (FIR 1997), congruently with the analysis of Berny et al. (1998) reporting that insecticide poisoning (especially with carbamates) was attributed to criminal baits whereas poisoning involving anticoagulant rodenticides (such as bromadiolone) was suspected to be secondary poisoning (i.e. accidental misuse).

Scientific background to the conflict: facts and unknowns

Overlap between hen harrier and grey partridge breeding phenology

The breeding phenology of hen harrier and grey partridge coincides. Egg laying of harriers lasts from mid-April to late June, and hatching commences after a 32-day incubation period (Millon et al. 2002). Maximum food requirements for nestlings and fledglings lasts from May to August. Male harriers supply food for females and nestlings until ca 15 days after hatching; thereafter the relative contribution of the female increases. Females prey upon larger and heavier prey than males, so composition of food brought to the nest is likely to change during summer (Schipper 1973). Hatching of partridge chicks peaks in mid-June (ONCFS, unpubl. data). Chicks do not fledge before 3–4 weeks of age (Birkan & Jacob 1988), and thus are particularly sensitive to predation at that stage. Incubating females and partridge chicks are therefore temporally available as food for harrier chicks.

Hen harrier migration

The hen harrier is partially migratory. Birds from northern Europe overwinter in France in addition to French sedentary or dispersing breeding birds (Yeatman-Berthelot & Jarry 1991). Migrants pass through France or arrive in France during September–December. Migration in the opposite direction occurs in March.

Demographic status of the hen harrier and the grey partridge

Both the hen harrier and the grey partridge were listed as 'Vulnerable' species at the European scale because of a large decline in numbers in the 1990s (Tucker & Heath 1994, BirdLife International 2004). The largest populations of western Europe occur in France for both species (see Table 1). The sustainability of the French population is therefore important to the long-term conservation status of both species in Europe (Rocamora & Yeatman-Berthelot 1999). However, harriers and partridges show opposite trends both in numbers and range in France.

Hen harriers have increased both spatially and numerically. Their breeding range expanded into northwestern France between the early 1970s and the late 1980s (Fig. 1). Breeding density has also increased at least in certain areas (see Table 1). Because of this recovery, the status of the hen harrier is not considered as unfavourable in France at the present (Rocamora & Yeatman-Berthelot 1999, Thiollay & Bretagnolle 2004). This expansion corresponded to a recent colonisation of cultivated

areas for breeding (Yeatman-Berthelot & Jarry 1994). Because many clutches and nestlings in cereals are likely to be destroyed during harvesting in this 'new' habitat, the population has been classified as 'to be monitored' despite the range expansion (Rocamora & Yeatman-Berthelot 1999).

In contrast, as a result of a declining national population, the status of the grey partridge in France is considered as unfavourable (Rocamora & Yeatman-Berthelot 1999). Indeed the range of the species has been reduced and its global abundance has decreased by ca 20% since the late 1970s, despite contrasting regional patterns (Reitz 2003b; Fig. 2). Long-term trends are, however, difficult to identify because of large year-to-year fluctuations and high between-site variability (Bro et al. 2005), and because data are scarce when densities are low. Moreover, systematic partridge counts have only been available since the late 1980s (data collected for hunting plans; see Fig. 2), which is after the assumed partridge decline. Partridges have declined due to a combination of factors, including changes in land use and agricultural practices (e.g. Chamberlain et al. 2000).

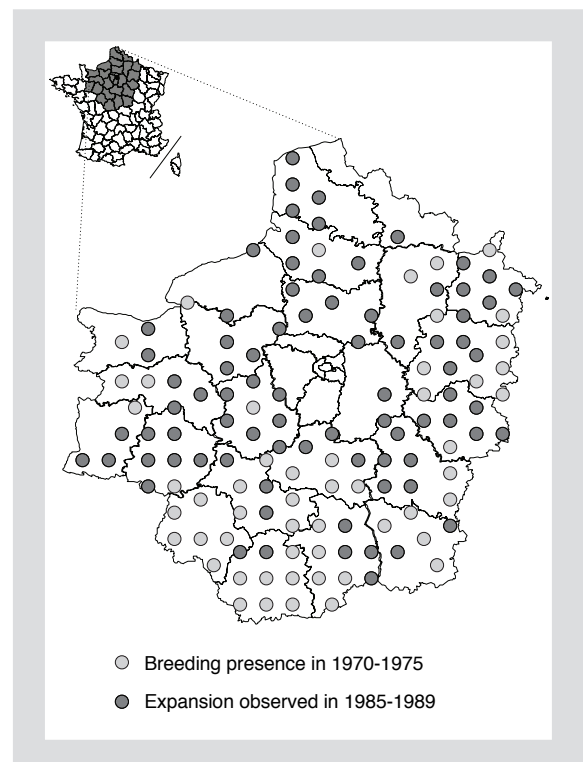


Figure 1. Recent change in distribution of breeding hen harrier in central northern France according to Yeatman-Berthelot & Jarry's (1994) bird atlas.

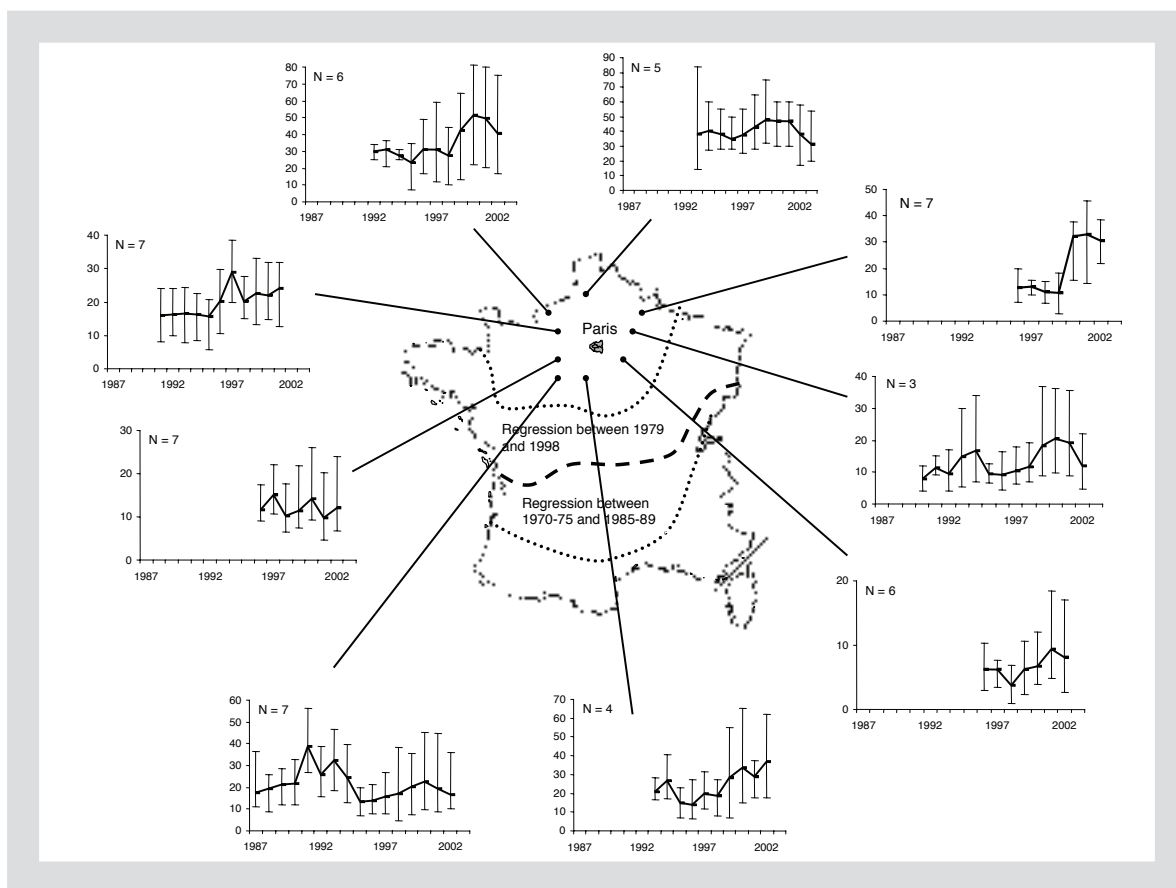


Figure 2. Recent change in national distribution of the grey partridge (from Yeatman-Berthelot & Jarry 1994, and Reitz 2003b). The graphs show year-to-year fluctuations in breeding densities (in pairs/100 ha; min, max) since 1987. N indicates the number of hunting estates.

Correlation between hen harrier and grey partridge presence, abundance and trends

Lack of extensive long-term monitoring of the avian community in farmland does not allow us to establish with accuracy whether the increase in hen harrier and the decrease in grey partridge coincided geographically and temporally. Fragmented data gathered from atlases and the national grey partridge survey (see Table 1, Figs. 1 and 2) may only roughly suggest such a correlation. Indeed, extensive monitoring of partridge populations started in the early or mid-1990s, only after the beginning of harrier colonisation and the assumed decline in partridge numbers in central northern France.

Quantification of raptor predation on grey partridge

To document robustly the importance of raptor predation on grey partridge mortality and its impact on population dynamics, a large-scale field study was conducted in central northern France during 1995-1997 (see Bro

et al. 2001). The mortality rate of partridges was estimated by radio-tracking ca 1,000 adult females on 10 contrasting sites in spring and summer to identify and quantify mortality causes. Simultaneously, the abundance of red foxes *Vulpes vulpes*, harriers and medium-sized mustelids was estimated in the same areas, and habitat characteristics were described.

Overall mortality rates of breeding females during March-September averaged 50% (values ranging within 35-75%; Bro et al. 2001). Similar results were found by Reitz et al. (1993) a few years before in the Beauce region. Mortality mainly occurred during May-July when females incubated their eggs (Bro et al. 2001). No increase in mortality was observed in late August-September when harriers migrate through France. Predation was the main mortality cause (75%), whereas farming practices were responsible for only a few mortality cases (Bro et al. 2001). Putative predators were identified through the state of the body remains. Raptor predation was identified through the presence of plucked feathers

and partially consumed prey, and mammal predation was identified through broken feathers and consumed viscera. However, predator species could not be identified from the remains.

These results confirmed that losses of adult partridges might be high during spring and summer, and associated the extent of the hen harrier problem with specific geographical regions (Fig. 3). The study also showed that the high mortality rates could not be attributed to scavenging (even though slight biases cannot be excluded) or sanitary problems (Bro et al. 2001). Biases due to radio-tagging were also taken into account (see Bro et al. 1999, Bro et al. 2001).

A series of correlations were drawn from the field data (Table 2). Partridge survival rate was negatively correlated with predation rate suggesting that predation was at least partially additive to other mortality causes. The relationship between the predation rate attributed to rap-

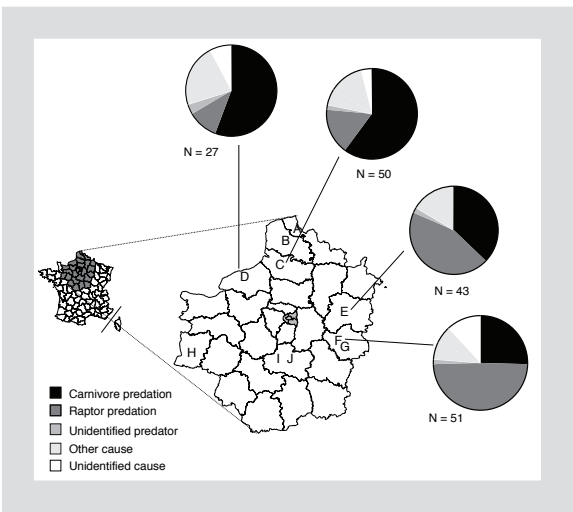


Figure 3. Mortality causes of breeding grey partridge in central northern France. N indicates numbers of dead radio-tagged partridges (see Bro et al. 2001).

Table 2. Scientific facts and unknowns that should be addressed to further understand the ecological basis of the conflict.

	Scientific facts	Further data and analyses needed
Correlation between hen harrier and grey partridge presence, abundance and trend	Negative correlation (spatial contrast) between hen harrier density in spring and partridge breeding density (Bro et al. 2001)	<ol style="list-style-type: none"> 1. Extensive monitoring of bird populations and their habitat on the long term and on a large geographic range using a rigorous design. 2. Joint analysis of partridge and harrier trends (spatial and temporal coincidence). In particular long-term survey of partridges and harriers in areas being colonised by harriers to assess the impact of harriers on partridge populations (replicated pseudo-experimental design to 'test' whether harriers limit partridge numbers and under which conditions they do so). 3. Estimation of harrier numbers and fluctuations throughout the year (spring-summer, winter, migration period)
Impact of hen harrier predation on grey partridge populations	<p>Expansion of breeding hen harrier in northwestern France in the early 1970s - late 1980s (see Fig. 1). Regression of partridge distribution in southern, eastern and western areas of its range (see Fig. 2).</p> <p>Since the mid-1990s: decline of partridge densities in some regions (Beauce; see Fig. 2), increase in hen harrier abundance (Champagne; Millon et al. 2002), but lack of data for the same areas.</p> <ul style="list-style-type: none"> • Adult partridge killed by raptors are likely to be healthy (Bro et al. 2001). • Mortality of breeding females peaks in May-July during incubation (Bro et al. 2001). • 40 and 20% of first and replacement clutches, respectively, fail due to the death of incubating females (Bro et al. 2000a). • The growth rate of partridge populations is most sensitive to breeding female mortality during incubation (Bro et al. 2000b). • Predation rate and raptor predation rate are positively correlated to harrier density (Bro et al. 2001). • Spring-to-summer survival of partridge females is negatively correlated to (raptor) predation rate (Bro et al. 2001). • Predation risk by a raptor is related to habitat characteristics, e.g. cover height (Reitz & Mayot 2002). 	<ol style="list-style-type: none"> 4. Importance of female versus male harriers as partridge predators. 5. Estimation of harrier predation rate on partridges (adults/chicks) throughout the year in relation to partridge total losses and life cycle stages (radio-tags with a 1-year lifetime on adults, continuous observation of harrier nests). 6. Use of modelling to assess the impact of harrier predation rate on partridge population dynamics under different scenarios (additivity vs compensation). 7. In addition to (2), an experimental study comparing partridge population dynamics in areas where harrier abundance or productivity would be reduced, and in areas where harriers are protected to test whether harrier predation is additive or not and limit partridge abundance and/or productivity. 8. Investigation of predation-habitat interactions (behavioural and landscape ecology), recently examined (Guyon 2005)
Hen harrier diet	<ul style="list-style-type: none"> • Numerous studies of diet composition in different years, seasons, regions and habitats. Hen harriers may feed on partridges in cultivated farmland both in spring-summer and winter (see Table 3). • Partridge contribution in numbers is low (< 5%), but contribution in weight may reach 15%. The proportion does not vary between years (Millon et al. 2002). 	<ol style="list-style-type: none"> 9. Long-term multi-site survey to draw the correlation between the proportion of partridges in harrier diet and partridge abundance (functional response) in relation to small mammal abundance at different stages of harrier and partridge life cycles. 10. Food provisioning experiment. 11. Diet composition of hen harriers in areas where partridge losses are high. 12. Diet composition of male vs females, changes in prey composition during chick provision. 13. Diet per nest to assess whether some harriers specialise on partridges in relation to local abundance of partridges

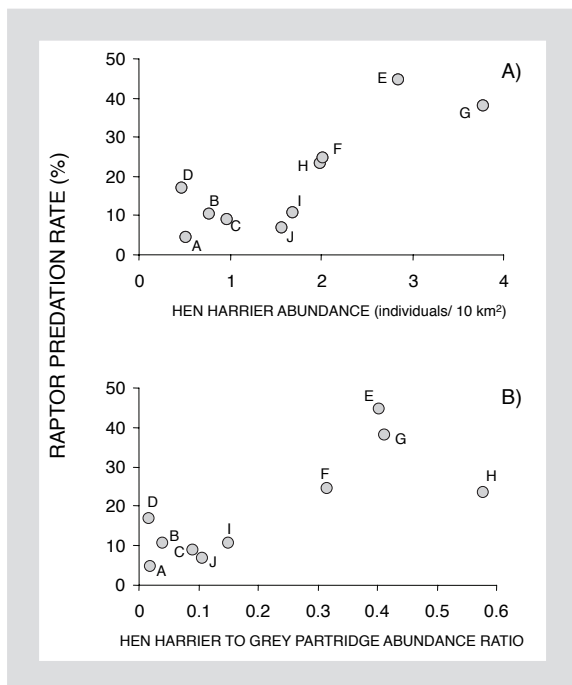


Figure 4. Positive correlations between spring-to-summer raptor predation rate on female radio-tagged partridges and hen harrier density (A) or hen harrier to grey partridge abundance ratio (B). Capital letters refer to study areas (see Fig. 3).

tors and hen harrier abundance was significantly positive (generalised linear model using a binomial distribution and a logit link function, $\chi^2_1 = 16.99$ $P < 0.001$; Fig. 4A). Similar results were observed between raptor predation rate and hen harrier to grey partridge abundance ratio ($\chi^2_1 = 16.66$ $P < 0.001$; see Fig. 4B). However, these relationships are correlative and may include potential confounding effects (see Bro et al. 2001, Evans 2004). Additionally, some questions remain open, e.g. whether analogous relationships exist between predation rate and partridge chick abundance, harrier productivity or abundance of harrier main prey. Scientific unknowns that should be addressed are further described in Table 2.

A high predation rate by raptors on partridges in autumn and winter was also observed (ONCFS, unpubl. data), but the data were not fully reliable due to a suspected high radio-tag bias (high mortality rate of tagged birds just after manipulation and release).

Mortality rates of chicks up to the age of six weeks ($N = 101$ broods with a radio-tagged female) ranged within 40–80%, but mortality causes could not be identified (ONCFS, unpubl. data).

Impact of raptor predation on grey partridge population dynamics

To investigate the impact of the mortality rates on partridge population dynamics, an elasticity analysis was carried out in a stochastic environment using a matrix model (see Bro et al. 2000b for further details). The analysis ranked model parameters in order of importance for the population growth rate (λ). The outputs showed that survival of females during breeding was the most crucial parameter for λ . Reproductive success appeared to be the second most crucial parameter after female survival (because nest success depended on female survival).

Hen harrier diet

Hen harrier diet in France has been analysed in several habitats and seasons (Table 3). Results indicate that diet composition varied greatly among studies. The feeding strategy probably depends upon prey availability (opportunism). Small mammals often represent the most important part of the diet of harrier populations, but harriers may feed on a large variety of prey: from arthropods and earthworms, to medium-sized mammals (including young lagomorphs) and a range of bird species including gamebirds (partridges and quails *Coturnix coturnix*). The species therefore displays in France a generalist predatory behaviour. Other diet studies in different countries reached the same conclusions (e.g. Schipper 1973, Clarke et al. 1993, 1997). The studies, however, did not document whether individual harriers might specialise on one type of occasional prey or forage in specific habitats.

Grey partridges appear in the diet of hen harriers inhabiting cultivated areas both in winter and spring-summer, although only occasionally (0–3% of diet composition by number; see Table 3). The most detailed study was carried out in the Champagne region (Millon et al. 2002), where Bro et al. (2001) found the highest grey partridge mortality rates. Millon et al. (2002) examined the spring and summer diet of the hen harrier during eight years (1993–2000). They found that the most important prey species by weight was microtine rodents (accounting for ca 45% of the diet) and passerines (ca 30%), but galliforms and lagomorphs accounted for ca 15 and 10% of the diet by weight, respectively (although only 3.2 and 1.2% by number). The shares of gamebirds and lagomorphs are much more important when results are given in weight contribution than when they are given by number. This discrepancy occurs because prey as large as partridges or young hares *Lepus* sp. or rabbits are highly profitable. So diet results may be reported in two different ways depending upon the message one

Table 3. Hen harrier diet composition in France expressed as % composition by number.

Season	Year	Area	Month	Sample size	Diet composition					Reference
					Small mammals	Lagomorphs	Game birds	Other birds	Other prey	
Winter	?	cultivated area and wetland and forest (Nord Pas-de-Calais)	/	83 pellets + 11 prey remains	52.7 mammals		2.1 (grey partridge)	33.3	11.8 (earthworms)	Tombal (1982)
	1983	? (Picardie)	February-March	177 pellets	81.2	0	0	18	0.7 (frogs)	Robert & Royer (1984)
	1989	cultivated area (Nord)	February	96 prey items	27.1	17.7	3.1 (grey partridge)	52.1	0	Clarke & Tombal (1989)
	1979-1981	wetland (Normandie)	January-March	214 pellets + prey remains	95.45	0.15	0	4.1	30	Chartier (1991)
Spring-summer	1976-1977?	forest (Picardie)		19 pellets	3.4	0	0	27.6	69 (invertebrates)	Delcourt (1977)
	1976-1977	? (Picardie)		26 pellets	4.6	0	4.7	39.5	51.2 (invertebrates)	Robert & Royer (1984)
	1991-1992	cultivated area (Pas-de-Calais)		66 pellets (5 nests)	29.2	7.7	1.5	58.2	3.1 (insects)	Farcy (1994)
	1993	?		415 prey items (1 nest)	90	?	?	?	?	Maurel (1995)
	1993-2000	cultivated area (Champagne crayeuse)	June-July	2049 prey items (pellets and prey remains)	63.7	1.2	3.2	29.9	0.8	Millon et al. (2002)
	1976-1978	livestock farming landscape - pastures,		26 prey items	15.4	11.5	3.8 (red-legged partridge)	61.5	7.7 unspecified mammals	Nore (1979)
	1972-1982	forests, hedges (Limousin)		43 prey items	25.6	7	2.3 (red-legged partridge)	65.1		Grafeuille (1983-1984)

wants to convey, and this is a source of conflict [authors' comment]. According to their data (Millon et al. 2002), the proportion of small game species did not increase over time and varied only slightly from year to year.

Do hen harriers limit partridge populations?

Field data together with the modelling simulations previously described suggest that raptor predation has an impact on partridge populations. Existing data, however, are insufficient evidence to confirm that harrier predation actually limits partridge densities both because essential information is lacking and because objective data are incomplete (see Table 2). First, the above-mentioned study on partridge mortality did not identify the species of raptor actually preying upon partridges. Second, the relationship between partridge predation and harrier abundance was correlative, not causal. Third, the studies of hen harrier diet were independent of partridge mortality data and did not quantify partridge abundance, which makes it impossible to evaluate the impact on partridge populations.

The conflict, in this particular case, is enhanced by the scarcity of quantitative data for certain aspects, which

allows stakeholders to bias perceptions in relation to the importance of concepts such as 'occasional prey' and 'increasing numbers'.

Hen harriers have recovered and colonised cereal agroecosystem during the few last decades and people tend to worry [authors' comment]. However, current scientific evidence does not prove, or disprove, that harriers actually limit partridge numbers.

Impact of predation on an occasional prey: theoretical considerations

The Alternative Prey Hypothesis (see review of Valkama et al. 2005) states that generalist predators do not limit prey populations, or only do so during short periods of time (e.g. when the main prey is scarce), because predators switch between prey species as their relative availability changes. However, more up-to-date theoretical work credited predation with a more important influence on populations of alternative prey. The Shared Predation Hypothesis (see Valkama et al. 2005) states that if predators are not so selective in killing their prey, then all prey are negatively affected when the densities of predators are high, because mortality of alternative

prey depends directly on predator encounter, and thus abundance. Known examples are goshawks *Accipiter gentilis* taking wild pheasants in areas where rabbits are abundant (Kenward 1986), hen harriers taking red grouse in moors with high passerine and vole densities (Redpath & Thirgood 1999), and red fox taking grey partridge in areas with abundant hare *Lepus europaeus* and rabbit populations (Reynolds & Tapper 1996). In these cases, the impact of predators on the alternative prey depends on the ratio of predators to the alternative prey, and not on the ratio of predators to the main prey as stated by the Alternative Prey Hypothesis. Under these conditions, predation may be destabilising, especially when predation is inversely density dependent (see Valkama et al. 2005 and references therein), and prey populations are particularly vulnerable when their density is low. So the impact of predation is dependent on the population status of the prey, which is likely to be governed by a number of factors other than predation. This means that, under particular circumstances, predators may trap their prey in a stable state of low density ('predation-pit', see Newsome et al. 1989, Evans 2004) and prevent any prey population growth.

Possible technical solutions to the conflict

The recovery of populations of predator species that were previously depressed has increased the call for solutions to predation problems. Potential solutions are numerous and fall into behavioural (e.g. diversionary feeding, or landscaping techniques to minimise predation risk), demographic (controlling predator numbers through intraguild predation, translocation or lethal methods) or financial solutions (incentives for maintenance of predator numbers, or compensation for loss of game). Potential solutions are discussed in the following sections in order of increasing severity of intervention with regard to protection laws. Further information can be found in Kenward (1999), Jimenez & Conover (2001) and Conover (2002).

Diversionary feeding

A 2-year experiment was carried out as a possible solution to alleviate harrier predation on grouse in British moors (Redpath et al. 2001). Harriers were provided with substitute food close to their nests, and predation on grouse chicks decreased significantly, suggesting that this technique is potentially efficient in reducing the impact of raptors on game species. Supplementary food might, however, have a positive effect on harrier numbers in the long term by increasing their overall reproductive success through polygyny rates, clutch size, productivity or fledgling survival (Simmons et al. 1986,

Amar & Redpath 2002), for which reason this solution is unpalatable to hunters until the possible effects have been determined (Redpath et al. 2004).

As this solution is costly (Redpath et al. 2001), time consuming and probably indefinite, it raises practical questions such as 'who should pay?' and 'who should do it?'. Hunters would probably be reluctant to spend time and money on feeding their 'enemy'. Raptor protectionists may disagree to spend time and money on feeding harriers just to enforce an existing law. However, this solution would be worth testing experimentally involving stakeholders, both to analyse harrier and partridge responses in the long term, and to assess stakeholder reactions to this very solution.

Landscaping techniques

A potentially valuable solution would involve habitat changes to minimise the risk of predation. Recent research showed that strips of tall cover could lead to a 'trap' for partridges in winter by concentrating both prey and predators on small isolated areas (Bro et al. 2005). Such a trap effect has often been reported (see Jimenez & Conover 2001). More research is therefore needed to find efficient habitat management schemes.

Land management for game purposes is difficult both because hunters do not always/often own the land where they hunt, and because agricultural producers are economically dependent on their land and most of them do not accept many constraints with regards to wildlife management (see Rambaud 1991). However, habitat management is a good candidate technique to solve the conflict, first because agriculture modernisation (e.g. pesticides use, monoculture and disappearance of idle land) is the primary cause of the overall wildlife decline in farmlands (Chamberlain et al. 2000), and because predation interacts with habitat in many different ways (Evans 2004). The European Common Agricultural Policy compelling the protection of the environment has been obligating farmers to restore habitat at a large scale in Europe since 2005 (recent CAP reform forcing the implementation by Member States of decoupling, modulation and cross-compliance on agricultural direct subsidies).

Intraguild predation

Another potential solution lies in restoring the primary community of predators by reintroducing or reinforcing top predators that interact competitively or prey upon medium-sized predators. Intraguild predation is recognised as a major influence on the abundance and distribution of some mammalian predators (e.g. Jimenez & Conover 2001).

The red fox is likely to reduce harrier breeding suc-

cess (Schüpbach 1996, Redpath et al. 2001). Potts (1998) reported cases where the abundance of harriers and red foxes were inversely proportional. However, the results of Green & Etheridge (1999) did not support this hypothesis. In fact, little is known about the impact of red fox predation on harrier populations. This issue could be documented experimentally, but an increase in fox numbers would almost certainly have detrimental effects on partridge populations because the red fox is a principal predator of partridges (Birkan & Jacob 1988, Bro et al. 2001).

Raptor translocation

Translocation was proposed in the UK to alleviate predation on grouse through maintaining harrier abundance at a level that does not negatively influence the economic viability of grouse moors (Potts 1998, Watson & Thirgood 2001). It has been used for goshawks at pheasant release sites (Marcström & Kenward 1981). Goshawks did not return to their capture site when they were translocated far enough.

Translocation is appealing because it is a non-lethal method that may improve the conservation status of the species, through an increase in their distribution range. However, this solution “seems unlikely to [...] play a major role in reducing conflicts” (Watson & Thirgood 2001). Indeed translocation could transfer the problem to other areas, unless these are areas with lower hunting interests, and it would have to continue indefinitely or for as long as gamebird areas attract raptors. Moreover, translocation is not generally recommended to solve bird problems because: 1) the translocated birds generally return home (at least adult birds), and 2) open territories are likely to be occupied by new breeders originating from non-territorial subpopulations (see Conover 2002).

Quotas

Potts (1998) discussed the possibility of allowing 'quotas' in the UK for the hen harrier (the removal of part of the harrier nests or nestlings up to an agreed level). This solution is highly controversial and unacceptable to the majority of the protectionist community as it goes against current European legislation. Such an approach has been defended by various scientists (“it is always better to accept a regulated and monitored control of predators than uncontrolled illegal actions” (Villafuerte et al. 1998) and “total protection does not prevent deliberate killing. [...] It also motivates illegal use of least selective techniques” (Kenward 2000)) because illegal practices are likely to decrease when legal methods to control targeted predators are undertaken (Reynolds & Tapper 1996).

This solution has not been tested in the field except as an opportunist quasi-experiment (see Etheridge et al. 1997). Hen harrier population dynamics was compared on grouse moors and other moors. Lower female survival and lower productivity as observed on grouse moors were not associated with a decrease in harrier pairs probably due to recruitment from other habitats. The study did not report an effect of illegal culling of harriers on grouse populations. Moreover, even if this option were acceptable, the application of such a solution would raise practical questions about how to define the quotas and how/ by whom they should be implemented.

Resolving the conflict

Resolving the described conflict is a conservation challenge in intensive farmland of central northern France. Illegal control of protected hen harriers highlights the fact that laws are not always sufficient to ensure effective protection of a given species.

Developing cooperation between stakeholder groups

The conflict results from divergent opinions about how wildlife should be managed. Addressing the social component of the conflict is therefore critical. The modern approach to tackle disagreement is the 'Consensus Building Approach' which is based on face-to-face meetings of the different stakeholder groups to seek to achieve resolution of their differences and the process is led by a mediator (see Redpath et al. 2004). The perspectives of the two groups of stakeholders are evaluated as are their acceptability of the different management solutions.

Such an approach was tested recently for the harrier-grouse conflict in the UK (Redpath et al. 2004). It has been proven to develop dialogue and be a valuable step towards cooperation. It also showed, however, that acceptance of a range of solutions by all stakeholders is difficult unless all parties are prepared to compromise.

It would be worth the effort developing such methods in France to establish dialogue and assess the acceptability of the different potential solutions, so that research efforts could tackle stakeholders' questions and be focused on those solutions that are perceived as a compromise. Diversionary feeding and habitat management appear to be good candidates (see above).

Research needs

Some critical aspects of the hen harrier - grey partridge relationships have not been documented and scientific

facts are fragmented in space and time (see Tables 1 and 2). Currently, the impact of harrier predation on partridge populations is not fully understood. Further research is essential. An experimental removal of harriers could be of scientific interest to document whether harrier predation is additive or compensatory, and ultimately whether harriers actually limit partridge numbers. This approach would be the most rigorous one but is not the only one, and it is currently unpalatable for some stakeholder groups. It would also be informative to concentrate efforts on a few areas as study cases to carry out long-term correlative studies evaluating simultaneously harrier numbers, partridge numbers, partridge mortality and harrier diet while measuring every possible explanatory factor, such as abundance of the main prey.

Experimental research on direct and indirect methods to reduce predation is also needed. As stated above, solutions may exist on paper, but little is known about their efficiency and effectiveness. All approaches depend on complex behavioural and ecological mechanisms. None of them is ideal and for all of them serious complications must be overcome.

Relative contributions of hunters, protectionists and government

Previous experimental studies showed that solutions are likely to be expensive, time consuming and some of them indefinite (Redpath et al. 2001, Bro et al. 2005). So the socio-economic issues of 'who should pay?' and 'who should do it?' will arise if a solution has to be applied at a large scale and on the long term. These issues are far from being trivial and they are also far from being resolved, but they should not be used as a delaying tactic to solving the conflict. Any application of a given measure or a combination of measures will need a prior concertation between stakeholders and government representatives.

Conclusions

Our understanding of the role of predation in prey population dynamics has changed considerably during the last 20 years, and it is now accepted that predation might limit gamebird populations. Following recent studies on the impact of raptor predation on gamebirds (see the review of Valkama et al. 2005), scientists (including those working within raptor protectionist NGOs) increasingly acknowledge that raptor predation may conflict with hunting interests. As an example, the World Working Group of Birds of Prey and Owls (WWGBP) met in 1998 for a world conference and adopted a Conference Res-

olution recognising that predation by raptors may create conflicts, waste resources and detract attention from long-term issues (see Kenward 2000). The interests of hunters, protectionists and farmers overlap and these groups should combine their efforts to manage wildlife. This team-effort approach to conservation would be a wise solution to the conflict (Vargas & Duarte 2001). However, dialogue is more likely to be constructive if objective knowledge of the ecological facts exists. Within this context, scientists need to communicate their results to the public in comprehensible words and effort should be put into education about wildlife conservation. The collaboration between scientists, protectionists and hunters would undoubtedly be fruitful for addressing the issue.

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