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Birds of prey as limiting factors of gamebird populations in Europe: a review

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ABSTRACT

Whether predators can limit their prey has been a topic of scientific debate for decades. Traditionally it was believed that predators take only wounded, sick, old or otherwise low-quality individuals, and thus have little impact on prey populations. However, there is increasing evidence that, at least under certain circumstances, vertebrate predators may indeed limit prey numbers. This potential role of predators as limiting factors of prey populations has created conflicts between predators and human hunters, because the hunters may see predators as competitors for the same resources. A particularly acute conflict has emerged over the past few decades between gamebird hunters and birds of prey in Europe. As a part of a European-wide research project, we reviewed literature on the relationships between birds of prey and gamebirds. We start by analysing available data on the diets of 52 European raptor and owl species. There are some 32 species, mostly specialist predators feeding on small mammals, small passerine birds or insects, which never or very rarely include game animals (e.g. hares, rabbits, gamebirds) in their diet. A second group (20 species) consists of medium-sized and large raptors which prey on game, but for which the proportion in the diet varies temporally and spatially. Only three raptor species can have rather large proportions of gamebirds in their diet, and another seven species may utilise gamebirds locally to a great extent. We point out that the percentage of a given prey species in the diet of an avian predator does not necessarily reflect the impact of that predator on densities of prey populations. Next, we summarise available data on the numerical responses of avian predators to changing gamebird numbers. In half of these studies, no numerical response was found, while in the remainder a response was detected such that either raptor density or breeding success increased with density of gamebirds. Data on the functional responses of raptors were scarce. Most studies of the interaction between raptors and gamebird populations give some estimate of the predation rate (per cent of prey population taken by predator), but less often do they evaluate the subsequent reduction in the pre-harvest population or the potential limiting effect on breeding numbers. The few existing studies indicate that, under certain conditions, raptor predation may limit gamebird populations and reduce gamebird harvests. However, the number and extent of such studies are too modest to draw firm conclusions. Furthermore, their geographical bias to northern Europe, where predator–prey communities are

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typically simpler than in the south, precludes extrapolation to more diverse southern European ecosystems. There is an urgent need to develop further studies, particularly in southern Europe, to determine the functional and numerical responses of raptors to gamebird populations in species and environments other than those already evaluated in existing studies. Furthermore, additional field experiments are needed in which raptor and possibly also mammalian predator numbers are manipulated on a sufficiently large spatial and temporal scale. Other aspects that have been little studied are the role of predation by the non-breeding part of the raptor population, or floaters, on the breeding success and survival of gamebirds, as well as the effect of intra-guild predation. Finally there is a need for further research on practical methods to reduce raptor predation on gamebirds and thus reduce conflict between raptor conservation and gamebird management.

Key words: conservation conflict, diet, functional response, grouse, intra-guild predation, non-breeder, numerical response, owl, population limitation, predation impact, raptor.

CONTENTS

I. INTRODUCTION

A new attitude towards wildlife has emerged in Europe during the last few decades, probably as a consequence of declining population trends or extinctions of many species due to human activities. Predator populations, and birds of prey in particular, have suffered from declines and range retractions (Bijleveld, 1974; Newton, 1998) owing to their naturally low population densities and their role as consumers of other species important to man (from poultry to game). Thus, raptors have been killed extensively in the past, in many cases to the point of extermination. Protective laws resulting from national legislation, recent international conventions (see Spellerberg, 1996) or European directives (e.g. 'Bird Directive' no. 79/409/CEE and 'Habitat Directive' no. 92/43/CEE) have been implemented to protect animals and their habitats. As a consequence, the populations of a range of predator species, that had been reduced previously through persecution, have been recovering during the last 20–30 years in Europe (Hagemeijer & Blair, 1997; Mitchell-Jones *et al.*, 1999). This recovery has induced tensions and divisions within interested sectors of society, especially where the prey of these predators are of socio-economic value (domestic animals, harvested or protected species). Similar tensions have arisen when hunters perceive protected predators to be a threat to game (Kenward, 1999, 2000; see also Lippert, Langgemach & Sömmer, 2000; Viñuela & Villafuerte, 2003). Conflicts between hunting and biodiversity conservation are particularly acute when predators are subjected to illegal, non-selective or excessive killing with the purpose of maximising hunting bags. This is the case, for example, for hen harriers *Circus cyaneus* and red grouse *Lagopus lagopus scoticus* in Scotland (Thirgood *et al.*, 2000*b*), and red kites *Milvus milvus* and rabbits *Oryctolagus cuniculus* in Spain (Villafuerte, Viñuela & Blanco, 1998). Furthermore, habitat loss has forced both gamebirds and raptors into increasingly small and fragmented habitat, which has probably been a contributory factor in generating conflict (Villafuerte *et al.*, 1998).

Since the early 1960s, the science of wildlife damage management has advanced to resolve human-wildlife conflicts (Conover, 2002; Woodroffe, Thirgood & Rabinowitz, 2004). A range of methods taking ecological and socio-economic aspects into account has been proposed. A recent European Concerted Action within the 5th Framework Program: Reconciling Gamebird Hunting And Biodiversity (REGHAB), involving Finland, France, Portugal, Spain and the UK addressed specifically conflicts involving gamebirds and raptors. This paper addresses a major aim of the project: to review the conflicts between predator control and raptor conservation in Europe within the context of predator–prey interactions. It is important to understand these interactions as they often have implications for land use, biodiversity and sustainable use of resources. Game management can only be optimised once a clear understanding of these issues has been reached. We first give a brief introduction to the theoretical background of the predator–prey system by reviewing relevant key concepts and terms. Second, we provide an overview of the diet of European bird of prey species and try to identify species that could potentially be harmful to game animals. Third, we assess the available data on the numerical and functional responses of these raptors to varying densities of gamebirds, and evaluate the importance of their predation on gamebird populations. We also give a brief overview of the relationships between raptors and gamebirds in North America, although the emphasis of this study is clearly on Europe. Finally, we summarise the results, identify areas where information is lacking and propose topics for future research.

(1) General background

In the middle of last century, following the work of Errington (1946, 1956, 1963), the general view amongst biologists was that predators had little effect on vertebrate prey populations as they only took those individuals which would have died from other causes – the so-called 'doomed surplus'. The idea of the 'doomed surplus' was supported by the influential early work on red grouse populations in Scotland (Jenkins, Watson & Miller, 1963, 1964; Watson, 1964). It was frequently assumed that the predated individuals were ill, injured, old or otherwise of low quality, and that predators acted as 'health officers' in nature. This 'Erringtonian view' was based on the assumption that the remaining individuals in the prey population are easily able to increase their reproduction and thus to compensate for predation mortality. Therefore, predators cannot cause any profound reduction of prey density. The 'Erringtonian view' has, however, been questioned in many studies conducted from 1980 onwards, which indicate that predation may, at least under certain conditions, be additive and thus have profound limiting effects on vertebrate prey populations (e.g. Marcström, Kenward & Engren, 1988; Krebs *et al.*, 1995; Korpimäki & Krebs, 1996; Tapper, Potts & Brockless, 1996; Hubbs & Boonstra, 1997; Korpimäki & Norrdahl, 1998; Byrom *et al.*, 2000; Thirgood *et al.*, 2000*a*,*c*; Bêty *et al.*, 2002; Korpimäki *et al.*, 2002; Nordström *et al.*, 2002, 2003; Banks *et al.*, 2004; Nordström & Korpimäki, 2004).

The theoretical background used to describe the ecology of predator–prey relationships relies on several concepts and definitions that are listed below in *italics*. The *mechanistic paradigm* searches for relationships between birth, death and movement rates, and the mechanisms controlling populations, such as disease, predation, food shortage and territoriality (Krebs, 1995, 2002*a*, *b*; see also Andrewartha & Birch, 1954). The more traditional *density paradigm* (see Krebs, 1995, 2002*b* for details) assumes that birth, death and movement rates will be related to population density (Sinclair, 1989; Sinclair & Pech, 1996). It has a central assumption that there is a point of equilibrium toward which the population moves if displaced. The density paradigm attempts to explain the regulation of numbers while the mechanistic paradigm attempts to explain the limitation of numbers. *Population regulation* here means the (usually density-dependent) processes by which a population returns to its equilibrium density (or 'carrying capacity'; Sinclair, 1989; Sinclair & Pech, 1996; Krebs, 2002*a*, *b*), and focuses on what stabilises/destabilises population density. *Population limitation* in turn means any factors that limit the size of the population below its carrying capacity (Sinclair, 1989; Sinclair & Pech, 1996; Krebs, 2002*a*,*b*). In this review, we are interested in factors that may limit game animal populations, and in particular, in the role of avian predators. This has a greater empirical and management importance than questions related to population regulation (Krebs, 2002*a*). The question of population limitation has been very useful in the management of both desirable and undesirable species. It has also been used as a major tool of wildlife and fisheries management. Because of that, here we have mainly adopted a mechanistic paradigm, to try to evaluate the role of raptors as limiting factors for game populations.

Compensation is a mechanism whereby the effects of mortality from one cause do not lead to an increase in the overall mortality rate within a population, because they are offset by reduction in mortality from another cause. By contrast, mortality which leads to an increase in overall mortality is *additive*. This distinction represents one attempt to avoid the problem of assigning causes of death and has mainly been applied to hunting mortality in comparison to natural sources of loss (Krebs, 2002*a*).

The effects of predation are dependent on the numbers and behaviour of both predators and prey. As an event, predation is rarely evenly distributed through a prey population, as it may be concentrated on certain localities, on particular age groups, sex or social classes, or it may vary through time (Newton, 1993). Predators have been schematically classified into two categories according to their diet selection (Andersson & Erlinge, 1977). They can be either *generalists* feeding on a variety of prey, or *specialists* taking only one or a few main prey species. However, in reality predators form a continuum from one extreme to another. Furthermore, some predators may change from being specialists to being more generalist over both temporal and spatial scales (Korpimäki & Krebs, 1996).

By nature, predation can be *regulatory* (stabilising or density-dependent) or *non-regulatory* (destabilising or density-independent) (Sinclair, 1989; Sinclair & Pech, 1996; Sinclair *et al.*, 1998). If predation is regulatory, then the proportion of prey that are killed increases with rising prey density, so that eventually prey numbers stop increasing. This is one mechanism through which a prey population could be held below the level that the carrying capacity would permit (Newton, 1998). Inverse density dependence, a form of non-regulatory predation, arises when predators remove approximately the same number of individuals from the prey population independent of the numbers of prey present. This leads to a situation in which a relatively greater proportion of the prey population is removed when prey numbers are low, preventing population growth.

(2) Responses of predators

There are two *responses* of predators, namely *numerical* and *functional* (Solomon, 1949) that describe the behaviour of predators to varying prey densities, promoting either direct or delayed density dependence, or inverse density dependence. The *numerical response* can be expressed as the number of territorial predators, total predator density or the number of offspring per predator territory in relation to the density of a particular prey (see e.g. Korpimäki & Norrdahl, 1991*b*; Tornberg, 2001). A numerical response of the predator occurs when the density or productivity of the predator depends on a given prey abundance rather than on total prey abundance. The numerical response is due to changes in natality, mortality, immigration, or emigration of the predator (Andersson & Erlinge, 1977; Korpimäki & Norrdahl, 1989*c*, 1991*b*; Salamolard *et al.*, 2000). Thus, the ability of predators to respond numerically to the fluctuations of prey populations may depend on the mobility, reproductive potential, generation time, territoriality or breeding system of the predator. High mobility (i.e. wide natal and breeding dispersal), large brood size, and early maturity and thus early initiation of reproductive life-span contribute to rapid numerical response of the predator. Quite often the densities of resident generalist and specialist predators lag well behind the prey populations (e.g. Pearson, 1966; Korpimäki, Norrdahl & Rinta-Jaskari, 1991; Nielsen, 1999). Nomadic specialist avian predators, on the other hand, show rapid numerical responses to changes in prey densities, being therefore able to track their prey populations without obvious time lags (Korpimäki & Norrdahl, 1989*a*, 1991*a*; Korpimäki, 1992*b*, 1994; Newton, 2002). Nomadism may not necessarily be the only way in which predator populations are able to track high prey densities, because recruitment from a non-breeding population may also explain the rapid numerical response (Salamolard *et al.*, 2000).

The *functional response* is expressed as the change in capture rate in response to changing prey density. This response is affected by the availability of main (i.e. preferred) and alternative prey, the ability to shift to alternative prey, and inter- and intra-specific competition for food (Andersson & Erlinge, 1977; Korpimäki, 1987; Korpimäki & Krebs, 1996). Functional responses of predators may be difficult to estimate and there can also be particular statistical problems in distinguishing between non-linear and linear responses with noisy field data (Trexler, McCullogh & Travis, 1988). Moreover, traditional methods (such as analyses of pellets and scats) to identify diets of predators may also include some shortcomings (see Section II for details).

Three different types of functional responses can be distinguished (Holling, 1959). In a Type I response, the relationship between prey density and the number of prey eaten per predator per unit time is linear. The number of prey eaten per predator increases indefinitely as prey density rises and thus the fraction of the prey population taken is density-dependent. In a Type II response (or convex functional response), a limit to the number of prey eaten per predator may be set by limited gut capacity or by restricted handling time resulting in an asymptotic curve. This will produce a declining (or inverse density-dependent) percentage kill. This model allows prey consumption to increase with prey density when prey are scarce and is more realistic at least in raptors because it takes into account the gut capacity and handling time of the predator. Third, foraging of the predator may be inefficient at low prey densities (sigmoid or type III functional response). This kind of functional response will produce a direct density dependence in the percentage kill at low prey densities but inverse density dependence at high prey densities. Theoretically, only the sigmoid curve (type III) has stabilising potential, whereas in the two other curves the percentage taken by predators either remains constant (type I) or declines (type II) with increasing prey numbers (Murdoch & Oaten, 1975; Taylor, 1984). If there are many alternative prey species in addition to the main prey, an ability to vary hunting techniques facilitates a wide functional response to fluctuating densities of the main prey (Korpimäki, 1992*b*).

The total response, also expressed as kill rate, is the result of the combination of the numerical and functional responses, and can be obtained by multiplying the number of a given prey killed per predator with predator density, and then plotting the outcome against prey density. Predation impact (predation rate) can be assessed through dividing the kill rate by the number of prey available (e.g. Kenward, 1986; Korpimäki & Norrdahl, 1989*c*, 1991*a*; Tornberg, 2001).

(3) Prey population cycles

Siivonen (1948), Hagen (1952), Angelstam, Lindström & Widén (1984, 1985) and Lindén (1988) have documented that populations of small game, such as hare and forest grouse, and small rodents in Fennoscandia and other areas (e.g. France; Salamolard *et al.*, 2000) fluctuate synchronously between years (short-term population fluctuations or the 3–4-year cycle). The cyclicity and synchrony of small rodents and the whole small game community are most marked in northern Fennoscandia and decrease southwards. In southern Sweden, populations of small game and small rodents are relatively stable between years (e.g. Angelstam *et al.*, 1985; Hansson & Henttonen, 1985). Although many factors (e.g. food supply, parasites, disease, weather) may influence population dynamics and have the potential to create population cycles (see Jędrzejewski & Jędrzejewska, 1996 and Turchin & Batzli, 2001), there is strong evidence that under certain circumstances, predation alone can generate cycles in prey populations and create the observed cyclic variation in the number of gamebirds (but see discussions in Graham & Lambin, 2002; Korpimäki *et al.*, 2003; Lambin & Graham, 2003 and Oli, 2003). On this matter, two main hypotheses have been proposed: (i) the alternative prey hypothesis (APH) and (ii) the predation hypothesis (also known as the specialist predation hypothesis; Rosenzweig & MacArthur, 1963; Begon, Harper & Townsend, 1990; Hanski, Hansson & Henttonen, 1991). Other hypotheses (for example, those related to parasites or intrinsic factors) have been developed to explain the observed cyclic dynamics of red grouse or ptarmigan populations in the UK where predators are strictly controlled by gamekeepers and are thus unlikely to be the primary cause of population cycles (Watson, 1998; Hudson, Dobson & Newborn, 1998, 2002; Moss & Watson, 2001; Mougeot *et al.*, 2003).

The alternative prey hypothesis (APH), first put forward by Hagen (1952) and Lack (1954), suggests that the nearly synchronous population fluctuations of small game and small mammals are caused by varying predation impact. If predators are selective in killing their prey, and if small rodents or lagomorphs are the main food of predators (because their densities in the peak phase are very high and they are easier to catch than gamebirds), then the APH predicts that predators partly shift their diet from the main prey to alternative prey (gamebirds) as the main prey decreases and back to the main prey as soon as small rodent numbers increase. A recent hypothesis, the shared predation hypothesis (SPH), which is an alternative to the APH, states that predators are less selective in killing their prey, and that all important prey species are negatively affected when the densities of predators are high; that is, at and immediately following the peak densities of the main prey (Norrdahl & Korpimäki, 2000). For prey species that constitute only a small share of the diet of predators (i.e. alternative prey), these two hypotheses have different predictions of the impact of predators on prey population dynamics. In the SPH, the mortality rate of the alternative prey is positively correlated to the encounter rate of predators, and the impact of predators on alternative prey largely depends on the abundance of hunting predators in an area. Although the proportion of alternative prey in the diet of predators is usually lower in years with high densities of main prey, predators eat alternative prey in all years. Due to a rapid numerical response of predator populations to density changes of main prey, the actual number of alternative prey killed by predators may be higher in years with high rather than low densities of main prey. In the APH, the impact of predators on alternative prey depends more on the density of the main prey than on the ratio of predators to alternative prey. Accordingly, the APH predicts that predation may have a limiting impact on alternative prey less often or during shorter periods than predicted by the SPH (Norrdahl & Korpimäki, 2000). In Europe, potential predators that may shift from small rodents or rabbits to gamebirds include carnivores, diurnal raptors, owls and corvids. As gamebirds are usually much larger than small rodents, small predators are able to take only their eggs and young and thus do not represent a threat to adult gamebirds (e.g. Angelstam *et al.*, 1984).

With respect to the predation hypothesis, it has been suggested that prey population cycles can be a consequence of predation by specialist predators (e.g. Henttonen *et al.*, 1987; Korpimäki *et al.*, 1991; Hanski *et al.*, 1993). At least four factors may create and/or maintain population cycles. First, there can be a time lag in the numerical response of the predator to changes in prey densities, arising because the rate of increase of predator populations is lower than that of their prey. The prey population grows faster than the predator population and overshoots an equilibrium density. Predators are not immediately affected when the prey begin to decline, and as a consequence they overshoot the carrying capacity of the prey and then decrease with a time lag (Keith, 1963; Keith & Windberg, 1978; see also Rohner, 1995). This process leads to an extended decline in the prey population, and only when predator densities have declined low enough can a new cycle begin. However, in reality predator–prey dynamics exceed simple two-species interactions (Rohner, 1995). Second, specialist predators are more likely to cause population cycles than generalist predators because they are less able to switch to alternative prey when prey populations decline. Third, population cycles may arise when there is a negative relationship between the kill rate of the predator and changes in prey population, i.e. when the total number of prey animals killed e.g. per area unit increases with decreasing numbers of prey. Consequently, cyclic variation may also be promoted if predation is highest at the decline and low phases of a prey population cycle driven mainly by another causal factor (e.g. Korpimäki *et al.*, 1991; Jędrzejewski & Jędrzejewska, 1996; Nielsen, 1999; Tornberg, 2001; Graham & Lambin, 2002).

(4) Current state of knowledge

Long-term studies on numerical and functional responses of raptors and owls to multiannual fluctuations of prey are scarce, and they relate mainly to the relationship between birds of prey and rodent fluctuations (e.g. Korpimäki & Norrdahl, 1989*c*, 1991*a*, *b*; Korpimäki, 1992*a*, *b*, 1994; Potapov, 1997; Wiklund, Kjellén & Isakson,1998; Salamolard *et al.*, 2000; Reif *et al.*, 2001; Redpath, Thirgood & Clarke, 2002), whereas studies on the relationship between raptors and variations in abundance of other prey are much more limited (but see Craighead & Craighead, 1956; Mindell, Albuquerque & White, 1987; Steenhof & Kochert, 1988; Rohner, 1996; Redpath & Thirgood, 1999). Similarly, a review of the scientific literature on predator-prey relationships indicates that there is extremely little information on whether raptor predation can limit populations of game animals. Some studies from northern Europe, particularly the relatively well-studied hen harrier – red grouse system in Scotland (e.g. Redpath & Thirgood, 1997, 1999; Thirgood *et al.*, 2000*a*, *b*, *c*; Thirgood & Redpath, 1997, 2004), and the goshawk – gamebird system in Fennoscandia and Russia (e.g. Galushin, 1970*a*, *b*, 1974; Lindén & Wikman, 1983; Kenward, 1986; Tornberg, 2001), suggest that in some cases or under particular circumstances, raptors may have significant effects on the population dynamics and hunting bags of gamebirds. However, there are virtually no studies from central or southern Europe (but see Ziesemer, 1983; Bro *et al.*, 2000, 2001). Given that the relationship between predators and gamebirds varies according to the availability of alternative prey and to the diversity of the predator assemblage (which can be highly disturbed through human activities and which also clearly varies between regions, diversity mainly increasing in southern latitudes), generalisation of results from studies in northern Europe to more southern latitudes is risky. There is almost no experimental evidence from Europe at an appropriate scale (but see Thirgood *et al.*, 2000*a* for a 'quasi-experimental' study), and existing relationships are in most cases dependent on data from only a few localities.

Here we present a review of the key findings from past or ongoing studies on the relationship between birds of prey and gamebirds across Europe. Diet and prey choice of various raptor species have been examined in many European countries and in North America (summarised by Marti, Korpimäki & Jaksic, 1993; Korpimäki & Marti, 1995), but here we aim to synthesise results from those European studies in which the impacts of raptor predation on their prey populations have been estimated (for comparison with North America, see Section VI, and also Rohner, 1995, 1996; Rohner, Doyle & Smith, 2001).

II. DIET OF RAPTORS IN EUROPE

Diet composition, given as proportion of main prey groups *by number*, of mammal- and bird-eating raptors and owls is shown in Table 1. An alternative method would be to report the proportion of different prey items *by weight*, but this has been used in few studies conducted previously, and therefore was not utilised here. In Table 1 we have included species which prey on gamebirds (at least 1 % of total prey number) or which feed to a greater extent (> 10 %) on other game animals (hares and rabbits, pigeons or waterfowl). The most recent diet studies were used where there were many from which to choose. Some species, for example Ural owl *Strix uralensis*, were included if there was evidence that they might at least temporarily feed on gamebirds (Korpimäki, Huhtala & Sulkava, 1990). We use the following prey categories: small mammals (including shrews, voles, mice and rats), hares (*Lepus* spp.) and rabbits (*Oryctolagus cuniculus*), pigeons, gamebirds (wild galliforms), waterfowl (mainly ducks, mergansers and goose), and others (including e.g. passerines, squirrels, reptiles, amphibians, insects, carrion and unidentified prey items). In the majority of these studies, prey remains and pellets were collected from nests and from the ground under nests. This method may have some shortcomings, e.g. the smallest prey animals, such as amphibians, can easily go undetected and so their relative importance may be underestimated (Mañosa & Cordero, 1992; Reif *et al.*, 2001; Redpath *et al.*, 2001*a*; Rutz, 2003). Diets studied from prey remains at nests may be further biased in favour of large items if the predator dismembers the prey away from the nest, and brings it back piecemeal; the observer may then record each piece as a separate prey item. In addition, diet samples collected from the nest sites may not represent accurately the diet of avian predators if they selectively consume small prey items at the capture site and bring only large prey items to the nest (Sonerud, 1992; but see Newton, 1986; Korpimäki, Tolonen & Valkama, 1994). In addition to these potential shortcomings there may be geographical differences in the attitudes of people towards game and their predators. Species that are considered as game in one country may not be considered such in another. Rabbits, for example, are considered a major game species in southern Europe whereas in the UK they have pest status. Consequently, raptor predation on rabbits in the UK does not lead to conflict unlike more southern European areas.

(1) Raptors not feeding on game

Some European bird of prey species have been omitted from Table 1 because their diets are known to consist almost entirely of non-game species or because no detailed information is available on their diet in Europe. These species are (main prey in parentheses): the osprey *Pandion haliaetus* (mainly fish; Häkkinen, 1978; Cramp & Simmons, 1980; Francour & Thibault, 1996), honey buzzard *Pernis apivorus* (mainly insects; Thiollay, 1967*a*; Glutz von Blotzheim, Bauer & Bezzel, 1971; Itämies & Mikkola, 1972; Cramp & Simmons, 1980), white-tailed eagle *Haliaeetus albicilla* (fish, waterbirds, carrion, only locally important consumption of lagomorphs or waterfowl; Cramp & Simmons, 1980; Watson, Leitch & Broad, 1992; Sulkava, Tornberg & Koivusaari, 1997; Zawadzka, 1999; Marquiss, Madders & Carrs, 2003), bearded vulture *Gypaetus barbatus* (carrion, mainly bones; Cramp & Simmons, 1980; Heredia & Heredia, 1991; Thibault, Vigne & Torre, 1993), other vultures (carrion; Cramp & Simmons, 1980; Fischer, 1982),

Table 1. Diet composition (proportion of prey items by number) of mammal- and bird-eating raptors and owls in Europe. Body mass (g) of male and female birds of prey in parentheses. *N*= number of prey items

Bird of prey species	Country	Small mammals	Hares and rabbits	Pigeons	Gamebirds	Waterfowl	Others	N	Source
Red kite *Milvus milvus* (947, 1213)	Italy	12.5	—	1.8	—	—	85.7	56	Manzi & Pellegrini (1992)
	Poland	7.9	2.1	3.0	0.6	4.3	82.1	531	Zawadzka (1999)
	Spain	—	29.2	—	—	15.9	54.9	634	Veiga & Hiraldo (1990)
	Spain (winter)	15.8	9.1	2.2	1.7	—	71.2	1577	Garcia *et al.* (1998)
	Spain (Madrid, winter)	19.0	21.7	1.1	10.6	0.3	47.3	7225	Ortega & Casado (1991)
	Spain (Doñana)	5.9	28.5	0.6	0.3	20.4	44.3	697	Delibes & García (1984)
	France	34.6	2.5	0.6	0.2	2.5	59.6	1215	Thiollay (1967 *a*)
	UK	21.8	6.7	0.7	0.1	1.5	69.2	1068	Walters Davies & Davis (1973)
	UK (England, summer)	25.1	36.7	18.0	5.3	—	14.8	338	Carter & Grice (2002) I. Carter (unpublished data)
	UK (England, winter)	39.9	31.1	9.1	6.5	1.9	11.5	537	Carter & Grice (2002) I. Carter (unpublished data)
	UK (Scotland)	3.9	55.6	8.2	1.9	—	30.4	259	Wildman *et al.* (1998)
	Germany	53.0	12.9	2.4	2.6	—	29.1	1395	Wuttky (1963)
	Germany	48.1	13.7	3.5	—	—	34.7	2967	Stubbe *et al.* (1991)
Black kite *Milvus migrans* (807, 850)	North Italy	5.0	0.7	3.9	—	—	90.4	307	Sergio & Boto (1999)
	Central Italy	9.9	7.3	—	0.4	—	82.4	273	De Giacomo *et al.* (1993)
	Poland	13.2	—	1.9	—	6.7	78.2	105	Zawadzka (1999)
	France	26.1	0.6	0.3	<0.1	1.2	71.8	2482	Thiollay (1967 *a*)
	Spain (Doñana)	—	24.4	—	—	21.9	75.6	1889	Veiga & Hiraldo (1990)
	Spain (Doñana)	0.9	30.7	0.1	0.4	5.9	62.0	3059	Viñuela (1991)
	Germany	44.4	9.5	2.1	—	—	44.0	662	Stubbe *et al.* (1991)
	West Spain	2.2	1.6	0.3	1.0	2.6	92.3	310	Fernández Cruz (1974)
	Central Spain	14.5	56.7	2.6	1.8	—	24.4	682	Arroyo (1980)
Hen harrier *Circus cyaneus* (346, 527)	France (winter)	27.1	17.7	—	3.1	—	52.1	?	Clarke & Tombal (1989)
	France (winter)	81.2	—	—	—	—	18.8	177(1)	Robert & Royer (1984)
	France	63.7	1.2	—	3.2	—	31.9	2049	Millon *et al.* (2002)
	Netherlands	6.5	20.4	0.1	12.7	1.9	58.4	857	Schipper (1973)
	Netherlands (winter)	26.9	14.9	2.7	6.5	9.8	39.2	879	Clarke *et al.* (1993)
	Norway	57.2	1.1	—	7.0	2.6	32.1	570	Hagen (1952)
	UK (winter)	11.2	10.5	2.6	5.7	0.1	69.9	3487	Clarke *et al.* (1997)
	UK (Scotland)	5.3	2.2	—	12.0	—	80.5	2324(2)	Redpath & Thirgood (1997)
	UK (Orkney, winter)	51.9	15.7	—	—	—	32.4	489	Picozzi & Cuthbert (1982)
	UK (Orkney)	5.2	47.3	0.8	6.6	—	40.1	482	Picozzi (1980)
	UK (Scotland)	2.2	11.3	0.1	34.5	—	51.9	758	Picozzi (1978)
	Central Spain	16.4	31.9	1.7	6.9	—	43.1	116	García (2003) and J. T. García (unpublished data)
Montagu's harrier *Circus pygargus* (261, 370)	France (Crayeuse)	49.4	1.1	—	1.1	—	40.1	2166	Millon *et al.* (2002)
	France (Barrois)	49.2	2.3	—	0.3	—	38.4	2837	Millon *et al.* (2002)
	France (Camargue)	3.8	—	—	2.2	—	94.0	182	Schipper (1973)
	South-west France	10.3	—	—	—	—	89.7	8817	Salamolard *et al.* (2000)
	Netherlands	11.9	2.3	—	1.7	0.8	83.3	1155	Schipper (1973)
	South-west Spain	2.4	1.2	0.5	5.4	—	90.5	3433	Hiraldo *et al.* (1975)

Table 1 (*cont.*)

Bird of prey species	Country	Small mammals	Hares and rabbits	Pigeons	Gamebirds	Waterfowl	Others	N	Source
	Central Spain	5.9	17.2	0.2	3.0	—	73.7	3096	Arroyo (1997)
	South-east Spain	0.7	2.9	—	—	—	96.4	139	Sánchez-Zapata & Calvo (1998)
	East Spain	18.5	—	—	—	—	81.5	305	Martínez *et al.* (1999)
	West Spain	3.0	0.7	—	1.0	—	95.3	1180	Corbacho *et al.* (1995)
	Portugal	0.5	<0.1	—	—	—	99.4	1739	Franco *et al.* (1998)
	UK	2.1	3.3	8.7	17.4	—	68.5	92	Underhill-Day (1993)
Marsh harrier *Circus aeruginosus* (500, 669)	Finland	35.3	—	—	—	16.0	48.7	187	Hildén & Kalinainen (1966)
	Poland	24.3	1.7	<0.1	0.7	27.7	46.2	1355	Witkowski (1989)
	North France	7.2	4.8	—	1.6	8.1	78.3	124	Schipper (1973)
	South France	3.8	25.6	0.2	0.7	9.8	59.9	570	Schipper (1973)
	South France (winter)	14.0	2.0	—	<1.0	56.0	27.0	272	Schipper (1973)
	France (autumn, winter)	27.1	7.6	—	—	—	65.3	3453	Bavoux *et al.* (1990)
	France (Lorraine)	78.3	0.8	0.1	—	3.8	17.0	937	Thiollay (1967 *a*)
	Netherlands (winter)	6.1	7.0	7.8	2.1	46.9	30.1	243	Clarke *et al.* (1993)
	Netherlands	3.9	32.6	—	23.6	8.1	31.8	233	Schipper (1973)
	Germany	54.5	0.9	1.2	0.5	4.5	38.4	1689	Lange & Hofmann (2002)
	UK	2.7	3.7	5.4	21.2	9.5	57.5	296	Underhill-Day (1985)
	Spain	23.0	22.8	1.8	2.5	14.7	35.2	1995	González (1991)
Goshawk *Accipiter gentilis* (712, 1140)	Denmark	—	0.8	40.0	5.0	0.8	53.4	20937	Nielsen & Drachmann (1999)
	Finland (Oulu)	4.2	3.8	2.3	44.4	8.9	36.4	1206	Tornberg & Sulkava (1991)
	Finland (Uusimaa)	3.5	3.0	8.1	15.6	3.3	66.5	1300	Wikman & Tarsa (1980)
	Finland (winter)	16.4	30.9	—	27.3	—	25.4	55	Tornberg & Colpaert (2001)
	France (Limousin)	1.5	5.5	(3)	3.5	—	89.5	199	Nore (1979 *a*, *b*)
	France (Lorraine)	1.2	1.2	6.7	0.4	6.3	84.2	510	Thiollay (1967 *a*)
	France (Corsica)	—	—	13.5	1.9	—	84.6	52	Thiollay (1967 *b*)
	Germany	0.2	14.5	37.1	10.4	0.8	37.0	3886	Brüll (1964)
	Germany	—	2.0	51.6	4.7	1.7	40.0	256	Warncke (1967)
	Germany	2.9	8.6	36.0	15.1	7.2	30.2	139(4)	Ziesemer (1983)
	Germany (Bavaria)	1.2	0.7	25.4	0.2	0.5	72.0	13342	Bezzel *et al.* (1997)
	Hungary	5.1	0.6	7.7	2.6	—	84.0	350	Zsolt & József (1993)
	Italy	(3)	—	8.5	(3)	—	91.5	782	Penteriani (1997)
	Germany/Netherlands	1.2	3.5	63.1	5.2	—	27.0	4825	Opdam *et al.* (1977)
	Poland	4.0	1.8	35.4	1.7	—	57.1	1054	Goszczyński & Piłatowski (1986)
	Poland	—	3.8	54.3	3.5	1.4	37.0	1086	Olech (1997)
	Poland	2.5	0.9	17.5	1.5	0.7	76.9	1539	Zawadzka & Zawadzki (1998)
	Poland (Silesia)	0.4	2.7	50.9	3.7	0.6	41.7	1166	Drazny & Adamski (1996)
	East Spain	7.0	22.3	17.6	4.7	—	48.2	85	Verdejo (1994)
	North-east Spain	—	16.6	14.1	19.1	—	50.2	2003	Mañosa (1994)
	South-east Spain	0.5	14.9	19.3	9.0	—	56.3	410	Padial *et al.* (1998)
	South Spain	1.2	15.6	16.9	8.9	0.3	57.1	563	Moreno-Arroyo *et al.* (2000)
	Sweden	—	0.7	15.6	22.2	—	61.5	904	Widén (1987)
	Sweden	0.7	0.7	6.4	24.7	3.4	64.1	1431	Höglund (1964)

	Sweden	—	14.0	5.5	28.0	—	52.5	127(4)	Kenward *et al.* (1981)
	South Norway	2.0(5)	1.0	?	14.0	10.0(6)	75.0	367	Selås (1989)
	UK	—	5.3	30.6	0.0	—	64.1	2213	Toyne (1998)
	UK	—	5.2	48.5	8.4	—	37.9	3980(7)	S. J. Petty (unpublished data)
	UK	7.8	20.3	42.2	4.7	1.6	23.4	64(4)	Kenward (1979)
Common buzzard *Buteo buteo* (762, 915)	Austria	90.6	0.5	?	—	?	8.9	202	Haberl (1995)
	Finland	50.4	4.3	—	7.4	—	37.9	1906	Reif *et al.* (2001)
	France	34.2	0.5	0.1	0.1	—	65.1	6740	Bayle & de Ruffray (1980)
	France (Lorraine)	47.8	0.2	0.2	<0.1	0.4	51.4	6146	Thiollay (1967*a*)
	Norway	41.3	—	—	2.5	0.6	55.6	719	Spidsø & Selås (1988)
	South Norway	44.6	0.8	0.8	2.5	0.5	50.8	839	Selås (2001)
	Hungary	34.4	0.4	—	1.4	0.7	63.1	279	Zsolt & József (1993)
	Poland	49.2	1.8	3.3	0.2	—	45.5	2109	Goszczyński & Piłatowski (1986)
	Poland (Bialowieza)	96.5	—	0.5	0.3	—	2.7	371	Jędrzejewski *et al.* (1994)
	North Spain	13.1	0.1	—	0.1	0.1	86.6	1103	Bustamante (1985)
	Spain	1.3	66.6	2.5	5.0	—	24.6	598	Mañosa & Cordero (1992)
	North-west Spain	26.2	—	—	—	—	73.8	65	Santamarina (1991)
	Italy	19.0	0.7	—	—	—	80.3	142	Sergio *et al.* (2002)
	UK	18.0	48.0	11.0	2.6	—	20.4	233	Kenward *et al.* (2001)
	UK	6.8	40.8	6.0	15.1	—	31.3	365	Graham *et al.* (1995)
	UK	5.1	56.1	2.4	5.1	—	31.3	253	Sim (2003)
	Germany	64.5	6.0	2.2	—	—	27.3	2223	Stubbe *et al.* (1991)
	South Germany	82.0(5)	0.5	?	?	?	17.5(8)	202	Haberl (1995)
Rough-legged buzzard *Buteo lagopus* (809, 1086)	Finland	43.8	—	—	9.3	—	46.9	203	Pasanen & Sulkava (1971)
Golden eagle *Aquila chrysaetos* (3572, 5194)	Estonia	—	27.0	—	34.0	3.0	36.0	279	Randla (1976)
	Norway	1.5	27.7	—	38.0	—	32.8	137	Hagen (1952)
	Finland(9)	—	32.7	—	35.7	7.0	24.6	5309	Sulkava *et al.* (1999)
	Finland(10)	—	30.2	—	51.2	4.4	14.2	1595	Sulkava *et al.* (1999)
	France	1.0	40.0	4.3	10.4	—	44.3	630	Fernandez (1991)
	France (Corsica)	0.9	—	0.9	3.6	—	94.6	111	Seguin & Thibault (1996)
	Italy	—	7.7	—	19.8	—	72.5	247	Pedrini & Sergio (2001)
	France/Spain (breeding)	—	47.7	—	11.3	—	41.0	44	Cheylan (1977)
	France/Italy (winter)	—	41.9	—	6.4	—	51.7	31	Cheylan (1977)
	Mediterranean areas	—	43.4	—	18.5	—	38.5	1142	Delibes *et al.* (1975); Rangni *et al.* (1986); Watson (1998)
	North-east Spain (Navarra)	1.9	38.3	5.2	10.2	—	44.4	478	Fernández & Purroy (1990)
	North-east Spain (Navarra)	—	52.9	3.9	10.3	—	32.9	816	Fernández (1993)
	Sweden	—	25.3	2.6	1.1	14.3	56.7	652	Högström & Wiss (1992)
	Sweden	1.2	20.6	—	54.1	3.5	20.6	2803	Tjernberg (1981)
	UK (Scotland)	—	25.1	—	19.0	—	55.9	1292	Watson *et al.* (1993)
	UK (West Scotland)	2.1	55.2	—	4.0	0.5	38.2	574	Watson *et al.* (1992)
Spanish imperial eagle *Aquila adalberti* (3200)	Central Spain	1.8	55.8	8.3	3.7	0.9	29.5	2188	González (1989)
	Doñana	0.8	55.6	3.6	1.3	22.7	16	910	González (1989)
	Doñana (winter)	1.3	27.4	0.9	2.0	51.0	17.4	1322	González (1989)
Eastern imperial eagle *Aquila heliaca* (2624, 3901)	Hungary	61.0	11.9	3.6	11.9	0.2	11.4	610	Haraszthy *et al.* (1996)
	Hungary	17.4	26.1	—	4.3	—	52.2	23	Zsolt & József (1993)
	Georgia	53.6	2.6	—	3.8	—	40	341	Abuladze (1996)

Table 1 (*cont.*)

Bird of prey species	Country	Small mammals	Hares and rabbits	Pigeons	Gamebirds	Waterfowl	Others	N	Source
Spotted eagle *Aquila clanga* (1770, 2135)	Estonia	63.0	—	—	<9.0	—	28.0	105(2)	Våli & Lõhmus (2002)
Bonelli's eagle *Hieraetus fasciatus* (2049)	France	—	16.1	6.2	11.7	—	66.0	1733	Real (1991)
	France	—	17.2	6.6	17.7	—	58.5	1718	Cheylan (1994)
	France	1.7	15.0	6.4	17.4	0.2	59.3	515	Simeon & Wilhelm (1988)
	France (Provence, breeding)	1.5	49.2	1.5	20.0	—	27.8	65	Cheylan (1977)
	France (winter)	—	12.0	—	28.0	28.0	32.0	25	Cheylan (1977)
	Italy (Sicily)	2	37.1	38.4	—	—	22.5	151	Di Vittorio *et al.* (2001)
	Portugal	—	21.2	28.4	7.9	—	42.5	165	Real (1991)
	South Portugal	—	12.6	47.3	17.0	0.6	22.6	541	L. Palma (unpublished data)
	Spain (Granada)	2.5	41.6	9.2	24.8	—	21.9	238	Gil-Sánchez (1998)
	Spain (Granada)	—	37.5	17.2	30.2	—	15.1	192	Ontiveros & Pleguezuelos (2000)
	Spain (Catalonia)	—	25.5	26.2	12.7	—	35.6	1556	Real (1991)
	North Spain	—	27.0	10.6	15.6	—	46.8	282	Real (1991)
	East Spain	—	39.2	34.7	10.5	—	15.6	380	Real (1991)
	Spain (Alicante)	0.3	42.5	39.0	3.8	—	14.4	630	Rico *et al.* (1990)
	Spain	—	13.7	23.4	—	—	62.9	124(2)	Real (1996)
	Spain (Murcia)	0.9	40.7	21.5	19.9	—	17.0	688	Martinez *et al.* (1994)
Booted eagle *Hieraetus pennatus* (709, 975)	Portugal	2.0	3.9	47.3	3.4	3.4	40.0	203	R. Borralho & N. Onofre (unpublished data)
	Spain	4.1	5.9	13.2	4.0	—	72.8	835	Martinez (2002)
	Spain (Central)	1.7	3.4	4.3	6.9	—	83.7	116	Garzon (1974)
	Spain (Ciudad Real)	14.0	60.0	—	15.0	—	11.0	100	Llandres & Otero (1985)
	Spain (Tietar valley)	2.8	8.4	4.6	1.9	—	82.3	1105	J. I. García-Dios & J. Viñuela (unpublished data)
	North-east Spain	—	11.9	20.8	4.0	—	63.3	101	Nevado *et al.* (1988)
	Spain (Guadarrama)	5.4	33.7	2.0	1.0	—	57.9	202	Veiga (1985)
	Spain (Navarra)	2.6	44.5	0.4	6.2	46.3	—	227	Iribarren & Rodriquez-Arbeola (1988)
Peregrine *Falco peregrinus* (666, 1113)	Finland	—	—	3.5	4.7	21.4	70.4	1075	Sulkava (1968)
	France	—	0.6	57.8	—	—	41.6	102	Bayle (1981)
	France (Corsica)	—	—	10.0	—	—	90.0	30	Thiollay (1967 *b*)
	Greenland	—	—	—	5.8	0.6	93.6	676	Rosenfield *et al.* (1995)
	Spain	—	3.0	35.5	1.3	—	60.2	820(11)	Oro & Tella (1995)
	Sweden	—	—	23.1	1.8	2.9	72.2	451	Lindberg (1975)
	UK	0.1	0.2	35.6	10.0	2.7	51.4	4130	Ratcliffe (1993)
	UK	—	0.3	48.7	15.4	—	35.6	876	Redpath & Thirgood (1997)
	UK (Scotland)	<0.1	<0.1	49.3	4.3	0.3	45.9	3579	Mearns (1983)
Gyrfalcon *Falco rusticolus* (1115, 1735)	Finland	5.2	1.2	—	65.0	2.3	26.6	729	Huhtala *et al.* (1996)
	Iceland	3.9	—	—	70.3	—	25.8	2316	Nielsen & Cade (1990)
	Iceland	—	—	0.04	71.7	19.8	8.5	31813	Nielsen (2003)
	Norway	3.8	0.4	1.9	84.0	0.4	9.5	468	Langvatn & Moksnes (1979)
	Sweden	25.8	0.6	—	67.7	—	5.9	1410	Lindberg (1983)

Lanner falcon *Falco biarmicus* (550, 675)	Italy	—	1.4	9.6	2.7	—	86.3	73	Mebs (1959)
	Italy (Sicily)	7.1	—	12.2	—	—	80.7	98	Mascara (1986)
	Italy (Tuscany)	11.5	—	6.4	—	—	82.1	78(1)	Morimando *et al.* (1997)
Saker falcon *Falco cherrug* (840, 1135)	Austria	71.4	—	14.3	14.3	—	0	42	Bauer (1955)
	Hungary	31.9	0.2	53.6	3.3	—	11	2272	Bagyura *et al.* (1994)
	Croatia	80.0	—	3.3	—	—	16.7	30	Suetens & Van Groenendael (1968)
Ural owl *Strix uralensis* (590, 870)	Finland	79.1	4.1	—	1.4	—	15.4	1812	Korpimäki *et al.* (1990)
	Finland	97.1	0.2	—	—	—	2.7	1739	Jäderholm (1987)
Eagle Owl *Bubo bubo* (1890, 2554)	Denmark	38.6	1.4	7.8	2.0	7.7	42.5	1091	Laursen (1999)
	Finland	82.5	4.3	—	2.2	—	11.0	2206	Korpimäki *et al.* (1990)
	France	54.2	11.9	1.9	4.4	—	39.5	2704	Bayle (1996)
	Germany	32.9	5.4	7.2	10.4	2.6	41.5	8766	Bezzel *et al.* (1976)
	Italy	39.3	(3)	3.2	(3)	(3)	57.5	751(11)	Marchesi *et al.* (2002)
	Norway	76.5	2.6	—	3.8	3.1	14.0	807	Mysterud & Dunker (1983)
	Norway	43.0	7.0	—	9.0	3.0	38.0	780	Bergman (1961)
	North Spain	54.8	20.1	3.2	2.6	1.6	17.7	2558	Donázar (1989)
	East Spain	17.9	35.0	3.9	6.5	—	36.7	1395	Martinez & Zuberogoitia (2001)
	North-east Spain	60.5	17.0	2.4	1.7	<0.1	17.9	3670	Serrano (1998)
	South-east Spain	20.3	55.2	2.5	2.9	—	19.1	2026	Martínez & Calvo (2001)
	Sweden	44.5	3.9	1.1	1.4	14.3	34.8	6450	Olsson (1979)
	Sweden	49.7	3.6	0.2	7.1	8.0	31.4	1214	Höglund (1966)
	Sweden	36.0	4.0	—	8.0	5.0	47.0	483	Bergman (1961)

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(1) number of pellets.

(2) number of prey items seen delivered to the nest.

(3) included in 'others'.

(4) number of prey taken by radio-tagged individuals.

(5) includes all other mammals than hare.

(6) includes also pigeons and woodcock.

(7) taken from Table 6 in Toyne, 1998.

(8) includes 1 bird and 17 reptiles.

(9) data from northern Finland (the Finnish reindeer husbandry area).

(10) data from central Finland (south of the reindeer husbandry area).

(11) numbers of pellet and prey remains combined.

short-toed eagle *Circaetus gallicus* (reptiles; Cramp & Simmons, 1980; Bakaloudis, Vlachus & Holloway, 1998), pallid harrier *Circus macrourus* (little detailed information, but mainly small rodents and birds, Cramp & Simmons, 1980), lesser spotted eagle *Aquila pomarina* (principally small mammals, reptiles and insects, game rarely consumed; Sladek, 1959; Glutz von Blotzheim *et al.*, 1971; Cramp & Simmons, 1980; Zawadzka, 1999; Stubbe *et al.*, 2000), steppe eagle *Aquila nipalensis* (present only in Russia, where specializes in ground squirrels, Cramp & Simmons, 1980), black-shouldered kite *Elanus caeruleus* (mainly rodents, small passerines and insects; Amat, 1979; Cramp & Simmons, 1980; Heredia, 1983; Parejo *et al.*, 2001), Levant sparrowhawk *Accipiter brevipes* (mainly lizards and insects, Cramp & Simmons, 1980), long-legged buzzard *Buteo rufinus* (few data available, but apparently mainly small mammals, reptiles and insects, Cramp & Simmons, 1980), hobby *Falco subbuteo* (mainly insects and small passerines, only occasionally hunting pigeons or gamebirds; Thiollay, 1967*a*; Glutz von Blotzheim *et al.*, 1971; Cramp & Simmons, 1980; Fiuczynski, 1988; Sergio & Bogliani, 1999; Sergio *et al.*, 2001), red-footed falcon *F. vespertinus* (mainly insects; Cramp & Simmons, 1980), lesser kestrel *F. naumanni* (invertebrates; Glutz von Blotzheim *et al.*, 1971; Cramp & Simmons, 1980; Negro, 1997), Eurasian kestrel *F. tinnunculus* (mainly small mammals; Hagen, 1952; Korpimäki, 1985; Village, 1990, 2001), Eleonora's falcon *F. eleonorae* (large insects and small birds; Cramp & Simmons, 1980), barn owl *Tyto alba* (small mammals; less than 0.5 % of *Lagopus* spp. chicks; Mikkola, 1983; Taylor, 1994), the Eurasian scops-owl *Otus scops* (mainly invertebrates, Mikkola, 1983), snowy owl *Nyctea scandiaca* (small mammals; Bergman, 1961; Mikkola, 1983), hawk owl *Surnia ulula* (small mammals, only occasional consumption of gamebirds; Hagen, 1952; Huhtala, Korpimäki & Pulliainen, 1987), pygmy owl *Glaucidium passerinum* (small mammals, small passerine birds; Bergman, 1961; Kellomäki, 1977; Schönn, 1980), little owl *Athene noctua* (mainly invertebrates and small mammals; Mikkola, 1983; Génot & Van Nieuwehuyse, 2002), tawny owl *Strix aluco* (small mammals, small passerine birds; Mikkola, 1983; Melde, 1984; Korpimäki, 1986; Petty, 1999; Galeotti, 2001), great grey owl *S. nebulosa* (small mammals; Bergman, 1961; Höglund & Lansgren, 1968; Mikkola, 1981, 1983), long-eared owl *Asio otus* (small mammals, small passerine birds; Hagen, 1952; Mikkola, 1983; Schimmelpfennig, 1991; Korpimäki, 1992*a*; García & Cervera, 2001), short-eared owl *A. flammeus* (small mammals; Hagen, 1952; Mikkola, 1983; Korpimäki & Norrdahl, 1991*a*) and Tengmalm's owl *Aegolius funereus* (small mammals; Hagen, 1952; Korpimäki, 1988; Schulenburg, 1991). It is likely that, in general, these species do not pose a threat to game animals, although during years of small mammal scarcity some of the species listed above may take small numbers of game animals instead of voles. In addition, the merlin *Falco columbarius* mainly preys on small passerine birds (Sulkava, 1971; Watson, 1979; Newton, Meek & Little, 1984; Bibby, 1987), although some predation on young *Tetraonidae* spp. has been reported in Norway (4.5 % of diet; Hagen, 1952). Finally, the diet of the sparrowhawk *Accipiter nisus* consists almost entirely of small passerine birds (Thiollay, 1967*b*; Sulkava, 1972; Newton, 1986; Möckel & Günther, 1991; Zsolt & József, 1993), but the larger females can take numbers of larger birds (such as wood pigeons or gamebirds, see Warncke, 1967; Thiollay, 1967*a*; Cramp & Simmons, 1980; Newton, 1986; Mañosa & Oro, 1991). However, consumption rates of pigeons (5 % of diet at most) and gamebirds (1–2 %) by sparrowhawks are low, and all authors consider that the impact of this species on game species is negligible (Bergman, 1961; Cramp & Simmons, 1980). Although the above-mentioned species do not generally take game, in Spain most of these species, such as tawny owl, long-eared owl or even Eurasian kestrel, may include small rabbits in their diet; the rabbit is considered a key species in Spanish Mediterranean ecosystems, and is also an important game species (Viñuela & Villafuerte, 2003; see Table 1). In fact, the diet of raptors in Spain appears to be much more lagomorph-based than elsewhere in Europe (mean ± S.D. proportion of hares and rabbits in the diet in Spain = 25.4 ± 18.3 %, $N = 44$; elsewhere in Europe = 9.8 ± 14 %, $N = 137$; Mann-Whitney U-test, $z = 5.1$, $P < 0.0001$; calculated from Table 1).

(2) Raptors feeding on game

This group comprises medium-sized and large raptors which feed on a variety of prey, including lagomorphs or gamebirds, but the proportion of these animals in their diet varies temporally and spatially. This group includes larger falcons (peregrines *Falco peregrinus*, gyrfalcons *F. rusticolus*, saker *F. cherrug* and Lanner falcons *F. biarmicus*), kites *Milvus* sp., harriers *Circus* sp., goshawks *Accipiter gentilis*, most eagle species (golden eagles *Aquila chrysaetos*, Spanish imperial eagles *A. adalberti*, eastern imperial eagles *A. heliaca*, spotted eagles *A. clanga*, Bonelli's eagles *Hieraaetus fasciatus*, booted eagles *H. pennatus*), buzzards *Buteo* sp., and the largest owl species (Table 1). The diets of raptors belonging to this group are discussed in detail below.

(*a*) *Kites*

Red kites and black kites *Milvus migrans* are relatively common in southern and central Europe, although their populations are suffering from alarming declines in some areas. They are virtually absent from all but the southern parts of Fennoscandian countries (see Cramp & Simmons, 1980; Forsman, 1999). Both species are predators and scavengers feeding on a wide range of species, and variations in diet reflect food availability and individual preferences (see Cramp & Simmons, 1980). In Spanish studies (Table 1), the proportion of gamebirds in kite diets was low, but rabbits were taken more frequently and their consumption rate profoundly affected the breeding performance of black kites (Viñuela & Veiga, 1992; Viñuela, 2000). It is not known to what extent game prey in the diet of these species is captured alive or taken as carrion, particularly during winter (Ortega & Casado, 1991; García, Viñuela & Sunyer, 1998), but it is known that during the breeding season they are able to catch young rabbits and gamebirds alive (Valverde, 1967; Viñuela, 1991; Villafuerte, 1994).

(*b*) *Harriers*

The diet of hen harriers differs between areas: in Norway small mammals were the most important single prey group, rabbits were the most frequent prey items in Orkney (but see Amar, Redpath & Thirgood (2003) for the importance of voles), and in mainland Scotland the diet largely consisted of meadow pipits *Anthus pratensis* and skylarks *Alauda arvensis* (Table 1). The proportion of gamebirds among the prey items seen delivered to the nest was high in Scotland (12 %), consisting mostly of red grouse (Redpath & Thirgood, 1997). In eastern France, the most important prey were also small mammals and secondarily passerine birds (Millon *et al.*, 2002).

The proportion of game species in Montagu's harriers' *Circus pygargus* diet also varied greatly between areas: in central Spain the proportion of hares in the diet was as high as 17 %; but in other Spanish areas the consumption of game species was negligible (Table 1). In the UK that of gamebirds was also around 17 %. By contrast, the proportion of either prey group in all other studies was less than 5 % with voles the most important prey in central Europe, and passerines and insects in southern Europe (see Butet & Leroux, 1993; Arroyo, 1997; Salamolard *et al.*, 2000; Millon *et al.*, 2002).

Remains of gamebirds were rather frequent in the diet of marsh harriers *Circus aeruginosus* in the UK (21 %) and the Netherlands (24 %), but were rare or totally absent in the diet in other countries such as Finland, France, Spain or Germany (Table 1). In most countries, small mammals appear as the main prey, although rabbits and waterfowl may be relevant in some areas or periods of the year. Small passerines and ducklings are also typical prey.

(*c*) *Goshawk*

Gamebirds are important prey items for goshawks particularly in northern Europe, where individual pairs may specialise almost completely in capturing gamebirds (Myrberget, 1970). For example, in Finland and Sweden their proportion in the diet varied from 15 to 44 % (Table 1; see also Sulkava, 1964). In central and southern Europe gamebirds may be partially substituted by lagomorphs, pigeons, corvids and thrushes, although partridges may still represent as much as almost 20 % of diet in NE Spain (Mañosa, 1991). In southern and western Finland, hazel grouse (*Bonasa bonasia*) was the most important prey species of the goshawk (percentage of hazel grouse in prey biomass during breeding season varied between 4 and 34 %; see Wikman & Tarsa, 1980; Lindén & Wikman, 1983, 1987; Forsman & Ehrnsten, 1985). In Swedish studies, radio-tracked goshawks fed almost exclusively on pheasants in autumn on an estate with pheasant release, and elsewhere wild pheasants were the most important source of winter biomass for male goshawks (Kenward, Marcström & Karlbom, 1981), whereas in Germany, the Netherlands, Poland and the UK, the diet contained far more pigeons than gamebirds (Table 1).

In northern Finland, the diet and breeding biology of goshawks has been studied since the 1960s (see Tornberg & Sulkava, 1991; Tornberg, 1997, 2000, 2001; Tornberg & Colpaert, 2001 for further details). Despite a remarkable decrease in forest grouse numbers during this period (Lindén & Rajala, 1981), their proportion in the diet of goshawks has remained relatively high, probably because they constitute the only sufficiently large and abundant prey for goshawks in this region. Therefore, in these northern forests, goshawks have relatively little scope for switching to other prey if the main prey decreases. Although the goshawk is considered a generalist predator (Marti *et al.*, 1993), it is more specialised in the north, especially during winter when migratory birds are absent. Grouse were clearly the preferred prey in early spring, especially the smallest species, the willow grouse (*Lagopus lagopus*) and the hazel grouse. Goshawks preyed on grouse during the nest-building and incubation periods, then shifted to ducks and then to thrushes, corvids and pigeons during the nestling period, then to grouse and leverets during the post-fledging period (Tornberg, 1997). The winter diet seemed to consist of mountain hares *Lepus timidus*, red squirrels *Sciurus vulgaris*, brown rats *Rattus norvegicus*, and forest grouse. Hares constituted 70 % of the biomass consumed by weight (Tornberg & Colpaert, 2001). In Sweden, the winter diet of goshawks (as revealed by radio-tracking) consisted mostly of red squirrels (80 % of winter prey) in a forest-dominated area (Widén, 1987), but only 33 % squirrels and 28 % gamebirds in farmland-dominated areas (Kenward *et al.*, 1981). It should also be noted that Widén's (1987) study was conducted during a squirrel population peak.

(*d*) *Buzzards*

Common buzzards *Buteo buteo* and rough-legged buzzards *B. lagopus* specialise more or less in small mammals in Europe, although both species can utilise alternative prey, such as game animals, during low vole years or in southern Europe where small mammals are less abundant (Table 1; see also Herrera & Hiraldo, 1976; Kowalski & Rzępala, 1997; Selås, 2001). *Microtus* spp. voles were the main prey of common buzzards in western Finland, and water voles, shrews, forest grouse and hares the most important alternative prey (Reif *et al.*, 2001). In this study, the proportion of forest grouse in the diet of buzzards was nearly independent of grouse abundance in the field and buzzards mainly took grouse chicks. The proportion of rabbits in the common buzzard's diet was considerable in the UK and particularly in Spain, where rabbits are the main prey of a large number of predators (Table 1; Viñuela & Villafuerte, 2003). Predation on gamebirds is relatively low when recorded at nests; however 15 % of prey were game in one UK study, and predation on pheasant poults can become heavy at poorly designed release pens after the breeding season (Kenward *et al.*, 2001).

(*e*) *Eagles*

Golden eagles appear to feed mainly on lagomorphs and gamebirds throughout Europe (Table 1). The proportion of gamebirds seems to be highest in northern Europe (Finland, Sweden and Norway) while in the more southern areas lagomorphs, particularly rabbits, are taken (Delibes, Calderon & Hiraldo, 1975; Fernández & Purroy, 1990; Fernández, 1993), except in Corsica where large mammals account for 40% and reptiles for 30% of the diet, respectively (Seguin & Thibault, 1996). In the reindeer husbandry area in northern Finland, reindeer calves were also included in the diet of golden eagles (8–12%; Sulkava *et al.*, 1999). The golden eagle is probably the only European raptor to include in the diet a percentage of other game predators (e.g. 15% carnivores, 11% corvids, and 4% raptors in NE Spain; Fernández & Purroy, 1990; see review in Watson, 1997). In fact, the presence of golden eagles in a hunting area could be beneficial, because they kill or keep away other species of predators, and thus they could reduce overall predation pressure on game species (Fielding *et al.*, 2003). Spanish imperial eagles feed mainly on medium-sized mammals, particularly rabbits, but also on medium-sized birds, particularly where these are abundant such as waterfowl in Doñana National Park or where rabbits are scarce (Table 1; Cramp & Simmons, 1980; Forsman, 1999; Ferrer, 2000). Since the estimated population comprises only 150–160 pairs (Forsman, 1999; Ferrer, 2000), possible negative effects on game numbers are likely to be highly localised. Eastern imperial eagles seem to specialise on small ground mammals, but the main alternative prey are lagomorphs and gamebirds (Table 1). Less information is available about the diet of spotted eagles, but the available data suggest that they also consume mainly small mammals. Bonelli's eagle and the booted eagle are also found in southern Europe, and their diets have been studied mostly in Spain and France (for Bonelli's and booted eagle see Table 1, for booted eagle see also Cramp & Simmons, 1980). Gamebirds are fairly typical in the diet of Bonelli's eagle (it is called the partridge-eating eagle in Spain), but booted eagles also take small to medium-sized birds, including red-legged and grey partridges (Cramp & Simmons, 1980).

(*f*) *Large falcons*

The share of gamebirds by number in the diet of peregrines was some 10–15% in the UK, but very low in Spain. Most prey items in Finland and the UK were pigeons, waders and ducks (Table 1). Gyrfalcons seem to be more or less specialised on gamebirds, especially rock ptarmigans *Lagopus mutus*, and their proportion in the diet exceeded 60% in all three studied areas. Less information is available about diets of lanner and saker falcons (Table 1). The diet of lanner falcons may include small numbers of pigeons, but apparently only rarely gamebirds or lagomorphs, while saker falcons may include at least locally significant percentages of gamebirds in the diet.

(*g*) *Owls*

The diet of eagle owls *Bubo bubo* varied greatly across areas, and the proportion of small mammals in the diet increased with latitude (France being an exception) (Table 1). With respect to game species, the relative importance of the eagle owl predation appears to be highest in Spain (proportion of rabbits in diet 17–55%) and in Germany (proportion of gamebirds 10%). However, the proportion of gamebirds in the diet of northern eagle owls and Ural owls *Strix uralensis* can be higher than Table 1 indicates, particularly during low vole years, when the owls can switch from voles to alternative prey. These owl species mainly feed on *Microtus* spp. voles, which show 3–4 year population cycles (e.g. Hansson & Henttonen, 1985). Korpimäki *et al.* (1990) found that yearly abundances of voles correlated positively with the proportions of voles in the diet of the eagle owl but were not related to the proportions of gamebirds in the diet of the owls (Fig. 1). For the Ural owl, the proportion of small game in the diet was negatively related to the abundance of voles in the field. Both owls also took more small game in poor vole years than in good ones, independent of the proportion of voles in the diet. In addition, the proportion of small game in the diet was nearly independent of its abundance in the field. The data indicate that both owl species behave as predicted by the APH (Korpimäki *et al.*, 1990), but their predation impact on small game requires more research to be accurately quantified.

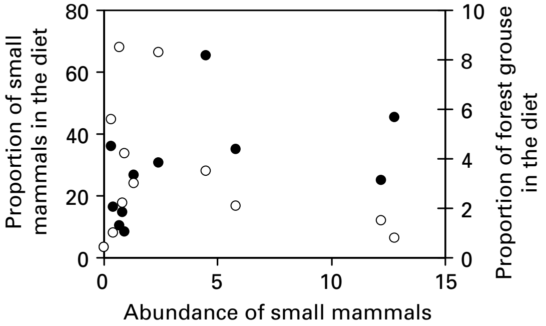

Fig. 1. Correlation between the spring abundance index (individuals per 100 trap nights) of *Microtus* spp. voles and the proportion of these voles in the diet of the eagle owl *Bubo bubo* (left y-axis, filled circles), and the proportion of forest grouse (the capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, hazel grouse *Bonasa bonasia* and willow grouse *Lagopus lagopus*) in the diet of the eagle owl (right y-axis, open circles) in western Finland during 1973–74, 1977–80 and 1982–87. The vole correlation is significant ($r_s = 0.57$, $P < 0.05$) while that of the grouse is not ($r_s = 0.11$, NS). Data from Korpimäki *et al.* (1990).

(3) Summary of raptor diets

The review of the literature reveals that more than half (32/52) of the European bird of prey species do not eat game animals as judged from existing diet studies and thus can be assumed to have negligible or nil effect on populations of game species. The remaining 20 species do prey on small game (lagomorphs or gamebirds), but there is much variation among species, and also among areas within the range of any given species in the contribution of game species to the diet (Table 1). Only three raptor species, the gyrfalcon, goshawk and golden eagle, can have rather large proportions of gamebirds in their diet, but locally also harriers, buzzards, Bonelli's eagles, booted eagles and peregrines may utilise gamebirds to some extent. A high percentage of a given prey species in the diet of a predator does not necessarily mean that this prey was taken alive, or that this predator has a negative impact on prey density. Some raptors, kites in particular, may take game animals partly or largely as carrion, which diminishes their effect on prey populations. Factors such as prey and predator densities, and the extent of mortality from other sources (e.g. from hunting or mammalian predators and other natural enemies) should be taken into account when evaluating the significance of avian predation. Further, for large territorial species at low densities (the golden eagle, for example), the amount of food required from a given area can also translate into relatively low effect on prey numbers even if the proportion of that prey species in the diet is relatively high (see Brown & Watson, 1964). On the other hand, if a prey population is at relatively low density or otherwise stressed, even a few prey individuals killed by a predator may have detrimental effects on prey population dynamics. In southern Europe, particularly Spain, the rabbit is the main prey of a wide range of predators, but rabbit populations have recently been decimated by rabbit haemorraghic disease (RHD). Thus, many predators in Spain may have to switch to other more abundant prey, including gamebirds, although more research is needed to confirm this (Serrano, 2000; Viñuela & Villafuerte, 2003). After irruption of RHD, golden eagles in northern Spain increased their consumption of partridges and hares (Fernández, 1993), behaving as generalist predators, and increasing their pressure on gamebird populations. However, eagle owls seem to be highly specialised on rabbits in some areas in Spain; their consumption rate of rabbits did not change significantly after RHD irruption, and rabbit scarcity may have caused declines in breeding success or population density of this predator (Serrano, 1998; Martínez & Calvo, 2001). On the other hand, rabbit populations may be suffering a 'predator-pit' situation, in which a population recovery may be hampered by predation, this contributing to the maintenance of this ecological and social problem (Viñuela & Villafuerte, 2003).

III. NUMERICAL RESPONSES

(1) Hen harriers, peregrines and red grouse

The numerical response of hen harriers and peregrines to red grouse and other moorland prey was studied in Scotland during 1992–2002 (Redpath & Thirgood, 1997, 1999; Thirgood *et al.*, 2000*a*, *b*, *c*; Thirgood & Redpath, 2004). Neither harriers nor peregrines showed a numerical response to red grouse abundance during the breeding season (Redpath & Thirgood, 1997, 1999), although both species were seen more frequently during winter in areas with more grouse (Thirgood *et al.*, 2002). Variation in hen harrier breeding density between areas was positively related to the abundance of meadow pipits *Anthus pratensis*, whilst variation within areas was related to the abundance of field voles (Redpath & Thirgood, 1997, 1999; Redpath *et al.*, 2002). The breeding densities of peregrines were highest in southern parts of the UK uplands and this was believed to be due to the abundance of racing pigeons. The ratio of hen harriers to grouse can be high compared with other territorial, monogamous predators, such as peregrines, which are not restricted to the same habitat as grouse.

(2) Goshawks and gamebirds

In southern Finland, the breeding densities of goshawks showed no clear numerical response to hazel grouse numbers. They shifted to feed on thrushes and crows when hazel grouse densities declined (Lindén & Wikman, 1983). Data collected from two sites in western Finland showed that brood size of goshawks increased with the relative density of hazel grouse (Lindén & Wikman, 1980) or with the total density of tetraonids (Huhtala & Sulkava, 1981; Sulkava, Huhtala & Tornberg, 1994). Tornberg (2001) found that goshawks in northern Finland showed a weak numerical response, measured as the number of nesting territories with a time-lag of one year, to the density of all grouse species pooled. Data from seven sites in Sweden and northern Germany indicated a weak sigmoidal numerical response by goshawks to pheasant densities in winter (Kenward, 1986) and goshawk dispersal behaviour also responded strongly to the availability of rabbits (Kenward, Marcström & Karlbom, 1993).

(3) Gyrfalcon and ptarmigan

In Iceland, the number of occupied gyrfalcon territories correlated with a three-year time-lag to numbers of rock ptarmigan, and total number of gyrfalcon (territorial adults and fledglings) in late summer correlated with ptarmigan numbers with a two-year time-lag (Nielsen, 1999). This study suggested that the factors contributing to the time-lag were the year-round residency of falcons on nesting territories and also late maturity. The delayed numerical response was seen as a destabilising effect of predation on ptarmigan populations.

(4) Summary of numerical responses

Studies on the numerical responses of avian predators to changing gamebird numbers are relatively scarce. In fact, this issue was clearly addressed in only 10 field studies, the main findings of which are summarised in Table 2. In half of these studies, no numerical response was found while in the remainder a response was detected. Among the latter studies, three (goshawks-forest grouse in northern Finland, common buzzard-forest grouse in western Finland and gyrfalcon-ptarmigan in Iceland) showed a time lag of one to three years; it is under such circumstances that predators are believed to induce cycles in prey populations (see Introduction).

IV. FUNCTIONAL RESPONSES AND TOTAL RESPONSES

Here, we summarise the main results of studies on the functional responses of birds of prey to changing gamebird

Table 2. Numerical (NR) and functional responses (FR) of raptors to changes in gamebird densities in Europe. Limit? = Does raptor predation limit the population size of gamebirds? BS = breeding season

Gamebird	Raptor	Country/area	NR	FR	Predation impact	Limit?	Source
Red grouse *Lagopus lagopus scoticus*	Hen harrier *Circus cyaneus*	UK/Scotland	No	Type III	(1)	Yes	Redpath & Thirgood (1997); Thirgood *et al.* (2000*c*)
Red grouse	Peregrine *Falco peregrinus*	UK/Scotland	No	Type II	(1)	Yes	Redpath & Thirgood (1997); Thirgood *et al.* (2000*c*)
Hazel grouse *Bonasa bonasia*	Goshawk *Accipiter gentilis*	Southern Finland	No	Type III	12 % of adults (BS)	?	Lindén & Wikman (1983)
Hazel grouse	Goshawk	Western Finland	Yes	?	?	?	Lindén & Wikman (1980)
Forest grouse(2)	Goshawk	Northern Finland	Weak (one-year lag)	Weak	7–32 % of all grouse (BS)	Yes	Tornberg (2001)
Forest grouse(3)	Common buzzard *Buteo buteo*	Western Finland	Yes (one-year lag)	No	(4)	(Yes)	Reif *et al.* (2001); V. Reif, unpublished data
Black grouse *Tetrao tetrix*	Goshawk	Sweden/Grimsö	?	No	(5)	—	Widén (1987)
Ptarmigan *Lagopus mutus*	Gyrfalcon *Falco rusticolus*	Iceland	Yes (two-year lag)	Type II	18 % of adults (BS)	Yes	Nielsen (1999)
Pheasant (wild) *Phasianus colchicus*	Goshawk	Sweden	Yes	Yes	(6)	Yes	Kenward *et al.* (1981); Kenward (1986)
Red-legged partridge *Alectoris rufa*	Goshawk	Spain/Catalonia	—	Yes?	(7)	?	Mañosa (1991, 1994)
Grey partridge *Perdix perdix*	Hen harrier, marsh harrier *Circus aeruginosus*	France	No	?	varies across areas, 15–70 % of total predation	?	Bro *et al.* (2001)
Forest grouse(2)	Eagle owl *Bubo bubo*	Western Finland	No	No	(8)	?	Korpimäki *et al.* (1990)

(1) Raptors were the cause of about 70 % of winter mortality and killed about 30 % of the grouse present in October. They also caused ⩾ 90 % of the early summer mortality of adult grouse. Summer raptor predation on adult grouse and chicks reduced autumn grouse densities by about 50 %.

(2) Including hazel grouse, black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus* and willow grouse *Lagopus lagopus*.

(3) Including hazel grouse and black grouse.

(4) Common buzzards responded both numerically and functionally to the densities of main prey (*Microtus* spp. voles) but there was a half- to one-year lag in their numerical response. At declining and low vole densities buzzards shifted to forest grouse chicks and apparently contributed to their density decline.

(5) During spring and summer goshawks removed 25 % of the female, and 14 % of the male black grouse population.

(6) Goshawk predation caused 88 % of 64 % total loss females and 23 % of 76 % total loss males.

(7) Goshawks removed 4.7 % of chicks and 6 % of autumn birds.

(8) Breeding eagle owls responded both numerically and functionally to cyclic density variations of small rodents, and shifted to alternative prey, such as forest grouse, at declining and low densities of small rodents.

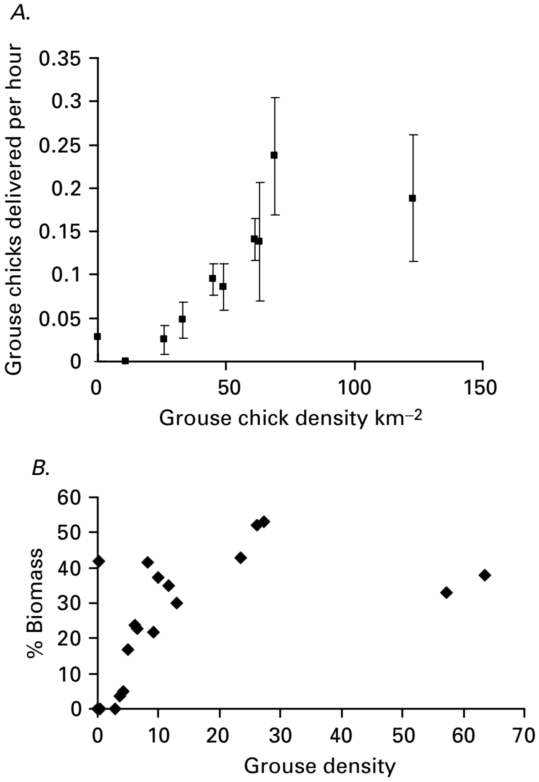

Fig. 2. *A*. Rate at which red grouse *Lagopus lagopus scoticus* chicks were brought to hen harrier *Circus cyaneus* nests by males and females combined in relation to the density of grouse chicks. Each point represents a mean ± S.E.M. for one moor in one year ($N = 1$–7). *B*. The percentage of grouse in peregrine prey (by biomass) in relation to estimates of grouse abundance within a 2-km radius of each eyrie. Data from Scotland (Redpath & Thirgood, 1999, 2003). Reproduced by kind permission of Blackwell Publishing, Oxford (Figs 6 and 8 in Redpath & Thirgood (1999)).

densities and also present results of studies that have attempted to quantify the effects of raptor predation on gamebird populations.

(1) Hen harriers, peregrines and red grouse in Scotland

Studies of raptor-grouse dynamics in Scotland suggest that the functional response of hen harriers to red grouse chicks is sigmoidal or type III, whilst that of peregrines to adult red grouse is asymptotic or type II (Redpath & Thirgood, 1999) (Table 2, Fig. 2). The shape of the hen harrier functional response suggests that the proportion of grouse chicks taken by harriers is highest at densities of 67 chicks km^{-2} (equivalent to 12 broods km^{-2}). The proportion of adult grouse taken by peregrines appeared to be inversely density dependent, such that increasing proportions of grouse were taken at densities below 20 grouse km^{-2}. The combined effect of the functional and numerical responses of hen harriers was that the impact of harrier predation was greatest on low-density grouse populations on moors where alternative prey, such as meadow pipits were most abundant (thus supporting higher numbers of harriers). There was direct density-dependence in the impact of hen harrier predation on red grouse chicks, but not in the impact of peregrine predation on adult red grouse. The suggestion was that predation by peregrines in the absence of other predators would not limit grouse numbers; but peregrine predation in addition to hen harrier predation was likely to reduce the ability of low-density grouse populations to increase (Redpath & Thirgood, 1999).

Seasonal trends in red grouse mortality, and the impact of predation, were studied by Thirgood *et al.* (2000*c*). Winter losses of red grouse between October and April averaged 33 %, and were density-dependent. Raptors were the cause of approximately 70 % of winter mortality, killing about 30 % of the red grouse present in October, but it was not known whether this source of mortality was additive to other losses. Summer losses of adult grouse between April and July averaged 30 %, and were also density-dependent. Raptors were the cause of more than 90 % of the early summer mortality of adult red grouse. Summer losses of red grouse chicks between May and July were estimated at 45 %, and were not density-dependent. Hen harriers killed approximately 28 % of red grouse chicks by late July, and about 37 % by the end of August. Summer raptor predation on adult red grouse and chicks appeared to be largely additive to other losses, and it was estimated that raptor predation reduced autumn grouse densities by 50 %. Thirgood *et al.* (2000*c*) developed a population model, combining the estimated reduction in autumn grouse density with the observed density dependence in winter loss, which suggested that in the absence of raptors for two years, red grouse densities in spring would be 1.9 times greater, and red grouse densities in autumn 3.9 times greater than in the presence of raptors. This model further suggested that raptor predation prevented the red grouse population from increasing and was thus a limiting factor.

Further evidence to suggest that predation by harriers and peregrines had a limiting effect on red grouse populations comes from analysis of red grouse shooting bags and a 'quasi-experimental' manipulation of hen harrier breeding densities. The numbers of red grouse harvested on Langholm moor in southern Scotland declined significantly during 1913–1990. Harriers and peregrines were absent or bred at low densities during this time but heather-dominant vegetation (favoured by the grouse) declined by 48 %. Harrier and peregrine breeding numbers increased to high levels following protection in 1990, whilst grouse density and grouse shooting bags declined year after year until shooting was abandoned in 1998. The prediction of a peak in grouse bags at Langholm in 1996, based on the patterns of bags during 1950–1990, was supported by the observed peaks in 1997 on two nearby moors with few raptors which formerly cycled in synchrony with Langholm moor. This study strongly suggested that, whilst long-term declines in grouse bags were most probably due to habitat loss, high levels of raptor predation subsequently limited the grouse population and suppressed a cycle (Thirgood *et al.*, 2000*a*).

(2) Goshawk and gamebirds in Sweden

Goshawks showed no functional response to fluctuations in black grouse *Tetrao tetrix* densities in Central Sweden (Widén, Angelstam & Lindström, 1987). It was estimated that during spring and early summer, goshawk predation removed 25 % of female and 14 % of male black grouse (Widén *et al.*, 1987). It was also estimated that goshawks killed more females than males of both black grouse and capercaillie (*Tetrao urogallus*) especially during low vole years (Widén *et al.*, 1987). In boreal forest, grouse form the staple food of goshawks in spring and summer. For comparison, in Norway approximately 50 % of the natural annual mortality among adult capercaillie hens was due to goshawk predation (Wegge, 1984). Therefore, goshawk predation on forest grouse can be a significant mortality factor.

In southern Sweden, goshawks took approximately 19 % of the 4300 released captive-born pheasants (*Phasianus colchicus*) (1/3 of those not shot by hunters or left wild in the spring) during the autumn and winter (Kenward, 1977). Goshawks were responsible for an estimated 88 % of the 64 % overwinter mortality among wild female pheasants, and for 23 % of the 76 % loss among wild male pheasants at one site (Kenward *et al.*, 1981). Combining data from this site and six others in Sweden and northern Germany where goshawks were radio-tracked to record predation, the functional response was found to be convex (Type II). The predation rate exceeded 5 % per month, which could only be sustained if the wild pheasants bred at the maximum rate for Scandinavia, at a second site where goshawks accumulated due to a high density of rabbits (Kenward, 1986; Kenward *et al.*, 1993). Interestingly, comparison of kills with population samples indicated an overrepresentation of females killed during periods of snow cover but not of individuals in poor condition. The demographic responses of the goshawks in these studies were used in a model that simulated survival in a predator–prey system from individual variation in functional responses; this showed that a one-predator-one-prey system could be stable, or exhibit cyclical variations, depending on the strength of the predator's breeding response (Kenward & Marcström, 1988).

(3) Goshawk and forest grouse in Finland

In southern Finland, goshawks showed a marked functional response to hazel grouse numbers, but the shape of the response curve was atypically concave (Lindén & Wikman, 1983). However, in reality it was perhaps of type III, but no data on goshawk diet composition were obtained at high hazel grouse densities. The average predation rate of goshawks on hazel grouse during the breeding season was estimated at 12 %, and the annual estimate was 36 %.

A weak functional response of goshawks to varying grouse numbers was found in the Oulu region of northern Finland, but here the density changes of grouse were rather small and goshawks presumably also killed grouse at maximum intensity at the lowest densities of grouse (Tornberg, 2001). This suggests a response type of a specialist predator not able to switch to other prey. In this situation, the shape of the functional response curve in goshawks was concave (type II). The total response of goshawks to grouse was inversely density-dependent, with predation rate being highest at low densities. Similar total responses of goshawks were also found in southern Finland (Wikman & Tarsa, 1980; Wikman & Lindén, 1981). Predation patterns of this kind indicate a delayed density-dependence and destabilising effect of the predator on prey populations (Sinclair & Pech, 1996). Predation impact of breeding goshawks on grouse varied from 7 to 32 % during the breeding season (highest for willow grouse, lowest for capercaillie) (Tornberg, 2001). On average, goshawks took 7 % of grouse chicks; on an annual basis the breeding goshawks took 2–24 % from the August grouse population. The goshawk's share of the total mortality was estimated to be 32 % of willow grouse, 9 % of black grouse males, 17 % of black grouse females, 7 % of capercaillie females, 20 % of hazel grouse and 6 % of grouse chicks of all species (Tornberg, 2001).

While predation by mammals on willow grouse has received much attention (see e.g. Marcström *et al.*, 1988), the effect of raptor predation is more poorly known, in spite of the fact that birds of prey, mainly gyrfalcons and goshawks, are frequently considered the main predators of willow grouse (Smith & Willebrand, 1999). In northern Finland, the decline in the willow grouse population from 1988 to 1998 was positively correlated with summer goshawk predation (Tornberg, 2000). It appeared that goshawk predation on willow grouse may be high and, in the presence of alternative prey (other grouse species, corvids, wood pigeons, pheasants, red squirrels), it may result in low density and stable grouse populations. Goshawks in northern Finland fulfilled rather well the criteria of predation theory, as they appeared to lag behind grouse numbers, they were fairly specialised on grouse, their kill rate of willow grouse was negatively related to changes in willow grouse densities and predation pressure was highest when grouse densities were lowest (Tornberg, 2001).

(4) Goshawk and gamebirds in south-western Europe

In north-eastern Spain, goshawk predation on red-legged partridges *Alectoris rufa* was high in spring (Mañosa, 1994), and it was estimated that 15 % of clutches were lost due to goshawk predation on adults (Mañosa, 1991). It is possible that this predation was partially additive to other sources of mortality. Although goshawk predation on partridge chicks and juveniles was relatively low, the combined effect of spring and summer predation resulted in a 22 % reduction in the number of birds available for shooting. It was estimated that goshawks consumed over winter only 6 % of the autumn partridge population, and were probably of little importance in influencing the population size of partridges next spring.

In a study aiming at reinforcing a pheasant population on a 2650 ha area in France (Mayot, Patillaud & Stahl, 1993), a total of 4500 hand-reared birds were released between 1985 and 1989, of which 257 were radio-tagged together with 72 wild birds. In the course of the study, 203 of the 257 hand-reared and 30 of the 72 wild birds were found dead with the cause of mortality identified. Predation appeared to be the most common cause of death for both hand-reared (89 %) and wild birds (87 %), and approximately 70 % of predated individuals were taken by red foxes. Some 10–20 % were taken by raptors, presumably goshawks (Mayot *et al.*, 1993).

(5) Buzzard predation on gamebirds

Kenward *et al.* (2001) examined predation by common buzzards on released pheasants in the UK from 1990 to 1995. Location data from 136 radio-tagged buzzards, together with prey remains from 40 nest areas, records from 10 gamekeepers and vegetation surveys, were used to investigate raptor predation at 28 pens from which pheasants were released in southern England. A total of 20725 juvenile pheasants was released in 1994–95, of which only 4.3 % were taken by buzzards. Although the predation impact exceeded 10 % at some sites, it was negligible at sites with good ground cover and few overhead perches for buzzards and a high density of released pheasants. Lloyd (1975) arrived at similar conclusions about cover for protecting pheasants from predation in that case mainly by tawny owls (*Strix aluco*).

Reif *et al.* (2001) found that breeding densities and reproductive success of common buzzards in western Finland responded to the fluctuating densities of *Microtus* spp. voles with a half- to one-year delay and that common buzzards shifted to forest grouse chicks and leverets during the decline and low phase of the vole cycle. Reif *et al.* (2001) concluded that common buzzards may, together with other generalist predators, reduce the breeding success of gamebirds and other small game (mostly young hares), in particular in the decline phase of the vole cycle when they shift to alternative prey and their breeding densities are still high. They may thus contribute to the existence of short-term population cycles of small game. Recent estimates indicate that the predation impact by breeding common buzzards on adult black grouse was 0.8 % (among-year variation 0.3–1.3 %), on black grouse juveniles 0.9 % (0.4–1.7 %), on hazel grouse 1.1 % (0.2–2.9 %), and on hazel grouse juveniles 1.4 % (0.4–3.3 %) produced during the summer (V. Reif, S. Jungell, E. Korpimäki & R. Tornberg, unpublished data).

(6) Gyrfalcon and ptarmigan in Iceland

Predation by raptors, particularly the gyrfalcon, is a major mortality cause of ptarmigan (as much as 91 % of mortality, affecting up to 15 % of adult population yearly; Cotter, Boag & Shank, 1992). The relationship between gyrfalcon and ptarmigan (*Lagopus mutus*) has been thoroughly studied in Iceland during 1981–1997 (Nielsen, 1999). The functional response curve of gyrfalcons was slightly convex or close to linear. Predation rate peaked during the decline and low phases of the ptarmigan cycle. Nielsen (1999) suggested that predation by gyrfalcons accelerates the decline, accentuates the amplitude and prolongs the low phase of the ptarmigan cycle. He also identified three potential destabilising factors: (1) gyrfalcons are resident specialist predators, (2) gyrfalcons show a delayed numerical response, and (3) gyrfalcons show a high utilisation of ptarmigan in all phases of the ptarmigan cycle. Consequently, the patterns of gyrfalcon predation on ptarmigan seem to fit well with the predictions of predation theory.

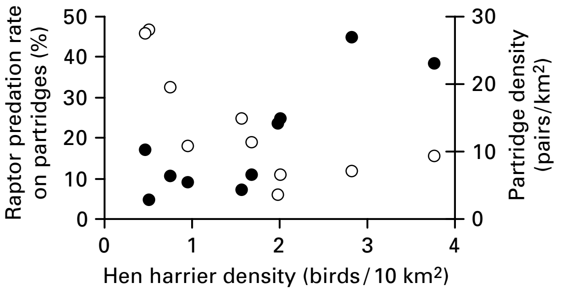

Fig. 3. Correlations between (i) raptor predation rate on grey partridges and hen harrier abundance (left *y*-axis, filled circles; $r_s = 0.83$, $P < 0.01$) and (ii) partridge spring densities and harrier abundance (right *y*-axis, open circles; $r_s = -0.72$, $P < 0.05$). Data from France (Bro *et al.*, 2001).

(7) Harrier predation on grey partridges in France

There is some correlative evidence to suggest that raptor predation may influence grey partridge (*Perdix perdix*) populations in France (Reitz *et al.*, 1993). Predation was the most common source of mortality among adult grey partridges during the breeding season: 54 % of the mortality was due to predation, and out of this, 59 % was attributed to birds of prey. Bro *et al.* (2001) subsequently showed that female partridges experienced high predation rates during spring and summer (varying from 32 % to 65 % across 10 study areas), 15–70 % of which was caused by raptors. Raptor predation rates on breeding females correlated with hen harrier abundance (measured as the total number of hen harriers seen during 2-h large-scale surveys with multiple observers) (Fig. 3), and partridge spring densities were negatively correlated with harrier abundance (Bro *et al.*, 2001). The ratio of harriers to partridges was thus high (on a relative scale) in some areas. Furthermore, the population growth rate of partridges was also negatively correlated with harrier abundance (Bro, 1998; Bro *et al.*, 2000). However, these findings may also result from confounding factors (spatial coincidence rather than causal factors). Indeed, the authors could not separate the interacting effect of predators from those of habitat (Bro *et al.*, 2001).

V. THE EFFECTS OF RAPTOR PREDATION ON GAMEBIRD POPULATIONS

Newton (1993, 1998) reviewed the role of predation in limiting bird populations and concluded that although mortality due to predation was unlikely to be always compensatory, many bird populations have reservoirs of nonbreeders which can replace territorial birds lost to predators. Recently, Nordström (2003) summarised 38 field experiments on ground-nesting birds in which either mammalian or avian predators had been experimentally removed to examine their impact on their avian prey (only one experiment included removal of raptors). Nest success of prey birds increased in 26/31 of these experiments after predator removal, post-breeding numbers increased in 14/20 cases and subsequent breeding numbers increased in 14/23 studies. As Newton (1993) also pointed out, two groups of ground-nesting birds – gamebirds and waterfowl – were particularly prone to limitation by predation. Amongst the gamebirds, only four experiments out of nine demonstrated that increased breeding success as a result of predator removal also resulted in increased breeding density (reviewed by Nordström, 2003). There was also some indication that experiments that had led to increased breeding densities had lasted for longer than those that had not, but this difference was not statistically significant.

Newton (1993, 1998) made three further relevant points. First, the majority of predator removal experiments have been carried out on ground-nesting prey species and on generalist predators, a combination in which predation is probably important. Although only one of these experiments included removal of raptors, there is no inherent reason why the removal of generalist raptors would give different results from generalist mammalian predators (Redpath & Thirgood, 1997). Second, in experiments where only one predator was removed, there was usually little increase in prey density because of compensatory increased predation by other species. Similarly, in predator removal experiments on small rodents, prey densities only increased when all the main predators were removed, not when only one predator species or group was removed (Norrdahl & Korpimäki, 1995*a*; Korpimäki & Norrdahl, 1998). Therefore, it seems that vertebrate predators have relatively high compensatory capacity when competition among predators is relaxed or risk of intra-guild predation is reduced. Third, in some experiments, predation was influenced by the availability of alternative prey (usually voles or rabbits) and habitat features such as nesting cover.

An additional caveat raised by Newton (1993, 1998) is the important difference between the effect of predation by raptors or other predators on breeding densities and on breeding production of game birds. The misunderstanding of these two aspects of population ecology also explains some of the differences of opinion between conservationists and hunters. Conservationists tend to be concerned with breeding densities of birds, whereas hunters are primarily concerned with the abundance of birds at the end of the breeding season and the onset of the hunting season. It is not contradictory that raptor predation might reduce the breeding production of gamebirds between hatching and the start of the hunting season, but have little or no impact on subsequent breeding densities because of compensatory reductions in other causes of mortality before the breeding season.

Our review of the literature up to 2003 indicates that there are rather few studies that have quantified both the numerical and functional responses of raptors to changes in gamebird densities (Table 2). Almost all of these studies were conducted in northern Europe and in fact most were conducted on goshawks. There were only single studies of other species (common buzzard, hen harriers, gyrfalcon and peregrine). The obvious reason for the lack of long-term studies is that they require considerable financial and logistic resources. Furthermore, it may be difficult to find areas with a full complement of unmolested predators and landowners that will agree not to persecute predators during the time of the experiment. A consequence of the relatively small number of detailed studies on raptor-gamebird dynamics is that it is difficult to develop general conclusions concerning the potential for raptor populations to limit game bird prey populations more widely.

Given the caveats listed above, what are the factors that might promote a high predation impact of raptors on game birds? Kenward (1986) noted how high rabbit density caused goshawks to accumulate in an area of Gotland and then prey unusually heavily on pheasants. In the case of red grouse and harriers in Scotland, it was suggested that the habitat loss and fragmentation caused by excessive sheep grazing resulted in high availability of alternative prey which increased the abundance of hen harriers and thus resulted in higher predation rates on red grouse (Redpath & Thirgood, 1999; Thirgood *et al.*, 2000*a*). Further, in this situation the authors concluded that the impact of raptor predation was greatest at relatively low grouse densities (below approximately 12 pairs per km^2). In Iceland, on the other hand, the fact that gyrfalcons are resident specialists showing a delayed numerical response and a high utilisation of ptarmigan seemed to promote the destabilising effects of predation (Nielsen, 1999). Similarly, goshawks in northern Finland are also resident specialists (especially in winter) feeding mainly on forest grouse, and their predation rate on adult grouse is highest at low grouse densities which can have a destabilising effect on grouse populations (Tornberg, 2001). In other words, in northern regions where alternative prey is absent or scarce, predation by resident specialists may induce grouse cycles.

VI. RAPTORS AND GAMEBIRDS IN NORTH AMERICA

In North America, gamebirds are an economically important natural resource which provide many state resource agencies with a significant proportion of their annual budget through hunting licence fees (Riley & Schulz, 2001). Forest grouse in particular may become more popular as game species due to their wide distributions on public land and relatively stable populations compared to other gamebirds in Northern America (Hewitt, Keppie & Stauffer, 2001). In the 1990s, a specific Predation Avian Recruitment Team (PART) was established in response to several public and private agencies and organisations. It had several objectives, including (i) conducting an analysis of predation and habitat interactions in the population dynamics of avian species, (ii) conducting the analyses and interpretation of information available, (iii) providing quality publications on the basis of these analyses and (iv) identifying additional research that may be required to assess fully the impact of predation on avian recruitment (Nelson, 2001).

Some existing studies indicate that raptor predation may be an important source of mortality for North American grouse species. For example, predation by raptors may account for as much as 50% of annual pheasant (*Phasianus* spp.) mortalities (Snyder, 1985; Riley, Wooley & Rybarczyk, 1994). Annual nest losses in forest grouse (blue grouse *Dendragapus obscurus*, spruce grouse *Falcipennis canadensis*, and ruffed grouse *Bonasa umbellus*) averaged 36% in 22 studies, with an average of 81% of these resulting from predation (Hewitt *et al.*, 2001). Chick losses were even higher, but the proportion of chicks lost to predators remained unknown. Overall mortality of subadult grouse during autumn and winter averaged 55%, and was most probably due to predators (Hewitt *et al.*, 2001). Primary predators of chicks were not known, but probably included most carnivores and raptors. Cooper's (*Accipiter cooperii*) and sharp-shinned hawks (*A. striatus*) probably preyed mostly on chicks, but goshawks and great-horned owls (*Bubo virginianus*) were important predators on grouse of all ages (Hewitt *et al.*, 2001).

In boreal forests of Canada, spruce grouse and ruffed grouse are alternative prey for birds of prey which primarily hunt snowshoe hares (*Lepus americanus*) that show 10-year cycles over much of Canada (Krebs *et al.*, 1995, 2001). During the increasing phase of a hare cycle, predator populations increase which results in higher predation pressure on sympatric spruce and ruffed grouse primarily during summer (Martin *et al.*, 2001). These grouse populations then start to decline after a peak density of hare populations (Boutin *et al.*, 1995). This has been suggested to be a by-product of predators shifting to alternative prey when hare populations crash (Martin *et al.*, 2001). However, in fact, only goshawks have been documented to shift to grouse during the decline phase of the hare cycle (Doyle & Smith, 2001). Furthermore, the exclusion of predators (mainly mammalian predators, but partially also avian predators) during a 10-year snowshoe hare cycle failed to change the population dynamics of spruce and ruffed grouse. The only indication of a positive predator reduction effect was a possible delay of one year in the decline of spruce grouse on the predator exclosure plot (Martin *et al.*, 2001). When hare populations crash, goshawks and great-horned owls migrate south during winter into the Lakes States region of the United States, where they increase ruffed grouse mortality during winter and may cause declines in grouse populations in the United States (Keith & Rusch, 1989). This indicates that where ruffed grouse populations are cyclic, predation by raptors has a strong effect on grouse density (Hewitt *et al.*, 2001).

Edminster (1939) found that predator control can increase nest success of ruffed grouse, but effects on grouse density were not consistent. Removal of 1324 avian and mammalian predators over four years in New York reduced nest loss but had little effect on brood mortality. Densities in removal areas decreased on average 1.5 ruffed grouse/100 ha (Edminster, 1939). In another study, 150 great-horned owls were removed over three years on a refuge without any noticeable effect on ruffed grouse abundance (Leopold, 1931). Four other studies conducted in the USA involved removal of both avian and mammalian predators of gallinaceous birds (reviewed in Newton, 1998). Only one of these resulted in increased post-breeding numbers and none resulted in increased breeding numbers in the following spring. Despite the degree of predation on nests, chicks, and juveniles of forest grouse, studies to date do not indicate that intense, local predator control can consistently increase forest grouse densities (Hewitt *et al.*, 2001). Carefully designed studies are necessary to understand fully how changes in predator populations affect grouse densities (Hewitt *et al.*, 2001).

In North America, direct predator control measures have rarely been recommended for prairie grouse (sage grouse *Centrocercus urophasianus*, sharp-tailed grouse *Tympanuchus phasianellus*, greater prairie-chicken *T. cupido* and lesser prairie-chicken *T. pallidicinctus*) management because there is not enough information on the long-term effects of predator removal on the behaviour, genetics, and abundance of these species and because predator control is relatively expensive (Schroeder & Baydack, 2001). Most direct attempts to control predator populations were conducted over a small spatial scale and were not motivated by a desire to increase numbers of prairie grouse. Thus, there are few examples of predator control in which populations of grouse were monitored (Schroeder & Baydack, 2001). Furthermore, the protected status of many predators and thereby concerns about public attitudes toward predator removal may have limited the use of this method (Schroeder & Baydack, 2001). Instead, indirect predator control through habitat management is believed to be the most economical, efficient, and viable long-term strategy to enhance populations of prairie grouse (Giesen & Connelly, 1993).

VII. SUGGESTIONS FOR FUTURE RESEARCH

Nearly all detailed studies on raptor-gamebird dynamics in Europe have been conducted in northern areas. Similar studies are needed in central and southern Europe where predator–prey systems are apparently more complex. Most studies on the interaction between raptors and gamebird populations give some estimate of the predation rate (per cent of population being taken by the predator), but less often have they evaluated the subsequent reduction in the pre-harvest population or the potential limiting effect on breeding numbers of gamebirds. The few studies that have evaluated the latter variable suggest that in at least some conflict situations, birds of prey take a significant amount of the gamebird breeding stock or chick production, and can thus limit their populations at least when gamebird breeding density is small. Cases of high predation rates were associated with reductions in the number of birds available for hunting in autumn (Kenward, 1977, 1986; Redpath & Thirgood, 1997; Thirgood *et al.*, 2000*a*, *c*).

Existing studies indicate that, under certain conditions, raptor predation may have detrimental consequences for breeding success and/or survival of gamebirds. However, so far the number and extent of studies may be too modest to draw any firm conclusions, except that predation pressures are variable and should be judged on local circumstances. In most cases, it also remained unclear whether the predation mortality was additive or compensatory. Thus, there is an urgent need to develop further such studies, to determine the functional and numerical responses of birds of prey to gamebird populations in species and environmental conditions other than those already evaluated in previous studies. Particularly important would be to evaluate the impact of birds of prey in guilds in which more than one predator and more than one prey coexist. The amount of intra-guild predation may be critical for evaluating the effects of predation on prey numbers, because many predators prey on other predators (Mikkola, 1983; Polis, Myers & Holt, 1989; Krüger, 2002; Petty *et al.*, 2003), and may increase their intraguild-predation rate when availability of a main prey declines (Korpimäki & Norrdahl 1989*a*, *b*; Tella & Mañosa, 1993; Serrano, 2000). Large avian predators in Fennoscandia and elsewhere can shift to alternative prey when the abundance of their main prey crashes (Korpimäki & Norrdahl, 1989*a*, *b*; Newton, 1998). Dietary shifts like this can result in increased predation on smaller predators, which in turn may increase the abundance of their prey (Palomares *et al.*, 1995). Korpimäki & Norrdahl (1989*a*, *b*) suggested that intra-guild predation might considerably lessen the impact of small mustelids on vole populations in the crash phase of the vole cycle. Sergio, Marchesi & Pedrini (2003) studied the impact of intraguild predation by eagle owls on black kites in the Italian Alps and found that within-population effects were most severe in areas with high owl densities and that kites responded to predation risk through predator spatial avoidance. Productivity of kites declined steeply with increasing predation risk by eagle owls. This finding indicates that heavy control (legal or illegal) of top predators may induce a strong potential for meso-predator release if their densities fall markedly. Overall, intraguild predation produces food-chain linkages that complicate generalisations about stability of food webs (Korpimäki & Krebs, 1996). Additionally, it would be useful to conduct extensive field experiments in which raptor numbers are manipulated on a sufficiently large spatial and temporal scale (see e.g. Norrdahl & Korpimäki, 1995*a*; Korpimäki *et al.*, 2002). Furthermore, in these experiments mammalian predator numbers should be estimated, and possibly experimentally manipulated, as there is strong evidence that mammalian predators also reduce gamebird breeding success and numbers (Marcström *et al.*, 1988; Lindström *et al.*, 1994; Norrdahl & Korpimäki, 1995*b*, 2000; Kurki *et al.*, 1997, 1998; Smedshaug *et al.*, 1999; Storaas, Kastdalen & Wegge, 1999; Kauhala, Helle & Helle, 2000), and that mammalian predators can compensate for reduced losses by avian predators, if avian predators alone are experimentally reduced (Parker, 1984; Norrdahl & Korpimäki, 1995*a*; Korpimäki & Norrdahl, 1998).

Finally, the fact that raptors may also benefit game animals has received little attention so far. It has been shown that goshawks may prey heavily on corvids during the breeding season (see e.g. Wikman & Tarsa, 1980) and thus could potentially reduce predation by corvids on gamebird clutches. Milonoff (1994) estimated that during the nestling period, one pair of goshawks (and offspring) consumes on average 25 adult grouse and 35 corvids. He then further estimated that if 'an average corvid' depredates more than two grouse nests, overall goshawks would benefit gamebirds. Furthermore, the proportions of medium-sized carnivores (red foxes, pine martens, American mink and raccoon dogs) in the diets of golden eagles, white-tailed eagles and eagle owls are approximately 0.5–1 % of prey number in Finland (Korpimäki & Nordström, 2004). Because densities of predators are usually an order of magnitude lower than the densities of herbivores, these top predators may act as an important mortality and risk factor for medium-sized carnivores. Of these, native red foxes and pine martens are enemies of small game (hare and grouse) (Kurki *et al.*, 1997, 1998) and alien American mink and raccoon dogs are enemies of waterfowl, *etc.* (Nordström *et al.*, 2002, 2003). In addition, the sublethal effects of top avian predators on carnivores may also be important, because smaller predators probably change their habitat use and foraging behaviour under the predation risk of top avian predators. Therefore, it has been suggested that the recent return of golden eagles in southern Finland and elsewhere, as well as the recent increase of white-tailed eagle populations in coastal areas of Finland and elsewhere could have beneficial effects on small game, because these top predators probably decrease the detrimental impacts of medium-sized carnivores on small game (Korpimäki & Nordström, 2004). In this way, these native top predators could potentially compensate for the losses induced by increasing eagle populations on small game. This might also reduce the recent need of gamekeepers to control medium-sized carnivore populations. Lastly, emphasis should be devoted to modelling, as simulation studies may help to disentangle complex situations, e.g. those ecosystems with multiple prey and both native and introduced predators. Such modelling work has only rarely been conducted on systems involving more than two predator species or two prey species, and little attention has yet been paid to the different types (avian *versus* mammalian, native *versus* alien) of predators and to intra-guild predation (but see Courchamp, Langlais & Sugihara, 1999, 2000; Roemer, Donlan & Courchamp, 2002).

Theoretical, observational and experimental studies suggest that specialist predators are able to cause multiannual cycles in the predator–prey systems when small mammals are the main prey items (Korpimäki *et al.*, 1991, 2002; Hanski *et al.*, 1993, 2001; Krebs *et al.*, 1995; Korpimäki & Krebs, 1996; Korpimäki & Norrdahl, 1998). Theoretically, the presence of alternative prey should lead to more stable prey populations (Maynard Smith, 1974; Andersson & Erlinge, 1977), providing that the predator has a rather strong impact on prey populations – as was the case e.g. in the goshawk-grouse interaction in southern Finland (Lindén & Wikman, 1983). Thus, more stable grouse numbers could be expected close to human habitation where there are more alternative prey items for goshawks. Again, this interesting aspect has not been studied so far, and remains to be addressed in the future. The continual decrease of grouse numbers has caused problems also to goshawks in southern Finland where their breeding densities have decreased (Lindén & Wikman, 1983; Forsman & Ehrnsten, 1985), as elsewhere in Fennoscandia (Tommeraas, 1993; Halley, 1996; Widén, 1997).

There is also an urgent need to investigate practical methods to reduce conflicts between raptor conservation and gamebird management (Thirgood & Redpath, 2004). Potential ways to reduce raptor predation include habitat management [to reduce predation risk for gamebirds (Thirgood *et al.*, 2002), or to reduce densities of alternative prey leading to reductions in raptor densities and their predation on gamebirds (Smith *et al.*, 2001)], diversionary feeding (to provide raptors with alternative food; Redpath, Thirgood & Leckie, 2001*b*), intraguild predation or competition with other raptor species (e.g. golden eagles or eagle owls; Mikkola, 1983; Thirgood *et al.*, 2000*b*; Sergio *et al.*, 2003, Korpimäki & Nordström, 2004), and direct control of raptor numbers by translocation (Watson & Thirgood, 2001), by reducing potential nest sites of raptors (Norrdahl & Korpimäki, 1995*a*) or by direct lethal control (Thirgood *et al.*, 2000*b*). All these techniques need further investigation and experimental testing for their efficacy. There is also some evidence from Fennoscandian countries that increased forest fragmentation, mainly caused by forestry practices, may improve the hunting success of goshawks on grouse (Wegge *et al.*, 1990). This view deserves more attention among researchers, and should probably be taken into account in forestry planning.

The degree of human intervention in the environment, particularly the eradication of the native top avian (eagles, eagle owls, *etc.*) and mammalian (wolves, bears, *etc.*) predators, may have a strong influence on the degree of 'problems' that raptors cause to gamebirds and how they are perceived by hunters. Therefore, as much of the conflict between raptors and gamebirds depends on legislation, history, human social culture and the type of gamebird hunting that occurs, ecological studies of the effects of raptors on gamebirds can only provide a partial solution.

Another aspect that is important to consider when evaluating the impact of raptors on gamebirds is that the influence of the non-breeding part of the raptor population, on breeding success and survival of prey populations, is relatively poorly known (Rohner, 1995, 1996; Korpimäki & Krebs, 1996). Most studies that have evaluated the predation rate on gamebirds have not separated between breeders and non-breeders, only total levels of predation having been assessed. Yet, for example, in the Oulu area in northern Finland one-third of wintering goshawks were estimated to be non-territorial floaters (Tornberg & Colpaert, 2001). Similarly, there was evidence that $<50\%$ of adult female goshawk were breeding in the island of Gotland in Sweden (Kenward, Marcström & Karlbom, 1999). Kenward *et al.* (2000) also found that in their study population of common buzzards in the UK only one bird out of every four was breeding. These results clearly indicate that the proportion of non-breeders can be high. If the non-breeders are nomadic 'floaters', their role may be especially important because they are probably easily able to track gamebird abundance and thereby potentially dampen and synchronise the prey populations over large areas, as has been detected for the relationship between nomadic birds of prey and voles (see e.g. Korpimäki & Norrdahl, 1989*c*, 1991*a*; Korpimäki & Krebs, 1996) and for the relationships between mobile avian and mammalian predators and snowshoe hares (*Lepus americanus*) (Krebs *et al.*, 2001). In north-eastern Spain, young Bonelli's eagles concentrate in areas in relation to the availability of gamebirds (Mañosa, Real & Codina, 1998). Therefore, more data are also needed on the existence and dynamics of non-breeders, as well as on gamebird chick predation in late summer. Intensive radio-telemetry studies on gamebirds and birds of prey simultaneously in the same area may be critical for evaluating this aspect.

VIII. CONCLUSIONS

(1) The comparison of diets of 52 European bird of prey species revealed that 20 preyed on small game (lagomorphs or gamebirds), but there was much variation among species, and also between areas within the range of any given species. The gyrfalcon, goshawk and golden eagle had the largest proportions of gamebirds in their diet, but locally also harriers, buzzards, Bonelli's eagles, booted eagles and peregrines utilised them to a great extent. A high percentage of gamebirds in the diet of a predator does not necessarily mean that this predator will have a negative impact on gamebird population densities.

(2) To date only 10 field studies have investigated numerical responses of avian predators to changing gamebird abundance. In half of these studies, no numerical response was found, while in the remainder at least a slight response was detected. Predators are believed to induce cycles in prey population dynamics especially if they show a time lag in their response to prey densities, and this appears to be the case for the predator–prey systems of goshawks and forest grouse in northern Finland, common buzzard and forest grouse in western Finland, and gyrfalcon and ptarmigan in Iceland.

(3) Even fewer studies have quantified both the numerical and functional responses of raptors to changes in gamebird densities. A direct consequence of the relatively small number of detailed studies on raptor-gamebird dynamics is that it is difficult to develop general conclusions concerning the potential for raptor populations to limit gamebird prey populations more widely. The few studies that have evaluated this potential limiting effect suggest that, in at least some situations, birds of prey may take an appreciable portion of the gamebird breeding stock or chick production.

(4) More studies are needed of species and environmental conditions other than those already evaluated previously, particularly in southern Europe, where the conflicts may be acute, and the predator–prey systems are more complex. Studies of the impact of birds of prey in guilds in which more than one predator and more than one prey coexist might be especially revealing. Moreover, it would be useful to conduct extensive field experiments in which numbers of raptors (and preferably also those of mammalian predators) are manipulated over a sufficiently large spatial and temporal scale.

(5) Finally, it is important to search for practical methods to reduce conflicts between raptor conservation and gamebird management. Several methods, including habitat management, eradication of alien predators, diversionary feeding, intraguild predation or competition with other

raptor species, and direct control of raptor numbers, have already been proposed and even tested for some species, but all these techniques require further investigation and wide-scale testing of their efficacy.

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