

RECONCILING GAMEBIRD HUNTING AND BIODIVERSITY (REGHAB)

PROPOSAL N°: **EKV-2000-00637**

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PROJECT WEBPAGE:

www.uclm.es/irec/Reghab/inicio.html

(Report on Workpackage 3 – Deliverable no 5).



Ecological background of the raptor-gamebird conflict: raptors as limiting factors of gamebird populations

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May 2002

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1. INTRODUCTION

1.1. General

The traditional Erringtonian view suggested that predators are generally not harmful to prey populations as they only take a doomed surplus of the prey population (Errington 1956). It was also frequently assumed that the predated individuals were ill, injured or otherwise of low quality and that predators acted as health officers in nature. This view has, however, been questioned in many studies conducted during 1980s and 1990s, and recent studies indicate that predation may, at least under certain environmental conditions, have profound effects on vertebrate prey populations (Marcström et al. 1988, Newton 1993, Krebs et al. 1995, Korpimäki and Krebs 1996, Tapper et al. 1996, Hubbs and Boonstra 1997, Korpimäki and Norrdahl 1998, Byrom et al. 2000, Thirgood et al. 2000b, Korpimäki et al. 2002). From a theoretical point of view, predators can either stabilise or destabilise prey populations, depending on the type of responses of the predator and carrying capacity of the prey (e.g. Hanski et al. 1991, Sinclair and Pech 1996). Increasing rate of generalist predation decreases the length and amplitude of the prey cycle which is driven by specialist predators, and with high enough density of generalist predators the prey cycle turns to a stable equilibrium point (Hanski et al. 1991).

The effects of predation are dependent of the numbers and behaviour of both predators and prey (Newton 1993). Predators can be either generalists feeding on a variety of prey, or specialists taking only one or a few main prey species. However, in the real world the division of predators is not necessarily so clear but rather they form a continuum. Furthermore, some predators may change from being specialists to being generalists in both seasonal and spatial scale (Korpimäki and Krebs 1996). As an event, predation is rarely evenly distributed through a prey population, as it may be concentrated in certain localities, on particular age groups, sex or social classes, or it may vary through time (Newton 1993). By nature, predation can be regulatory (stabilising or density-dependent) or nonregulatory

(destabilising or density-independent). Another form of nonregulatory predation, inverse density dependence, 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. There are two responses of predators, namely functional and numerical, that may promote density-dependence (these two types of responses will be discussed below).

Several researchers, e.g. Siivonen (1948), Hagen (1952), Angelstam et al. (1984, 1985) and Lindén (1988), documented that populations of small game, such as hare and grouse, and small rodents in Fennoscandia fluctuate synchronously between years (short-term population fluctuations or the 3-4-year cycle). The cyclicity and synchrony of 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 and Henttonen 1985). In general, it is thought that predation alone may cause cycles in prey populations (but see Dobson and Hudson 1995), and for the cyclic variation in the number of gamebirds two main hypotheses have been proposed: (i) the alternative prey hypothesis (APH) and (ii) the predation theory (Rosenzweig and MacArthur 1963, Begon et al. 1990, Hanski et al. 1991).

The alternative prey hypothesis (APH) first put forward by Hagen (1952) and Lack (1954) says that synchronous population fluctuations of small game 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 small game), then APH predicts that predators partly shift their diet from main prey to alternative prey (small game) as main prey decreases and back to main prey as soon as small rodents increase. A recent substitute hypothesis, the Shared Predation Hypothesis (SPH) in turn states that predators are not selective in killing their prey, and then all important prey species are negatively affected when the densities of

predators are high; that is, at and after the peak densities of main prey (Norrdahl and Korpimäki 2000). With respect to the prey species that constitute only a small share of the diet of predators (i.e. alternative prey), these two hypotheses have different presumptions 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 and Korpimäki 2000). In Europe, potential predators that may shift from small rodents or rabbits to small game are, e.g. carnivores, diurnal raptors, owls and corvids. As lagomorphs and galliformes are much larger than small rodents, small predators are able to take only eggs and young of small game (e.g. Angelstam et al. 1984).

1.2. Responses of predators

Responses of predators to fluctuations in prey abundance may be numerical and/or functional (Solomon 1949). Numerical response can be expressed as e.g. number of territorial predators, total predator density or as the number of offspring per territory which are plotted against density of prey (see e.g. Korpimäki and Norrdahl 1991a, Tornberg 2001). A numerical response of the predator occurs when the demography 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, and emigration (Andersson and

Erlinge 1977, Korpimäki and Norrdahl 1991a, Salamolard et al. 2000). Thus, the ability of predators to respond numerically to the fluctuations of prey populations depends on the mobility, reproductive potential, and generation time of the predator. High mobility (i.e. wide natal and breeding dispersal), large clutch and brood sizes, 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, Nielsen 1999). Nomadic specialist, on the other hand, show rapid numerical responses to changes in prey densities, being therefore able to track their prey populations without time lags (Korpimäki and Norrdahl 1989, 1991). Nomadism may not necessarily be the only way in which predator populations are able to track high prey densities, as it has been detected that recruitment from a floating population may explain the rapid numerical response (Salamolard et al. 2000).

Functional response, in turn, is expressed as the proportion of a given prey in predator's diet plotted against density of that prey. The availability of main (i.e. preferred) and alternative prey, the ability to shift to alternative prey, and inter- and intraspecific competition for food affect the functional response of the predator (Andersson and Erlinge 1977, Korpimäki 1987, Korpimäki and Krebs 1996). Functional responses of predators may be difficult to estimate and there can also be particular statistical problems to distinguish between nonlinear and linear responses with noisy field data (Trexler et al. 1988). Moreover, traditional methods (such as analyses of pellets and scats) to identify diets of predators may also include some shortcomings, e.g. the fact that smallest prey animals can easily go undetected in the analyses and thus their relative importance may be biased. Usually three different types of functional responses can be distinguished (Holling 1959). First, the relationship between prey density and the number of prey eaten per predator per unit time can be linear. This will produce a constant percentage kill, i.e. while the number of prey eaten per predator increases indefinitely as prey density rises, the fraction of the prey population taken is density-dependent. Second, 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 (convex or type II functional response). This will produce a declining (or inverse density-dependent) percentage kill. This model is more realistic because it allows prey consumption to increase with prey density when prey are scarce and also 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 direct density-dependence in percentage kill at low prey densities but inverse density-dependence at high. Theoretically, only the sigmoid curve 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 and Oaten 1975, Taylor 1984). It has been found that usually the functional response curves of avian and mammalian predators are convex (Murdoch and Oaten 1975). If there are many alternative prey species in addition to the main prey, a large body size and an ability to vary hunting techniques accordingly, facilitate a wide functional response to fluctuating densities of the main prey. In addition, if the intensity of food competition is low, predators are better able to respond functionally to varying prey densities.

The total response, also expressed as kill rate, can be obtained by multiplying the number of a given prey killed per predator with their density and then plotting the outcome against the prey density. Predation impact (predation rate) can be assessed through dividing the kill rate by the number of prey available (e.g. Korpimäki and Norrdahl 1991b, Tornberg 2001).

Responses of birds of prey (i.e. diurnal raptors and owls) to population fluctuations of voles and small game are of great interest for three reasons. First, numerical responses of wintering raptors and owls in northern latitudes are usually synchronous with fluctuations in vole densities (Galushin 1974, Korpimäki 1994, Norrdahl and Korpimäki 2002). This is probably due to the high mobility of birds of prey outside the breeding season. Populations of breeding birds of prey may not respond or may show delayed density-dependent responses to changing prey densities (e.g. Keith et al. 1977, Erlinge et al.

1983). However, many studies indicate that breeding densities of some nomadic raptors track population fluctuations of voles without obvious time lags (Korpimäki 1985b, Korpimäki and Norrdahl 1989, 1991a). Second, at high latitudes vole-eating raptors exhibit strong numerical responses to fluctuating prey densities during the breeding season, whereas at lower latitudes they mainly respond functionally (e.g. Luttich et al. 1971, Newton 1976, Phelan and Robertson 1978, Korpimäki 1986a, but see Salamolard et al. 2000). Third, the shape of functional response curve is important in predicting effects of predators on prey populations (see above; Murdoch and Oaten 1975, Taylor 1984, Fujii et al. 1986).

1.3. Prey population cycles

It has been suggested that population cycles of prey can be a consequence of predation by specialist predators. At least four factors may create and/or maintain this cyclicity. First, there can be a time lag in the numerical response of the predator to changes in prey densities, meaning that 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 their own equilibrium density and then decrease with a time lag (see 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, it must be kept in mind that in reality predator-prey dynamics exceed simple two-species interactions (Rohner 1995). Second, specialist predators are more likely to cause cyclicity than generalist predators because they are unable to switch to alternative prey when prey populations decline. Third, cyclicity may arise when there is negative relationship between 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 the prey population cycle (e.g. Korpimäki et al. 1991, Nielsen 1999, Tornberg 2001).

1.4. State of the current research

Long-term studies on numerical and functional responses of raptors to multiannual fluctuations of prey are scarce, and they relate mainly to the relationship between raptors and rodent fluctuations (e.g. Adamcik et al. 1978, 1979, Korpimäki and Norrdahl 1989, 1991a, 1991b, Korpimäki 1992, 1994, Salamolard et al. 2000, Reif et al. 2001), whereas studies on the relationship between raptors and variations in abundance of other prey are much more limited. Similarly, and even more so, a revision of the scientific literature on predator-prey relationships indicate that there is extremely little information on whether raptors may and do limit populations of game animals. Some studies from western and northern Europe, particularly the thoroughly studied system of hen harriers and red grouse in Scotland (e.g. Redpath and Thirgood 1997, 1999), and the goshawk and tetraonids in Fennoscandia (e.g. Lindén and Wikman 1983, Tornberg 2001), suggest that in some cases or under particular circumstances, raptors may have an obvious effect on population dynamics and hunting bags of game birds. However, there are virtually no studies from central or southern Europe (but see Bro et al. 2000, 2001), and because the relationship between predators and game birds varies according to the availability of alternative prey and to the diversity of the predator (including mammalian predators) assemblage (which clearly vary between regions), generalisation from studies from northern Europe is difficult. There is no experimental evidence at an appropriate scale, and existing relationships are in most cases dependent on only a few data points. Thus, there is a real need to produce a research proposal to compare (preferably experimentally) the impact of raptors on gamebirds in different parts of Europe.

Here we present a review of the of the key findings from past or ongoing studies on the relationship between birds of prey and game birds across Europe. Diet and prey selection of various raptor species have been examined in many European countries (e.g. Höglund 1964, Sulkava 1964, Opdam et al. 1977, Korpimäki 1986b, Korpimäki et al. 1990, Mañosa 1994, Tornberg 1997, Tornberg et al. 1999; reviewed by Marti et al. 1993, Korpimäki and Marti 1995), but in here we aim at synthesising results from those studies in which the impact of raptor predation on their prey populations have been estimated. There are surprisingly few studies of this kind, and most of those existing have been carried out in western and northern Europe while data were almost completely lacking from central and eastern Europe.

2. DIET OF RAPTORS IN EUROPE

In this section, we briefly summarize available data on prey selection of raptors and owls across Europe. Diet composition, given as proportion of main prey groups **by number**, of mammal- and bird-eating raptors and owls are shown in Table 1. An alternative way would be to report the proportion of different prey items **by weight**, but this method has been used in only few studies conducted so far, and therefore this approach was not used in this review. We have grouped the prey categories as “small mammals” (including shrews, voles, mice and rats), “hares (*Lepus* sp.) and rabbits (*Oryctolagus cuniculus*)”, “gamebirds” (pheasants, partridges and forest grouse) and “others” (mostly pigeons, waterfowl, passerines and also unidentified prey items). In the majority of these studies, prey remains and pellets were collected from nests and on the ground under the nests. This method may be biased, as it may underestimate the proportion of small prey items, such as amphibians, and overestimate the proportions of large prey items, like water voles *Arvicola terrestris*, lagomorphs and grouse in the diet (see e.g. Reif et al. 2001). Thus, these potential shortcomings should be kept in mind when evaluating the data shown in Table 1. Furthermore, a high percentage of a given prey species in the diet of a predator does not necessarily mean that this predator will have a negative impact on densities of prey populations. Factors

like prey and predator density, and the extent of mortality from other sources (e.g. from hunting or by mammalian predators and other natural enemies) should also be taken into account when evaluating the significance of raptor predation. On the other hand, if prey population is threatened or population size low, even a few prey individuals killed by a predator may have detrimental effects on prey population dynamics.

Some European bird of prey species have been omitted from Table 1 because their diets are known to consist almost entirely of other than game species. Therefore, the following species were excluded from the table (main prey in parenthesis): **honey buzzard** *Pernis apivorus* (mainly insects; Glutz von Blotzheim et al. 1971, Cramp 1980), **white-tailed eagle** *Haliaeetus albicilla* (fish, waterbirds, carrion; Cramp 1980), vultures (carrion; Cramp 1980), **short-toed eagle** *Circaetus gallicus* (reptiles; Cramp 1980, Bakaloudis et al. 1998), **the hobby** *Falco subbuteo* (insects, small passerine birds; Glutz von Blotzheim et al. 1971, Cramp 1980), **lesser kestrel** *F. naumanni* (invertebrates; Glutz von Blotzheim et al. 1971, Cramp 1980), **the kestrel** *F. tinnunculus* (small mammals; Korpimäki 1985a), **the merlin** *F. columbarius* (small passerine birds; Sulkava 1971, Watson 1979, Newton et al. 1984, Bibby 1987), **barn owl** *Tyto alba* (small mammals; Mikkola 1983), **the snowy owl** *Nyctea scandiaca* (small mammals; Mikkola 1983), **the hawk owl** *Surnia ulula* (small mammals; Hagen 1952, Huhtala et al. 1987), **pygmy owl** *Glaucidium passerinum* (small mammals, small passerine birds; Kellomäki 1977), **little owl** *Athene noctua* (mainly invertebrates; Mikkola 1983), **tawny owl** *Strix aluco* (small mammals, small passerine birds; Mikkola 1983, Korpimäki 1986c, Petty 1999), **great grey owl** *S. nebulosa* (small mammals; Höglund and Lansgren 1968, Mikkola 1983), **long-eared owl** *Asio otus* (small mammals; Mikkola 1983, Korpimäki 1992), **short-eared owl** *A. flammeus* (small mammals; Hagen 1952, Mikkola 1983, Korpimäki and Norrdahl 1991b) and **Tengmalm's owl** *Aegolius funereus* (small mammals; Korpimäki 1988). It is likely that in general these species do not possess a threat to game animals, although during years of small mammal scarcity some of the species listed above may use small amounts of game animals instead of voles. In addition, the diet of **the sparrowhawk** *Accipiter nisus* consists

almost entirely of small passerine birds, but the larger females can take considerable amounts of larger birds too (such as wood pigeons, see Newton 1986).

The second group comprises medium-sized and large raptors which feed on a variety of prey, that includes also lagomorphs or gamebirds, but the proportion of these animals in their diet varies between years and seasons and also spatially. This group includes **peregrines** *Falco peregrinus* and **gyrfalcons** *F. rusticolus*, kites, harriers, **goshawks** *Accipiter gentilis*, **golden eagles** *Aquila chrysaetos*, **Spanish imperial eagles** *A. adalberti*, **Bonelli's eagles** *Hieraetus fasciatus*, **booted eagles** *H. pennatus*, buzzards, and the largest owl species. The diets of raptors belonging to this group will be discussed below.

Red kites *Milvus milvus* and **black kites** *M. migrans* are relatively common raptors in southern and central Europe, but they are virtually absent from Fennoscandian countries (see Cramp 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 1980). In Spanish studies (Table 1) the proportion of gamebirds in kite diets was reasonably low, but rabbits were taken more frequently.

The diet of **hen harriers** *Circus cyaneus* differed between areas: in Norway small mammals were the most important single prey group, rabbits were the most frequent prey items in Orkney, and in Scotland the majority of diet consisted of meadow pipits *Anthus pratensis* and skylarks *Alauda arvensis*. The proportion of gamebirds among the prey items delivered to the nest was highest in Scotland (12%), consisting mostly of red grouse *Lagopus lagopus scoticus*. In eastern France, most important prey was also voles, secondarily passerines (Millon et al. 2002). Also the proportion of game species in **Montagu's harriers'** *C. pygargus* diet varied greatly between areas: in Spain the proportion of hares in the diet was approximately 17% ; in the UK that of gamebirds was also around 17%. In contrast, the proportion of either in almost any other study is less than 5% and voles are the most important prey in

central Europe, and passerines and insects in southern Europe (see Arroyo 1997, Millon et al. 2002, Salamolard et al. 2000). Remains of gamebirds were rather frequent in the diet of **marsh harriers** *C. aeruginosus* in the UK (21%) whereas they were totally absent in the diet of Finnish conspecifics and in Spain/France they feed mainly on waterfowl (Clarke et al. 1993, Bavoux et al. 1990, Gonzalez 1991). In fact, the proportion of small mammals in the diet was quite high in Finland (36%), and in all areas small passerines and ducklings were among the most typical prey items.

Gamebirds are important prey items for **goshawks** particularly in northern Europe, where their proportion in the diet varied from 22 to 72% by number. In central and southern Europe gamebirds are substituted by lagomorphs, pigeons, corvids and thrushes. In southern and western Finland, hazel grouse (*Bonasa bonasia*) was the most important prey species of the goshawk (percentage of hazel grouse of prey biomass during breeding season varied between 4 and 34%; see Forsman and Ehrnsten 1985, Lindén and Wikman 1983, 1987, Wikman and Tarsa 1980). In northern Finland, the breeding biology of goshawks has been studied since 1960s (see Tornberg 1997, 2000, 2001, Tornberg & Colpaert 2001, Tornberg & Sulkava 1991 for further details). Despite a remarkable decrease in forest grouse since 1960s (Lindén and Rajala 1981), their proportion in the diet of goshawk has remained relatively high, probably because they constitute the only sufficiently large and abundant prey for goshawks in this area. Therefore, in natural conditions, goshawks have relatively little scope for switching to other prey if the main prey decreases. Although goshawk is considered as a generalist predator (Marti et al. 1993) it is fairly specialised in the north, especially during winter when migratory birds are absent. Grouse were clearly the most preferred prey in early spring, especially the smallest species, the willow grouse (*Lagopus lagopus*) and the hazel grouse. Goshawks preyed on grouse during 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 fledging period (Tornberg 1997). Winter diet consisted 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 and Colpaert 2001).

Common buzzards *Buteo buteo* and **rough-legged buzzards** *B. lagopus* have specialised more or less in small mammals in northern Europe, although both species can utilise alternative prey, such as game animals, during low vole years (Pasanen and Sulkava 1971, Reif et al. 2001). *Microtus* voles were the main prey of 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 common buzzard's diet was considerable in the UK and particularly so in Spain.

Golden eagles appear to feed mainly on lagomorphs and gamebirds throughout Europe. The proportion of gamebirds seems to be highest in northern Europe (Finland, Sweden and Norway) while in the more southern areas the role of hares and rabbits is probably more important. 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). Spanish imperial eagles feed mainly on medium-sized mammals, particularly rabbits, but also on medium-sized birds (Cramp 1980, Forsman 1999). Since the estimated population comprises only 150-160 pairs (Forsman 1999), the possible negative effects on game welfare are likely to be rather localised. Bonelli's eagle and booted eagle are also south European raptors, whose diets have been examined mostly in Spain and France (for Bonelli's eagle see Table 1, for booted eagle Cramp 1980). Gamebirds are fairly typical in the diet of Bonelli's eagle, but also booted eagles take small to medium-sized birds, and red-legged and grey partridges are often found as prey items (Cramp 1980).

The share of gamebirds by number in the diet of peregrines was some 10-15% in the UK, but most prey items in Finland and UK fell to category "others" including mostly pigeons, waders and ducks. 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.

The diet of **eagle owls** *Bubo bubo* varied notably across areas, such that the proportion of small mammals in the diet increased with latitude (France being an exception). With respect to game species, the relative importance of eagle owl as their predator appears to be highest in Spain (proportion of rabbits in diet 35%) 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* voles, which show 3-4-yr population cycles (e.g. Hansson and Henttonen 1985). Korpimäki et al. (1990) found that yearly abundances of voles correlated positively with the proportions of voles in the diet. 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, independently of the proportion of voles in the diet. In addition, the proportion of small game in diet was nearly independent of its abundance in the field. The data indicate that both owl species behave as APH predicts, but their predation impact on small game requires more research to be accurately quantified.

To summarise, Table 1 indicates that only three raptor species, gyrfalcon, goshawk and golden eagle, can have rather large proportions of gamebirds in their diet, but locally also harriers, buzzards, Bonelli's eagles and peregrines may utilise them to a great extent.

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

<i>Bird of prey species</i>	<i>Country</i>	<i>Small mammals</i>	<i>Hares and rabbits</i>	<i>Gamebirds</i>	<i>Others</i>	<i>N</i>	<i>Source</i>
<i>Red kite</i> (1015)	Spain	-	29.2	-	70.8	634	Veiga & Hiraldo 1990
	Spain	15.8	9.1	1.7	73.4	1577	Garcia et al. 1998
	UK	21.8	6.7	0.1	71.4	1068	Walters Davies & Davis 1973
<i>Black kite</i> (830)	Spain	-	24.4	-	75.6	1889	Veiga & Hiraldo 1990
<i>Hen Harrier</i> (430)	Norway	57.2	1.1	7.0	34.7	570	Hagen 1952
	UK (winter)	11.2	10.5	5.7	72.6	3487	Clarke et al. 1997
	UK (Scotland)	5.3	2.2	12.0	80.5	2324 ¹⁾	Redpath & Thirgood 1997a
	UK (Orkney)	5.2	47.3	6.6	40.9	482	Picozzi 1980
	Netherlands (winter)	26.9	14.9	6.5	51.7	879	Clarke et al. 1993
	France (winter)	27.1	17.7	3.1	52.1	?	Clarke & Tombal 1989
<i>Montagu's Harrier</i> (310)	UK	2.1	3.3	17.4	77.2	92	Underhill-Day 1993
	Spain	5.9	17.2	3.0	73.9	3096	Arroyo 1997

<i>Bird of prey species</i>	<i>Country</i>	<i>Small mammals</i>	<i>Hares and rabbits</i>	<i>Gamebirds</i>	<i>Others</i>	<i>N</i>	<i>Source</i>
<i>Marsh Harrier</i> (640)	Finland	36.1	-	-	63.9	183	Hildén & Kalinainen 1966
	Netherlands (winter)	6.1	7.0	2.1	84.8	243	Clarke et al. 1993
	UK	2.7	3.7	21.2	72.4	296	Underhill-Day 1985
	France (autumn, winter)	27.1	7.6	-	65.3	3453	Bavoux et al. 1990
<i>Goshawk</i> (1150)	Finland (Oulu)	4.2	3.8	44.4	47.6	1206	Tornberg & Sulkava 1991
	Finland (Uusimaa)	3.5	3.0	15.6	77.9	1300	Wikman & Tarsa 1980
	UK	-	5.3	0.0	94.7	2213	Toyne 1998
	UK	-	5.2	8.4	86.4	3980	S. J. Petty unpubl. data ²⁾
	Sweden	-	0.7	22.2	77.1	904	Widén 1987
	Sweden	0.7	0.7	24.7	73.9	1431	Höglund 1964
	Sweden	-	14.0	28.0	58.0	127	Kenward et al. 1981 ³⁾
	Netherlands	-	3.5	5.2	91.3	4821	Opdam et al. 1977
	Spain	-	16.6	19.1	64.3	2003	Mañosa 1994

<i>Bird of prey species</i>	<i>Country</i>	<i>Small mammals</i>	<i>Hares and rabbits</i>	<i>Gamebirds</i>	<i>Others</i>	<i>N</i>	<i>Source</i>
<i>Common Buzzard (710)</i>	Finland	50.4	4.3	7.4	37.9	1906	Reif et al. 2001
	Norway	41.3	-	2.5	56.2	719	Spidsø & Selås 1988
	UK	18.0	48.0	2.6	31.4	233	Kenward et al. 2001
	UK	6.8	40.8	15.1	37.3	365	Graham et al. 1995
	Spain	1.3	66.6	5.0	27.1	598	Mañosa & Cordero 1992
	Austria	90.6	0.5	-	8.9	202	Haberl 1995
	France	34.2	0.5	0.1	65.2	6740	Bayle and de Ruffray 1980
<i>Rough-legged Buzzard (920)</i>	Finland	40.8	-	10.7	48.5	169	Pasanen & Sulkava 1971
<i>Golden eagle (4170)</i>	Finland ⁴⁾	-	32.7	35.7	31.6	5309	Sulkava et al. 1999
	Finland ⁵⁾	-	30.2	51.2	18.6	1595	Sulkava et al. 1999
	Norway	-	10.7	52.0	37.3	513	Högström & Wiss 1992
	Estonia	-	27.0	34.0	39.0	279	Randla 1976
	UK	-	25.1	19.0	55.9	1292	Watson et al. 1993
	Sweden	1.2	20.6	53.8	24.4	2803	Tjernberg 1981
	Medit. areas	-	43.4	18.5	38.5	1142	Delibes et al. 1975, Ragni et al. 1986, Watson 1998
	France	1.0	40.0	10.4	48.6	630	Fernandez 1991

<i>Bird of prey species</i>	<i>Country</i>	<i>Small mammals</i>	<i>Hares and rabbits</i>	<i>Gamebirds</i>	<i>Others</i>	<i>N</i>	<i>Source</i>
<i>Bonelli's eagle</i> (2049)	Spain	-	37.5	30.2	32.3	192	Ontiveros & Pleguezuelos 2000
	Spain	-	13.7	-	86.3	124 ¹⁾	Real 1996
	France	-	17.2	17.7	65.1	1718	Cheyland 1994
<i>Peregrine</i> (890)	Finland	-	-	4.7	95.3	1075	Sulkava 1968
	UK	0.1	0.2	10.0	89.7	4130	Ratcliffe 1993
	UK	-	0.3	15.4	84.3	876	Redpath & Thirgood 1997a
	France	-	0.6	-	99.4	102	Bayle 1981
<i>Gyr Falcon</i> (1430)	Sweden	25.8	0.6	67.7	5.9	1410	Lindberg 1983
	Iceland	3.9	-	70.3	25.8	2316	Nielsen & Cade 1990
	Finland	5.2	1.2	65.0	28.9	729	Huhtala et al. 1996
<i>Ural Owl</i> (800)	Finland	79.1	4.1	1.4	15.4	1812	Korpimäki et al. 1990

<i>Bird of prey species</i>	<i>Country</i>	<i>Small mammals</i>	<i>Hares and rabbits</i>	<i>Gamebirds</i>	<i>Others</i>	<i>N</i>	<i>Source</i>
<i>Eagle Owl (2630)</i>	Finland	82.5	4.3	2.2	11.0	2206	Korpimäki et al. 1990
	Norway	76.5	2.6	3.8	17.1	807	Mysterud & Dunker 1983
	Sweden	44.5	3.9	1.4	50.2	6450	Olsson 1979
	Sweden	49.7	3.6	7.1	39.6	1214	Höglund 1966
	Germany	32.9	5.4	10.4	51.3	8766	Bezzel et al. 1976
	Spain	17.9	35.0	6.5	40.6	1395	Martinez & Zuberogoitia 2001
	France	54.2	11.9	4.4	41.4	2704	Bayle 1996

¹⁾ number of prey items seen delivered to the nest

²⁾ taken from Table 6 in Toyne 1998

³⁾ number of prey taken by radio-tagged individuals

⁴⁾ data from the Finnish reindeer area

⁵⁾ data from south of the reindeer area

3. NUMERICAL RESPONSES

The relationships between red grouse (*Lagopus lagopus scoticus*) and their main predators, hen harriers and peregrines, have been studied in Scotland since 1992 (Redpath & Thirgood 1997a, b, 1999, Thirgood and Redpath 1997, Thirgood et al. 2000a, b, c). Neither harriers nor peregrines showed numerical response to grouse abundance, but hen harrier density was significantly associated with meadow pipit density (Redpath & Thirgood 1999). In turn, peregrine density was highest in areas where racing pigeons were abundant but was not correlated with red grouse density. 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.

In southern Finland, 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). Instead, the data collected from western Finland showed that brood size of goshawks increased with the relative density of hazel grouse (Lindén and Wikman 1980). Tornberg (2001) found that for goshawks in northern Finland there was a weak numerical response, measured as number of nestlings / territory with a time-lag of 1 year for the density of all grouse species pooled.

In Iceland, number of gyrfalcon territories correlated with a 3-yr time lag to ptarmigan numbers, and that of total gyrfalcon numbers (territorial adults and fledglings) in late summer with a 2-yr time lag (Nielsen 1999). The authors suggested that the factors contributing to the time-lag were the year-around residency of falcons on nesting territories and also late maturity. This delayed numerical response, in turn, was seen as a destabilising effect of predation.

To summarize, data on numerical responses of avian predators to changing gamebird numbers are relatively scarce. In fact, this issue was clearly addressed in only eight 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 rest of them a more or less obvious response was detected. Among the latter ones, two (goshawks-forest grouse in northern Finland and gyrfalcon-ptarmigan in Iceland) showed a time lag of one to three years, and it is under this kind of circumstances when predators are believed to induce cyclicity in prey populations (see introduction).

4. FUNCTIONAL RESPONSES, TOTAL RESPONSES, AND EFFECT OF RAPTOR PREDATION ON PREY POPULATIONS

It appeared that the data on functional responses were even more scarce than those on numerical ones. In this section, we summarize the main results of studies on functional responses of birds of prey to changing gamebird densities and also present results of studies that have attempted to quantify the effects of raptor predation on gamebird populations.

4.1. Predators and red grouse in Scotland

In Scotland, the functional response curve of hen harriers to red grouse numbers was sigmoidal or type III and that of peregrines was type II (Table 2). Impact of hen harriers on red grouse populations was greatest on moors where alternative prey, such as meadow pipits, and thus also hen harriers were most abundant. There was direct density-dependence in hen harrier predation impact on red grouse chicks, but not in peregrine predation impact on adult red grouse. The conclusion 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 is likely to reduce the ability of low-density grouse populations to increase (Redpath & Thirgood 1999). Seasonal trends in red grouse mortality and predation pressure were studied

by Thirgood et al. (2000b). Winter losses of red grouse between October – August averaged 33%, and were density-dependent. Raptors were the cause of about 70% of winter mortality and they killed 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 between April – 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 to July were estimated at 45%, and were not density-dependent. Hen harriers killed about 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 reduced autumn grouse densities by 50%. Thirgood et al. (2000b) developed population model which suggested that in the absence of raptors for 2 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 (Thirgood et al. 2000b). This model further suggested that raptor predation may have prevented the red grouse population from increasing and was thus a limiting factor.

4.2. Goshawk and gamebirds in Sweden

In central Sweden (Grimsö area), goshawks showed no functional response to fluctuations in black grouse *Tetrao tetrix* density. However, there were only 6 goshawk nests in the study area and the study lasted for only 5 years and therefore the results should be interpreted with caution. It was estimated that during spring and early summer goshawk predation removed 25% of the female and 14% of male black grouse population. It was also estimated that goshawks killed more females than males of both black grouse and capercaillie (*Tetrao urogallus*; females of this species were more vulnerable than males due to their smaller size), especially during low vole years (Widén et al. 1987). In boreal forest, forest grouse are of vital importance as staple food of goshawks in spring and summer. For comparison, in Norway about 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 severe and a dominating mortality factor.

In southern Sweden, goshawks took about 19% of the 4300 released captive-born pheasants (*Phasianus colchicus*) (1/3 of those not harvested by man or left wild in the spring) during the autumn and winter (Kenward 1977). On the other hand, goshawks were responsible for an estimated 88% of the 64% overwinter mortality among female wild pheasants, and for 23% of the 76% loss among male pheasants (Kenward et al. 1981). It was concluded that wintering goshawks can show both numerical and functional responses to their prey because of their high density and their high predation on pheasants. Interestingly, there was no indication that individuals in poor condition were preyed upon.

4.3. 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 and Wikman 1983). However, it is likely that in reality it was perhaps of type III because there was no data on goshawk diet composition 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, northern Finland, but in this area density changes of grouse were rather small and goshawks presumably killed grouse at maximum intensity, also at the lowest densities of grouse. This suggests a response type of a specialist predator not being able to switch to other prey. The shape of the functional response curve in goshawks was probably concave (type II). The total response of goshawks on grouse was inversely density-dependent, predation rate being highest at low densities. Similar total responses of goshawks

were also found in southern Finland (Wikman and Linden 1981, Wikman and Tarsa 1980). Predation patterns of this kind indicate a delayed density-dependence and destabilising effect of predator on prey populations (Sinclair and Pech 1996). Predation impact of the breeding goshawks on grouse varied from 7-32% during the breeding season (highest for willow grouse, lowest for capercaillie) (Tornberg 2001). On average, goshawks took 7% of grouse chicks; on annual basis breeding birds took 2-24% and when floaters were included 4-42% from the August grouse population. Goshawk's share of the total mortality was estimated to be 32% of willow grouse, 9% of black grouse males, 17% 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 has been less examined, in spite of the fact that birds of prey, mainly gyrfalcons and goshawks, are frequently considered as the main predators of willow grouse (Smith and Willebrand 1999). In northern Finland, the decline in the willow grouse population in 1988-1998 was positively correlated with summer goshawk predation (Tornberg 2000). Under these circumstances, goshawk predation was thought to be able to regulate grouse populations. 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, squirrels), it may result in low density and stable grouse populations. Goshawks in northern Finland fulfilled rather well the criteria of the predation theory, as they appeared to lag behind grouse numbers, they were fairly specialised on grouse, their kill rate of willow grouse related negatively to changes in willow grouse densities and predation pressure was highest when grouse densities were lowest (Tornberg 2001).

4.4. Goshawk and red-legged partridge in Spain

In northeastern Spain, goshawk predation on red-legged partridges *Alectoris rufa* was particularly heavy in spring, and it was estimated that 15% of the breeding stock was predated by goshawks (Mañosa

1994). It is possible that this predation was additive to other sources of mortality, because goshawks mainly took breeding (reproducing) birds. Although goshawk predation on partridge chicks and young was relatively low, the combined effect of spring and summer predation resulted in a 22% reduction in the number of birds available for shooting. During winter, it was estimated that goshawks consumed only 6% of the autumn partridge population, and was probably of small importance in determining the population size next spring.

4.5. Buzzard predation on gamebirds

Kenward et al. (2001) examined the predation pressure 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 were released 1994-95 and out of these, 4.3% were taken by buzzards. In the study conducted in western Finland by Reif et al. (2001 and unpubl.) it was found that breeding densities and reproductive success of common buzzards responded to fluctuating densities of main food (*Microtus 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 population cycle of main prey. Reif et al. (2001) concluded that common buzzards may reduce the breeding success of small game, in particular in the decline phase of the vole cycle when they shift to alternative prey and their breeding densities are still high, and thus may contribute to the existence of short-term population cycles of small game.

4.6. Gyrfalcon and ptarmigan in Iceland

The relationship between gyrfalcon and ptarmigan (*Lagopus mutus*) was studied in Iceland during 1981-1997 (Nielsen 1999). 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 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, also the patterns of gyrfalcon predation on ptarmigan seem to fit well with the predictions of the predation theory.

4.7. 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. It was found that predation was the most common source of mortality among adult grey partridges during the breeding season. Reitz et al. (1993) found that 54% of the mortality was due to predation, and out of this, 59% was attributed to birds of prey. Some years later, Bro et al. (2001) showed that female partridges experienced high predation rates during spring and summer (varying from 32% to 65% across study areas), 15-70% of which was caused by raptors. Predation rates (combining predation by mammals and by raptors) on adults correlated with harrier abundance and chick mortality increased with estimates of harrier abundance (Bro et al. 2000). Furthermore, partridge spring densities were negatively associated with harrier abundance (Bro et al. 2001) and population growth rate of partridges decreased when harrier abundance increased (Bro 1998). However, all these findings may also result from confounding factors. The authors could not separate the effect of predators from those of habitat, and an interference between them is likely (Bro et al. 2001).

4.8. Summary on the effects of predation

Newton (1993) made a comprehensive review of 31 field experiments in which either mammalian or avian (or both; only one experiment included removal of raptors) predators had been experimentally removed to find the impact of these predators on their avian prey. Prey nest success increased in 24/28 of these experiments after predator removal, post-breeding numbers increased in 11/16 cases and subsequent breeding numbers increased in 10/16 studies. Similarly, Côté and Sutherland (1997) meta-analysed 20 published studies of predator removal programs and found that predator removal increased hatching success and post-breeding population sizes. From the game management point of view, the size of the post-breeding population is of great importance because it will determine how many birds can be sustainably hunted. These reviews and also a mathematical model for the red grouse in the absence of its predators (Thirgood et al. 2000) indicate that removal of avian predators may increase autumn population sizes. Newton (1993) also suggested that when only one predator species was removed no subsequent increases in prey populations were detected, and the reason for this might have been compensatory predation by other predator species. Moreover, levels of predation were probably also influenced by the availability of alternative prey (such as voles or rabbits) and by habitat features (Newton 1993).

As already stated, there are rather few studies conducted so far that have quantified both numerical and functional responses of birds of prey to changes in gamebird densities. Most of them were conducted on one single species (goshawk), and there were only single studies of other species (one on buzzard, one on harriers, one on gyrfalcon, one on peregrine). The most apparent reason for this scarcity is that these kind of studies require a lot of time and financial and other resources. What then are the factors that might promote high predation impact of raptors on gamebirds? In the case of red grouse and harriers in Scotland, it was suggested that the higher availability of alternative prey (meadow pipits and small mammals) would increase the abundance of hen harriers and thus result in higher predation rates on red

grouse (Redpath and Thirgood 1999). Further, the authors concluded that the impact of raptor predation will be greatest when grouse densities fall below approximately 12 pairs per km². 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).

Table 2. Numerical and functional responses of raptors to changes in gamebird densities in Europe. BS = breeding season.

Gamebird species	Raptor species	Country / area	Numerical response?	Functional response?	Predation impact	Does raptor predation affect population size of gamebirds?	Source
Red grouse	Hen harrier	UK/Scotland	No	Type III	¹⁾	Yes	Redpath & Thirgood 1997a, Thirgood et al. 2000
Red grouse	Peregrine	UK/Scotland	No	Type II	¹⁾	Yes	Redpath & Thirgood 1997a, Thirgood et al. 2000
Hazel grouse	Goshawk	southern Finland	No	Type III	12% of adults (BS)	?	Lindén & Wikman 1983
Hazel grouse	Goshawk	western Finland	Yes	?	?	?	Lindén & Wikman 1980
Forest grouse	Goshawk	northern Finland	Weak	Weak	7-32% of all grouse (BS)	Yes	Tornberg 2001
Forest grouse	Common buzzard	western Finland	Yes, 1-yr lag	No	²⁾	(Yes)	Reif et al. 2001 and unpubl.
Black grouse	Goshawk	Sweden/Grimsö	?	No	³⁾	-	Widén 1987
Ptarmigan	Gyrfalcon	Iceland	Yes (2-yr lag)	Type II	18% of adults (BS)	Yes	Nielsen 1999

Gamebird species	Raptor species	Country / area	Numerical response?	Functional response?	Predation impact	Does raptor predation affect population size of gamebirds?	Source
Pheasant (wild)	Goshawk	Sweden	Yes	Yes	⁴⁾	Yes	Kenward et al. 1981
Red-legged partridge	Goshawk	Spain/Catalonia	-	Yes?	⁵⁾	?	Mañosa 1991, 1994
Grey partridge	Harriers	France	No	?	varies across areas, 15-70% of total predation	?	Bro et al. 2001

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

²⁾ common buzzards responded both numerically and functionally to the densities of main prey (*Microtus voles*) but there was a half- to one-year lag in their numerical responses. At declining and low vole densities buzzards shifted to forest grouse chicks and apparently contributed to their density decline.

³⁾ during spring and summer goshawks removed 25% of the female, and 14% of the male black grouse population

⁴⁾ goshawk predation caused 88% of 64% total loss females and 23% of 76% total loss males

⁵⁾ goshawks removed 4.7% of chicks and 6% of autumn birds

5. TENTATIVE CONCLUSIONS AND SUGGESTIONS FOR FUTURE DIRECTIONS OF RESEARCH

Most of the studies on the interaction between raptors and gamebird populations give some estimate of the predation rate (percent of population being taken by the predator), but less often have they evaluated the subsequent reduction on the pre-harvest population or the potential limiting effect on breeding numbers. The few studies that have evaluated the latter suggest that in at least some conflict situations, birds of prey may take a significant amount of the gamebird breeding stocks or chick production. As expected, high predation rates were often associated with severe reductions in the number of birds available for hunting in autumn (Kenward 1977, Kenward et al. 1981, Redpath and Thirgood 1997a).

Existing studies indicate that, under certain conditions, raptor predation may have detrimental consequences for breeding success and / or survival of game birds. However, so far the number and extent of studies may be too modest to draw any firm conclusions. 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 raptors to gamebird populations in species and environmental conditions other than those already evaluated in the existing studies. Particularly important would be to evaluate the impact of raptors in guilds in which more than one predator and more than one prey coexist. The amount of intraguild predation may be critical for evaluating the effects of predation on prey numbers, because many predators prey on other predators (Polis et al. 1989). It has been shown that large avian predators in Fennoscandia can shift to alternative prey when the abundance of their main prey crashes (Korpimäki and Norrdahl 1989). Dietary shifts like this can result in increased predation on smaller predators which in turn may increase the abundance of their prey. Korpimäki and Norrdahl (1989) pointed out that intraguild predation might considerably lessen the impact of small mustelids on vole populations in the crash phase of the vole cycle. Overall, intraguild predation produces food-chain linkages that complicate generalizations about stability of food

webs (Korpimäki and Krebs 1996). Additionally, it would be useful to conduct extensive field experiments in which raptor numbers are manipulated in a sufficiently large spatial and temporal scale (see e.g. Norrdahl and Korpimäki 1995a, Korpimäki et al. 2002). Furthermore, in these experiments also mammalian predator numbers should be estimated, and possibly experimentally manipulated, as there is some evidence that mammalian predators may reduce gamebird breeding success and numbers (Lindström et al. 1994, Norrdahl and Korpimäki 1995b, 2000, Kurki et al. 1997, 1998, Marcström et al. 1988, Smedshaug et al. 1999, Storaas et al. 1999), and that mammalian predators can compensate for reduced losses by avian predators, if only avian predators are experimentally reduced (Norrdahl and Korpimäki 1995a, Korpimäki and Norrdahl 1998). Furthermore, the fact that raptors may also benefit game animals has received little attention so far. It has been shown that e.g. goshawks may prey heavily on corvids during the breeding season (see e.g. Wikman and Tarsa 1980) and thus they can potentially reduce predation by corvids on gamebird nests (Milonoff 1994). 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, goshawks would actually be beneficial to gamebirds.

Theoretical, observational and experimental field studies suggest that resident specialist predators are able to cause multiannual cycles in the predator-prey systems when small mammals are the main prey items (Hanski et al. 1993, 2001, Krebs et al. 1995, Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998, Korpimäki et al. 1991, 2002). Theoretically, the presence of alternative prey should lead to more stable prey populations (Maynard Smith 1974, Andersson and 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 (Linden and Wikman 1983). Thus, more stable grouse numbers could be expected close to habitation where there are more alternative prey items for goshawks. Again, this interesting aspect has not been studied so far and remains to be thoroughly addressed in the future. The continual decrease of grouse has caused problems also to goshawks in southern Finland where their breeding

densities have decreased (Linden and Wikman 1983, Forsman and Ehrnsten 1985), like elsewhere in Fennoscandia (Tommeraas 1993, Halley 1996, Widen 1997).

Potential ways to reduce raptor predation include habitat management (to reduce predation risk for the gamebirds, or to reduce densities of alternative prey, leading to reductions in raptor densities and their predation on gamebirds), diversionary feeding (i.e., provide raptors with alternative food), utilisation (or introduction) of other raptor species (e.g. eagle owls) and direct control of raptor numbers by translocation (Thirgood et al. 2000a) or by reducing potential nest sites of raptors (Norrdahl and Korpimäki 1995a). There is also some evidence from Fennoscandian countries that increased forest fragmentation, mainly caused by effective 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 forest planning.

Another aspect that would be important to consider when evaluating the impact of raptors on gamebirds is that the influence of floaters, or the non-breeding part of the raptor population, on breeding success and survival of grouse is relatively poorly known (Rohner 1995,1996, Korpimäki and Krebs 1996). However, most studies that have evaluated the predation rate on gamebirds have not separated between breeders and non-breeders, only levels of predation have been assessed. Yet, for example, in the Oulu area in northern Finland 1/3 of wintering goshawks were estimated to be non-territorial floaters (Tornberg and Colpaert 2001). Similarly, there was evidence that only less than 50% of adult female goshawk were breeding in the island of Gotland in Sweden (Kenward et al. 1999). Kenward et al. (2000) also found that in their study population of common buzzards in the UK only one bird of four was breeding. These results clearly indicate that the proportion of non-breeders can be high. The role of floaters may be important because they are probably easily able to track gamebird abundance and thereby potentially dampen and synchronise the prey populations as has been detected for the relationship between nomadic birds of prey and voles (see e.g. Korpimäki and Norrdahl 1989, 1991,

Korpimäki and Krebs 1996). 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.

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