Pattern of goshawk Accipiter gentilis predation on four forest grouse species in northern Finland

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I studied predator-prey relationships between goshawk *Accipiter gentilis* and four species of forest grouse (Tetraonidae) in northern Finland during 1988-1998. The main purpose of my study was to evaluate the impact of goshawk predation and its possible effect on multiannual cycling patterns in grouse numbers. Theoretically specialist predators should tend to cause stable-limit cycles in prey populations if there is a time-lag in the predator's response to prey density and the prey species should be most affected at low densities. Four grouse species, willow grouse *Lagopus lagopus*, black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus* and hazel grouse *Bonasa bonasia*, form the main food of the goshawk in boreal forests in northern Finland. Grouse constituted >40% of the goshawk's diet during the breeding season. The impact of predation by breeding goshawks on grouse varied depending on grouse species within 7-32% during the breeding season. Losses were highest for willow grouse and lowest for capercaillie. On average, goshawks took 6% of grouse chicks. On an annual basis breeding goshawks took 2-31% of the August grouse population. The goshawk's share of the total mortality in grouse was also species related. The most reliable estimates were found for black grouse of which 35% were removed and for hazel grouse of which 40% were removed. Goshawks are relatively specialised on forest grouse in northern boreal forests as was demonstrated by a weak functional response of the hawks to changes in grouse density. Breeding goshawks showed no numerical response to changes in grouse density but the production of young tended to lag one year behind black grouse density. The predation rate of goshawks was inversely density dependent on changes in grouse density, which may have had a destabilising effect on the grouse populations. A positive relationship existed between summer predation on willow grouse and changes in the population the previous year.

Key words: Accipiter gentilis, cyclicity, goshawk, grouse, population regulation, predation

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The role of predators in limiting or regulating prey populations has recently become a hot topic in research and debate (Andersson & Erlinge 1977, Angelstam, Lindström & Widén 1984, Erlinge, Göransson, Högstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylvén 1984, Hansson 1984, Kenward 1986, Henttonen 1987, Korpimäki 1993, Hanski, Hansson & Henttonen 1991, Korpimäki & Krebs 1996, Krebs 1996, Redpath & Thirgood 1999, Thirgood, Redpath, Rothery & Aebischer 2000). The traditional Erringtonian view states that predators only take a 'doomed surplus' of the prey population, which is regulated by either food shortage or intrinsic feed-back mechanisms such as genetic and social interactions (Errington 1956, Kenward 1986, Krebs 1996). Population regulation is a density dependent feed-back process which keeps populations within certain limits (Korpimäki 1993, Murdoch 1994, Sinclair & Pech 1996). Theoretically, the predator's effect on prey populations can be stabilising or destabilising, depending on the predator's functional response type, searching efficiency and carrying capacity of the prey (Hanski et al. 1991, Sinclair & Pech 1996). A predator numerical response with a time lag to a change in prey density tends to destabilise prey populations and cause stable-limit predator-prey cycles (Begon, Harper & Townsend 1990, Korpimäki, Norrdahl & Rinta-Jaskari 1991, Hanski et al. 1991).

Grouse (Tetraonidae) form a prominent part of the diet of the goshawk *Accipiter gentilis* throughout the year in boreal forests (Sulkava 1964, Höglund 1964, Lindén & Wikman 1983, Widén 1987, Selås 1989, Tornberg & Sulkava 1991, Tornberg 1997). Goshawk predation has also been found to play a major role in grouse demography (Angelstam 1984, Wegge, Rolstad, Gjerde & Storaas 1989, Swenson 1991, Valkeajärvi & Ijäs 1994). Two studies have estimated that goshawks remove roughly 15-25% of the grouse population during the breeding season (Lindén & Wikman 1983, Widén 1987). Yet, there have been relatively few discussions on the possible role of goshawk predation in the cycling of grouse populations (but see Ranta, Lindström & Lindén 1995). Lindén & Wikman (1983) found a concave functional response curve of goshawks to changes in hazel grouse *Bonasa bonasia* densities and a positive although delayed density-dependent impact on the density suggesting a stabilising effect on the hazel grouse population. In contrast, Angelstam et al. (1984) considered goshawks to have only a minor effect on grouse populations.

Three forest grouse species in Fennoscandia, capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix* and hazel grouse, tend to show multiannual cycles in abundance; the length of these cycles varies from 3-4 to 6-7 years with a relatively synchronous pattern (Angelstam, Lindström & Widén 1985, Lindén 1989, Lindström 1994, Ranta et al. 1995). The periodicity is longer in southern and central Finland than in northern Finland and Scandinavia. Willow grouse *Lagopus lagopus* living both in forested and subalpine areas show a 3-4 year pattern in cyclicity (Myrberget 1984). Many hypotheses have been put forward to explain the cyclicity of grouse populations (*cf.* Lindström 1994). Predation is thought to cause cycles in prey populations, and for grouse species two main hypotheses have been suggested: 1) the alternative prey hypothesis (APH), originally proposed by Hagen (1952) and Lack (1954), later defined by Angelstam et al. (1984), suggests that microtine predators switch to grouse when microtine populations crash causing a synchronous but delayed crash in grouse populations; and 2) the predation theory (Rosenzweig & MacArthur 1963, Begon et al. 1990, Hanski et al. 1991) which suggests that grouse population cycles may be caused by specialist predators (here goshawk). This theory predicts that cycles in prey populations may occur when (i) there is a time lag in the numerical response of the predators, (ii) predators are specialists, i.e. they do not show functional responses to the prey, (iii) there is a negative relationship between kill rate and changes in the prey population, and (iv) predation rates are highest at the decline or bottom phases of the prey population (see Korpimäki et al. 1991, Nielsen 1999).

In this article, I present both the functional and the numerical responses of goshawks to changes in grouse numbers and estimate the impact of goshawk predation on four grouse species. Finally, I test the predictions derived from the predation theory concerning the causes for stable-limit cycles between predator and prey.

Study area

The main research area is situated in the vicinity of Oulu (65°00'N, 25°30'E), Finland, within a radius of 30 km from the city centre (Fig.1). The isle of Hailuoto in the Bothnian Bay was also included. The study area covers ca 1,500 km^2 and is characterised by flat terrain, where a mixture of coniferous forests and bogs covers 2/3 of the total area, the rest being fields, lakes and settlements. Only 25% of forests are in their mature stage; for a more detailed description of the area, see Tornberg (1997).

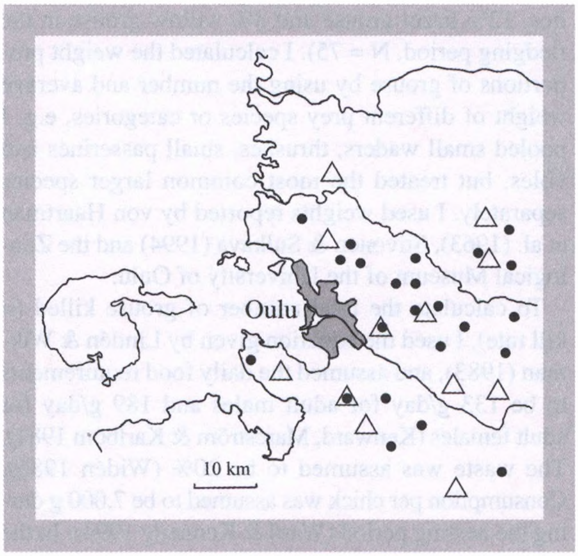

Figure 1. The study area near Oulu with indications of nesting sites of goshawks (●) and wildlife triangles (Δ) used during 1989-1998. Nests deviate non-randomly from their original positions.

Methods

Collection of breeding data and food remains

Nesting sites of the goshawk were located in the study area during 1989-1998. During this period all known sites were visited yearly to collect food remains and to check nesting results. The number of known territories was 10 in 1989; by 1998 the number had increased to 22 (see Table 3). Some territories were apparently deserted in the course of the study due to clear-cutting, but these were also included in the counting because nesting sites were not totally destroyed. The status of the territories was checked to see whether they were occupied, eggs were laid and young fledged. Sometimes nesting was not recorded until fledging time. Some goshawks (26 birds) were monitored by radio-telemetry during 1991-1995 to get information on winter diet and structure of the goshawk population (Tornberg & Colpaert 2001).

Food remains were collected in the course of the breeding season at least three times: during incubation, at the end of the nesting period and at the end of the fledging period. In total 2,456 prey items were identified from the samples; for further details, see Tornberg (1997).

Grouse densities

Data on grouse densities and breeding success were obtained from the Finnish Game and Fisheries Research Institute (see Table 2). Grouse censuses, based on 12 km long routes shaped as triangles, were carried out each year in early August (Anon. 1992, Lindén, Wikman & Helle 1989), and each year 10-12 triangles were counted in my study area. The location of the triangles and goshawk nests in the study area are shown in Figure 1. Because censuses recorded grouse densities in late summer, I estimated densities in spring the same year by adding the number of grouse killed by goshawks to the number of adults found in the August censuses (see also Lindén & Wikman 1983). I calculated chick production assuming that every female laid eggs (Marjakangas & Törmälä 1997). I further assumed an even sex ratio for willow grouse and hazel grouse, but a female biased sex ratio for black grouse and capercaillie (60% females; Rajala 1974). I used species specific clutch sizes found in the literature (von Haartman, Hilden, Linkola & Tenovuo 1963, Lindén 1989). I assumed a nest loss rate of 30% for all species (Marjakangas & Törmälä 1997) and an early loss rate of chicks due to unknown factors of 20% (Lindén 1981, Kastdalen & Wegge 1989, Thirgood et al. 2000). I calculated annual mortality of the different grouse species according to the following equation:

$$\text{Mortality} = \text{adult}_{\text{year+1}}/\text{adult} + \text{juvenile}_{\text{year t}}.$$

To compare the predation on grouse with their availability, I calculated grouse density for each goshawk pair using the following equation:

$$D_{ij} = \left(\sum_{j=0}^{5} D_j \times d_{ij}\right) / \sum_{j=0}^{5} D_{ij},$$

where density of grouse (D_{ij}) for the ith pair is a weighted average of the five nearest wildlife triangles. The density value D_j of jth triangle is multiplied by a weighting factor dij, where dij is the distance between triangle j and the nest.

Goshawk population

I estimated the density of the territorial goshawks based on the number of the nest sites found. Nests were fairly regularly spaced in areas of continuous habitat. I assumed that the same nesting sites were used year after year. The nearest-neighbour distance between the nests in the area, where most nests were found, was 4.0 km (see method in Newton 1986). As more nests were found near settled areas, where the density may be higher than in unsettled areas, I used a nearest-neighbour distance of 4.5 km (see Fig. 1), leading to a breeding bird density of 4.7 pairs/100 km^2, given that no pairs hunted farther than 3 km from their nesting sites.

Predation estimate

To calculate predation estimates, I used data on diet based on collection of food remains at the breeding sites. I divided the breeding season into three periods: the nest-building and incubation period (60 days), the nesting period (45 days) and the fledging period (30 days). The percentage of each prey species or group was calculated as an average of percentages of each sample in each year separately for the incubation, nesting and fledging periods. I only accepted samples that contained ≥5 prey items.

I divided the non-breeding period into two parts; the first part lasted from mid-August to the end of November (105 days; snowless period), and the last part from December to the end of March (120 days; snowy period). Due to the lack of yearly data on goshawk winter diet, I used the average percentage of grouse in the winter diet from the years 1991-1995 (Tornberg & Colpaert 2001). As the data mostly represented the diet of female goshawks which primarily hunted mountain hares *Lepus timidus*, a prey species not taken by males, I corrected data for males by expanding the percentage of the hares' biomass to the other prey objects. Thus black grouse constituted 10.3% of female, but 52.0% of male winter diet. The respective values for capercaillie were 8.9 and 0% (male goshawks do not kill capercaillie cocks), for willow grouse 0.8 and 3.8%, and for hazel grouse 1.9 and 9.6%. Due to lack of data on autumn diet, I used the mean proportions from the fledging period and the winter for that period. The proportion of grouse during the fledging period was the sum of proportions of adults and grouse chicks in the diet (56% of grouse chicks were found to be black grouse, 24% capercaillies, 12% hazel grouse and 8% willow grouse in the fledging period, N = 75). I calculated the weight proportions of grouse by using the number and average weight of different prey species or categories, e.g. I pooled small waders, thrushes, small passerines and voles, but treated the most common larger species separately. I used weights reported by von Haartman et al. (1963), Siivonen & Sulkava (1994) and the Zoological Museum of the University of Oulu.

To calculate the total number of grouse killed (= kill rate), I used the equation given by Lindén & Wikman (1983), and assumed the daily food requirements to be 133 g/day for adult males and 189 g/day for adult females (Kenward, Marcström & Karlbom 1981). The waste was assumed to be 20% (Widén 1985). Consumption per chick was assumed to be 7,000 g during the nesting period (Ward & Kennedy 1994). In the fledging period their consumption was assumed to be the same as for adults.

Functional and numerical response

The functional response was defined as the percentage of each grouse species and all species pooled, plotted against the adult grouse density found in the August censuses. I examined for pair specific responses by including data from the five nearest wildlife triangles and by including prey samples containing ≥10 prey specimens to avoid randomness in prey percentages.

I used five breeding parameters as numerical parameters of the goshawk population: number of territorial goshawks/100 km^2, number of juveniles/100 km^2 (= production of young in each year), total goshawk density (adults + juveniles)/100 km^2, number of adults/

Table 1. Mean percentages (upper figures) and standard errors (lower figures) of the prey species willow grouse (WG), black grouse males (BGm) and females (BGf), capercaillie females (Cf), hazel grouse (HG), and the groups grouse chicks (Gc), other birds (OB) and mammals (M), by number in the diet of the goshawk in the Oulu region during 1989-1998.

	Year									
Prey	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
WG	3.8	3.2	7.5	6.8	3.8	6.0	7.1	5.5	15.5	5.9
	0.9	1.3	2.4	1.8	2.0	1.5	1.5	2.6	5.8	2.0
BGm	5.7	5.6	4.8	2.8	1.4	4.2	4.3	3.8	2.0	2.7
	1.9	1.3	2.6	1.1	0.8	1.4	1.9	1.9	1.4	0.9
BGf	10.4	9.5	4.7	7.4	10.7	7.3	15.4	12.6	10.1	10.7
	2.5	2.2	2.0	2.2	2.7	1.5	3.6	2.2	2.4	2.6
Cf	0.4	0.7	1.1	1.1	1.0	1.3	7.6	2.5	8.0	2.9
	0.4	0.5	1.1	0.6	1.0	0.6	3.4	1.0	3.1	2.1
HG	8.8	6.0	11.4	9.3	11.8	16.6	17.0	10.5	10.5	8.5
	4.7	1.6	3.5	3.0	2.2	2.6	4.0	2.9	3.9	2.1
Gc	5.8	10.3	4.6	10.2	12.4	14.3	5.8	8.5	3.7	13.1
	2.6	3.3	1.8	2.8	3.2	2.4	2.7	3.0	0.9	1.9
OB	37.0	36.4	46.8	37.3	34.3	40.3	35.1	34.8	32.0	37.1
	5.1	4.6	7.6	4.4	7.2	5.1	8.9	7.1	6.6	5.1
M	28.1	28.3	19.1	25.0	24.5	10.0	7.6	17.5	12.3	19.2
	2.8	4.2	1.5	5.5	10.6	2.7	2.7	4.1	3.4	3.3
Nests	8	7	8	10	6	11	9	8	7	12
N	204	318	235	363	216	350	131	190	193	256

Table 2. Mean densities (individuals/km^2; upper figures) and standard errors of the means (lower figures) of adults and juveniles of willow grouse, black grouse, capercaillie and hazel grouse in August based on 12 wildlife triangle censuses in the vicinity of Oulu for 1989-1998.

	Willow grouse		Black grouse		Capercaillie		Hazel grouse	
Year	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.
1989	0.6	1.4	7.2	4.4	1.2	0.5	3.4	4.0
	0.4	1.0	1.3	1.5	0.3	0.4	1.1	1.8
1990	1.7	1.3	4.7	1.9	11.9	2.0	2.6	1.3
	1.1	1.2	1.0	0.8	0.6	0.9	0.9	0.6
1991	1.4	0.0	3.7	5.6	1.7	2.3	1.6	1.8
	0.7	0.0	1.0	2.9	0.5	1.0	0.5	0.8
1992	0.4	1.1	3.0	2.4	1.7	0.9	1.7	3.4
	0.4	1.0	0.8	1.1	0.7	0.5	0.6	1.1
1993	0.8	0.0	6.2	8.9	3.1	4.6	4.0	4.9
	0.6	0.0	1.3	3.3	1.1	3.4	1.0	2.2
1994	0.4	0.0	5.4	1.7	1.7	2.1	3.4	1.9
	0.4	0.0	1.4	0.9	0.4	1.5	1.2	1.0
1995	1.4	0.9	3.3	7.4	2.1	1.5	3.9	3.0
	1.1	0.9	1.1	3.0	0.9	1.0	1.1	1.3
1996	2.8	1.0	8.1	7.9	2.2	1.1	2.8	2.5
	2.1	0.7	1.2	1.2	0.9	1.0	0.8	1.5
1997	0.6	0.6	4.3	5.2	1.4	0.8	3.6	3.5
	0.4	0.6	1.4	2.0	0.6	0.6	1.1	1.9
1998	0.3	1.2	3.2	3.3	2.3	2.7	2.7	3.4
	0.2	1.2	0.6	1.0	0.6	1.3	1.3	1.8

checked territory (= territory occupancy) and number of nestlings/checked territory (= productivity). The numerical response was obtained by plotting the five parameters against the autumn density of grouse for the years t, t-1 and t-2. The total response (= kill rate) was obtained by 1) multiplying the number of grouse killed per predator with their density, and 2) plotting the outcome against the density of adult grouse found in the August censures. I used Spearman correlations to test dependencies between the variables.

Predation rate

An estimate of the predation impact (= predation rate) was obtained by dividing the kill rate by the number of grouse available (see Keith, Todd, Brand, Adamcik & Rusch 1977). I calculated predation rates for the breeding season for the different grouse species and for all grouse pooled. The whole-year estimate was calculated as an average for the years 1991-1995 for which data on winter diet was available. I included only the consumption of the resident birds (= birds having their own breeding territory) and that of their offspring. I made a cautious assumption that juveniles stayed or survived in the study area at least until the end of November (Widén 1985, R. Tornberg, pers. obs.). For the first part (mid-August - end of November) of the non-breeding period I included only the consumption of resident adults. For the latter part (beginning of December - end of March) of the non-breeding period I included only the resident adults.

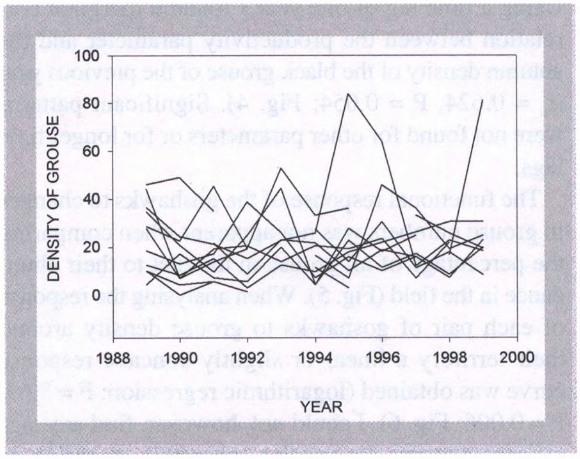

Figure 2. Changes in density (individuals/100 km^2) of grouse (all species pooled) at 12 wildlife triangles used in the study area in August censuses near Oulu during 1989-1998.

Results

Goshawk diet

Four grouse species including adults and chicks constituted 43% of the diet by number in the breeding season during the study years (Table 1). The most important grouse prey were black grouse hens (10%). The proportion of grouse in the diet of goshawks tended to increase during the study years. This was most obvious for willow grouse and capercaillie hens. The changes in the proportion of grouse were not synchronous. The percentage of other birds in the diet remained fairly stable but the percentage of mammals decreased.

Table 3. Densities of goshawks during the breeding season (individuals/100 km^2) for breeding birds (B), nestlings (N), nestlings per goshawk territory (N/T), goshawks (T) and the number of goshawk territories checked (NT) in the study area during 1989-1998.

Year	B	N	N/T	T	NT
1989	8.5	11.7	2.8	20.2	10
1990	9.4	11.5	2.4	20.9	10
1991	9.4	5.1	1.1	14.5	12
1992	9.4	10.1	2.2	19.5	13
1993	8.2	5.0	1.2	13.2	16
1994	6.4	5.4	1.7	11.8	19
1995	7.2	2.6	0.7	9.7	21
1996	7.6	6.3	1.7	14.0	21
1997	7.3	6.8	1.9	14.1	18
1998	7.7	8.0	2.1	15.7	22

Grouse density during the study years

During the study years grouse density peaked in 1993 and 1996 (Table 2). The highest density (33.5 grouse/km^2) was reached in 1993 and the lowest (14.5 grouse/km^2) in 1992. The proportion of juveniles reached a maximum (59%) in the peak year 1993 and the pre-peak year 1995 and a minimum (34%) in the crash year 1994. Grouse species fluctuated asynchronously with each other (i.e. there was no correlation in year-to-year variation between the species, $P > 0.05$). Synchrony in the fluctuation of grouse species between the wildlife triangles was also absent or weak. Of all the triangles in my study area only the data sets of two correlated significantly positively with each other (Fig. 2).

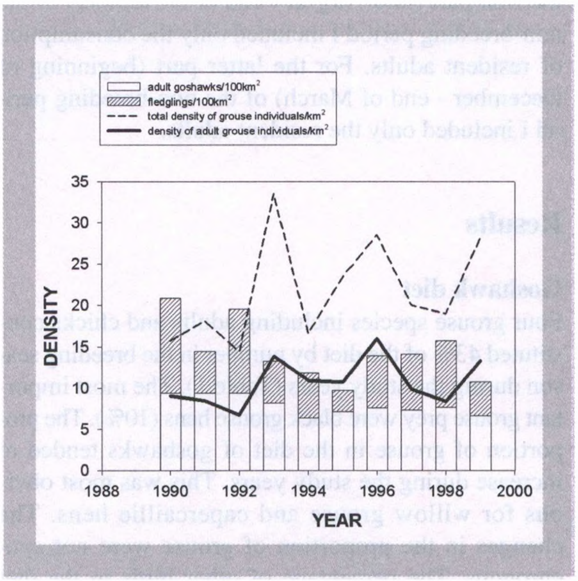

Figure 3. Density of breeding goshawks (parents and offspring) related to the total density of grouse and the density of adult grouse in August in the study area near Oulu during 1989-1998.

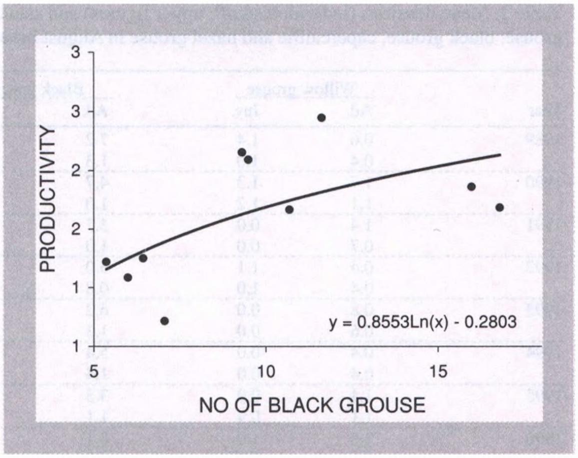

Figure 4. Relationship between productivity of the goshawk population (expressed as number of nestlings per checked goshawk territory) and density (individuals/km^2 in year t-1) of the black grouse in the previous autumn near Oulu during 1989-1998.

Goshawk population

The density of breeding goshawks was highest during 1989-1992 and decreased during 1993-1998 (Table 3). The breeding success of the goshawk population, expressed both as the total number of fledglings and as the number of fledglings per checked territory, also decreased during this time. The breeding success in 1989 was 4-fold what it was in the poorest year 1995.

Numerical, functional and total responses

The numerical response of the breeding goshawks to the density of adult grouse (= spring density) and total density (= August density) was unclear (Fig. 3). Density parameters of the breeding goshawks tended to be negatively correlated to changes in grouse abundance. Using a time lag of one year I found a marginal correlation between the productivity parameter and the autumn density of the black grouse of the previous year ($r_s = 0.624$, $P = 0.054$; Fig. 4). Significant patterns were not found for other parameters or for longer time lags.

The functional response of the goshawks to changes in grouse numbers was not apparent when comparing the percentage of all grouse in the diet to their abundance in the field (Fig. 5). When analysing the response of each pair of goshawks to grouse density around their territory a linear or slightly concave response curve was obtained (logarithmic regression: $F = 8.59$, $P = 0.006$; Fig. 6). I could not, however, find any significant patterns for species separately in spring or later in the breeding season (Fig. 7). When I plotted the number of separate grouse species killed by the goshawk

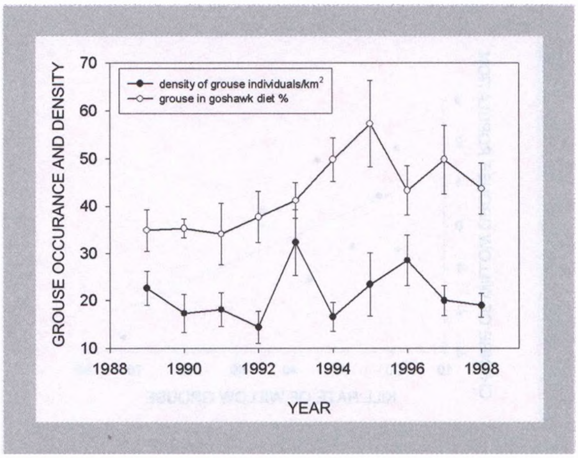

Figure 5. Relative occurrence (in %) of grouse in the diet of the goshawks during the breeding season and the corresponding densities (individuals/km²) of grouse in the study area during 1989 -1998. Standard error of the means are indicated.

population/100 km² (= kill rate) against the density of each grouse, no significant patterns were found.

Impact of predation during the breeding season

During the breeding season resident goshawks and their offspring removed, on average, 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 (Table 4). There was a marked between-year variation in the impact. When I plotted the yearly proportions of grouse removed during the breeding season against the density of adult grouse of each year, a significant negative

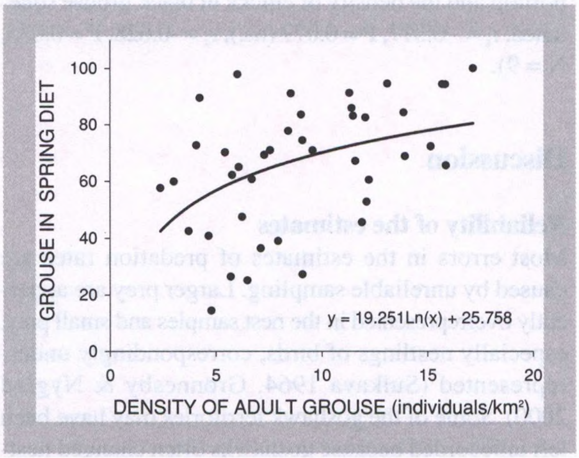

Figure 6. Functional response of breeding goshawks (expressed as % grouse in the goshawk spring diet) to changes in the density (individuals/100 km²) of adult grouse for all species pooled during spring 1989-1998.

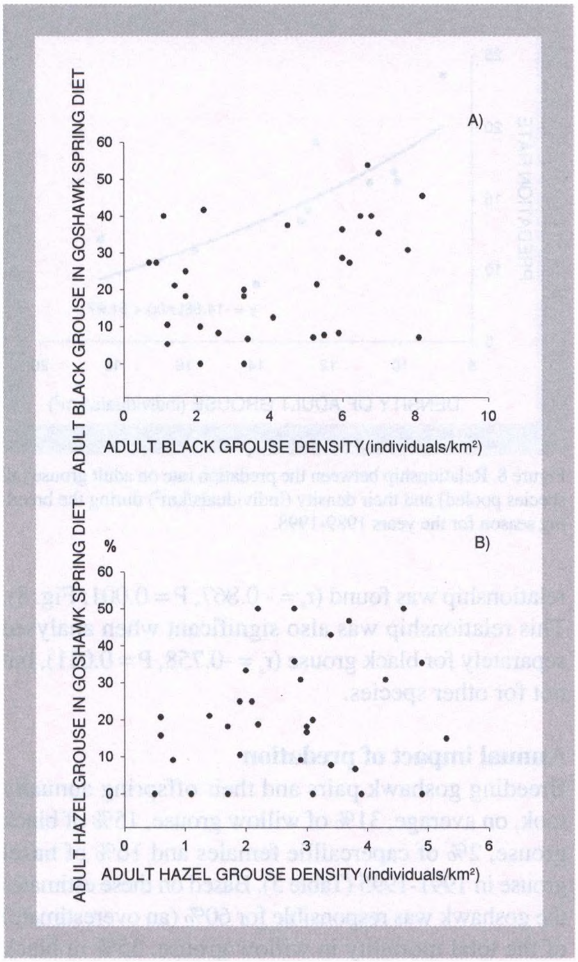

Figure 7. Functional response of breeding goshawks (expressed as % grouse in the goshawk spring diet) to changes in the density (individuals/100 km²) of the black grouse (A) and hazel grouse (B) during spring in the years 1989-1998.

Table 4. Predation impact of the goshawk on willow grouse (WG), black grouse males (BGm) and females (BGf), capercaillie females (Cf), hazel grouse (HG) and grouse chicks (Gc) during the breeding season calculated from spring densities in 1989-1998.

	Grouse species					
Year	WG	BGm	BGf	Cf	HG	Gc
1989	19.4	6.7	9.9	3.9	10.2	
1990	25.9	13.4	21.8	5.1	17.0	9.7
1991	20.3	10.6	10.5	2.3	33.0	4.7
1992	53.6	12.6	27.5	8.0	30.4	7.7
1993	18.0	3.9	15.0	5.7	15.5	5.2
1994	41.7	7.0	9.1	4.1	20.6	6.6
1995	12.4	9.6	21.0	11.2	16.5	3.5
1996	10.9	4.7	12.6	7.5	24.5	2.3
1997	54.9	7.2	18.4	18.7	16.5	1.5
1998	58.3	10.2	22.9	4.4	16.1	11.0
Mean	31.5	8.6	16.9	7.1	20.0	5.8

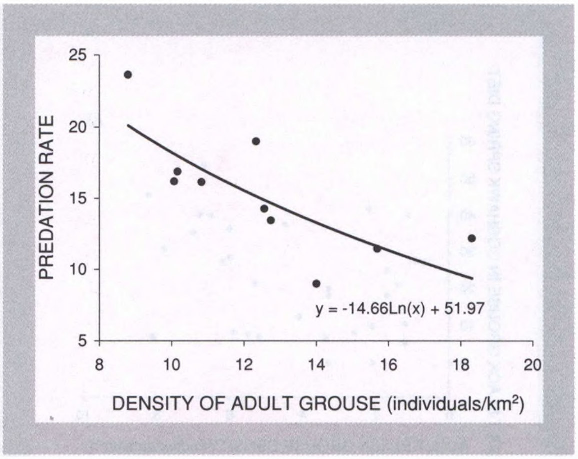

Figure 8. Relationship between the predation rate on adult grouse (all species pooled) and their density (individuals/km^2) during the breeding season for the years 1989-1998.

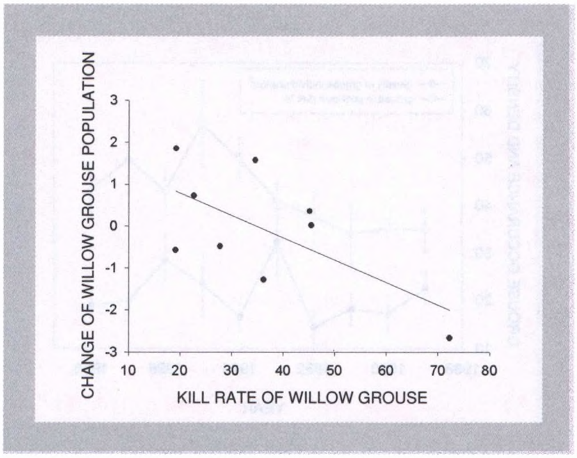

Figure 9. Relationship between changes in the population of the willow grouse from year t-1 to year t and the kill rate of willow grouse during the breeding season in year t.

relationship was found (r_s = - 0.867, P = 0.001; Fig. 8). This relationship was also significant when analysed separately for black grouse (r_s = -0.758, P = 0.011), but not for other species.

Annual impact of predation

Breeding goshawk pairs and their offspring annually took, on average, 31% of willow grouse, 15% of black grouse, 2% of capercaillie females and 16% of hazel grouse in 1991-1995 (Table 5). Based on these estimates the goshawk was responsible for 60% (an overestimate) of the total mortality in willow grouse, 35% in black grouse, 5% in capercaillie and 40% in hazel grouse, annually.

Goshawk predation and grouse population parameters

To estimate the effect of goshawk predation on grouse dynamics I analysed the relationships between the kill rate of adults and population parameters (mortality, population change and production of young) of each grouse species. I analysed the kill rate of the year and the mortality/population change from August of the previous year because this period was the 'handling unit' in my calculations. I found no significant relationships between the kill rate and the mortality/population change of the grouse of the previous winter except for the mortality of willow grouse (one-tailed: r_s = 0.745, P = 0.011, N = 9; Fig. 9).

To examine the effect of goshawk predation on the breeding parameters I made correlation tests between the kill rate of adults of each grouse species and the proportion of chicks/chick density in August censuses. The only significant correlation was between the kill rate of capercaillie hens and the proportion of their chicks (one-tailed: r_s = - 0.661, P = 0.019). The kill rate of grouse chicks related negatively to the juvenile proportion and the density of chicks in black grouse (one-tailed: r_s = - 0.517, P = 0.077 (ns.), r_s = -0.628, P = 0.035, N = 9).

Table 5. Average predation impact of breeding goshawks and their offspring on willow grouse (WG), black grouse (BG), capercaillie (C) and hazel grouse (HG) during the breeding (summer) and non-breeding seasons (autumn, winter) in 1991-1995 expressed as the numbers taken. Predation rates for each season are calculated from average August densities of the years 1990-1994.

	Grouse species			
Season	WG	BG	C	HG
Summer	18.1	7.2	1.8	10.1
Autumn	9.0	4.2	0.3	5.4
Winter	4.2	3.4	0.2	0.8
Total	31.2	14.8	2.3	16.4
% of total mortality	59.7	34.8	5.0	39.7

Discussion

Reliability of the estimates

Most errors in the estimates of predation rates are caused by unreliable sampling. Larger prey are apparently overrepresented in the nest samples and small prey, especially nestlings of birds, correspondingly underrepresented (Sulkava 1964, Grønnesby & Nygård 2000). Some of the goshawk territories may have been left unrecorded because goshawks often changed nesting sites due to disturbance. Usually, however, a successful nest was detected during the fledging period. Grouse densities were based on wildlife triangles, which are considered to provide relatively reliable estimates on grouse numbers (Lindén et al. 1989). The combined length of the census line each year in my study area is probably sufficient to obtain accurate densities (*cf.* Lindén & Wikman 1983). Backcalculating spring densities by adding the number of grouse killed by the goshawk to the number of adults counted in the August censuses ignores mortality caused by other factors (e.g. mammalian predators), and therefore may underestimate the spring density of grouse.

Functional and numerical response

The numerical response of goshawks to grouse was relatively weak. The density and occupancy of the breeding goshawks fluctuated only negligibly, which is typical of Finnish goshawks (Väisänen, Koskimies & Lammi 1998). In the boreal forests of North America fluctuations in goshawk density are more pronounced and closely linked to the population dynamics of the snow-shoe hare *Lepus americana* (Doyle & Smith 1994). In my study the production of young goshawks lagged one year behind black grouse reproduction as was also found by Sulkava, Huhtala & Tornberg (1994) in western Finland. Time lags in the density and occupancy rate of the breeding adults are difficult to detect in short time-series such as in my study. It is noteworthy that the fluctuation of grouse populations has dampened and the cycling pattern of the different species has not been synchronous during the 1990s (*cf.* Lindén & Rajala 1981, Ranta et al. 1995). Thus, changes in goshawk dynamics are not apparent. In a countrywide investigation using longer time series, breeding goshawks seem to lag two years behind the black grouse population (Väisänen et al. 1998). Two-year time lags have been reported for gyrfalcons *Falco rusticolus* in relation to ptarmigans in Iceland (Nielsen 1999) and for great horned owl *Bubo virginianus* in relation to snow-shoe hares in North America (Keith et al. 1977, Rohner 1995). Theoretically, time lags of two years would be enough to generate grouse cycles in northern boreal forests because a predator driven cyclicity of a prey population requires a time lag of $^1/_4$ of the cycle length (May 1981).

A functional response of the goshawks to changes in grouse numbers was found only in spring for the percentage of grouse combined. No patterns were found for the individual species, which probably is due to goshawks switching between grouse species. This implies that goshawks consider different grouse species as one (Tornberg 1997). The shape of the response curve was almost linear or slightly concave referred to as a type II curve which is probably the most basic one for the goshawk-grouse relationship, as was also stated in earlier studies (Wikman & Tarsa 1980, Tornberg & Sulkava 1991), and for other raptors too (e.g. Keith et al. 1977, Nielsen 1999, Redpath & Thirgood 1999). The point where the functional response curve starts to level-off is difficult to determine, which is probably due to the fact that pairs which nested close to settled areas consumed less grouse at the same grouse densities than pairs nesting in unsettled forested areas, thus bending the curve down at the lower densities. Lindén & Wikman (1983) reported a concave functional response curve for hazel grouse in southern Finland. Elements of concavity could also be seen in my data for hazel grouse. As a refuging species hazel grouse may have a threshold density above which the predation rate accelerates causing a sigmoidal response curve (see Lindén & Wikman 1983), which would include an element of density-dependent predation (*cf.* Redpath & Thirgood 1999).

Goshawk predation and regulation of grouse populations

The goshawk predation pattern on grouse was inversely density-dependent, which was due to the absent response of the kill rate to changes in grouse density. Corresponding patterns have also been found for large falcons hunting on *Lagopus* species (Nielsen 1999, Redpath & Thirgood 1999). A depensatory response is thought to be associated with a generalist predator having a type II functional response (Sinclair & Pech 1996, Redpath & Thirgood 1999). However, the same effect will be obtained when specialist predators show a time lag in relation to their prey (Nielsen 1999). In northern conditions, where alternative prey is scarcer than in southern areas, the ascending part of the response curve is not visible because the predator either cannot survive or breed at the lowest prey densities. Depensatory predation in northern regions may destabilise the grouse cycle by increasing the amplitude and/or extending the low phase of the cycle. In southern Finland, the goshawks' numerical, functional and total responses to hazel grouse tended to increase, or even accelerate, when hazel grouse density increased (Lindén & Wikman 1980, 1983). Hence, a stabilising effect of the goshawk predation on grouse populations might be possible in southern Finland.

I did not consider floaters of the goshawk population that may complicate the scheme by aggregative responses (Kenward 1977, Kenward et al. 1981). Floaters may easily track grouse abundance and thus probably dampen and synchronise the prey population within and among the species, as was found for the relationship between nomadic birds of prey and voles (Korpimäki

1986, 1993, Korpimäki & Norrdahl 1989, 1991, Korpimäki & Krebs 1996).

Even though the level of predation was fairly high this did not seem to have a great impact on the overall patterns of grouse mortality. This may have been due to the incomplete nature of my predation estimates from the breeding season which thus may have failed to reflect predation for the whole year. Willow grouse may have been an exception from this pattern as the species may be more vulnerable to raptor predation than other grouse species. Thirgood et al. (2000) showed that raptor predation could lower spring and autumn densities in red grouse *Lagopus lagopus scoticus* and probably also dampen multiannual cycling in the species. Willow grouse may be in real danger of being driven into local extinction under depensatory predation from raptors in addition to heavy mammalian predation (see Sinclair & Pech 1996). Habitat deterioration (draining of bogs) may be one of the most serious threats that willow grouse are faced with. It is also worth mentioning that the probable shortening of the snowy period due to the green-house effect will test the adaptability of the species, e.g. in regard to its change into winter/spring plumage.

The recruitment rate in grouse is largely determined by early chick mortality (Lindén 1981, 1989), in which mammalian predators have been suggested to play a major part (Angelstam et al. 1984, Henttonen 1989, Kurki, Helle, Lindén & Nikula 1997), but predation by raptors may also have a large impact on grouse chick mortality as has been shown for red grouse (Thirgood et al. 2000). Although goshawks seem to play a minor role in grouse chick mortality based on predation rates found, the total impact may be greater taking into account the bias in the estimates and the predation on hens, which has been found to be very heavy in spring (Angelstam 1984, Widén 1987, Valkeajärvi & Ijäs 1994, Tornberg 1997). I found direct and indirect effects of goshawk predation on the proportion and density of black grouse and capercaillie chicks which are the most preferred among grouse chicks (Sulkava 1964, this study). Therefore, goshawk predation on the most preferred capercaillie chicks may cause fairly high losses for this species, especially when fragmentation of their preferred habitat, i.e. old forests, may increase their vulnerability to predation (Kastdalen & Wegge 1989, Wegge et al. 1990, Storaas et al. 1999).

In conclusion, goshawk predation on the four forest grouse species partially fulfilled the predictions of the predation theory. First, goshawks showed a tendency to lag behind grouse numbers even though this was shown only for the productivity parameter of the goshawk population. Second, goshawks were fairly specialised on grouse and were not able to switch to another prey in winter and in the beginning of the breeding season to any large extent. Third, the kill rate of willow grouse related negatively to annual population changes in this species, but not to those of other grouse species. Finally, the predation pressure of the goshawks was highest when grouse densities were lowest.

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