

# The impact of predator abundance on grouse populations in Finland — a study based on wildlife monitoring counts

Kaarina Kauhala & Pekka Helle

*Kauhala, K., Finnish Game and Fisheries Research Institute, Evo Game Research Station, Kaitalammintie 75, FIN-16970 Evo, Finland. E-mail: kaarina.kauhala@rktl.fi*  
*Helle, P., Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2 A, FIN-90570 Oulu, Finland*

*Received 30 January 2001, accepted 29 October 2001*



The relationships between grouse (Capercaillie, Black Grouse and Hazel Grouse) populations and red fox and pine marten abundance were studied in Finland using the wildlife triangle counts from 1989 to 1999. Spatially, a negative relationship existed between predator indices and grouse breeding success, but predator indices and grouse density did not correlate. When temporal variation was concerned, there was a negative relationship between the fox index and grouse breeding success in some areas of southern and western Finland, and between the marten index and grouse breeding success in north-east Finland. Only in 4 areas out of 27 was there a negative relationship between predator indices and grouse density, all areas being in northern or eastern Finland. The growth rate of grouse populations had a stronger negative relationship with grouse density than with predator indices; predator numbers thus were of minor importance when determining the trends in grouse populations.

## 1. Introduction

Because predation is the major cause of non-hunting mortality in many grouse species (Willebrand 1988, Cotter *et al.* 1992, Caizergues & Ellison 1997, Smith & Willebrand 1999), changes in predator numbers have been connected to the changes in the density of grouse populations in many areas (Marcström *et al.* 1988, Henttonen 1989, Lindström *et al.* 1994, Selås 1998, Smedshaug *et al.* 1999, Kurki *et al.* 2000). Many studies (e.g. Marcström *et al.* 1988, Lindström *et al.* 1994, Smedshaug *et al.* 1999) suggest that predators, especially the red fox (*Vulpes vulpes*), have an impact on the breeding success of grouse. The evidence against predators affecting the growth rate and density of grouse populations over the

long-term is, however, less convincing. Some studies point to the conclusion that habitat changes, mainly fragmentation of forests, are largely responsible for the decline in grouse numbers (e.g. Conneli & Braun 1997, Macdonald *et al.* 1999, Storch 2000).

In Finland, we have a wildlife monitoring system, the wildlife triangles (see Lindén *et al.* 1996), that can be used to study the relationships between game species. We have studied earlier the interactions between predator and mountain hare (*Lepus timidus*) populations using wildlife triangles (Kauhala & Helle 2000). The aim of the present paper is to study the relationships between 3 grouse species (Capercaillie *Tetrao urogallus*, Black Grouse *T. tetrix* and Hazel Grouse *Bonasa bonasia*) and their mammalian

predators (red fox and pine marten *Martes martes*), i.e. whether foxes or martens can affect grouse breeding success, the growth rate and density of grouse populations.

## 2. Material and methods

### 2.1. Data collection

The data were collected using wildlife triangle counts (see Lindén *et al.* 1996) from 1989 to 1999. The number of both adult and young grouse is counted each August from the same triangles. Volunteer assistants perform the counts each year. The triangles are equilateral and each side is 4 km long, the total length of each inventory route thus being 12 km. A 3-person team counts the grouse and covers a census belt 60 m in width, i.e. each triangle equals 0.72 km<sup>2</sup>. These counts thus give the density of grouse/km<sup>2</sup> of forested land. Grouse densities are slightly underestimated, since the census efficiency is about 70–80% (see Brittas & Karlbom 1990). Besides, females with brood are observed with higher probability than broodless females and males (Brittas & Karlbom 1990), and therefore breeding success may be subtly overestimated. These inaccuracies do not bias the analyses markedly (see Helle & Lindström 1991). The snow tracks of red fox and pine marten were counted from the same triangles each winter (15 Jan–15 March), i.e. about 6 months earlier than grouse numbers; the data used here are from Kauhala and Helle (2000). The winter counts give the predator index (tracks crossing the transect line/10 km per 24 h). We assumed here that there is a linear relationship between predator indices and predator abundance.

Finland was divided into 27 squares (100 km × 100 km, i.e. 10 000 km<sup>2</sup>, Fig. 1). The mean number of triangles was 35/square per year (range 14–91), which equals 420 km of transect line or 25 km<sup>2</sup>. The total data were 10 454 triangles (125 448 km of transect line or 7527 km<sup>2</sup>). The data consisted of 20 862 Capercaillie, 60 170 Black Grouse and 53 437 Hazel Grouse observations. The mean proportion of young was 0.37 for Capercaillie, 0.44 for Black Grouse and 0.42 for Hazel Grouse. The mean of 97.2 Capercaillies

was seen per square per year (SD = 45.02), the corresponding figures being 202.6 (121.28) for Black Grouse and 179.9 (72.81) for Hazel Grouse. The total number of snow tracks was 72 128 for the red fox and 10 647 for the pine marten, the means per square and year being 242.9 (SD = 133.91) for the fox and 35.9 (15.86) for the marten. Spatial autocorrelation is inherent in these kind of data. This means, among other things, that population changes of species between neighbouring areas are more synchronous than changes between more distant areas (Koenig 1999, Ranta *et al.* 1999), which may raise a question of independence of samples. In order to reveal major geographical patterns in the data, we also divided the country into 4 larger areas: southern (S), western (W), eastern (E) and northern (N) Finland (Fig. 1).

We calculated the persistence of the grouse populations from August of year  $t$  to August of year  $t+1$  for each grouse species. It includes, besides survival, the effects of immigration and emigration, but since the areas were large (100 × 100 km), the effect of migration is probably of minor importance, immigration and emigration compensating for each other:

$$\text{Persistence} = \frac{\text{adult density in August of year } t+1}{\text{total density in August of year } t} \quad (1)$$

We also calculated the population growth rate from August of year  $t$  to August of year  $t+1$  for each grouse species:

$$\text{Growth rate} = \log a_{t+1} - \log a_t \quad (2)$$

where  $a_{t+1}$  is the total density of grouse in August of year  $t+1$  and  $a_t$  the total density in August of year  $t$ .

The growth rate (from August of year  $t$  to August of year  $t+1$ ) thus includes 2 components: 1) persistence of adult and young grouse (from August of year  $t$  to August of year  $t+1$ ); and 2) the breeding success during summer (year  $t+1$ ). Component 1 determines the number of adults and component 2 mainly the number of young in the August population. Because the density of the August population, and thus also the growth rate of the population, is affected both by what happens to the birds that are in the population the previous August (component 1) and the breeding success the current summer (component 2), it is

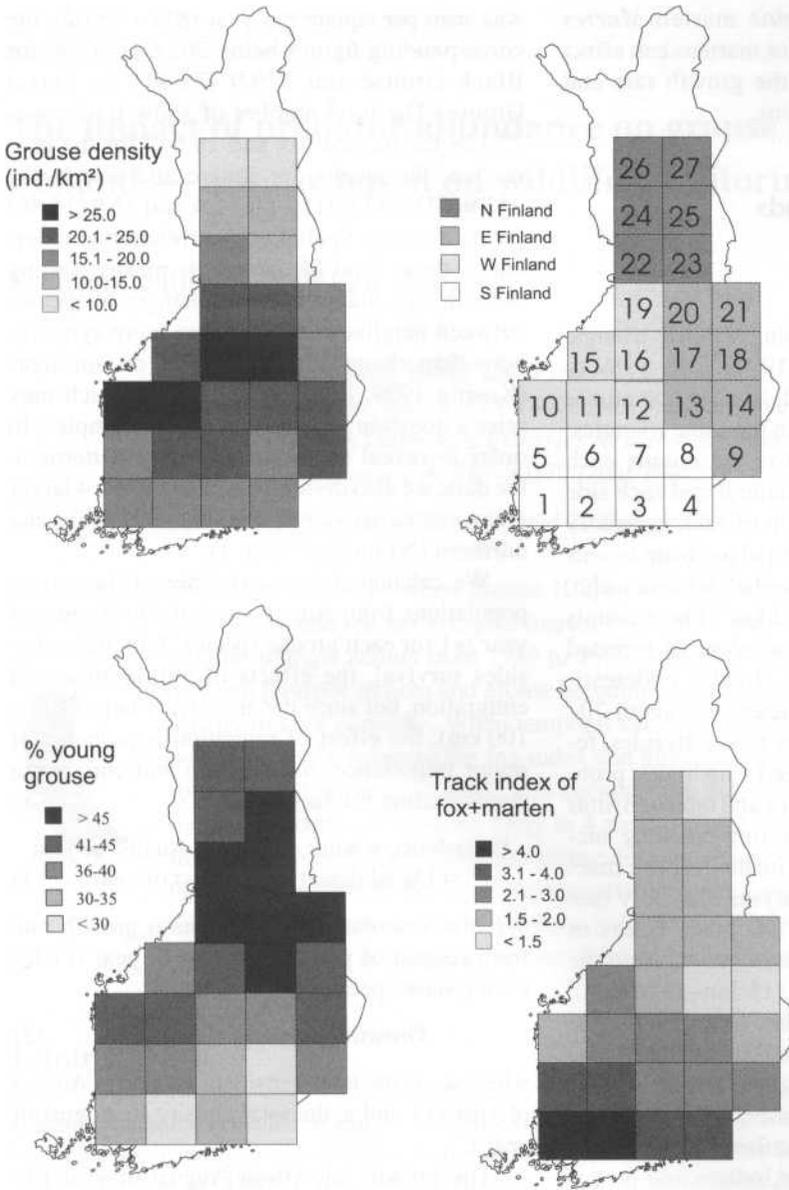


Fig. 1. Mean density and breeding success (% young) of grouse in each square during the study period from 1989 to 1999, based on the wildlife triangle counts from August each year. The mean predator index in each square is also given, being the sum of snow track indices of fox and marten from the wildlife triangle winter counts (number of tracks/10 km per 24 h). Finland was divided into 27 squares (100 km × 100 km) and 4 larger areas (southern, western, eastern and northern Finland) for the study.

important to divide the growth rate into these two components. We wanted to test the effect of predator numbers on the two components and also, which component is more important for the growth rate of the population. The proportion of young grouse in the August population was used as an index of breeding success. In the analyses, we used the log transformations of densities and predator indices.

## 2.2. Statistical analyses

We used correlation analyses to test spatial relationships between grouse density, breeding success and predator indices and ANOVA to test the differences between areas.

When studying temporal variation, we first tested whether the trends in population densities/predator indices were significant by regression of

the population densities/predator indices against year. We also calculated the change (%) in predator indices by comparing the means of the three first and the three last years of the study period. We then tested the relationships between predator indices and the density, breeding success, persistence and growth rate of grouse populations using stepwise regression analysis. We also used stepwise regression analysis to determine which was more important for the growth rate of the grouse populations: the breeding success or the persistence of the August populations of grouse until the next August.

We tested the impact of predator indices on total grouse density with a time-lag of 18 months (predators late winter of year *t* and grouse August of year *t*+1) and with a time-lag of 6 months (predators and grouse the same calendar year). The level of significance was 0.05. We used bonferroni-corrected P-values in some tables (Rice 1989).

### 3. Results

#### 3.1. Spatial variation

##### 3.1.1. Grouse density

Total grouse density was highest in west Finland (Fig. 1): Capercaillie and Black Grouse densities were highest in western Finland, while Hazel Grouse density was highest in southern Finland (Fig. 2). Black Grouse and Hazel Grouse densi-

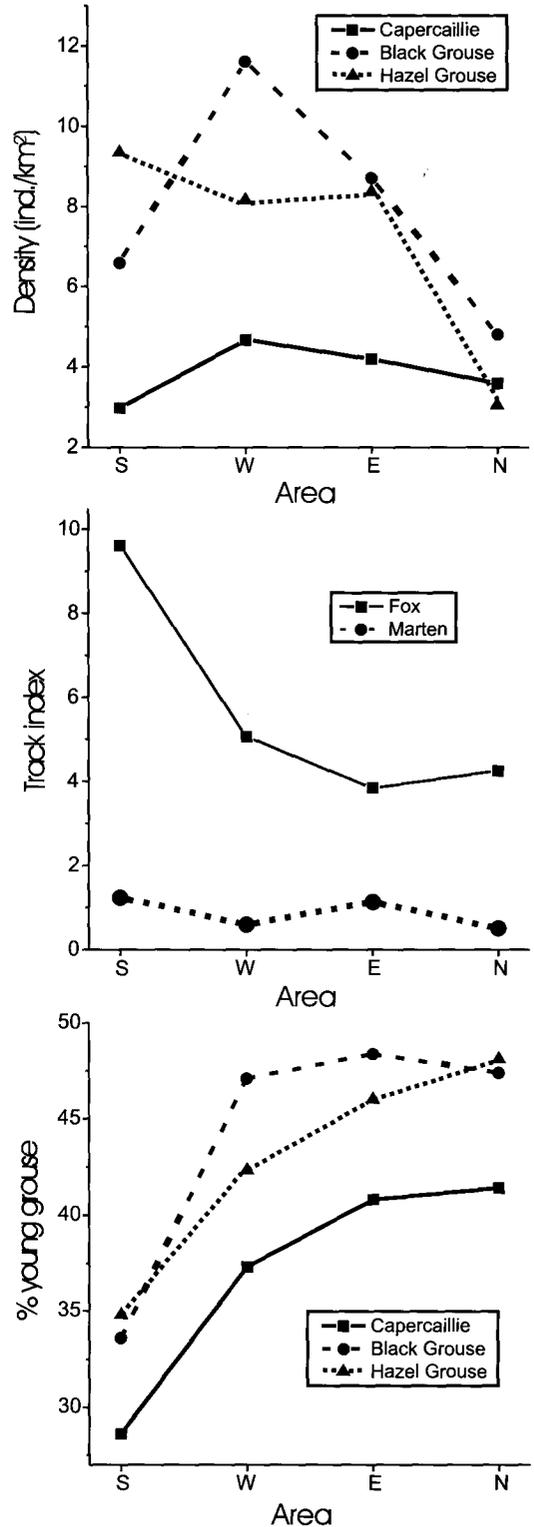


Fig. 2 (right). Density and breeding success (% young) of Capercaillie, Black Grouse and Hazel Grouse populations and fox and marten indices in different areas of Finland. S = southern Finland, W = western Finland, E = eastern Finland and N = northern Finland. Differences between areas were significant in all cases (ANOVA): Capercaillie density:  $F_{3,23} = 5.31$ ,  $P = 0.006$ ; Black Grouse density:  $F_{3,23} = 12.96$ ,  $P < 0.001$ ; Hazel Grouse density:  $F_{3,23} = 18.19$ ,  $P < 0.001$ ; Capercaillie breeding success:  $F_{3,23} = 15.58$ ,  $P < 0.001$ ; Black Grouse breeding success:  $F_{3,23} = 14.94$ ,  $P < 0.001$ ; Hazel Grouse breeding success:  $F_{3,23} = 15.38$ ,  $P < 0.001$ ; fox index:  $F_{3,23} = 14.22$ ,  $P < 0.001$ ; and marten index:  $F_{3,23} = 6.67$ ,  $P = 0.002$ .

ties correlated positively with each other and with total grouse density, while Capercaillie density did not correlate significantly with total grouse density, using the means of the 27 squares (Table 1). The total predator index was highest in southern Finland, the fox index being highest in southern Finland and decreasing towards the east and north, and the marten index being highest in southern and eastern Finland (Fig. 2). The fox index correlated better than the marten index with the total predator index. Grouse densities did not correlate significantly with the predator indices (Fig. 3 and Table 1).

### 3.1.2. Grouse reproductive success

Reproductive success (% young in August) of different grouse species correlated positively being lowest in southern Finland and highest in eastern and northern Finland (Figs. 1, 2, and Table 1). The mean fox and marten indices correlated negatively with the breeding success of all grouse species (Fig. 3 and Table 1). Density and breeding success of grouse did not correlate.

## 3.2. Temporal variation

### 3.2.1. Trends in grouse density and predator indices

There was a negative trend in grouse populations in 5 of 81 cases (3 grouse species  $\times$  27 squares), but the fox or marten index did not increase in any square (Table 2). The Hazel Grouse density increased in 3 squares in northern Finland (1 where the fox index decreased and 2 where the marten index decreased). Capercaillie or Black Grouse densities did not increase in any square, although the fox index decreased in 10 squares (areas 6, 8–14, 22 and 26) and the marten index in 6 squares (areas 1, 10, 14 and 25–27); the predator indices thus declined in 13 different squares. The change in the fox index varied between –38% and –62%, the mean being –48% (SD = 8.5), and that of the marten index between –63% and –83%, the mean being –73% (SD = 8.5).

### 3.2.2. Relationship between predator indices and grouse density

When grouse density in August (year  $t$ ) was regressed against log track indices of predators (in late winter of year  $t$ , i.e. about 6 months earlier) in each square, fox was included in 3 models as a significant variable (one in E Finland and 2 in N Finland) and marten in two models in northern Finland (Table 3). When the same analyses were done with a time-lag of 1.5 yr (predators winter of year  $t$ , grouse summer of year  $t+1$ ), only 3 models out of 81 were significant, a negative relationship existing between Hazel Grouse density and the marten index in squares 21 and 27, and between Black Grouse density and the marten index in square 27. The predator indices and grouse density did not show any significant relationship in southern or western Finland.

### 3.2.3. Relationship between predator indices and grouse breeding success

When the breeding success of grouse (% young in August of year  $t$ ) was regressed against log track indices of predators (in late winter of year  $t$ ), the fox index was included in 9 and the marten index in 4 models (Table 4). The marten index was included in some models of eastern and northern Finland (squares 21, 23, 25 and 27), and the fox index in those of mainly southern and western Finland. Altogether 12 (14.8%) models were significant with a negative relationship between grouse breeding success and a predator index.

### 3.2.4. Relationship between predator indices, grouse density and persistence

When the persistence of grouse (from August of year  $t$  to August of year  $t+1$ ) was regressed against the density of the grouse species concerned (August of year  $t$ ) and predator indices (late winter of year  $t$ ), grouse density was most often included in the models. The fox index was included only in 4 (5%) models of southern Finland and the marten index in 12 (15%) models. Grouse density was included in 58 (72%) models.

Table 1. Spatial correlations ( $r$ ) between the mean log grouse density, the breeding success of grouse (% young) and the mean log predator indices in different areas. Data are based on wildlife triangle counts from 1989 to 1999. C = Capercaillie, B = Black Grouse and H = Hazel Grouse.

	C dens.	B dens.	H dens.	Total dens.	C % young	B % young	H % young	Total % young	fox	marten	fox + marten
C dens.	1.00										
B dens.	0.52	1.00									
H dens.	0.06	0.66	1.00								
Total gr. dens.	0.43	0.93	0.88	1.00							
C % young	0.56	0.22	-0.41	-0.05	1.00						
B % young	0.57	0.30	-0.37	0.02	0.94	1.00					
H % young	0.45	0.10	-0.45	-0.15	0.94	0.87	1.00				
Total % young	0.55	0.22	-0.42	-0.06	0.99	0.97	0.96	1.00			
fox	-0.55	-0.04	0.35	0.11	-0.72	-0.74	-0.68	-0.74	1.00		
marten	-0.40	-0.09	0.54	0.19	-0.68	-0.69	-0.67	-0.70	0.42	1.00	
fox + marten	-0.57	-0.05	0.43	0.14	-0.78	-0.80	-0.74	-0.80	0.98	0.58	1.00

Matrix of Bonferroni-corrected probabilities:

	C dens.	B dens.	H dens.	Total dens.	C % young	B % young	H % young	Total % young	fox	marten	fox + marten
C dens.	0.000										
B dens.	0.345	0.000									
H dens.	1.000	0.011	0.000								
Total gr. dens.	1.000	0.000	0.000	0.000							
C % young	0.138	1.000	1.000	1.000	0.000						
B % young	0.113	1.000	1.000	1.000	0.000	0.000					
H % young	0.957	1.000	0.982	1.000	0.000	0.000	0.000				
Total % young	0.180	1.000	1.000	1.000	0.000	0.000	0.000	0.000			
fox	0.182	1.000	1.000	1.000	0.001	0.001	0.006	0.001	0.000		
marten	1.000	1.000	0.190	1.000	0.006	0.004	0.007	0.003	1.000	0.000	
fox + marten	0.100	1.000	1.000	1.000	0.000	0.000	0.001	0.000	0.000	0.080	0.000

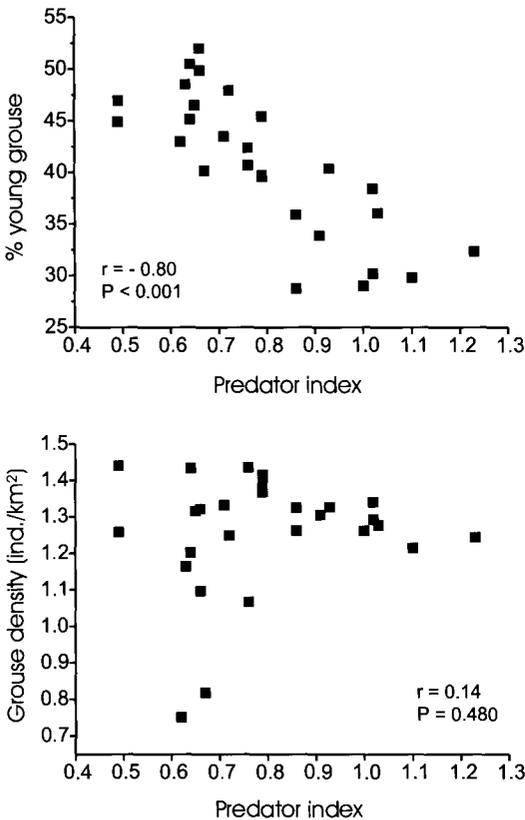


Fig. 3. Relationship between breeding success of grouse (% young grouse) and predator index, and between grouse density and predator index. The means for each square ( $n = 27$ ) were used in the analyses, data based on the wildlife triangle counts from August each year between 1989 and 1999.

### 3.2.5. Impact of breeding success and persistence on the growth rate of grouse populations

Persistence of grouse (component 1) explained most of the variation in the population growth rate when tested using stepwise regression analysis; persistence was the first variable included in the model in 94% of the cases, and the breeding success (component 2) in 6% of the cases.

### 3.2.6. Relationship between predator indices, grouse density and the growth rate of grouse populations

When the growth rate of grouse populations (from August of year  $t$  to August of year  $t+1$ )

was regressed against grouse density (August of year  $t$ ) and predator indices (year  $t$ ), grouse density was included in 61 (75.3%) models (Table 5). The fox index was included in 7 (8.6%) and the marten index in 14 (17.3%) models.

## 4. Discussion

### 4.1. Predator numbers and grouse breeding success

Breeding success of grouse correlated negatively with predator indices when spatial variation was tested. Also Kurki *et al.* (1997) found that fox and marten indices correlated negatively with grouse breeding success; predator indices were higher and grouse breeding success lower in southern Finland than in northern Finland. We must, however, be cautious when drawing conclusions from spatial correlations; the low breeding success of grouse in southern Finland may be due to other factors besides the abundance of predators. Fragmentation of forests and a low proportion of older forests may be among the causes; nest predation by generalist predators may be heavier in fragmented landscapes because of higher predator activity (Yahner & Mahan 1997). Habitat loss may also have reduced the quantity and quality of nesting and early brood-rearing habitat causing population declines (Connelly & Braun 1997). Differences in habitats and in predator numbers may thus both be responsible for the spatial differences in the breeding success of grouse.

Also the abundance of the fox explained some of the temporal variation in the breeding success of grouse in southern and western Finland: fox numbers are higher and edge-related nest predation by the fox may be heavier in more fragmented landscapes of southern and western Finland than in forested landscapes in eastern and northern Finland (Huhta *et al.* 1998). Predator removal experiments also suggest that foxes and martens have an impact on grouse breeding success (Marcström *et al.* 1988, Côté & Sutherland 1997, Kauhala *et al.* 2000).

Table 2. Trends in grouse populations in relation to fox and marten trends in different areas (27 squares) of Finland. Squares with a significant trend in any grouse population are included. Data are based on wildlife triangle counts from 1989 to 1999. Trends were tested by regressing the density against time. 0 = no trend, – = decreasing. Neither the fox nor the marten index increased in any square.

Dependent variable: log Capercaillie density

Independent variable: year

Area	t	r <sup>2</sup>	F <sub>1,9</sub>	P	fox	marten
Square16	-2.49	0.41	6.22	0.034	0	0
Square19	-2.68	0.44	7.16	0.025	0	0
Square24	-2.87	0.48	8.23	0.019	0	0

Dependent variable: log Black Grouse density

Independent variable: year

Area	t	r <sup>2</sup>	F <sub>1,9</sub>	P	fox	marten
Square1	-3.55	0.58	12.63	0.006	0	–
Square26	-2.88	0.48	8.28	0.018	–	–

Dependent variable: log Hazel Grouse density

Independent variable: year

Area	t	r <sup>2</sup>	F <sub>1,9</sub>	P	fox	marten
Square22	3.19	0.56	10.20	0.013	–	0
Square25	2.82	0.47	7.93	0.020	0	–
Square27	2.33	0.40	5.43	0.048	0	–

Table 3a. Relationship between predator indices (late winter of year *t*) and the density of different grouse species (August of year *t*), data based on wildlife triangle counts from 1989 to 1999. Independent variables with  $P < 0.05$  were included in the models. All independent variables had a negative relationship with grouse density.

Area	r <sup>2</sup>	F <sub>1,8</sub>	P	Dep. variable	Indep. variables
E Finland: Squares21	0.45	6.56	0.034	Hazel Grouse	fox
N Finland: Square23	0.47	8.02	0.020	Capercaillie	marten
	0.37	5.33	0.046	Hazel Grouse	fox
Square24	0.38	5.60	0.042	Hazel Grouse	fox
Square27	0.66	15.62	0.004	Hazel Grouse	marten

Table 3b. Relationship between predator indices (late winter of year *t*) and the density of different grouse species (August of year *t*+1), data as above.

Area	r <sup>2</sup>	F <sub>1,7</sub>	P	Dep. variable	Indep. variables
Square21	0.71	16.86	0.005	Hazel Grouse	marten
Square27	0.68	14.77	0.006	Black Grouse	marten
	0.71	16.96	0.004	Hazel Grouse	marten

#### 4.2. Persistence and growth rate of grouse populations

Grouse density was strongly and negatively connected with the yearly persistence of grouse (from August to next August), predator numbers being of minor importance. Also Marcström *et al.* (1988) found that high grouse breeding success in one summer (and thus high population density in autumn) was associated with low counts of adult grouse the next year, and Robertson and Hudson (1997) reported that losses of Red Grouse (*Lagopus lagopus scoticus*) were highest in years when population density was high.

Persistence of grouse was associated more strongly than the breeding success with the growth rate of grouse populations. Caizergues and Ellison (1997) also found that population growth of Black Grouse is influenced more by adult survival than by reproductive success. Spidsø *et al.* (1997) found that predation was the most important cause of mortality in a Black Grouse population in Norway, mortality rate being highest during winter, and the Goshawk (*Accipiter gentilis*) being responsible for most deaths. Thus, although numbers of foxes and martens were negatively connected with

grouse breeding success, their effect on the growth rate of grouse populations may be of minor importance. Macdonald *et al.* (1999) found that predation was a significant threatening factor for (grouse) populations only when it occurred at a high and constant rate and affected all age classes. Chick predation alone does not usually threaten grouse populations, because many animals, including foxes and grouse, have adapted to high juvenile mortality.

Grouse populations were rather stable during the study period and were probably density-dependent, significant trends existing in only a few cases (Table 2). The lack of suitable habitats or food, functional response of predators (including man), diseases or parasites may be responsible for the density-dependence of grouse populations. Mortality caused by hunting may also be important; more grouse are probably hunted in years with high numbers of grouse in August than in years with low numbers. Modelling of Finnish grouse population dynamics by a stage-structured population model with delayed density dependence yielded a good fit (e.g. Lindström 1996), but the data used originated from the period 1964–84 when grouse populations were cyclic. The cyclicity is not evident in the present

Table 4. Relationship between predator indices (late winter of year  $t$ ) and the breeding success of different grouse species (August of year  $t$ ), data based on wildlife triangle counts from 1989 to 1999. Independent variables with  $P < 0.05$  were included in the models. All independent variables had a negative relationship with grouse breeding success.

Area	$r^2$	$F_{1,9}$	P	Dep. variable	Indep. variables
S Finland:					
Square3	0.50	9.29	0.014	Black Grouse	fox
Square4	0.43	6.91	0.027	Capercaillie	fox
Square8	0.38	5.50	0.044	Hazel Grouse	fox
W Finland:					
Square11	0.49	8.79	0.016	Capercaillie	fox
Square12	0.75	26.8	0.001	Capercaillie	fox
	0.44	7.02	0.026	Black Grouse	fox
Square19	0.43	6.74	0.029	Black Grouse	fox
E Finland:					
Square20	0.45	7.23	0.025	Capercaillie	fox
Square21	0.54	9.46	0.015	Black Grouse	marten
N Finland:					
Square23	0.64	15.8	0.003	Capercaillie	marten
Square25	0.41	6.12	0.035	Hazel Grouse	marten
Square27	0.64	13.89	0.006	Hazel Grouse	fox + marten

data, however, and density fluctuations seem to be less pronounced and erratic. Furthermore, Smith and Willebrand (1999) found that hunting mortality in Willow Grouse (*Lagopus lagopus lagopus*) was mostly additive to natural mortality.

### 4.3. Grouse density

Although fox numbers declined in 10 areas and marten in 6 during the study, grouse populations in these areas did not increase, excluding 3 areas

in northern Finland where Hazel Grouse populations increased. Predator abundance is thus not a key factor affecting grouse density in Finland, probably with the exception of Hazel Grouse populations in northern Finland. In southern and western Finland the connection between predator numbers and grouse density was minimal (Tables 2 and 3). In Sweden and Norway, however, grouse numbers increased when fox numbers declined because of sarcoptic mange infestation (Lindström *et al.* 1994, Selås 1998). On the other hand, Small *et al.* (1993) found that grouse indices started to

Table 5. Growth rate of grouse populations (from year  $t$  to year  $t+1$ ) was regressed against predator indices (late winter of year  $t$ ) and the density of the grouse species concerned (August of year  $t$ ), data based on wildlife triangle counts from 1989 to 1999. Independent variables with  $P < 0.05$  were included in the models. All independent variables had a negative relationship with the growth rate of grouse populations.

Area	Independent variables included in the models		
	Capercaillie	Black Grouse	Hazel Grouse
S Finland:			
Square1	–	density	–
Square2	density + fox	–	–
Square3	density	marten	–
Square4	density	density	density + marten
Square5	–	density	density + fox
Square6	density	density	density
Square7	density	density	density
Square8	density	density + fox	density
W Finland:			
Square10	–	density	density + fox
Square11	density	density	density + fox
Square12	density	–	–
Square15	density	density	density
Square16	density	density	density
Square19	density + marten	density + marten	density + marten
E Finland:			
Square9	density	density + marten	density
Square13	density + marten	density + marten	density + marten
Square14	density	density + fox	density + marten
Square17	density	density	density
Square18	density	density	density
Square20	density + marten	density	density + marten
Square21	density	density + marten	density + marten
N Finland:			
Square22	density	density	–
Square23	density	density	density
Square24	–	–	density
Square25	density + fox	–	density
Square26	–	–	density
Square27	–	–	–

increase sharply in Sweden — in synchrony with fox numbers — two years before the crash in fox numbers. In Germany, the decline of Capercaillie populations has been connected to the decline of the abundance of bilberry (*Vaccinium myrtillus*), which is essential to Capercaillie for food and cover (Klaus *et al.* 1997). In Finland also the abundance of bilberry has declined since the 1950s because the average age of forests is younger than in the 1950s (Reinikainen *et al.* 2000).

In the predator removal experiment in Finland we also found that the density of adult grouse did not increase in the predator removal areas, although grouse breeding success increased (Kauhala *et al.* 2000). Also Côté and Sutherland (1997) found that predator removal had a positive effect on the breeding success and post-breeding (autumn) size of bird populations, while the effect of predator removal on the size of breeding bird populations was not evident. The Swedish experiment showed, however, that the density of adult Capercaillie and Black Grouse increased after two years of predator removal, but the results were not very clear and the authors concluded that more research is needed (Marcström *et al.* 1988).

#### 4.4. Conclusions

The abundance of mammalian predators and grouse density are not strongly linked in Finland; especially in southern and western Finland the association between predator abundance and yearly grouse density is minimal, although predator abundance is negatively connected with grouse breeding success. In northern Finland, predator numbers may, however, affect Hazel Grouse density. The growth rate of grouse populations is more strongly related to what happens to the birds after August than by the breeding success of grouse. This means that other factors than the abundance of predators, including forest fragmentation and decline in bilberry abundance, probably are responsible for the low population densities of grouse in southern Finland. The functional response of predators, including hunters and avian predators, may also affect yearly grouse densities. Predation pressure may thus be involved, but the *abundance* of mammalian predators does not play a key role in determining grouse density in the long term.

*Acknowledgements.* We are grateful to all those volunteers who have participated in wildlife triangle counts and two anonymous referees for constructive comments on the manuscript.

### Selostus: Petojen runsauden vaikutus kanalintukantoihin Suomessa — riistakolmioaineistoon perustuva tutkimus

Kanalintujen (metso, teeri ja pyy) ja pienpetojen (kettu ja näätä) runsauden välistä suhdetta tutkittiin Suomessa riistakolmioaineiston perusteella vuosina 1989–1999. Alueellisesti tarkasteltuna petoindeksien ja kanalintujen lisääntymismenestyksen välillä oli negatiivinen korrelaatio, mutta petoindeksien ja kanalintujen tiheyden välillä ei ollut korrelaatiota. Kun tarkasteltiin ajallista vaihtelua, kettuindeksin ja kanalintujen lisääntymismenestyksen välillä oli negatiivinen suhde joillakin alueilla Etelä- ja Länsi-Suomessa. Näätäindeksi ja kanalintujen lisääntymismenestys korreloivat negatiivisesti joillakin alueilla Itä- ja Pohjois-Suomessa. Petoindeksien ja kanalintutiheyden välillä oli negatiivinen suhde vain neljällä alueella 27:stä, kaikki alueet olivat Itä- tai Pohjois-Suomessa. Kanalintukantojen tiheys vaikutti enemmän kuin petojen runsaus kanalintukantojen kasvukertoimeen; petotiheydellä oli siten vain vähäinen merkitys kanalintukantojen kehitykselle.

#### References

- Brittas, R. & Karlbom, M. 1990: A field evaluation of the Finnish 3-men chain: a method for estimating forest grouse numbers and habitat use. — *Ornis Fennica* 67:18–23.
- Caizergues, A. & Ellison, L. N. 1997: Survival of black grouse *Tetrao tetrix* in the French Alps. — *Wildlife Biology* 3: 177–186.
- Connelly, J. W. & Braun C. E. 1997: Long-term changes in sage grouse *Centrocercus urophasianus* populations in Western North America. — *Wildlife Biology* 3: 229–234.
- Côté, I. M. & Sutherland, W. J. 1997: The effectiveness of removing predators to protect bird populations. — *Conservation Biology* 11: 395–405.
- Cotter, R. C., Boag, D. A. & Shank, C. C. 1992: Raptor predation on rock ptarmigan (*Lagopus mutus*) in the central Canadian Arctic. — *Journal of Raptor Research* 26: 146–151.

- Helle, P. & Lindström, J. 1991: Censusing tetraonids by the Finnish wildlife triangle methods: principles and some applications. — *Ornis Fennica* 68: 148–157.
- Henttonen, H. 1989: Does an increase in the rodent and predator densities, resulting from modern forestry, contribute to the long-term decline in Finnish tetraonids? — *Suomen Riista* 35: 83–90.
- Huhta, E., Jokimäki, J. & Helle, P. 1998: Predation on artificial nests in a forest dominated landscape — the effects of nest type, patch size and edge structure. — *Ecography* 21: 464–471.
- Kauhala, K. & Helle, P. 2000: The interactions of predator and hare populations in Finland — a study based on wildlife monitoring counts. — *Annales Zoologici Fennici* 37: 151–160.
- Kauhala, K., Helle, P. & Helle, E. 2000: Predator control and the density and reproductive success of grouse populations in Finland. — *Ecography* 23: 161–168.
- Klaus, S., Berger, D. & Huhn, J. 1997: Capercaillie *Tetrao urogallus* decline and emissions from the iron industry. — *Wildlife Biology* 3: 131–136.
- Koenig, W.D. 1999: Spatial autocorrelation of ecological phenomena. — *Trends in Ecology and Evolution* 14: 22–26.
- Kurki, S., Helle, P., Lindén, H. & Nikula, A. 1997: Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. — *Oikos* 79: 301–310.
- Kurki, S., Nikula, A., Helle, P. & Lindén, H. 2000: Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. — *Ecology* 81: 1985–1997.
- Lindén, H., Helle, E., Helle, P. & Wikman, M. 1996: Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. — *Finnish Game Research* 49: 4–11.
- Lindström, J. 1996: Modelling grouse population dynamics. — Ph.D. thesis, Department of Ecology and Systematics, University of Helsinki, Helsinki. 142 pp.
- Lindström, E. R., Andrén, H., Angelstam, P., Cederlund, G., Hörmfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. — *Ecology* 75: 1042–1049.
- Macdonald, D. W., Mace, G. M. & Barretto, G. R. 1999: The effects of predators on fragmented prey populations: A case study for the conservation of endangered prey. — *Journal of Zoology (London)* 247: 487–506.
- Marcström, V., Kenward, R. E. & Engren, E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. — *Journal of Animal Ecology* 57: 859–872.
- Ranta, E., Kaitala, V. & Lindström, J. 1999: Spatially autocorrelated disturbances and patterns in population synchrony. — Royal Society of London. Proceedings. *Biological Sciences* 266: 1851–1856.
- Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.) 2000: Kasvit muuttuvassa metsäluonnossa. (Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950.) — Tammi, Helsinki. 384 pp.
- Rice, W. R. 1989: Analyzing tables of statistical tests. — *Evolution* 43: 223–225.
- Robertson, P. A. & Hudson, P. J. 1997: Patterns of density dependence within and between populations of red grouse *Lagopus lagopus scoticus* in Britain. — *Wildlife Biology* 3: 292.
- Selås, V. 1998: Does food competition from red fox (*Vulpes vulpes*) influence the breeding density of goshawk (*Accipiter gentilis*)? Evidence from a natural experiment. — *Journal of Zoology (London)* 246: 325–335.
- Small, R. J., Marcström, V. & Willebrand, T. 1993: Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. — *Ecography* 16: 360–364.
- Smedshaug, C. A., Selås, V., Lund, S. E. & Sonerud, G. A. 1999: The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. — *Wildlife Biology* 5: 157–166.
- Smith, A. & Willebrand, T. 1999: Mortality causes and survival rates of hunted and un hunted willow grouse. — *Journal of Wildlife Management* 63: 722–730.
- Spidsø, T. K., Hjeljord, O. & Dokk, J. G. 1997: Seasonal mortality of black grouse *Tetrao tetrix* during a year with little snow. — *Wildlife Biology* 3: 205–209.
- Storch, I. (ed.) 2000: Grouse Status Survey and Conservation Action Plan 2000–2004. — WPA/BirdLife/SSC Grouse Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK and the World Pheasant Association, Reading, UK. 112 pp.
- Willebrand, T. 1988: Demography and ecology of a black grouse (*Tetrao tetrix* L.) population. — Dissertation, Uppsala University, Uppsala, Sweden. 44 pp.
- Yahner, R. H. & Mahan, C. G. 1997: Effects of logging roads on depredation of artificial ground nests in a forested landscape. — *Wildlife Society Bulletin* 25: 158–162.