THE IMPACT OF PREDATION ON BOREAL TETRAONIDS DURING VOLE CYCLES: AN EXPERIMENTAL STUDY

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SUMMARY

(1) Predators were removed in an experiment to study the impact of mammal predation on woodland tetraonid populations during vole cycles. Foxes and martens were killed from 1976 to 1980 on one of two similar islands in the northern Baltic. The treatment was then reversed until 1984.

(2) When predators were killed, tetraonid brood sizes averaged 5.52 in August, and 77% of hens had chicks. When predator were not killed, broods averaged 3.29 chicks and 59% of hens had chicks.

(3) Counts of adult capercaillie and black grouse during July and August increased by 56–80% after 2 years of predator removal. Counts at leks increased by 166–174%.

(4) Removing foxes and martens had no significant effect on vole abundance during two 4-year cycles.

(5) When predators were not removed, tetraonid brood sizes and the proportion of females that bred successfully were each positively correlated with vole abundance in summer. There were most chicks per adult hen when vole numbers were high and increasing slowly from summer to autumn. When foxes and martens were killed, neither brood size nor subsequent adult numbers were significantly correlated with vole abundance in summer, although losses of whole broods increased slightly when vole numbers grew most rapidly from summer to autumn. We conclude that large vole populations resulted in large autumn grouse populations mainly because they reduced predation on breeding grouse.

(6) The vole numbers and increase rates that were associated with high grouse breeding success in one summer were also associated with low counts of adult grouse the next year, and thus with an increase in grouse losses from one summer to the next.

INTRODUCTION

Associations or correlations have often been reported between numbers of small mammals, autumn bags of shot grouse, and predator abundance in Scandinavia (Hagen 1952; Myrberget 1970, 1984; Hörnfeldt 1978; Marcström & Höglund 1980; Haukioja et al. 1983; Angelstam, Lindström & Widén 1984; Hörnfeldt, Löfgren & Carlsson 1986), with similar records for hares (Lepus americanus) and predators in North America (Keith 1963, 1974). Two hypotheses to explain the herbivore population synchrony are that there is cyclic variation in quantity or quality of food plants (Svärdsön 1957; Sivonen 1957; Kalela 1962) or shifts in predation pressure (Cabot 1912; Hagen 1952; Lack 1954).
Predation on tetraonids

There is evidence that predatory mammals can reduce the breeding success of birds (reviewed by Sih et al. 1985; Potts 1986), and some mammals increase their predation on birds when their main mammal prey become scarce (e.g. Maclean, Fitzgerald & Pitelka 1974; Dunn 1977; Tapper 1979). However, there is little to show that mammals can depress autumn populations of tetraonids, or breeding populations of any bird species. On the contrary, most studies support the view that bird populations are limited by food (Newton 1980).

This paper describes a 9-year study of tetraonid populations on two similar islands in northern Sweden. Experimental removal of foxes (Vulpes vulpes L.) and martens (Martes martes L.) showed that their predation not only reduced tetraonid breeding success, but also reduced the number of adult tetraonids and was mainly responsible for synchronizing tetraonid productivity with vole abundance. A similar impact of fox and marten predation on hares (Lepus timidus L.) is reported in a second paper (Marström et al. 1988).

STUDY AREA

The study islands were Bergön (18.0 km²) and Rånön (23.5 km²), at 66°N in the northern Gulf of Bothnia, which lay 3–4 km from the mainland and a similar distance apart. Both islands were almost entirely covered by forest, primarily pine (Pinus silvestris L.) and spruce (Picea abies Karst). Less than 10% of the trees were birch (Betula pubescens Ehrh., B. pendula Roth.), or other deciduous trees (Alnus incana Moench, Salix phylicifolia L., Salix pentandra L.) which occurred primarily as a narrow zone along the coast (Elveland 1970). The habitat resembled that used by tetraonids in much of northern Sweden, but included a higher proportion of mature trees. Both islands lacked roads, but had a few summer houses.

METHODS

Predator removal

The main tetraonid predators on these islands were foxes and martens. These were killed on Bergön from 1976 to spring 1980. They were then allowed to recolonize that island across the sea-ice, which lasted from December to May, and were removed from Rånön from autumn 1980 until spring 1984. The sea-ice let predators reach the removal island, so that trapping was necessary each winter, but also permitted emigration from the other island, as would occur at a mainland site.

While the sea-ice was solid, snow-scooters were used to visit both islands almost every day, and to check the snow surface for tracks of foxes or martens. Most immigrants were killed within a few weeks, although a few left the island again. Martens were caught in carrion-baited box traps, or shot after they had been driven from lairs. Foxes were usually taken with spring-loaded foot snares (Nordic Sport Ab, S-93100 Skellefteå) hidden under the snow (von Schantz 1979; Englund 1982), or shot when snow crusting made snaring impossible.

No foxes bred on the island where they were killed, but it was seldom possible to remove them completely. One or two remained there most summers. In contrast, two to three fox litters were reared each year on the other island, including the spring following treatment reversal. Although we could not count foxes in summer, we checked their numbers at the first snowfall, usually before there was enough sea-ice for foxes to leave the islands. After
TABLE 1. The numbers of foxes and martens present in winter or killed on Rånön and Bergön in each phase of the study

<table>
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<tr>
<td>Present on Rånön</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Foxes</td>
<td>7–8</td>
<td>11</td>
<td>14</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>Martens</td>
<td>2–3</td>
<td>4</td>
<td>4</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Removed from Bergön</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foxes</td>
<td>3</td>
<td>12</td>
<td>12</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>Martens</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
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<td>Phase 2</td>
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<tr>
<td>Present on Bergön</td>
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<tr>
<td>Foxes</td>
<td>7</td>
<td>7–8</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Martens</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
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<tr>
<td>Removed from Rånön</td>
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<tr>
<td>Foxes</td>
<td>11</td>
<td>10</td>
<td>6</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Martens</td>
<td>5</td>
<td>2</td>
<td>2</td>
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1976, the island without predator removal always had nine to twenty foxes at the first snowfall.

Foxes could be counted fairly easily in winter, because they were reluctant to cross fresh ski tracks on the islands. After a snowfall, a third of the island was marked off by a ski-track, and next day all fox tracks in that area were followed until the foxes were found. The rest of the island was examined in the next 2 days. These counts showed that seven or eight foxes were on Rånön in the winter of 1976, and ten to fourteen from 1977 to 1980. Only three foxes could be killed on Bergön in 1976 (possibly because they had been shot for sport on both islands into the 1975 winter), but eleven to seventeen were removed annually from 1977 to 1980 (Table 1). Similarly, three to eight foxes were present each winter from 1981 to 1984 on Bergön, and six to eleven were killed on Rånön.

No martens bred on the experimental island, although one trap-shy adult survived there through the summer of 1978. Winter counts, by following tracks to lairs after a fresh snowfall, showed that two to six martens wintered on the island with no predator removal, and up to five were killed on the experimental island.

It was impractical to remove other predators. These were present on both islands, but generally in low numbers. Mink (*Mustela vison* L.) occurred infrequently along the shoreline. Stoat (*Mustela erminea* L.) numbers were low and variable: their tracks became most common in the 1978–79 and 1981–82 winters, when small mammals were abundant or declining after a peak. There were a few crows (*Corvus cornix* L.) and ravens (*C. corax* L.), as potential egg predators, but only the jay (*Garrulus glandarius* L.) was relatively common. The goshawk (*Accipiter gentilis* L.) is an important predator of both adult tetraonids and chicks in Fennoscandia (Höglund 1964; Sulkava 1964; Lindén & Wikman 1983; Widén 1985), but did not breed on the islands, and few raptor kills were found.

**Tetraonids**

Both islands contained populations of capercaillie (*Tetrao urogallus* L.), black grouse (*Tetrao tetrix* L.), hazel grouse (*Bonasa bonasia* L.) and willow grouse (*Lagopus lagopus* L.). Tetraonid numbers and brood sizes were assessed when chicks were 2–8 weeks old, when chicks could fly if disturbed but before the broods started to break up. The main technique was the Finnish three-man-chain (Rajala 1962, 1974), in which three people...
walk in line abreast, 20 m apart. Each person records all birds rising within 10 m on either side, and the chain thus covers a 60-m strip.

One count was made on each island in August 1976. Subsequently, there was one count in July and another in August, except that the August count had to be abandoned in 1980 because weather conditions were unfavourable and broods had already split up. The two islands were surveyed within the same week, using marked routes which traversed them at 400-m intervals. Counts therefore covered 15% of each island.

Adults of each species could almost always be sexed when flushed. Hazel grouse were the exception because cocks and hens are similar, and counts of hazel grouse were generally unreliable because some well-grown young were mistaken for adults. To increase the number of brood records, dogs were used to find broods on both islands from 1978 onwards. A dog-handler was sent to a separate part of each island immediately after the August chain counts, and avoided recounting broods by working in one direction through each area.

Between 23 April and 24 May each year, capercaillie and black grouse leks were watched by at least two people for seven to eight mornings on each island, to determine the maximum number of displaying cocks and to count all the hens that visited. The observations coincided with the peak of display activity.

Small mammals

The dominant small mammals were Clethrionomys glareolus Schreb. and Sorex araneus L., with smaller numbers of Microtus agrestis L. and Microtus oeconomus L. To assess their abundance, twenty groups of five snap traps were set systematically at similar marked sites on each island, for 7 days at a time. One session of 1400 trap-days was mainly in June, to give an index of small mammal numbers while tetraonids were hatching, followed by a second session mainly in August, to assess the increase in shrew and vole numbers while chicks were reared. The trap sites were the same throughout the study, with half on relatively dry ground and half in damp habitats.

RESULTS

Breeding success

Broods of the different tetraonid species were generally similar in size within each island, except that willow grouse had significantly more young than one or more of the other species on Bergøn in 1980 and 1981 and on Rånøn in 1983 (Mann–Whitney U-tests, \( P < 0.05 \)).

In 1976, three-man-chains found only three broods on Rånøn and seven on Bergøn, with no young willow grouse on either island (Fig. 1). Broods on Bergøn, where foxes and martens were killed, were significantly larger than on Rånøn only if data from capercaillie, black grouse and hazel grouse were pooled (Mann–Whitney U-test, \( P < 0.05 \)). Very few broods were found on either island in 1977, probably because there had been frequent falls of sleet and rain during the hatching period.

From 1978 onwards, three-man-chains counted an average of 0.4 young per brood fewer than the dog handlers, probably because dogs found some young that did not flush from chains. The difference was significant for black grouse on Rånøn in 1980 (Mann–Whitney U-test, \( P = 0.0202 \)) and 1981 (\( P = 0.0023 \)). During 1978–84, testing for inter-island differences in brood size was based on broods recorded with dogs.
Broods were significantly larger \((P < 0.05)\) on the island with predator removal in 6 of the 9 study years for capercaillie, in 6 years for black grouse, in 5 years for hazel grouse and in 2 years for willow grouse. When probabilities for each species were combined (Fisher 1954), the difference was significant at the 1% level in 1978, 1979 and 1984, and at the 0.1% level for 1980–83 (Fig. 1). On average, broods contained 68% more young (5.52, S.D. = 0.11, \(n = 378\)) where foxes and martens had been killed than on the control island (3.29, S.D. = 0.11, \(n = 314\)).

The proportion of females with broods was also higher in 8 out of 9 years on the island with predator removal (Wilcoxon matched-pair test, one-tailed \(P = 0.008\)). The proportion of hens with broods did not differ significantly between species, averaging 77% in August when there was predator removal and 59% when there was none; thus, 31% more hens had broods when foxes and martens were killed.

The overall effect of predation on tetraonid productivity could be estimated by combining the data on brood size with those on hens with broods: productivity was 4.25 young per hen when predators were removed, 2.2 times higher than the 1.94 young per hen when there was no predator removal.

**Adult populations**

There were considerable fluctuations in the adult tetraonid numbers counted by threeman-chains (Fig. 2) and at leks (Fig. 3). The July count on Rånön was especially low in 1982 (Fig. 2a) because hot weather made the birds reluctant to fly: only one willow grouse
Predation on tetraonids

was counted, and no hazel grouse at all, compared with eight and seven, respectively, in August. In July 1983 the count on Bergón was inflated by a large flock of male black grouse which had formed unusually early. A black grouse lek formed on the ice between the two islands in 1981. The count at this lek was attributed to the nearest island, resulting in a very high count for Ránön that year (Fig. 3b), but some birds may also have come from the other island. Cock black grouse were also unusually abundant on Ránön that July (Fig. 2).

Nevertheless, the trend in all counts on Bergón was positive relative to counts on Ránön in 1976–80, while foxes and martens were killed on Bergón. This was at least partly because of a fall in numbers on Ránön (Figs 1b, 2a), perhaps as a result of an increase in numbers of predators there (Table 1). When the predators were killed on Ránön, from late 1980 to 1984, it was the Ránön population which showed a clear relative gain in all counts except those from three-man-chains in July.

The significance of the changes could be tested by comparing counts on the two islands in 1976–77 (the first 2 years of the study), in 1979–80 (the last 2 years of predator removal on Bergón) and in 1983–84 (the last 2 years of predator removal on Ránön). Since lek

FIG. 2. The numbers of adult tetraonids counted by three-man chains on Ránön (●—○) and Bergón (□—■) in July (a) and August (b). Predator removal, shown by open symbols, was on Bergón in 1976–80 (□) and on Ránön in 1980–84 (○).
counts were not statistically independent between years, probabilities were estimated (Fisher exact tests) for each possible combination of years (e.g. 1976 vs. 1979, 1976 vs. 1980, 1977 vs. 1979, 1977 vs. 1980) and expressed as a geometric mean. On this basis, lek counts of hen capercaillie increased significantly on Bergön relative to Rånön when foxes and martens were killed on Bergön (one-tailed $P=0.030$), and on Rånön relative to Bergön after treatment reversal ($P=0.009$), with similar, but not significant, changes for cocks ($P=0.116$, $P=0.097$). The changes for black grouse were more significant for cocks ($P=0.048$, $P<0.001$) than for the relatively small counts of hens ($P=0.517$, $P=0.018$).

Counts of individual species by three-man-chains were too low to show significant changes in exact probability tests. However, the consecutive chain counts were reasonably independent samples from each island population, because the 60-m chain 'width' was small compared with the 800–2200 m summer range diameters of black grouse and capercaillie in northern Sweden (T. Willebrand, unpublished data; R. Brittas, unpun-
lished data), and the numbers counted on each of 301 July transects explained only 15% of the variance in counts on the same transects in August. On this basis, each count gave a virtually independent density estimate for the local population: the difference in density on the two islands could be compared for three counts in 1976–77, three in 1979–80 and four in 1983–84. From 1976–77 to 1979–80, the density increase on Bergön relative to Råön approached significance for capercaillie (Mann–Whitney U-test, one-tailed \( P = 0.063 \)) and black grouse (\( P = 0.063 \)), and was significant at the 5% level if probability values for all four species were combined (Fisher 1954). Capercaillie and black grouse densities on Bergön doubled during this period, from 0.9 to 1.7 km\(^{-2} \) and from 1.5 to 3.0 km\(^{-2} \), respectively, but declined on Råön from 2.0 to 1.5 and from 2.6 to 2.1 km\(^{-2} \), a 19–25% decrease.

From 1979–80 to 1983–74, the relative increase in density on Råön approached significance for willow grouse (\( P = 0.054 \)), and for black grouse if the July count for 1983 was omitted (\( P = 0.063 \)), in which case the combined probabilities were significant at the 5% level. Once again, capercaillie and black grouse densities doubled when predators were removed, from 1.5 to 3.3 and from 2.1 to 4.8 birds km\(^{-2} \). However, their densities also increased somewhat on Bergön, from 1.7 to 2.4 and from 3.0 to 3.8 birds km\(^{-2} \), so the relative improvement was only 56% for capercaillie and 80% for black grouse. This compared with changes of 174% and 166%, respectively, in counts at leks.

**Tetraonid breeding and small mammal numbers**

Predator removal had no detectable effect on vole or shrew numbers in the June or the August trap sessions, or on their growth in numbers between the sessions (combined probabilities from Wilcoxon matched-pair tests, one-tailed \( P > 0.1 \)). Fewer shrews than voles were trapped throughout the study, with no relationships between shrew numbers and any tetraonid variables. Analyses were therefore based on vole numbers alone. Since vole numbers fluctuated synchronously on both islands, sample sizes were increased by combining data from both islands. There were two maxima and minima in vole numbers between 1975 and 1984, at 4-year intervals (Fig. 4). Confidence limits are over-estimates.
because they could only be calculated for variation between consecutive days, and therefore include a fall in local populations as voles died in the snap traps.

When no predators were removed, there was a strong positive correlation \( (r^2 = 0.891, P < 0.002) \) between vole abundance in June and the mean tetraonid brood size (Fig. 5). The relationship was similar during both vole cycles on both islands, and for each


Predation on tetraonids

Table 2. Simple and partial correlations between tetraonid breeding success and vole population indices, with and without the killing of foxes and martens

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<th>Predators preserved</th>
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<th>Predators killed</th>
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<tr>
<td></td>
<td>Simple r</td>
<td>Partial r</td>
<td>Simple r</td>
<td>Partial r</td>
</tr>
<tr>
<td>Brood size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>with vole numbers (1)</td>
<td>0.890**1</td>
<td>0.775*1</td>
<td>0.157</td>
<td>0.092</td>
</tr>
<tr>
<td>Brood size</td>
<td>0.707*</td>
<td></td>
<td>-0.197</td>
<td></td>
</tr>
<tr>
<td>with vole increase (2)</td>
<td>(constant 2)</td>
<td>(constant 1)</td>
<td>(constant 2)</td>
<td>(constant 1)</td>
</tr>
<tr>
<td>% of hens with broods</td>
<td>0.644</td>
<td>0.736*</td>
<td>-0.299</td>
<td>0.768*</td>
</tr>
<tr>
<td>with vole numbers (1)</td>
<td>(constant 2)</td>
<td>(constant 2)</td>
<td>(constant 2)</td>
<td>(constant 1)</td>
</tr>
<tr>
<td>% of hens with broods</td>
<td>0.324</td>
<td>-0.548</td>
<td>-0.697*</td>
<td>-0.877**1</td>
</tr>
<tr>
<td>with vole increase (2)</td>
<td>(constant 1)</td>
<td></td>
<td>(constant 1)</td>
<td></td>
</tr>
<tr>
<td>Young per hen</td>
<td>0.789*1</td>
<td>0.812*1</td>
<td>0.017</td>
<td>0.434</td>
</tr>
<tr>
<td>with vole numbers (1)</td>
<td>(constant 2)</td>
<td>(constant 2)</td>
<td>(constant 2)</td>
<td>(constant 1)</td>
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<tr>
<td>Young per hen</td>
<td>0.487</td>
<td>-0.559</td>
<td>-0.243</td>
<td>-0.486</td>
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<tr>
<td>with vole increase (2)</td>
<td>(constant 1)</td>
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* P < 0.05, ** P < 0.02, *** P < 0.01, **** P < 0.005.

tetraonid species. On average, broods contained 2.8 young at the two vole population minima, and about one chick more at the vole peaks. There was a weak correlation between brood size and the vole population growth from June to August, but this relationship vanished if vole abundance in June was also taken into account (Table 2). There was no correlation between brood size and vole abundance or vole population growth when foxes and martens were killed.

When no predators were killed, the proportion of females with broods increased with vole abundance in June, although the correlation was significant only if subsequent vole population growth was also taken into account (Table 2). The equation

\[
\%\text{with-broods} = (20.94 \times \text{vole-numbers}) - (3.55 \times \text{vole-increase}) + 54.97
\]  

(1)

was dominated by the effect of vole abundance in June, and predicted a 24% increase in the proportion of hens with young through the observed range of vole data (0.07-2.64 per 100 trap-days in June, with increases of 0.14-8.79 per 100 trap-days by August).

When foxes and martens were killed the strongest effect in a similar regression equation

\[
\%\text{with-broods} = (11.60 \times \text{vole-numbers}) - (4.98 \times \text{vole-increase}) + 88.26
\]  

(2)

was the tendency for fewer females to raise broods when vole populations grew rapidly from June to August (Fig. 6, Table 2). The equation therefore predicted a 13% decrease in tetraonid breeding success over the observed range of vole data.

Table 3. Simple and partial correlations between numbers of adult tetraonids and vole population indices, with and without the killing of foxes and martens

<table>
<thead>
<tr>
<th></th>
<th>Predators preserved</th>
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<th>Predators killed</th>
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<tr>
<td></td>
<td>Simple r</td>
<td>Partial r</td>
<td>Simple r</td>
<td>Partial r</td>
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<tr>
<td>July counts in year (N)</td>
<td></td>
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<tr>
<td>with vole numbers in (N-1) (1)</td>
<td>0.685</td>
<td>-0.922**1</td>
<td>0.206</td>
<td>0.099</td>
</tr>
<tr>
<td></td>
<td>(constant 2)</td>
<td></td>
<td>(constant 1)</td>
<td></td>
</tr>
<tr>
<td>July counts in year (N)</td>
<td>0.461</td>
<td>0.881**</td>
<td>0.246</td>
<td>-0.169</td>
</tr>
<tr>
<td>with vole increase in (N-1) (2)</td>
<td></td>
<td>(constant 1)</td>
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** P < 0.01, *** P < 0.005.
The production of young per adult hen, which was estimated as the product of brood size and the proportion of hens with broods, was strongly correlated with June vole abundance when no predators were killed (Table 2). The correlation improved slightly, from $r = 0.789$ (with 7 d.f., $P < 0.02$) to $R = 0.861$ (with 6 d.f., $P < 0.01$), if the negative effect of vole population growth was also taken into account ($F_{1,6} = 4.24$, $0.1 > P > 0.05$). There were no significant correlations between young per hen and the vole population indices when foxes and martens were killed.

**Tetraonid winter survival and small mammal numbers**

Although tetraonids produced most young when vole populations were large and increasing slowly, numbers of adult tetraonids did not peak the next summer. Instead, the numbers of adult tetraonids tended to fall after years of high productivity (young per adult hen), provided that no foxes and martens were killed. Decrease in the June chain-counts could be predicted most accurately by a combination of high vole numbers and low vole population growth in the previous year ($R_{05} = 0.940$, $P < 0.002$, Table 3). This relationship reversed the correlations which were found between the vole indices and grouse productivity. High vole numbers and low vole population growth were associated with high productivity in the same summer, but low numbers of adults the following year. There were no significant correlations between chain-counts and vole indices when foxes and martens were killed.

**DISCUSSION**

*The impact of predation*

When foxes and martens were killed, 77% of tetraonid hens had broods in August and brood size averaged 5.52 chicks: there were 4.25 young per hen. Without predator removal, 59% of hens had a brood, and broods averaged 3.29 chicks: there were 1.94 chicks per hen. Removal of predators thus produced a 2.2-fold improvement in productivity. This is a minimum estimate of predation’s impact on breeding, because (i) there were usually one or two non-breeding foxes or martens left on the removal island, (ii) no other predators were removed, and (iii) the measures exclude females killed with their broods.

It is more difficult to assess how much the adult populations were increased by predator removal. Although capercaillie and black grouse densities doubled between 1976–77 and 1979–80 in chain counts on Bergön, the increase could at least in part have resulted from factors other than predator removal. The impact of predation on numbers of adult capercaillie and black grouse is indicated less ambiguously by the population changes on both islands after treatment removal. During predator removal on Rånön, population estimates increased there relative to Bergön by 1.6-fold for capercaillie and 1.8-fold for black grouse in chain counts, and by about 2.7-fold for each species in lek counts.

If population growth were determined by productivity, two summers with a 2.2-fold difference in breeding success should have produced a 2.5-fold increase in Rånön’s population by 1983, relative to Bergön, with a larger difference by 1984. The 2.7-fold change in lek counts was consistent with this prediction, but there was less change in the chain counts. The population changes may also have been influenced by fox and marten predation on adults, and by compensatory differences between the islands in immigration, emigration or survival. Further research, preferably using radio-tagging to monitor
movements, mortality and the accuracy of counts, would be needed to show the
importance of predation relative to resources during prolonged predator control.

_Tetraonid breeding and vole cycles_

Tetraonid brood size was strongly correlated with vole abundance only where no foxes
and martens were killed (Table 2, Fig. 5). The relationship must therefore have stemmed
mainly from predation, and not from a parallel effect of weather or food on both small
mammals and tetraonid populations. The brood size reduction reflected partial brood
loss by most of the hens, rather than a tendency for some broods to remain large while
others were depleted (Fig. 1). It seems that the predators found most of the broods, but
that they often failed to kill all the brood members.

Since all radio-tagged black grouse hens normally lay at least one clutch each spring
(Willebrand 1988), lone hen tetraonids were presumably birds that had lost all their eggs
or young. Like the partial brood losses, total brood losses were least frequent when voles
were abundant in June. This trend was at least partly due to predation, because it was
most marked where predators were preserved, but it also occurred where foxes and
martens were killed. Perhaps this was because we did not remove all the predators.
Alternatively, good feeding conditions in spring, which can enhance tetraonid breeding
(Moss, Watson & Parr 1975), may also benefit vole numbers in early summer (e.g.
other hand, the correlation between growth in vole populations and total brood loss in
tetraonids was enhanced by killing predators (Table 2, Fig. 6), and was therefore not a
product of fox and marten predation.

Predation may not have been the only factor linking grouse breeding to vole
abundance, but its minimum contribution can be estimated. At low vole numbers and no
predator removal, 50% of the hens reared young, with an average brood of 2-8: i.e. 1-4
young per hen. At high vole numbers, 90% of the hens had broods, which averaged 3-8
chicks (3-4 young per hen), a 2-4-fold increase. The contribution of reduced predation to
the decrease in total brood losses could be estimated by comparing the positive regression
coefficients in eqns (1) and (2). On this basis, reduced predation was responsible for 45%
of the observed increase in the proportion of hens with broods, equivalent to an increase
from 50% to 68% (instead of to the maximum 90%). With reduced predation responsible
for an increase to 3-8 chicks with 68% of the hens (to 2-6 young per hen), it would account
for 60% of the observed increase from 1-4 to 3-4 young per hen.

This is a minimum estimate of predation’s role as a synchronizer, partly because
predator removal was incomplete, partly because we could not record hens killed with
their broods, and partly because vole numbers reached a maximum of only 2-64 per 100
trap-days in June. Mainland sites frequently record five captures per 100 trap-days at that
time, and occasionally more than ten (V. Marcström & N. H. Höglund, unpublished
data). With fox and marten predation, tetraonid brood sizes would average 6-7 at a vole
level of ten per 100 trap-days (similar to the maximum of 7-2 young per brood during
predator removal), provided that the relationship in Fig. 5 remained linear. The estimate
of predation’s minimum contribution would then be 68%, if 90% of hens had broods (this
includes renesting). There would also be six young per adult hen in the autumn, which
agrees rather well with the best production figures for tetraonids in northern Sweden (V.
Marcström, unpublished data).

Although tetraonid breeding was enhanced by vole peaks, there was no lasting effect on
population size. Instead, there were fewest adult grouse in years after vole peaks,
especially in the July counts (Table 3), provided that no foxes and martens were killed. A possible explanation is that the predators bred most successfully when voles were abundant, and then killed more tetraonids in winter snow-holes or at the start of the following breeding season.

We conclude that predation was the dominating factor synchronizing tetraonid productivity with vole abundance, but that predation may also have prevented growth of the tetraonid populations in years following vole peaks.

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Predation on tetraonids


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