THE RESPONSE OF THE GOSHAWK *ACCIPITER GENTILIS* TO CHANGING GROUSE *TETRAONIDAE SP.* POPULATIONS

RISTO TORNBERG

Department of Biology, Box 3000, FIN-90014 University of Oulu, Finland, risto.tornberg@oulu.fi

Goshawk's diet and breeding success was studied in northern Finland in the vicinity of Oulu during years 1989–2004 in order to evaluate predation impact on four grouse species, the Black Grouse *Tetrao tetrix,* Capercaillie *Tetrao urogallus,* Hazel Grouse *Bonasa bonasia* and Willow Grouse *Lagopus lagopus.* Sporadic food data was also used from years 1965–1988. Number of studied territories raised from 12 to 37 during the study years. Food remains were collected from territories at least three times per year: in spring (around the nesting site, n = 1420), in summer (from the nest after chicks fledged, n = 1782) and late summer (around the nesting site, n = 826). Winter diet was assessed by telemetry and from museum samples (n = 88). Diet composed mainly of grouse species totalling highest in spring, around 50%, and lowest in winter, around 30%, by number. Black Grouse were the most numerous among grouse, but juvenile grouse outnumbered them during late summer. Preference of different grouse species in Goshawk's diet was measured by a simple catch/supply index. Willow Grouse was taken twice more among grouse than their abundance in the field suggested, while Black Grouse and Hazel Grouse were taken at the same ratio as their abundance in the field. Capercaillies (only females) were taken around half compared to their relative abundance. Goshawk's functional response (grouse found/nesting site as a response variable) against grouse density of the previous autumn was typically concave. Occupancy rate and productivity (chicks fledged/occupied territory) of the Goshawk territories declined as the grouse density declined but brood size remained at the same level. Combining functional and numerical responses for total response (kill rate) declined as well with grouse density implying that Goshawk's predation impact on grouse has remained in a stable level. During years 1989–1998 year to year variation of total response tended to lag grouse density by two years, which implies destabilising effect of the Goshawk on grouse population. After 1999 this pattern, however, disappeared when grouse density fell to a very low level. Applied for the whole period, correlation with two year lag was observed but it was far from significant. Predation impact calculated for years 1989–1998 was 31% for the Willow Grouse, 15% for the Black Grouse, 2% for the Capercaillie and 16% for the Hazel Grouse.

Key words: Goshawk, grouse, diet, breeding, predation.

РЕАКЦИЯ ТЕТЕРЕВЯТНИКА (*Accipiter gentilis*) НА ИЗМЕНЕНИЯ В ПОПУЛЯЦИЯХ ТЕТЕРЕВИНЫХ ПТИЦ (TETRAONIDAE Spp.). Р. Торнберг. Университет Оулу, Финляндия.

Питание и успешность гнездования тетеревятника изучались на севере Финляндии, в районе Оулу, в 1989–2004 гг. для оценки воздействия его охоты на четыре вида тетеревиных птиц: тетерева *Tetrao tetrix,* глухаря *Tetrao urogallus,* рябчика *Bonasa bonasia* и белую куропатку *Lagopus lagopus.* Привлекались также разрозненные данные по питанию вида в 1965–1988 гг. За годы исследований число обследуемых территорий выросло с 12 до 37. Остатки пищи с территорий собирались не реже 3 раз в год: весной (вокруг гнезда, n = 1420), летом (из гнезда после вылета птенцов, n = 1782) и поздним летом (вокруг гнезда, n = 826). Питание в зимний период оценивалось по данным телеметрии и по музейным образцам (n = 88). Рацион состоял, в основном, из тетеревиных птиц, чья доля в питании была выше всего весной – около 50% (по числу объектов), и ниже всего зимой – около 30%. Тетерев был наиболее многочисленным среди прочих тетеревиных, но поздним летом птенцы тетеревиных опережали его по количеству объектов в рационе. Пищевые предпочтения тетеревятника по видам тетеревиных оценивались при помощи простого отношения добыча/ресурс. Белых куропаток добывалось вдвое больше, чем предполагала их относительная численность на территории, тетерев и рябчик добывались пропорционально их численности. На глухаря (только на самок) тетеревятник охотился примерно вдвое меньше, чем предполагало его наличие. Функциональная реакция тетеревятника (число тетеревиных на одно гнездо как функция отклика) на плотность населения тетеревиных птиц предыдущей осенью обычно была вогнутой. Индекс занятости территорий тетеревятника и их продуктивность (число слетков на территорию) снижались при сокращении плотности населения тетеревиных, но размер выводков оставался прежним. Объединив функциональный и количественный отклик, мы видим, что общая реакция – частота добыч, также снижалась при сокращении плотности тетеревиных птиц, что говорит о неизменном уровне воздействия на них охоты тетеревятника. В 1989–1998 гг., межгодовые колебания общей реакции отставали на 2 года от изменений плотности населения тетеревиных, указывая на дестабилизирующее воздействие тетеревятника на их популяцию. Однако после 1999 г., когда плотность

тетеревиных птиц упала до крайне низкого уровня, эта закономерность исчезла. Анализируя весь период исследований в целом, корреляция с запозданием на 2 года существовала, но была совсем незначительной. Расчетное воздействие хищничества в период 1989–1998 гг. составило 31% для белой куропатки, 15% – для тетерева, 2% – для глухаря и 16% – для рябчика.

Ключевые слова: тетеревятник, тетеревиные птицы, питание, гнездование, хтщничество.

INTRODUCTION

The response of a predator to changes of prey availability can be divided into functional (dietary) and numerical response (Keith et al. 1977, Begon et al. 1996). Further, functional response is usually divided into three main types according to shape of the response curve: linear, concave and sigmoid shaped (Holling 1959). Combining functional and numerical response a total response is obtained (Doyle & Smith 2001, Tornberg 2001). It means a total number of prey specimens killed by predators in a given area. This so called kill rate divided by density of prey yields predation rate, often called predation impact (Lindén & Wikman 1983). Predators can be placed, based on their food habits, on a continuum from specialist to generalist predators. Utmost specialists respond only numerically while utmost generalists only functionally to prey changes (Reif et al. 2004a).

Predator´s response on changes of the availability of prey can have impact on prey population. Some predators, typically the species wandering around like nomads, respond immediately to the changes of prey numbers, while others, mainly small mammalian predators and certain site-tenacious raptorial birds, lag one or several years behind their prey (Galushin 1974, Korpimäki & Norrdahl 1989, Nielsen 1999, Tornberg et al. 2005). Former type of predation tends to stabilize prey population while latter destabilize it. Effect may also be influenced by predator type; i.e. whether it is a specialist or a generalist predator. Specialists can have both effects while generalists mainly stabilize prey populations (Hanski et al. 1991).

Goshawks *Accipiter gentiles* hunt in boreal forests mainly on four grouse species: Black Grouse *Tetrao tetrix,* Capercaillie *Tetrao urogallus*, Hazel Grouse *Bonasa bonasia* and Willow Grouse *Lagopus lagopus* throughout the year. These species account for 30–50% of the diet by number in northern Finland (Tornberg 1997, Tornberg & Colpaert 2001). Goshawk's breeding output is also highly dependent on grouse density (Sulkava et al. 1994, Byholm et al. 2002, Tornberg et al. 2005). Since the beginning of the 1960s, densities of all grouse species have continually declined in Finland (see Ranta et al. 1995, Helle et al. 2002). This has reflected in the diet of the Goshawk (Tornberg & Sulkava 1991). Some recent studies also show that Goshawk populations have declined in many regions in Fennoscandia (Lindén & Wikman 1983, Widen 1997, Selås 1998, Gundersen et al. 2004). In Finland, however, clear evidence of steady decline is still only local. The total population seems to be declining slightly (e.g. Björklund et al. 2002).

Aim of the present study is to document recent changes in the dietary and numerical responses of the Goshawk to varying grouse density, as well as to analyse Goshawk's possible effect on this variation. I am especially interested in how keenly Goshawks react to grouse density in northern Finland. I also present newest data about preference of the Goshawk for different grouse species, and whether there has appeared any change in the course of time.

STUDY AREA, MATERIAL AND METHODS

The study has been carried out in the vicinity of the city of Oulu (25° 30' E, 65° 00' N), mainly from 1989 to 2005, but some scattered data is also available since the year 1965. The landscape in the study area is typical for the region, i.e. lowland with few lakes and many rivers and brooks. The area is characterized by coniferous forests, with pines *Pinus sylvestris* and Norway spruce *Picea abies* mixed with birches *Betula pubescens* and aspens *Populus tremula* covering around 65% of the area. Around 30% of the area comprises of peat bogs, of which 2/3 are drained for forestry. The rest of the area are covered by fields, sandpits and human settlements.

Data on prey

Prey species eaten by Goshawks were monitored by collecting their remains around nesting sites during three phases of the nesting period: (1) nest-building and incubation period (hereafter spring), (2) nestling period (hereafter summer), and (3) during and after fledgling period. Prey remains were identified by using reference material of the Zoological museum, University of Oulu. Prey remains collected after the year 1989 total as follows: 1782 individuals from spring, 1420 from summer, and 826 individuals from fledging period, respectively. Data collected before 1989 sum up to 413 prey specimens from spring, and 395 from summer. Diet outside the breeding season was assessed by radio tracking during 1991–1995 (see Tornberg & Colpaert 2001), and during 2000–2003. Also stomach contents of Goshawks found dead in the study area or near-by, and sent to the Zoological Museum, were included in the data set (in total 88 prey specimens).

Data on Goshawk nesting

Nesting territories were checked in spring to detect whether they were occupied or not. Territory was stated to be occupied if fresh twigs of spruce or pine were brought to the nest. During May occupied nests were checked to see whether eggs were laid or not. Number of eggs was counted, and the eggs were measured whenever possible. Sometimes a new nest was found not until the young were already hatched. In successful nests the nestlings were counted and ringed as well as weighed, and their wing lengths were measured. The annual number of territories checked varied between 14 (1989) and 35 (2004).

Data on grouse populations

Since 1989 density estimates of grouse species were obtained from wildlife triangle censuses organized by Finnish Game Research Institute (Lindén et al. 1989). Census routes are triangles, with four kilometres long sides. A triangle is walked by three observers 20 m apart, and all grouse met in this transect line are counted. The following information is recorded: species, sex (Black Grouse and Capercaillie), number of lone females and those with a brood, and the number of juveniles. Each observation is plotted on a map. In the beginning, there were 10–12 triangles counted in my study area annually, but recently not more than 7–8. Grouse were counted by a similar line transect method also from the year 1963 to 1988, but in that period the transects were walked along the most suitable habitats for broods of grouse (Rajala 1974). Wildlife triangles give more representative densities for the landscape in general, but the older route censuses indicate more optimal habitats. However, there seems to be no abrupt shift in density estimates between route and triangle censuses (see Lindén et al. 1989).

Statistical analysis

For prey data I calculated percentage of each prey species or species group in a sample. I further calculated the mean of all samples from each year to have an annual average estimate of each species. For grouse I also used the number of grouse species found per sample, and calculated annual estimates for them as described above. This parameter measured the functional response.

For Goshawk nest data I defined occupancy rate as the number of territories occupied per number of territories checked. The number of fledglings per occupied territory (Steenhof 1987) indicated breeding productivity. Index for the numerical response of the Goshawk can be defined as 2 x occupancy rate (=number of parents) + productivity (=number of young). I further calculated an index for the total response by multiplying both response types (functional response x numerical response). Preference index for the different grouse species was calculated by dividing the relative proportion of each grouse species in the diet by the relative density of the species in the field. This so called catch per supply ratio results as 1.0 when a prey species is consumed in the same proportion as predicted by its abundance alone.

I used regression analysis to analyse trends in the time series, and cross correlation analysis for making pair-wise tests with different time-lags between the grouse data and the Goshawk parameters. Before running cross correlation analysis I removed trends from time series by residual techniques. For testing whether Goshawks preferred any of the grouse species when hunting, I used one-sample t-test.

RESULTS

Seasonal diet composition

Grouse species account for more than 50% of the diet during spring but drop till about 30% during summer. Their proportion increases again up to ca. 40% during the fledging period (fig. 1). In winter the percentage of grouses tends to be lower than during the breeding season. Proportion of mammals is less than 20% during the breeding season, but it increases up to almost 50% outside the breeding season. In addition to grouse, only ducks and corvids are important during the breeding season. Corvids are especially important prey during the nestling period.

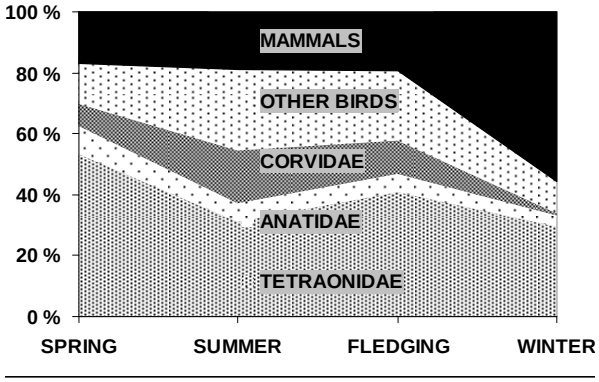

Figure 1. Seasonal change in the diet of the Goshawk near Oulu during 1989–2003.

The Black Grouse is the most important prey, accounting for 15–20% of the Goshawk's diet throughout the year (fig. 2). The Hazel Grouse and the Willow Grouse are numerous during spring, but their proportion tends to decline strongly during the breeding season. In winter, Hazel Grouse are relatively important prey for Goshawks. Capercaillies, of which only females are found in the diet during the breeding season, are rarely taken by the Goshawks. Capercaillie cocks are found in the diet only outside the breeding season. Only female Goshawks kill full-grown Capercaillie cocks.

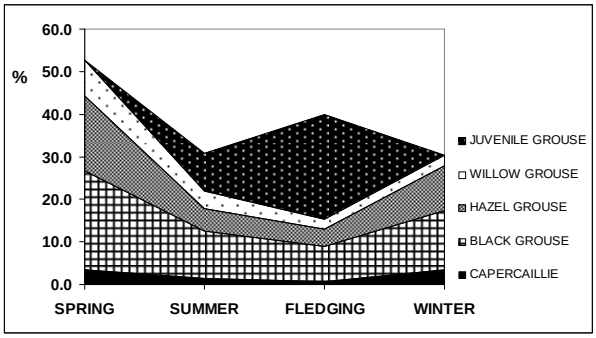

Figure 2. Seasonal change of grouse species in the diet of the Goshawk near Oulu during 1989–2003.

Goshawk's preference for different grouse species

Goshawks clearly prefer Willow Grouse over other grouse species as their prey in spring ($t = 3.725$, $df = 32$, $p = 0.001$, one-sample t-test). The Black Grouse and the Hazel Grouse are consumed roughly at the same ratio as found in the field, but Capercaillie females are taken in considerably lower proportion than available ($t = -7.653$, $p < 0.001$) (fig. 3). There was a slight increase in the preference for Black Grouse and Capercaillie females during the study years.

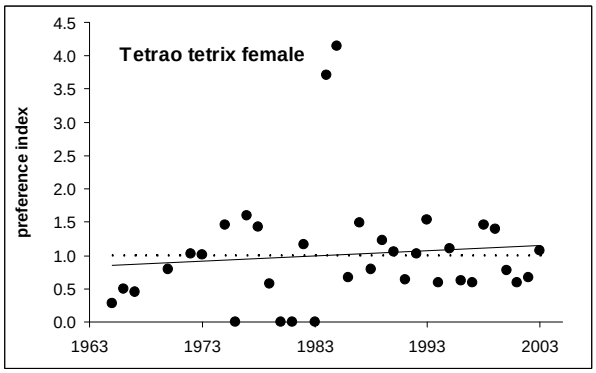

Figure 3. The change of the Goshawk's preference for Black Grouse females during the breeding season near Oulu in 1965–2003. Each dot represents a catch–supply ratio (proportion of prey in the diet per proportion in the field) of one year. Prey is preferred when dot is above the dashed line (ratio =1).

Goshawk's functional response for grouse density

The number of grouse killed by the Goshawk follows fairly well both the annual changes as well as the long-term trends of grouse populations in the field (fig. 4). After removal of the trends, cross-correlation analysis revealed that best correlation was obtained with 1-year lag, i.e. when comparing the number of killed grouse to the grouse density of the previous year ($r = 0.410$, $p < 0.05$). When the number of killed grouse is plotted against the density of grouse of the previous autumn, a functional response curve is obtained. Best fit was obtained for logarithmic function ($F = 21.62$, $df = 30$, $r^2 = 0.429$, $p < 0.001$) (fig. 5).

Goshawk's numerical and total responses related to grouse density

Goshawk's occupancy rate, productivity and combination of these two declined at the same rate as the grouse density (fig. 6). The clutch size declined slightly, but the brood size remained stable. I correlated all these variables with grouse density with different time lags after removal of the trends. Of these variables only the clutch and brood sizes correlated significantly with grouse density with a one year time lag ($r = 0.566$ and $r = 0.526$, $p < 0.05$, respectively). Total response correlated best with 2-year time lag but correlation was not significant ($r = 0.376$, n.s.). During the 1990's (1990–1999), however, correlation was close to significant ($r = 0.631$ vs. confidence limit = 0.708) (fig. 7).

DISCUSSION

Grouse typically dominate in the diet of Goshawks in boreal forests in spring (Sulkava 1964, Höglund 1964, Lindén & Wikman 1983, Widen 1987, Tornberg 1997). It must be remembered that spring diet consists prey specimens predated by males only. It, hence, cannot be considered representative for the diet selection of the whole population. In the Goshawk, having a marked sexual dimorphism, sexes differ remarkably in prey choice (Kenward et al. 1981, Tornberg & Colpaert 2001). Small grouse species, the Willow Grouse and the Hazel Grouse, dominate in early spring, but the bigger Black Grouse become more important during the breeding season (Tornberg 1997). Especially Black Grouse hens become most important during the nestling period, while importance of the cocks vanishes, likely due to the end of lekking period, which follows increasing difficulties to find them.

The decline of the proportion of grouse species in the diet of the Goshawk during the breeding season is clearly due to the increase in numbers of young birds, mainly thrushes and corvids, which are easier to hunt (Lindén & Wikman 1983, Tornberg 1997). Grouse chicks become more important prey towards late summer, when they grow and become more profitable as prey (Tornberg 1997). Young of large grouse species seem to be more preferred than smaller ones (Sulkava 1964, Reif et al. 2004b). It is likely that predation on young grouse remains at the same level later in autumn as observed in August. When females start to hunt in the late nestling period, they likely hunt similar prey as males (Gronnesby & Nygård 2000, Reif & Tornberg unpubl.). Later in autumn, however, females start to kill full-grown hares, and they also take more Capercaillies, even adult cocks (Tornberg & Colpaert 2001).

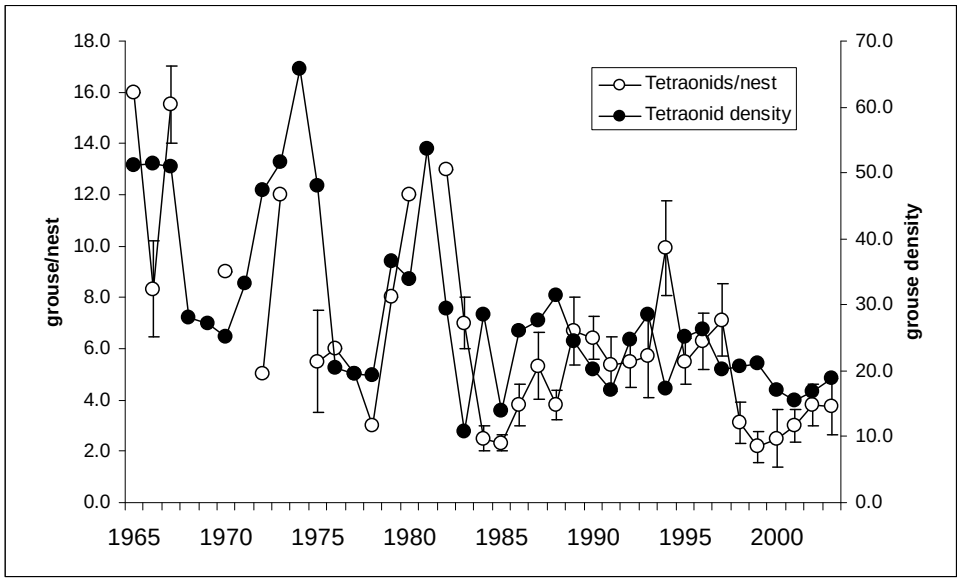

Figure 4. The mean annual number, with standard error of mean, of grouse specimens found in the nests, and the total density of grouses near Oulu during 1965–2003.

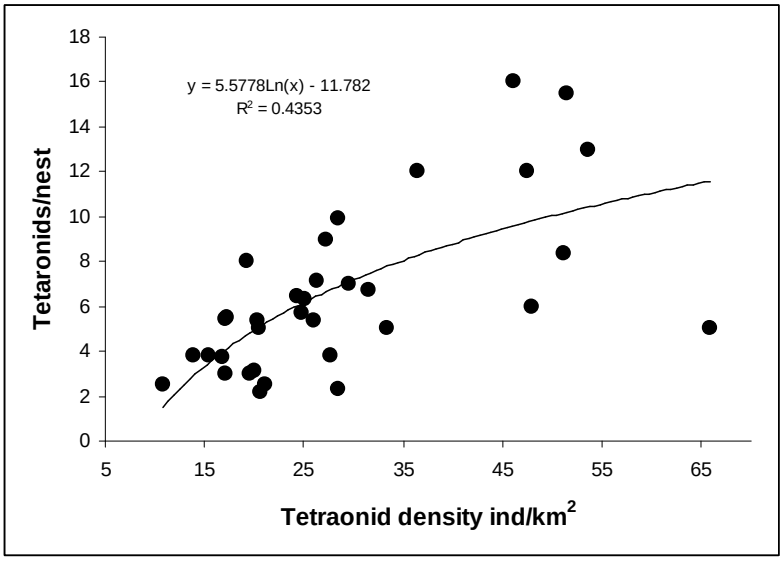

Figure 5. The mean annual number of grouses found as prey of the Goshawk plotted against the total density of grouses (individuals/km^2) near Oulu during 1965–2003.

Hares can account up to 30% of diet by number, and 70% by weight, in winter, but they are killed only by female Goshawks. Therefore, the proportion of grouse in the diet of males is somewhat higher than in that of females (about 40%, Tornberg unpubl.). When squirrels are abundant, they form an important winter food for both sexes (Widén 1987). In boreal forests of North America, Goshawks hunt mainly on mammals, especially snowshoe hares *Lepus americana* (Doyle & Smith 2001).

Goshawk's preferences for different grouse species show interesting patterns. Willow Grouses are strongly favoured as a prey while Capercaillie females are taken remarkably less than expected by their abundance in the field. Tornberg & Sulkava (1991) found that preference of the Willow Grouse population declined during the 1980s in my study area. New data show that this species is taken with as high a rate as previously. Reasons for this probably lie in the high vulnerability of the Willow Grouse to Goshawk´s predation during the lekking period. Willow Grouse males are white and noisy in spring, which inevitably makes it easier for the Goshawk to hunt them compared with other grouse. Avoidance of Capercaillie females might be due to their relatively large size for hunting by male Goshawks.

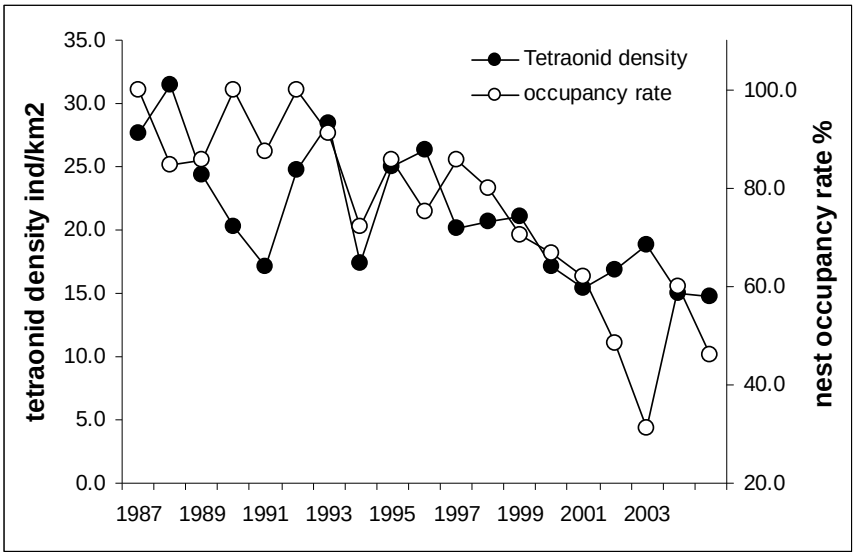

Figure 6. The occupancy rate of Goshawk territories and the grouse density near Oulu during 1987–2005.

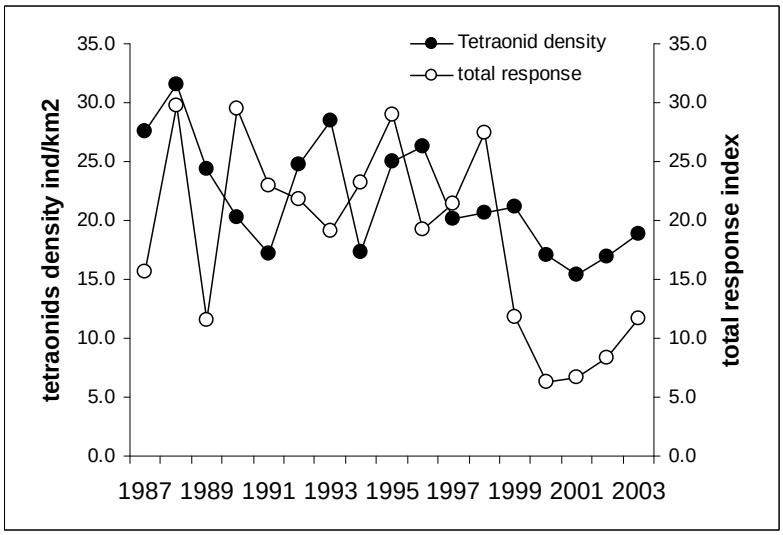

Figure 7. Total response of the Goshawks and the grouse density near Oulu during 1987–2005.

In comparison, the preferences of the Golden Eagle *Aquila chrysaetos* for grouse species are strongly related to the size of prey. Capercaillie females are taken twice more often than they are found in the field, respectively. However, Willow Grouse are more preferred than Black Grouse hens (Sulkava et al. 2003). In the Goshawk, size-related preference is not so clear, while the males tend to take relatively less Black Grouse cocks than hens during winter (Tornberg unpubl.). Similar pattern has been observed in relation to sexes of Pheasants *Phasianus colchicus* (Kenward et al. 1981).

The number of grouse in Goshawk's diet followed in accordance the density of grouse. My response variable, grouse remains found per nesting site, is independent of other prey species taken (in opposite to percentages that depend on the number of other prey). Therefore measuring response in this way might indicate more reliably the true response percentages than percentages that have been used in most other studies. Shape of the functional response curve obtained was concave, when diet variable was plotted against grouse density. Tornberg & Sulkava (1991) observed a similar pattern when using grouse proportions as a dependent variable. In North America, Goshawks responded in a similar way for snowshoe hares (Doyle & Smith 2001). Lindén & Wikman (1983) observed, however, a convex shaped curve for the Hazel Grouse. Generally, a concave curve (type 2) refers to a generalist predator that has a strong preference for main prey (Kenward 1986). This sort of pre-

dation possesses inherently a destabilising effect on prey (Begon et al. 1996). Predator having a convex shaped functional response curve (type 3) possesses an ability to regulate prey population at low density. It indicates also that prey has a refuge at low density, as might be the case for Hazel Grouse–Goshawk interaction (Lindén & Wikman 1983), or alternative prey is richly available. This is a very likely explanation for type 3 response curve in southern boreal forests. More northern areas, where alternative prey is less available, type 2 curve is expected. In areas where alternative prey is very scarce, functional response may be lacking, because Goshawks cannot breed at all when grouse are scarce. Functional response may also be lacking if grouse are abundantly available, as was the case in Finland during the 1960s and 1970s with high grouse densities (Kauko Huhtala, unpubl. data). Icelandic Gyrfalcons *Falco rusticolus* which are very dependent on Ptarmigans *Lagopus mutus* during breeding season showed no functional response for changes in the density of prey (Nielsen 1999).

Dependence of Goshawk's breeding success on grouses has been shown in many studies in Finland (Huhtala & Sulkava 1981, Tornberg & Sulkava 1991, Sulkava et al. 1994, Tornberg 2001, Byholm et al. 2002, Tornberg et al. 2005), and in Norway (Selås 1997, 1998, Gundersen et al. 2004). Time lag of 0.5–1 year after grouse population cycles is typical in clutch and brood sizes of Goshawks (Sulkava et al. 1994, Tornberg 2001, this study). In North America, Goshawks lag one year after snowshoe hare peak expressed as sightings and productivity (Doyle & Smith 1994, 2001). Tornberg et al. (2005) observed that Goshawk's occupancy rate lagged two years after grouse peak in western Finland. A similar tendency in total response was also observed in the present study but, likely due to relatively weak cyclicity of grouse population during the study years, this phenomenon remained obscure. These studies show that Goshawks might have a strong destabilizing effect on grouse populations, which raises Goshawk predation as one candidate for grouse cycles in northern latitudes. Because cyclicity in Finnish grouse populations has practically ceased, the idea could be tested only in large intact areas of Russian taiga forests, where cyclicity might still be going on in grouse populations (see Beskariev et al. 1994, but see Bortcevski 1993).

Goshawk's important role in grouse mortality is proved in many grouse studies (e.g. Angelstam 1984, Willebrand 1988, Wegge et al. 1990, Bortchevski 1993, Valkeajärvi & Ijäs 1994). Based on several studies, predation impact on different grouse species by breeding Goshawks has varied from 2 to 20% (Lindén & Wikman 1983, Widén 1987, Tornberg 2001). Goshawk's percentage of annual mortality was estimated from 5% (in Capercaillie) up to 60% (Willow Grouse) in northern Finland (Tornberg 2001). In western Russian taiga forest, Goshawks were responsible for 70–90% of annual mortality of Capercaillies (Bortchevski 1993). It is likely that in intact taiga forest Capercaillies are Goshawk's most important prey species because Black Grouse and Hazel Grouse are relatively scarce there, as well as important winter prey animals, hares and squirrels (Bortchevski 1993).

In the future, densities and food habits of the Goshawk should be studied in large intact areas of Russian middle and north boreal forests, from where there are practically no data at present. This might give important insight to the dynamics of grouse species in natural conditions.

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