

**EFFECT OF CHANGING  
LANDSCAPE STRUCTURE ON  
THE PREDATOR-PREY  
INTERACTION BETWEEN  
GOSHAWK AND GROUSE**

**RISTO  
TORNBORG**

Department of Biology

OULU 2000



*RISTO TORNBERG*

**EFFECT OF CHANGING LANDSCAPE  
STRUCTURE ON THE PREDATOR-  
PREY INTERACTION BETWEEN  
GOSHAWK AND GROUSE**

Academic dissertation to be presented with the assent of  
the Faculty of Science, University of Oulu, for public  
discussion in Kuusamonsali (Auditorium YB 210),  
Linnanmaa, on May 27th, 2000, at 12 noon.

Copyright © 2000  
Oulu University Library, 2000

Manuscript received 28 April 2000  
Accepted 3 May 2000

Communicated by  
Professor Robert Kenward  
Doctor Torgeir Nygård

ISBN 951-42-5637-9

ALSO AVAILABLE IN PRINTED FORMAT

ISBN 951-42-5636-0  
ISSN 0355-3191 (URL: <http://herkules.oulu.fi/issn03553191/>)

OULU UNIVERSITY LIBRARY  
OULU 2000

**Tornberg, Risto, Effects of changing landscape structure on the predator-prey interaction between goshawk and grouse**

Department of Biology, University of Oulu. P.O.Box 3000, FIN-90014

2000

Oulu, Finland

(Manuscript received April 28, 2000)

***Abstract***

I studied the ecology of the goshawk-grouse relationship in Oulu, northern Finland, during and outside the breeding season, by radio-telemetry. This included museum samples of goshawk to obtain a better ecological as well as a better evolutionary understanding of it.

The proportion of grouse in the diet of goshawks has decreased since the 1960's, in accordance with the decline of grouse populations. The main prey groups replacing the lacking grouse were corvids, squirrels and hares. The proportion of grouse was highest in spring and it decreased towards the end of the nestling phase. The most preferred grouse species were hazel grouse *Bonasa bonasia* and willow grouse *Lagopus lagopus*. Preferences for different prey types are not explained by active choices of goshawk, but by changes in the vulnerability of the prey species. The nestling phase, when food demand is highest, is not adjusted to when prey supply is highest, but before it.

The size and shape of the goshawks has changed from the 1960's. Adult males became smaller but females larger. Both became relatively longer winged and tailed. Decrease of male's size may be a response to the change in the food supply. Prey types replacing grouse are generally smaller, which may cause the change in the male's morphology. Females being less active during the breeding season may not be affected. For the female to be larger is advantageous in winter when they kill 'over large' prey like mountain hares *Lepus timidus* and capercaillie cocks *Tetrao urogallus*.

Wintering goshawks were mainly females in adult plumage that tended to stay in the study area. However, only one third bred locally. More than one quarter of all hawks died during the study. Although known to be inhabitants of old forests, which this study supports, goshawks are fairly well adapted to mosaic landscape resulting from modern forestry, providing that suitable sized prey is available. Females have less problems, probably because hares, the main winter prey for females, are not affected negatively by forestry, like grouse and squirrels are, the main prey for males.

Goshawks have a remarkable impact on grouse populations, especially when non-territorial hawks, 'floaters' are also included. About one half of the total mortality rate of grouse may be due to goshawk predation. Goshawk predation accords to predictions of general predation theory and may be a noticeable factor contributing to cyclicity in grouse.

Key words: goshawk, grouse, predation, reversed sexual size dimorphism, population regulation

## Acknowledgements

This work was carried out in the Department of Biology of University of Oulu. I thank Professor Markku Orell for pleasant working conditions and especially the emeritus Professor Seppo Sulkava, a pioneer in the research of birds of preys in Finland, who lead me into the fascinating world of birds of prey through the analysis of prey remains, which many consider unpleasant tasks. However, studying food remains of the goshawk is like going bird watching excursion in the wings of a hawk. Talks with Seppo and another senior 'man of bird of prey', field naturalist Kauko Huhtala were unforgettable. I am happy to have for supervisors such top ecologists as Erkki Korpimäki and Mikko Mönkkönen. By encouraging, advising, and above all through his incredible production of high quality papers on the ecology of birds of prey, has Erkki provided an impressive model of how to study in the difficult and labourous field of raptors and owls. Mikko's support in statistics, working up with manuscripts and planning the work was irreplaceable. Though younger than the defendent, Mikko's experience and versatility in the field of ecology is amazing. Alfred Colpaert, expert in GIS, made possible the analysis of habitat use of the hawks, and Maarit Pakkala helped analyse the museum data.

Several amateur and professional ornithologists helped me in the field work. Pentti and Markku Hukkanen, father and son, men devoted to birds of prey, searched many new nesting sites of goshawks to me. Seppo Haapala 'nursed' the nests on the Isle of Hailuoto, Kari Koivula and Seppo Rytönen gave hints of the hawks living in 'tit area, Wytham wood of Oulu'. The Zoo of the Department of Biology lead by Jari Ylönen gave important technical assistance in catching the hawks and Henry Sormunen the same in the field. Samuli Heikkinen liberated me several times from pinches I got stuck in with my computer.

The staff of the Zoological museum with former head Eino Erkinaro and present one Juhani Itämies showed patience during the field work when I successfully skipped the routine museum works. Especially this concerns my colleagues Eero Lindgren and Pasi Paaso, who had to do the 'dirty work', handling dead animals in the museum when I enjoyed of pleasant field trips in beautiful mornings. No wonder if they sometimes had been envious.

I thank the Finnish Game and Fisheries Research Institute and there especially Marcus Wikman for providing census data of game animals. I also thank the Finnish Game

Management Foundation, Jenny and Antti Wihuri Foundation and the Faculty of Sciences of the University of Oulu for financial support.

Finally I thank my wife, Tuija, and our five children, Tiia, Riku, Sini, Juho and Ossi, who brought joy to my life and resisted only little my continuous field trips also during the weekends.

Oulu, May 2000

Risto Tornberg

## List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Tornberg R & Sulkava S (1991) The effect of changing tetraonid populations on the nutrition and breeding success of the goshawk (*Accipiter gentilis L.*) in Northern Finland. *Aquilo Ser. Zool.* 28: 23-33.
- II Tornberg R (1997) Prey selection of the goshawk *Accipiter gentilis* during the breeding season: The role of prey profitability and vulnerability. *Ornis Fenn.* 74: 15-28.
- III Tornberg R Mönkkönen M & Pakkala M (1999) Changes in diet and morphology of Finnish goshawks from 1960s to 1990s. *Oecologia (Berlin)* 121: 369-376.
- IV Tornberg R & Colpaert A (2000) Survival, ranging, habitat choice and winter diet of the northern goshawk in Northern Finland. *Ibis* (in press).
- V Tornberg R (2000) Can the goshawk regulate grouse populations? *Wildlife Biology* (submitted).

## Contents

Abstract	
Acknowledgements	
List of original papers	
1. Introduction .....	13
1.1. Background .....	13
1.2. Long-term change in the diet of the goshawk.....	15
1.3. Prey choice and timing of breeding in the goshawk .....	16
1.4. Evolutionary response of the goshawk for change in grouse.....	16
1.5. Winter ecology of goshawks .....	17
1.6. Goshawk's impact on grouse populations .....	17
1.7. Aim of this study .....	18
2. Study area, material and methods .....	19
2.1. Study area.....	19
2.2. Collection of food remains and breeding data.....	19
2.3. Density indices of prey animals.....	20
2.4. Radio-tracking of the goshawks .....	20
2.5. Museum data .....	21
3. Results and discussion.....	23
3.1. Dietary response of the goshawk to the decrease of grouse.....	23
3.2. Prey choice and timing of breeding in the goshawk .....	24
3.3. Evolutionary response to decrease of grouse.....	26
3.4. Winter ecology of goshawks .....	27
3.5. Goshawk and grouse. Are they coupled?.....	29
4. Conclusions .....	34
5. References .....	35

# 1. Introduction

## 1.1. Background

Predation is a violent interaction in nature, where one part loses its life. Almost all animals are destined for a violent death, which is often caused by predation. This excludes top predators – although they are often the prey of man. Conventionally, predation was considered only to keep track prey population killing rather ‘doomed surplus’ (Errington 1956). Also prey individuals fallen as an offer were often assumed to be injured or ill and predators as ‘health officers’ in nature. Predation was, thus, considered mainly compensatory (Kenward 1986, Korpimäki & Krebs 1996). A classic example of predator-prey interaction, snowshoe hare - lynx time series from the 19th century, based on statistics from Hudson Bay company, suggested a predator driven cyclicity of prey but it can also be interpreted in a conventional way. The early, simple, Lotka-Volterra model suggests a fluctuating nature of predator-prey interaction (see Begon *et al.* 1990). In more realistic models, the stability of the system depends mainly on prey recruitment rate, the predator’s searching efficiency and a time-lag between predator and prey (Rosenzweig & MacArthur 1963, May 1973, Maynard-Smith 1974, Hanski *et al.* 1991). A lot of work done in the ecology of voles and snowshoe hares produced several hypotheses attempting to explain their periodic fluctuations (Korpimäki & Krebs 1996, Krebs 1996). However, most population regulation theories put forward in the 1960s stressed social and even genetic feed-back mechanisms not to mention plant-herbivore interactions as a cause of population fluctuations (see review Krebs 1996). Starting in the beginning of the 1980’s, several field and theoretical studies on small mammals turned their interest towards the role of predation in regulating prey populations (Keith *et al.* 1977, Angelstam *et al.* 1984, Erlinge *et al.* 1984, Hansson 1984, Kenward 1986, Henttonen 1987, Korpimäki *et al.* 1991, Hanski *et al.* 1991, 1993, Norrdahl & Korpimäki 1995, Korpimäki & Krebs 1996).

The ‘armsraces’ between prey and predator, co-evolution, is probably responsible for many specific adaptations found in animals. For example camouflage, mimicry and different anti-predator behaviours like flocking are cases where avoidance of predation is

apparent. Most of these adaptations have a genetic basis but also, especially in higher vertebrates, some behaviours can be learned (Taylor 1984). According to the life-history theory, animals tend to increase the proportion of their genes in future generations. Thus the predator that can allocate the most energy for breeding also obviously increases its genes most in the next generation. The predator must therefore decide where to hunt and what to hunt. Optimising energy gain will, according to the optimal foraging theory, sometimes lead to specialisation in prey choice, but sometimes a more beneficial way is to attack every potential prey. (Charnov 1976, Pyke *et al.* 1977, Pyke 1984, Stephen & Krebs 1986, Reynolds *et al.* 1988). The responses of a predator to changing prey numbers can be classified into numerical and functional responses according to Solomon (1949). The shape of the response curve is considered to be important in the regulation of prey population (Holling 1959, Taylor 1984). A sigmoid shaped response curve hints to stabilising of prey population while a convex shaped curve to destabilising it.

The goshawk is a large, relatively common and widely distributed raptor species in the northern hemisphere (Fischer 1980). It captures bird and mammal species varying greatly in size, from small mammals weighing a few grams up to the size of hares and capercaillie cocks weighing 4kg (Höglund 1964, Sulkava 1964, Brull & Fischer 1981). Because many small game species, interesting also man, include goshawk's diet, its foraging habits have been studied in Europe since the 1940's (see Brull & Fischer 1981). In Central Europe, the goshawk's food base depends greatly on pigeons, corvids, thrushes and rabbits (e.g. Opdam *et al.* 1977, Cozszynski & Pilatowski 1986), while in the boreal forests of Northern Europe goshawks hunt mainly grouse species; black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus*, hazel grouse, *Bonasa bonasia* and willow grouse, *Lagopus lagopus* (Sulkava 1964, Höglund 1964, Linden & Wikman 1983, Widen 1987, I, II). In the boreal forests of North American mammals, primarily the snowshoe hare *Lepus americanus* constitutes the main prey base (Storer 1966, McGowan 1975). Because of a high proportion of game animals in the diet, the goshawk has caused a lot of controversy between protectionists and game managers. Recent studies on game animals adopting radio-telemetry as a research tool have revealed predation to be their most marked proximate cause of death (Angelstam 1984, Willebrand 1988, Kastdalen & Wegge 1989, Wegge *et al.* 1990, Swenson 1991, Marjakangas 1992, Valkeajärvi & Ijäs 1994). The goshawk has turned out to be one of the most important predators of adult grouse. When goshawk predation was studied in Sweden on pheasant *Phasianus colchicus*, population decreases of up to 60-70 % were found, depending on the density of pheasants (Kenward *et al.* 1981). When a similar study was conducted in boreal forests for winter predation on grouse, very low predation was apparent (Widen 1987). Yet, the highest losses of grouse taking place in the early phase of breeding as depredated eggs and chicks are presumably not due to goshawk predation. Recently, changes in forest structure are considered to be the most important cause for the poor success of grouse (e.g. Henttonen 1989, Andren 1995, Wegge *et al.* 1990, Kurki *et al.* 1997). Forest fragmentation has probably increased voles and their predators; red foxes *Vulpes vulpes*, stoats *Mustela erminea* and martens *Martes martes*, which would also increase grouse kills.

Goshawk is considered an old forest species based on its nest site selection (e.g. Link 1986). Decrease of the amount of old forests has probably negatively affected on its living conditions via loss of nesting and hunting habitats (Widen 1997). However, goshawk is fairly well adapted to agricultural landscape of central Europe (Kenward 1982).

Therefore, its adaptation to modern man-dominated boreal forest might mainly be a question of sufficient food supply, especially in winter.

## **1.2. Long-term change in the diet of the goshawk**

Grouse, as a stable food source for goshawks, have dramatically decreased in Finland since the start of grouse censuses in the beginning of the 1960's. (Linden & Rajala 1981). However, the goshawk population has not decreased by the same amount, as would be expected, based on the central importance of grouse in the goshawk's diet (Saurola 1985, Haapala *et al.* 1994, Väisänen *et al.* 1996). On the other hand, changing forests might have created new sources of food. At least the vole has benefited from clear-cutting, which increases the growth of grasses and bushes; the favourite food of field voles (Larsson & Hansson 1977, Henttonen 1989), and possibly also of hares. The continual rise in man's standard of living produces more waste, utilised by corvid birds and rats, which are suitable food for raptors and owls. The number of corvids has markedly increased since the 1950s, in particular, in the last two decades (Väisänen *et al.* 1996). Therefore, one can ask if these potential alternative prey types have been sufficient to make up for the lack of grouse in the goshawk's diet.

## **1.3. Prey choice and timing of breeding**

According to the life history theory, animals tend to increase their genes in future generations by maximising their reproductive output, measured as the number of offspring surviving until reproductive age (Williams 1966). This can be reached by making the right decisions in the different breeding stages. Firstly, the predator has to get extra energy to produce eggs and rear its young by choosing its prey properly. This can be achieved by searching for prey that give the most energy/time used for its provision. The main prediction of this optimal foraging theory states that predators should continue consuming the main prey if available, irrespective of the abundance of secondary prey (Pyke *et al.* 1977, Pyke 1984, Stephens & Krebs 1986). Predators that have a short searching time for prey compared to handling time should specialise in their foraging and generalise in the opposite situation (Reynolds *et al.* 1988). Therefore goshawks should specialise in spring and hunt mostly grouse and generalise in summer when more easily catchable birds are available. Secondly, predators should adjust their breeding so that a maximum number of nestlings reach independence (Lack 1954). On the other hand, the value of this decision is not manifested until the first breeding attempt of the offspring. Therefore, the survival of offspring during the first year, being lowest then, largely determines the value of parental choices. Birds can time their breeding period so that the highest demand for food in the nestling phase coincides with the highest supply (Lack 1954), or they can start as early as possible and give the offspring time to prepare for harsh winter conditions. This might be profitable in raptors, whose style of life, hunting, demands a lot of experience (Perrins 1970, Newton 1986, Village 1990).

## 1.4. Evolutionary response to decrease of grouse

The goshawk, like all raptor species, shows a remarkable reverse sexual size dimorphism. The female can be 1.5 times larger than the male. Typically, in goshawks and also in other raptors, the roles of the sexes are clearly segregated during the breeding season. The male provides food for the female and offspring for most of the breeding season (Newton 1979). Thus food data, which is collected at that time, reflects primarily the prey choice of males. Because of the large size difference between mates, divergence in the diets of sexes could be expected (Reynolds 1972). Data gathered during the non-breeding season sometimes showed no difference in prey choice between sexes (Opdam *et al.* 1977, Widen 1987) but implied differences in some cases (Kenward *et al.* 1981, IV). The avoidance of food competition between sexes has been a favoured explanation for the sexual size dimorphism in raptors (Reynolds 1972). Numerous hypotheses have been put forward to explain this unique reversed dimorphism in hawks and owls (Hakkarainen *et al.* 1991). However, many of them remain untestable or can be tested only indirectly in ecological time by studying the reproductive output of pairs that have different male/female size ratios (Hakkarainen *et al.* 1991). Because only the male delivers prey for the brood during the critical period of hatching, its hunting skills are of essential importance for the survival of nestlings. This time may also be a period of strong natural selection, affecting or maintaining the reversed nature of size dimorphism in hawks or even their morphology (III). The agility of the male, partly due to its small size, is considered to be important in this sense (Storer 1966, Reynolds 1972, Andersson & Norberg 1981, Hakkarainen *et al.* 1995). Due to the decline of grouse populations their proportion in goshawks diet has respectively decreased. Alternative prey types are smaller, on average, than grouse. Therefore small sized males could be more efficient capturing alternative prey, which would have resulted in smaller males at present than in the good grouse years of the 1960's and 1970's. Females, on the contrary, do not start hunting until late in the nestling phase. In winter they rely heavily on hares as a stable food, which has increased rather than decreased. Therefore less or no changes in female size are expected.

## 1.5. Winter ecology of goshawks

Winter is a time of extreme conditions in the north. Temperatures can drop to -30 C. Another harmful point for diurnal animals is a short day length, which reduces the time for searching for food. This is especially problematic for raptors whose food source, prey animals, is not very predictable. In addition, prey animals adopt different anti-predator behaviours, like flocking (Angelstam 1984) and snow-roosting (Marjakangas 1990). Crypticity of prey also decreases finding probabilities of prey. Yet, in spite of these difficulties goshawks are able to spend winter in the north. Due to their secretive life habits very little is known about their habits outside the breeding season. By adopting radio-telemetry as a research tool new information about the goshawk's winter ecology has recently been obtained. (Kenward 1977, Kenward *et al.* 1981, Kenward 1982, Ziesemer 1981, Widen 1985, Widen 1989, Kenward *et al.* 1991, 1993). Important questions like population structure, demography, movements, survival, causes of death,

habitat selection and winter diet can be cleared up more accurately than before. A crucial aspect in the conservation of the goshawk derived from these themes is its response to change in forest structure due to modern forestry. Goshawks are known to be old forest dwellers based on nest site preferences (e.g. Link 1986). Clear-cuts have produced a mosaic landscape where old forest patches are becoming smaller and smaller. In landscape ecology it has been found that beyond a certain limit of habitat loss the population will decrease more than the habitat loss alone would explain (Andren 1994). There are indications that the goshawk might have decreased in recent decades in Fennoscandia, at least locally (Linden & Wikman 1983, Forsman & Ehrnsten 1985, Tommerraas 1993, Halley 1996, Widen 1997). However, in agricultural areas of Sweden and Central Europe goshawks are rather well adapted to landscape containing less than 50% forest (Kenward *et al.* 1981, Kenward 1982, Ziesemer 1982).

## **1.6. Goshawk's impact on grouse populations**

Due to the high proportion of grouse in the diet, the goshawk, being a relatively common raptor, might have a fairly high impact on grouse populations. Depending on the strength and timing of the impact, the predator can limit the prey population or even regulate it (May 1973, 1981, Hanski *et al.* 1991, Korpimäki 1993, Murdoch 1994, Korpimäki & Krebs 1996). A typical feature of many northern species, periodic fluctuation of abundances, also considers grouse that show multiannual fluctuation, with a cycle length of 6-7 years in most parts of Finland (Linden 1988). A somewhat shorter cycle length, 3-5 years, is found in northern Finland and Scandinavia (Myrberget 1984, Angelstam *et al.* 1985, Linden 1988, 1989). There are two hypotheses presented to explain grouse cycles by predation. Angelstam *et al.* (1984) brought up and defined an old theory originally proposed by Hagen (1952) and Lack (1954), the so called alternative prey hypothesis (APH), which explains population cycles of small game to be formed by varying predation pressure, caused by vole-eating predators. Population fluctuation of grouse may also be driven by a specialist predator, according to the general predation theory (Rosenzweig & MacArthur 1963, May 1973, Hanski *et al.* 1991, 1993). Although known as a generalist predator, the goshawk is relatively specialised on grouse in northern conditions. If a predator were to cause cyclic fluctuations in the prey population it firstly should be relatively specialised on it e.g. show no functional response for prey. Secondly, it should respond numerically with a time-lag to prey population and thirdly, predation pressure should be highest during low phase of prey population and there should be a negative correlation between the kill rates of the predator and the change in the prey population (Korpimäki *et al.* 1991, Nielsen 1999).

## **1.7. Aim of this study**

The main idea of this work is to declare the goshawk's role in the population dynamics of grouse. Due to the interactive nature of the goshawk-grouse relationship, both participants are naturally affected. There have been two interesting processes in grouse dynamics: 6-7 year periodicity in the fluctuation and the long-term decrease in their

numbers (Linden & Rajala 1981, Ranta *et al.* 1995). Because grouse are the main prey of goshawks in Finland, there is special interest as to how the goshawk has responded to these changes; dietary, numerically and evolutionary.

## **2. Study area, material and methods**

### **2.1. Study area**

The study was carried out in the surroundings of the city of Oulu (65°00'N, 25°30'). The study area totals about 245 km<sup>2</sup>. It is typical coastal lowland with the highest hilltops reaching 100 m a.s.l. with a lot of rivers, small lakes and ponds. About 60 % of the total area is covered by a mosaic of forests and bogs. The proportion of bogs is very high, roughly half of the woodland area. At present, however, about 60 % of the bogs are dry (Kaila 1993). The forests are dominated by pine *Pinus silvestris* mixed with Norwegian spruce *Picea abies* and birch *Betula* sp. Modern forestry with clear-cuts and pine plantations tends to increase the mosaic pattern of the landscape. About 25% of the forests are in a mature stage. The diversity of successional stages is increased by the secondary succession of dried bogs and abandoned fields. Cultivated fields comprise 14 % of the area.

### **2.2. Collection of food remains and breeding data**

Food remains have been collected from 38 different goshawk nesting sites since 1965 in Oulu district. The total material contains some 4341 prey specimens. From 1965 to 1988 collection was fairly sporadic, then it became more systematic. Material collected from the surroundings was separated from that found in the nests. During the breeding season prey remains can be found outside the nest during the incubation period but also during the fledging period when goshawk broods forage near the nest for about one month after fledging (Sulkava 1964, Huhtala 1976, Kenward *et al.* 1993). From 1988 to 1994 collection was done at two week intervals to get a more detailed understanding of the prey choice during the breeding season. Breeding status of all known nesting territories was checked in the course of the collection of food remains. Nests without any signs of new building were considered unoccupied. Nests 'decorated' with fresh twigs were classified as occupied. In all successful nests, the nestlings were weighed, wing length measured and ringed. In most cases the eggs were also counted and measured. In some

cases, successful nesting wasn't noticed until the fledging period when noisy chicks revealed the nesting site.

### **2.3. Density indices of prey animals**

Density estimates of grouse were provided by The Finnish Game and Fisheries Institute. Estimates are based on the so-called route (until 1989) and triangle censuses (1989 on). In both methods three men patrols move in chains 20 m apart along a certain route (route censuses) or along compass lines designed in the form of triangles, each side 4 km long. Counters, mainly hunters, record all grouse in the line, determining their species, sex and age. Censuses are carried out in early August. The same triangles are used for snow track counting of mammals in February-March. I used yearly data from 10-12 triangles, which were situated within a circle with a radius of 30 km, the city of Oulu as a centre point. Data from 10-15 triangles outside that area were used to back up the estimates (more about method see Linden *et al.* 1996). Track indices of mammals were transformed to density estimates by a formula  $Z = 1.57 \times s/md$ , where  $Z$  = animals/1000 ha,  $s$  = number of tracks crossing the line,  $m$  = length of the census route and  $d$  = length of animal's day track (Formosov & Priklonski, cited in Havas & Sulkava 1987). Density estimates for other land birds were given by Mikola (1986), Rauhala (1994) and Inkeroinen & Mönkkönen (unpubl. data) and for waterfowl by Tynjälä (unpubl. data). All bird estimates except grouse were based on spring censuses. I calculated summertime estimates taking into account the productivity and mortality rate of different species found in handbooks or research reports (Coombs 1978, Rajala 1979, Valkeajärvi & Ijäs 1994). Density of adult grouse in August censuses included mortality caused by goshawks and was used in their spring density estimates. Productivity of mammals was also obtained from literature (Siivonen 1956, Angerbjörn 1986, Wauters & Dhondt 1990).

### **2.4. Radio tracking of goshawks**

In 1990-1995 goshawks were trapped in cages baited with live pidgeon *Columba livia*, provided by the university zoo. Trappings started in October-November and continued until the end of January. Usually there were 5-10 cages operating, excluding the weekends and latter half of December. The amount of hawks caught (including retrapped individuals) during 1990-95 was 38. Each trapped hawk was sexed, aged, weighed, wing length (straightened) measured and ringed. In a pilot study in winter 1990-91, 10 hawks were trapped but only 3 of them had been radio-tagged. The proper study began in October 1991. All hawks caught, excluding 2 individuals, were radio-tagged (Biotrack, TW-2 or TW-3 modifications) weighing 15 g. Tags with activity sensors were attached to central rectrics of hawks (Kenward 1978). The number of tagged hawks in 1991-1995 was 26, which was distributed as follows: 1991-92 5 males and 2 females, 1992-1993 3 males and 6 females, 1993-1994 1 male and 5 females, and 1994-1995 1 male and 4 females. Of these, 16 were accepted for final range and habitat analysis. Radio-tagged hawks were located by triangulation using portable radio receivers (RX-81, Televilt and CE-12, Custom Electronics of Urbana, Illinois) equipped with 3 or 5 element Yagi

antenna. Three or more bearings were required for a reliable estimate of the hawk's position. During tracking sessions each hawk was located 1-3 times per day and then finally at the night roost site. A low tracking frequency probably assured the independence of the locations (Kenward 1987). The whole data consisted of 331 day-time locations and 299 night-roost locations. An activity sensor on the radio-tag revealed when the hawk was sitting or flying, from the difference in pulse rates. An irregular pulse rate was detected when a hawk was eating prey. Using this cue it was possible to find foraging places and recognise the prey species. During 1990-1995 40 such occurrences were located. Additional winter prey were identified from pellets that hawks left in cages and also from a stomach of one radio-tagged hawk just killed by an eagle owl *Bubo bubo*. Preys the size of red squirrel *Sciurus vulgaris* and brown rat *Rattus norvegicus* could be recognised because their foraging lasted long enough to find the feeding site.

## 2.5. Museum data

Skin and bone samples of the Northern Goshawk were used in the morphological analysis from the collection of the Zoological museum of the University of Oulu. In total, 258 specimens were used in the analysis. The collection originates from northern Finland in 1961-1997. From each skin the following measurements were taken: body, length, tail, bill, tarsus and total length. Wing lengths were taken from flattened and straightened wings and tail length from the root of central retrics to the tip of them. Because these measurements were made during the preparation by several people, they are open to criticism. However, the same people have prepared hawks of both sex and age categories. When possible all measurements were checked from the museum skins. Skeletons were measured as follows: sternum length: from the tip of the *spina* to the median back edge of the *sternum*, breadth (median) and height (maximum), maximum lengths of *coracoid* and *femur*, *humerus*: from the proximal tip (*caput humeri*) to the tip of the trochlea, length of the pelvic bone (length of the *sacrum*) and breadth of it: distance between the lower (outer) edges of *acetabulum* (see Bährmann 1974). The outer bones of limbs were excluded from the analysis, because these bones are mostly left on the skin.

All birds were classified according to plumage, adults and juveniles. Cause of death was considered by grouping the sample together, birds in normal condition and starved birds. If the cause of death was not accurately determined we considered the adult male starved or under the risk of starvation if it weighed less than 700 g and a juvenile when weighing less than 650 g. The respective limits for females were 1100 g for adults and 1000 g for juveniles. If starvation was caused by injury, such birds were excluded from the analysis.

## **3. Results and discussion**

### **3.1. Dietary response of goshawks to decrease of grouse**

In spite of a remarkable decrease in grouse since the 1960s (Linden & Rajala 1981), their proportion in the diet of northern goshawk has remained relatively high (I, II, V). In northern boreal forests grouse constitute the only sufficiently large and abundant prey for goshawk sized raptors. Really, the black grouse is the most important bird species in boreal forests if estimated by biomass (Järvinen *et al.* 1977). In natural conditions therefore, the goshawk has relatively little scope for switching to other prey if the main prey decreases (c.f. McCowan 1975, Rohner 1995). Although considered as a generalist predator (Marti *et al.* 1993), the goshawk is actually fairly specialised in the north. Particularly in winter time when migratory birds are absent (McCowan 1975, IV). The only possible alternatives are mountain hares and red squirrels (I,IV). Of these, mountain hare is too large a prey for male goshawks but for females they constituted the main prey in winter (IV). Therefore, one might expect that the goshawk would decrease in proportion with the grouse. This has probably not taken place, despite the fact the goshawk was also heavily persecuted until 1989, before it became totally protected (Haukioja & Haukioja 1970, Saurola 1976, 1985, Väisänen *et al.* 1996). How did the goshawk persist with such expansive harvesting and the simultaneous decrease of the main prey, grouse? Harvesting was probably not very harmful because it removed mainly juveniles. It was probably compensated for by improved survival and reproduction of breeding birds (Haukioja & Haukioja 1970, Kenward *et al.* 1991). Since protection the juvenile mortality rate has not decreased because the majority of them, in particular males, die of starvation (Tornberg & Virtanen 1997, IV). However, the continual decrease of grouse has caused problems for goshawks. In southern Finland their population density has decreased (Linden & Wikman 1983, Forsman & Ehrnsten 1985). Also, elsewhere in Fennoscandia goshawks have been reported to be declining markedly, especially in Norway (Tommeraaas 1993, Halley 1996, Widen 1997). In the province of Oulu the breeding success of goshawks dipped in the 1980's when grouse had an exceptionally long low phase, but it recovered in the late 1980's. In my study area the number of occupied territories continually decreased during the study period in the

1990's, but this might fit within the limits of normal population fluctuation (c.f. Haapala *et al.* 1994, I, V). Goshawks have partly been able to compensate for the loss of grouse by switching to other prey found near settlements (I, II). Corvids could, as a relatively large prey, be a realistic alternate prey in winter. They were, however, not found in the diet during the winter study, but brown rats that were taken from the city dump were found (IV). Probably corvids, mainly hooded crows, forming huge flocks in winter are not an easy prey for goshawks. The significance of corvids probably increases the further south you go. In southern Ostrobothnia in western Finland corvids were the main prey in nestling phase, constituting up to 40% of prey specimens (Tornberg, unpubl.). In Häme grouse constituted 50% in the spring diet in the 1950's. Now that figure is about 15%. Corvids increased simultaneously in the spring diet from 10% to 28% and thrushes from 4% to 16% (Sulkava, pers. comm.). They were clearly the most important compensating prey type. In summer the changes in diet were not so pronounced.

### **3.2. Prey choice and timing of breeding**

Grouse were clearly the most preferred prey in early spring, especially the smallest species willow grouse and hazel grouse (II). The preference of grouse species and also other species varied markedly between years and within the breeding season (I, II, V). The main prediction of the optimal foraging theory predicts the diets accurately when the prey is immobile (Pyke *et al.* 1977, Sih 1990). However, in mobile higher vertebrates behaviour and learning changes the vulnerability of prey and the properties of predator (Hughes 1979). For example, the proportion of black grouse hens in the diet has been found to vary depending on the phase of the vole cycle, independent of its abundance in the field (Widen *et al.* 1987, Selås 1998, V). This is caused, probably, by the change in the behaviour of hens. The theory predicts a preference for large prey if handling times are equal for all preys. This is surely not the case. Changes in preference are clearly affected by changes in handling times. Chicks are easier to catch than adult birds. In spite of the preference shift to small prey in summer, mainly chicks over adult birds, adult grouse maintained their relatively high preference even then (II). The preferred species were not always very important in the nutrition of the goshawks, at least in summer. This might suggest that some prey species were exceptionally vulnerable to predation and were taken every time they were encountered. The weak point in testing OFT with diets is that they are assumed to be the outcome of prey choices. Yet, they are rather the outcome of successful attacks of a predator (Sih 1990, Sih & Moore 1990). Attacks are probably launched much more often, also for species not found in the diet (Cresswell 1995). Preference for prey size was clearest in late summer when goshawks switched to grouse chicks. Grouse broods can be kept as 'patches' where the predator can visit several times in succession (Sulkava 1964, Redpath *et al.* 1997). The predictability of such a patch probably depends much on the structure of the habitat. Grouse broods move mainly after hatching, which may be an anti-predator behaviour against avian predation (Sonerud 1985). If the habitat fragments it would be easier for the predator to locate the 'patch' again. This might be the case, at least for capercaillies, the most tightly bound to old forests (Wegge *et al.* 1990, Storaas *et al.* 1999). Soon, predator searching time decreases for the prey, which leads to an increase in the profitability.

The availability of suitable prey in early spring is crucial for starting breeding. In raptors, there is a clear division of roles in sexes (Newton 1979). Males provide the food for the female and brood until fledging (Sulkava 1964, Kenward *et al.* 1993a). During the radio-tracking study I found that females essentially reduced their wintering range and activities were concentrated near the breeding site by the beginning of March (c.f. Zieseimer 1981, Newton 1986). Females rarely moved more than one kilometre from the nest. However, it was not often I found many prey remains in the breeding sites before April. Females were probably still hunting in March. This is based on hare pellets found very often near the nests in early spring. Mountain hare is profitable prey for females due to its large size. After killing a hare, females don't need to move over wide areas searching for more prey for 3-5 days, which helps raise the body condition for egg production (Widen 1985, Newton 1986, Meijer *et al.* 1988).

Starting the breeding very early is probably selected for in goshawks (c.f. Lack 1954, Perrins 1970, Newton 1979). The egg laying period overlaps with the start of grouse displaying and leking, when they are more vulnerable to predation (Angelstam 1984, Willebrand 1988, Nielsen & Cade 1992, Valkeajärvi & Ijäs 1994). Starting early ensures that fledglings reach their independence respectively early, which gives them more time to train their hunting skills in relatively favourable conditions before the harsh winter time (II). Better survival rates in early broods have been documented in several raptor species (Marquiss & Newton 1984, Newton 1986, Village 1990). Thus, the timing of breeding in the goshawk supports Perrin's (1970) theory which is to start breeding as early as possible, in contrast to Lack's (1954) theory that predicts adjusting the highest demand of offspring in nestling phase to the best supply, which in the goshawk's case would be a much later date (II). On the other hand, availability of easily catchable nestlings and fledglings of song birds and corvids may be highest during the nestling phase of the goshawk (Toyne 1998). Selection for early breeding can cause difficulties in two other critical phases of the breeding in raptors, namely starting the breeding and hatching the chicks (Newton 1979). By postponing the breeding goshawks would avoid food shortages in early spring and early summer, in particular during cold springs, when grouse can cease leking and females gather in flocks (Marjakangas 1986, Elkins 1988, Nielsen & Cade 1992), which makes hunting them more difficult. At the hatching phase, the food demand of the hawk family sharply increases (Tolonen 1994, Kennedy & Ward 1994). In late springs males may have difficulties providing enough food, when the growth of vegetation impairs the perceptiveness of ground dwelling prey. Goshawks rely a lot on thrushes, corvids and their nestlings in this phase. (Linden & Wikman 1983, II, S. Sulkava, pers. comm.). If prey, even small ones, are not delivered to the nest often enough the weakest chick or chicks will easily die. It is at this time that brood reduction in goshawk is most common (Huhtala & Sulkava 1981).

### **3.3. Evolutionary response of goshawks to decrease of grouse**

The capability to catch small avian prey depends a great deal on the agility of the raptor. Being smaller is then beneficial (Andersson & Norberg 1981). One of the earliest hypothesis for reversed sexual size-dimorphism in raptors was the so-called small male hypothesis, the reasoning is based on the males higher capability to catch small prey,

which are encountered most frequently (Storer 1966, Reynolds 1972, Andersson & Norberg 1981, von Schantz & Nilsson 1981, Ydenberg & Forbes 1991, Hakkarainen *et al.* 1991). As already stated this skill may be crucial in early nestling phase. Because large grouse have remarkably decreased, goshawks have switched to corvids and passerines, which are smaller and have different flying properties than grouse (I,II). They are probably more capable of sudden turns than grouse, which rely more on power flight; rapid spurts and out-climbing (Pennycuick *et al.* 1995). Thus small, agile hawks could be better adapted to present conditions. This, really, seems to have happened in goshawks. Adult males have become smaller since the beginning of the 1960s (III). The faith of juveniles in their first year gives hints what is selected for and what against. All dead hawks, in particular ones that died of starvation, have failed in their life. Thus their quality might explain something about the properties that were selected against. Hawks that died in accidents may give a more random sample of the population. Probably goshawks have not yet been able to adapt to windows, cars and power lines. Starved juvenile hawks were larger than hawks that died in accidents in the 1960's to 1970's while the reverse was true in the 1980's to 1990's, which supports the idea of selection against large size of males at present. Not only did the size change but the shape, too. Adult males became longer winged and tailed, which also might increase agility and the ability to turn suddenly (Andersson & Norberg 1981). In contrast, the size of adults females increased. Females stay most of the breeding season in the nest, guarding the chicks. Inverse size relations in the sex of raptors is also assumed to depend on the female's properties. Large females can store more fat than males and can stand periodic interruptions in prey deliveries during the incubation period (Lunberg 1986, Korpimäki 1986). Large females can also defend chicks against predators or even from aggressiveness from the male (Smith 1982, Mueller & Meier 1985). These aspects may well be a reason why the size of the female increased. However, it is known that a female's size varies greatly over the distribution area, e.g. in Europe. Nest predators are the same in Europe, which goes against the latter theory. However, the predictability of prey becomes poorer in the north, which could, indeed, favour larger females according to the 'starvation' hypothesis (Lundberg 1986). Northern variants of the goshawk are larger than southern ones (Fischer 1980, Eck 1982). Female size could also be determined by the size of winter prey. Mountain hare was the most important prey for females in winter (IV). Also, capercaillie cocks are within a female's reach. Because of the decrease of grouse, hares may have become a more important food source for females (Höglund 1964, Widen 1987, Kenward *et al.* 1981, IV). In North America, the snow-shoe hare is the main prey of goshawks. The snow-shoe hare weighs only about 1.5 kg so males can also catch it. The reason why the degree of sexual dimorphism in North American goshawks is less than in Europe may be caused by this (Storer 1966, Kenward 1996). The different diets of the sexes decreases the competition between them, which was also presented as a cause for RSD (Reynolds 1972, Newton 1979, Andersson & Norberg 1981). The problem with this hypothesis is, however, that avoiding competition will not explain the reversed nature of sexual size-dimorphism.

### 3.4. Winter ecology of goshawks

Wintering hawks tended to be female (IV). They also tended to be more site tenacious, contrary to the general idea that females are less site tenacious in raptors and owls (Newton 1979). This has also been stated about goshawks in earlier studies (Sulkava 1964, Höglund 1964, Kenward *et al.* 1981, Widen 1985, Marcström & Kenward 1981, Halley 1996). To my mind it was reasonable that females had been more numerous in winter, because their food base is larger due to the fact males are unable to hunt hares. In a Swedish study goshawks ate almost barely squirrels in winter in boreal forests (Widen 1987). This probably resulted from a peak year of squirrels during the study years (Andren & Lemnell 1992). Red squirrels are suitable winter prey for goshawks and I also found a preference for squirrels when they were abundant in the first study year (IV). Almost all juveniles that were marked stayed wintering. More than half of them, however, died during the winter, some quite soon after marking. In these cases winter came suddenly with very cold periods and snow storms. It may, however, be possible that some hawks suffered from trapping and marking, although no injuries were found in those birds except one adult male that lost part of its head feathers. The mortality rate of juveniles in their first year has been stated to be very high 40-50%, also in more southern latitudes (Ziesemer 1982, Kenward *et al.* 1991). Therefore the mortality rate I found matches well with those estimates.

About one third of the marked hawks left the study area relatively soon after marking. Furthermore, one third of the hawks (33%) remained nesting in the study area or nearby, and the rest that wintered in the area disappeared quite suddenly just before the breeding season. Disappearance may also have been caused by battery-failures of the tags. Territory defences were clearly seen from March onwards. Once, a radio-marked adult male with a female tried to intrude in the middle of three territories. The attempt was not successful and the intruders were chased away. My results imply therefore that less than half of the goshawks were local birds. Yet I assume that many of those that moved may have had their own territory somewhere else. Three of these birds were in their third year but three were older. In Gotland, Sweden, where juvenile goshawks also mainly stay over winter, the population model has recently been able to build (Kenward *et al.* 1991, 1999). Juvenile males had a higher mortality rate and they started breeding at a younger age than females, on average. In the second year 82% of males were breeding but only 25% of females (Kenward *et al.* 1991). In open populations, like mine, the dynamics might be more complicated. Based on controls of ringed hawks in Oulu (n = 10), seven of them were controlled near Oulu (mean 23 km) and three were controlled abroad (mean 974 km) during the study period. This suggests that most juveniles may not disperse very far (see also Sulkava 1964, Halley 1996). It may, on the contrary, be possible that Oulu region attracts hawks based on controls of ringed hawks from 200 km south of Oulu. Hawks controlled as adults were born on average 71 km from their birth places (n = 5).

Wintering hawks in the study area ranged over areas extending from 2223 ha to 17030 ha. Males tended to have larger areas than females defined by the convex popygon method (Kenward 1987) (9894 km<sup>2</sup>, n=4, and 6484 km<sup>2</sup>, n=11, respectively). Goshawks ranged in similar sized areas than in the boreal forest of central Sweden (Widen 1985). Because the goshawk is considered an old forest species one would expect that size ranges would depend on the amount of old forest in the area (Kenward 1982). It might be

deduced that the goshawk needs a certain amount of preferred habitat in its range, when the amount of old forest should be independent of the size range. I found, however, a positive correlation between these variables, though not significant ( $r_s = 0.446$ , n.s.). On the other hand, the percentage of old forest in the range was inversely depending on the range size ( $r_s = -0.604$ ,  $p = 0.021$ ), which witness for the expectation.

What was the preferred habitat? The goshawk, expectedly, preferred old forest stands, above all, spruce forests but also deciduous forests, mainly birch stands. This is also well documented in other studies (Kenward 1982, Widen 1989, Iverson & al. 1996, Bright-Smith & Mannan 1994, Hargris *et al.* 1994, Drennan & Beier 1997). Goshawks also used much younger forest stands but clearly avoided open areas. Clear-cuts were an exception. They were rather highly ranked. Because in every location point the surroundings were also considered within a circle with 100 m radius, it often included many different habitat types, yet, less than random points. The high rank of clear-cuts might refer to perching at forest edges, when hawk might get access to species living in forests and those living in clear-cut or plantations. It must be remembered that the satellite-image was from 1987 and the last locations were from 1995 when clear-cut areas were already covered by young trees. It seems that goshawks are fairly well adapted to mosaic forest landscape produced by modern forestry provided that there is suitable prey available. However, forestry has reduced grouse numbers (Kurki *et al.* 1997), which harms goshawks. On the other hand, mountain hares might have benefited from forestry that creates new growth edible for hares. Female goshawks can kill hares and they constituted more than 70% of the diet by biomass. Males are, however, not able to kill hares. So they have, essentially, a narrower food base. The average hare biomass per km<sup>2</sup> is roughly 32 kg while that of grouse and squirrels is 18kg and 3kg respectively, excluding capercaillie males, that makes more than 10 kg out of the male's reach (II, V). Thus, females have 63kg prey/km<sup>2</sup> and males only 21kg! If grouse decrease still further goshawks will encounter poor wintering possibilities for males, which on the other hand is contrary to their tendency to stay in their territories (Sulkava 1964, Kenward *et al.* 1981, Halley 1996).

### **3.5. Goshawks and grouse. Are they coupled?**

Grouse constitute the main prey for goshawks throughout the year (II, IV). Although their proportion clearly decreases in winter, at least for females, it probably accounts for 10-50% by biomass (IV). During the breeding season goshawks accounted for the loss of between 2 and 22% of adult grouse, depending on species. In earlier investigations similar estimates have been stated with regard to raptor predation on grouse (Linden & Wikman 1983, Widen 1987, Redpath & Thirgood 1999, Nielsen 1999, Thirgood *et al.* 2000). Studies on grouse also show that mortality, caused mainly by goshawks, has been on the same magnitude (Angelstam 1984, Willebrand 1988, Valkeajärvi & Ijäs 1994, Wegge *et al.* 1990). Smaller species, like willow grouse and hazel grouse, were depredated more intensively than larger black grouse and capercaillie, which suffered relatively little from goshawk predation (V). In Scandinavia, goshawks killed more black grouse and capercaillie females, probably based on the lower availability of smaller grouse species being highly preferred in my study area (I, II, Widen 1985, Selås 1989). Predation on grouse chicks was fairly low, only 7% of hatched chicks. Estimating predation on juvenile

birds is problematic because very little remains are left, rarely allowing quantitative estimates (Sulkava 1964, Höglund 1964, Huhtala 1976, II). Therefore, the grouse chick proportion is underestimated in nest samples. It is possible to obtain more quantitative estimates in fledging time (Huhtala 1976, II). On the other hand, large prey is probably respectively overestimated, (Sulkava 1964). In Scotland, hen harriers *Circus cyaneus* took between 30 and 40% of red grouse chicks. However, hen harriers are probably much more efficient chick predators than larger goshawks. Predation on grouse is very much age related in autumn but very little is known about it. Taking non-territorial birds, floaters, into account much higher predation losses are found. This part of raptor and owl populations is the least well known (Rohner 1995, 1996, Nielsen 1999, Korpimäki & Krebs 1996). I calculated that 1/3 of wintering hawks may be non-territorials, which may even be a cautious estimate (IV). In addition, a good food supply will attract hawks from other regions (Kenward 1977, Kenward *et al.* 1981), which will yield higher raptor densities than the assumed balanced population model (see Kenward *et al.* 1991, 1999).

I found no functional response of the goshawk for varying grouse numbers. However, density changes of grouse were rather mild and goshawks presumably were able to kill grouse at maximum intensity and also at the lowest stated density level of grouse, but not essentially to raise the killing rate at higher densities. This suggests the response type that is typical for a specialist predator, not being able to switch to other prey (Korpimäki *et al.* 1991, Nielsen 1999). In fact, goshawks have potentially alternative prey during the breeding season in my study area (I, II), but in early spring, hawks nesting in remote sites do not have many real alternatives. Although goshawk is considered to be a generalist predator, the lack of suitable sized prey compels it to be a specialist in certain circumstances, as also found in other raptors (Galushin 1974, Korpimäki & Norrdahl 1989, Huhtala *et al.* 1996, Nielsen 1999). The shape of the functional response curve in goshawks is probably concave (type II) (Wikman & Tarsa 1980, I, but see Linden & Wikman 1983). Similar response types have also been found in peregrines *Falco peregrinus* and grey falcon *Falco rusticolus* (Redpath & Thirgood 1999, Nielsen 1999).

I could state a weak numerical response, expressed as number of goshawk nestlings/territory with a time-lag of one year for the density all grouse species pooled ( $r = 0.601$ ,  $p = 0.066$ ). Sulkava *et al.* (1994) comparing grouse densities of the previous year and the breeding performance of the goshawk contained significant positive correlations, which proves a time lag of one year (see also Huhtala & Sulkava 1981). In winter, study capture indices tracked the productivity of the local population (own obs.). In Alaska, sightings of goshawks peaked one year after a peak year for the snow-shoe hare (Smith & Doyle 1994). Thus, the total population (breeders and non-breeders) lag at least 14-15 months behind the grouse. Traditionally, time-lags are connected to the response pattern of mammalian predators, while avian predation would rather track prey density changes without time-lags (Galushin 1974, Korpimäki & Norrdahl 1989, 1991, Korpimäki 1994). This concerns, in particular, nomadic specialists that are not bound to stationary territories (Korpimäki 1993). The goshawk is a species that more or less stays all year round in its territory and neither are juveniles particularly migratory (Sulkava 1964, Höglund 1964, Saurola 1976, Marcström & Kenward 1981, Halley 1996). Because of this relatively high residency and synchronous fluctuations of grouse over large areas, time-lags are to be expected. Nielsen (1999) found gyrfalcons (breeding adults + nestlings) to lag two years behind ptarmigans in Iceland. In Canada, the breeding population of great

horned owls *Bubo virginianus* also lagged two years behind the snow-shoe hare peak (Rohner 1996). Rohner (1995) suggested that time-lag arises when the defence of territories decreases during prey decline creating scope for new territories. It may also rise from the lack of recruits to fill empty territories after high mortality rate of breeding birds in years of poor prey populations (Nielsen 1999).

The total response of the goshawk on grouse was inversely density dependent. Thus predation rate was higher in low grouse abundance than in peak densities. Similar total responses have been found in earlier goshawk studies (Wikman & Linden 1981, Wikman & Tarsa 1980) and in large falcons hunting on *Lagopus* species (Redpath & Thirgood 1999, Nielsen 1999). Predation patterns of this kind will prove a delayed density-dependence and destabilising effect of predator on prey population (Sinclair & Pech 1996). This relationship is based on predation of breeding birds, which corresponded with a time-lag in changes of prey. However, not much is known about the response of non-breeding birds, which are free to move to any site of good prey supply. Studies on goshawks in more southern regions and on great horned owls suggest that non-breeders are less residential and probably do not show extended delays for changes of prey (Kenward *et al.* 1981, Doyle & Smith 1994, Rohner 1996). This part of the population probably behaves similarly to nomadic raptors and owls, yet, not over such vast areas like true nomads. (Galushin 1974). By this dataset it is, however, not possible to say much about this issue because very little is known about the total response of the whole goshawk population, including breeders and non-territorial parts of a population. It is in any way clear that 'floaters' constitute a remarkable part of a goshawk population like they do in great horned owls (Rohner 1996, IV). They probably show aggregative responses for prey accumulations (Kenward 1977), which have a stabilising effect on prey fluctuations (Korpimäki & Krebs 1996).

In Southern Finland and also in nearby settlements in northern Finland alternative prey is available (I. S. Sulkava, pers.comm.). This enables relatively stable breeding for goshawks and probably a more rapid response for grouse density variations, which might dampen the grouse cycle. The goshawk operates in line with other general predators, like foxes and martens, which have the highest densities in the south (Linden *et al.* 1996). Hence, we might expect lower grouse densities on average and weaker cyclicity in southern Finland. According to Linden (1989) grouse populations in Southern Finland are partly non-cyclic, while strongest cyclicity and highest densities are found in Central Finland. This is what is stated for vole cycles: large number of general predators switching between prey types and dampening and shortening vole cycles in the south. In the north, where fewer generalist predators are present, resident specialists, mainly small mustelids, (*Mustela erimea*, *M. nivalis*) drive the vole cycle (Erlinge *et al.* 1984, Hansson 1984, Henttonen 1987, Korpimäki *et al.* 1991, Hanski *et al.* 1991, 1993). This might also suit the grouse cycle, with the exception being that the resident specialist is an avian predator in the north, but the same species acts as a generalist in the south, in connection with other generalists. The vole cycle clearly affects the grouse cycle via an APH type effect (Angelstam *et al.* 1984). Irregularities in the grouse cycle may, in fact, result from such interference, which increases as significance of the small mammal community increases as a result of changes in landscape structure. Grouse declined three times during the study period, in 1990, 1994 and 1997, which were also the crash years of voles. The disappearance of the regular 6-7 year pattern in the grouse cycle may partly result from

the strong impact of small mammal predators on grouse after vole crashes sensu APH. The fragmentation of forests have created suitable habitats for *Microtus* voles, which have increased average vole and predator densities, respectively (Henttonen 1989, Kurki *et al.* 1997). It has also been hypothesised that disturbances reducing breeding success of a population every now and then may sustain periodic fluctuation in a population that is otherwise regulated by a delayed density dependent manner (Kaitala *et al.* 1996). Korpimäki & Norrdahl (1997) suggested vole crashes to be one such a source of disturbance in grouse dynamics.

The general predation theory makes several predictions on the outcome of predator-prey interaction (Rosenzweig & MacArthur 1963, May 1973, Begon *et al.* 1990). Stability of the system is reached when the predator is relatively inefficient but unstable in the opposite situation. At some point in between the system tends to show limit cycles, which are stable in their own way (Taylor 1984). Theoretical and field studies imply that resident specialist predators acting in a delay are able to cause limit cycles in the predator-prey system, while nomadic specialists and generalists tend to dampen cycles (Korpimäki & Norrdahl 1989, 1991, Korpimäki 1993, Hanski *et al.* 1991,1993, Korpimäki & Krebs 1996). Goshawk fulfilled the main criteria of the theory. However, to get a better understanding of it, a more detailed analysis is needed of the goshawk's impact on grouse populations, especially during the non-breeding season. We need more data on the dynamics of non-territorial hawks, floaters, and also more data on grouse chick predation in late summer. To reach these goals intensive radio-telemetry studies on grouse and goshawks are needed in the same area simultaneously.

## 4. Conclusions

Continual decrease of the grouse since the 1960's in Finland has been considered to be a consequence of changes in the forest structure. Although grouse are the main prey of the goshawk, goshawk has probably not decreased so markedly. This witnesses for its adaptiveness that is documented in dietary and in evolutionary respect. Goshawk has thus found new sources of food. Evidently increase of the amount of clear-cuts and young forests has elevated the average density of voles but also that of hares that seem to form a remarkable source of winter food for females. Because hares are out of male's reach the controversy between the sexes in respect to food supply has increased, which probably explains the opposing changes in the size of the sexes. Males could, however, compensate for the losses of grouse by moving to settlements and dump sites where rats, corvids and domestic pigeons are available in winter. Changes in the structure of forests, the diet and the morphology of the goshawks may have several consequences to the relationship between the goshawk and the grouse. In spite that decrease of old forests has adversely affected the biotopes of the grouse, the fragmentation of the forests may also have altered the searching efficiency of the goshawks. Depending on the grade of fragmentation and the goshawks' possibilities to compensate for the loss of grouse by some alternative prey the final outcome in this predator-prey interaction may lead to dampening out of the cyclicality and a lower average density of the main prey as predicted by the general predation theory. Thus, goshawks, may have contributed to the decline of the grouse populations in Finland while they also have suffered and will suffer if the decline of the grouse will continue. Goshawks are not the main reason for the decline of the grouse but may play in concert with other predators the whole process ultimately hanging on the large scale changes in the forest structure caused by man.

## 5 References

- Andersson M & Norberg Å (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds with a size scaling of flight performance. *Biol J Linn Soc* (1981) 15: 105-130.
- Andren H (1992) Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* 73: 794-804.
- Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: review. *Oikos* 71: 355-366.
- Andren H (1995) Effects of landscape composition on perdition rates at habitat edges. In: *Mosaic landscapes and ecological processes* Hansson L Fahrig L et Merriam G (eds) Chapman et Hall London.
- Andren H & Lemnell P (1992) Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. *Ecography* 15: 303-307.
- Angelstam P (1984) Sexual and seasonal differences in mortality of the black grouse (*Tetrao tetrix*) in boreal Sweden. *Ornis Scand* 15: 123-134.
- Angelstam P Lindström E and Widen P (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* (Berlin) 62: 199-208.
- Angelstam P Lindström E & Widen P (1985) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. *Holarctic Ecol* 8: 285-298.
- Angerbjörn A (1986) Reproduction of mountain hare (*Lepus timidus*) in relation to density and physical conditions. *J Zool Lond* (A) 208: 559-568.
- Begon M Harper J L & Townsend C R (1990) *Individuals populations and communities*. Blackwell Sci Publ Boston.
- Beier P & Drennan J E (1997) Forest structure and prey abundance in foraging areas of northern goshawks. *Ecol Appl* 7(2): 564-571.
- Brull H & Fischer G (1984) *Das leben europäischer Greifvögel*. Gustav Fischer Verlag Stuttgart.
- Bährmann U (1974) Vergleichende osteometrische untersuchungen an rumpfskelett-teilen und extremitäten von einigen tagraubvögeln aus den familien Accipitridae Pandeionidae und Falconidae. *Zoologische Abhandlungen Staatliches Museum für Tierkunde in Dresden* Band 33 (3): 33-62.

- Charnov E L (1976) Optimal foraging: Attack strategy of a mantid. *Am Nat* 110: 141-151.
- Coombs F (1978) *The Crows*. BT Batsford Ltd London
- Cresswell W & Whitfield D P (1994) The effects of raptor predation on wintering wader populations at the Tynninghame Estuary Southeast Scotland. *Ibis* 136: 223-232.
- Cresswell W (1995) Selection of avian prey by wintering sparrowhawks (*Accipiter nisus*) in southern Scotland. *Ardea* 83: 381-389.
- Daan S Dijkstra C Drent R & Meijer T (1988) Food supply and the annual timing of avian reproduction. *Proc XIX Int Ornith Congress Ottawa*.
- Dixon K R & Chapman J A (1980) Harmonic mean measure of animal activity areas. *Ecology* 61(5): 1040-1044.
- Doyle F I & Smith J M N (1994) Population responses of northern goshawks to the 10-year cycle in numbers of snowshoe hares. *Studies Avian Biol* 16: 122-129.
- Eck S (1982) Weitere untersuchungen an *Accipiter gentilis gallinarum* (Brehm 1827). *Zoologische Abhandlungen Staatliches Museum für Tierkunde in Dresden Band 38* (3).
- Elkins N (1988) *Weather and bird behaviour*. T & AD Poyser Ltd Calton.
- Erlinge S Göransson G Högstedt G Jansson G Liberg O Loman J Nilsson IN von Schantz T & Sylven M (1984) Can vertebrate predators regulate their prey? *Am Nat* 123: 125-133.
- Errington P (1956) Factors limiting higher vertebrate populations. *Science* 124: 304-307.
- Fischer W (1980) *Die Habichte*. Die Neue Brehm-Bucherei Band 158 A Ziemsen Verlag Wittenberg Lutherstadt.
- Forsman D & Ehrnsten B (1985) Is the goshawk declining? *Lintumies* 20: 83-88 (in Finnish with English summary).
- Goszczyński J & Pilatowski T (1986) Diet of common buzzards (*Buteo buteo* L) and goshawks (*Accipiter gentilis* L) in nesting period. *Ekol Polska* 34(4): 655-667.
- Galushin V M (1974) Synchronous fluctuations in populations of some raptors and their prey. *Ibis* 116: 127-133.
- Haapala J Korhonen J & Saurola P (1994) Breeding and population trends of common raptors and owls in Finland in 1994. *Linnut* 30(2): 20-25 (in Finnish with English summary).
- Haartman von L Hilden O Linkola P & Tenovuo R (1963) *Pohjolan linnut värikuvin*. Otava Helsinki.
- Hagen Y (1952) *Rovfuglene og viltpleien Gyldendal*. Norsk forlag Oslo Norway (In Norwegian).
- Hakkarainen H and Korpimäki E (1991) Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? *Oikos* 61: 337-46.
- Hakkarainen H & Korpimäki E (1995) Contrasting phenotypic correlations in food provision of male Tengmalm's owls (*Aegolius funereus*) in a temporally heterogenous environment. *Evolutionary Ecology* 9: 30-37.
- Hakkarainen H Huhta E Lahti K Lundvall P Mappes T Tolonen P and Wiehn J (1996a) A test of male mating and hunting success in the kestrel: the advantages of smallness. *Behav Ecol Sociobiol* 39: 375-380.

- Hakkarainen H Koivunen V Korpimäki E & Kurki S (1996b) Clear-cut areas and breeding success of Tengmalm's owls *Aegolius funereus*. *Wildlife Biology* 2(4): 253-258.
- Halley D J (1996) Movements and mortality of Norwegian goshawks *Accipiter gentilis*: an analysis of ringing data. *Fauna Nor Ser C Cinclus* 19: 55-67.
- Hanski I Hansson L & Henttonen H (1991) Specialist predators generalist predators and the microtine rodent cycle. *J Anim Ecol* 60: 353-367.
- Hanski I Turchin P Korpimäki E & Henttonen H (1993) Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364: 232-235.
- Hansson L (1984) Predation as a factor causing extended low densities in microtine cycles. *Oikos* 43: 255-256.
- Hansson L (1994) Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecol* 9(2): 105-116.
- Haukioja E & Haukioja M (1970) Mortality rates of Finnish and Swedish goshawks (*Accipiter gentilis*). *Finn Game Res* 31: 13-20.
- Havas P & Sulkava S (1987) Suomen luonnon talvi. Kirjayhtymä Oy Länsi-Suomi Rauma (In Finnish).
- Helle P (1984) Effects of habitat area on breeding bird communities in Northeastern Finland. *Ann Zool Fenn* 21: 421-425.
- Henttonen H (1987) The impact of spacing behaviour in microtine rodents on the dynamics of least weasels *Mustela nivalis* - a hypothesis. *Oikos* 50: 366-370.
- 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 (in Finnish with English summary)
- Holling C S (1959) Some characteristics of simple types of predation and parasitism. *Can Ent* 91: 385-398
- Hughes R N (1979) Optimal diets under the energy maximisation premise: The effects of recognition time and learning. *Am Nat* 113: 209-221.
- Huhtala K (1976) On the food of the goshawk. *Suomen Luonto* 35: 305-309 (in Finnish with English summary).
- Huhtala K & Sulkava S (1981) Environmental influences on Goshawk breeding in Finland. In: Kenward R E & Lindsay I M (eds): *Understanding the Goshawk*. The International Association for Falconry and Conservation of Birds of Prey Oxford. p. 89-104.
- Höglund N (1964) Über die Ernährung des Habichts (*Accipiter gentilis* L) in Schweden. *Viltrevy* 2: 271-328.
- Iverson G C Hayward G D Kimberly T DeGayner E Lowell R E Crocker-Bedford C Schempf P E & Lindell J (1996) Conservation assessment for northern goshawk in Southeast Alaska. U S Forest technical report PNM 0(387).
- Kaila A (1993) (ed): *Yearbook of Forest Statistics 1992*. Institute of Forest Research Gummerus Jyväskylä.
- Kaitala V Ranta E & Lindström J (1996) External perturbations and cyclic dynamics in stable populations. *Ann Zool Fenn* 33: 275-282.
- Kastdalen L & Wegge P (1989) Why and when do Capercaillie chicks die- Preliminary results based on radio-instrumented broods in south-east Norway. *Int Grouse Symp IV*: 65-76.

- Keith L B Todd A W Brand C J Adamcik R S & Rusch D H (1977) An analysis of predation during a cyclic fluctuation of snowshoe hares. XIII Int Congr Game Biol: 151-175.
- Kenward R E (1977) Predation on released pheasants (*Phasianus colchicus*) by goshawks (*Accipiter gentilis*) in Central Sweden. Viltrevy 10(4): 79-109.
- Kenward R E (1978) Radio transmitters tail-mounted on hawks. Ornis Scand 9: 220-223.
- Kenward R E (1982) Goshawk hunting behaviour and range size as a function of food and habitat availability J Anim Ecol 51 69-80
- Kenward R E (1986) Problems of goshawk predation on pigeons and other game Proc XVIII Int Orn Congr: 666-678.
- Kenward R E (1987) Wildlife radio tracking. Academic Press London.
- Kenward R E (1996) Goshawk adaptation to deforestation: Does Europe differ from North America? In D M Bird & D E Warland (eds) Raptors adapting to modified environments. Academic Press New York. p. 233-243.
- Kenward R E Marcström V & Karlbom M (1981) Goshawk winter ecology in Swedish pheasant habitats. J Wildl Mgmt 45: 397-408.
- Kenward R E Marcström V & Karlbom M (1991) The goshawk (*Accipiter gentilis*) as predator and renewable resource. Gibier Faune Sauvage 8: 367-378.
- Kenward R E Marcström V & Karlbom M (1993) Post-nestling behaviour in goshawks *Accipiter gentilis* I The causes of dispersal. Anim Behav 46: 365-370.
- Kenward R E Marcström V & Karlbom M (1999) Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. J Anim Ecol 68: 1020-1033.
- Korpimäki E (1986) Reversed size dimorphism in birds of prey especially in Tengmalm's Owl *Aegolius funereus*: a test of the "starvation hypothesis". Ornis Scand 17: 236-332.
- Korpimäki E (1993) Regulation of multiannual vole cycles by density-dependent avian and mammalian predation? Oikos 66: 359-363.
- Korpimäki E & Norrdahl K (1989) Predation of Tengmalm's owls: numerical responses functional responses and dampening impact on population fluctuations of voles. Oikos 54: 154-164.
- Korpimäki E & Norrdahl K (1991) Numerical and functional responses of Kestrels, Short-eared owls and Long-eared owls to vole densities . Ecology 72: 814-826.
- Korpimäki E Norrdahl K and Rinta-Jaskari T (1991) Responses of stoats and least weasels to fluctuating food abundance: is the low phase of the vole cycle due to mustelid predation? Oecologia (Berlin) 88: 552-561.
- Korpimäki, E & Norrdahl K (1997) Can the Alternative Prey Hypothesis explain the occurrence of short-term population cycles of small game in Finland? Suomen Riista 43: 72-84 (in Finnish with English summary).
- Korpimäki E & Krebs CJ (1996) Predation and population cycles of small mammals A reassessment of the predation hypothesis. Bioscience 46: 754-764.
- Krebs CJ (1996) Population cycles revisited. J Mammal 77: 8-24.
- Kurki S Helle P Linden 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.
- Lack D (1954) The natural regulation of animal numbers. Clarendon Press London.

- Larsson T-B & Hansson L (1977) Vole diet on experimentally managed afforestation areas in northern Sweden. *Oikos* 28: 242-249.
- Levins R (1968) Evolution in changing environments. Princeton Univ Press Princeton.
- Linden H (1981) Estimation of juvenile mortality in the capercaillie *Tetrao urogallus* and the black grouse *Tetrao tetrix* from indirect evidence. *Finn Game Res* 39: 35-51.
- Linden H (1988) Latitudinal gradients in predator-prey interactions cyclicity and synchronism in voles and small game populations in Finland. *Oikos* 52: 341-349.
- Linden H (1989) Characteristics of tetraonid cycles in Finland. *Finn Game Res* 46: 34-42.
- Linden H & Rajala P (1981) Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland 1964-1977. *Finn Game Res* 39:13-34.
- Linden H & Wikman M (1983) Goshawk predation on tetraonids: Availability of prey and diet of the predator in the breeding season. *J Anim Ecol* 52: 953-968.
- Linden H Wikman M & Helle E (1989) Tetraonid populations in Finland 1988: A comparison between the route censuses and the wildlife triangles. *Suomen Riista* 35: 36-42 (in Finnish with English summary).
- Lindström J (1994) Tetraonid population studies - state of the art. *Ann Zool Fenn* 31: 347-364.
- Link H (1986) Untersuchungen am Habicht (*Accipiter gentilis*). Deutscher Falkenorden Blomberg.
- Lundberg A (1986) Adaptive advantages of reversed sexual size dimorphism in European owls. *Ornis Scand* 17: 133-140.
- MacGowan J D (1975) Distribution density and productivity of goshawks in interior Alaska. Final Report Federal Aid in Wildlife Restoration Alaska Dept of Fish and Game Juneau Alaska.
- Marcström V & Kenward RE (1981) Movements of wintering goshawks in Sweden. *Swed Wildl Res* 12: 1-36.
- Marcström V Kenward R E & Engren E (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *J Anim Ecol* 57: 859-872.
- Marjakangas A (1986) On the winter ecology of the black grouse, *Tetrao tetrix*, in Central Finland. *Acta Univ Oul ser A* 183. p. 87.
- Marjakangas A (1990) A suggested antipredator function for snow roosting behaviour in the Black grouse *Tetrao terix*. *Ornis Scand* 21: 77-78.
- Marjakangas A (1992) Pienpedot rajoittavat teeren poikastuotantoa. *Metsästäjä* 41(1): 32-33(in Finnish).
- Marti C D Korpimäki E & Jaksic F M (1993) Trophic structure of raptor communities: A three-continent comparison and synthesis. In: Power DM (ed) *Current Ornithology* 10: 47-137.
- May R M (1973) Complexity and stability in Model Ecosystems. Princeton University Press Princeton.
- May R M (1981) Models for two interacting populations. In: May R M (ed) *Theoretical Ecology*. Blackwell Sci Publ. p. 78-104.
- Maynard-Smith J (1974) *Models in Ecology*. Cambridge University Press England.
- Meijer T Daan S & Dijkstra C (1989) Female condition and reproduction: effects of food manipulation in freeliving and captive Kestrels. *The Auk* 106: 549-559.
- Mikola J (1985) Pöllöjen ravinnosta ja saalistuspaineesta Oulun Sanginjoella vuosina 1981-1984. Unpubl MS thesis Dept Zool Univ Oulu (in Finnish).

- Mueller H C and Meyer K (1985) The evolution of reversed sexual dimorphism in size A comparative analysis of the falconiformes of the Western Palearctic. Current Ornithology 2 Plenum Press New York & London.
- Mueller H C Berger D D & Allez G (1981) Age and sex differences in wing loading and other aerodynamic characteristics of sharp-shinned hawks. Wilson Bull 93(4): 491-499.
- Murdoch W W (1994) Population regulation in theory and practice. Ecology 75: 271-287.
- Myrberget S (1984) Population dynamics of willow grouse *Lagopus lagopus* in an island in North Norway Fauna Nor Ser C Cinclus 7: 95-105.
- Newton I (1979) Population ecology of raptors. Poyser Berhamsted
- Newton I (1986) The sparrowhawk Poyser Calton
- Newton I & Marquiss M (1984) Seasonal trend in the breeding performance of sparrowhawks. J Anim Ecol 53: 809-829.
- Nielsen O (1999) Gyrfalcon predation on ptarmigan: numerical and functional responses. J Anim Ecol 68: 1034-1050.
- Nielsen O K & Cade T J (1990) Seasonal changes in food habits of gyr falcons in NE-Iceland. Ornis Scand 21: 202-211.
- Nieminen M Tornberg R Sulkava S & Marjakangas A (1995) Habitat selection in the hazel grouse. Suomen Riista 41: 35-41 (in Finnish with English summary).
- Norrdahl K & Korpimäki E (1995) Mortality factors in a cyclic vole population. Proc R Soc Lond B 261: 49-53.
- Opdam P Thiessen J Verschuren P & Muskens G (1977) Feeding ecology of a population of goshawk (*Accipiter gentilis*). J Orn 118: 35-51.
- Paton P W C Messina F J & Griffin C R (1994) A phylogenetic approach to reversed size dimorphism in diurnal raptors. Oikos 71: 492-498.
- Perrins C M (1970) The timing of birds' breeding seasons. Ibis 112: 242-255.
- Pyke G H (1984) Optimal foraging theory: a critical review. Ann Rev Ecol Syst 15: 523-575.
- Pyke G H Pulliam H R & Charnov E L (1977) Optimal foraging: A selective review of theory and tests. Quart Rev Biol 52: 137-154.
- Rajala E (1979) Rastaiden (*Turdus* sp) pesimisbiologiasta Koillis-Lapissa. Unpubl MS thesis Dept Zool Univ Oulu (in Finnish).
- Ranta E Lindström J and Linden H (1995) Synchrony in tetraonid population dynamics. J Anim Ecol 64: 767-776.
- Rauhala P (1994) Kemin -Tornion seudun linnusto 2. Raahen Kirjatyö Oy (in Finnish).
- Redpath S M (1995) Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. J Anim Ecol 64: 652-661.
- Redpath S M & Thirgood S J (1997) Birds of prey and red grouse. London: Stationery Office.
- Redpath S M & Thirgood S J (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. J Anim Ecol 68: 879-892.
- Reynolds R T (1972) Sexual dimorphism in *accipiter* hawks: a new hypothesis. The Condor 74 191-197.

- Reynolds J C Angelstam P & Redpath S (1988) Predators their ecology and impact on gamebird populations. In: Hudson P J & Rands M R W (eds) Ecology and Management of Gamebirds. Blackwell Scientific Publ Oxford. p. 72-97.
- Rohner C (1995) Great horned owls and snowshoe hares: what causes the time lag in the numerical response of predators to cyclic prey. *Oikos* 74: 61-68.
- Rolstad J & Wegge P (1987) Distribution and size of capercaillie leks in relation to forest fragmentation. *Oecologia* (Berlin) 72: 389-394.
- Rosenzweig M L & MacArthur R H (1963) Graphical representation and stability conditions of predator-prey interactions. *Am Nat* 97: 209-223.
- Saurola P (197) Kanahaukan kuolevuus ja kuolinsyyt. *Suomen Luonto* 35: 310-314 (in Finnish with English summary).
- Saurola P (1985) Finnish birds of prey: status and population changes. *Ornis Fenn* 62: 64-72.
- Schantz T & Nilsson I N (1981) The reversed size dimorphism in birds of prey: a new hypothesis. *Oikos* 36: 129-132.
- Seiskari P (1962) On the winter ecology of the capercaillie *Tetrao urogallus* and the black grouse *Lyrurus tetrix* in Finland. *Papers Game Res* 22: 1-119.
- Selås (1989) Byttedyrvalg hos honsehauk *Accipiter gentilis* i hekketida. *Fauna Nor Ser C Cinclus* 42: 104-110.
- Selås V (1997) Annual variation in female black grouse vulnerability to goshawk predation during vole cycle: Is food quality of importance? In: Population ecology of forest-living hawks in Southern Norway PhD thesis Dept Biol and Nature Cons Agricultural Univ of Norway.
- Sih A (1993) Effects of ecological interactions on forager diets: competition predation risk parasitism and prey behaviour. In: Hughes R N (ed): Diet selection Blackwell Sci Publ. p. 182-211.
- Sih A & Moore R D (1990) Interacting effects of predator and prey behaviour in determining diets. In Hughes R N (ed): Behavioural Mechanisms of Food selection. NATO ASI Series vol G 20 Springer-Verlag Berlin Heidelberg.
- Siivonen L & Sulkava S (1994) Pohjolan nisäkkäät. Otava Keuruu (in Finnish).
- Siivonen L (1956) Suuri nisäkäskirja. Suomalaisen Kirjallisuuden Kirjapaino Oy Helsinki (in Finnish).
- Sinclair A R E & Pech R P (1996) Density dependence stochasticity compensation and predator regulation. *Oikos* 75: 164-173.
- Smith S M (1982) Raptor "reverse" dimorphism revisited: a new hypothesis. *Oikos* 39: 118-122.
- Solomon ME (1949) The natural control of animal populations. *J Anim Ecol* 18: 1-35.
- Sonerud G A (1985) Brood movements in grouse and waders as defense against win-stay search in their predators. *Oikos* 44: 287-300.
- Sonerud G A (1992) Functional responses of birds of prey: biases due to load-size effect in central place foragers. *Oikos* 63: 223-232.
- Stephens D W & Krebs J R (1986) Foraging theory. Princeton University Press.
- Storaas T & Wegge P (1987) Nesting habitats and nest predation in sympatric populations of Capercaillie and Black Grouse. *J Wildl Mgmt* 51: 167-172.

- Storaas T Kastdalen L & Wegge P (1999) Detection of grouse by mammalian predators: A possible explanation for higher brood losses in fragmented landscapes. *Wildl Biol* 5: 187-192.
- Storer R W (1966) Sexual dimorphism and food habits in three North American accipiters. *The Auk* 83: 423-436.
- Sulkava S & Huhtala K & Tornberg R (1994) Regulation of Goshawk *Accipiter gentilis* breeding in Western Finland over the last 30 years. In: Meyburg B-U & Chancellor R D (eds): *Raptor Conservation Today* WWGBP Pica Press. p. 67-76.
- Sulkava S (1964) Zur Nahrungsbiologie des Habichts. *Accipiter gentilis L Aquilo Ser Zool* 3: 1-103.
- Swenson J E (1991) Social organisation of hazel grouse. PhD thesis University of Alberta Edmonton Alberta.
- Tanner J.T (1975) The stability and the intrinsic growth rates of prey and predator populations. *Ecology* 56: 855-867.
- Thirgood S J Redpath SM & Aebischer N (2000) Raptor predation and population limitation in red grouse. *J Anim Ecol* (in press).
- Taylor R J (1984) *Predation*. Chapman & Hall New York.
- Tommerås P J (1993) Hønsø hauk i Liksvik - et offer for det moderne skogbruket. *Fauna* 46: 180-195.
- Tolonen P & Korpimäki E (1994) Determinants of parental effort: a behavioural study in the Eurasian Kestrel *Falco tinnunculus*. *Behav Ecol Sociobiol* 35: 355-362.
- Tornberg R & Huhtala K (1993) Kanahaukka ja metsäkanalinnut. Riistantutkimusosaston tiedote nro 122 Finnish Game Research Institute Helsinki (in Finnish).
- Tornberg R & Virtanen V (1997) When and why do goshawks die? *Linnut* 32 (1): 10-13 (in Finnish with English summary).
- Toyne E P (1998) Breeding season diet of the Goshawk *Accipiter gentilis* in Wales *Ibis* 140: 569-579.
- Underhill-Day J C (1988) The effect of predation by marsh harriers *Circus aeruginosus* on the survival of ducklings and game bird chicks. *Ardea* 77: 47-55.
- Valkeajärvi P & Ijäs L (1994) Comparison at breeding success between fed and unfed black grouse in Central Finland (in Finnish with English summary). *Suomen Riista* 40: 98-109.
- Ward J M & Kennedy P L (1994) Approaches to investigating food limitation hypothesis in raptor populations: An example using the northern goshawk. *Studies Avian Biol* 16: 114-118.
- Wauters L & Dhont; A A (1990) Reproduction and recruitment in a red squirrel population. *Trans the XIX IUGB Congress Trondheim 1989*: 157-162.
- Wegge P Gjerde I Kastdalen L Rolstad J & Storaas T (1990) Does forest fragmentation increase the mortality rate of capercaillie? *Trans the XIX IUGB Congress Trondheim*.
- Widen P (1985) Population ecology of the goshawk (*Accipiter gentilis L*) in the boreal forest. *Acta Univ Upsal* 777 PhD thesis.
- Widen P (1987) Goshawk predation during winter spring and summer in a boreal forest area of central Sweden. *Holarct Ecol* 10: 157-162.
- Widen P (1989) The hunting habitats of goshawks *Accipiter gentilis* in boreal forests of Central Sweden. *Ibis* 131: 205-235.

- Widen P (1997) How and why is the goshawk (*Accipiter gentilis*) affected by modern forest management in Fennoscandia? *J Raptor Res* 31: 107-113.
- Widen P Angelstam P & Lindström E (1987) The effect of prey vulnerability: goshawk predation and population fluctuations of small game. *Oikos* 49: 233-235.
- Wiklund C G (1996) Body length and wing length provide univariate estimates of overall body size in the Merlin. *The Condor* 98: 581-588.
- Wikman M & Tarsa V (1980) Food habits of the goshawk during the breeding season in southwestern Finland 1968-1977. *Suomen Riista* 27: 63-68 (in Finnish with English summary).
- Village A (1990) *The Kestrel*. Poyser London.
- Willebrand T (1988) Demography and ecology of a black grouse (*Tetrao tetrix L*) population. *Acta Univ Upsal* 148: 1-44.
- Williams GC (1966) *Adaptation and Natural selection*. Princeton University press Princeton N J:
- Väisänen R Lammi E & Koskimies P (1996) Muuttuva pesimälinnusto. Otava Keuruu (in Finnish).
- Ydenberg R C & Forbes L S (1991) The survival-reproduction selection equilibrium and reversed size dimorphism in raptors. *Oikos* 60: 115-120.
- Ziesemer F (1983) Untersuchungen zum Einfluss des Habichts (*Accipiter gentilis*) auf Populationen seiner Beutetiere. *Beiträge zur Wildbiologie* Häft 2.