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Prey selection of the Goshawk *Accipiter gentilis* during the breeding season: The role of prey profitability and vulnerability

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Seasonal changes in the diet of the Goshawk *Accipiter gentilis* during the breeding season were studied in northern Finland from 1988 to 1994. The Goshawk preyed mostly on grouse during the nest-building and the incubation period (60–70% by weight). Then shifting first to ducks and later during the nestling time to corvids, thrushes and pigeons. During fledging predation shifted to grouse chicks and leverets. Goshawks preferred grouse, mostly Willow Grouse *Lagopus lagopus* and Hazel Grouse *Bonasa bonasia* in the early phase of breeding. The preference for Black Grouse *Tetrao tetrix*, especially that of the females, increased throughout the breeding season. Capercaillies *Tetrao urogallus* on the contrary were avoided. Other prey species or groups had sharp 'preference peaks' at some part of the breeding season, ducks in May, corvids in June (nestling phase), pigeons in July and grouse chicks in August. Preferences found were not well explained by the predictions of the Optimal Diet Theory (active decisions of the predator to attack), but rather by the changes in the behaviour and the vulnerability of the prey. Goshawks adjusted their breeding time, following Perrins' (1970) theory, to start breeding as early as possible, thus ensuring the maximal food availability for the post-fledged juveniles.

1. Introduction

Predatory birds, as all birds in general, have three critical phases during breeding: production of the clutch, hatching and post-fledging time, when young become independent (Newton 1979). Food is involved with all these phases. During laying, females need extra food to produce the clutch. In experiments, where extra food was offered for laying females, larger clutches and an earlier laying date were observed (Newton & Marquis 1984, Korpimäki 1986a, Meijer et al. 1989). High availability of food is emphasized by the fact that the male alone provides the food for the laying female (Newton 1979). After hatching, the energy need of the family increases sharply (e.g. Tolonen & Korpimäki 1993). Finally, when the young become independent they need an abundance of easily catchable prey (Korpimäki 1986).

Birds have two ways to maximize the number of offspring entering the breeding population, firstly, by adjusting their breeding time optimally in relation to food availability and, secondly, by harvesting food optimally, i.e. maximizing energy gain in relation to energy invested for its provision. There are two main theories explaining the timing of the breeding in birds. Lack's (1954) theory states that the greatest food demand (during the nestling phase) is met with the largest food supply. Perrins' (1970) theory emphasizes the early phase of breeding by hypothesizing that birds tend to start breeding as early as possible.

The optimal diet theory (ODT) is the main conceptual framework which attempts to explain food harvesting problems (Schoener 1971, Pulliam 1974, Charnov 1976, Pyke et al. 1977, Pyke 1984, Stephens & Krebs 1986). The theory proposes that organisms tend to maximize their energy gain. This especially concerns predators (Schoener 1971). Therefore, consuming relatively large prey should be most profitable for the consumer. The theory further predicts that the diversity of the diet should increase as the abundance of the most profitable prey decreases and vice versa. Thirdly, the number of lower ranked prey do not affect the diet, but the absolute abundance of higher ranked prey does. ODT has been criticized because of its mechanistic nature, especially regarding the third prediction (i.e. Hughes 1979). According to Sih (1993) and Sih and Moore (1990), the prey choice is not solely the decision of the predator as ODT assumes, but the behaviour of the prey also affects the value (profitability) of the prey. The refuges, crypticity and activity of the prey also effect the encounter rate between the prey and predator. Thus increased preference is simply a result of better capture success, not the active decision of the predator to attack or not to attack (Sih & Moore 1990).

The Goshawk starts breeding in early spring (Huhtala & Sulkava 1981). The breeding season is relatively long, about 160 days or even more (Kenward et al. 1992). The breeding result is dependent on the abundance of grouse, which are their main prey in the boreal region (Höglund 1964, Sulkava 1964, Huhtala 1976, Huhtala & Sulkava 1981, Linden & Wikman 1983, Widen 1987, Tornberg & Sulkava 1991, Sulkava et al. 1994). Most losses in brood sizes take place during hatching or just after it (Sulkava et al. 1994), but there are no data on the survival of the early vs. late broods. The diet of the Goshawk, especially during the breeding season, is well described throughout Europe (e.g., Höglund 1964, Sulkava 1964, Opdam et al. 1977, Brull & Fischer 1984). There are, however, few studies where the availability of prey is considered (but see Selås 1989). When estimating the significance of the predator to the population dynamics of its prey, it is important to detect whether it selects its prey randomly or not (Sih & Moore 1990). Since the grouse population has remarkably decreased since the 1960s (Rajala & Linden 1981), there is special interest to see how the Goshawk has adapted to this change. Tornberg and Sulkava (1991) found that Goshawks hunted corvids more, for example, in the 1980s than in the 1960s.

The aim of this paper is to study any dietary changes of the Goshawk during breeding in relation to food availability, while keeping in mind the critical phases of the breeding cycle and the theories involved. Secondly, the hunting strategy of the Goshawk was studied by calculating its preferences for different prey types, using data on diets and availability. The results are examined in light of ODT and Sih's (1993) and Sih and Moore's (1990) more stochastic views.

2. 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´E). The study area totals about 245 km^2. It is typical coastal lowland, with the highest hilltops reaching 100 m a.s.l., characterized by 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 dried (Kaila 1993). Forests are dominated by pine *Pinus silvestris,* mixed with Norwegian spruce *Picea abies* and birch *Betula* sp. Modern forestry with clearcuts 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 make up about 14% of the area.

2.2. Collection of the food samples

Most prey remnants and pellets were collected in Oulu at nests and in their vicinity in 1988–94. In two territories older material was also available, which was then added to the data. Samples smaller than 14 specimens were excluded from the analysis. Altogether 2 159 prey specimens were identified from the samples collected from 12 different territories. The collection of the material was carried out fortnightly from early April to mid-August. During the nest-building and incubation phase, Goshawks feed near the nest on hummocks and tree trunks, where remnants were carefully collected each time to avoid double counting of prey (see Sulkava 1964, Huhtala 1976). After hatching, the male brings the prey to the nest, whereafter remnants were collected there. In the early nestling phase, normally very few remnants were found at the nest because the female cleans the nest carefully after each meal. Therefore, collecting was done with extra care at that time. In the late nestling phase, remnants often accumulate in large amounts when also the female starts to hunt.

After fledging, collection could often be continued for 3–4 weeks in the vicinity of the nest. The collection method gives quite a reliable estimate of prey distribution during the nest-building and incubation phase and again during the fledging phase, but it is somewhat biased during the nestling phase, when only feathers are left of juvenile birds, which gives limited possibilities for quantitative analysis (Sulkava 1964).

Chicks were weighed and wing-lengths measured since 1990 to determine the hatching date. Prey remnants were identified by using comparison material from the Zoological Museum at the University of Oulu. The remnants found of Black Grouse and capercaillies were sexed, based on their large sexual dimorphism. Prey weights were given by Von Haartmann et al. (1963–72) for birds. Weights of mammals and also of some birds were calculated from the collection at the Zoological Museum. The growth of leverets and grouse chicks were taken into account by measuring femur and tibia lengths of leverets and humerus lengths of grouse chicks. Lengths were compared with curves showing correspondence between weight and bone length. The growth curve for leverets is given by Mikola (1986), and the curve for grouse bones was calculated from the museum material.

2.3. Prey availability

2.3.1. Grouse

Grouse densities were given by the Finnish Game Research Insitute. These estimates are based on triangle censuses made by hunters in August. Three persons patrol, walking at a distance of 20 m from each other along the sides of a triangle, one side being 4 km long (Linden et al. 1989). These censuses give almost the real densities and breeding success of grouse: number of adults, number of young, average brood size and percentage of hens with brood. In this study data from 12 triangles, located within a radius of 30 km around the city of Oulu, were used. Because there were no density estimates of adult grouse in spring, I calculated spring and summer densities using the total grouse density of the previous year (for each species separately) as a starting point, and adult density of the year as an end point assuming linear mortality. To estimate the abundance of grouse chicks hatched, I assumed 30% nest losses (Linden 1981, Valkeajärvi & Ijäs 1994). In fact, I used this estimate for all ground-nesting bird species because nest predators do not seek nests of any particular species (Storaas & Wegge 1987). The average clutch sizes were given by Haartman et al. (1963–72). I estimated densities in July by comparing the number of hatched to that counted in August, making a slight correction downwards due to a concavity in the mortality pattern of young chicks (Linden 1981).

2.3.2. Ducks

Ducks were counted on small ponds and lakes during May and June in 1994–95. Each male found at the end of May was interpreted as a breeding pair (Koskimies & Väisänen 1988). Summer densities were calculated, assuming 30% nest losses and an average clutch size, as given by Haartman et al. (1963–72). I assumed a 10% monthly mortality for ducklings and 2% mortality for adult ducks.

2.3.3. Waders, doves, corvids and thrushes

Densities of these species are based on transect line censuses done during 1981–84 (Mikola 1986) and 1986–92 (Mönkkönen & Inkeroinen unpubl.) in the study area. Because waders are basically open terrain birds and transect lines were placed principally in woods, I corrected these estimates by taking into account the relative area of open terrain (fields and swamps). Densities of waders in fields were given by Rauhala (1994) from the Kemi region about 100 km north of Oulu. I used counts of swamp birds made by students during summer courses in the study area during 1982–1992 and those given by Rauhala (1994). A similar correction was made for corvids and the Fieldfare *Turdus pilaris*, but this was made by the amount of settlements because these birds (especially Hooded Crows *Corvus corone* and Magpies *Pica pica*) favour settled areas.

There were no realistic estimates of corvid densities near villages available in Oulu. Rauhala (1994) reports a corvid density of 6.7 pairs per km^2 in the Kemi region. Bird counts made by students in Hietasaari, a suburb of Oulu, during 1982–95 gave densities of 7.3 pairs per km^2 for magpies and 4.9 pairs per km^2 for crows. I used densities of 6 pairs per km^2 for both species in the countryside and 0.1 and 0.2 in forests, respectively. This calculation gave average pair densities of 1.2 pairs per km^2 for crows and 0.9 pairs per km^2 for magpies.

I assumed nest losses of 50% for corvids (Coombs 1978), 60% for large thrushes and 70% for smaller thrush species (Rajala 1979). About half of the redwings were assumed to have a second brood (Rajala 1979). The Wood Pigeon *Columba palumbus* was the only dove among the prey items during breeding. For this species I assumed two broods. I considered average hatching dates given by Haartman et al. (1963–72) for all prey species. A 10% monthly mortality rate was suggested for all young birds and a rate of 2% for adult birds.

2.3.3. Hares and squirrels

Mountain Hare *Lepus timidus* and Red Squirrel *Sciurus vulgaris* densities were based on triangle censuses made in the winters of 1989–1994, when snow tracks were counted (Linden et al. 1989). Tracks crossing the census line were transformed to densities, according to the formula $Z = 1.57 \times s/md$, where Z = animals/1 000 ha, s = number of tracks crossing the line, m = length of the census route and d = length of the animal's day track (Formozov & Priklonski, cited in Havas & Sulkava 1987). These calculations gave average densities of 9 individuals per km^2 for hares and 10 individuals per km^2 for squirrels. I assumed two broods for hares per breeding season (Siivonen 1956, Angerbjörn 1986). The first brood was assumed to be born in April–May and the second in June–July. I assumed that 1.5 young per female were born in the first brood and 3.0 in the second. I further assumed that 30% of broods were lost before weaning and that there was a 10% monthly mortality rate for leverets and one of 5% for adults. When calculating biomass, the growth of leverets was taken into account. According to the population model for squirrels by Wauters and Dhondt (1991), the first brood yields 24% of the potential recruits (all females reproduce maximally) and the second brood 15%. I assumed a 10% monthly mortality rate for young squirrels and a 5% rate for adults.

2.4. Data handling

When assessing preferences, the most frequent definition is the proportion of used, divided by the proportion of available (Krebs 1989). Using proportions, where the sum of parts is one, contains a serious problem of dependency. This prevents defining absolute preference/avoidance of habitat or prey. Further, this independency allows for no testing of values of preference indices. The compositional analysis offers a possibility to exclude such dependencies by using log-ratio transformation ($y_i = \ln(x_i/x_j)$, where x_i is the proportion of the ith resource class and x_j is any component of a composition resulting in each y_i being linearly independent (Aebischer et al. 1993). This transformation is done for each used and available resource class and individual. Pair-wise differences $d = Y_{used} - Y_{available}$ yields a data matrix, where Ho is $d = 0$ meaning random use of resource classes. Multivariate analysis was used to test the randomness of use. The test value Λ (Wilks' test) follows χ^2 distribution with df equaling the number of variables in the data after a transformation $- N \ln \Lambda$ (for more details, see Aebischer et al. 1993).

Rank order was assessed by calculating a matrix for each Goshawk pair, where use and availability of each resource class in each cell was compared as follows: $\ln(x_{ui}/x_{uj}) - \ln(x_{ai}/x_{aj})$ $(= Y_{ui} - Y_{ai})$, where x_{ui} is utilization of the ith resource and x_{ai} is the availability of the ith resource, respectively (see Aebischer et al. 1993). The means of several nests were calculated to yield a matrix, where the number of positive elements in each row directly gives the rank of each resource class, 0 being the worst and D – 1 the best (D = number of resource classes). The ratio of mean to standard error gives a t value (df = n – 1) pointing to where non-random use occurs.

2.5. Sources of error

Densities of prey in each month are given in Table 1. For species such as grouse, squirrels and hares the densities are averages for all study years. It is also known that populations of these animals may fluctuate greatly. Therefore, using averages calculated over years to represent their availability may be misleading, particularly when calculating preference estimates. During the study years, however, populations of these animals fluctuated only moderately. Grouse reached the highest densities in 1989 (23.5 indiv. per km^2) and 1993 (26.8 indiv. per km^2), while the lows were in 1991 (17.2 indiv. per km^2) and 1994 (17.9 indiv. per km^2). The squirrel's track index was highest in 1990 (16.7 tracks per 10 km) and lowest in 1994 (6.5 tracks per 10 km). Hares had two peaks, the first in 1990 (10.9 tracks per 10 km) and the second in 1994 (11.5 tracks per 10 km). The low phase was in 1992, when the index gave a value of 5.9 tracks per 10 km. Ducks were counted only during 1994 and 1995, and the latter year was not in the diet analysis. Duck populations also fluctuated remarkably (see Pöysä et al. 1995). During the study, Teals *Anas crecca* and Mallards *Anas platyrhynchos* had one peak and one low phase during 1994–95, representing the average situation (Pöysä et al. 1995). Thus, the densities of ducks used in analysis might describe an average for the study years. In spite of the heterogeneous sources of the availability data, causing a certain failure in estimates, this may not invalidate the idea of ranking the preferences for the most important prey species or prey classes.

The same availability of prey was assumed for all Goshawk pairs, which of course is not strictly true. However, all prey classes were probably available for all pairs. The largest variation in the availability for different pairs may have been in corvids and pigeons, which favour human settlements. Pairs living near urban areas had a higher availability of these prey. This especially concerns one pair living near the dump site of the city, which supported high numbers of corvids.

3. Results

3.1. Dietary shifts during the breeding season

Grouse species composed the most important part of the diet throughout the breeding season. Their proportion was highest in spring, it dropped to less than half (by weight) in June and rose again up to 60–70% during the fledging phase (Tables 2 and 3). The Black Grouse was the most important grouse species by both number and weight, and the capercaillie was the least significant. Migratory birds were added to the diet almost immediately after their arrival in May. At that time, ducks, mostly teals and mallards, were the most important. Corvids were consumed during the whole breeding season with the peak in June. Hooded Crows dominated in April and May, while magpies and Jays *Carrulus glandarius* dominated later in the breeding season. The proportion of juveniles of these corvids was about 70% in June–July. The proportion of juveniles was 70% for thrushes, and roughly 50% for waders and Wood Pigeons. Goshawks hunted relatively few ducklings. They made up only 14–27% of preyed-upon-ducks in June–July. Mammals were used during the whole breed-

Table 1. Densities of the most important prey species or prey classes during the breeding time. Values in the table are individuals per km^2.

	April	May	June	July	August
Willow Grouse	1.2	1.1	1.1	1.0	1.0
Black Grouse	6.3	6.1	5.8	5.6	5.4
Capercaillie female	2.0	1.9	1.8	1.8	1.7
Hazel Grouse	3.5	3.3	3.1	3.0	2.8
Grouse chicks			29.5	16.7	8.3
Ducks	0.4	0.8	1.9	1.8	1.7
Waders		4.9	9.9	11.5	10.8
Wood Pigeon	0.4	0.8	1.2	1.5	1.5
Corvids	4.1	4.0	7.5	7.9	7.6
Thrushes	0.1	6.3	17.9	21.7	20.5
Leverets	0.5	4.6	13.1	11.1	9.4
Red Squirrels	9.0	8.1	12.3	14.4	13.7

ing season. Red Squirrels and small mammals outnumbered leverets, while the latter were more important by weight especially late in the breeding season due to their growth. The diversity of the diet was highest in June (Table 2).

3.2. Changes in the preference of prey

The prey choice of the Goshawk was non-random during all months (MANOVA, $p < 0.01$). The data from August was not tested because of a

Table 2. Proportions of different prey by number during the breeding time. Each value is an average of proportions over several territories. Standard error of the mean is presented in parentheses.

	April		May		June		July		August	
	%	S.E	%	S.E.	%	S.E.	%	S.E.	%	S.E.
Willow Grouse	7.8	(2.3)	11.1	(2.6)	2.2	(0.9)	2.7	(0.8)	3.7	(2.4)
Black Grouse	21.9	(4.3)	16.9	(2.5)	8.0	(2.0)	7.1	(0.9)	5.5	(2.4)
Capercaillie	0.6	(0.6)	1.5	(0.4)	1.0	(0.5)	1.8	(0.6)	0.0	(0.0)
Hazel Grouse	26.8	(5.5)	16.6	(1.6)	5.4	(0.6)	5.4	(0.9)	1.2	(1.2)
Grouse chicks	0.0	(0.0)	0.0	(0.0)	6.8	(1.2)	23.7	(2.6)	40.9	(5.8)
Ducks	6.3	(2.7)	11.2	(2.5)	3.8	(1.1)	3.9	(1.0)	3.7	(2.4)
Waders	0.0	(0.0)	4.6	(1.2)	4.3	(1.1)	5.9	(1.7)	5.5	(3.3)
Wood Pigeon	1.0	(0.7)	1.9	(0.8)	4.4	(1.6)	4.6	(0.9)	2.9	(2.3)
Corvids	9.2	(3.0)	10.5	(3.5)	19.0	(2.7)	12.8	(1.3)	5.4	(4.2)
Thrushes	0.8	(0.5)	4.4	(1.1)	11.0	(1.7)	11.5	(1.4)	4.2	(1.8)
Small passerines	3.4	(1.2)	2.1	(0.8)	4.7	(1.1)	2.5	(0.7)	0.0	(0.0)
Other birds	2.8	(1.1)	1.9	(0.6)	6.2	(1.6)	3.1	(0.7)	0.6	(0.6)
Mountain Hare adults	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.1	(0.1)	0.0	(0.0)
Mountain Hare juveniles	0.7	(0.7)	1.6	(0.8)	6.0	(1.3)	4.8	(0.9)	11.6	(5.4)
Red Squirrel	11.3	(2.8)	6.5	(1.5)	12.9	(2.5)	7.6	(1.1)	13.6	(9.9)
Small mammals	7.6	(4.8)	9.3	(1.6)	4.2	(1.0)	2.5	(0.8)	0.6	(0.6)
Number of nests	9		9		10		12		4	
Diet width	6.7		9.6		12.5		9.7		4.7	

Table 3. Proportions of different prey by weight during the breeding time.

	April		May		June		July		August	
	%	S.E.	%	S.E.	%	S.E.	%	S.E.	%	S.E.
Willow Grouse	9.0	(2.8)	12.6	(2.8)	3.4	(1.4)	3.8	(1.1)	3.7	(2.5)
Black Grouse	38.8	(6.3)	33.6	(3.9)	20.7	(4.6)	14.9	(2.1)	7.2	(3.1)
Capercaillie	1.4	(1.4)	5.1	(1.4)	4.0	(2.0)	6.9	(2.1)	0.0	(0.0)
Hazel Grouse	20.4	(4.9)	11.2	(1.1)	5.2	(0.8)	4.5	(0.8)	0.5	(0.5)
Grouse chicks	0.0	(0.0)	0.0	(0.0)	1.9	(0.4)	23.9	(2.3)	52.3	(7.2)
Ducks	6.1	(2.6)	10.7	(2.8)	3.8	(1.0)	3.6	(0.9)	1.8	(1.2)
Waders	0.0	(0.0)	1.5	(0.4)	2.6	(0.6)	5.8	(1.4)	4.5	(2.5)
Wood Pigeon	1.0	(0.7)	1.9	(0.8)	6.0	(2.3)	5.0	(0.8)	2.0	(1.4)
Corvids	9.6	(3.7)	10.7	(3.5)	14.5	(2.5)	7.5	(0.7)	1.5	(1.1)
Thrushes	0.1	(0.0)	0.7	(0.2)	2.5	(0.5)	2.2	(0.3)	0.6	(0.3)
Small passerines	0.1	(0.0)	0.1	(0.0)	0.3	(0.1)	0.1	(0.0)	0.0	(0.0)
Other birds	2.2	(0.8)	0.7	(0.2)	3.5	(0.8)	1.4	(0.3)	0.1	(0.1)
Mountain Hare adults	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.8	(0.8)	0.0	(0.0)
Mountain Hare juveniles	0.7	(0.7)	3.3	(1.6)	19.1	(3.8)	13.0	(2.2)	18.2	(8.8)
Red Squirrel	6.1	(1.5)	3.8	(0.8)	10.8	(2.3)	5.4	(0.9)	7.5	(6.0)
Small mammals	4.6	(3.6)	4.2	(0.8)	1.8	(0.4)	0.9	(0.3)	0.1	(0.1)
Number of nests	9		9		10		12		4	

scarcity of cases (too few nests). Matrices described above were calculated for each month. Some groups of small species were left out, such as small passerines and voles, which were little used as prey despite being highly available.

The preference orders of each month are given in Table 4. The rank of the Hazel Grouse and Black Grouse females stayed rather high during the breeding season till August. In contrast, the rank of the Black Grouse males and the Willow Grouse dropped in June and July. Some prey species or groups had a 'preference peak' such as ducks in May and corvids in June. The preference for Wood Pigeons peaked in July. Grouse chicks rose monotonically in rank order till August. Capercaillie females, leverets, thrushes and squirrels were in the lowest rankings.

Statistical differences (t distribution, df = n – 1, $p < 0.05$) found between each rank are described in Fig. 1. During May, June and 3–5 July, the highest rank differed from the lower ranks. In April differences were found only between the last and higher ranks, and in August between the first and lower ranks.

3.3. What explains preferences?

To analyse causes for preferences, I made pairwise correlation tests to see what properties of the prey best explain its preference or avoidance. Four variables were chosen. The first variable, weight of the prey, was chosen assuming that Goshawks select their prey according to the energy maximization principle. This is also the best measure of the profitability, assuming that handling times for each prey are the same. The second variable chosen was the density of the prey, which is comparable to the encounter frequency of the prey and predator. It is inversely related to searching time. The third variable chosen was the combination of these two (weight × density), which measures biomass of the prey in the field. For the fourth variable I chose the proportion of the prey by weight in the diet (importance).

The results of the correlation tests are shown in Table 5. Density of the prey correlated negatively with rank in all months, as did biomass, except in August. Prey weight correlated positively with the preference in April and August.

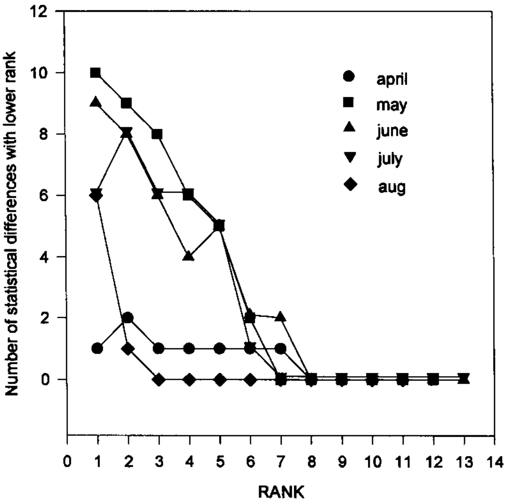

Fig. 1. Number of statistical differences of each rank with lower ranks in each month. See text for further explanation.

Because some prey classes include very different sized species, I also calculated separate ranks for teals, mallards, Hooded Crows and Curlews *Numenius arquata*. Analysis with these changes did not, however, alter the result, except that the correlation between weight and preference for April also changed to a negative one. 'Importance' most often correlated positively. Correlations were statistically significant only in May and August.

Table 4. Relative ranks of different prey during April–August. Highest rank is denoted by 1 and the lowest rank by 0.

	April	May	June	July	August
Willow Grouse	0.86	0.91	0.42	0.58	0.90
Black Grouse male	0.43	0.64	0.17	0.00	
Black Grouse female	0.57	0.73	0.75	0.92	0.80
Capercaillie female			0.09	0.00	0.08
Hazel Grouse	1.00	0.82	0.92	0.83	0.20
Grouse chicks			0.08	0.67	1.00
Ducks	0.71	1.00	0.58	0.50	0.40
Waders		0.36	0.25	0.17	0.30
Wood Pigeon		0.45	0.83	1.00	0.70
Corvids	0.29	0.64	1.00	0.75	0.00
Thrushes		0.27	0.50	0.42	0.10
Leverets		0.00	0.33	0.25	0.30
Red Squirrel	0.14	0.18	0.67	0.33	0.60

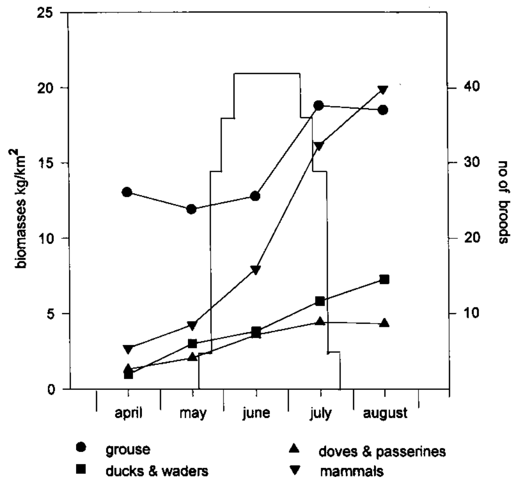

Fig. 2. Change in the amount of available biomass of four prey groups during the breeding season and timing of the nestling phase in 1990–1994. Histogram represents how many nests had nestlings at three-day periods.

3.4. Timing of breeding in relation to food abundance

The median hatching time was 27 May. The time span between the earliest and the latest hatch date was about 20 days. However, most hatchings took place within a week (Fig. 2). The median start of the laying took place on the 15th of April, provided that the incubation period was 42 days as reported by Sulkava (1964). There were no statistical differences between early and late clutches or brood sizes (clutch size 4.0 n = 17 before median day vs. 3.8 n = 13 after it and brood sizes 3.1 and 2.7 respectively). The biomass of grouse, ducks, waders, corvids and leverets clearly peaked after the nestling time.

4. Discussion

4.1. Prey selection

In the boreal zone grouse form the main food supply for the Goshawk as stated in many earlier studies (Höglund 1964, Sulkava 1964, Huhtala 1976, Linden & Wikman 1983, Wikman 1987, Tornberg & Sulkava 1991). The proportion of grouse in the Goshawk's diet has decreased since the 1950s, when it comprised 80–90% of the total catch during the nest building and incubation period (Sulkava 1964). This is caused by the continual decrease of the grouse populations since the 1960s (Linden & Rajala 1981). In the Oulu region a clear change in the diet took place in the 1980s (Tornberg & Sulkava 1991). However, grouse still make up a major proportion of the nutrition, especially in spring. Later in the breeding season Goshawks switch immediately to new prey species as they appeared (migratory birds, mostly ducks). Earlier during 'good grouse populations', no noticeable switching to other prey species during the first half of the breeding season was found (Sulkava 1964, Huhtala 1976, Tornberg & Huhtala 1993). In southern Finland, the diet also became more diverse relatively rapidly after hatching of the young hawks (Linden & Wikman 1983). Compared with other studies in Scandinavia, the diet contains more small grouse species like Willow Grouse and Hazel Grouse, but less capercaillies (Widen 1987, Selås 1989).

Food data collected from nests may include a bias because of the load size effect of the predator. At greater distances from the nests, small prey are not worth bringing to the nest, but rather are consumed by the predator itself (Pyke 1984, Stephen & Krebs 1986). Sonerud (1992) suggested that if the alternative prey is smaller than primary

Table 5. Spearmann correlations between rank and weight of prey, density, profitability and 'importance' of prey (proportion by weight in the diet) during April–August. Two-tailed significance levels * $p < 0.05$.

	April	May	June	July	August
Weight	0.306	– 0.028	– 0.274	– 0.248	0.687 *
Density	– 0.451	– 0.528	– 0.140	– 0.182	– 0.260
Biomass	– 0.393	– 0.424	– 0.550	– 0.484 *	0.105
'Importance'	0.357	0.662 *	0.371	– 0.061	0.706 *
N	7	12	13	13	11

prey, large prey become overestimated in the diet based on nest samples because the male himself consumes small prey items. This bias is difficult to estimate in the Goshawk because of its lurking hunting habits. If true, the preference values of small prey like squirrels, voles and passerine birds would be higher than estimated from nest samples. Supposedly the values for different months are comparable with each other, and preference estimates are relative rather than absolute. Male Goshawks often consume part of a larger prey. For example, the heads of the grouse have regularly been eaten when brought to the nest. Even half of the whole grouse may have been eaten, which can be deduced from the lack of, e.g. pelvic and leg bones in the prey remains.

The predation activity of the Goshawks was non-random throughout the breeding season. These kind of predators can have an affect on the community structure and the numbers of their prey (Sih & Moore 1990). The Goshawk does not appear to regulate grouse numbers (e.g. Angelstam et al. 1984). There may, however, be a greater impact than previously thought. High predation on young grouse, especially in late summer, and which probably continues till winter, may affect grouse numbers. Moreover, juvenile Goshawks tend to gather at sites of high prey abundance and are able to respond numerically to prey numbers (see Kenward et al. 1981). During all the months the 3–5 most preferred prey classes differed from the lower ranks, possibly forming the so-called optimal set of prey (see Charnov 1976). The composition of this 'optimal set' varied, however, from month to month. It is somewhat difficult to define any certain 'main prey', although this 'optimal set' always included 2–3 grouse species. Highly, but occasionally preferred prey types like ducks, corvids and Wood Pigeons are, in spite of their high rank, complementary rather than main prey.

Goshawks showed a preference for the size of prey in April and August, but weight and preference correlated negatively during other months. In April, Goshawks preferred medium-sized prey and avoided very small and very large prey species. Selås (1989) found that Goshawks in Norway (the prey composition resembling that in Finland) favoured large species, but he only looked at adult prey specimens. With smaller hawk species, such as, Kestrels *Falco tinnunculus* and the Sparrowhawk *Accipiter nisus*, a positive correlation between prey weight and preference during breeding have usually been found (Korpimäki 1985, Selås 1993). Creswell (1995) reported that Sparrowhawks hunted mostly on medium-sized prey in relation to its availability in winter in Scotland.

If Goshawks had hunted according to the Optimal Diet Theory, a positive correlation between weight (profitability) and preference should have been found (Charnov 1976, Pyke et al. 1977, Pyke 1984, Stephens & Krebs 1986). Sih (1993) notes that ODT predicts preferences well, when prey is immobile. The behaviour of the prey, on the contrary, changes encounter rates of the prey and predator, which affects the value of the prey.

ODT assumes that preferences are the result of active predator choice focusing only on the prey, which increases the net energy gain ('optimal set'). Sih and Moore (1990) note that predator choice is only one component of the preference. For example, certain prey types may be pursued but seldom caught, resulting in low preference values. Cresswell and Whitfield (1994) found that wintering hawks attacked almost all wader species available, but were successful only with some species. Obviously hawks attack almost all items available of suitable size, i.e. recognition of the prey is incomplete.

The high preference for grouse in spring is clearly due to their behaviour changes at the start of the reproduction period. Hens of Black Grouse and capercaillies depart from winter flocks to prepare for clutch production, which results in more movements and lower vigilance. This may increase their vulnerability to predation (Angelstam 1984, Widen et al. 1987, Marjakangas et al. 1991, Swensson 1991, Valkeajärvi & Ijäs 1994).

Small grouse species, such as the Hazel and the Willow Grouse, were the most preferred species. These species are territorial and probably easier to find by the predator than freely moving larger grouse, such as the Black Grouse and the capercaillie. Low preference for capercaillie females may be due to their larger size (but see Widen et al. 1987). The decreased preference for adult grouse later in the breeding season is mostly explained by their decreased activity (cocks finish their courtship, females incubate) and simultaneous growth of the vegetation, while predation may also have depleted their numbers.

Other important factors affecting encounter rates are crypticity and refuges (e.g. Hughes 1979, Sih & Moore 1990). Snow melt, which takes place on average in late April, affects the perceptibility of the grouse feeding on the ground. Cryptic species like the Hazel Grouse, the Black Grouse and the capercaillie females benefit from this. The Willow Grouse, on the other hand, may suffer as they, especially males, are still partially white in May. Higher consumption of and preference for Willow Grouse in May is possibly a result. Snow cover has been found to be a good predictor of the diets of owls (Sonerud 1986, Jacobsen & Sonerud 1993). During deep snow cover Tengmalm's Owls *Aegolius funereus* and Hawk Owls *Surnia ulula* consumed more Bank Voles *Clethrionomys glareolus* than microtus voles, because the former species move about more on the snow surface. The situation reversed when the snow melted and microtus became more vulnerable to predation.

The Hazel Grouse is an example of the importance of refuge. Linden and Wikman (1983) found that Goshawk predation on the Hazel Grouse increased at high densities, when a part of the population moved to less favourable habitats. Leverets may also be an example of a prey dependent on refuge. Their proportion by weight was high in August (20%), but the preference value was relatively low. Hares are active in twilight, when Goshawks, in contrast, are less active. Refuge use is thus one factor which confuses the correlation between profitability and preference.

Vulnerability, i.e. the prey's capability to hide or flee once it is detected and its defence ability after attack, is one of the most important factors affecting preference (Sih & Moore 1990, Sih 1993). Goshawks frequently catch young animals (Sulkava 1964, Opdam et al. 1977, Selås 1989). In my study this prey class was very vulnerable to predation and was extensively consumed during the nestling and fledging time. Handling times for young animals are probably lower than for adults, which increase their profitability (Charnov 1976). Young birds seem to be still more vulnerable than adults in late winter, as suggested by Cresswell and Whitfield (1994). Palmer (1981) showed theoretically that predators gain more energy by taking prey that have short handling times rather than opting for a higher net energy content. This factor may be one of the most important in removing the correlation between prey weight and preference in June and July.

Broods of birds form food patches, which predators can visit several times. Broods of altricial birds, like those of corvids, thrushes and pigeons are very predictable, for they generally do not move until post-fledging time. In contrast, broods of precoccious birds like grouse and waders move continuously and therefore are less predictable (Sonerud 1985). Broods of corvids may be easy to find, for young corvids are noisy and easily detectable (especially magpies) at the beginning of the fledging period, in late June. Experienced old Goshawk males obviously learn where corvid and pigeon territories and nests are usually situated, which shortens the searching time and thus increases the net energy intake per unit time. Korpimäki (1992) found that Long-eared Owls *Asio otus* preferred Common Voles *Microtus epiroticus*, although they were less adundant than other small mammals. The gregarious life style of Common Voles probably made them more profitable than more solitary prey species. The high preference for ducks in May might also be explained by the 'patch idea', because they may be found in certain small ponds or brooks year after year. The reason why Goshawks shifted from predation broods of altricial birds to grouse chicks in July may be related to the increased profitability of the grouse chicks due to their rapid growth. The quality of the habitat for grouse broods, due to forest fragmentation, may largely affect their being caught as suggested by Tornberg and Sulkava (1991).

The Goshawk's diet broadened in June. This is also found in other Goshawk studies (Sulkava 1964, Huhtala 1976, Linden & Wikman 1983) and, for example, in Kestrels (Korpimäki 1986b). There is a discrepancy between theory and reality because prey numbers usually increase during summer, which ought to reduce the variety of the diet according to ODT. Korpimäki (1986b) supposed that the lowered availability of voles, due to the growth of vegetation, and the high number of vulnerable alternative prey resulted in the variety of the diet. Earlier, during 'good grouse populations', Goshawks continued to consume more grouse even during the nestling phase (Sulkava 1964, Huhtala 1976, Tornberg & Huhtala 1993). Sulkava (1964) made direct observations in nests and found that grouse chicks made up more than 40% of the total number of prey. Korpimäki (1992) found, accordingly, that an increase in secondary prey did not affect the diet of the Long-eared Owl if the main prey (Common Voles) were readily available. Thus, the overall decrease in grouse numbers has steadily resulted in a dietary shift from grouse to alternative prey species in Goshawks during the nestling phase.

4.2. Timing of breeding

Goshawks start breeding relatively early in March, mostly depending on the temperature. Laying may start, at the earliest, in the beginning of April (Huhtala 1981, Sulkava et al. 1994). This is well synchronised with the start of courtship in grouse as their winter flocks are dissolved (Marjakangas et al. 1991). These events increase the vulnerability and thus the availability of grouse as stated above, enabling the higher hunting success of the male hawks. Meijer et al. (1989) considered that the initiation breeding in voles affected higher strike frequencies and the success of kestrels, which enabled the male to provide extra food for the female to produce a clutch. Gyr Falcons *Falco rusticolus* start breeding when ptarmigans arrive at their breeding territories (Nielsen & Cade 1990). Correspondingly, cold spells in spring hinder the courtship of grouse, which affects the start of laying in the Goshawk. This phenomenon may explain the correlations between the spring temperature and the laying date in the Goshawk (Huhtala & Sulkava 1981, Sulkava et al. 1994).

Prey abundance was lowest during the laying phase before the arrival of migratory birds, whereafter it increased till late breeding. Thus, the nestling phase did not fit with the highest food abundance as Lack's (1954) theory predicts. Rather the breeding strategy of the Goshawk follows Perrins's (1970) idea to start breeding as early as possible. This phenomenon is general in several predatory bird species (e.g. Newton & Marquiss 1984, Korpimäki 1986a, Meijer et al. 1989, Village 1990). Most brood losses in the Goshawk take place during the first few days after hatching (Sulkava 1964, Huhtala & Sulkava 1981, Sulkava et al. 1994). The diet in June was most diverse, related to difficulties in prey deliveries by the male. Thus, postponing the laying date would yield better food conditions for the nestlings. Predator birds seem, however, to invest more in post-fledging time by starting early, which yields better overall fitness for the parents (Drent et al. 1988, Meijer et al. 1989). Birds from early clutches have generally better chances to enter the breeding population than birds from late ones (Newton & Marquiss 1984, Village 1990).

Goshawks shifted hunting to growing grouse chicks during the fledging time. Before completion of the post-juvenile moult, by September, grouse are obviously relatively easy to catch. Another important prey class, leverets, grow beyond the hunting capability of the males during August (cf. Kenward et al. 1993). Hence, young hawks starting independent life in September encounter much poorer hunting choices than earlier hatched ones, and get less experience before the harsh conditions of winter.

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Selostus: **Kanahaukan ravinnonvalinta pesimäkauden aikana: Saaliin saatavuuden ja saalistettavuuden merkitys**

Kanahaukan saaliin pesimäaikaista saaliinvalintaa tutkittiin Oulun ympäristössä vuosina 1988–94. Näytteitä kerättiin 12 eri reviiriltä. Niistä määritettiin yhteensä 2 159 saalisyksilöä. Erisaalislajeista tai ryhmistä laskettiin kuukausittaiset lukumäärien ja painon mukaiset osuudet. Eri lähteistä, pääasiassa Riistantutkimuslaitoksen tilastoista kerättyjen saaliseläinten tiheyksien tai tiheysindeksien ja e.m. osuuksien avulla laskettiin eri saalisryhmille kuukausittaiset suosituimmuusindeksit. Kanahaukkojen pesinnän ajoittumista verrattiin tarjollaolevan ravinnon määrään.

Kanahaukat saalistivat eniten metsäkanalintuja sekä lukumäärän että painon mukaan arvioiden. Kanalintujen osuus oli suurimmillaan keväällä, 60–70% painon mukaan laskien pesäpoikasaikana 30–40%:iin, mutta nousten jälleen lentopoikasaikana yli 50%. Sekä lukumääräisesti että painon mukaan teeri oli tärkein yksittäinen kanalintulaji. Metson, josta saalistettiin vain naaraita, merkitys oli vähäisin. Tästä huolimatta kanahaukat saalistivat (suosivat) saatavillaoloon nähden eniten riekkoja ja pyitä.

Pesimäkauden edetessä kanahaukat saalistivat enenevässä määrin muita lintuja ja nisäkkäistä jäniksiä. Toukokuussa suosituin saalisryhmä olivat vesilinnut, kesäkuussa varislinnut ja heinäkuussa sepelkyyhkyt. Näiden saalisryhmien paino-osuudet ravinnossa eivät kuitenkaan missään vaiheessa ylittäneet kanalintujen osuutta. Kanalintujen poikasia alettiin saalistaa enenevässä määrin kesäkuun loppupuolelta lähtien. Heinä–elokuussa kanalinnunpoikasten lukumääräosuus läheni 30–40%, jolloin ne olivat myös suosituin saalisryhmä.

Optimaalisen ravinnonhankintateorian mukaan peto suosii saaliita, joista saatava energia saaliin hankintaan käytettyyn energiaan nähden on suurin. Näinollen pedon tulisi suosia suurikokoisia saaliita. Saaliin koko, 'hyötyisyys' selitti kuitenkin saaliiden suosituimuutta vain elokuussa. Ilmeisestikin saaliseläinten valintaan vaikuttaa, ei vain itse peto, vaan myös saaliin käyttäytyminen. Kanalintujen osuus ravinnossa ja niiden suosituimmuus on suurimmillaan aikaisin keväällä, jolloin ne soidinpuuhiensa vuoksi ovat ilmeisesti haavoittuvimmillaan. Tämä koskee erityisesti munintaan valmistautuvia kanoja, jotka runsaan ruokailuntarpeen vuoksi joutuvat helposti pedon yllättämiksi. Toinen saaliiksijoutumista lisäävä tekijä on talviparvien hajaantuminen. Kesällä muiden saalisryhmien suosituimmuus selittyi pääasiassa nuorten yksilöiden saalistuksella, jotka ovat aikuisia yksilöitä haavoittuvampia. Lentopoikasvaiheen aikana kanalintujen poikasten suosittuimmuus kasvoi voimakkaasti, mikä puolestaan selittynee niiden voimakkaasta kasvusta johtuvan 'hyötyisyyden' lisääntymisestä.

Kanahaukkojen pesinnänajoitus ei noudata Lackin (1954) teoriaa, jonka mukaan pesäpoikasaika osuisi runsaimman ravinnontarjonnan aikaan. Pikemminkin pesintä pyritään aloittamaan Perrinsin (1970) teorian mukaan niin aikaisin kuin se on mahdollista, jolloin runsaimman ravinnontarjonnan aika osuu poikasten itsenäistymisvaiheeseen. Ilmeisesti näin menetellen kanahaukat kykenevät parhaiten maksimoimaan lisääntymisiän saavuttavien jälkeläistensä määrän.

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