

## JUVENILE GROUSE IN THE DIET OF SOME RAPTORS

VITALI REIF<sup>1</sup> AND RISTO TORNBERG

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

KAUKO HUHTALA

Tehtaanpuistokatu 3, FIN-85310 Sievi, Finland

**ABSTRACT.**—Grouse (e.g., *Tetrao*) constitute a significant part of the diet for some raptors. Especially grouse chicks are important for several avian predators including species that normally prey upon small mammals. To evaluate the impact of avian predation on grouse, we need to know which raptors are hunting which species and when juvenile grouse suffer from the heaviest predation. Because grouse chicks are difficult to identify in prey samples based on morphological characteristics, we made an attempt to address this problem by measuring the humerus size of grouse chicks found in prey remains of Northern Goshawks (*Accipiter gentilis*), Eurasian Sparrowhawks (*Accipiter nisus*), Common Buzzards (*Buteo buteo*), and Northern Harriers (*Circus cyaneus*). Then, we plotted humerus sizes from prey remains against growth curves of chicks of Capercaillie (*Tetrao urogallus*), Black Grouse (*Tetrao tetrix*), Willow Grouse (*Lagopus lagopus*), and Hazel Grouse (*Bonasa bonasia*). We found that the size of grouse chicks in the diet was best explained by the mass of raptors, but not the fledging date of their young. Ranges of grouse size in the raptor diets were overlapping, suggesting that all four raptor species hunt grouse chicks at about the same dates. Pressure of the avian predator assemblage on juvenile grouse does not appear to be uniform; smaller grouse species suffer from heavier predation during a longer period than larger grouse.

**KEY WORDS:** Northern Goshawk; *Accipiter gentilis*; Eurasian Sparrowhawk; *Accipiter nisus*; Common Buzzard; *Buteo buteo*; Northern Harrier; *Circus cyaneus*; grouse; predation; Finland.

---

### LAGOPODOS JUVENILES EN LA DIETA DE ALGUNAS AVES RAPACES

**RESUMEN.**—El lagopodo (*Tetrao*) constituye una parte significativa en la dieta de algunas rapaces, en especial los pichones del lagopodo son importantes para muchos depredadores de aves incluyendo especies que normalmente se alimentan de pequeños mamíferos. Para evaluar el impacto de la depredación sobre el lagopodo, necesitamos saber cuales rapaces están cazado a cuales especies y cuando los juveniles del lagopodo se ven afectados por la mayor depredación. Debido a que los pichones de lagopodo son difíciles de identificar en los restos de presas basados en características morfológicas, hicimos un ensayo para resolver el problema mediante la medición del tamaño del número de los pichones de lagopodo encontrados en los restos del azor (*Accipiter gentilis*), el gavilán euroasiático (*Accipiter nisus*), el ratonero común (*Buteo buteo*), y el aguilucho norteño (*Circus cyaneus*). Posteriormente planteamos el tamaño del número de los restos de presas versus las curvas de crecimiento de, los pichones de *Tetrao urogallus*, *Tetrao tetrix*, *Lagopus lagopus*, y *Bonasa bonasia*. Encontramos que el tamaño de los pichones de lagopodo en la dieta se entiende mejor a partir de la masa de las rapaces y por la fecha del emplumamiento de los juveniles. Los rangos del tamaño del lagopodo en la dieta de las rapaces se sobre pusieron, lo cual sugiere que las cuatro especies de rapaces cazan pichones aproximadamente en las mismas fechas. La presión del ensamblaje de los depredadores aviares en los juveniles de lagopodo, es aparentemente uniforme; las especies menores de lagopodo sufren una mayor depredación durante un periodo mas largo que las especies de lagopodo de mayor tamaño.

[Traducción de César Márquez]

The tetraonids constitute a significant portion in the diet of some birds of prey. For some of them

(e.g., Northern Goshawk [*Accipiter gentilis*], Gyrfalcon [*Falco rusticolus*], Golden Eagle [*Aquila chrysaetos*]) small game are commonly-taken prey (Huhtala et al. 1996, Tornberg 1997, Sulkava et al. 1998, Nielsen 1999). For others, such as those that feed

---

<sup>1</sup> E-mail address: vitali.reif@oulu.fi

mainly on small mammals (e.g., Common Buzzard [*Buteo buteo*], Northern Harrier [*Circus cyaneus*], Eurasian Eagle-Owl [*Bubo bubo*], Ural Owl [*Strix uralensis*]), the tetraonids may become an alternative prey in poor vole (*Microtus* spp.) years (Angelstam et al. 1984, Korpimäki et al. 1990, Redpath and Thirgood 1999, Reif et al. 2001), when they can be an important source of food to support breeding.

Depending on their size and hunting capacity, raptors kill both juvenile and adult grouse (e.g., P. Sulkava 1964, S. Sulkava 1964, Tornberg 1997, Sulkava et al. 1998, Reif et al. 2001). There are few quantitative studies regarding raptor predation on grouse chicks (S. Sulkava 1964, Höglund 1964, Grønnesby and Nygård 2000, Thirgood et al. 2000), in part because the latter are difficult to identify to the species level in prey remains. Five grouse species (Capercaillie [*Tetrao urogallus*], Black Grouse [*Tetrao tetrix*], Hazel Grouse [*Bonasa bonasia*], Willow Grouse [*Lagopus lagopus*], and Ptarmigan [*Lagopus mutus*]) found in Fennoscandia come in a variety of sizes from 350 g (Hazel Grouse) to 4000 g (Capercaillie cock). The growth rate of their chicks varies correspondingly (e.g., Semenov-Tian-Shansky 1959, Lindén 1981, Klaus et al. 1990). Large raptor species might prey relatively little on grouse chicks generally (e.g., Golden Eagle; Sulkava et al. 1998) or mainly on chicks of large grouse species (e.g., Northern Goshawk; S. Sulkava 1964, Tornberg 2001). However, the latter soon escape predation of small raptor species, such as Eurasian Sparrowhawks (*Accipiter nisus*) and the Northern Harriers.

To assess the predation impact of the whole community of raptors on different grouse species, we need to know the variation in the size of grouse chicks in the diet of different avian predators. In our study area, goshawks, sparrowhawks, buzzards, and harriers hunt small game on a regular basis. The aim of this study was to determine how these predators partition this common food resource—grouse chicks. We used a large existing prey-remains collection of the Zoological Museum, University of Oulu, and published data. We expected that the selection of juvenile grouse by these predators would depend: (1) on the size of the raptor that generally accords with the size of the prey and, (2) because of rapid growth of grouse chicks and temporal variations in breeding times of the raptors, on the date of capture. In addition, we attempted to assess which species of grouse are most vulnerable to raptor predation and during which

time period this occurred. We compared the appearance and the growth of grouse chicks in the field with the size of juvenile grouse in the diet of these four avian predators during the late nesting period in July, when most prey remains accumulate in raptor nests.

#### MATERIAL AND METHODS

The prey material was collected in Finland in the following areas: Oulu (goshawk, sparrowhawk, harrier), Kuusamo (goshawk), and Central Ostrobothnia (harrier, buzzard). Most of the material was collected in Oulu (65°00'N, 25°30'E) and Central Ostrobothnia (64°00'N, 24°00'E). These areas represent coastal lowland with many small rivers and lakes. Roughly 67% of the area is covered by mosaic of spruce (*Picea abies*) and pine forests (*Pinus sylvestris*) mixed with birch (*Betula pubescens*). About half of the forested area includes bogs, a large number of them being drained. Cultivated areas with settlements are situated mainly in river valleys. Kuusamo (66°00'N, 29°00'E) is a rolling highland area, the highest hilltops reaching 450 m above the sea level. Area is also characterized by large lakes. Coniferous forests comprise more than 70% of the area, with fewer bogs than the previous area. Due to lower population density, the area cultivated is less in Kuusamo than in the Oulu-Ostrobothnia area.

The prey remains analyzed were collected during different years between 1966–2003 (Table 1). Prey remains and pellets were collected from the nests after fledging once a year. Prey remains for goshawks were collected also from the area surrounding the nest during the post-fledging period (after the young leave the nest, but stay in the nesting area). The total number of collected samples varied among the species as follows: goshawks, 32 (and 14 from nest areas); buzzards, 74; sparrowhawks, 14; harriers, 7. We assumed that most collected prey remains were accumulated in the nests shortly before fledging, because females often clean their nests when they rear small chicks (Dement'ev and Gladkov 1951, pers. observ.).

To determine the size of grouse chicks in the diet we measured the length of humeri. The humeri of juvenile grouse were distinguished from the adults' by the degree of ossification. There are four grouse species present in the study area: Willow Grouse, Black Grouse, Capercaillie, and Hazel Grouse. However, the bones of grouse chicks were not sorted by species because they could not be identified with certainty. When two opposite humeri of the same size were found, we counted this material as one animal.

We compared the size of grouse chicks (expressed in humerus length) found in the diet of each raptor at the end of its nestling period (and post-fledging period for the goshawk) with sizes of grouse chicks of different species derived from growth curves (Fig. 1). Given the scarcity of grouse remains in many nests, we were not able to consider each nest as a unit for analysis; therefore, each grouse chick was considered an experimental unit instead. Fledging dates of raptors were calculated by adding the length of the nestling periods (Cramp and Simmons 1980) to hatching dates. We calculated hatching

Table 1. Juvenile grouse in the prey-remain collections at raptor nests in Finland.

SPECIES	NO. OF	TOTAL	MEAN		YEARS OF COLLECTION
	SAMPLES WITH JUV. GROUSE HUMERI	NO. OF JUV. GROUSE HUMERI	HUMERI IN A SAMPLE	SE	
Northern Goshawk (nest)	21	40	1.9	0.18	1967, 1970-73, 1975, 1978, 1980, 1984, 1987-90
Northern Goshawk (nest area)	9	18	2.0	0.44	1994-96, 1998, 2001
Common Buzzard (nest)	14	22	1.6	0.29	1997, 1984, 1986-91, 1996
Eurasian Sparrowhawk (nest)	13	22	1.7	0.16	1985, 1988-91, 1995
Northern Harrier (nest)	7	19	2.7	0.62	1966, 1971, 1976-77

dates by estimating the age of chicks from wing lengths based measurement data on known-aged birds and a nonlinear-regression model:  $y = x^3 - 0.002x^2 + 0.325x - 0.534$  (Tornberg unpubl. data). The wing-growth pattern has been found to be fairly similar for raptors weighing around 1 kg (Kenward et al. 2000). For the sparrowhawk, we used a growth curve developed by Moss (1979). We found the following hatching dates (in Julian days) for different birds of prey: goshawk,  $154.18 \pm 0.67$  (SE; 2 June;  $N = 146$ ); buzzard,  $151.94 \pm 0.44$  (31 May;  $N = 282$ ); harrier,  $167.77 \pm 1.01$  (16 June;  $N = 52$ ); sparrowhawk,  $172.58 \pm 0.52$  (21 June;  $N = 90$ ).

The growth patterns of grouse chicks (in terms of body mass) were taken from Lindén (1981) for Capercaillie, from Klaus et al. (1990) for Black Grouse, and from Semenov-Tian-Shansky (1959) for Hazel and Willow grouse. For the latter two species, the growth patterns were given with calendar dates without exact age reference; therefore, we aged those Hazel and Willow grouse with given masses according to our own observations and by comparing their mass/age ratios to that of Black Grouse. The body mass of chicks was converted into humerus length

using a curve calculated from material of the Zoological Museum, University of Oulu (Power model:  $y = 4.8104x^{0.4234}$ ,  $r^2 = 0.962$ ,  $N = 16$ ,  $P < 0.001$ ; Fig. 1). Given the lack of data for newly-hatched chicks, the growth curves start at the age of 10 d. The hatching time of grouse was obtained from literature (von Haartman et al 1963-72, Lindén 1983, Marjakangas and Törmälä 1997), P. Helle (pers. comm.), and our own observations. Variation of hatching dates is available only for Black Grouse studied by radiotelemetry in Kainuu, 200 km east of Oulu (Marjakangas and Törmälä 1997, Marjakangas unpubl. data). The mean hatching date for 126 Black Grouse broods in 1991-95 was  $165.8 \pm 0.421$  Julian days (14 June). We assumed that the correspondent time span of hatching period was similar for all other grouse species.

Because sample sizes differed among the raptor species, and were relatively small for all but goshawks, only variations in mean grouse size in the diet (Fig. 2) were tested statistically. Correspondence of the size of juvenile grouse in the diet to the size of different grouse species in the wild was analyzed only visually on the graphs (Figs 2-4). Capability of the raptors to kill juvenile grouse of different size (i.e., the whole size range; Fig. 4) was derived based on single specimens of maximal and minimal size. In order to find the time period when juvenile grouse suffer from the heaviest predation, we plotted dimension zones on graphs that corresponded to the full ranges of grouse size taken in raptor diets. On the time scale, these "predation zones" begin at the point when any of the grouse species reaches the minimal size hunted by the raptor (Figs. 3a-d). The growth curves of grouse species plotted over the zones indicate when grouse grow in and out of the "predation zones." This analysis was done based on the assumption that the full range of grouse size in raptor diet does not change through the summer. Because all these raptors are capable of killing even adults of the smallest grouse, the "predation zones" are not limited on the right side (toward the end of the summer). These zones, when plotted together indicate an overlapping area in which the size of grouse chicks makes them vulnerable to predation by all four raptor species (Fig. 4).

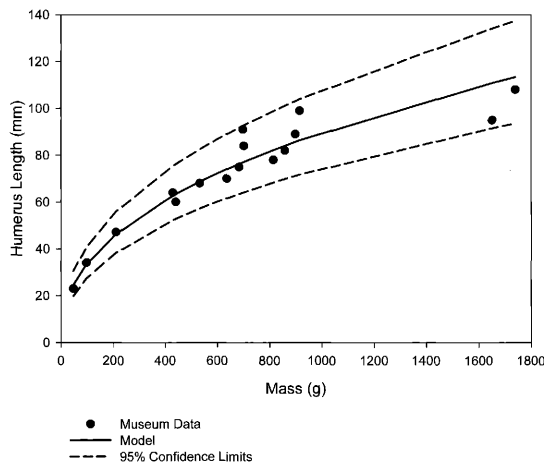


Figure 1. Model employed to estimate juvenile grouse humerus size based on mass.

RESULTS

The size of juvenile grouse (expressed as humerus length) found in the raptor nests differed

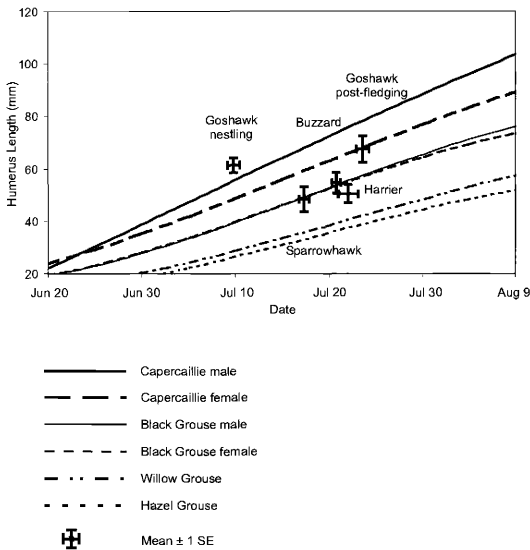


Figure 2. Mean size of humeri of grouse chicks in the diet of raptors in relation to fledging dates of raptors. The growth curves of humeri of different grouse species are also presented (see Materials and Methods). Crosses show relationship of fledging periods (horizontal bars) to humeri lengths of grouse remains (vertical bars). For Northern Goshawks two crosses are shown; (1) late nestling period (about fledging date) and (2) data collected during the post-fledging period.

significantly among the species (one-way ANOVA,  $F = 11.64$ ,  $P < 0.001$ ). The grouse chicks in the prey remains of goshawks were larger than those from the nests of other raptors (Tukey test: sparrowhawks,  $P < 0.001$ ; buzzards,  $P < 0.05$ ; harriers,  $P < 0.001$ ; Fig. 2, Table 2). The largest grouse chicks were also found among the goshawk prey, whereas sparrowhawks killed the smallest grouse (Fig. 2, Table 2). During the post-fledging period, the goshawks killed larger grouse chicks ( $\bar{x}$  length = 68 mm) than during the late-nestling period (62 mm;  $t = -2.26$ ,  $df = 56$ ,  $P < 0.05$ ). Using stepwise-linear regression, we found that the size of the grouse chicks in the diet was explained by the mass of the raptor female ( $F = 14.5$ ,  $B = 0.0116$ ,  $R^2 = 0.26$ ,  $P < 0.001$ ), but not by the date of fledging or mean mass of the male.

We plotted variations of grouse size in the raptor diets against the growth curves of grouse according to the time when the prey remains were presumably accumulated (Figs. 3a–d). This enables visual analysis of the correspondence between the grouse size in the diet and the size of chicks of different

grouse species in the wild at the same time. The smallest chick (the minimal value of humerus size) was found in the sparrowhawk nests (Fig. 3b). According to the regression model, this chick's mass was 84 g, which corresponds to the age of about 10 d for Capercaillie, 20 d for Black Grouse, 25 d for Willow Grouse and Hazel Grouse. Grouse chicks taken by goshawks in the nestling period were clearly larger than chicks of any grouse species (Fig. 2). Sparrowhawks delivered chicks to the nest around the size of the Black Grouse, which were larger than Willow and Hazel grouse chicks but smaller than female Capercaillie chicks. Chicks killed by buzzards were closest to the size of Black Grouse chicks, but were smaller than female chicks of Capercaillie and larger than Willow Grouse chicks. The size of grouse chicks taken by harriers was close to the size of Black Grouse, and larger than that of Willow Grouse chicks. Finally, grouse chicks found in goshawk diet during the post-fledging period were about the size of female Capercaillie, but smaller than male chicks of Capercaillie and larger than Black Grouse chicks (Fig. 2).

The lowest size limit of the “four-species predation zone” (i.e., when grouse chicks were hunted by all the raptor species) was 45-mm humerus, which was limited by the goshawk's diet (Fig. 4), and corresponds to the age of about 20 d for Capercaillie, 30 d for Black Grouse, 35 d for Willow Grouse, and 40 d for Hazel Grouse. The upper size boundary of the zone (65 mm humerus) is limited by the harrier's diet and ca. corresponds to 30-d-old males and 35-d-old females of Capercaillie, 45-d-old Black Grouse, 65-d-old Willow Grouse and older than 80-d (adult-size) Hazel Grouse.

#### DISCUSSION

The size of grouse chicks in prey remains of raptor species differed significantly. However, variances of sizes within each class overlap considerably (Fig. 4). Thus, we were not able to determine exactly which grouse species each raptor was taking. We found that the goshawk took relatively larger grouse chicks than sparrowhawks (Fig. 2). This was clearly related to the size of the raptors (Table 2). In the diet of goshawks, grouse chicks comprised 7% in June, 24% in July, and 41% in August by number (Tornberg 1997). This can be explained by the growth of the different grouse species, which makes them more profitable as a food item toward late summer. In the beginning of July, only the Capercaillie chicks seem to reach the size that

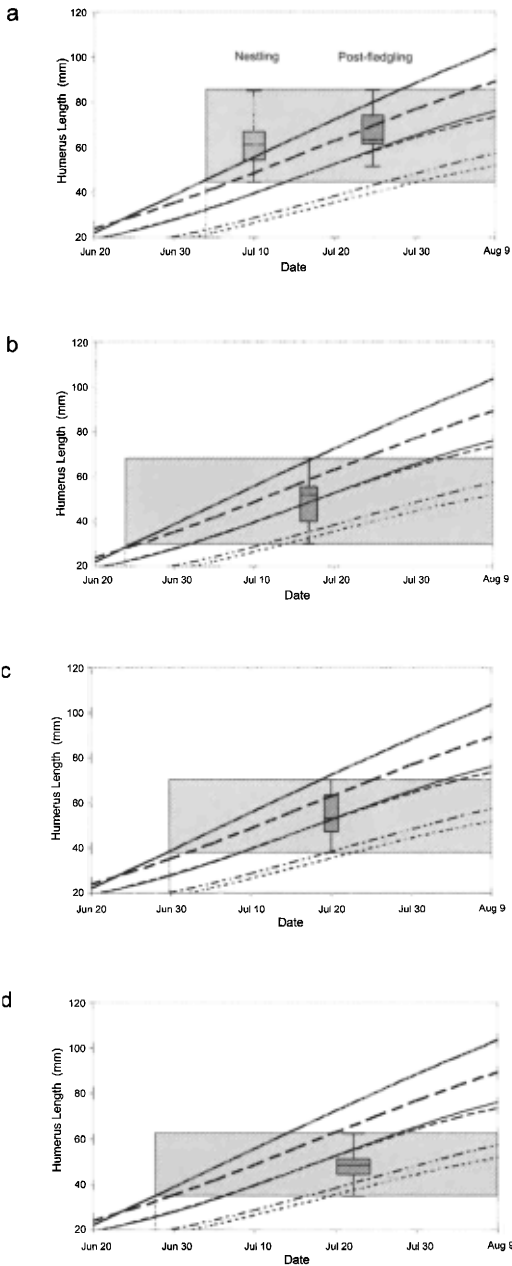


Figure 3. The size range of humeri of grouse chicks in the diet of raptors in relation to fledging dates of raptors: (a) goshawk, (b) sparrowhawk, (c) buzzard, and (d) harrier. The boxes contain the median and the 50% of values falling between 25th and 75th percentiles, the whiskers represent the highest and the lowest value. The position of the boxes on the date scale correspond to the mean fledging date and the width of the boxes is  $2 \times SE$  (same as horizontal bars in Fig. 2). The growth curves

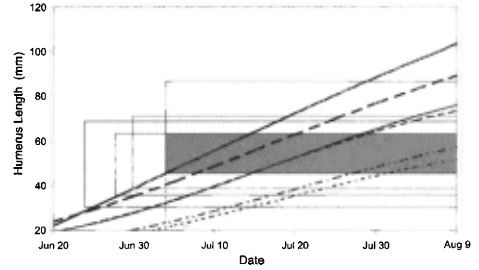


Figure 4. Overlap of size range of humeri of grouse chicks in the diet of raptors. The empty boxes are the size range (correspond to the shaded boxes in Fig. 3) and the growth curves of grouse species as in Fig. 2. The overlap (the shaded zone) indicates the time period when all the raptor species can hunt the grouse of given size range.

is suitable for the goshawk, while in August chicks of the smallest grouse species, Hazel Grouse, are also large enough to be taken (Fig. 3a). This fits with S. Sulkava's (1964) and Tornberg's (2001) findings that goshawks hunt chicks of Capercaillie and Black Grouse relatively more frequently than smaller grouse species. However, the mean size of juvenile grouse found in goshawk nests was larger than that of available Black Grouse and Capercaillie chicks. This could be due to feeding young hawks on the nest during post-fledging period or because of large age difference between the chicks (the youngest stays on the nest long after the older ones have left).

For sparrowhawks, grouse are not very important prey (P. Sulkava 1964). The mean size of chicks taken by sparrowhawks were closest to the size of Black Grouse (Fig. 2). This pattern appears reasonable, because grouse chicks are usually found at the end of the Sparrowhawk's nestling period, which may result from the females' hunting. At that time Black Grouse chicks are ca. the same mass as adult Hazel Grouse, which sparrowhawk females often kill in spring before laying (P. Sulkava 1964). This may have contributed to our finding that raptor female size appeared to be the best predictor for the size of juvenile grouse in the diet.

←

of grouse species as in Fig. 2. The shaded boxes are the "predation zones" and indicate the whole size range of grouse in raptor diet (see Materials and Methods).

Table 2. The mean body mass of the avian predators (Cramp and Simmons 1980) and mean body mass of young grouse in raptor diet (estimated with regression model) during the raptor fledging period.

	MEAN MASS OF RAPTORS, G		MEAN MASS OF GROUSE, G	
	MALE	FEMALE	MEAN	SD
Eurasian Sparrowhawk	140	260	261	125
Northern Harrier	350	530	274	95
Common Buzzard	690	860	322	141
Northern Goshawk	860	1410	428	146

Grouse, especially juveniles, are important alternative prey for the Common Buzzard (Reif et al. 2001), which took on average larger grouse chicks than sparrowhawks (Fig. 2). The buzzard is capable of hunting even adult Black Grouse (Reif et al. 2001). Therefore, at the end of nestling period the maximal size of grouse in the buzzard's diet most likely was limited by available chicks in the field (Fig. 3c). Thus, during the post-fledging period, buzzards probably hunt larger grouse chicks too. Scanty data for harriers also suggested that grouse were a fairly prominent part in their diet during poor vole years (Thirgood et al. 2000, R. Tornberg and K. Huhtala unpubl. data). The mean sizes of chicks found in the harrier's diet corresponded best to those of Black Grouse chicks (Fig. 3d). However, they could be also large chicks of Willow Grouse, because the habitat used by both species was similar (Redpath and Thirgood 1999).

Based on the size ranges of grouse in the diet of these four raptors, in the course of development, grouse chicks undergo predation pressure by all raptor species studied. The smallest chicks are preyed upon by sparrowhawks only (Fig. 3b). Later on, while growing, they reach the size suitable for harriers and buzzards (Figs. 3c, 3d). Finally, juvenile grouse suffer from the heaviest predation (by all four raptors) when they reach the size hunted by goshawks (Fig. 3a) and thus fall within the "four-species predation zone" (Fig. 4). Chicks of different grouse species become vulnerable to goshawk predation at different ages (i.e., the youngest were Capercaillie and the oldest were Hazel Grouse). The time periods when chicks were under predation pressure by all four raptor species also varied according to the growth patterns in grouse (Fig. 4). While juvenile Capercaillie escape

from harrier predation in 10–15 d, chicks of Willow Grouse stay in the "four-species predation zone" more than 30 d and all Hazel Grouse chicks older than 40 d and adults can be preyed upon by all the raptors. Thus, predation pressure on juvenile grouse from the assemblage of the avian predators would not be even; smaller grouse species are under heaviest predation during a longer period than larger grouse. However, the correspondence of the mean size of grouse chicks in the diet of raptors at the end of their nestling periods to available juvenile grouse in the wild suggests that juvenile Black Grouse are preyed upon by most of these raptor species—sparrowhawks, buzzards, and harriers (Fig. 2). Although the goshawk certainly takes the largest share of grouse, the other three predators may have a high cumulative effect, especially in years of poor vole abundance when buzzards and harriers switch to juvenile grouse as their alternative prey.

We acknowledge that there were possible biases in our data. Because of the scarcity of grouse remains, we had to use each grouse chick found in the nest as a unit for the analysis. Multiple grouse remains in one nest cannot be considered independent, because more than likely they were taken by the same hawk. Furthermore, in some samples the sizes of grouse bones were very close to each other, which may be due to the fact that the prey belonged to the same brood (i.e., once found, the whole brood may have been killed by the same raptor). However, because the numbers of grouse chicks found per nest were low (Table 1), we believe that these limitations have not resulted in serious pseudoreplication. Moreover, we suggest that the small sample sizes of the data we used most likely affected the evaluation of hunting capabilities of raptors only as an underestimation of maximum and minimum sizes of grouse. Because the upper limit of the "four-raptor predation zone" is defined by the size of juvenile grouse in the harrier's diet, underestimation of maximum grouse sizes in other raptors would not have an effect on determining the heaviest predation period.

In conclusion, we have found that several birds of prey share by size a common resource, grouse chicks, during their nestling periods. Juvenile grouse were vulnerable to different avian predators in the course of their development. Our data clearly indicate that the impact of predation of the whole raptor community on grouse needs to be considered when examining predation on grouse.

## ACKNOWLEDGMENTS

We are grateful to Erkki Korpimäki for the idea of this study and to Sven Jungell for providing the prey and ringing material. Markku Hukkanen and the Ringing Centre of the Natural Museum of Helsinki University provided the ringing data. Pekka Helle communicated information on the hatching dates of grouse and Arto Marjakangas provided his unpublished data. Mikko Mönkkönen, Harto Lindén, and two anonymous referees gave valuable comments on the early versions of the manuscript. The study at various stages was financially supported by the Centre for International Mobility (CIMO) of the Finnish Ministry of Education, the Jenny and Antti Wihuri Foundation, and the Environmental Graduate School of EnviroNet of the University of Oulu (to V. Reif).

## LITERATURE CITED

- ANGELSTAM, P., E. LINDSTRÖM, AND P. WIDÉN. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199–208.
- CRAMP, S. AND K.E.L. SIMMONS (EDS.). 1980. The birds of the western Palearctic. Vol. 2. Oxford Univ. Press, Oxford, U.K.
- DEMENT'EV, G.P. AND N.A. GLADKOV (EDS.). 1951. Birds of the Soviet Union. Vol. 1. Israel Program for Scientific Translations, Jerusalem, Israel.
- GRÖNNESBY, S. AND T. NYGÅRD. 2000. Using time-lapse video monitoring to study prey selection by breeding goshawks *Accipiter gentilis* in central Norway. *Ornis Fenn.* 77:117–129.
- HÖGLUND, N. 1964. Über die Ernährung des Habichts (*Accipiter gentilis* L.) in Schweden. *Viltrevy* 2:271–328.
- HUHTALA, K., E. PULLIAINEN, P. JUSSILA, AND P.S. TUNKKARI. 1996. Food niche of the Gyrfalcon *Falco rusticolus* nesting in the far north of Finland as compared with other choices of the species. *Ornis Fenn.* 73:78–87.
- KENWARD, R.E., V. MARCSTRÖM, AND M. KARLBOM. 1993. Post-nestling behaviour in goshawks *Accipiter gentilis*: the causes of dispersal. *Anim. Behav.* 46:365–370.
- , R.H. PFEFFER, M.A. AL-BOWARD, N.C. FOX, K.E. RIDDLE, E.A. BRAGIN, A. LEVIN, S.S. WALLS, AND K.H. HODDER. 2000. Setting harness sizes and other marking techniques for falcon with strong sexual dimorphism. *J. Field Ornithol.* 72:244–257.
- KLAUS, S., H.-H. BERGMANN, C. MARTI, F. MÜLLER, O.A. VITOVIĆ, AND J. WIESNER. 1990. Die Birkhühner. Wittenberg Lutherstadt, Ziemsen, Germany.
- KORPIMÄKI, E., K. HUHTALA, AND S. SULKAVA. 1990. Does the year-to-year variation in the diet of Eagle and Ural Owls support the alternative prey hypothesis? *Oikos* 58:47–54.
- LINDÉN, H. 1981. Growth rates and early energy requirements of captive juvenile Capercaillie, *Tetrao urogallus* *Finn. Game Res.* 39:53–67.
- . 1983. Metson ja teeren muna- ja pesyekoon vaihtelusta. (Variations in clutch size and egg size of Capercaillie and Black Grouse.) *Suomen Riista* 30:44–50.
- MARJAKANGAS, A. AND L. TÖRMÄLÄ. 1997. Female age and breeding performance in a cyclic population of Black Grouse *Tetrao tetrix*. *Wildl. Biol.* 3:195–203.
- MOSS, D. 1979. Growth of nestling Sparrowhawks (*Accipiter nisus*). *J. Zool. Lond.* 187:297–314.
- NIELSEN, O.K. 1999. Gyrfalcon predation on Ptarmigan numerical and functional responses. *J. Anim. Ecol.* 68. 1034–1050.
- REDPATH, S.M. AND S.J. THIRGOOD. 1999. Numerical and functional responses in generalist predators: Hen Harriers and peregrines on Scottish grouse moors. *J. Anim. Ecol.* 68:879–892.
- REIF, V., R. TORNBORG, S. JUNGELL, AND E. KORPIMÄKI. 2001. Diet variation of Common Buzzards in Finland supports the alternative prey hypothesis. *Ecography* 24:267–274.
- SEMENOV-TIAN-SHANSKY, O.I. 1959. On ecology of tetraonids. Lapland State Reserve, Moscow, U.S.S.R.
- SULKAVA, P. 1964. Varpushaukan pesimisaikaisesta käyttäytymisestä ja ravinnosta. *Suomen Riista* 17:93–105.
- SULKAVA, S. 1964. Zur nahrungsbioologie des habichts, *Accipiter gentilis*. *Aquilo Ser. Zool.* 3:1–103.
- , K. HUHTALA, P. RAJALA, AND R. TORNBORG. 1998. Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland in 1957–96. *Ornis Fenn.* 76:1–16.
- THIRGOOD, S.J., S.M. REDPATH, P. ROTHERY, AND N.J. AEBISCHER. 2000. Raptor predation and population limitation in red grouse. *J. Anim. Ecol.* 69:504–516.
- TORNBORG, 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.
- . 2001. Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildl. Biol.* 7:245–256.
- VON HAARTMAN, L., O. HILDÉN, P. LINKOLA, P. SOUMALAINEN, AND R. TENOVUO. 1963–72. Pohjolan linnut varikuvien. Vol. 4–5. Otava, Helsinki, Finland.

Received 2 December 2002; accepted 7 April 2004

Associate Editor: Juan José Negro