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of the Rough-legged Buzzard *Buteo lagopus*
in Northern Finnish Lapland



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Piekana *Buteo lagopus*
Rough-legged Buzzard
(kuva / *photo*: Seppo Keränen)

Diet and breeding biology of the Rough-legged Buzzard *Buteo lagopus* in Northern Finnish Lapland

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Breeding biology of Rough-legged Buzzards *Buteo lagopus* at Kilpisjärvi, NW Finnish Lapland, in relation to rodent cycles

Johan Tast¹, Asko Kaikusalo & Martti Lagerström

Breeding of Rough-legged Buzzards was studied at Kilpisjärvi, the northwesternmost corner of Finnish Lapland almost annually in July in 1963-1985, when nestlings were "in age of ringing" close to fledging. In our study area the diet of buzzards consists almost exclusively of small microtine rodents. During deepest cyclic lows of violently fluctuating microtines, buzzards do not breed at all or they do not succeed to produce fledged young. Breeding processes in spring are released only if there are small rodents enough. Consequently, microtines regulate the size of the breeding population and productivity of the Rough-legged Buzzard. The number of occupied buzzard territories varied between 0 and 40 in the whole study area in parallel with fluctuations of their main prey. When rodent populations were at their highest in 1974, 18 or 19 pairs of buzzards bred within an area of 100 km². In the "best" sub-area there were five occupied nests within 3 km². Breeding success varied. During rodent peaks more than four young per nest fledged. On the contrary, during deepest rodent lows, no nestlings survived. The number of fledged young produced correlated positively with the available prey abundance.

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Introduction

Populations of five microtine rodents fluctuate cyclically and violently at Kilpisjärvi, in the northwesternmost tip of Finland (69° N; 20° 50' E) about 100 km north of the coniferous forest line. The area consists of both subalpine mountain birch forests and low alpine vegetation.

Kilpisjärvi region is inhabited by five small rodent species, the grey-sided vole, *Clethrionomys rufocanus*, the red vole, *Clethrionomys rutilus*, the root vole, *Microtus oeconomus*, the field vole, *Microtus agrestis*

and the Norwegian lemming, *Lemmus lemmus*.

When population cycles are investigated, comparisons of population development in several areas are needed, in order to get a reliable view of rodent cycles, because vole numbers do not increase beyond a maximum which in optimal habitats may be reached already before the ordinary population peak.

The main avian predator of small rodents is the Rough-legged Buzzard, *Buteo lagopus*, whose breeding in the area will be treated in this paper in relation to its prey abundance.

Material and methods

The nest-sites of Rough-legged Buzzards were visited in mid-July close to the time of fledging of the young, which were ringed when possible. Some nests were situated in inaccessible places and it was even impossible to count the exact number of nestlings. As the young were relatively close to fledging, obviously almost all ringed young birds survived. At this time we were also able to determine if empty nests had been occupied earlier in summer. Every breeding site where Rough-legged Buzzards had bred at least once was regarded as a nesting territory. If a new nest-site was found in a place visited already during earlier summers, it was counted among territories investigated every year when the place was visited also before the observed breeding.

Data concerning rodent abundance derives from four trapping activities. The overall fluctuations are shown from results of standard line trappings carried out annually since the late 1940's. In this paper the years from 1963 to 1987 are treated. The trapping was performed in June at the time of snow melt and in autumn from mid-August to mid-September. Traps were set in lines straight up the mountain slopes from the shore of Lake Kilpisjärvi (altitude 475 m) to the tree-line (600 m). The traps were placed in pairs at about 7 m intervals. Most trap sites were in different forest habitats, but partially also in shrubs and small bog areas. The catches of all five small rodent species made in different habitats have been combined. Number of trap-nights usually varied between 500 and 1700, but in 1974 and 1975 they were about 2500.

In three study plots in open habitats snap-trapping was performed annually at the end of June and beginning of July, a few weeks before buzzard nestlings fledged. Site A is a highly luxuriant and productive open bog area close to Lake Kilpisjärvi (altitude about 500 m). Two traps were placed in each and the same point every summer. Trap-nights per annum were about 80. Site B is a peatland study plot near the tree-line. Here traps were set in groups of five every year in the same suitable places.

This site is somewhat less productive than site A. Number of trap-nights was annually about 180. Site C is in Saananvankka, an alpine valley between the fjells Saana and Jehkats above the tree-line consisting of low alpine meadows and grassy thickets, some of which are seasonally subject to flood. Groups of five traps were set every summer in same places (altitude 600-700 m). Number of trap-nights was about 200 annually. Saananvankka is a favourite hunting area of Rough-legged Buzzards. During some years, for instance in 1974, five pairs searched their food there.

Rodents

During the 25 years 1963-1987 there occurred 6 cyclic highs and 5 cyclic lows of microtine rodents. The most luxuriant study plot A is an optimal habitat for root voles, where they were caught almost every summer. Only during two cyclic lows, 1979 and 1985, no root voles were caught there. The water vole, *Arvicola terrestris*, does not belong to the species occurring regularly at Kilpisjärvi, but in study plot A the species lived for a short period in late 1970's (Tast 1986). Water voles were caught in 1979, when no other rodents were trapped in this study plot.

The total number of years with no rodents obtained was 2 on plot A, 3 on plot B and 4 on plot C, and summers with less than 1 rodent per 100 trap-nights were 2 on plot A, 5 on plot B and 7 on plot C. These figures indicate that cyclic lows of microtines are deeper in the alpine zone and in less productive areas than in lower altitudes in luxuriant habitats.

Most often the culmination of population cycles takes place in winter. The line trapping results presented in Table 1 show that during 15 winters populations decreased. However, there were only five winters with great changes in numbers. Highest spring populations were in the following years (corresponding figures of the previous autumn are given in parentheses): 1974 26.7 (19.7); 1982 20.7 (18.0); 1978 16.5 (16.3); 1983 16.5 (27.0); 1964 13.0 (14.0) and 1987 12.1 (19.2). Highest autumn populations were (spring figures are given in parentheses): 1969 38.1 (7.9); 1978 30.9 (16.5); 1982 27.0 (20.7); 1983 25.8 (16.5); 1973 19.7 (5.9);

Table 1. Fluctuations in relative numbers of microtines according to standard line trappings performed in the mountain birch zone. Figures denote combined numbers of five small rodent species per 100 trap-nights. Change from autumn to next spring shows the winter survival of voles and their probable winter reproduction.

	Spring	Autumn	Change from spring to autumn	Change from autumn to next spring
1963	7.6	14.0	+6.4	-1.0
1964	13.0	15.4	+2.4	-14.4
1965	1.0	0.3	-0.7	-0.3
1966	0.0	1.8	+1.8	-0.5
1967	1.3	1.8	+0.5	-0.7
1968	1.1	7.8	+6.7	+0.1
1969	7.9	38.1	+30.2	-31.1
1970	7.0	9.8	+2.8	-9.7
1971	0.1	0.8	+0.7	-0.2
1972	0.6	5.4	+4.8	+0.5
1973	5.9	19.7	+13.8	+7.0
1974	26.7	16.2	+10.5	-6.5
1975	9.7	3.7	+6.0	-3.6
1976	0.1	0.3	+0.2	+3.8
1977	4.1	16.3	+2.2	+0.2
1978	16.5	30.9	+14.4	-30.7
1979	0.2	0.5	+0.3	-0.2
1980	0.3	2.1	+1.8	+0.9
1981	3.0	18.0	+15.0	+2.7
1982	20.7	27.0	+6.3	-10.5
1983	16.5	25.8	+10.3	-25.7
1984	0.1	0.1	0.0	+0.1
1985	0.2	1.5	+1.3	+0.6
1986	2.1	19.2	+17.1	-7.1
1987	12.1	18.9	+6.7	

1986 19.2 (2.1); 1987 18.9 (12.1) and 1981 18.0 (3.0). When the above figures are compared, it is easily seen that there seems to be no correlation between population size and winter mortality, as the numbers of microtine rodents in spring after high autumn populations may be either high or low. In conclusion, wintering success of microtine rodents is not density-dependent.

Although small rodent populations usually decrease during winters, in nine cases vole catches in the autumn standard line trapping (mid-August to mid-September) were smaller than during the following spring. The interpretation is not the same for all years. In some winters microtines reproduce (Tast & Kaikusalo 1976, Kaikusalo & Tast 1984) and this took place at least in 1963/64, 1968/69, 1972/73, 1973/74, 1977/78 and 1980/81. In summers with low numbers of microtines their

breeding continues longer than during dense populations (Kalela 1957, 1982, Tast & Kalela 1971, Viitala 1977, Henttonen & Järvinen 1981). Probably trapping ceased before the youngest voles reached trappable age in three years, and hence the spring density indices were higher after winters of 1980/81, 1984/85 and 1985/86.

Results of line trappings performed in subalpine mountain birch forests (Table 1) tallies well with those obtained in more open habitats A, B and C (Table 2). Usually rodent populations fluctuate in parallel in alpine and subalpine habitats. The only exception in our data is summer 1984. During the winter of 1983/1984 rodent populations collapsed in the forest region, while voles were still abundant in the alpine zone in early summer, as can be seen in Table 3 where results of line trappings in forest region and snap trappings in the open habitats

Table 2. Results of snap-trapping in three study plots in open habitats. Trapping was performed annually at the end of June and beginning of July. Figures denote the combined numbers of five small rodents species per 100 trap-nights. Further details in text.

	A	B	C
1963		10.9	3.4
1964	34.1		15.5
1965		1.2	1.4
1966	4.5		0.0
1967	10.8	4.2	3.3
1968	7.5	4.9	1.4
1969	21.5	18.4	20.3
1970	54.6	25.8	10.1
1971	1.6	0.0	0.0
1972	8.3	0.6	0.0
1973	50.0	12.3	17.0
1974	27.9	44.5	41.4
1975	19.3	13.8	13.6
1976	1.5	0.0	0.5
1977	6.2	15.3	4.3
1978	26.2	27.5	38.7
1979	0.0	0.0	0.5
1980	10.9	0.7	0.0
1981	34.3	10.9	10.2
1982	25.0	29.8	36.9
1983	38.3	21.1	41.0
1984	5.0	1.5	11.6
1985	0.0	1.8	0.6
1986	17.6	6.6	13.0
1987	5.5	20.8	20.8

A, B and the alpine study plot C are given for years 1983 - 1985. The culmination of population cycle took place in the alpine habitats by mid-summer. Rodents almost totally disappeared also from the alpine zone in July.

As to population development during summer, in most years rodent numbers increased. In 1974 rodents were most abundant in the total area, although numbers decreased in line trapping and study plot A. This was

owing to dispersal, as from overdense areas population thins out to suboptimal habitats in higher altitudes, as can be seen from Table 2 of plots B and C. During cyclic lows in 1965, 1966, 1967, 1971, 1976, 1979, 1980, 1984 and 1985 populations remained at a low level for the whole summer.

Average body weight of microtines varied during different phases of the cycles. Among microtines studied at Kilpisjärvi it has been established that weights of grey-sided voles

Table 3. Comparison of line-trapping results in subalpine forest zone (spring and autumn), in the open habitats A and B, and in the alpine study plot C in 1983 - 1985.

	Spring	Autumn	Plot A	Plot B	Plot C
1983	16.5	25.8	38.3	21.1	41.0
1984	0.1	0.1	5.0	1.5	11.6
1985	0.2	1.5	0.0	1.8	0.6

(Kalela 1957) and root voles (Tast 1966) were heaviest during population peaks indicating that fluctuations in their abundance are linked with plant production biology (Kalela 1962, Tast & Kalela 1971).

The species composition changed during population cycles. When root vole numbers increased, their population density decreased in optimal habitats, because they dispersed to less luxuriant habitats both in the forest and the alpine zone. Then the inferior competitor, the field vole, had to give way to its "big brother". During some root vole peak years the field vole almost totally disappeared from the study area, for instance in 1960 (Tast 1968). Similarly, owing to interspecific competition between the two *Clethrionomys* voles, during some of cyclic highs the red voles were almost totally lacking (Viitala 1984).

Breeding population of Rough-legged Buzzards

Rough-legged Buzzards arrive to the Kilpisjärvi area every spring in April, when the whole area is covered with thick snow. Recently Koi-vula & Viitala (1999) found that buzzards are able to see ultraviolet (UV) light and these raptors are attracted to voles' scent marks, which are visible in UV light. Microtine rodents mark their territories with urine and faeces, which they use as scent marks. Buzzards apparently estimate the abundance of available food and then decide whether to breed or to emigrate. During our study period there were three such years when no buzzards occupied a territory for breeding (1965, 1971 and 1985). In 1985 the first Rough-legged Buzzard was observed at Kilpisjärvi on April 20. But buzzards disappeared from the area soon after their arrival, last ones by the end of May. One bird was seen by us on July 5. Neither in the northeastern Lapland at Utsjoki (Iso-Iivari & Saari 1997) took any successful breeding place that summer. The last non-breeding year at Kilpisjärvi was 2009, when no breeding buzzards were observed in the region nor in other parts of Finnish Lapland (Tast 2009).

During the cyclic low of 1966, no rodents were caught neither in the alpine study plot C nor in the spring line trapping. In the most luxuriant open bog study plot A trapping resulted in 4.5 root voles per 100 trap-nights (Table 2). This result shows that there were in some places rodents, which produced enough food to those two buzzard pairs which bred in the Kilpisjärvi area that summer. They succeeded to produce one fledgling each. In 1968, 1976 and 1979 some territories were occupied in early summer, but no young were found in nests in mid-July. These years were such that rodent populations did not increase during the summer with the exception of 1968, when two territories were occupied, but no young were in nests in July, although rodent numbers increased that summer. Successful breeding requires first that in spring there are rodents above a threshold level so that buzzards remain in the region and begin nesting activities. But also during the summer rodent populations must increase or at least remain on so high a level that food is available to nestlings.

The number of occupied buzzard territories varied between 0 and 40 in the whole study area (Table 4). When rodent populations were at their highest in 1974, 18 or 19 buzzard pairs bred within an area of 100 km². In optimal places with many good nest-sites, buzzards bred quite close to each other. The shortest distance between two nests was only 400 m. At best there were simultaneously five occupied nests within 3 km².

The size of breeding Rough-legged Buzzard population was not limited by the availability of nest-sites. From Table 4 it can be seen that every summer also during the highest numbers of buzzards there were several such empty nest-sites where the species had bred during some other year.

The number of breeding buzzard pairs correlated significantly with small rodent abundance.

Table 4. Annual variations in the breeding population and the nestling success of the Rough-legged Buzzard in Kilpisjärvi.

	Territories studied	Territories occupied	Nests with young	Youngs per nest
1963	8	4	3	1.0
1964	15	8	6	4.3
1965	10	0	0	0
1966	13	2	2	1.0
1968	10	2	0	0
1970	34	20	8	4.3
1973	19	11	5	1.6
1974	38	31	26	4.2
1975	43	30	22	3.8
1976	35	6	0	0
1977	31	24	5	2.3
1978	47	40	26	3.9
1979	34	20	0	0
1980	37	14	0	0
1981	34	25	13	2.5
1984	41	27	2	1.0
1985	10	0	0	0

Breeding success of Buzzards

In 1974 38 nesting territories were investigated. At 31 of these breeding started, and in mid-July at the time of ringing the young, in 26 nests a total of 109 young were found. The average number of young per nest of successful breeding was 4.2. Corresponding figures for 1975 were 43 investigated territories, with 30 ones where breeding had started. In July 22 nests had a total of 84 nestlings with an average of 3.8 young per successful brood. In 1984 breeding started at 27 of 41 studied territories, but in mid-July only in two nests any young were still alive, one in each. During rodent peaks buzzards have more voles to capture and they are on average heavier than during other phases of rodent cycles.

We have no observations of the clutch size, but in some investigations it has been shown that there is a tendency for larger clutches during years when food is abundant (e.g. Hagen 1969, Potapov 1997). However, the observed variation in nestling numbers depends almost exclusively on nestling mortality, which is a result of food conditions, i.e., the rodent abundance. Hatching in Rough-legged Buzzard nests is

asynchronous, as incubation starts with the first egg. In years with food shortage, the youngest siblings do not get enough food and starve. There are many observations of cannibalism when older chicks eat younger, weaker ones (e.g. Barth 1952, Hagen 1952, 1969, Potapov 1997). In Potapov's study siblicide seemed to be the most significant factor reducing the brood size. Also parents have been observed to eat their nestlings but this can be suspected to happen after the nestling had already died.

Discussion

Rough-legged Buzzards are nomadic in their breeding. When they arrive to their previous nesting territories in spring, they estimate the food situation on the basis of their UV-sight. If food is scarce, they emigrate to other areas with adequate food. So they can move long distances from their birthplaces or previous breeding places and breed there. There are several supporting observations. According data presented by Galushin (1974) breeding season recoveries of birds aged 2 years or more show mean movement of 1955 km from the place of ringing. Glutz et al. (1971) and Cramp & Simmons (1985) give two examples. A young

Rough-legged Buzzard which was ringed in Norway was found in the breeding season 4 years later in Yamal in Russia 2700 km to east from its birth place. A nestling ringed in Sweden was found three years later in Russia close to the arctic circle at the end of May 1450 km east of its ringing place.

Although the species usually breeds in high latitudes in subarctic and arctic areas, it can occasionally breed south of its normal breeding range in years when microtines are abundant there and scarce in northern areas. This was the case in Finland in 2009 when in Lapland no breeding pairs were observed (Tast 2009), but several pairs were found breeding for example in the Suomenselkä area in central Finland (Sulkava 2010, Rajala 2010). Also a few pairs were found breeding in northern Pirkanmaa, where the species has not been observed breeding before (Seppälä 2009, Tast 2009). Although tens of Rough-legged Buzzards overwintered in Pirkanmaa, the breeding places were not in areas where wintering took place. Mysterud (1964) reported of Rough-legged Buzzards breeding in 1962 in lowlands north of Oslo, south of their normal Norwegian breeding range.

Many studies have demonstrated a close positive correlation between rodent abundance and the density of raptors (e.g. Barth 1952, Hagen 1969, Virkkala 1992, Korpimäki 1994). Hagen (1969) suggested that there is a threshold in rodent abundance, below which Rough-legged Buzzards do not settle down and breed. He estimated that in his study area in Norway this is 2 rodents per 100 trap-nights. There surely are differences in the trapping techniques of different investigators but Hagen's estimate fits fairly well with our observations.

During rodent peaks there is more food available to buzzards and the voles are bigger. In addition, also changes in species composition favour raptors since during population highs the most abundant species, the lemming and the root vole, are the heaviest microtines in our study area. Also Potapov (1997) stated that in his study areas in Siberia prey species composition changed during

rodent cycles and Rough-legged Buzzards produced most offspring in years when biggest small mammal species were most abundant.

Small rodents belong to the second trophic level being mostly herbivores. At Kilpisjärvi their amount during cyclic lows is very small. During population peaks the most abundant species, the grey-sided vole, can reach densities up to 35 females per hectare as estimated from live-trapping data (Kalela 1957, Viitala 1977, 1987). This means a biomass of about 210 kg per km². The root vole can reach about 100 kg per km² (Tast 1966, 1974, 1982), while the figure for the smallest and least abundant red vole is about 10 kg per km².

In the Kilpisjärvi area land bird biomass has been estimated to be about 2.5 kg per km² according to line transect investigations (Lahti 1976, Järvinen 1976, Lagerström 1993). This figure is less than 1 % of the available rodent food. In forest Lapland land bird biomass is about 10 kg per km², i.e., fourfold to that at Kilpisjärvi (Järvinen 1976), and in open bog areas with numerous waders the figure is ten times higher than in our study area.

In Kittilä some 200 km to south from Kilpisjärvi in the coniferous forest zone, Pasanen & Sulkava (1971) and Pasanen (1972) found that during good rodent years the share of small mammals in buzzard diet was about the same as in our study area, about 90 %. But during one breeding season rodent populations collapsed similarly as in our study area in 1984. However, Rough-legged Buzzards succeeded in their breeding also that summer by changing to an alternative prey item, birds (mostly waders, especially ruffs, *Philomachus pugnax* and juvenile ducks and thrushes).

Thus, the species can be regarded as a generalist predator in areas with greater biodiversity as stated by Hanski et al. (1991) but in our study area and also elsewhere in tundra habitats the species is a typical specialist consuming almost exclusively small rodents (e.g. Hagen 1952, 1969, Galushin 1974, Mindell et al. 1987, Whitaker et al. 1996, Potapov 1997), and its abundance and breeding success depends totally on microtine rodents.

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Diet composition of breeding Rough-legged Buzzards *Buteo lagopus* at Kilpisjärvi, NW Finnish Lapland

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The diet of breeding Rough-legged Buzzards at Kilpisjärvi consisted almost exclusively of small rodents. Populations of their primary prey exhibit regular cycles. During deepest cyclic lows buzzards do not start nesting activities. When prey abundance is a little higher, breeding begins, but young do not survive. Only during rodent peaks many pairs breed and produce several fledglings. Hence, their diet can be studied in detail only when small rodents are abundant. Pellets and fresh prey animals were gathered at buzzard nests during two rodent peak years, 1974 and 1975. In addition, fresh prey animals at nest-sites were sampled in 1970 – 1987 in mid-July in connection with ringing buzzard nestlings. Hints of widening of diet when the main food item is scarce are seen when comparing the composition of fresh prey animals at nests in different phases of rodent cycles. The share of birds increased, when rodents were less abundant. However, at Kilpisjärvi buzzards' successful breeding can occur only when rodents are available throughout the nesting period. The year 1984 was exceptional. In the autumn of 1983 rodent populations were high both in the alpine and subalpine habitats. During winter 1983/1984 vole populations crashed in forests, while in alpine habitats they were relatively high still in spring 1984, and dropped distinctively by mid-summer. As a result, buzzards began to breed in the alpine area, but in most nests young failed to fledge. That summer the share of birds among fresh prey animals found at nests was significantly higher than during years with higher vole numbers indicating that in our study area birds are a secondary food item of buzzards, which enables adults to survive, but not their young.

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Introduction

Rough-legged Buzzards, *Buteo lagopus*, occupy circumpolar habitats in the tundra areas and adjacent northern parts of taiga forests. At Kilpisjärvi (69°N), nesting takes place both in the alpine tundra and in the subalpine mountain birch region. The species is a nomadic raptor, whose populations vary greatly from year to year in parallel with their

main food, small rodents (e.g. Hagen 1952, 1969, Galushin 1974, Springer 1975, Mindell et al. 1987, Mindell & White 1988, Poole & Bromley 1988, Virkkala 1992, Whitaker et al. 1996, Potapov 1997). However, in northern Russia, in years with high numbers of snowy owls, *Nyctea scandiaca*, populations of Rough-legged Buzzards were regulated more by these owls than of the abundance of small rodents (Wiklund et al. 1998).

Fluctuations in numbers of microtine rodents have been monitored at Kilpisjärvi annually beginning in 1946. Changes in rodent numbers are cyclical with more or less regular intervals between successive peaks (e.g. Kalela 1962, Tast & Kalela 1971, Henttonen et al. 1984, Hansen et al. 1999 a, 1999b, Tast et al. 2005). Since 1964 also multiannual fluctuations in numbers of the common shrew, *Sorex araneus*, have been studied. Shrew populations are also cyclical, their numbers being highest a year before rodent peak (Tast et al. 2005).

Kilpisjärvi area is inhabited by five small rodent species. The grey-sided vole, *Clethrionomys rufocanus*, is the most frequent species in most habitats both in the alpine and subalpine region (e.g. Kalela 1957, 1962). The root vole, *Microtus oeconomus*, ranks highest on peatland and in areas subject to flooding and in man-made habitats (Tast 1966, 1968). The field vole, *Microtus agrestis*, is sometimes abundant in meadows especially in low alpine areas and in meadow forests, but owing to interspecific competition between the two *Microtus* species, the weaker field vole is often scarce during actual population peaks (Tast 1968, Viitala 1977, Henttonen et al. 1977). The red voles, *Clethrionomys rutilus*, are least abundant (Kalela et al. 1971, Henttonen et al. 1977, Viitala 1977, 1984). The Norwegian lemming, *Lemmus lemmus*, occurs only during so called lemming years, which always coincide with the cyclic highs of the other small rodents, but intervals between lemming peaks are often longer, as they are not abundant during every cyclic high (Tast & Kalela 1971, Lahti et al. 1976, Tast 1991).

Shrews are living both in alpine and subalpine habitats (Kaikusalo 1980, Kaikusalo & Hanski 1985, Kaikusalo & Tast 1994), the common shrew *Sorex araneus*, probably being the most numerous mammalian species at Kilpisjärvi. In the area three other shrew species, *Sorex minutus*, *Sorex caecutiens* and *Neomys fodiens* occur, too.

The Rough-legged Buzzard feeds mainly on living prey, although it also eats some carrion. In our study area its main prey, voles

and lemmings, are visible almost exclusively in snowless season. Consequently, buzzards are forced to migrate for winter south of areas where they can find rodent food. In addition, as they are diurnal, they are unable to hunt in our study area in winter far north of the Arctic Circle, where sun is not shining at all during two months in mid-winter. Normal winter ranges of our Rough-legged Buzzards lie in central and eastern Europe (Glutz et al. 1971, Cramp et al. 1980), but they can occasionally winter even in southern Finland, if rodent populations are high there (Mikkola 1968, Tast 2009).

Buzzards arrive at Kilpisjärvi every spring in April and begin their breeding activities, if rodent populations exceed a threshold. If not, most buzzards emigrate to areas with better food conditions, but a few may stay in the area without nesting. In non-breeding years most buzzards leave the area by end of May.

Koivula & Viitala (1999) showed that Rough-legged Buzzards are able to see ultraviolet (UV) light and these raptors are attracted to voles' scent marks, which are visible in UV light. Small rodents mark their territories with urine and faeces, which they use as scent marks.

Buzzards apparently estimate abundance of their food availability in the spring before deciding whether to breed or to emigrate. If overwintering rodent populations have been high and their decrease has taken place late in the winter, buzzards can begin to breed also in a poor rodent year attracted by abundant scent marks, but do not succeed in producing fledglings.

Material and methods

The investigations were carried out at Kilpisjärvi in the northwesternmost tip of Finland (69° 03' N, 20° 50' E) about 100 km north of the coniferous forest line. The area consists of both subalpine mountain birch forests and low alpine vegetation.

When raptor diets are examined, the best and the most accurate results are obtained by direct observations. However, in most studies indirect methods have been used, i.e. analysis

of pellets and counting fresh prey animals found at nest-sites.

Pellets and food remains were gathered at Rough-legged Buzzards' nests at the end of the breeding season. In 1974 samples were collected at seven nests, two of which were in the alpine and five in the subalpine region. In addition, some pellets were gathered from further three breeding territories. In 1975 eight nest-sites were examined, five of which were in the alpine and three in the subalpine region.

When pellets were analyzed, first the number of skulls was counted. Then jaws, feet and other bones were combined together. The numbers presented here are minimum values, as for example skulls and feet combined together could have belonged to different specimens. When possible, the bones were determined to the species. Extra bones were thereafter determined to the genus level, i.e. either *Clethrionomys* or *Microtus*. If the bones could not be told even to generic level, then they were grouped to the family Microtinae.

Bone determination was based mainly on large bone reference material collected by Asko Kaikusalo in 1955-1974. Comparisons were made also with data presented by Siivonen (1967).

Prey animals are not necessarily represented in pellets in same proportions as their frequency is in the food of the predator. Hence, the efficiency of pellet analysis was tested by feeding experiments at Loppi, Ojajoki, in southern Finland in the field station of the Finnish Forest Research Institute.

A young Rough-legged Buzzard, youngest in its brood from the Kilpisjärvi area, was used in the experiments. Obviously this bird had not survived to fledgling state in its original nest. Among many raptors, including the Rough-legged Buzzard, the male is mostly responsible for hunting especially in the beginning of breeding, while the female feeds the nestlings. As the young hatch at several days intervals, the older chicks receive more food than the younger ones. During food

Table 1. The efficiency of pellet analyses as tested with a young Rough-legged Buzzard in feeding experiments. Fl = adult, juv = juvenile.

Prey species	Eaten	Found
<i>Micromys minutus</i>	8	7
<i>Mus musculus</i>	121	113
<i>Rattus norvegicus</i>	42	42
<i>Lemmus lemmus</i>	7	7
<i>Microtus agrestis</i>	98	94
<i>Microtus oeconomus</i>	21	21
<i>Clethrionomus glareolus</i>	62	59
<i>Clethrionomus rufocanus</i>	16	16
<i>Arvicola terrestris</i>	36	36
<i>Sorex araneus</i>	16	16
<i>Sorex minutus</i>	6	6
<i>Mustela nivalis</i>	1	1
Mammals total	434	418
<i>Phylloscopus</i> sp. fl	2	2
<i>Anthus pratensis</i> fl	4	3
<i>Fringilla coelebs</i> fl	3	3
<i>Turdus</i> sp. juv	3	2
<i>Turdus</i> sp. fl	14	14
<i>Tetrastes bonasia</i> juv	1	1
<i>Lagopus lagopus</i> juv	2	2
<i>Lagopus lagopus</i> fl	3	3
Aves total	32	30

Table 2. The diet of the Rough-legged Buzzard in the Kilpisjärvi area during the breeding seasons of 1974 and 1975.

Prey species	1974	1975	Total	Total percentage (%)
<i>Lemmus lemmus</i>	51	121	172	
<i>Clethrionomys rufocanus</i>	197	156	353	
<i>Clethrionomys rutilus</i>	49	13	62	
<i>Clethrionomys sp.</i>	21	24	45	
<i>Microtus oeconomus</i>	157	165	322	
<i>Microtus agrestis</i>	55	15	70	
<i>Microtus sp.</i>	43	38	81	
Rodentia sp.	83	61	144	
<i>Neomys fodiens</i>	1		1	
<i>Sorex araneus</i>		2	2	
<i>Mustela nivalis</i>	1		1	
<i>Lepus timidus</i>	2	2	4	
<i>Lagopus sp.</i>	1	1	2	
Passerines	5	1	6	
Total	566	599	1265	
Rodentia			1249	98.7
Insectivora			3	0.3
Lepidomorpha			4	0.3
Mustelidae			1	0.1
Aves			8	0.6

shortage, the youngest nestlings perish first. Even cannibalism is known to occur among Rough-legged Buzzard broods.

Permission to use wild animals including Rough-legged Buzzards, in experiments at Ojajoki field station was given by Finland's Ministry of Agriculture and Forestry on January 21st, 1974, diary number 6401/64M-MM 1973. The food consumption of this young buzzard was measured, and its gaining of weight was followed to late autumn.

Mammals offered to the buzzards were mostly white laboratory house mice and snap-trapped wild small rodents. In feeding experiments we used also birds, which were found dead, most of them after flying against cars or windows. All animals given to the buzzard were whole, not torn in pieces. Food remains were collected from the bird's cage during the following day.

At Rough-legged Buzzard nests fresh prey animals are found quite frequently. These were recorded and determined to the species at 62 nest-sites in the period of 1970–1987.

Results

Efficiency of pellet analysis

Results of feeding experiments are summarized in Table 1. Almost all animals offered to the buzzard were found in pellets. Only 3.9 % of a total of 466 prey animals were not detected when the pellets were examined. All of these specimens were among the smallest given. Of avian food items 6.3 % was not revealed in pellets, while the corresponding figure for small rodents was 3.7 %. The difference between birds and mammals is insignificant.

Pasanen (1972) was able to find 40 % of the animals given to Rough-legged Buzzards in his feeding experiments. All frogs “disappeared” and less of eaten birds than mammals were found in pellets.

Diet composition according to pellet analyses

The distribution of different prey items in the pellets analyzed is given in Table 2. A total of

1265 prey items were determined. The great majority of them were mammals, their number being 1257. The bulk of them were small rodents which totalled 1249. Their proportion was 98.7 % by number, and about 97 % by weight.

The weights of small rodents vary from about 10 g to 100 g (the biggest lemmings and root voles). However, most rodents captured by buzzards are from 25 g to 60 g. Intraspecific weight variation is almost as great as interspecific. Consequently, the importance of different microtines in the diet of Rough-legged Buzzards is seen almost equally well when compared by number as by weight. Four mountain hares, *Lepus timidus*, were found. One of them was a carrion, and the others juveniles. Their share was 0.3 % by number and some 2 % by weight. So, the hares are not important in buzzards' diet during rodent peak years, nor have buzzards any impact upon hare populations at least in years, when small rodents are abundantly available. Only three shrews were recorded, one of them was a water shrew, *Neomys fodiens*, and two were common

shrews, *Sorex araneus*. Eight of the prey animals were birds belonging to five species.

Fresh prey animals found at nests

152 fresh prey animals were found at 62 nests in 1970 - 1987. Results are summarized in Table 3. In principle the results are rather similar to pellet analyses. Small rodents consisted 90.0% (n = 153) of total sample. If the rodent peak years 1974 and 1975 are excluded, the share of small rodents decreases to 87.0 %. The share of birds is significantly higher in nests (8.8 %, n = 15, P < 0.001) than in pellets (0.6 %, n = 6).

Rough-legged Buzzards do not breed at all in our study area in years when small rodent populations are low. As to 1984, rodent populations in birch forest region collapsed in the autumn of 1983, but in alpine habitats they were in early spring so high that buzzards started to breed, but by the mid-summer vole populations collapsed. Buzzards changed to alternative prey, birds, as the main food item, small rodents, disappeared. In poor food conditions nestlings perished, as adult birds were unable to get enough food to their young.

Table 3. Fresh prey animals found at Rough-legged Buzzard nests in the Kilpisjärvi area in 1970 - 1987. Ad=adult, juv=juvenile.

Prey species	Total	Total percentage (%)	Remarks
<i>Lemmus lemmus</i>	42		
<i>Clethrionomys rufocanus</i>	104		
<i>Clethrionomys rutilus</i>	2		
<i>Microtus oeconomus</i>	3		
<i>Microtus agrestis</i>	2		
Rodents	153	90.0 %	
<i>Mustela nivalis</i>	2		
Mammals total	155	91.2 %	
<i>Anas crecca</i>	1		
<i>Lagopus lagopus</i>	3		2 ad + 1 juv
<i>Lagopus sp.</i>	2		ad
<i>Pluvialis apricaria</i>	1		juv
<i>Anthus pratensis</i>	1		
<i>Luscinia svecica</i>	1		
<i>Oenanthe oenanthe</i>	2		
<i>Turdus iliacus</i>	1		
<i>Corvus corone</i>	1		
Small passerine	1		juv
Small wader	1		juv
Aves total	15	8.8 %	

Breeding activities were started at 27 nests, but only in two nests one young in each survived to fledgling state.

Of the 15 birds among fresh prey animals gathered at nest-sites, seven were from the 1984 sample. In the large samples of rodent peak years 1974 and 1975 only one bird was found at nest-sites, showing that avian prey is a secondary food item of Rough-legged Buzzards in our study area.

Discussion

The feeding habits of Rough-legged Buzzards during breeding season in Kilpisjärvi region were similar to those found in several other areas. All studies have shown that they generally prefer small rodents as their main food item. Food composition of breeding Rough-legged Buzzards has been studied in many places, e.g. in Norway (Hagen 1952, 1969, Mysterud 1964), Alaska (Cade 1955, 1960, White & Cade 1971), Russia (Osmolovskaja 1948, Potapov 1997, Wiklund et al. 1998) and Finland (Pasanen & Sulkava 1971, Pasanen 1972, Virkkala 1992). In alpine areas Rough-legged Buzzards are specialists consuming almost exclusively small rodents. In areas with richer bird fauna these raptors are able to change their dietary habits successfully to avian prey if rodent populations decrease during breeding season. At Kilpisjärvi estimates of bird biomass is 2.5 kg/km² according to line-transect censuses (Lahti 1976, Järvinen 1976, Lagerström 1993). In Kittilä some 200 km to south of our study area in the coniferous forest region Pasanen & Sulkava (1971) and Pasanen (1972) found that during their three study years, the share of small mammals during two good rodent years was about 90 % of buzzards' diet. But during the third breeding season rodent populations collapsed. However, Rough-legged Buzzards succeeded in their breeding also that summer by changing to avian food. Now their food consisted almost exclusively of birds, 47 % of their food was ruffs, *Philomachus pugnax*, 23 % of juvenile ducks, and 18 % of thrushes and other birds. In forest Lapland land bird biomass is about 10 kg/km² (Järvinen 1976)

and in open bog areas with numerous waders, the figure is about ten times higher than in our study area.

In fact, the alternative food item of Rough-legged Buzzards in Kittilä consisted of waders which frequented the bogs of their investigation area.

Small rodents belong mostly to the second trophic level being mostly herbivores. At Kilpisjärvi during cyclic lows they are almost totally lacking. According to our live trapping data the biomass of small rodents during peak years can be estimated. The most abundant species, *Clethrionomys rufocanus*, can reach densities up to 15 females per hectare (Kalela 1957, Viitala 1977, 1987), which means a biomass of about 200 kg/km². *Microtus oeconomus* can come up to 100 kg/km² (Tast 1966), while figures for the least abundant species, *Clethrionomys rutilus*, are at highest about 10 kg/km² (Viitala 1977, 1987).

No doubt, Rough-legged Buzzards are generalists in their hunting in areas where alternative prey items are available in abundance. But in main distribution range of this raptor ecosystems are relatively simple. So, in areas with small biodiversity, they are obliged to the only abundant food item, small rodents, and hence are there specialists. Hanski et al. (1991) classified Rough-legged Buzzards among generalists obviously owing to diet studies of the species in coniferous forest regions, e.g. those of Pasanen & Sulkava (1971).

Although shrews are abundant in our study area, they are rarely eaten by buzzards. Perhaps they are too small to release attacks of these raptors. Pasanen (1972) observed that all frogs which he gave to Rough-legged Buzzard "disappeared". We have no observations indicating that in Kilpisjärvi area frogs would belong to the diet of buzzards. Frogs are scarce in our study area and, hence, have not any importance as a probable source of food to these raptors.

Birds are rare also in winter food of the species. Henshav (1875 as cited by Springer 1975) found remains of four birds in the stomach contents of 173 wintering *Buteo*

lagopus in America. Craighead & Craighead (1956) reported that four passerine birds were found among 203 prey identified from pellets of wintering Rough-legged Buzzards. Microtine rodents constituted the bulk of prey taken by this raptor species both in their wintering areas in America and Central Europe (Sladek 1960).

One of the predictions of the optimal diet theory (for further details see e.g. Emlen 1966, Mac Arthur & Planka 1966, Stenseth & Hansson 1979, Korpimäki 1986) is that the diet of the predator should expand when the abundance of their preferred prey decreases. Our observations seem to fit well with that, as the share of avian food items increased when rodent population began to decrease during the breeding season of Rough-legged Buzzards.

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Individual selectivity in the prey choice of breeding Rough-legged Buzzards *Buteo lagopus* at Kilpisjärvi, NW Finnish Lapland

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During two rodent peak years, 1974 and 1975, the bulk of the diet of fifteen breeding pairs of Rough-legged Buzzard, *Buteo lagopus*, consisted mostly of small rodents. However, food composition varied at different nests, and vole species did not occur in buzzard diets in the same proportions as in the field. At fourteen nests these raptors were clearly selective in their prey choice. At twelve nests the proportion of main prey species exceeded 50 % of the total number of prey items. Unexpectedly, the dominating species varied: at four nests it was *Clethrionomys rufocanus*, and at other four nests *Microtus oeconomus*. At three nests it was *Lemmus lemmus* and at one nest *Clethrionomys rutilus*, the least abundant rodent species in the area. Apparently buzzards in spring adopt their hunting strategies by successful experiences when searching food. Consequently, their responses to their mammalian prey become selective by some kind of inlearning process to a special prey in a special habitat. As a result, the diet width of individual pairs was surprisingly narrow.

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Introduction

At Kilpisjärvi, in the northwesternmost corner of Finnish Lapland (69° 03'N, 20° 50'E) about 100 km north of the coniferous forest line, small mammals and their characteristic multiannual population cycles have been studied continuously since 1946 (e.g. Kalela 1949, 1957, 1962, Tast & Kalela 1971, Kaikusalo & Tast 1984, 1994, Tast 1966, 1968, 1984, 1991, Lahti et al. 1976, Henttonen et al. 1977, Henttonen & Hanski 2000, Tast et al. 2005). Thus, the abundance of small rodent species in different years and in different habitats is known fairly exactly. In addition, we know how microtine rodents living in the area change

their habitat seasonally during different phases of cycles (Kalela et al. 1961, 1971 a and b, Tast 1966, 1968, Viitala 1977). Furthermore, both intraspecific and interspecific social relationships of cycling microtine populations are known fairly well (Kalela 1957, Tast 1966, 1968, Lahti et al. 1976, Henttonen et al. 1977, Viitala 1977, 1984a, 1987, Viitala & Ylönen 1993).

The main avian predator of small rodents is the Rough-legged Buzzard. This raptor does not succeed in breeding when rodent populations are at a low level. Hence, the breeding of buzzards in our study area depends totally on the availability of small rodents.

The aim of this paper is to present food choice of fifteen buzzard families during their breeding season.

Material and methods

Pellets and food remains were gathered at fifteen Rough-legged Buzzard nests in 1974 and 1975 at the end of breeding season. In 1974 samples were collected at seven nests, two of which were in the alpine and five in the subalpine region. In 1975 eight nest-sites were examined, five of which were in the alpine and three in the subalpine region. The analysis of the material is described in another paper (Tast et al. 2010).

Fluctuations of small rodent numbers were studied by snap-trapping annually in different habitats beginning in the 1950's. The indices used in this study were obtained from the following snap trappings:

A) Line trapping (Kalela 1957, p.139) performed in the subalpine birch region in June and autumn annually since 1954. In this study, results of June trappings of 1974 and 1975 are presented. Traps were set in lines straight up the mountain slopes from the shore of Lake Kilpisjärvi to the tree line. The traps were placed in pairs at about 7 m intervals. Most trap sites were in different forest habitats, but partially also in shrubs and small bog areas. The catches made in different habitats have been combined. The lines began at a height of 460 m a.s.l. and continued to about 600 m. a.s.l.

B) Trapping (Tast 1966, 1968) in an open bog area at a height of about 500 m a.s.l. close to Lake Kilpisjärvi. Here two traps were placed at each point which were every summer the same. This study plot is a favourite habitat of *Microtus oeconomus*. The trapping was performed at the end of June and beginning of July.

C) Trapping (Tast 1966, 1968) in a peatland study plot near the tree line at about 600 m a.s.l. Traps were set in groups of five annually in the same suitable places at the end of June and beginning of July.

D) Trapping in Saananvankka, an alpine valley between the fjelds Saana and Jehkats above the tree line consisting of low alpine

meadows and grassy thickets, some of which are seasonally subject to flood. The trapping was performed at the end of June and early July. Groups of five traps were set annually in same suitable places at heights from 600 m a.s.l. to 700 m a.s.l.

Saananvankka is a favourite hunting area of Rough-legged Buzzards. During some years, e.g. in 1974, five pairs searched their food there.

Results

Rodent populations during the study years

The abundance of small rodents fluctuates at Kilpisjärvi cyclically. The cycles vary both in their amplitude and length. Also species composition differs from peak to peak. Peaks may last from one to three years. In most years populations increase during summer time, but during some winters microtines may reproduce (Tast & Kaikusalo 1976, Kaikusalo & Tast 1984). In such cases, for example after the winter of 1973/1974, vole populations can be higher in spring than during the previous autumn. The summer peak of 1974 was highest during the total study period of 1950 - 2002. This peak was also reflected in the numbers and occurrence of other rodentivorous predators. For instance, the snowy owl, *Nyctea scandiaca*, nested in Finnish Lapland probably for the first time for four decades (Hakala et al. 1974, Järvinen 1983).

Tables 1 and 2 present results of snap trappings in the four study areas. Although rodent populations reached a high level already in autumn 1973, they remained high till late 1975. The species composition changed by time. It has been already earlier established that when *Microtus oeconomus* numbers increase, the weaker *Microtus agrestis* disappears from most of its optimal habitats (Tast 1968, Viitala 1977). Similarly the expansion of *Clethrionomys rufocanus* results in disappearing of *Clethrionomys rutilus* from its best habitats (Viitala 1977, 1984, 1987). These changes can be seen when comparing Tables 1 and 2.

Lemmings bred in 1974 only in the open

Table 1. Results of rodent trapping in four habitats in 1974. A = line trapping in subalpine birch forests from 560 m to 600 m a.s.l., B = an open bog area in the subalpine region close to Lake Kilpisjärvi at about 500 m a.s.l., C = a bog area at the tree line 600 m a.s.l., D = low alpine meadows and willow thickets from 600 m to 700 m. a.s.l. Figures given denote vole numbers per 100 trap-nights. Numbers for trap-nights of study area A include also autumn trapping.

Study area	<i>L.lemmus</i>	<i>C.rufocanus</i>	<i>C.rutilus</i>	<i>M.oeconomus</i>	<i>M.agrestris</i>	Total	Trap nights
A		15.5	0.9	1.8	3.8	22.0	2512
B		1.3	1.3	25.3		27.9	75
C	9.0	6.3	1.8	27.2		44.3	110
D		5.6		33.8	2.0	41.4	143

Table 2. Results of snap-trappings in 1975 in the same areas as in Table 1.

Study area	<i>L.lemmus</i>	<i>C.rufocanus</i>	<i>C.rutilus</i>	<i>M.oeconomus</i>	<i>M.agrestris</i>	Total	Trap nights
A		5.8	0.3	0.5	0.3	6.9	2464
B	1.3			18.0		19.3	78
C	0.8	5.7		7.3		13.8	123
D	1.1	6.5		6.0		13.6	183

bog area at timber line, while in 1975 they were caught also in other open habitats but not in forests. In years with high lemming numbers they are commonly caught also in forests.

Diets of Rough-legged Buzzard families

The diets of different buzzard families varied greatly (Table 3). A peculiar feature is that at almost every nest one prey species dominated. In twelve of the fifteen cases the proportion of the main rodent species exceeded 50 % of the total number of prey animals. Unexpectedly, the dominating food item was not the same, neither when the two study years were compared nor when the main habitats (alpine/subalpine region) were treated. Four of the five small rodent species living in the Kilpisjärvi area were among the favourite food items at least at one nest.

At four nests *Clethrionomys rufocanus* was the most abundant food item. In 1974 the bulk of prey animals consisted of this species at two alpine nests, and in 1975 at one nest both in the alpine and in the subalpine region. These results tally well with the fact that the abundance of grey-sided voles is in most

years highest of all rodents both in most alpine and subalpine habitats. But at one nest (7/1974) in the subalpine region not a single grey-sided vole was found, and at further six nests their share did not exceed one fourth.

Especially interesting is the nest 7/1974 where food consisted mostly of red voles. This vole occurs only in small numbers in the area. According to multiannual live trapping experiences the numbers of breeding females in best habitats is two per hectare as compared with the corresponding figure for grey-sided voles, 35 breeding females per hectare (Viitala 1977, 1984a, 1987). The male of this buzzard pair had for some reason specialized in hunting red voles, although grey-sided voles and root voles were much more abundant at that time.

Norwegian lemmings formed the main food at three alpine nests in 1975, but in none a year before.

The principal food consisted of root voles at two subalpine nests in both years. Only field voles did not occur among the most abundant prey animals at any of the nests investigated.

Field voles and root voles resemble each

Table 3. Composition of the diets of fifteen Rough-legged Buzzard families according to pellet analysis. Figures given are numbers of prey animals. With **bold** are shown figures which constitute at least 50 % of all prey at that nest. Nests 1, 2, 8, 9, 10, 11 and 12 are from alpine habitats; nests 3, 4, 5, 6, 7, 13, 14 and 15 from subalpine habitats.

Nests of 1974

Nests	1	2	3	4	5	6	7	Total
<i>L. lemmus</i>		12		18	5	8	1	44
<i>C. rufocanus</i>	69	41	8	29	13	33		193
<i>C. rutilus</i>	4	3	3	1		7	31	49
<i>M. oeconomus</i>	2	10	17	57	27	40		153
<i>M. agrestis</i>	2		5	13	2	15	18	55
Total	77	66	33	118	47	103	50	494
Proportion of main prey (%)	90	62	52	48	57	39	62	

Nests of 1975

Nests	8	9	10	11	12	13	14	15	Total
<i>L. lemmus</i>	21	29	9	25	31	3	2	1	121
<i>C. rufocanus</i>	16	9	3	6	46	24	14	38	156
<i>C. rutilus</i>						7	2	4	13
<i>M. oeconomus</i>	23	12	3	19	12	52	41	3	165
<i>M. agrestis</i>	4	2				5	3	1	15
Total	64	52	15	50	89	91	62	47	470
Proportion of main prey (%)	36	56	60	50	52	57	66	81	

other both as to their colour, behaviour and habitat selection. If the two *Microtus* species were treated jointly, at further two nests their combined numbers would exceed half of the total diet (4/1974 59.3% and 6/1974 53.4%).

At all fifteen nests the numbers of voles differed significantly from which would be expected on the basis of their occurrence in field.

Usually Rough-legged Buzzards are hunting in open habitats, not in forests. When their combined numbers at all nest-sites are compared with rodent frequencies in all open study habitats, i.e. areas B, C and D, the following conclusions can be drawn. In 1974 at the alpine buzzard nests lemmings, red voles and field voles were found in relation to their availability, while grey-sided voles were caught highly significantly ($P < 0.001$) more often than expected. On the contrary the proportion of root voles was highly significantly smaller than expected ($P < 0.001$). Also in 1975

their numbers were highly significantly smaller than expected, while all other species occurred among prey significantly more often than expected.

Owing to interspecific competition between field voles and root voles and correspondingly between red voles and grey sided voles, the numbers of the weaker species in 1975 were highly significantly lower than in 1974 ($P < 0.001$). The numbers of lemmings were highly significantly higher in 1975 than in 1974 ($P < 0.001$), while in proportions of root voles and grey-sided voles no difference between years was observed.

Discussion

The dominating prey item in the diets of Rough-legged Buzzard families had a disproportionally large share. Its amount did not correlate with observed abundances of different microtine species in the field. And further, the dominating species varied at

different nests. A predator is selective if it takes some or all prey in different proportions than those that are present in habitats where the predator hunts. Prey may be chosen on the basis of its species or size. The sizes of the small rodents living in Kilpisjärvi area are in order from heaviest: the lemming, the root vole, the field vole, the grey-sided vole and the red vole (e. g. Henttonen et al. 1977). There seems to be no correlation in the preferences of Rough-legged Buzzards and the sizes of their prey rodents. Obviously the size of a prey mammal is not of importance for hunting buzzards, if it exceeds 15 grams, i.e. is larger than shrews. On the other hand, the prey animals ought to be smaller than 100 g. This means that buzzards avoid mammals which exceed sizes of lemmings and root voles.

Apparently the search of Rough-legged Buzzards was influenced by their first successful prey captures in the spring. Consequently, the searching image was formed, and buzzards learned to use a certain prey or a certain hunting habitat, or most likely both.

Of the rodents occurring at Kilpisjärvi, the Norwegian lemmings are by far the most conspicuous, especially when migrating. First, they have bright colours, most of fir being yellow/orange with large black areas in the back. And, furthermore, migrating lemmings are aggressive and noisy, their voice can be heard at distances of several hundred meters (Arvola et al. 1962, Myllymäki et al. 1962). Aggressively behaving migrating lemmings are not prone to escape. On the contrary, they may attack animals which they meet on their way, even so big ones as reindeer and dogs and even cars. Hence, an avian predator has no difficulties to catch them. Consequently, it is easy to understand that the share of lemmings during years of lemming migrations is unproportionally high in buzzard diets.

The impact of grazing lemmings on the vegetation of their home ranges is so heavy that they cannot settle down to the same territories in successive peak years (e.g. Kalela et al. 1961, Tast 1991). Hence, in 1975 lemmings were forced to migrate longer distances from

their wintering sites to summer habitats than in 1974. In the beginning of buzzards' breeding season in 1975, most lemmings were exposed to avian predators when moving in areas unfamiliar to them without any runways or burrows where to escape.

The Rough-legged Buzzards which fed mostly on root voles surely hunted in open bog patches where this rodent species is often the only regularly occurring microtine (Tast 1966, 1968).

It is difficult to understand how one buzzard family (7/1974) breeding in forest region was able to live on the two in least numbers occurring vole species. However, both red voles and field voles are species which are inferior to grey-sided voles and root voles, respectively, and when the populations of the latter species are growing, the former are forced to leave their territories (Tast 1968, Viitala 1977, 1987). Hence, in 1974 red voles and field voles had to disperse to suboptimal habitats. Transient voles without well-known home ranges will probably experience higher predation. There is scattered evidence supporting this view (Metzgar 1967). Almost all avian predators are unable to capture rodents within burrows, and hence they mainly catch them when voles are exposed in the terrain. Steen (1994) observed when following root voles which were equipped with transmitters that dispersing voles had very high mortality rate during or immediately after dispersal. As residents they survived if they made it through the first couple of days.

Jacsic (1989) determined that a predator is opportunistic, if it takes all prey in the same relative abundance as present in those patches where it hunts. Thus, an opportunistic predator has a diet that correlates with prey abundances. All buzzards which we studied were selective in their prey choice.

Obviously the learning of a definite hunting habit is a common phenomenon among avian predators. Räber (1949) stated that in tawny owl *Strix aluco* and long-eared owl *Asio otus* a searching image was formed. Those owls that had been accustomed to catch birds did not try to capture small mammals. On the other

hand, Wendland (1963) observed that the same owl species in the parks of Berlin had adopted habit to hunt both mammals and birds. Sulkava (1966) found 26 hedgehogs *Erinaceus europaeus* among 80 prey animals of the eagle owl *Bubo bubo*. Usually hedgehogs are only rarely found among the prey of eagle owls. Several investigators have reported corresponding observations concerning the pygmy owl *Glaucidium passerinum* (e.g. Sonerud et al. 1972, Kellomäki 1977, Jedrzejewska & Jedrzejewski 1993). For example, a pygmy owl brought to its young ten nestlings of wryneck *Jynx torquilla* in succession (Sonerud et al. 1972). According to Mueller (1971), in North American raptors american kestrel *Falco sparverius* and broad-winged hawk *Buteo platypterus* searching image was the most important factor for the choice of prey.

Several injured raptors have been brought to the field station of the Finnish Forest Research Institute at Loppi, Ojajoki, in southern Finland, where these birds have been taken care of so long that it has been possible to release them after their curing. Many times odd and curious searching images were formed and adopted in captivity. A kestrel, *Falco tinnunculus*, was first fed with naturally coloured mice, but when white laboratory mice were offered to it, it avoided them for a long period. An ural owl, *Strix uralensis*, was first fed exclusively with field voles. When food item was changed to water vole, *Arvicola terrestris*, the owl refused to eat them during a whole week. And worst of all was a honey buzzard, *Pernis apivorus*, which had received bananas as its food in its first host family. It was not at all interested in animal food.

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Subarctic rodents compensate predation losses caused by Rough-legged Buzzards *Buteo lagopus*

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A Rough-legged Buzzard pair with four young consumes about 2 000 voles or lemmings during the breeding season. In 1974 numbers of breeding buzzards were highest in our study area with 18 or 19 pairs having their nests in an area of 100 km². So, on average, there was one buzzard pair per 5 km². Their main prey, small rodents, produce three litters during the breeding period of buzzards. During increase and peak phases of rodent cycles voles may produce more than 600 young per hectare in optimal habitats. If one third of vole offspring survives, then 10 ha could produce the voles needed for one buzzard family. This is less than 1 % of the total territory of one buzzard family. Of course, whole of this area is not optimal habitat for small rodents, and several buzzard pairs may be hunting in same places. However, no doubt the predation of buzzards has only small effect on rodent populations during increase and peak phases of rodent cycles. During cyclic lows buzzards do not nest at all in our study area. As to the influence of buzzards' predation upon rodent populations, the social status of captured voles must be taken into consideration. Most prey animals caught by buzzards are individuals that have only small influence on the rodent population development, as rodents without own territories are most exposed to predation. Buzzards take all food on ground being unable to caught voles from their burrows. So, usually rodents captured do not belong to the breeding cohort. Thus, in most cases predation of Rough-legged Buzzards has only marginal effect on small rodent populations, because these are capable to compensate predation losses to a great extent. On the contrary mammalian predators, especially mustelids, surely have an important influence on rodent cycles.

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Introduction

Generally, when prey and predator relationships are investigated, the influence of predation is perhaps overestimated. The fact of predation should be distinguished from its effect on prey populations as claimed already long ago by Errington (1967). However, often this has been neglected. It is rather easy

to get exact data on the diet of an avian predator by analyzing pellets and food remains. Many specialist raptors are nomadic in their breeding habits. Correlations between the numbers of rodent prey and breeding densities and nesting success of rodentivorous raptors can be measured. In arctic and subarctic environments small rodents fluctuate violently cyclically, and so do their avian predators. But

when the influence of predators on prey populations is considered, an essential point of view is to which extent prey populations are able to compensate their predation losses. This paper is aimed to show how small rodents living in subarctic Finnish Lapland compensate losses caused by their main avian predator, the holarctic raptor Rough-legged Buzzard *Buteo lagopus*.

At Kilpisjärvi, in the northwesternmost corner of Finnish Lapland (69° 03'N, 20° 50'E) about 100 km north of the coniferous forest line, small mammals and their characteristic multiannual population cycles have been studied continuously since 1946 (e.g. Kalela 1957, 1962, Tast 1966, 1968, Tast & Kalela 1971, Henttonen et al. 1977, Hansen et al. 1999, Henttonen & Hanski 2000, Tast et al. 2005).

The breeding biology and population densities of the five small rodents living in the area are known fairly exactly in detail. They are presented for the grey-sided vole *Clethrionomys rufocanus* e.g. in Kalela (1957) and Viitala (1977), for the red vole *Clethrionomys rutilus* in Viitala (1977, 1984) and Henttonen & Peiponen (1982), for the root vole *Microtus oeconomus* in Tast (1966), and for the field vole *Microtus agrestis* in Viitala (1977, 1984) and Tast (1980), and for the Norwegian lemming *Lemmus lemmus* in Kalela et al. (1961, 1971a, 1982) and Tast (1982). The occurrence of the species in different habitats is summarized e.g. in Kalela et al. (1971b) and Henttonen et al. (1977).

Food intake of breeding Rough-legged Buzzards

A young Rough-legged Buzzard, youngest in its brood from the Kilpisjärvi area, was used in feeding experiments. Permission to use wild animals including Rough-legged Buzzards, in experiments at Ojajoki field station in Loppi, was given by Finland's Ministry of Agriculture and Forestry on January 21, 1974, diary number 6401/ 64 M –MM 1973. The food consumption of this young buzzard was measured, and its gaining of weight was followed to late autumn. Its daily food intake averaged 140 g. This means about 5 or 6

specimens of small voles (*Clethrionomys rufocanus* and *rutilus* and *Microtus agrestis*) and 3 or 4 lemmings or root voles.

During rodent peaks a buzzard nest often consists of four nestlings (Hagen 1952, 1969, Barth 1952, Potapov 1997, own observations in Tast et al. 2010). The nestling period is from 39 to 43 days. So a nestling consumes about 6 kg rodents when being in its nest and another 6 kg while fledged before migrating from the area. The adult birds take roughly the same amount as nestlings. So a buzzard family will use some 35 kg during the nestling period and 80 kg during the whole summer season. This means roughly 2000 to 2500 small voles or 1500 to 2000 root voles or lemmings.

Reproduction of small rodents

The reproductive potential of predators is much less efficient than that of microtine rodents. All avian predators living in arctic and subarctic environments have seasonal reproduction which is restricted to a rather short period following snowmelt. They produce only one brood during the breeding season. Litters of microtine rodents in optimal circumstances follow one another in succession every 3 weeks (Kalela 1957, Kalela et al. 1961, 1971a, Tast 1966, 1980, Koponen 1970, Viitala 1977, 1987). Post partum oestrus occurs commonly. First litters of all five small rodent species are produced already under snow at the time when buzzards are laying their eggs. So rodents are able to produce three litters during buzzard's incubation (28 – 31 days) and nestling period and still one litter after buzzards have fledged before their migrating to wintering areas. And furthermore, in suitable circumstances young rodents of first litters can attain sexual maturity at an age of 3 to 5 weeks and give birth to their first litters before buzzard young fledge. Their maturation depends on population density. Maturation of both males and females is restricted by social factors. In all five rodents males of the year achieve sexual maturity only, if no mature males are living in close vicinity (Kalela 1957, 1982, Tast 1966, Viitala 1977, 1987). If there are few overwintered males in spring,

almost all the males of the first litters mature immediately after weaning. But when the population includes more mature males than can attain dominant status, a hierarchy is established, and subordinate males must disperse to unoccupied areas.

Young *Clethrionomys* females of both species reach sexual maturity only if they have occupied a home range of their own (Viitala 1977, 1987). Thus, their maturation is territorially regulated (Viitala 1977, 1984, 1987, Viitala & Ylönen 1993). But the maturation of young red vole females is prohibited also by presence of grey-sided voles. Also the puberty of both *Microtus* species and the lemmings is density dependent (Tast 1966, Koponen 1970, Viitala 1987).

Microtus females can form breeding colonies (Tast 1966, Viitala 1975, 1977, 1987, Viitala & Ylönen 1993), but also among them reproduction ends in overdense populations and young females remain immature.

When rodent populations are dense, their reproduction ceases earlier. Among lemmings variation in the ending of breeding can be several months (Koponen 1970, Kalela 1982). In 1970, when lemmings were most abundant during our study period, their breeding ended already by the end of June, while in other years in suitable habitats their breeding can continue to the late autumn, in some years as long as to November (Kalela 1982).

During good rodent years reproduction of microtines begins in spring at the time when buzzards arrive to the area. Thus, vole yearlings are independently moving distinctly before buzzard eggs hatch. The average litter sizes of the rodent species in Kilpisjärvi region are the following: *Lemmus lemmus* 6.1 (n = 364) according Kalela & Oksala (1966), *Clethrionomys rufocanus* 6.0 (n = 285) Kalela

1957, *Clethrionomys rutilus* 7.3 (n = 41) Henttonen & Peiponen (1982), *Microtus agrestis* 6.0 (n = 285) Tast (1980), and *Microtus oeconomus* 7.1 (n = 361) Tast (1966, 1980).

The size of territories occupied by microtines in Kilpisjärvi area have been estimated on the basis of live trapping of voles. Female microtines are territorial, the minimum size of a home range of a female *Clethrionomys rufocanus* is 300 m², while that of a *Clethrionomys rutilus* is 5000 m² (Viitala 1987). Thus, there can live in good habitats 35 female grey-sided voles per hectare, while the ha-density of red voles is 2 females.

Microtus agrestis females can attain sexual maturity although they have not occupied a home range. When the young females of the first litter of the year attain maturity, almost half of the territories are common with two or more females (Viitala 1977). Next litter is delivered in another place, while voles become territorial. This mechanism enables them to occupy suboptimal habitats when population density increases. The size of their territories is smaller than that of grey-sided voles, at the highest there have been 70 females per ha. As to root voles, their breeding biology resembles in principle that of field voles. Average size of a female territory was 500 m², and also among root voles in late summer common territories of several females exist (Tast 1966). We have not live-trapped lemmings, but according to snap trapping results their densities can be at least of the same magnitude as for grey-sided voles.

As a conclusion during the nesting period of Rough-legged Buzzards, all microtine species may produce at least three litters, and the females from first litters, one litter. Rodent reproduction per one hectare in optimal circumstances is presented in Table 1.

Table 1. Microtine reproduction in optimal circumstances (females x litters x litter size) per 1 hectare.

<i>Clethrionomys rufocanus</i>	35 x 3 x 6 = 630 individuals
<i>Clethrionomys rutilus</i>	2 x 3 x 7 = 42
<i>Microtus agrestis</i>	70 x 3 x 6 = 1260
<i>Microtus oeconomus</i>	20 x 3 x 7 = 420
Our estimate of <i>Lemmus</i> production is about	500

Although mortality among young rodents is high, there are surely still several hundreds of young voles per ha available for buzzards.

Influence of Buzzards' predation on rodent populations

When the actual influence of a predation act is estimated, the social status of the small rodent captured must be taken into consideration. And also the phase of rodent cycle has its influence.

Generally, the voles most vulnerable for avian predation are those without any established home ranges, as buzzards take their food on ground being unable to catch rodents from their burrows. In dense small rodent populations all animals are not actively taking part in reproduction. These subordinate ones are most easily captured by raptors, and their removal has in principal no effect on the numbers of breeding rodents. If an immature vole is caught, its disappearance has no effect on population development, as it did not belong to the reproductive cohort. If a mature male is caught, then to a subordinate one is given possibility to mature and fill the "male vacuum". Among lemmings, migrating individuals are most exposed to avian predation.

The initially overdense population thins out towards optimum level because of dispersal. In males it is brought about by aggressiveness in old males, but in females by a territorial avoidance reaction in young females. Steen (1994) followed radiomarked root voles and found that the survival of transient dispersing voles was poor, but there was a distinct positive change in their survival after they had occupied own territories. And mostly dispersing voles are young voles which have not yet attained sexual maturity or in the case of both *Microtus* species, young females which are pregnant for the second time and searching a home range for themselves in suboptimal habitats (Tast 1966, Viitala 1977). As to sexes, obviously males are caught by avian predators more often than females. Fresh prey animals found by us at Rough-legged Buzzard nests support this view.

In all small rodent populations studied at Kilpisjärvi, males move more than females and mature males move within the home ranges of several females. If a predator catches such a male, this has almost no effect on the rodent numbers. Firstly, there are several males whose ranges are overlapping. Surviving males are able to fertilize females. Secondly, now some of young males have possibility to attain sexual maturity, as the dominating male is absent.

When immatures are captured, the effect is not of any importance perhaps with the exception of summers after cyclic lows, when all of the young produced in early summer attain sexual maturity and take part in reproduction already in the season of their birth.

If a mature *Clethrionomys* female is captured by a predator, the influence depends on the phase of rodent cycle. In live trappings conducted by Viitala (1987) in 1973 and 1974, during increasing phase and the actual peak, immediately after removing a female, a young one occupied the home range and attained sexual maturity. So the loss caused by predation was compensated within a few days. In 1972, all females in the study plot were mature yearlings. Now, theoretically the situation could be such that no young immature females were present and so not available to fill the vacant home range. If so, then predation had a real effect on the population development of the *Clethrionomys* species in question.

In the case of *Microtus* species, the situation is more complicated, because in a given phase females are able to attain sexual maturity without having at that time a home range of their own. But also in the best habitats of the two *Microtus* species, there are limits after which no new habitats can be occupied. During some of the population peaks, e.g. in 1960, field voles almost totally disappeared from Kilpisjärvi, as the root voles occupied the habitats suitable to both species (Tast 1968). In optimal habitats surely after disappearing of a mature female, a young female occupies this vacant home range. It is only in suboptimal habitats were avian

predation can have a real influence on the *Microtus* population.

In good habitats where more than 30 *Clethrionomys* females are living, they can produce three litters each totalling 100 litters during Buzzard's breeding period. If one third of the young survive, the rodent production is 300 voles. This means that an area of 10 hectares is large enough to support one Buzzard family. As the area covered by a Buzzard family is about 5 km², this means that less than one per cent of the Buzzard's hunting area will give enough rodent food to these raptors. And the area needed to produce 2000 *Microtus* voles is even smaller than that of the corresponding area with *Clethrionomys* voles. As a consequence, during years with increasing or high microtine numbers, the effect of buzzard hunting on vole populations is not of any importance.

During cyclic lows buzzards do not nest at all in our study area. If rodent numbers in spring exceed the threshold needed for buzzards to onset nesting activities, and then vole populations collapse during the summer, as happened in 1984, nestlings of buzzards starved. Surely, the disappearance of rodents was not caused by avian predation.

The influence of mammalian predators, especially that of mustelids, which are able to capture voles also from their burrows and overwintering colonies, is quite different than the effect of avian predators, most of which live in the Kilpisjärvi region only during the snowless season. Usually the culmination of rodent cycles takes place during winter.

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Kilpisjärven biologinen asema Helsingin yliopisto

Kilpisjärven biologinen asema (perustettu 1964) on Helsingin yliopiston luonnontieteellinen tutkimusasema. Asema (69°03'N, 20°50'E) sijaitsee subalpiinisessa tunturikoivuvyöhykkeessä. Koivuvyöhyke ulottuu noin 600 metrin korkeuteen. Suomessa ainoastaan Kilpisjärven seudulla on yli 1000 metrin korkeuteen kohoavia tuntureita. Tammikuun keskilämpötila on -13,5°C, helmikuun -13,1°C, kesäkuun +7,4°C ja heinäkuun +10,8 °C. Lumi sulaa tunturikoivikosta kesäkuun alussa. Kilpisjärven luonto on monipuolinen, mikä johtuu alueen sijainnista ilmastollisella ja geologisella rajavyöhykkeellä. Erityisesti muusta Suomesta poikkeavat eläimistö ja kasvisto ovat houkuttelleet biologeja Kilpisjärvelle.

Kilpisjärvi Biological Station University of Helsinki

Kilpisjärvi Biological Station (founded in 1964) is a scientific research station belonging to the University of Helsinki. The station (69°03'N, 20°50'E) is situated in the subalpine birch forest zone in Finnish Lapland. The upper boundary of the birch forest lies at about 600 m. Kilpisjärvi is the only part of Finland with altitudes of 1000 m or more. The mean temperature in January is -13,5°C, in February -13,1°C, in June +7,4°C and in July +10,8°C. The snow in the birch forest melts in early June. The situation of Kilpisjärvi in a climatic and geologic border zone results in a great variety of habitats within a restricted area. The unique fauna and flora, which differ from those of any other part of Finland have made the region especially attractive to biologists.



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