

Diet, nesting density, and breeding success of rough-legged buzzards (*Buteo lagopus*) on the Nenetsky Ridge, Arctic Russia

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Abstract The rough-legged buzzard, a circumpolar avian predator, is usually defined as rodent specialist in the tundra but as a generalist in the boreal zone, leaving open the question of where the shift in feeding strategy occurs. Here, we investigated the diet and breeding biology of buzzards as well as abundance of their possible prey during 5 years in the low-Arctic shrub tundra on the Nenetsky Ridge, Russia. We employed three complementary methods to assess the diet of this Arctic predator—pellet dissection, identification of prey remains on nests, and stable isotope analysis—to overcome their respective limitations. We documented fluctuations in abundances of the likely prey, namely rodents, ptarmigans, and hares. Nesting density of buzzards changed substantially over the years, but did not track the abundance cycle of the rodents. The

number of buzzard fledglings was relatively low (1.08 ± 0.3) and did not change according to the density of rodents. In the year when rodents were at their lowest abundance, diet analyses of nestlings documented a shift from rodents to alternative prey, with a decrease in the proportion of tundra voles and an increase in proportion of hares, ptarmigans, and ducks. Here, we argue that buzzards may adopt different feeding strategies along the gradient from generalists to specialists. While the rough-legged buzzard is usually considered a small rodent specialist, our study shows that it can shift to alternative prey where or when rodents are scarce and when alternative prey are sufficiently abundant to provide subsistence for breeding.

Keywords Rough-legged buzzards · *Buteo lagopus* · Diet shift · Stable isotopes · Predator–prey interactions · Arctic

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Introduction

Small rodents (voles and lemmings) are often dominant primary consumers in terrestrial boreal and arctic ecosystems and therefore key prey for many predator species in such ecosystems (Wiklund et al. 1999; Ims and Fuglei 2005). Still northern predator species differ in their reliance on rodents. They can be classified as specialists if the proportion of their prey (here rodents) is always dominant in the diet, independently of the prey's abundance, or they can be considered as generalists when they target different prey in the same proportion as they appear within their environment (Andersson and Erlinge 1977; Jaksic 1989; Hanski et al. 1991; Dawson et al. 2011). Among rodent specialists, breeding success and population density usually vary with rodent availability; generalists on the contrary

are able to shift from one type of prey to another, and their density and reproduction are thus less dependent of prey availability (Hagen 1969; Korpimäki 1985; Korpimäki and Norrdahl 1989; Redpath and Thirgood 1999; Redpath et al. 2001). Some predators, however, do not have a single fixed feeding strategy, and they occupy an intermediate position along the gradient from generalists to pure specialists (Glasser 1982; Hanski et al. 1991; Malo et al. 2004). Unravelling the degree to which abundant arctic predator species behave as specialists or generalists is central to understanding their population dynamics, their function in the food web, as well as their response to environmental changes (Newton 1979; Hanski et al. 1991; Ives et al. 2005; Dawson et al. 2011).

The rough-legged buzzard (*Buteo lagopus*) is a bird of prey with a circumpolar distribution. The optimal breeding areas for these birds are the southern bioclimatic subzones of the Arctic (Snow et al. 1998; Ferguson-Lees and Christie 2001). The rough-legged buzzard (hereafter buzzard) is usually defined as a small rodent specialist (Osmolovskaya 1948; Mindell et al. 1987; Tast et al. 2010a, b). In tundra habitats, the density of small rodents is known to undergo periodic fluctuations (population cycles, usually with a period of 3–4 years), and buzzards track this prey dynamics, translating into a cyclical pattern in nesting density and reproductive performance (Galushin 1974; Potapov 1997; Sokolov 2002; Sundell et al. 2004). However, some authors have classified the rough-legged buzzard as a generalist predator (Hanski et al. 1991) or as a predator able to shift to alternative prey, such as grouse, ducks, and hares, in years of low small rodent abundance (Pasanen and Sulkava 1971; Kalyakin 1989). Tast et al. (2010a) explain this dichotomy by the differences in prey diversity available in different parts of the buzzard's range: according to these authors, in the northern part of the boreal zone, where they argue that biodiversity is higher than on the tundra, buzzards are likely generalists, whereas in the tundra, they are small rodent specialists. In contrast to Tast et al.'s suggestion, Kondratyev et al. (2006, 2007, 2008, 2011) and Glazov (2011) noted that buzzards were successfully nesting in tundra habitats on Kolguev Island (in the Barents Sea), despite small rodents are absent from the island.

Here, we investigate the diet and breeding performance of buzzards on the Nenetsky Ridge, located in the south-western part of the Russian Arctic. In this region, the small rodent community is dominated by tundra voles (*Microtus oeconomus*), and lemmings (two species: *Lemmus sibiricus* and *Dicrostonyx torquatus*) are practically absent (van Eerden 2000). We expected that buzzards either could compensate for the low availability of small rodents (mainly caused by the low number of lemmings) in the area by generally using alternative prey such as willow ptarmigan (*Lagopus lagopus*) and mountain hare (*Lepus*

timidus) or that they could compensate for the temporally low abundance of small rodents by using alternative prey in the low phase of the rodent cycle. The main objectives of our investigation were to (1) estimate the temporal variation of relative abundance of the three potential prey for buzzards—rodents, ptarmigans, and hares; and (2) determine how buzzards respond to the temporal variation of their prey in terms of diet composition, nesting density, and breeding success. We employed three complementary methods to assess the buzzard's diet: pellet dissection, identification of prey remains on active nests, and stable isotope analysis. This allows us to reveal whether buzzards act as specialists or generalists in our study area.

Materials and methods

Study area

Our investigations were carried out as part of the 'Arctic Predators' project (www.arctic-predators.uit.no) in the Nenetsky Nature Reserve (68°20'N 53°18'E), Russian Arctic, from mid-June to mid-August 2007–2011. This region belongs to the low-shrub tundra zone (Walker et al., 2005). Our study area included the Sediyaha, Sengruyaha, and Nyudiako-Pendermayaha rivers with relatively deep (ca. 50 m) and narrow (ca. 300 m wide) valleys. The valleys are characterized by lush meadow vegetation and dense willow thickets over 2 m high. The surrounding tundra landscape harbours sand cliffs up to 40–50 m above sea level. The small mammal community is dominated by tundra voles; other herbivores in this area are predominantly mountain hare and willow ptarmigan (cf. Ehrlich et al. 2012).

Abundance of prey

We estimated abundance indices for small rodents and the two main alternative types of prey (hares and ptarmigans), using, respectively, snap trapping and faeces counts on 36 study plots covering three widespread habitat types (meadows at the edge of willow thickets, hummock tundra, and dwarf shrub tundra). Spatially, the plots were arranged as triplets with one plot in each of the tree habitats (Ehrlich et al. 2012). Rodent trapping was done according to the small quadrat method (Myllymäki et al. 1971). Three snap traps were placed in each corner of 15 × 15 m plots for two successive nights at the end of June and in the middle of August and baited with raisins and rolled oats. Faeces counts were carried out at the same time as snap trapping in eight 50 × 50 cm quadrates, which were evenly distributed around the study plots. In total, the yearly abundance

indices were thus based on 1,728 traps/night (36 plots \times 12 traps \times 2 nights \times 2 trapping sessions) and 576 faeces quadrates (36 plots \times 8 quadrates \times 2 counts).

Monitoring of buzzard breeding performance

We monitored an area of ca. 150 km², targeting river and lake banks during walking excursions, using 8–10 \times binoculars to search for buzzard nests. To secure constant search effort and zone, we only used the nests found in the part of the study area that was surveyed during all 5 years. To collect samples for diet analysis and to record nesting success (a successful nest being a nest producing at least one fledgling), we regularly visited active nests (approx. every 5–10 days) until fledging time. The breeding success of buzzards was estimated as the mean number of fledglings (young that reached 35 days of age—ca. 4 days before average fledging) per territorial pair in a particular year, following Marti et al. (2007). The nesting density of buzzards was estimated as the number of territorial pairs, which had a clutch (one egg or more) in the monitoring area in a given year.

Diet analysis

The most widely used methods for investigating raptor diet (especially for nestlings) are the analysis of pellets and prey remains left at the nest; however, these methods lead to biases in estimating prey proportions (Simmons et al. 1991; Marti et al. 2007; Tornberg and Reif 2007). Large prey may be underestimated by pellet analysis because adults dissect large prey and often feed only the meat to their nestlings, a tissue they digest completely. On the other hand, large prey may also be overestimated by analysis of prey remains. Nestlings require more time to consume larger prey items compared to smaller items, which can be swallowed in one piece; thus, the remains of large prey have a greater chance to be found at the nest (Redpath et al. 2001; Lewis et al. 2004). In addition, ptarmigan chicks that are soft-boned may be totally digested and underestimated (Tornberg and Reif 2007). The combination of these methods can also lead to overestimation of some prey in the diet because of double counting, i.e. fur from one hare could be found in pellets and as prey remains on the nest. Furthermore, errors may arise from different ways of calculating prey proportion in the diet (Redpath et al. 2001). For instance, proportions based on the number of prey may overestimate small prey items (Sonerud 1992). Estimating proportions based on the weight of prey is often difficult due to our inability to evaluate the precise weight of the consumed prey, particularly when prey fragments (e.g. femur or humerus) are absent.

Stable isotope analysis is another powerful method to estimate diet composition (e.g. DeNiro and Epstein 1977;

Hobson and Clark 1992; Inger and Bearhop 2008). One of the advantages of this method is that it addresses proportions of assimilated food and avoids thus the biases described above. However, the inference of diet composition using stable isotopes requires knowing discrimination factors for the analysed consumers (e.g. Lecomte et al. 2011); though this is not necessary for documenting a diet shift over time as it can be assumed that discrimination factors are constant in time. In the present study, we used a combination of all three methods (prey remains, pellets, and stable isotopes) to get a more complete picture of diet change over time.

During visits to nests, pellets were collected at the nests, as well as from most of the resting places within the breeder's territory. We assumed that pellets at the nests were from nestlings, while pellets found at resting places were from the adults of the nearest nest. A minimum number of prey items was determined for each species or group of prey in each batch of pellets (i.e. all pellets found at one place on one collection date). Uncountable remains (feathers, fur) were registered as one prey item for each batch of pellets where they were found, but only if there were no other remains of this species. Prey remains found at the nests were identified to species level and counted (we did not find any prey remains at the resting places).

For stable isotope analyses, we sampled down and blood from nestlings at each nest visit. In 2007–2010, ca. 5 down feathers (2–3 pinches) from each young were collected dry and stored in individual paper bags. In 2009–2010, 0.5 mL blood samples were collected from the brachial vein of nestlings weighing over 100 g using a 1-mL insulin syringe with a 25-gauge needle. The blood was immediately transferred to Eppendorf tubes containing 1 mL of 70 % ethanol. To obtain prey isotopic signatures, we collected 1 cm³ samples of muscle from each possible prey, preserving the samples in 15-mL tubes with 10 mL of 70 % ethanol.

Tissue samples of small rodents were collected during snap trapping; samples of other prey were collected during nest visits (only if fresh). All materials for stable isotope analysis were stored in 70 % ethanol (muscle, blood) or dry at room temperature (down) until being transferred to the University of Tromsø where it was prepared for analysis before being sent to Stable Isotopes in Nature Laboratory (SINLAB, University of New Brunswick, Canada) for final analysis. Sample preparation included fat extraction (for down), drying in the oven at 65 °C, grinding, weighing, and packaging into tin capsules (for details see Ehrich et al. 2011).

In total, we analysed 949 pellets, 139 prey remains, 79 down, and 54 blood samples, as well as 87 samples of prey. Pellets, prey remains, and prey samples for stable isotope analyses were collected from 34 nest sites from 2007 to

Table 1 Number of nests and sample sizes used to describe the diet of rough-legged buzzards in 2007–2010, Nenetsky Nature Reserve, Russia

Year	Number of nests	Pellets on the nests	Pellets on the roosts	Remains	Stable isotope analysis		
					Down	Blood	Prey
2007	6	31	100	6	5	0	42
2008	10	63	126	37	8	0	32
2009	14	195	256	37	51	40	13
2010	4	46	132	59	15	14	0
Total	34	335	614	139	79	54	87

2010 (Table 1). Data from 2011 were not included because only one successful nest was found in the study area in that year.

Data analysis

The relative abundance of small rodents was estimated for each season in each year as the number of animals trapped per triplet of sampling plots. These estimates were summarized as the mean number of individuals trapped per 100 trap nights in each triplet and presented with a 95 % confidence interval (CI). The relative abundance of ptarmigan and hare was quantified as the number of small quadrates per triplet of study plots where faeces of the respective species were registered and summarized as means per year and season with CI.

We quantified buzzard diet in the following way. First, we estimated the range of prey species consumed by buzzards using pellets and prey remains analysis. Then, we calculated the number of prey items for each nest, separating prey remains consumed by adults and nestlings. To avoid double counting, the number of prey items for each nest was the maximum number of individuals of a particular species found in the pellets and prey remains together (not the sum). For instance, when we discovered the remains of three ptarmigans in the pellets, but found the remains of four ptarmigans in the nest on the same date, we counted a total of four birds consumed. To summarize the diet for a particular year, we calculated the percentage of each prey species (group) for each nest and then used the mean and CI of these percentages (Korpimäki et al. 1994; Reif et al. 2001). Proportions of prey were estimated in two different ways: (1) based on the number of prey; and (2) based on the weight of each prey, which was derived from the literature (for birds from Snow et al. (1998); for mammals from Nowak and Walker (1991)), assuming that the maximum weight of any prey could not exceed 1,000 g (Bechard and Swem 2002).

To estimate how the diet of buzzard nestlings varied between years using stable isotopes, we calculated the mean and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each year (down and blood were analysed separately). As for

pellets and prey remains, we first combined the values for each nest to derive an average for each year. We calculated the mean values of stable isotope ratios determined for each prey species or group of prey. Because $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ diet-tissue discrimination factors for blood and down of buzzards are unknown, we did not quantify nestling diet composition using mixing models. Instead, we used the diet proportions obtained from the pellet and prey remains analyses to predict values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for buzzards each year. Finally, we compared the changes from year to year in the predicted values to the observed changes in stable isotope values of down and blood of nestlings. To plot that comparison in a clear manner, we plotted the predicted isotopic values using the discrimination factor of the peregrine falcons (*Falco peregrinus*) determined by Hobson and Clark (1992).

All calculations were done using the statistical platform R 2.15.0 (R Development Core Team 2012). When analysing differences between years in the relative abundance of prey and in diet proportions, we used CI instead of significance tests, because CI conveys more information about the biological significance (Gardner and Altman 1986; Yoccoz 1991). We presented the means and CIs for all estimates and considered differences with non-overlapping CIs as providing strong evidence for a difference (see Schenker and Gentleman 2001).

Results

Prey abundance

During our trapping sessions, we caught 323 small mammals (rodents and insectivores). This total included 286 tundra voles, 18 shrews (*Sorex* sp.), seven northern birch mice (*Sicista betulina*), five water voles (*Arvicola terrestris*), four grey-sided voles (*Myodes rufocanus*), as well as three collared lemmings (*Dicrostonyx torquatus*). The abundance of small rodents (i.e. predominantly tundra voles) increased from 2007 to 2008, but then declined to low levels until spring 2011, and densities reached a new peak in autumn 2011 (Fig. 1). Most small mammals (95 %)

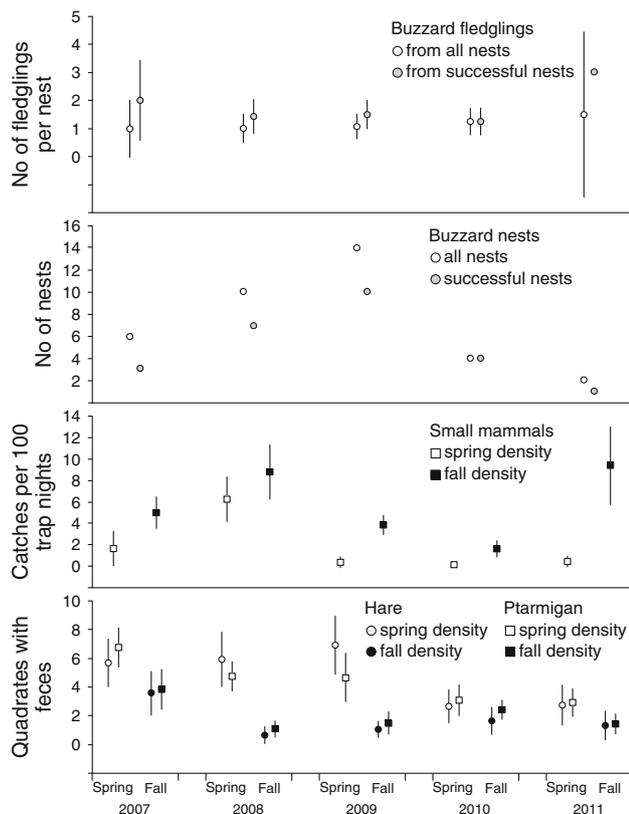


Fig. 1 Nesting density and breeding success of rough-legged buzzards, and prey abundance indices, Nenetsky Nature Reserve, Russia (2007–2011). Error bars represent 95 % confidence intervals

were trapped close to willow thickets and spring numbers were always lower than autumn numbers. Faeces counts indicated a decrease in the spring presence of ptarmigan from 2007 to 2011, while spring presence of hares was stable from 2007 to 2009, but dropped in 2010–2011 (Fig. 1; see also Ehrich et al. 2012).

Diet analysis

The diet of buzzards consisted of 11 species of mammals, 18 species of birds, one species of amphibian, as well as one species of fish. Frog (*Rana temporaria*) only occurred once, and fish (*Coregonus* sp.) twice; due to their rarity, they were not included in the analysis. Mammals were the most numerous group of prey for all 4 years (83 % of all prey items); tundra vole, water vole, and collared lemming were the most common mammalian species (73, 10, and 8 % of all mammalian prey items, respectively). The proportion of bird prey items was 17 %, with willow ptarmigan representing 49 % of all bird prey items. The number of different prey species increased from 2007 to 2010, mostly because of an increase in the number of bird species (Online Resource 1).

The number of tundra voles found in the diet of nestlings was constant from 2007 to 2009 (57–65 % of all prey

items), but dropped in 2010 (10 % of all prey items). The number of hares, ptarmigans, and ducks was low from 2007 to 2009 (0–10 % of all prey items), but increased in 2010 (13–39 % of all prey items). The numbers of collared lemmings, water voles, and other mammals remained low in all 4 years. In addition, the number of passerine birds and waders were at the same level for all 4 years. Compared to nestlings, the diet of adults showed a high proportion of tundra voles while the proportion of other prey was relatively low and stable for all years (Fig. 2). When compared to the proportions estimated from the number of prey, proportions based on the weight of prey showed a lower percentage of rodents and a higher percentage of hares, ptarmigans, and ducks (Fig. 2).

The stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of water voles and tundra voles were similar and the same was true for hares and ptarmigans (see Table 2 for signatures and confidence intervals of all pairwise differences between the prey species). Isotope signatures of the other prey species were distinct for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Table 2; Fig. 3). Mean values of $\delta^{13}\text{C}$ for nestling down remained similar from 2007 to 2009 (-24.34 ± 0.31 to -24.26 ± 0.38 ‰), but in 2010, down samples contained a greater proportion of the heavier carbon isotope (-23.58 ± 0.43 ‰). In contrast, the mean values of $\delta^{15}\text{N}$ in the down samples were at the same level during all 4 years (6.64 ± 0.35 – 7.24 ± 0.84 ‰, Fig. 3c). Blood samples in 2010 contained a greater proportion of the heavier carbon and lighter nitrogen isotopes compared to 2009 (-25.81 ± 0.25 ‰ $\delta^{13}\text{C}$ and 6.51 ± 0.34 ‰ $\delta^{15}\text{N}$ for 2009; -25.26 ± 0.25 ‰ $\delta^{13}\text{C}$ and 5.49 ± 0.19 ‰ $\delta^{15}\text{N}$ for 2010, Fig. 3d). Predicted signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for buzzards based on the results from pellets and prey remains analysis did not differ between years neither when calculating proportions using the number of prey items (Fig. 3a) nor when using the weight of prey (Fig. 3b).

Nesting density and breeding success

Density of breeding buzzards increased from a total of six nests in 2007 to 14 in 2009, but then decreased to two nests in 2011. However, breeding success of buzzards did not change over the 5 years of the study and was on average 1.08 ± 0.3 (95 % CI) fledglings per nest (Fig. 1).

Discussion

Nesting density and breeding success of buzzards

In our study area, we documented all phases of the rodent cycle: increase, peak, decrease, and crash. The relative presence of ptarmigans declined over the 5 years of the study, while the abundance of hares was stable for the first

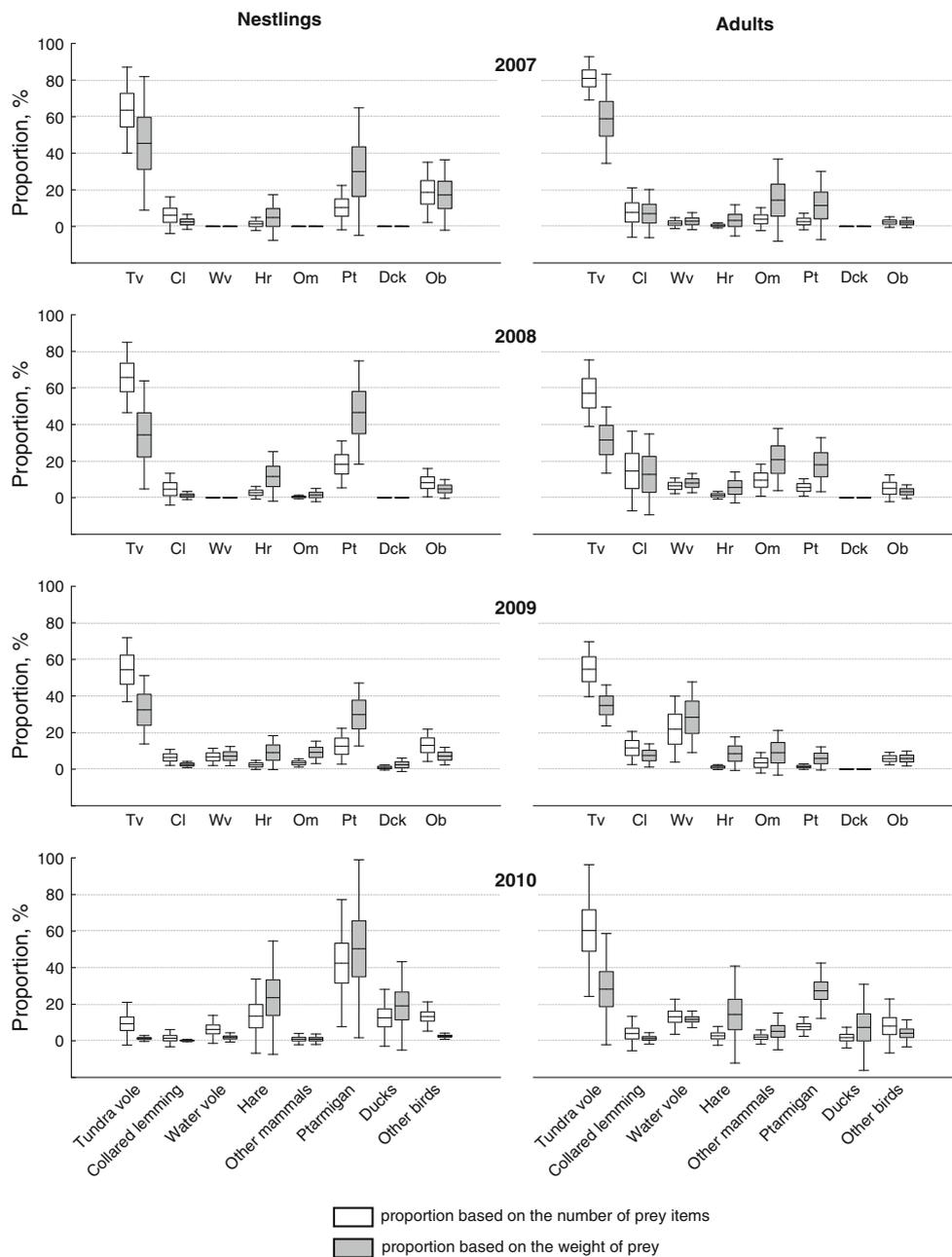


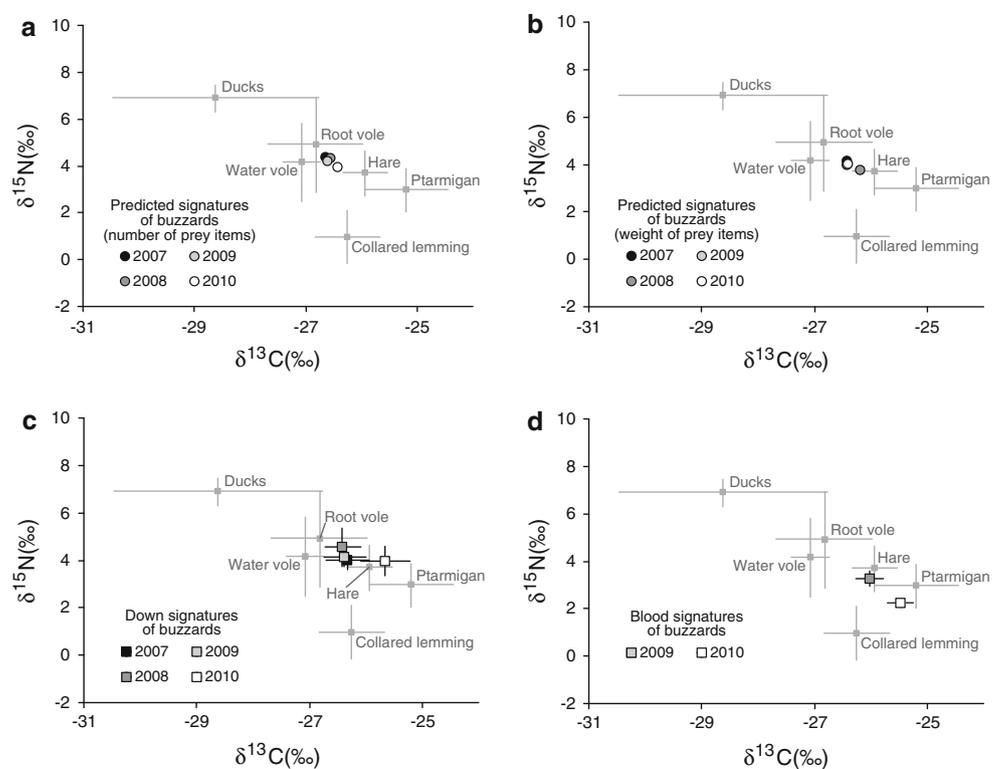
Fig. 2 Diet of rough-legged buzzards, Nenetsky Nature Reserve, Russia (2007–2010). Proportions are given with 95 % confidence intervals

3 years and declined thereafter (see also Ehrich et al. 2012). Contrary to our expectations based on other studies in the Arctic (Osmolovskaya 1948; Galushin 1974; Potapov 1997; Sokolov 2002; Tast et al. 2010a), nesting density of buzzards in the Nenetsky Ridge did not follow the abundance of small rodents. Such a discrepancy between the dynamics of buzzards and small rodents has also been documented for populations in the boreal zone, where the density of buzzards sometimes did not decrease during years of low rodent densities (Pasanen and Sulkava 1971; Kalyakin 1989). In alpine and sub-alpine regions of

Fennoscandia, nesting density of buzzards was low in years with peak abundance of small rodents (Hagen 1969). These discrepancies could be explained by the influence of the cumulative abundance of rodents and alternative prey; however, in our study, the cumulative abundance of all prey was highest in 2008, and the highest density of buzzards was observed the year after. Other studies have concluded that such a lag between vole abundance indices and raptors' breeding performance (i.e. peak numbers of breeding buzzard one year after the peak of voles) may be due to a delayed numerical response to voles (Reif et al.

Table 2 Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of prey species (mean \pm SD) and differences between them (mean \pm 0.95 CI of the difference), Nenetsky Nature Reserve, Russia (2007–2010). Upper part—for $\delta^{15}\text{N}$, bottom part—for $\delta^{13}\text{C}$, n —number of samples

	Tundra vole ($n = 43$)	Collared lemming ($n = 7$)	Water vole ($n = 7$)	Hare ($n = 9$)	Ptarmigan ($n = 13$)	Duck ($n = 7$)
$\delta^{13}\text{C}$	-26.83 ± 0.84	-26.25 ± 0.58	-27.07 ± 0.34	-25.94 ± 0.43	-25.21 ± 0.59	-28.61 ± 1.84
$\delta^{15}\text{N}$	4.91 ± 2.02	0.97 ± 1.12	4.17 ± 1.67	3.81 ± 0.86	2.99 ± 1.11	6.90 ± 0.58
Tundra vole		3.94 ± 1.12	0.74 ± 0.11	1.10 ± 0.86	1.92 ± 0.88	1.99 ± 0.75
Collared lemming	0.58 ± 0.56		3.20 ± 1.68	2.84 ± 1.12	2.02 ± 1.13	5.93 ± 1.07
Water vole	0.24 ± 0.11	0.82 ± 0.57		0.36 ± 0.86	1.18 ± 0.76	2.73 ± 1.55
Hare	0.89 ± 0.40	0.31 ± 0.58	1.13 ± 0.41		0.82 ± 0.75	3.09 ± 0.75
Ptarmigan	1.62 ± 0.43	1.04 ± 0.60	1.86 ± 0.44	0.73 ± 0.45		3.91 ± 0.77
Ducks	1.78 ± 1.55	2.36 ± 1.57	1.54 ± 1.52	2.67 ± 1.55	3.40 ± 1.55	

Fig. 3 Signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for rough-legged buzzard nestlings and their main prey, Nenetsky Nature Reserve, Russia (2007–2010). **a**, **b** signatures of nestlings calculated on the basis of the proportions of six main prey estimated from pellets and prey remains analysis (**a** proportions based on number of prey items, **b** proportions based on weight of prey); **c**, **d** observed signatures of nestlings, corrected for discrimination factors according to Hobson and Clark (1992); **c** down samples, **d** blood samples. Mean values \pm SD

2004). Although our observation is consistent with such a delayed response, we cannot confirm it because our 5-year study only covered one rodent cycle of 4 years. It is likely that rodent abundance (or abundance of prey in general) is not the only factor determining the density of buzzards, other factors such as a weather condition may have a stronger impact in certain regions and years. Influential weather conditions could be the amount of snow as well as the timing of snow melting during spring. When buzzards arrive to the nesting territory during late spring years, territories can still be covered by snow, preventing them from building their nest in time for a successful reproduction. In this case, buzzards will likely move to other

nesting locations free of snow despite a high abundance of prey because delaying breeding can negatively affect their breeding success. Despite our lack of quantitative data on snow cover and melting patterns, we suggest that this hypothesis could explain that nesting density was lower than expected in 2008 (rodent peak year), when we crudely estimated ca. three times more territory covered with snow than in any other year in the end of June.

The breeding success of buzzards in our study area was stable over the study period at a relatively low level (ca. 1 fledgling per nest). In other Arctic regions, the mean breeding success of buzzards may range from 0 to 4.3 fledglings per nest (Osmolovskaya 1948; Galushin 1974;

Potapov 1997; Sokolov 2002; Tast et al. 2010a). Stable breeding success could be explained by a combination of two opposing factors. On the one hand, the use of alternative prey increased the lower limit of breeding success, which never reached zero. On the other hand, the abundance of small mammals in the investigated region seems quite low, and the populations fluctuated with moderate amplitude compared to other study areas in the boreal and Arctic regions (Henttonen et al. 1977; Ims et al. 2011). These characteristics of the small rodent cycle may have played a role in decreasing the upper limit of breeding success, thereby buffering fluctuations in breeding success of buzzards. Also, the rodent community in the study region consisted mainly of tundra voles (lemmings and grey-sided voles were very rare). Different behaviour and habitat use of tundra voles, lemmings, and grey-sided voles may render them to be more or less accessible to avian predators (Batzli and Lesieutre 1991; Oksanen and Oksanen 1992). In particular, we suspect that tundra voles residing under the cover of dense thickets of tall willow may be less accessible to predators than lemmings and grey-sided voles in the more barren tundra habitats, which are characterized by sparser and more low-statured vegetation.

The observed increase in nesting success during the year of low abundance of rodents (up to 100 % in 2010) might be due to a nesting cohort of old and experienced pairs, which are able to shift to alternative prey and breed in a situation where their main food resource was scarce. This has also been shown for other raptors (Formozov 1934; Andersson 1976, 1981; Korpimäki 1988, 1990), but only suggested for buzzards so far (Mechnikova 2009). Marking adults in our study area may be one way to test such a hypothesis.

Diet shift

The diet analysis of buzzards documented a shift from main to alternative prey. Analysis of pellets and prey remains showed a decrease in the proportion of tundra voles and an increase in proportion of hares, ptarmigans, and ducks in 2010, compared to three preceding years. The stable isotope analysis showed the same pattern of between-year variation. Analysis of $\delta^{13}\text{C}$ in the down from growing nestlings indicated a similar diet for three consecutive years (2007–2009), with a change in 2010, compatible with a shift from rodents to ptarmigans and hares (towards the lighter nitrogen isotope and towards the heavier carbon isotope). Analysis of nestling blood samples in 2009–2010 also supported these conclusions. In contrast, adults fed mostly on rodents in all 4 years, signalling possible diet segregation between parents and nestlings.

Despite such congruence among prey remains, pellets, and stable isotopes, the signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for buzzards predicted on the basis of diet proportions resulting

from pellet and prey remains analysis were not congruent with the observed results from down and blood analysis. This could be explained by the layout of prey stable isotope signatures (Fig. 3): the main prey (here tundra and water voles) were located between two alternative prey groups (ducks on one side and hares together with ptarmigans on the other side). Thus, when buzzards shifted to alternative prey, the input of ptarmigans and hares (with low values of $\delta^{15}\text{N}$ and high values of $\delta^{13}\text{C}$) was compensated by ducks (with high values of $\delta^{15}\text{N}$ and low values of $\delta^{13}\text{C}$), and the overall predicted isotopic signature of buzzards remained the same. The actual detection of a shift from main to alternative prey using down and blood isotopic signatures indicates a bias in pellet and prey remains analyses, with either an overestimation of ducks or an underestimation of ptarmigan and hare (or both of them). The latter seems a likely explanation, as ptarmigan chicks can be digested completely. Ducklings, on the contrary, were not observed among the prey (Online resource 1), making a similar bias less probable for ducks. A methodological framework combining both traditional methods (pellets and prey remains analysis) and newer methods (stable isotope analysis) provide thus more accurate and trustful information about the diet of birds of prey.

As discussed with regard to nesting success above, prey abundance may not be the only factor determining the diet of buzzards. Buzzards are known to be nomadic raptors that, in general, track local variations in small rodent densities; it is thus likely that some of the buzzards studied here may have been recruited from other regions with different feeding habits. The diet shift in 2010 was observed for four pairs, whose foraging behaviour could be affected by nesting in previous years in an area with no rodents (e.g. Kolguev Island, ca. 150–200 km from our study region). This hypothesis could be tested by future investigation of dispersal patterns of buzzard.

Whether buzzards are specialists or generalists

Buzzards did not always feed primarily on small rodents, but instead, shifted to other prey species, when rodents started to be scarce; so, one could argue that buzzards are not true rodent specialists. In addition, the proportion of main prey in their diet did not track changes in abundance of this prey, a behaviour that is typical of generalists. Although nesting density of buzzards varied from year to year as predicted for specialists, this temporal variation was not directly linked to the abundance of any particular prey group. Moreover, the breeding success of buzzards was stable, that is, typical for generalist predators. Therefore, buzzards at this low-Arctic site act more as generalists than specialists. To feed their nestlings, buzzards brought rodents to their nest, but shifted to alternative prey, when

the abundance of rodents decreased. Whether buzzards are able to implement, this shift may depend on two conditions. First, their functional response may depend on the relative abundance of key versus alternative prey, a pattern likely to differ from region to region. Second, buzzards rely on two hunting strategies: relatively high-altitude flights to locate rodents versus flights at only few meters above willow thickets when searching for ptarmigans and hares (Osmolovskaya 1948; Kalyakin 1989), and thus may depend on the presence of willow thickets to hunt alternative prey effectively. Ehrich et al. (2012) found that the percentage of willow cover is related to the abundance of ptarmigan and hare. A study on the shrub–tundra on Yamal peninsula is consistent with this suggestion. Here, the percentage of willow cover, and therefore the abundance of hares and ptarmigans, was lower than in our study area, and buzzards in Yamal did not shift from rodent to alternative prey (Sokolov 2002).

To conclude, we argue that the buzzards' feeding strategies may be considered within a continuum between clear generalists and pure specialists. Buzzards are rodent specialists, but are able to shift to alternative prey when rodents become scarce, as seen with another top predator in tundra ecosystems, the arctic fox (*Vulpes lagopus*; Elmhagen et al. 2000). Our results showing that rough-legged buzzards can be decoupled from variations in rodent abundance suggest that further research is needed to find out how general this pattern is across the species distribution range and what are the underlying causes. Long-term monitoring of diet shift and population dynamics could help decipher the complex trophic interactions occurring at the fringe of the Arctic and boreal zones, where density dependence between predator and prey is not yet well understood. Our study provides an additional piece of the puzzle to understand how the role of predators may vary in different ecosystem contexts.

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