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The structure of vertebrate predator community in north-eastern Belarus before and after naturalization of the American mink and raccoon dog

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A b s t r a c t . The structure of the vertebrate predator community in north-eastern Belarus has been examined before and after naturalization of the American mink and raccoon dog. Species composition of the community, population density and biomass, portion of each species in the pooled community density and biomass, species body mass and size structure of the community were investigated. The community consisted of 36 native predator species, and 11 other predator species were sporadically registered in the area in both periods before the American mink and raccoon dog expansion and after the introduced species have reached a high population density. Separating predator species into four size groups, we found that in terms of total density the largest portion of the community belonged to small predators, while large predators formed the smallest portion. In terms of total biomass, the larger medium-sized predator group predominated over other size groups. Despite decline in the populations of ten native predator species, the total community density and biomass as well as portions of different size groups appeared to be very similar before and after naturalization of the introduced predator species.

Key words: predator species richness, predator weight, predator density and biomass, introduced predators

Introduction

This paper is addressed to the structure of the vertebrate predator community in north-eastern Belarus, where the semi-natural terrain and vertebrate fauna are rather typical for the European forest zone. The community is still species-rich and consists of 36 native predator species, and 11 other predator species sporadically appear in the area. We were aimed to examine the species richness of the community, estimate population density and biomass, portion of each species in the pooled community density and biomass, and size structure of the community against the background of the expansion and naturalization of the two introduced predators – the American mink *Mustela vison* and raccoon dog *Nyctereutes procyonoides*. Having studied vertebrate predators in north-eastern Belarus for 23 years (since 1986), we have an opportunity to compare the community structure in two situations: (1) before the American mink arrival into the area and when the population density of the raccoon dog was low, and (2) when both introduced predators appeared to be numerous in 1992–1995 (S i d o r o v i c h et al. 2000, S i d o r o v i c h & M a c d o n a l d 2001). Impact of the alien predators on the structure of the whole community of aboriginal predator species in semi-natural habitats has not been investigated before in Europe, while there is numerical literature on predator fauna, species population density and biomass. Also, there are few studies analyzing structure of whole predator community dealing with all predator taxa i.e. carnivores, falconiformes, strigiformes, and serpentes (M a r t i et al. 1993, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998, K r e b s et al. 2001).

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Size is a crucial factor enabling predators to hunt larger prey, which provide bigger amount of food. Also, larger predators have a higher chance to survive through interference interactions that is common between predators (Holt & Polis 1997, Palomares & Caro 1999, Linnell & Strand 2000). There are many studies involving size parameters (mainly weight) to analyse vertebrate communities (e.g. Rosenzweig 1968, Mikkola 1983, Gittleman 1985, Damuth 1987, Jaksic 1989, Nee et al. 1991, Marti et al. 1993, Dayan & Simberloff 1996, Jędrzejewska & Jędrzejewski 1998, Tumanov 2003). However, the study fulfilled in the Białowieża Forest, eastern Poland (Jędrzejewska & Jędrzejewski 1998) is the only one in Europe that gives a detailed analysis of size relationships between predators with implication for demography success. However, the community investigated in Białowieża Forest already included the alien predator species that could affect the size relationships between predators.

Study Area

North-eastern Belarus has mostly hilly relief originating from the last glaciation (Matveev et al. 1988). It is a part of the extended region of the European forest zone, which is characterised by transitional structure of woodlands and located between more southern deciduous (mostly broad-leaved) forests and boreal coniferous forests. The spruce *Picea abies* and pine *Pinus sylvestris* are the dominant coniferous trees. The black alder *Alnus glutinosa* and grey alder *Alnus incana*, birches *Betula pendula*, *Betula pubescens*, and aspen *Populus tremula* are the most common deciduous trees.

In north-eastern Belarus the given study on vertebrate predators was mainly carried out in a semi-natural forested area in the Lovat river head, Gorodok district (55°°N, 31°°E) that is typical for the region. There is much clay in the surface ground deposits, resulting in good water supply and abundant trace elements, producing rich soil. Plant communities have high species diversity and productivity, and habitats with high carrying capacity for herbivores and, in turn, for their predators dominate. Thus, animal species diversity is high there, too (Sidorovich et al. 2001b). In the woodland, either premature coniferous stands (32% of the area) or mid-successional, small-leaved forests (14%) or black alder swampy woods (16%) predominate. There is an extensive aquatic network. Mean density of rivers is about 0.7 km/km^2, and there are small and medium-sized glacial lakes (0.3–2 km^2). Open grassy marshes occupy about 11% of the area and are mostly common in valleys of rivers and glacial lakes. Manmade landscape elements (fields, hay meadows, villages, roads etc.) make up about 8% of the habitats available.

In north-eastern Belarus, the cold season with snow cover and the average air temperature below 0°C normally lasts from early November until early April. Some winters are rather mild with a short snowy period (about two months). Most winters are quite severe, usually with a deep snow cover (30–90 cm) and air temperatures of about -20°C and lower often lasting for several weeks. Usually such frosty periods alternate with thaws lasting for a week.

The study area was relevant for such a research on vertebrate predator community due to: (1) low disturbance of the community by humans in terms of both habitat deterioration and direct impact on animal populations; (2) high species diversity of the community dwelling in semi-natural rich habitats on clay soil; (3) long-term and quite detailed study on vertebrate predator community that results in various data available for analysis of the community structure; (4) monitoring of changes in the community structure in relation to naturalization of the American mink and raccoon dog has been undertaken.

Material and Methods

Sources for the initial data in relation to predator and prey body mass, population density and biomass of various predator species that were used in the study are given in Table 1. The census methods applied for counting different predator species were described in published papers (Sidorovich & Macdonald 2001, Sidorovich et al. 2003d, 2005a, 2006a, Dombrovski & Ivanovskij 2005, Sidorovich & Solovej 2007). Various information related to the census of predators conducted by the methods (e.g. sample size of unit census plots or routes, census area) is pointed out there. Therefore, in the given paper, to make it shorter, only a brief description of the census methods applied is presented.

In valley habitats (valleys of rivers, brooks and glacial lakes) the European mink *Mustela lutreola,* American mink, Eurasian otter *Lutra lutra* and polecat *Mustela putorius* were censused along various aquatic ecosystems during winter by searching the banks, shores and floodplains for tracks of the riparian mustelid species (Sidorovich & Macdonald 2001). In winter, fresh tracks of individuals of the same species (or sometimes family groups for the otter) usually form concentrations in valley habitats separated by distances of variable length, where tracks of the species were either absent or only old tracks were found. Harsh winter conditions are characterized by low prey availability, when predators are believed disperse. Extensive winter trapping undertaken within the demography study on riparian mustelids (Sidorovich 1997, Sidorovich & Macdonald 2001) showed that the removal of an individual was followed by an absence of fresh tracks for quite a long time (at least, 10 days): in 14 out of 14 cases for the European mink, in 216 out of 222 cases for the American mink, in 34 out of 35 cases for the polecat, and in 23 out of 23 cases for the stoat.

Similarly, but following a shuttle-shaped census route covering a particular plot of 1–2 km^2, we counted track concentrations of weasels *Mustela nivalis* and stoats *Mustela erminea*

Table 1. Sources for the initial data used in the study.

Parameters	Sources
Body mass and length of carnivore species	Geptner et al. 1967, Pucek 1981, Banad & Kozlo 1985, Sidorovich 1997, Sidorovich et al. 1999, Sidorovich & Solovej 2007, authors' unpublished data.
Craniometrical parameters of carnivore species	Sidorovich 1997, authors' unpublished data.
Body mass of owl species	Fedushin & Dolbik 1967, Mikkola 1983, authors' unpublished data.
Body mass of diurnal raptor species	Fedushin & Dolbik 1967, Cramp 1994.
Reptilian body mass	Authors' unpublished data.
Owl density	Sidorovich et al. 2003c, authors' unpublished data.
Diurnal raptor density	Dombrovski & Ivanovskij 2005, Sidorovich et al. 2003c, authors' unpublished data.
Carnivore density	Sidorovich 1997, Sidorovich & Macdonald 2001, Sidorovich et al. 2003c, 2005, 2006a, Sidorovich & Solovej 2007.
Snake density	Sidorovich et al. 2003c, authors' unpublished data.

in the variety of habitats used by the species in early winter in the conditions of little snow cover (up to 15 cm deep) one or two days since the last snowing (S i d o r o v i c h & S o l o v e j 2007). Such a track concentration was associated with presence of an individual of the species.

To estimate population densities of pine martens *Martes martes* and red foxes *Vulpes vulpes* we counted the species trails crossed established census route and calculated abundance index as number of trails per 1 km per day. Then we recalculate the abundance index into population density with Priklonsky's formula (P r i k l o n s k y 1965), which was adapted to the habitat conditions of north-eastern Belarus by using estimates of the daily movement distance of the species in the conditions of different snow cover (S i d o r o v i c h et al. 2005a, 2006a). Daily movement distances of the two species were assessed by combining snowtracking and radiotracking as it was recommended by Z a l e w s k i et al. (1995).

To reveal the number of badgers *Meles meles* in a particular area, in the warm season we found their setts, did visual observations at the setts from a hide, inspected frequently the sett entrances searching for badger tracks, and did filming with cameras equipped with movement detector (S i d o r o v i c h & R o t e n k o , unpubl. results).

Population density of raccoon dogs was assessed by total inspection of an area in late winter and early spring (S i d o r o v i c h et al. 2007), when raccoon dogs begin to be active in some degree at hibernation places (such as badger setts and beaver burrows), but, nevertheless, they do not walk far away and mainly stay there around.

Census of wolves *Canis lupus* and lynxes *Lynx lynx* was done in winter by total inspection of an area with a vehicle that was driven through the dense net of forest and other roads a few days after the last snowfall. We mapped all crossings of the species trails. Such a census approach of the species was used in Białowieża Forest (J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998). Similar method was applied for counting brown bears *Ursus arctos* in the warm season using the recommendations provided by P a z h e t n o v (1990).

To detect owls, we used the published methods (F u l l e r & M o s h e r 1981, J o h n s o n et al. 1981), which were based on owl territorial calls. To call owls, a tape-recorder was applied, while going by census routes that were twice investigated during each owl counting. Taking into account our previous experience obtained during numerous attempts to listen to such calling from a distance, we assumed that 600 m would be an appropriate width for the census transect. If a territorial calling of an individual owl was registered, we assumed that pair or at least lone individual were present (S i d o r o v i c h et al. 2003d). The neighbouring territories of an owl species were separated from each other on the basis of simultaneous registrations of two or more calling individuals as well as by fairly long distance without any territorial call of this owl species.

Diurnal raptor species were mainly censused by visual observation with the help of binoculars and telescopes (20–60x) from a series of points at 2–3 km from each other (D o m b r o v s k i & I v a n o v s k i j 2005). Such a census point was either an opening or a top of a tall tree. The majority of census plots were inspected twice: at the end of April and May during the period of active displays for main part of species of diurnal raptors, and at the end of June and July, when adults actively forage to feed the nestlings. The greater spotted eagle *Aquila clanga*, lesser spotted eagle *Aquila pomarina*, black kite *Milvus migrans*, hobby *Falco subbuteo*, merlin *Falco collumbarius*, sparrowhawk *Accipiter nisus*, goshawk *Accipiter gentiles*, white-tailed eagle *Haliaeetus albicilla*, short-toed eagle *Circaetus gallicus*, and honey buzzard *Pernis apivorus* were counted by the method (D o m b r o v s k i & I v a n o v s k i j 2005). In the cold season the rough-legged buzzard

Buteo lagopus was censused by visual observation not only from the points, but also by traveling transects densely covering relevant habitats in the census plot. Several species of diurnal raptors (the common buzzard *Buteo buteo*, golden eagle *Aquila chrysaetos*, osprey *Pandion haliaetus* and marsh harrier *Circus aeruginosus*) were censused not only by visual observation from the points, but also searching for their nests and checking them.

The grass snake *Natrix natrix* and adder *Vipera berus* were visually censused in 3 m wide transects in the variety of habitats in May during suitable weather and daytime.

Census of vertebrate predators was conducted in the study area over the period from 1986 until 2007. Not all the species were involved in the survey each year, because it is time and labour consuming work and there was a limitation to fulfill the whole amount of work each year. The number of years, when the census was conducted, varies from 4 for several species of diurnal raptors to 22 for carnivores. Nevertheless, the majority of predator species were counted in both most important periods: 1986–1990, when the presence of the introduced predator species and their negative influence on the aboriginal predator species were negligible; and since 1992, when the invaders have established dense populations and impacted on many species of the native fauna.

Counting of predators was mainly conducted in pre-reproduction periods (when it was relevant to do such census): carnivores (with exception of the brown bear and badger) in winter, owls in late March-mid April, snakes in May, and diurnal raptors in May-early June (before fledglings appeared). Census of brown bears and badgers was done in summer, but calculating their densities, we exclude juveniles in order to get the data that are comparable with those of other predator species. So, the data on density and biomass of predator species gained are more or less contemporized and characterise their populations before reproduction. Population biomass of each predator species was computed as its density multiplied by mean body mass. To be comparable, population density and biomass of all species were calculated per unit area of 100 km^2. The maximal census area used for the majority of predator species (with exception of the adder, grass snake and weasel) was 500 km^2.

One of the research tasks was to examine the size structure of the predator community. Mean body mass in adults was used as a proxy of a species size for comparative analyses of the community structure. Having a large variation in the average body mass of different predator species, to investigate the size structure of the community, we separated predator species formally into four weight-related groups: (1) large predators (hereafter LP) including the brown bear, wolf and lynx, which have the mean body mass higher than 20 kg; (2) larger medium-sized predators (LMP) including the red fox, raccoon dog, badger, otter, golden eagle, white-tailed eagle, and eagle owl *Bubo bubo,* the mean body mass is between 2.5 and 15 kg; (3) smaller medium-sized predators (SMP) including the pine marten, polecat, American mink, European mink, marsh harrier, short-toed eagle, honey buzzard, osprey, black kite, lesser spotted eagle, greater spotted eagle, goshawk, common buzzard, rough-legged buzzard, great grey owl *Strix nebulosa*, Ural owl *Strix uralensis*, and tawny owl *Strix aluco*, the mean body mass is between 0.5 and 2 kg; and (4) small predators (SP) including the stoat, weasel, hobby, merlin, sparrowhawk, short-eared owl *Asio flammeus*, long-eared owl *Asio otus*, Tengmalm's owl *Aegolius fureneus*, pygmy owl *Glaucidium passerinum* and adder weighting up to 0.4 kg.

Food niche breadth was applied as one of the factors to analyze relationships between weight and population density and biomass of predators. To calculate food niche breadth of various predator species, we used the published data on predator diets (Dorofeev & Ivanovskij 1980, Ivanovskij & Umanskaya 1981, Ivanovskij 1983, 1990a,b, 1992, 1996a,b, 1998, Sidorovich 1997, 2000a, 2006a,b, Sidorovich et al. 2000, 2001a, 2003a,c,e, 2005a, 2006a,b, 2008a,b, Januta et al. 2002, Sidorovich & Solovej 2007).

We used simple descriptive statistics and the Spearman rank correlation coefficient (r_s) from the software STATISTICA Analysis System (release 6.0) for statistical analysis of the data obtained. G-test was used to examine heterogeneity of percentages (Sokal & Rohlf 1995).

Results

Species composition of the vertebrate predator community

During the study period of 1986–2007 the following 38 predator species were found to be present in the study area and were involved in the analysis: the brown bear, lynx, wolf, red fox, raccoon dog, pine marten, weasel, stoat, polecat, badger, European mink, American mink, otter, marsh harrier, short-toed eagle, osprey, white-tailed eagle, hobby, merlin, honey buzzard, golden eagle, black kite, greater spotted eagle, lesser spotted eagle, goshawk, sparrowhawk, common buzzard, rough-legged buzzard, great grey owl, Ural owl, tawny owl, Tengmalm's owl, pygmy owl, long-eared owl, short-eared owl, eagle owl, grass snake and adder. The other predator species recorded mostly in rural landscape spotted-distributed in the forested study area had a low population density there and hence were not considered in the study. Among them there are five species: the stone marten *Martes foina*, hen harrier *Circus cyaneus*, Montagu's harrier *Circus pygargus*, kestrel *Falco tinnunculus* and little owl *Athene noctua*. Sporadically registered and plausibly short-time present predator species such as the scops owl *Otus scops*, snowy owl *Nyctea scandiaca*, hawk owl *Surnia ulula,* red kite *Milvus milvus*, booted eagle *Aquila pennata* and peregrine *Falco peregrinus* were excluded from the data analysis either.

In the period of 1986–1988 the American mink was absent in the study area, the first single individual was captured in late autumn of 1988 (Sidorovich 1997, Sidorovich & Macdonald 2001). Since 1992 the American mink has become common there (Fig. 1). Aggressive interference from the naturalized American mink towards the European mink and polecat strongly affected the populations of these native predator species resulting in their declines (Sidorovich 2001, Macdonald et al. 2002b). The density decrease and gradual extinction of the European mink in the study area is shown in Fig. 2. Also, predation by numerous American mink negatively influenced riparian voles (the water vole *Arvicola terrestris* and root vole *Microtus oeconomus*), and this consequently affected their predator guild, first of all, the populations of the stoat, polecat, short-eared owl and eagle owl (Macdonald et al. 2002a, Sidorovich 2000b, Sidorovich et al. 2005b, 2006b, unpubl. results, Sidorovich & Solovej 2007). The decline in stoats led to increased numbers of weasels, in particular in marshlands (Sidorovich & Solovej 2007).

When we started investigating vertebrate predators in the study area in 1986, raccoon dogs had already populated the area, but the species density was fairly low. The outbreak in raccoon dogs happened only since 1995 (Sidorovich et al. 2000) as it is shown in Fig. 3. Competition over carrion in late winter and early spring between naturalized raccoon dogs and aboriginal forest generalist predators negatively influenced the guild, especially the populations of the polecat, red fox and pine marten in extended forested areas

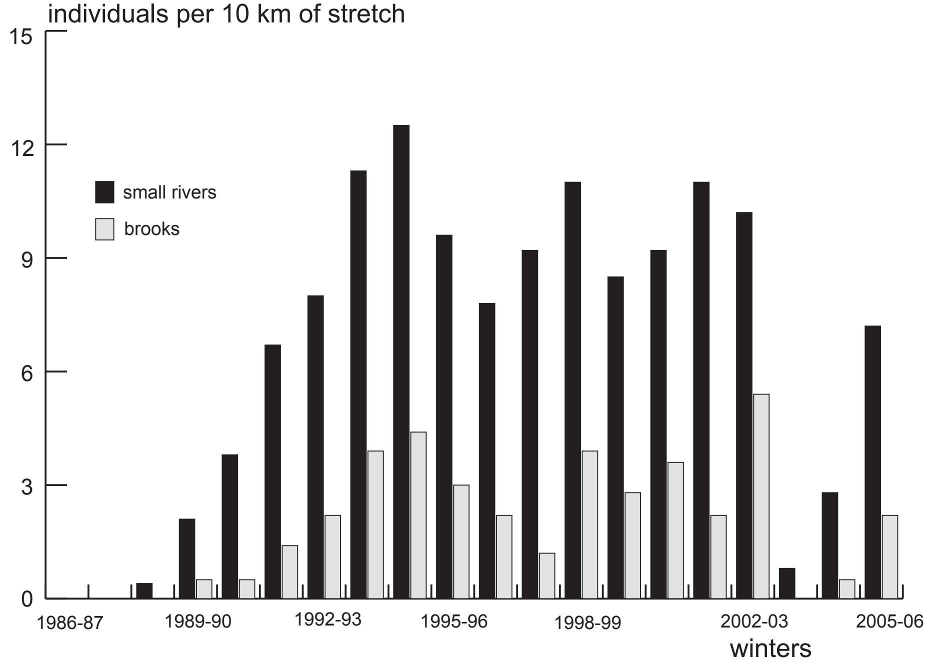

Fig. 1. Changes in the American mink density during the expansion and further population dynamics in the study area in north-eastern Belarus, 1986–2007.

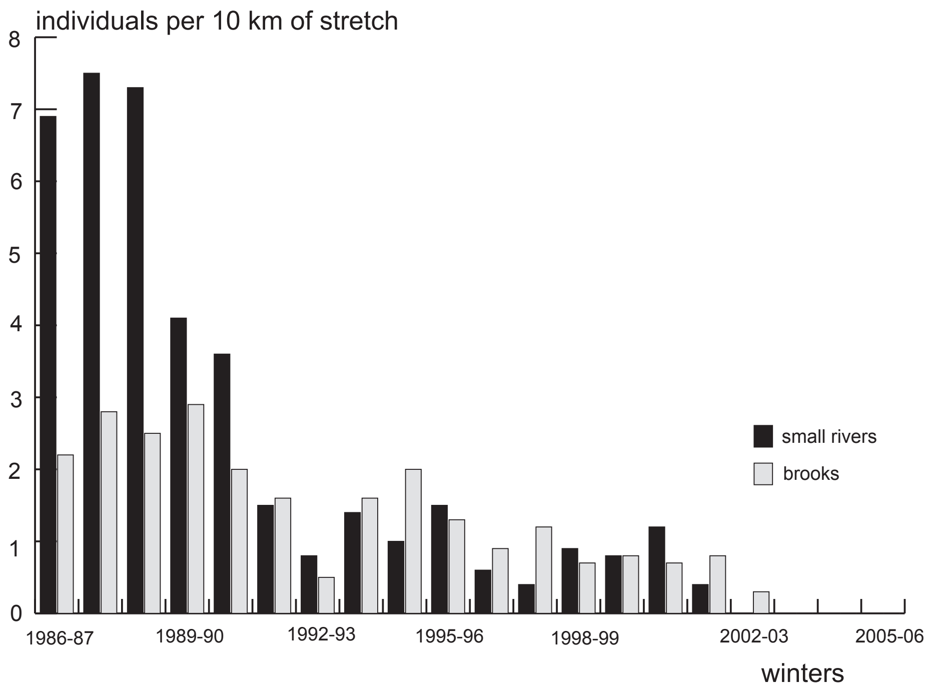

Fig. 2. Population decline of the European mink in the study area in north-eastern Belarus, 1986–2007.

(Sidorovich et al. 2000) and plausibly the golden eagle (Tjernberg 1981). Also, the badger population decreased in numbers, when raccoon dogs appeared to be common in the area (Sidorovich et al. 2000), though particular causes of the evident decline of the badger population are seemingly still unknown.

After naturalization of the American mink and raccoon dog these two introduced species appeared to be commoner than the majority of native predator species. Indeed, in the period of 1992–2007 only the grass snake, adder, red fox and weasel had higher population density than the invaders. In terms of biomass, only four native species (the brown bear, red fox, adder and grass snake) overweighed the raccoon dog and six native species (additionally the otter and badger) overweighed the American mink.

Overall, we revealed negative influence of the naturalized alien predators on thirteen native predator species: the European mink, polecat, stoat, red fox, badger, pine marten, brown bear, short-eared owl, eagle owl, great grey owl, greater spotted eagle, marsh harrier and golden eagle (Sidorovich et al. 2000, 2005a, 2006, unpubl. results, Sidorovich 2001, Sidorovich & Macdonald 2001, Macdonald et al. 2002a, Sidorovich & Solovej 2007). This negative influence found resulted in either density decrease or only exacerbated competition for food suggesting possible population decline in future. During the study period we were able to estimate the density decrease for ten aboriginal predator species as well as the increased density of weasels, raccoon dogs and American minks were recorded (Table 2). For the other native predator species that were either only slightly affected or unaffected by the introduced invaders, we used density values averaged for all estimates available for the area obtained in both periods.

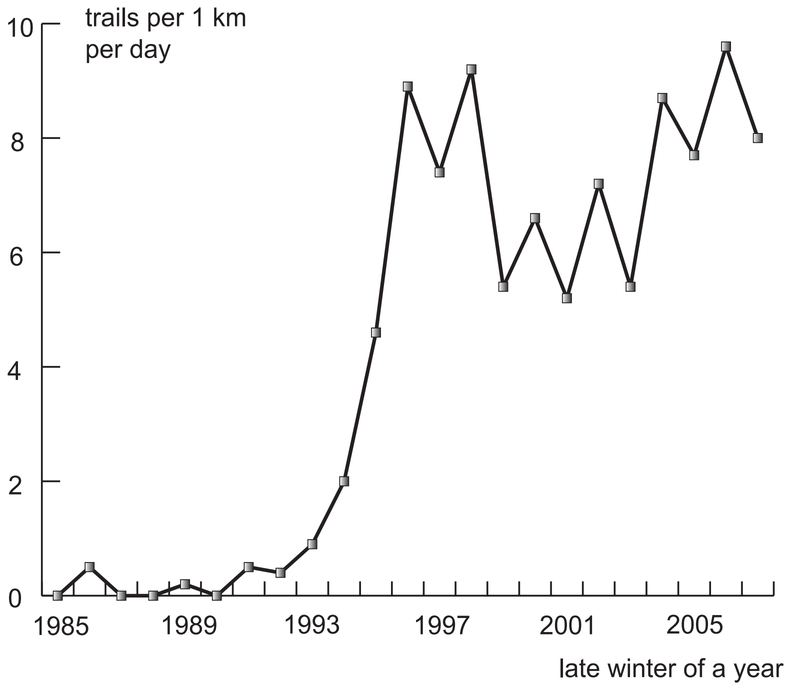

Fig. 3. Between-year changes in abundance index of raccoon dogs in the study area in north-eastern Belarus, 1985–2007. Number of raccoon dog trails crossed the same 36 km census route averaged per one km per day in late winter was used as an abundance index of the species.

Despite the recorded decrease in numbers of ten aboriginal predator species (Table 2) we found the same predator species composition in the study area of 500 km^2 in both periods, i.e. before and after the introduced American mink and raccoon dog got a high population density. The European mink has finally disappeared from the area somewhen in 2003 (Fig. 3). The main trend was density and biomass decreases in the populations of many aboriginal predator species, while the two introduced predator species grew in numbers and biomass (Table 2).

Before the American mink and raccoon dog expansion the pooled predator density comprised approximately 20152 inds/100 km^2 in summer and 1029 inds/100 km^2 in winter, taking into account active overwintering predator species only. The pooled predator biomass assessed was 6286 kg/100 km^2 and 1504 kg/100 km^2, respectively. In summer the grass snake markedly prevailed over all other species, and it composed about 88% of the pooled predator density and 49% of their biomass. The pooled winter density of active predators was 19.6 fold lower than that in summer, and biomass – 4.2 fold lower. The seasonal decrease in the pooled predator density and biomass happened mainly because grass snakes start to hibernate in mid autumn. Also, disappearance of migratory birds, and hibernation of the adder, brown bear and badger determined partly the trend. In summer wide variation in the population density of different predator species was found (coefficient of variation, CV = 527%). The predator density varied from 0.2 individuals per 100 km^2 for the black kite and white-tailed eagle to 17721 inds/100 km^2 for the grass snake. Similarly, predator biomass largely ranged from 0.2 kg/100 km^2 in black kites and merlins to 3066 kg/100 km^2 in grass snakes (CV = 312%). In winter the variation in the population density of different predator species was lower – CV = 167%, and in the biomass – CV = 234%.

Since the naturalized predator species densely populated the study area and in spite of the populations of ten native predator species declined and the weasel density increased, there was a small change in the pooled predator density and biomass (Table 2). The ratio between the summer and winter pooled predator density and biomass was similar as it was before the American mink and raccoon dog expansion – 18.2 and 3.5 fold, respectively. Again, in summer wide variation in the population density and biomass of different predator species was found (CV = 533% and 314%, respectively), and in winter it was markedly lower – CV = 207% and 204% respectively.

Body mass of predators related to their population density and biomass

We revealed great variation in the mean body mass between different vertebrate predator species. This ranged from 66 g for the pygmy owl to 173.6 kg for the brown bear (Table 2), and the coefficient of variation equaled 323%.

Portions of differently sized predators in the community, i.e. small predators, smaller medium-sized predators, larger medium-sized predators, and large predators are shown in Fig. 4. In spite of the pronounced changes in the density and biomass of eleven native predator species, the shares of each size group in the pooled predator density and biomass before and after the American mink and raccoon dog expansion were similar (Fig. 4), and the small differences found were statistically insignificant ($G < 1.05$; $P > 0.30$). In the warm and cold seasons both before and after the outbreaks in the alien species, the maximal portion in pooled predator density belonged to the group of small predators (WS, 96.7–97.0%; CS, 52.1–55.0%), and the larger predator group had the smallest portion (WS, < 0.1%; CS,

Table 2. Presence in the warm (WS) and cold (CS) seasons, seasonal activity, mean body mass of adults, population density and biomass of various species of vertebrate predators in north-eastern Belarus.

Species	Seasonal presence and activity	Mean body mass in adults, g	Before naturalization of Am and Rd				After naturalization of Am and Rd			
			Density		Biomass		Density		Biomass	
			Inds per 100 km^2	% WS(CS)	Kg per 100 km^2	% WS(CS)	Inds per 100 km^2	% WS(CS)	Kg per 100 km^2	% WS(CS)
Ursus arctos	Present WS CS, inactive CS	173600	5.2	0.03 (0)	902.7	14.39 (0)	4.2	0.02 (0)	729.1	11.74 (0)
Lynx lynx	Present, active WS CS	23500	3.1	0.02 (0.30)	35.3	0.56 (2.35)	3.1	0.02 (0.28)	35.3	0.57 (1.98)
Canis lupus	Present, active WS CS	39000	1.8	0.01 (0.17)	70.2	1.12 (4.67)	1.8	0.01 (0.16)	70.2	1.13 (3.94)
Vulpes vulpes	Present, active WS CS	6112	136.0	0.68 (13.21)	831.2	13.25 (55.25)	121.0	0.60 (10.95)	739.6	11.91 (41.56)
Nyctereutes procyonoides	Present WS CS, inactive half time CS	6487	4.0	0.02 (0.39)	25.9	0.41 (1.72)	65.0	0.32 (5.88)	421.7	6.79 (23.70)
Martes martes	Present, active WS CS	1008	87.4	0.43 (8.49)	88.1	1.40 (5.86)	54.6	0.27 (4.94)	55.2	0.89 (3.10)
Mustela nivalis	Present, active WS CS	67.1	356	1.77 (34.59)	23.9	0.38 (1.59)	484	2.40 (43.79)	32.4	0.52 (1.82)
Mustela erminea	Present, active WS CS	159.9	92.3	0.46 (8.97)	14.7	0.23 (0.98)	36.1	0.18 (3.27)	5.6	0.09 (0.31)
Mustela putorius	Present, active WS CS	831	55.7	0.28 (5.41)	46.2	0.74 (3.07)	20.1	0.10 (1.82)	16.7	0.27 (0.94)
Mustela vison	Present, active WS CS	1007	0	0 (0)	0	0 (0)	71.4	0.35 (6.46)	71.9	1.16 (4.04)
Mustela lutreola	Present, active WS CS	814	51.1	0.25 (4.97)	41.6	0.66 (2.77)	7.7	0.04 (0.70)	6.3	0.10 (0.35)
Lutra lutra	Present, active WS CS	7613	28.0	0.14 (2.72)	213.2	3.40 (14.77)	28.0	0.14 (2.53)	213.2	3.43 (11.98)
Meles meles	Present WS CS, inactive CS	10900	22.7	0.11 (0)	247.4	3.94 (0)	8.4	0.04 (0)	91.6	1.48 (0)
Circus aeruginosus	Present, active WS	539	34.0	0.17 (0)	18.4	0.29 (0)	34.0	0.17 (0)	18.4	0.30 (0)

Table 2. continued

Circaetus gallicus	Present, active WS	1680	0.4	<0.01 (0)	0.7	0.01 (0)	0.4	<0.01 (0)	0.7	0.01 (0)
Falco subbuteo	Present, active WS	225	3.6	0.02 (0)	0.8	0.01 (0)	3.6	0.02 (0)	0.8	0.01 (0)
Falco collumbarius	Present, active WS	171	1.4	0.01 (0)	0.2	0.01 (0)	1.4	0.01 (0)	0.2	0.01 (0)
Pernis apivorus	Present, active WS	793	9.6	0.05 (0)	7.6	0.12 (0)	9.6	0.05 (0)	7.6	0.12 (0)
Aquila chrysaetos	Present, active WS CS	4448	0.4	<0.01 (0.04)	1.8	0.03 (0.12)	0.4	<0.01 (0.04)	1.8	0.03 (0.10)
Pandion haliaetus	Present, active WS	1592	0.8	<0.01 (0)	1.3	0.02 (0)	0.8	<0.01 (0)	1.3	0.02 (0)
Haliaeetus albicilla	Present, active WS CS	4500	0.2	<0.01 (0.02)	0.9	0.01 (0.06)	0.2	<0.01 (0.02)	0.9	0.01 (0.05)
Milvus migrans	Present, active WS	829	0.2	<0.01 (0)	0.2	<0.01 (0)	0.2	<0.01 (0)	0.2	<0.01 (0)
Aquila clanga	Present, active WS	1865	1.0	<0.01 (0)	1.9	0.03 (0)	1.0	<0.01 (0)	1.9	0.03 (0)
Aquila pomarina	Present, active WS	1329	8.4	0.04 (0)	11.2	0.18 (0)	8.4	0.04 (0)	11.2	0.18 (0)
Accipiter gentiles	Present, active WS CS	1036	4.8	0.02 (0.47)	5.0	0.08 (0.33)	4.8	0.02 (0.43)	5.0	0.08 (0.28)
Accipiter nisus	Present, active WS CS	199	4.4	0.02 (0.43)	0.9	0.01 (0.06)	4.4	0.02 (0.40)	0.9	0.01 (0.05)
Buteo buteo	Present, active WS	844	38.0	0.19 (0)	32.1	0.51 (0)	38.0	0.19 (0)	32.1	0.52 (0)
Buteo lagopus	Present, active CS	954	12.0	0 (1.17)	11.5	0 (0.76)	12.0	0 (1.09)	11.5	0 (0.65)
Asio otus	Present, active WS	308	26.0	0.13 (0)	8.0	0.13 (0)	26.0	0.13 (0)	8.0	0.13 (0)
Asio flammeus	Present, active WS	381	32.0	0.16 (0)	12.2	0.19 (0)	2.0	0.01 (0)	0.8	0.01 (0)
Bubo bubo	Present, active WS CS	2666	1.2	0.01 (012)	3.2	0.05 (0.21)	0.4	<0.01 (0.04)	1.1	0.02 (0.06)

Table 2. continued

Strix nebulosa	Present, active WS CS	1057	0.8	<0.01 (0.08)	0.9	0.01 (0.06)	0.4	<0.01 (0.04)	0.4	0.01 (0.02)
Strix uralensis	Present, active WS CS	796	74.0	0.37 (7.19)	58.9	0.94 (3.91)	74.0	0.37 (6.69)	58.9	0.95 (3.31)
Strix aluco	Present, active WS CS	557	42.0	0.21 (4.08)	23.4	0.37 (1.56)	42.0	0.21 (3.80)	23.4	0.38 (1.31)
Aegolius funereus	Present, active WS CS	145	36.0	0.18 (3.50)	5.2	0.08 (0.35)	36.0	0.18 (3.26)	5.2	0.08 (0.29)
Glaucidium passerinum	Present, active WS CS	66.0	38.0	0.19 (3.69)	2.5	0.04 (0.17)	38.0	0.19 (3.44)	2.5	0.04 (0.14)
Vipera berus (>40 cm, on average73 cm)	Present WS CS, inactive CS	387	1218	6.05 (0)	471	7.51 (0)	1218	6.04 (0)	471	7.59 (0)
Natrix natrix (>40 cm, on average 77 cm)	Present WS CS, inactive CS	173	17721	87.99 (0)	3066	48.86 (0)	17721	87.86 (0)	3066	49.38 (0)
Total, WS(CS)			20151.5 (1028.8)	100 (100)	6286.2 (1503.5)	100 (100)	20182.4 (1106.2)	100 (100)	6220.6 (1781.3)	100 (100)

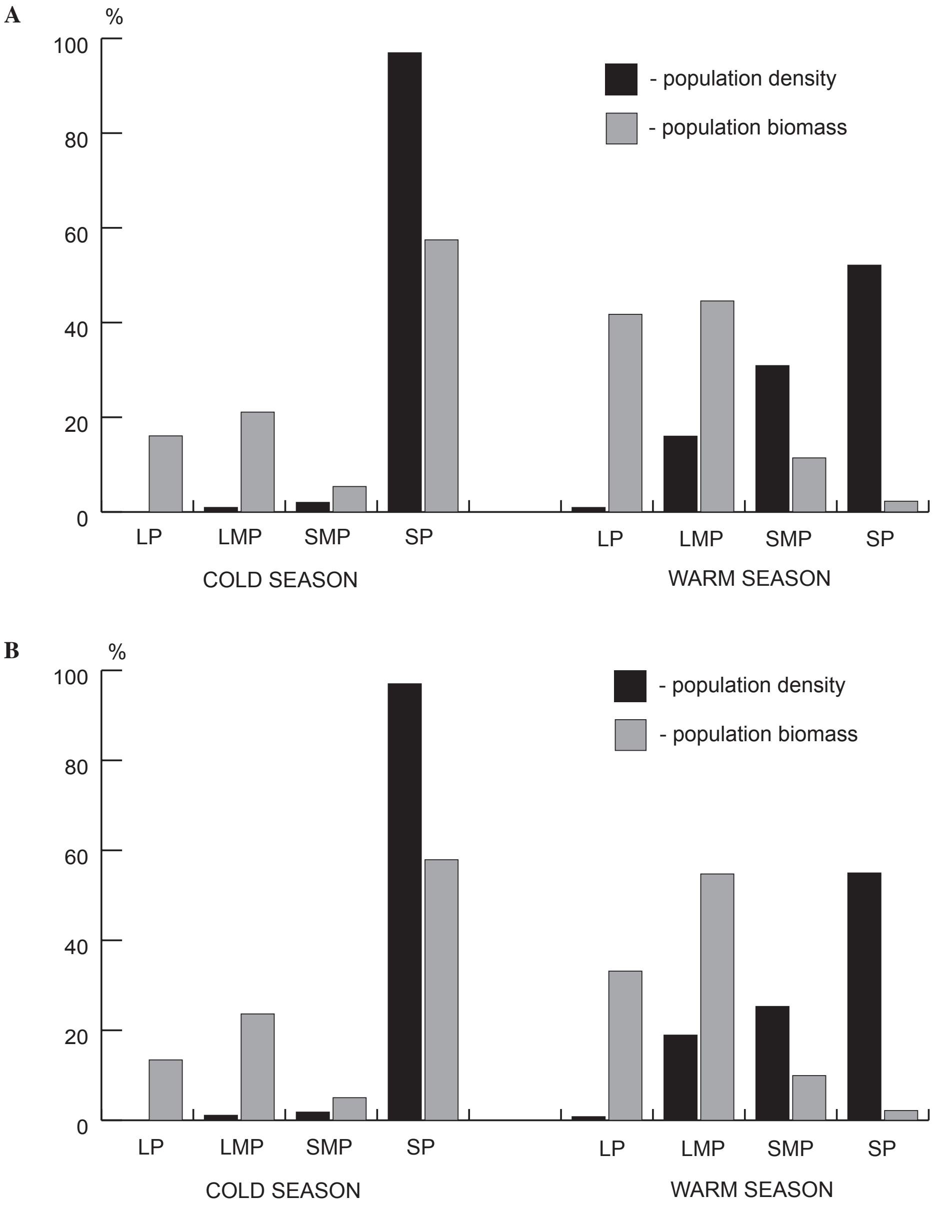

Fig. 4. Portion of differently sized predator groups in the predator community in north-eastern Belarus: A – Before the American mink and raccoon dog expansion, B – After the American mink and raccoon dog expansion.

0.8–1.0%). In terms of biomass, in the warm season the largest portion belonged to the group of small predators, too (57.5–58.0%), while in the cold season larger medium-sized predators forged (44.6–54.8%), and small predator group comprised the smallest portion (2.1–2.3%).

Before the American mink and raccoon dog expansion significant negative correlations between the mean body mass of aboriginal predator species and their densities were found (r_s = -0.48, P = 0.003). Interestingly, that this pattern is also attributable and even higher pronounced if we consider carnivores (r_s = -0.85, P = 0.001) and falconiformes (r_s = -0.52, P = 0.05) separately, while it is nearly absent in strigiformes (r_s = -0.29, P = 0.49). After the alien species became common the above correlations slightly declined. Any statistically significant correlations between body mass of various predator species and their population biomass were not revealed.

Discussion

The presented results suggest the following features. First, since the American mink and raccoon dog densely populated the study area in north-eastern Belarus, the predator species richness has remained nearly the same with exception of the recorded gradual demise of the European mink (Macdonald et al. 2002b). Nevertheless, the density of nine other native predator species was found to decrease and one native species increased in numbers. American minks and raccoon dogs appeared to be commoner than the majority of native predator species. However, in spite of the changes mentioned the pooled density and biomass of the predator community shifted slightly as well as there was a little change in the portion of the predator size groups. This result suggests that the observed substitution of the aboriginal predators by the competitive invaders (i.e. the American mink and the raccoon dog) was rather adjusted to an ecologically potential total biomass and its distribution at various size levels of predators that, in turn, is plausibly determined by habitat carrying capacity. Such an inference would follow the known consistent patterns of ecology (Begon et al. 1996, Krebs 2001), but having investigated the changes we confirmed the inference and showed that a saturation of habitat carrying capacity in destructed predator community can happen in a rather short-term period. Also, the above results give a little support to the idea that the productivity and functioning in the vertebrate predator community has been altered drastically after the naturalization of the American mink and raccoon dog since the pooled predator density and biomass and their distribution at different size levels shifted slightly. Nevertheless, with respect to the species diversity concept the invader influence led to the detrimental effect in the predator species diversity.

Second, we found that small predators appeared to be commoner and, in turn, ecologically more effective than larger predators, especially in the warm season (Fig. 4). Similar results on predators (even without involving snakes) were gained in the Białowieża Forest (eastern Poland), where prevalence of small predators in numbers was connected with huge supply of small prey and small predator adaptations for hunting small prey (Jędrzejewska & Jędrzejewski 1998). In the cold season in terms of biomass the groups of large predators and larger medium-sized predators predominated over small predators (Fig. 4). That shows higher efficiency of larger predators in the harsh conditions of cold winter, perhaps, due to acting of the well-known bioenergetic factors that favour larger body (Kleiber 1975, Shmidt-Nielsen 1984).

Third, we found that mean body mass of various predator species negatively correlated with their density, i.e. smaller predators usually have higher population density, and strength of this relationship is different between the predator assemblages. The pattern was found to be the most pronounced for carnivores, but weakly attributable to strigiformes. Mikkola (1983) suggests that ecological isolation mechanism and, in turn, diversity of demography strategies and ecological niches of owls do not seem to have evolved as completely as it is attributed to other predator assemblages. The inverse relationship between predator body mass and population density, being obvious for the whole predator community, nevertheless,

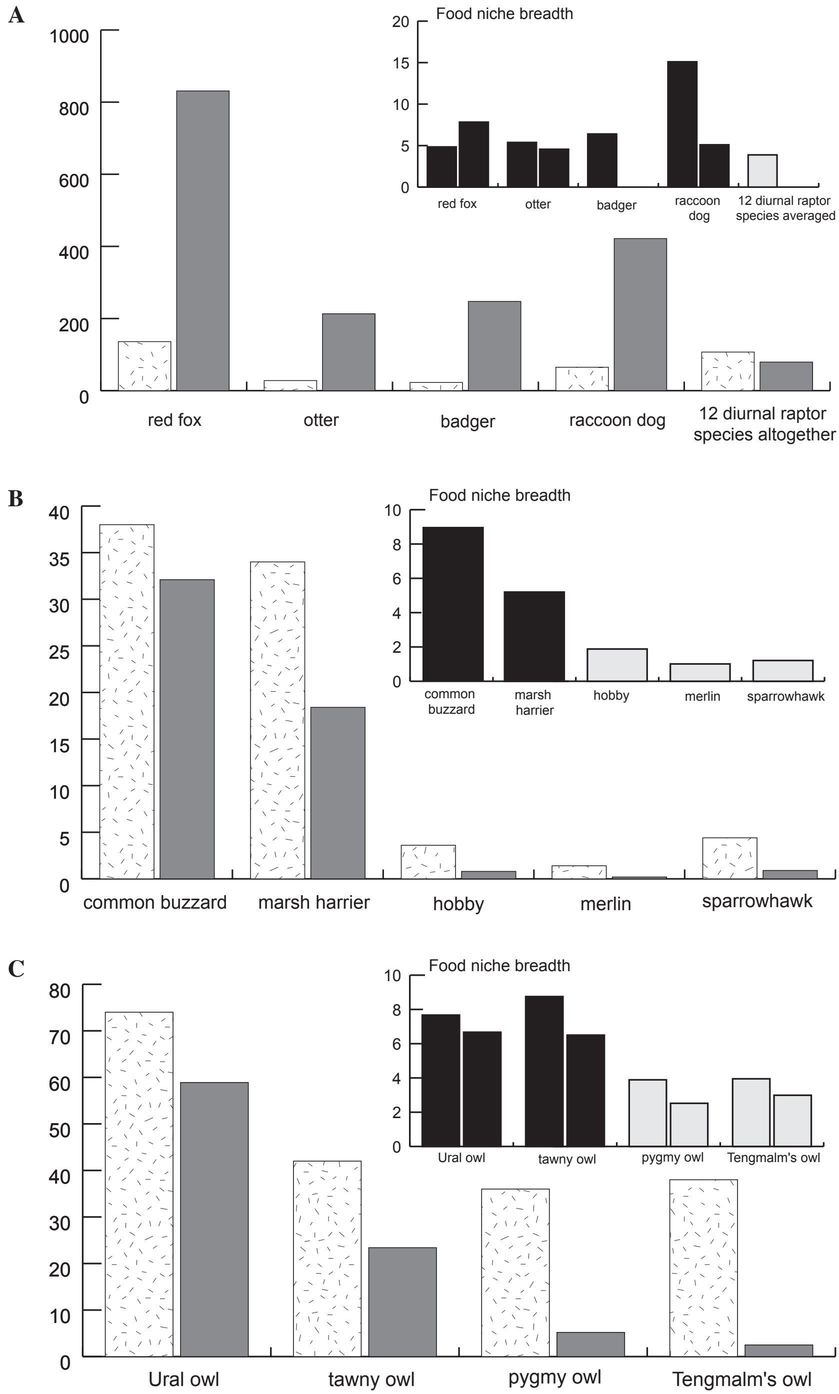

Fig. 5. Population density and biomass, food niche breadth of exceptional predator species. A– Exceptional carnivore species versus smaller 12 diurnal raptor species, B – Common buzzard and marsh harrier versus the smaller species: hobby, merlin and sparrowhawk, C – Ural owl and tawny owl versus smaller pygmy owl and Tengmalm’s owl.

has many exceptions. The most pronounced exceptional species is the grass snake that was markedly more (364–15484 times) abundant compared to the other small predator species of similar weight, e.g. the weasel, stoat, Tengmalm's owl, pygmy owl and sparrowhawk. The grass snake specializes in feeding on amphibians, first of all, common frogs (D r o b e n k o v 1995), and there are only a few other species consuming this common prey (S i d o r o v i c h et al. 2001a, 2003b). So, the grass snake food niche was exclusively established on widespread and plenty prey category and that led to the high demographic success and determined an outstanding position of the species in the relationship between body mass and population density in the predator community. Similar pattern is attributable to the otter that is the most adapted species in foraging water-living prey (fish, crayfish and water-dwelling frogs), and therefore, the predator mainly uses these food resources (S i d o r o v i c h 2000a, J ę d r z e j e w s k a et al. 2001). Other exceptions relate to the predator species having wide food niche. In north-eastern Belarus among aboriginal predator species the red fox, badger and the naturalized raccoon dog, being medium-sized predators, had rather high density compared to many raptorial species (short-toed eagle, hobby, merlin, honey buzzard, osprey, goshawk, greater spotted eagle and sparrowhawk) that are smaller, but have lower population density (Table 2, Fig. 5A). In turn, among diurnal raptors the marsh harrier and common buzzard are bigger than hobby, merlin and sparrowhawk, but the formers were characterized by higher population density than the latters (Fig. 5B). Again among owls the Ural owl and tawny owl being bigger were commoner than smaller pygmy owl and Tengmalm's owl (Fig. 5C). Indeed, the mentioned exceptional species are characterized by wider food niche (Figs 5A-C) and opportunistic feeding habits (S i d o r o v i c h 1997, J a n u t a et al. 2002, S i d o r o v i c h et al. 2003c, 2006a, 2008b). Feeding plasticity in kind of (1) wide food niche, (2) substitution of less available prey for more available prey in seasonal dynamics, (3) quite large home range and tracking of prey concentration etc. usually provides efficient feeding and leads to higher population density and biomass (B e g o n et al. 1996, K r e b s et al. 2001, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998). On the other hand, environmental conditions in north-eastern Belarus are characterized by dramatic shifts in prey abundance and availability due to (1) the pronounced seasonal changes from warm (sometimes hot) summer to frequently cold winter with deep snow cover and freezing-over of aquatic ecosystems; (2) predominance of migratory bird prey; (3) inactivity and low availability of amphibians in winter that are one of the most common prey category in summer; (4) breeding in prey species during the warm season only etc. (S i d o r o v i c h et al. 2001a,b, 2003d, 2005a). Undoubtedly, such changeable environmental conditions favour predator species with flexible feeding habits.

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