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Niche separation between the weasel *Mustela nivalis* and the stoat *M. erminea* in Belarus

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We investigated three main niche components (diet composition, habitat use and diel activity rhythms) to examine how the weasel *Mustela nivalis* and the stoat *M. erminea*, both specialised predators of small rodents, could permanently coexist in Belarus. Our research was carried out in temperate forests of Belarus, in two study areas with different environmental conditions: 1) continuous dry-land forest interspersed by a variety of swampy biotopes and aquatic ecosystems (Paazerre, northern Belarus) and 2) extended wetland with large forest patches (Palesse, southern Belarus). The habitat use and diel activity rhythms of seven weasels and eight stoats were analysed by radio-tracking over about 300 km² in Paazerre. Snow-tracking was also applied to study habitat use by the two mustelid species. Diet composition was examined by analysing 365 weasel scats and 606 stoat scats. Our results suggest that while the weasel and stoat occur in close proximity to each other, they use different micro-habitats, are most active during different times of the day, and prey primarily on different small rodent species. Most weasels selected forest and forest edge habitats, where they predominantly preyed on smaller rodent species (bank voles *Clethrionomys glareolus* and *Apodemus* mice); stoats selected wetlands, especially open grassy marshes, and preyed more frequently on larger rodents such as water voles *Arvicola terrestris* and *Microtus* voles. Weasels were mostly diurnal and adjusted their activity to the seasonally changing length of daylight, whereas stoats were much more active in twilight and during the night.

Key words: Belarus, diel activity rhythm, diet, habitat selection, stoat, weasel

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Several studies have addressed the ecological separation between the weasel *Mustela nivalis* and the stoat *M. erminea* in Europe, in the environmental

conditions of boreal Scandinavia (Erlinge 1975, 1979, 1981, Andersen 1978, Erlinge & Sandell 1988, Klemola et al. 1999) or in the milder climate of

farmlands and fragmented forests of western Europe (Day 1968, King & Moors 1979, McDonald et al. 2000, McDonald 2002). No studies have been carried out in the transitional coniferous/small-leaved woodlands that form the typical landscape of Belarus. Additionally, few studies on the ecological separation between the two species have managed to analyse all niche components (King & Moors 1979, Powell & Zielinski 1983, Erlinge & Sandell 1988, King 1989, McDonald et al. 2000), with the exception of a detailed analysis carried out in a semi-natural environment of Sweden (Erlinge 1975, 1979, 1981, Erlinge & Sandell 1988). In the present study we focused on an analysis of the two species' niches in semi-natural landscapes of the temperate forest zone of Europe.

Study area

Our study was conducted during 1997-2003 in two study areas in Belarus (Fig. 1), Paazerre in the northern and Palesse in the southern part of the country. The two study areas were markedly different in habitat composition, vegetation and climate (severity of winters). We investigated small mustelid populations in forests with limited man-made landscape elements (such as fields, hay meadows, villages and roads, which covered about 8% of the available habitats).

Paazerre, a hilly area originating from the last glaciation (Matveev et al. 1988), is part of the extended region of the European forest zone and has intermediate conditions between the more southern deciduous (mostly broad-leaved) forests and the boreal coniferous forests. Spruce *Picea abies* and pine *Pinus sylvestris* are dominant coniferous trees, and small-leaved trees (black alder *Alnus glutinosa* and birches *Betula pendula*, *B. pubescens*) are the most common deciduous trees. Paazerre is also characterised by an extensive aquatic network (mean density of rivers being 0.7 km/km²; numerous small and medium-sized residual glacial lakes ranging in size within 0.3-2 km²). Open grassy marshes do not account for a large portion of the territory and are most common in valleys of rivers and glacial lakes. The study was carried out in a 300-km² area located in the Gorodok district (see Fig. 1; habitat composition of the study area is given in Table 1). The cold season in Paazerre, defined as the season with snow cover and average air temperature usually dropping below 0°C, normally lasts from early November until early April. Most winters are quite



Figure 1. Location of our study are in Belarus with indication of the study methods used: R=radio-tracking, S=snow-tracking, SC=scat collection, and SRC=small rodent census.

severe, with deep snow cover of 30-90 cm varying between habitats and years, and air temperatures of around -20°C and lower often lasting for several weeks. Usually such frosty periods alternate with thaws lasting for a week. Some winters, however, are rather mild with a short snowy period lasting around two months.

The Palesse study area is mostly flat and much swampier. Open grassy marshes are especially extensive, but raised bogs are less common than in Paazerre. Density of river network is relatively low (0.2-0.4 km/km²). Residual glacial lakes are rare, but there are many floodplain waterbodies in old

Table 1. Habitat composition (%) in the main study areas in Paazerre and Palesse, Belarus.

Habitat types	Paazerre	Palesse
Forest types dominated by spruce >60 years old	22.7	0.0
Dry-land pine stands >60 years old	9.6	12.1
Raised bogs with a suppressed pine overgrowth	4.7	3.7
Forests dominated by broad-leaved trees	0.0	14.4
Mid-succession deciduous woods	13.8	12.5
Black alder swampy woods	16.4	14.7
Ecotones between forest and open grassland	1.8	1.7
Aquatic ecosystems	2.7	2.0
Stream banksides and lake shores	0.4	0.3
Recent (≤ 2 years old) clearcuts	2.6	4.6
Clearcuts with some reforestation >2 years old	7.0	12.3
Open grassy marshes	10.7	13.8
Dry meadows	6.8	4.2
Intensively used fields	0.6	2.4
Villages	0.2	1.3
Total length of transects inspected, km	178	102

riverbeds in valleys of medium-sized and big rivers. Forest habitats mostly consist of broad-leaved forests, black alder swamps, and dry-land pine stands. Amongst the broad-leaved trees, the oak *Quercus robur* is the dominating species. The study area, covering ca 170 km², was located in the Lełchitsy and Stolin districts (see Fig. 1; see Table 1 for habitat composition). In Palesse, winters are much milder and one month shorter than in Paazerre.

Material and methods

Habitat investigation

In the Paazerre study area, proportions of the various habitat types (the landscape structure) were estimated by travelling 18 transects. The transects were about 10 km long and covered a total of 178 km. They were directed northwards and to cover all parts of the study area they were placed as densely as possible. In Palesse, the landscape structure was investigated using 10 transects, covering a total of 102 km. We estimated the length of each habitat patch in the transects and calculated the proportion of each habitat type. Various ecotones were accepted to being 10 m wide. The proportion of biotopes and ecotones for both study areas are reported in Table 1.

Capture

Weasels and stoats were live-caught in wooden flip-door box-traps with a separate bait compartment (Jędrzejewski et al. 2000). Two live laboratory mice provided with food and shelter were used as bait in each trap. The traps were checked every two hours. The captured weasels and stoats were carefully immobilised by injection of Vetalar, and then radio-tagged. We kept the radio-tagged small mustelids in a big box with hay for several hours, and sometimes up to two days, until they began to kill laboratory mice normally (Jędrzejewski et al. 2000). We released each individual at the site of capture. During live capturing, the box-traps were equally distributed in forests, dry meadows and grassy marshes. The mean trapping effort to live-catch one small mustelid varied between trapping sessions from 51 to 246 trap-nights. In total, we captured and radio-tagged 34 small mustelids, but only seven weasels (three females and four males) and eight stoats (four females and four males) were radio-tracked long enough to allow data analyses (4–11 months, average eight months). During the period of radio-tracking the

estimated current home range of the individuals had stabilised.

Radio-tracking

In Paazerre, the radio-tracking study was carried out during 1997–2001. Receivers were provided by Telonics Inc. (Mesa, Arizona), and neck-collars with transmitters were made by Biotrack Ltd. (Wareham, UK). Animals were located by detecting bearings at short-distance from at least two locations, with the support of detailed maps and GPSs; radio-tracking was carried out simultaneously by experienced operators, familiar with the study areas and in constant contact by either walkie-talkie or mobile phone. Radio-location error, estimated by locating hidden collars, was minimal, and difference among the three researchers involved was < 10%. In most cases when radio-tagged individuals were inactive, we approached them in order to identify precise habitat type of the shelter. During the snowy period, precise location was identified by snow-tracking. Animals were usually tracked continuously over 4-hour periods, with locations generally collected every 15 minutes. The number of fixes for each individual varied from 434 to 1,235 and totalled 6,203 for weasels and 6,328 for stoats. We used all radio-tracking data in the calculations of habitat selection by the species, because both stoats and weasels, mostly using short-distance moving, stayed within the same habitat patch for quite a long time. To avoid risks of autocorrelation in the data on habitat use by the radio-tracked small mustelids, we mostly did 4-hour long radio-tracking sessions, and secondly, we usually did not return to do radio-tracking of the same radio-tagged individual until at least one day had passed since the last radio-tracking session; normally we conducted one radio-tracking bout for each individual per 2–4 days.

Preferences among habitat types was estimated using Ivlev's electivity index D (after Jacobs 1974). According to Krebs' suggestion (Krebs 1998), the least biased Morisita's index C (Morisita 1959) was used to evaluate habitat use overlap between the two species.

Snow-tracking

Habitat selection in winter was also investigated by snow-tracking in both study areas. Transects and additional paths were walked, all mustelid tracks were recorded and proportion of tracks in each habitat type calculated. Species were identified by tail marks in the snow which were markedly longer

and wider for the stoat. This method of identification was tested on radio-tracked animals and proved to be very precise (three mistakes in >800 trials).

Scat collecting and diet analysis

Scats of weasels and stoats were collected: 1) during radio-tracking (inspecting places where they were active or inactive for long and in four nesting sites discovered), 2) during live catching and 3) during snow-tracking. We also collected scats by digging holes made by small rodent species, that were frequently used by weasels or stoats, as shown by radio-tracking and/or snow-tracking. A total sample of 426 weasel scats and 606 stoat scats were used for diet analysis. We identified 459 prey individuals in weasel scats and 823 in stoat scats. We found on average 1.07 prey individuals per scat for the weasel and 1.36 prey individuals per scat for the stoat.

To identify mammal prey species, we washed the scats, picked 10 hairs at random and inspected them microscopically (Teerink 1991). Frequency of occurrence was calculated as the proportion of each prey species in the total of identified prey species (%OC). Percentage of consumed food biomass (%BC) was calculated following Jędrzejewska & Jędrzejewski (1998), using a coefficient of digestibility for each food item. As these coefficients were unknown for small mustelids, we used the parameters calculated for the polecat *Mustela putorius*, which phylogenetically and ecologically is a closely related species. To compare overall dietary diversity (breadth of the food niche) in different seasons and regions, and between the species, we calculated Levins' B index (Levins 1968), which varies from one (narrowest niche) to 15 (broadest possible niche), for 15 food categories. In accordance with Krebs' suggestion (Krebs 1998), we used the least biased Morisita's index C (Morisita 1959) to evaluate dietary similarity. To assess preference for small rodent species, we used Ivlev's electivity index D (after Jacobs 1974): $D = (r - p) / (r + p - 2rp)$, where r is the fraction of the species or species group among all small rodents consumed in the total number of small rodents in scats, and p is the fraction of the species or species group in the living community of small rodents. D ranges from -1 (total avoidance of a species) over 0 (selection proportional to occurrence) to +1 (maximum positive selection).

Small rodent census

Abundance index and species composition of small rodents were estimated by snap-trapping in three

trapping sessions: in pre-reproduction period (April), mid-reproduction period (June-August), and post-reproduction period (October-early November). Snap-trapping as a method of small rodent census involving killing of the individuals captured is allowed under the legal framework in Belarus. Rodent censuses were carried out simultaneously to scat analysis (during 1997-2000 in Paazerre and in 1997, 2002 and 2003 in Palesse). Trapping data (average) gathered in the October-early November sessions were used to define rodent species structure, mean abundance and weight. Census plots were placed in the main woodland habitat types: premature forest dominated by spruce (only in Paazerre), old broad-leaved forest (only in Palesse), ecotones of the above forest types with open grasslands, pine stands, clearcuts, black alder swamps, mid-succession deciduous forest, and open grassy marsh. In each habitat type, five plots were investigated during each trapping session, and to avoid autocorrelation, plots were changed in the following sessions. Traps were baited with fried bread in forest habitats, and also with carrots in grassy marshes. We set 20-50 snap-traps at approximately 5-m intervals. The traps were up for three days and they were checked daily. In total, censuses were done in 735 plots. Captured individuals were identified using Pucek's (1981) key.

The number of individuals captured during 100 snap-trap nights was used as a proxy of small rodent density, total and by habitat. The species' proportions in trapping bags were applied to approximate their proportions in the living community. The species structure of rodents available for weasels and stoats was estimated as mean weighted values based on habitat use by the predatory species and the prey species structure in the above variety of habitats investigated by snap-trapping. We used the mean weighted species structure of rodents to assess the preferences of weasels and stoats for various species of this prey group. Mean abundance index of rodents available for weasels and stoats was assessed the same way, based on mean abundance index of the prey species in the variety of habitats where snap-trapping was conducted. We used the mean abundance index of rodents available for weasels and stoats to compare quality of different habitat types used by small mustelids.

Statistical analysis

For statistical analysis of our data we used Spearman rank correlation coefficient (r_s), Mann-Whitney

U-test, Student's t-test for difference between two means, and G-test for homogeneity of percentages (Sokal & Rohlf 1995).

Results

Habitat separation

In Paazerre, the radio-tracked weasels did not change habitat use across seasons ($C=0.93$; Table 2A). They stayed within forest of different types (41.9–43.1% of fixes), and less often used more open places such as forest edges, i.e. forest ecotones with grassy openings and aquatic ecosystems (27.1–30.1%), grassy openings, i.e. dry meadows and open marshes (11.0–16.4%), and clearcuts with some reforestation (13.2–16.8%). Within woodland weasels mostly used fairly old forest dominated by spruce year-round (18.9–21.4%), mid-succession small-leaved forest in the warm season (16.5%) and black alder swampy wood in the cold season (11.3%). Year-round, weasels significantly selected ecotones between forest and open grassland ($D=0.86-0.91$), river banksides or lake shores ($D=0.77-0.91$), and clearcuts with some reforestation ($D=0.28-0.41$), whereas they evidently avoided raised bogs ($D=-0.92$), dry-land pine forest ($D=-0.69- -0.72$) year-round, and open grassy marshes ($D=-0.51$) and black alder swamps ($D=-0.61$) in the warm season. In the cold season similar data on the habitat use by weasels were obtained by snow-tracking (see Table 2B), and their overlap with the respective radio-tracking data was remarkably high ($C=0.96$).

Comparing snow-tracking data gained in Palesse and Paazerre, we found a significant difference between the two study areas ($C=0.62$; $G=65.1$, $P<0.001$), likely due to the marked differences between them. In Palesse, weasels did not use spruce forest ($G=19.8$, $P<0.01$), which is nearly absent in that area, but spent much time in deciduous forests dominated by broad-leaved trees ($G=32.3$, $P<0.01$), which, on the other hand, is a rare habitat in Paazerre. In Paazerre weasels used forest edges twice as often as in Palesse ($G=4.2$, $P=0.03$). In the warm season in Palesse, weasels selected old broad-leaved forest ($D=0.29$), ecotones between forest and open grassland ($D=0.79$), stream banksides ($D=0.94$) and dry meadows ($D=0.44$).

According to the radio-tracking data obtained in Paazerre (see Table 2A), the habitat use by stoats did not change from the warm season to the cold season ($C=0.97$). In contrast with the weasels

radio-tracked in the same area, the radio-tagged stoats generally avoided dry-land forest (only 4.3–5.5% of the recorded locations, $D=-0.53- -0.95$). Black alder swampy woods were used by stoats approximately in proportion to the landscape structure or slightly less (10.7–15.7% of fixes, $D=-0.03- -0.24$). Year-round, stoats selected open grassy marshes (35.6–46.4%, $D=0.64-0.76$), forest edges especially at the border between forest and marshland (13.9–16.0%, $D=0.80-0.82$), stream banksides and lake shores (11.5–11.9%, $D=0.94$). Dry meadows were, to some extent, slightly selected by stoats (10.0–11.2%, $D=0.21-0.27$). Snow-tracking data collected in Paazerre showed similar habitat use by stoats, and results largely overlapped with those of radio-tracking ($C=0.93$). Snow-tracking showed no significant differences in habitat use by stoats between Palesse and Paazerre ($C=0.97$). In both areas, the most used habitats of stoats were swampy biotopes such as open grassy marshes (44.0–46.4%) and swampy river banks (16.9–19.6%), but black alder swamps were used more frequently in Palesse than in Paazerre (15.9 vs 5.0%; $G=6.1$, $P=0.03$).

Radio-tracking data gathered in the warm season in Paazerre showed a markedly significant difference in habitat use between stoats and weasels ($C=0.36$, $G=96.8$, $P<0.001$), and so did radio-tracking data collected in Paazerre in the cold season ($C=0.61$, $G=56.7$, $P<0.001$) and snow-tracking data collected in Paazerre ($C=0.43$, $G=80.4$, $P<0.001$) and in Palesse ($C=0.42$, $G=61.5$, $P<0.001$). The main differences were due to the fact that swampy habitats were used much more frequently by stoats than by weasels (63.2–76.8% vs 11.3–30.0% of locations recorded; $G\geq 21.4$, $P>0.01$), and by the fact that stoats showed a higher preference for open grassy marshes than did weasels (35.6–46.4% vs 3.6–8.7%; $G\geq 19.3$, $P<0.01$, $D=0.64-0.76$). Weasels on the other hand used forest habitats more than stoats (33.9–48.3% vs 6.7–20.0%; $G\geq 8.6$, $P<0.01$). In particular, dry-land forest appeared to be used almost exclusively by weasels and was only rarely used by stoats (24.7–37.3% vs 1.7–5.5%; $G\geq 12.5$, $P<0.01$).

Abundance and species structure of small rodents

We estimated the structure of the small rodent communities in the main habitat types of weasels and stoats, i.e. woodland and marshland, respectively (Table 3). In Paazerre in the warm season, small rodents were almost equally common in woodland and marshland, but in the cold season they were almost two times more abundant in

Table 2. Habitat used by weasels and stoats in Belarus given as percentages for the warm (WS) and cold (CS) seasons with Ivlev's electivity index D given in parentheses. G-test for homogeneity of percentages is given to show the differences between habitat use by weasels and stoats in the warm and cold seasons, respectively.

A) Radio-tracking data, Paazerre	Weasels		Stoats		G(p)	
	WS	CS	WS	CS	WS	CS
Habitat types						
Forest types dominated by spruce > 60 years old	18.9 (-0.12)	21.4 (-0.04)	0.8 (-0.95)	0.7 (-0.95)	20.62 (<0.01)	24.43 (<0.01)
Dry-land pine stands > 60 years old	1.9 (-0.69)	1.7 (-0.72)	0 (-1.0)	0.5 (-0.91)	2.63 (>0.1)	0.69 (>0.1)
Raised bogs with a suppressed pine overgrowth	0.2 (-0.92)	0.2 (-0.92)	0.9 (-0.69)	1.5 (-0.53)	0.48 (>0.1)	1.13 (>0.1)
Mid-succession deciduous (mostly small-leaved) woods	16.5 (0.1)	8.7 (-0.25)	4.7 (-0.53)	3.1 (-0.67)	6.96 (<0.01)	2.77 (0.08)
Black alder swampy woods	4.6 (-0.61)	11.3 (-0.21)	10.7 (-0.24)	15.7 (-0.03)	2.50 (>0.1)	0.72 (>0.1)
Ecotones between forest and open grassland	27.1 (0.91)	19.2 (0.86)	13.9 (0.80)	16.0 (0.82)	4.33 (0.03)	0.29 (>0.1)
Stream banksides and lake shores	3.0 (0.77)	7.9 (0.91)	11.5 (0.94)	11.9 (0.94)	5.32 (0.02)	0.81 (>0.1)
Recent (≤ 2 years old) clearcuts	1.6 (-0.24)	1.5 (-0.27)	0 (-1.0)	0 (-1.0)	2.22 (>0.1)	2.08 (>0.1)
Clearcuts with some reforestation > 2 years old	15.2 (0.41)	11.7 (0.28)	0 (-1.0)	0.6 (-0.85)	21.07 (<0.01)	12.26 (<0.01)
Open grassy marshes	3.7 (-0.51)	8.7 (-0.11)	46.4 (0.76)	35.6 (0.64)	43.05 (<0.01)	17.52 (<0.01)
Dry meadows	7.3 (0.04)	7.7 (0.07)	10.0 (0.21)	11.2 (0.27)	0.42 (>0.1)	0.65 (>0.1)
Intensively used fields	0 (-1.0)	0 (-1.0)	1.1 (0.30)	1.2 (0.34)	1.52 (>0.1)	1.66 (>0.1)
Villages	0 (-1.0)	0 (-1.0)	0 (-1.0)	2.0 (0.82)	-	2.77 (0.08)
Pooled number of radio-locations (number of individuals)	2963 (5)	240 (4)	1716 (3)	612 (6)	-	-

B) Snow-tracking data, Paazerre and Palesse	Weasels		Stoats		G(p)	
	Paazerre	Palesse	Paazerre	Palesse	Paazerre	Palesse
Habitat types						
Forest types dominated by spruce > 60 years old	14.3 (-0.28)	-	0.6 (-0.96)	-	15.63 (<0.01)	-
Dry-land pine stands > 60 years old	2.0 (-0.68)	4.6 (-0.48)	0 (-1.0)	0 (-1.0)	2.77 (0.08)	6.30(0.02)
Raised bogs with a suppressed pine overgrowth	0.4 (-0.81)	0.5 (-0.77)	0.6 (-0.78)	0.4 (-0.81)	0.04 (>0.1)	0.01(>0.1)
Old forests dominated by broad-leaved deciduous trees	-	23.3 (0.29)	-	1.8 (-0.80)	-	21.84(<0.01)
Mid-succession deciduous (mostly small-leaved) woods	8.4 (-0.27)	3.6 (-0.59)	1.1 (-0.87)	0.7 (-0.91)	6.36 (0.02)	2.14(>0.1)
Black alder swampy woods	9.2 (-0.32)	16.8 (0.08)	5.0 (-0.58)	15.9 (0.05)	1.26 (>0.1)	0.02(>0.1)
Ecotones between forest and open grassland	25.2 (0.90)	12.7 (0.79)	10.1 (0.72)	9.2 (0.71)	6.67 (<0.01)	0.56(>0.1)
Stream banksides and lake shores	7.2 (0.90)	9.6 (0.94)	19.6 (0.97)	16.9 (0.97)	5.96 (0.02)	2.04(>0.1)
Recent (≤ 2 years old) clearcuts	0.9 (-0.49)	1.0 (-0.65)	0 (-1.0)	0.4 (-0.85)	1.25 (>0.1)	0.27(>0.1)
Clearcuts with some reforestation > 2 years old	14.5 (0.39)	9.1 (-0.17)	2.2 (-0.54)	2.1 (-0.73)	10.14 (<0.01)	4.72(0.03)
Open grassy marshes	.8 (-0.24)	3.6 (-0.62)	46.4 (0.76)	44.0 (0.66)	33.08 (<0.01)	40.48(<0.01)
Dry meadows	8.3 (0.11)	10.2 (0.44)	9.5 (0.18)	5.3 (0.12)	0.08 (>0.1)	1.58(>0.1)
Intensively used fields	1.6 (0.47)	3.0 (0.11)	2.8 (0.65)	2.1 (-0.07)	0.33 (>0.1)	0.16(>0.1)
Villages	1.2 (0.72)	2.0 (0.22)	2.2 (0.84)	1.1 (-0.08)	0.30 (>0.1)	0.27(>0.1)
Number of individuals recorded by tracks (one track concentration means one individual)	942	197	179	284	-	-

Table 3. Abundance index (in %) and species structure of small rodents in Paazerre and Palesse. The values are given for the warm (WS) and cold (CS) seasons. Mean abundance is given as rodents captured per 100 snap-trap nights.

Parameter	Paazerre								Palesse							
	Woodland		Marshland		Estimated prey availability for				Woodland		Marshland		Estimated prey availability for			
					Weasel		Stoat						Weasel		Stoat	
	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS
<i>Arvicola terrestris</i>	0	0	10.4	11.9	0.3	1.3	5.4	5.7	0	0	27.8	32.7	4.9	2.6	13.1	17.0
<i>Microtus vole</i>	1.1	1.9	20.0	36.1	11.8	21.8	27.7	37.2	12.8	13.3	22.8	21.2	13.7	37.2	17.7	14.0
<i>Apodemus mouse</i>	15.7	19.3	39.3	20.9	20.5	23.6	30.9	26.8	19.7	36.6	36.0	33.5	23.1	26.8	22.8	34.8
<i>Clethrionomys glareolus</i>	82.5	77.7	28.6	29.9	65.8	51.1	33.8	28.1	60.6	40.0	10.6	9.9	52.8	26.7	21.0	24.4
Other species	0.7	1.1	1.7	1.2	1.6	2.2	2.2	2.2	6.9	10.0	2.8	2.7	6.7	5.5	29.2	6.1
Total number of census plots	240		60		420				180		45		315			
Mean abundance index	28.0	15.9	24.4	24.1	32.2	22.5	31.4	31.7	34.6	27.9	21.4	11.6	30.7	34.4	32.9	16.4

marshland ($t=9.8$, $P<0.01$). Year-round in Paazerre woodland bank voles *Clethrionomys glareolus* were the most common small rodents, *Apodemus* mice were also fairly common prey, while *Microtus* voles were rather rare (see Table 3). Similar small rodent communities inhabited woodlands in Palesse with the exception of *Microtus* voles which were more common there. Compared to woodland, in marshland we found significantly more *Microtus* voles in Paazerre only ($G=20.0$ - 37.5 , $P<0.01$) and water voles *Arvicola terrestris* in both Palesse and Paazerre ($G=10.2$ - 39.0 , $P<0.01$). Water voles were more common in Palesse (see Table 3).

Having investigated the structures of small rodent communities in the main habitat types of weasels and stoats, we also needed to synthesise data on the structures of small rodent communities that were available for the two mustelid species taking into account their habitat usage. The data given in Table 3 were necessary to calculate the selectivity in predation of small rodents by weasels and stoats.

Weight of small rodents

Weight of the available prey species (summarised in Table 4) may be another indicator of habitat quality. The data collected indicate that mean bodymass of prey species was lower in the warm than in the cold season. Amongst 12 rodent species, the water vole was the largest prey species of stoats and weasels. The root vole *Microtus oeconomus*, the field vole *M. agrestis*, and the yellow-necked mouse *Apodemus flavicollis* were also relatively big prey species, but smaller than the water vole ($t=13.2$ - 31.7 , $P<0.001$). Other rodent species available for small mustelids in the study areas were markedly smaller.

Diet differences

Diet data (Table 5) indicate that in the warm season in Paazerre, weasels mostly rely on small rodents, which provided 80.8%BC. The most common prey species in Paazerre was the bank vole (48.3%OC), while *Microtus* voles were preyed on less frequently (18.0%OC). In the cold season, the diet of the weasel was very similar ($C=0.96$ for %OC and 0.96 for

Table 4. Bodymass (in g) of various rodent species in Belarus for the cold (CS) and warm (WS) seasons. Seasonal difference was tested using Student's t-test for difference between two means.

Species	N		Min		Max		Mean		SD		t	P
	CS	WS	CS	WS	CS	WS	CS	WS	CS	WS		
Water vole <i>Arvicola terrestris</i>	51	176	153	24	287	284	200.7	90.1	37.2	55.2	16.6	<0.01
Root vole <i>Microtus oeconomus</i>	193	444	27	14	81	79	44.9	34.3	7.7	14.2	12.2	<0.01
Field vole <i>Microtus agrestis</i>	79	152	19	11	57	56	34.7	30.2	9.8	12.1	3.1	<0.01
Common vole <i>Microtus arvalis</i>	70	423	18	11	50	50	26.8	23.3	7.3	9.9	3.5	<0.01
European pine vole <i>Microtus subteraneus</i>	27	21	12	9	46	34	25.1	20.1	11.3	8.4	1.8	0.06
Striped field mouse <i>Apodemus agrarius</i>	47	198	18	10	55	41	29.9	22.9	8.5	9.3	5.0	<0.01
Wood mouse <i>Apodemus sylvaticus</i>	41	184	17	9	43	40	28.2	20.5	6.9	7.7	6.3	<0.01
Pygmy field mouse <i>Apodemus uralensis</i>	29	27	16	8	26	26	19.7	14.8	4.0	4.3	4.4	<0.01
Yellow-necked mouse <i>Apodemus flavicollis</i>	142	519	20	14	56	45	34.5	30.2	7.6	18.4	4.2	<0.01
Bank vole <i>Clethrionomys glareolus</i>	432	4035	15	8	35	32	21.6	19.7	6.0	4.7	6.4	<0.01
Harvest mouse <i>Micromys minutus</i>	116	109	5	4	14	13	7.8	6.9	2.0	1.9	3.5	<0.01
Birch mouse <i>Sicista betulina</i>	20	51	6	4	13	15	9.2	8.5	1.9	1.7	1.4	0.89

Table 5. Diet of the weasel in Belarus during 1994-2003. Percentage of frequency of prey occurrence in the diet (%OC), and percentage of food biomass consumed (%BC) is shown for the warm (WS) and cold (CS) seasons.

Prey species or category	Paazerre				Palesse			
	WS		CS		WS		CS	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	0.7	0.1	1.1	0.1	1.4	0.1	-	-
Amphibians	-	-	0.5	0.7	-	-	-	-
Reptiles	0.7	0.2	-	-	-	-	-	-
Shrews	15.0	5.9	10.0	3.5	1.4	0.5	3.9	1.2
Mole	2.0	2.6	2.6	3.6	2.9	3.1	1.9	2.2
Water vole	-	-	1.1	1.5	1.4	1.5	-	-
Bank vole	48.3	49.2	63.9	63.5	38.6	36.4	42.3	37.2
<i>Apodemus</i> mice	4.4	5.2	2.2	2.1	27.1	29.2	34.6	39.6
<i>Microtus</i> voles	18.0	23.4	14.9	20.1	20.0	21.5	15.4	17.6
Other rodent species	2.7	3.0	2.1	2.8	2.9	3.1	1.9	2.2
Birds	8.2	10.4	1.6	2.1	4.3	4.6	-	-
Number of scats	134		178		66		48	
Number of prey items	147		190		70		52	
Food niche breadth	3.35	3.08	2.26	2.22	3.75	3.73	3.08	3.05

%BC). By comparing the small rodent structure by habitat (see Tables 3 and 5), weasels appeared to select *Microtus* voles in the warm season ($D=0.42$) and bank voles in the cold season ($D=0.50$). *Apodemus* mice were consumed by weasels in markedly lower proportions than available in the used habitats ($D=-0.89$ - -0.94). Weasels in Palesse had a slightly different diet year-round (warm season: $C=0.86$ for %OC and 0.86 for %BC, $G=36.3$ - 55.9 , $P<0.001$; cold season: $C=0.80$ for %OC and 0.73 for %BC, $G=30.5$ - 46.4 , $P<0.001$) than weasels in Paazerre. In this area, weasels appeared to be even more specialised in preying on small rodents (mostly taking bank voles and *Apodemus* mice). *Apodemus* mice were eaten 6-16 times more frequently than in Paazerre ($G=18.2$ - 41.2 , $P<0.01$; see Table 5). Conversely, in Palesse the proportion of bank voles in weasel diet was markedly lower than in Paazerre, but the difference was statistically significant only in the cold season ($G=3.2$ - 6.9 , $P=0.01$ - 0.05). In Palesse, weasels did not show any marked preference or avoidance in their predation on small rodents and used different small rodent species approximately proportionally to their presence in the living community.

Diet analysis showed that stoats predominantly ate water voles and *Microtus* voles, which together accounted for a large proportion of their diet (55.2 - 81.7% OC and 63.8 - 88.6% BC; D varied from 0.31 to 0.72 and the mean was 0.50). In Palesse, stoats fed markedly more on water voles than in Paazerre in both the warm (57.7 vs 10.7% BC; $G=35.4$, $P<0.01$) and the cold season (45.8 vs 24.7% BC; $G=6.5$, $P=0.01$). Conversely, the proportion of *Microtus*

voles in stoat diet was higher in Paazerre than in Palesse in both the warm (53.2 vs 30.9% BC; $G=6.0$, $P=0.02$) and the cold season (39.1 vs 20.8% BC; $G=5.8$, $P=0.01$). Similar to weasels, stoats in Palesse were more specialised in feeding on small rodents (Table 6). In general, stoat diet in Palesse was quite different from that in Paazerre in both the warm ($C=0.65$ for %OC and 0.63 for %BC; $G=68.1$ - 66.9 , $P<0.001$), and the cold season ($C=0.79$ for %OC and 0.82 for %BC; $G=30.9$ - 35.4 , $P<0.009$). Overall, stoat diet was similar in the cold and warm seasons ($C=0.78$ - 0.97), but with significant differences in the consumption of several food items ($G=25.4$ - 41.7 , $P<0.05$); in the cold season, stoats in Paazerre consumed more water voles and carrion and less *Microtus* voles than in the warm season. In the cold season, stoats in Palesse fed more on bank voles and *Apodemus* mice, but less on water voles and *Microtus* voles (see Table 6). Interestingly, the weasel was found, although rarely, amongst prey remains in stoat scats in both Paazerre and Palesse.

Our results indicate a marked difference in the feeding habits of the two species, accounting for a limited dietary overlap: $C=0.29$ - 0.70 for %OC ($G=78.8$ - 130.7 , $P<0.001$) and 0.25 - 0.51 for %BC ($G=100.5$ - 119.9 , $P<0.001$). Stoats preyed more often on water voles and *Microtus* voles, while weasels mostly ate bank voles and *Apodemus* mice. The differences were statistically significant ($G=5.1$ - 57.8 , $P<0.03$), with the exception of *Microtus* voles in Palesse and *Apodemus* mice in Paazerre. Compared to weasel, the stoat was a less specialised predator of small rodents (see Table 6) and ate a wider range of food

Table 6. Diet of the stoat in Belarus during 1994–2003. Percentage of frequency of prey occurrence in the diet (%OC) and percentage of food biomass consumed (%BC) is shown for the warm (WS) and cold (CS) seasons.

Prey species or category	Paazerre				Palesse			
	WS		CS		WS		CS	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	-	-	1.2	<0.1	-	-	-	-
Amphibians	2.5	4.0	1.9	1.7	2.0	1.2	-	-
Reptiles	1.6	1.7	-	-	-	-	-	-
Shrews	5.0	1.3	7.2	1.4	1.1	0.3	4.0	0.7
Mole	-	-	2.9	4.8	2.0	2.3	4.0	6.6
Water vole	8.0	10.6	14.9	24.7	49.6	57.7	28.0	45.8
Bank vole	10.6	6.1	13.4	6.9	3.0	1.4	24.0	12.2
<i>Apodemus</i> mice	1.7	0.9	0.8	0.4	2.0	1.0	13.0	6.3
<i>Microtus</i> voles	47.2	53.2	40.8	39.1	32.1	30.9	20.0	20.8
Other rodent species	-	-	0.5	0.1	2.0	0.3	-	-
Muskrat	2.9	4.0	1.2	1.6	-	-	-	-
Hares	2.9	3.8	-	-	2.1	2.3	-	-
Weasels	1.0	1.3	1.4	1.7	-	-	0.5	0.8
Carriion	-	-	4.2	8.1	-	-	2.5	4.0
Birds	13.8	13.0	9.6	9.9	4.1	2.6	4.0	2.8
Herbs	2.9	<0.1	-	-	-	-	-	-
Number of scats	136		157		142		171	
Number of prey items	204		213		206		200	
Food niche breadth	3.76	3.18	4.43	4.09	2.83	2.53	4.50	3.20

items, e.g. young hares *Lepus europaeus* and *L. timidus*, muskrat *Ondatra zibethicus*, weasel, carrion of wild ungulates and beavers *Castor fiber*.

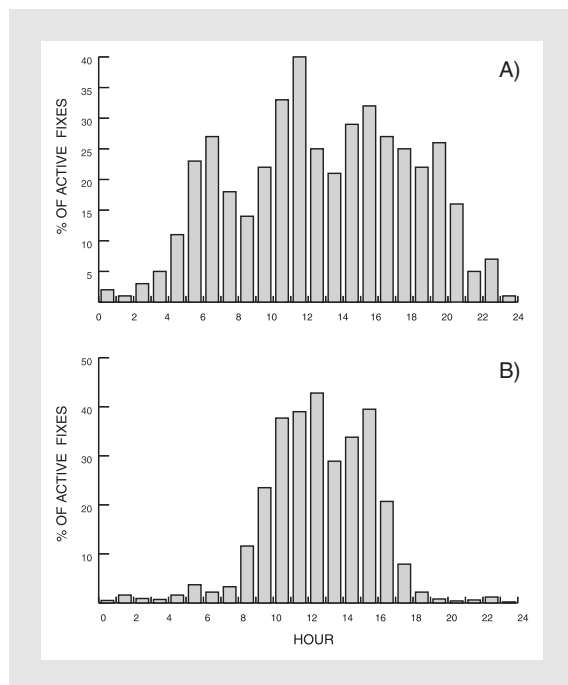


Figure 2. Diel activity rhythm of weasels in Paazerre during A) the warm season (April–October), according to data pooled for five individuals (in total, 2,963 fixes taken at 15-minute intervals) and B) the cold season (November–March), according to data pooled for four individuals (in total, 3,240 fixes taken at 15-minute intervals).

Difference in the diel activity rhythms

Diel activity rhythms of the radio-tagged weasels and stoats based on the pooled data gained from all radio-tracked individuals are shown in Figures 2 and 3. In the warm season, weasels were mostly diurnal and were hardly active at night. The mean duration of daily activity was 4.2 hours (17.5% of 24 hours). The pattern of weasel daily activity in the cold season was similar (see Fig. 2B), but the mean duration of daily activity was significantly lower than that in the warm season (3.1 hours, or 12.7% of 24 hours; $U=377.0$, $P=0.04$). Also in the cold season, the weasel diel activity rhythm was differently distributed over different times of the day ($G=149.2$, $P<0.001$) and adjusted to the changed daytime.

In the warm season, stoat diel activity rhythm was very different from that of weasels ($G=134.1$, $P<0.001$), with stoats being almost equally active during day and night and most active in twilight (see Fig. 3A). But the total duration of daily activity of stoats was nearly the same as that of weasels (4.4 hours, or 18.3% of 24 hours). In the cold season, stoats were more active at night than in the warm season ($G=49.7$, $P=0.002$; Fig. 3B). The total duration of daily activity of stoats in the cold season was slightly lower (3.7 hours, or 16.1% of 24 hours (no statistical difference)). Stoats and weasels differed in both duration ($U=383$, $P=0.04$) and distribution between hours ($G=312.9$, $P<0.001$) of activity in the cold

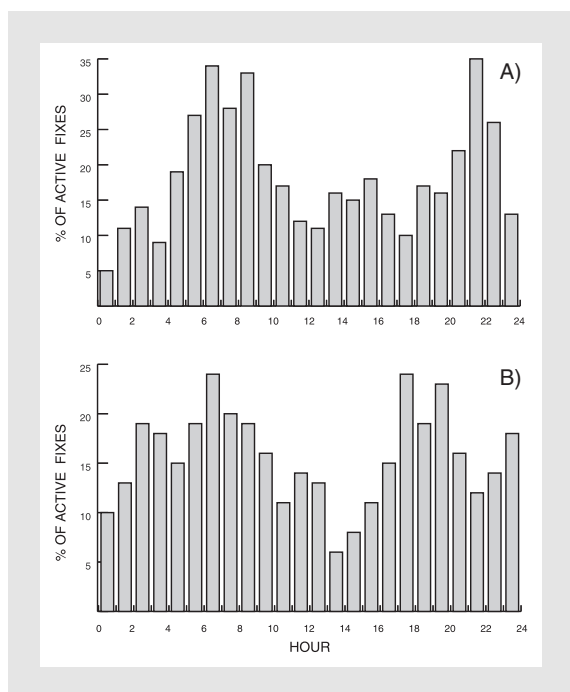


Figure 3. Diel activity rhythm of stoats in Paazerre during A) the warm season (April-October), according to data pooled for three individuals (in total 1,716 fixes taken at 15-minute intervals) and B) the cold season (November-March), according to data pooled for six individuals (in total 4,612 fixes taken at 15-minute intervals).

season. Stoat activity was longer and mainly concentrated during night and twilight (see Figs. 2B and 3B).

Discussion

Our results suggest that in the semi-natural landscapes of Belarus, where the weasel and stoat occur in close proximity, they use different micro-habitats, are active primarily during different times of the day, and prey primarily on different small rodent species. Most weasels selected forest and forest edge habitats, where this smaller predator mostly preyed on smaller rodents (bank voles and *Apodemus* mice). Stoats selected wetlands, especially open grassy marshes, and mostly fed on larger rodent species such as water voles and *Microtus* voles. Moreover, open grassy marshes were characterised by more abundant larger rodent species, in particular during the cold season, when it is harder for predators to survive. The daily activity patterns of stoats and weasels were markedly different. The weasel was mostly diurnal and appeared to adjust its activity to the seasonal changes of day light, whereas the stoat

was much more active in twilight and during the night. These results are similar to those gathered in previous studies (Debrot et al. 1985, Zielinski 1986, 1988, Jędrzejewski et al. 2000).

Based on the results of our study, we hypothesise that coexistence of the stoat and the weasel in a semi-natural landscape within the temperate forest zone in Belarus can be explained as follows. The larger stoat selects either the larger prey species in the community, such as the water vole and root vole, or rodent populations with high density and biomass, such as several species of the genus *Microtus*. Stoats appear to get their daily food intake in the easiest possible way, that is to prey on larger prey species. Also, foraging on a wider array of prey species increases its hunting efficiency. The stoat has been described as a less effective small rodent killer than the weasel, because it is too large to enter burrows of smaller rodent species (King & Moors 1979, Erlinge & Sandell 1988, King 1989), and therefore, preying on larger rodents is a way for stoats to survive. Conversely, the smaller weasel exploits populations of small rodents more efficiently than the stoat, because the weasel can gain access to smaller tunnels (Lockie 1966, King 1989). Therefore, weasels usually rely on smaller rodents such as bank voles.

In general, the pattern of niche separation between the weasel and the stoat as shown by our study appears to be similar to what was found in other regions (King & Moors 1979, Erlinge 1975, 1981, Powell & Zielinski 1983, Erlinge & Sandell 1988, King 1989, McDonald et al. 2000), where the stoat was found to forage on rodent and other suitable prey species that were larger than those foraged upon by the weasel, and also to more frequently use habitats where such nourishing prey species are common. In the temperate woodlands of Belarus, the stoat uses feeding habitats that are different from the ones it uses in other regions, e.g. western European farmlands (Day 1968, King & Moors 1979, McDonald et al. 2000, McDonald 2002). The daily activity patterns of weasels and stoats in Belarus appear fairly different from those recorded in some areas (Zielinski 1986, 1988 and references therein), but are similar to those found in other regions (stoat: Debrot et al. 1985; weasel: Jędrzejewski et al. 2000).

Surprisingly, our study showed that in Belarus the weasel is less common in wetlands than the stoat, and feeds less frequently on water voles and *Microtus* voles. The latter observation is probably due to the specific habitat use of this predator, which in

our study areas lived in forest habitats, clearcuts and forest edges, where water voles and *Microtus* voles were less common. However, from the published literature it is well known that weasels can kill rodents as large as water voles, and moreover, *Microtus* voles and sometimes water voles may form a large proportions of the species' diet (Day 1968, King 1989, McDonald et al. 2000). Therefore, it remains unclear why weasels in Belarus frequently refrained from using the wetlands that support this attractive large prey species. Considering that our field work showed that many weasels live in swamps, we tend to rule out that this habitat is unsuitable for the species. Thus, we hypothesise that the avoidance of this specific habitat may be due to agonistic interactions with the stoat, e.g. interspecific territoriality, predation attempt and interference competition. In aggressive encounters the larger predator is more likely to be dominant, and, therefore, such interactions could have strongly influenced habitat selection by weasels. In the published literature, there are studies which clearly suggest that direct aggression and scent communication from the stoat, as the larger and socially dominant species, excludes weasels from habitats with high vole densities and biomass (King & Moors 1979, Erlinge & Sandell 1988, King 1989). This interference can occasionally lead to predation, as shown by weasel remains in stoat scats in our study and earlier findings by Erlinge (1981).

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