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Seasonal variations in distribution patterns and movements of bats in relation to habitat characteristics

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Abstract

Different types of land use, such as forestry and agriculture, change the distribution and composition of habitats in the landscape. In order to understand the consequences of that for different organisms, and to find methods for combining conservation with production of crops, timber and other products it is important to collect information on distribution pattern, habitat selection and movements of different organisms. By using ultrasound detectors, mist-nets and radio telemetry distribution patterns, abundance and species richness of bats in relation to habitat characteristics among different forest patches in "Lower Dniester" Ramsar Site, Republic of Moldova was studied. The area consists mainly of agricultural lands and highly fragmented inundated and upland forest remnants. In each habitat patch data were collected on forest age, abundance of standing dead and living trees, size of forest patches, occurrence of villages and availability of water. Data were collected during two different periods: July-August and September-October, in order to investigate potential seasonal differences on habitat selection. The result shows that the distribution pattern of bats varies significantly during different seasons. During critical periods (late in autumn), bats are restricted to some specific key habitats and there are movements of bats between key habitats and suboptimal habitats. A multivariate analysis revealed importance of standing dead tree density. From this study, it is obvious that key habitats play an important role for bat populations and that more information on habitat selection and movements of bats during critical periods is needed to improve the conservation of bats.

Keywords: key habitats, bats, Moldova, critical seasons, distribution, movements.

Contents

Introduction

One of the most important reasons for population decline among animals and plants is degradation and fragmentation of their habitats (Fahrig 2003; Wade *et al.* 2003). In order to understand the consequences of this, and how to manage and restore habitats, more information about habitat selection, characterisation of critical habitats and movements between habitats of animals and plants is needed.

Habitat selection is one of the principal components of the species ecology, which permits species to coexist (Rosenzweig 1981). In order to choose an appropriate habitat, animals should consider many different factors, such as foraging benefits, diel period, shelter, and potential predators (Pierce *et al.* 2004; Di Stefano *et al.* 2009). Often habitats are not optimal, and therefore animals have to select habitat based on a trade-off between the costs and benefits (Orians & Wittenberger 1991; Mysterud & Ims 1998). For example, open habitats might provide the best foraging opportunity, while close habitats provide animals with shelters against predators and/or weather (Godvik *et al.* 2009).

Bats are a species-rich order of mammals with approximately 1 100 species (Simmons 2005) in the world, and several species are very abundant. Therefore, they play an important role in different ecosystems from the pollination of plants and dispersing of seeds to regulation of insect populations (Hill & Smith 1988; Galindo-Gonzales *et al.* 2000; Aluri *et al.* 2005; Williams-Guillen *et al.* 2008). On the other hand, several species belongs to the most vulnerable animals. Among mammals of their size, bats are unique in having long lives, low reproductive rates, and relatively long periods of infant dependency. This makes bats more dependent on stable conditions (Findley 1993).

There are a large number of field studies on the relationship between species richness and abundance of bats, and habitat area, but most of the data have been collected during the mid-summer period when the insect abundance in general is high in most habitats. In general, these studies show that most species of bats use many different habitats without any very specific requirements (de Jong & Ahlén 1991; Brooks & Ford 2005; Yates & Muzika 2006). On the other hand, there are indications that bats move to other habitats as soon as the insect abundance decrease and therefore the habitat selection is more critical during spring and autumn (de Jong & Ahlén 1991; Kusch & Idelberger 2005; Rakotoarivelo *et al.* 2007). For conservation purposes, it is important to find out the characteristics and function of these specific habitats. Therefore, more studies on movements and habitats selection of bats during spring and autumn, when insect abundance in general is low, are needed.

Habitat use, distribution patterns and abundance of bats are known to be influenced by many factors at different scales (Grindal & Brigham 1999; Hagan & Meehan 2002). In general, availability of roosts and foraging resources are important, and these factors are mainly affected by the composition and distribution of habitats in the forest or agricultural landscape. At the local scale size and distribution of trees and snags (Crampton & Barclay 1998; Yates & Muzika 2006), stand openness (Kusch *et al.* 2004; Brooks & Ford 2005), presence of water (Kusch *et al.* 2004; Brooks & Ford 2005; Biscardi *et al.* 2007) and solar exposure (Lacki & Schwierjohann 2001) may affect the presence of bats. Patch size, composition of matrix habitats, extent of fragmentation, distribution of prey and availability of linear landscape elements are main factors at the landscape level (Grindal & Brigham 1999; Law *et al.* 1999; Zimmerman & Glanz 2000; Estrada & Coates-Estrada 2002; Kusch *et al.* 2004; Menzel *et al.* 2005; Rogers *et al.* 2006; Zahn *et al.* 2007).

However, our knowledge of basic biology, habitat selection and response to management activities are still limited for most bat species (Fenton 1997; Arnett 2003). Current changes in structure and arrangement of forests at different landscape scales (Sampson & De Coster 2000; Yates & Muzika 2006) and agricultural intensification (Hutson *et al.* 2001; Wickramasinghe *et al.* 2003, 2004; Pocock & Jennings 2008) may influence the distribution of bat populations by affecting roosting and foraging habitats.

The Republic of Moldova has a small and highly fragmented forest area, which covers 10.7 percent (338 051 ha) of the country area (Anonym 2006), and old forests are conserved in small patches. At present, the forest of Moldova is exposed to a high anthropogenic impact, which will affect roost availability, the structure of the forest, and insect production.

In the Republic of Moldova 21 species of bats are revealed and of these 16 species are protected by the State (Anonym 1999), and for six species the status is estimated as critical (Anonym 2001). However, the bats fauna of Moldova is poorly studied and habitat selection of bats has not been investigated at all.

All bat species in Moldova are associated with forest and/or agricultural areas, for foraging, roosting or commuting. In order to understand how to manage the landscape for conservation of bats it is important to understand which factors that are affecting the distribution pattern of bats in the landscape exist and which components that are important for habitat selection can be.

Study aim and research questions

The overall aim of the study was to examine distribution patterns, abundance, species richness and movements of bats in the forest landscape of "Lower Dniester" Ramsar Site during different seasons to upgrade conservational management from the viewpoint of bats conservation.

The following specific questions were addressed in this study:
(1) Are there any differences in distribution patterns, abundance and species richness of bats between different forest habitats and during different seasons?

(2) How do different forest habitat characteristics affect distribution patterns, abundance and species richness of bats and which of them are important for bat populations?

(3) Which habitats are important for bats during periods of low food availability (e.g. September-October) and how can these habitats be identified?

(4) Are there movements of bats between forest habitats during periods of low food availability?

Methods

Study area

Field research was conducted from 01 July 2008 until 31 October 2008 in the territory of "Lower Dniester" Ramsar Site, in the Republic of Moldova (46°34'N 29°49'E). I selected six research plots in the north-western part of the Ramsar Site where research was undertaken: Grădina Turcească (GT), Copanca-Leuntea (CL), Valea Moşului (VM), Valea Tetii (VT), Ciobruciu de Munte (CM) and Lunca Talmaz (LT) (Fig. 1).

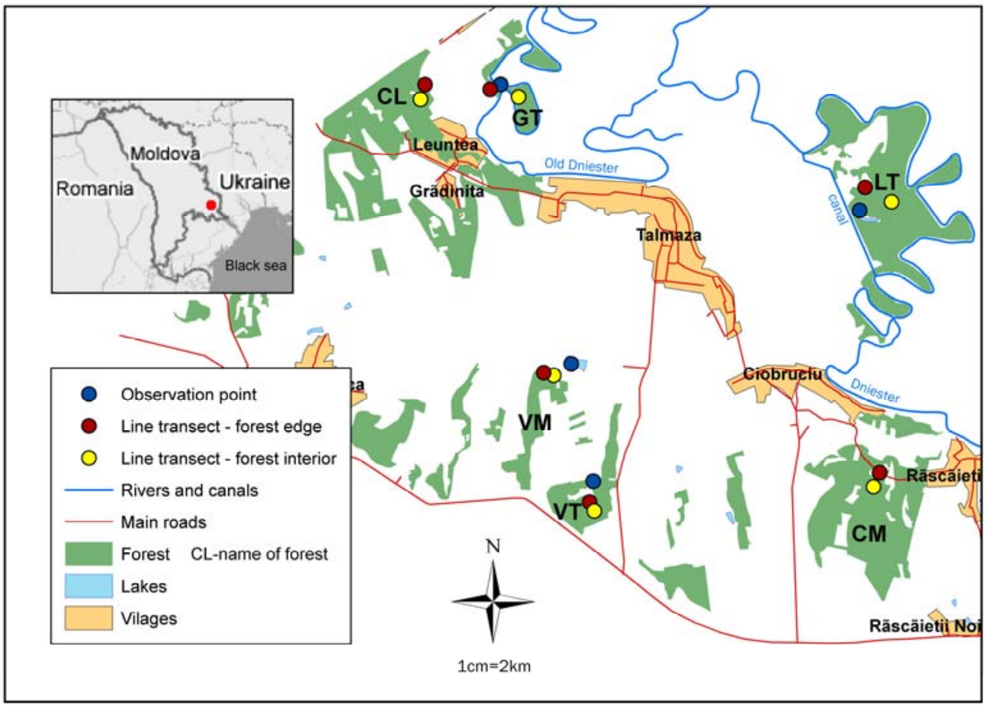

Fig. 1. Location of study area and sampling design.

The LT forest is located in a big bend of Dniester River in the downstream. The wetland area includes old and young forest stands with many glades, meadows, a lake (24 ha), permanent and intermittent water canals and swamps. The forest area is about 1 503 ha. The GT forest is located alongshore of the Old Dniester River and includes calm water body bordered by diverse riparian forests as well as glades, pastures and agriculture areas. The forest area is about 226 ha. The dominant tree species in both research plots are White poplar (*Populus alba*), White willow (*Salix alba*) and Common ash (*Fraxinus excelsior*) followed by Black poplar (*P. nigra*) and Pedunculate oak (*Quercus robur*). There are mature forest stands with the age over 100 years. Both LT and GT plots are characterized by flood-plain forest.

The CL, VM, VT and CM woodlands are upland habitats, which include forest stands with different age, ponds, small intermittent and permanent streams, meadows, glades, pastures, grasslands, and agriculture areas. The dominant tree species are Black locust (*Robinia pseudoacacia*), Downy oak (*Q. pubescens*) and Pedunculate oak (Andreev *et al.* 2004).

The zone of proposed researches is within the territory of potential "Lower Dniester" National Park and "Lower Dniester" Ecological Network. Therefore, undertaken investigations in this area contribute to development of scientific basis for appropriate planning of conservational activities.

Seasons and habitat categories

During the first period of data collection (July and August), insect abundance in general is high, and foraging conditions for bats are optimal (optimal time). During the second period (September and October), insect abundance is lower and therefore, the differences between habitats increase (critical time).

Various habitats provide bats with different living conditions. Therefore, some of them can play key role for existing bats on the territory, others can assign good conditions for bats only during a certain season and can be important as a temporal habitat. Thus, in this study I tried to identify two types of habitats within the research territory: optimal habitats (or key habitats) and suboptimal habitats.

Bats sampling – line-transects and observation points

The active monitoring survey based on walking transects, observation points and using of ultrasound detectors was used for estimation of distribution, species richness and abundance of bats in different habitats.

Six line-transects were established (one in each research plot). Each transect was 1 km long and divided into two parts: forest (0.5 km) and edge (0.5 km). The forest part of transect was located inside the forest patch and the edge part of transect was located between the forest edge and the agriculture area (Fig. 1). The survey started 30-50 minutes after sunset and the forest part of transect was conducted first, while the forest edge part was conducted later on, since bats usually start to fly earlier in close habitats. Each transect took 6-12 minutes to finish.

Observation points were established along the water in GT (along the Old Dniester River), VM (along the lake), VT (along the lake) and LT (along the

Adana lake) habitats (Fig. 1). Six observation points were established for each water body with the distance 100 m between points. The survey started immediately after finishing the survey along the line-transects and 10 minutes was spent at each point. In some cases when only observation points were being conducted, the survey started 90-120 minutes after sunset in order to make all observations approximately at the same time.

Each line-transect and observation point was visited three times during optimal (July-August) and critical (September-October) periods. Totally 36 surveys were made along the line-transects and 144 surveys were made at the observation points for the period July-October.

The line-transects were chosen depending on habitat conditions, because linear transects had to be more or less reachable by car, motorbike or foot. The observation points were selected based on quick access to them after finishing survey on transects and depending on natural conditions.

For identification of bats, the heterodyne ultrasound bat detector Pettersson D-200 (Pettersson Elektronik AB, Sweden) was used combined with visual observation by using headlamps (Ahlén 1990; Ahlén & Baagoøe 1999). The following characters were registered during identification of bats in flight: hunting environment, flight stile, rhythm of sound, frequency of sound (kHz) and quality of the pulse (dry clicks or smacks).

The time expansion detector (Tranquility II, United Kingdom) was used to check the presence and abundance of some species: Soprano pipistrelle *Pipistrellus pygmaeus*, Nathusius' pipistrelle *P. nathusii*, Common pipistrelle *P. pipistrellus*, Noctule bat *Nyctalus noctula* and Serotine bat *Eptesicus serotinus* (Ahlén 1990; Ahlén & Baagoøe 1999).

In the forest it was difficult to distinguish between *N. noctula* and Lieisler's bat *N. leisleri* due to similarity in echolocation calls. Therefore, these species were identified as "*N. noctula/leisleri*" in the forest. It was possible to identify *N. noctula* and *N. leisleri* in the open habitat. It is difficult to identify Whiskered bat *Myotis mystacinus* and Brandt's bat *M. brandtii* with ultrasound detectors and they were referred as "*M. mystacinus/brandtii*".

Bat calls were recorded with Transcend T. sonic 630 (Transcend Information Inc., USA) digital MP3 player. In total, the fieldwork resulted in about 25 hours of records. Bat calls were analyzed with BatSound Standard 3.31 software (Petterson Elektronik AB, Sweden). The following characters of bat sounds were used to identify bat species: intervals between pulses, pulse length and peak frequency (Ahlén 1981; Ahlén 1990; Ahlén & Baagoøe 1999). I used sequences of pulses in order to identify number of bat passes. One sequence of several pulses was considered as one individual (a pass). Only records with good quality were used for analysis. The separate or individual calls were not used.

Bats sampling – bat captures

Since, it is difficult to identify some bat species, for instance Grey long-eared bat *Plecotus austriacus*, *M. mystacinus/brandtii*, *N. noctula/leisleri* (in cluttered habitats), by using ultrasound detectors, I used capturing methods to check species richness of bats in forest. Bat capturing methods also helped to prove the results of bats identification with ultrasound detectors. Thus, in addition to ultrasound identification bats were captured with the help of mist nets and mobile trap (Kunz & Kurta 1988; Borissenko 1999). Mobile trap was found as a handy device for capturing of bats within this project. I used ultra thin nylon monofilament (0.08 mm) mist nets with mesh 14x14 mm, height 2.4 m, length 9 m, and 4 shelves (ECOTONE, Poland).

Usually, bat trapping started immediately after finishing monitoring survey. Sometimes it was possible to perform monitoring survey and bats capturing at the same time. Some expeditions were organized only for bats capturing. I used both methods in the same area since on some days, abundance of bats was low and mobile trap was more suitable then mist nets. Bats were captured for the period July-October. I trapped bats two times in each research plot.

Bats were captured under licence from Ministry of Ecology and Nature recourses of Moldova and were handled carefully in order to avoid any further disturbance or harm. Captured bats were released immediately after registration of all necessary data in the area where they had been caught.

Bats sampling – radio tracking

In order to investigate movements of bats between habitats radio tracking technique was used. *P. pygmaeus* was chosen for radio tracking because this species is common in the research area, which made it possible to catch this species in different habitats and during different seasons (Bondarenco & Andreev 2006).

Radio telemetry was performed from 21 August 2008 until 02 November 2008. For practical reasons the research was mainly concentrated on studying movements between the GT and CL forests during the critical period (September-October). These habitats were selected because they are located close to each other (about 2 km) and represent two types of habitat: flood-plain forest near water (GT) and upland forest far away from water (CL). Bats were caught individually by mobile trap.

Five individuals were marked with radio transmitters glued on the fur in the middle of the back between scapulae. It is suggested that the weight of added transmitter should be <5 percent of the weight of flying animals (Aldridge & Brigham 1988). However, researchers successfully added and tracked *P. pygmaeus* with weight of transmitters between 4.9-7 percent of body mass (Davidson-Watts & Jones 2006; Nicholls & Racey 2006 a, b). I used the lightest available transmitters model LB-2N, with weight about 0.35g and nominal life 12 days (Holohil Systems Ltd., Canada). The hair between the scapulae was trimmed and tags were added close to bat's skin using surgical glue (Ellsworth Adhesives AB, Sweden) enabling the transmitter to stay adhered to the bat's back for about 2-3 weeks. The weight of tags with adhesive was about 7 percent of body mass according to experimental data of some authors who used the same method for the same species (Nicholls & Racey 2006 a, b).

All bats marked with radio transmitters also were fitted with aluminium alloy rings with reflective tapes of different colour combinations on the right forearm with internal width 2.9 mm, and metal height and gauge 5.5x0.38 mm (Porzana Ltd., United Kingdom) (Barclay & Bell 1988). The marking of bats with reflective tapes made it possible to observe bats marked at different time in flight with halogen torch.

Hand receiver model RX-98H (TPV Positioning AB, Sweden) was used to locate bats at the research area. The presence of bats at the area where they were marked was checked every first, second or third day after marking depending on the different circumstances (weather, nature conditions, bats behaviour, or necessity to be in another part of the project area). If the marked bat was not found the whole area within 2 km from the last roost or trapping site was investigated for two weeks. The range of the transmitters is approximately 0.5-1 km depending on the terrain.

All necessary permissions for the work with radio transmitters on the protected area were obtained from Ministry of Ecology and Nature recourses of Moldova.

Sampling data and habitat/landscape variables

The following data were recorded during the monitoring survey: bat species, number of bat passes (number of individuals), and meteorological data such as temperature, wind speed (calm, light wind, moderate wind, strong wind, very strong wind), extend of cloud cover, occurrence of mist and rain.

In order to understand how different habitat components affect species composition and abundance of bats a number of habitat/landscape variables were recorded: age of forest stands, tree density and standing dead tree density, the size of forest patches, distance to the nearest water body, area of water cover within each forest patch and distance from the forest patch to the nearest village (Table 1). These variables were selected because of their potential influence on insect abundance, roost availability, manoeuvrability and protection against predators (Krusic *et al.* 1996; Crampton & Barclay 1998; Law *et al.* 1999; Ciechanowski 2002; Erickson & West 2003; Patriquin & Barclay 2003; Gorresen & Willig 2004; Kusch *et al.* 2004; Brooks & Ford 2005; Loeb & O'Keefe 2006; Rogers *et al.* 2006; Yates & Muzika 2006; Biscardi *et al.* 2007; Perry *et al.* 2007).

Table 1. Description of the seven tested environmental variables measured in all forest habitats.

Place	Average forest age	Tree density (16 samples/ № of trees)	Standing dead tree density (16 samples/ № of trees)	Size of forest patch (ha)	Distance to the nearest water body (km)	Area of water cover (ha)	Distance to the nearest village (km)
Code	(ForAge)	(TreeDens)	(DeadTree)	(ForSize)	(DistWat)	(WatArea)	(DistVill)
GT	60.71	21.81	1.00	226	0.0	70	1.5
CL	34.68	31.43	0.56	2 226	2.6	0.0	0.8
VM	21.46	25.62	0.06	216	0.9	29	3.8
VT	28.22	15.81	0.06	282	0.0	0.5	0.5
CM	40.34	12.62	0.37	954	3.0	0.0	1.7
LT	44.60	12.50	0.93	1 503	0.0	327	3
p-forest model	ns	ns	<0.002	ns	collinear	<0.006 collinear	ns collinear
p-water model	<0.0020	ns	<0.002	collinear	collinear	collinear	<0.014

P values are from ordination redundancy analysis (RDA). Variables were tested together using the automatic forward selection in CANOCO. Collinear–variable was collinear with the other environmental variables in the model.

Information about forest age was derived from the analysis of the vegetation maps obtained from the State Forest Agency "MOLDSILVA". Information about tree density and standing dead tree density was collected by the direct survey along line-transects. Each line-transect was divided into 20 m sections. At each section a plot (a circle with radius 5.6 m=100 m²) was set up in which the number of living and dead trees (trunk's diameter >10 cm) was calculated. Other landscape data were analysed by using maps of project area gained from the Institute of Ecology and Geography of Moldova and vegetation map obtained from the State Forest Agency "MOLDSILVA". The maps were analysed with ArcGIS 9.2 software (Environmental Systems Research Institute, Redlands, California, USA).

Data analysis

Constrained linear ordination redundancy analysis (RDA, CANOCO 4.5; ter Braak & Smilauer 1998) was used to estimate the effect of different environmental factors on bats community (Jongman *et al.* 1995; Leps & Smilauer 2003).

Since it is difficult to choose the accurate ordination method to analyse a particular data set it is good to estimate heterogeneity in the species data first. It is possible to calculate it using one of the detrended ordination methods in CANOCO software (Leps & Smilauer 2003). Detrended canonical correspondence analysis (DCCA) was used to calculate heterogeneity in the species data. DCCA calculate the length of the community composition gradients, which measures the beta diversity in community composition (Leps & Smilauer 2003). The authors suggest using linear models if the larger value of the gradient is shorter than 3.0. The length of the gradient calculated for the forest habitat data set is 0.838 and for the water habitat data set is 2.518 that verified that linear ordination method could be used (i.e. RDA) (Jongman *et al.* 1995; ter Braak & Smilauer 1998; Leps & Smilauer 2003). To analyse data with RDA method, species and measured environmental variables data sets from each forest plot were created. For each environmental variable, Monte Carlo Permutation Test was carried out using the automatic forward selection option in the CANOCO, in order to reveal variables that had statistically significant influence on bats community. Only habitat variables significant at the $p<0.05$ were included to the final model. Rare species of bats (Pond bat *M. dasycneme* and Kuhl's pipistrelle *P. kuhlii*) were excluded from the model.

Standardization by error variance was selected while performing RDA test. In this case, CANOCO calculate for each species an error of how many variations in bat species were not explained by the environmental variables. Each species then is weighted by the inverse value of calculated error. This kind of standardisation is the best choice when using RDA analysis with environmental variables available (Leps & Smilauer 2003).

Finally, RDA ordination diagrams with bat species and environmental variables were drawn for the forest and water habitats to reveal the relationship between the species and environmental variables. The diagrams were created by using CanoDraw for Windows 4.1 software. The ordination diagrams represent relative effects of environmental variables on bats community and linear correlation between species and environmental variables (Leps & Smilauer 2003).

Nonparametric Wilcoxon Signed Rank Test was used to compare abundance of each bat species in each habitat between summer and autumn (SPSS 16.0). Effect size was calculated for each analysed group of species to reveal the strength of the relationship between two variables using Cohen (1988) criteria: 0.1=small effect, 0.3=medium effect, 0.5=large effect.

Spearman's correlation was used to reveal relationships between number of bat passes and number of species in each research plot (SPSS 16.0). Coefficient of determination was estimated for each correlative group to see how much variance two variables share (Pallant 2007).

Results

Forest bat assemblages

Altogether 10 402 passes of bats were recorded, 991 of them were registered within the forest habitat and 9 411 passes along or above the water bodies. In total, nine species of bats were identified by ultrasound detectors: *P. pygmaeus*, *P. pipistrellus*, *P. nathusii*, *P. kuhlii*, *N. noctula*, *N. leisleri*, *M. dasycneme*, Daubenton's bat *M. daubentonii*, *E. serotinus* and one group of species *M. mystacinus/brandtii*. *P. pygmaeus*, *P. nathusii* and *N. noctula* were registered in all research plots. *M. dasycneme* and *P. kuhlii* were registered only in LT forest. *M. daubentonii* was a common species in forest habitats where water was present (Table 2).

Table 2. Bat species recorded in six forest patches by ultrasound detectors (D) and captures (C) during summer and autumn periods.

Species	GT		CL		CM		VT		VM		LT		Code
	D	C	D	C	D	C	D	C	D	C	D	C	
Pipistrellus pygmaeus (Leach 1825)	+	+	+	+	+	+	+	+	+	+	+	+	Ppyg
P. pipistrellus (Schreber 1774)	+	+	+		+				+		+	+	Ppip
P. nathusii (Keyserling and Blasius 1839)	+	+	+		+	+	+		+		+	+	Pnat
P. kuhlii (Kuhl 1817)											+	+	Pkuh
Nyctalus noctula (Schreber 1774)	+	+	+		+	+	+	+	+	+	+	+	Nnoc
N. leisleri (Kuhl 1817)	+	+				+		+	+	+	+	+	Nlei
N. noctula/ leisleri	+				+		+		+		+		Nnoc/lei
Myotis dasycneme (Boie 1825)											+	+	Mdas
M. mystacinus (Kuhl 1817)		+		+								+	Mmys
M. mystacinus/ brandtii	+		+						+		+		Mmys/br
M. daubentonii (Kuhl 1817)	+	+				+	+		+		+	+	Mdau
Eptesicus serotinus (Schreber 1774)	+		+				+		+				Eser
Plecotus austriacus (Fischer 1829)		+		+		+		+		+		+	Plaus

Only four species registered in the forest habitat and five species found near the water habitat were recorded in more than five percent of the samples. The most common and frequent species were *P. pygmaeus* (frequency of occurrence=37.13 percent) and *N. noctula/leisleri* (34.31 percent) registered in the forest and *P. pygmaeus* (45.58 percent) and *M. daubentonii* (23 percent) registered near the water bodies. *M. mystacinus/brandtii* (4.44 percent) and *E. serotinus* (3.13 percent) were rare species in the forest and *P. pipistrellus* (1.35 percent), *N. leisleri* (0.5 percent), *M. mystacinus/brandtii* (0.24 percent), *P. kuhlii* (0.07 percent) and *M. dasycneme* (0.06 percent) were very rare species registered along the ponds (Figs. 2 & 3).

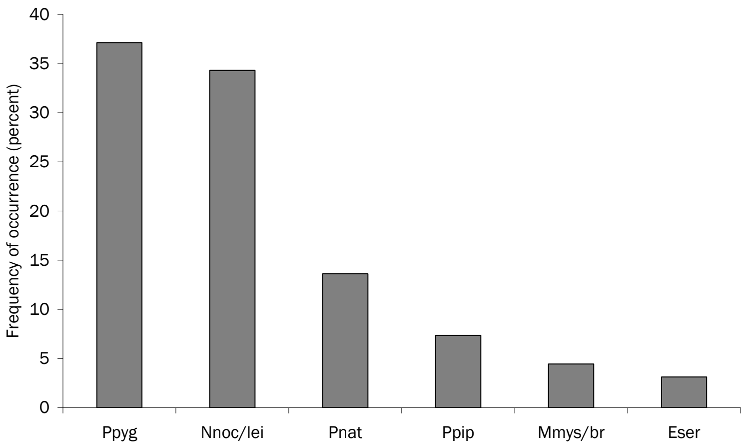

Fig. 2. Frequency of occurrence of bats registered in the forest habitat (total n=991 passes). Species abbreviations see Table 2.

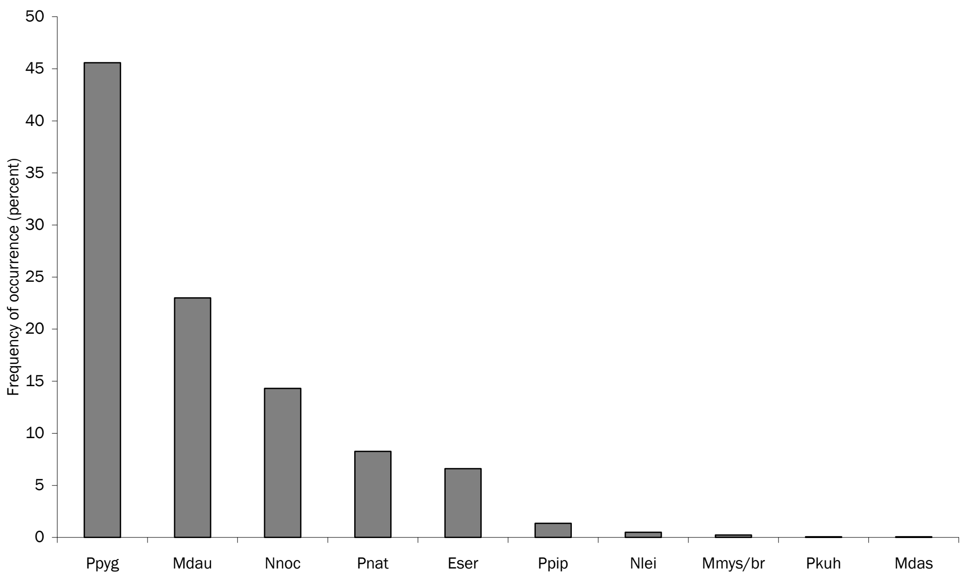

Fig. 3. Frequency of occurrence of bats registered in the water habitat (total n=9 411 passes). Species abbreviations see Table 2.

In total, 121 individuals of ten species of bats were captured: *P. pygmaeus* (40 individuals), *P. pipistrellus* (3), *P. nathusii* (10), *P. kuhlii* (2), *N. noctula* (15), *N. leisleri* (26), *M. dasycneme* (2), *M. mystacinus* (4), *M. daubentonii* (12) and *P. austriacus* (7). *P. pygmaeus* and *P. austriacus* were found in all habitats and *M. dasycneme* and *P. kuhlii* were captured only in the LT forest (Table 2).

There was a strong positive correlation between number of passes and number of species registered in the forest ($r=0.709$, $n=36$, $p< 0.0015$), and water habitats ($r=0.817$, $n=72$, $p< 0.0015$). Coefficient of determination was 50.26 percent for the forest habitat and 66.74 percent for the water environment, which means that the number of recorded passes may explain nearly 50.26 percent and 66.74 percent of the variance in recorded data on the species richness of bats.

Habitat preferences

Multivariate analysis of data from different forest patches showed the effect of the different environmental variables on the bat community. The standing dead tree density and area of water cover in the forest model, as well as forest age, standing dead tree density and distance to the nearest village in the water model had significant influence on bats community in RDA analysis (Monte-Carlo permutation test, $p<0.05$; Table 1). Both forest and water models were statistically significant (Monte-Carlo permutation test, $p<0.001$). The amount of variability in the bat counts data explained by the tested variables in the forest model is 23 percent and 35.1 percent in the water model (Table 3).

Table 3. Relationships between bats community and recorded environmental variables derived from the redundancy analysis. It corresponds to Figs. 4 & 5.

Summary RDA parameters	Canonical axes		
	Axis 1	Axis 2	Axis 3
		Forest model	
Species-environment correlations	0.677	0.317	-
Eigenvalues	0.221	0.009	-
Total canonical eigenvalues (Percent variance explained)		0.23 (23)	
		Water model	
Species-environment correlations	0.845	0.694	0.331
Eigenvalues	0.273	0.068	0.010
Total canonical eigenvalues (Percent variance explained)		0.351 (35.1)	

The explanatory power of the environmental variables is given in Table 4. The variables ordered from the highest to the minimum explanatory power show the ability to explain differences in the species data. The variables with highest explanatory power were standing dead tree density (18 percent) and area of water cover (18 percent) in the forest model and standing dead tree density (27 percent) and average forest age (25 percent) in the water model (Table 4).

Table 4. The marginal effects (explanatory power) of the environmental variables analysed in RDA analysis.

Forest model		Water model	
Variable	Lambda1 (percent)	Variable	Lambda1 (percent)
Standing dead tree density	**0.18 (18)**	Standing dead tree density	**0.27 (27)**
Area of water cover	**0.18 (18)**	Average forest age	**0.25 (25)**
Average forest age	0.13 (13)	Area of water cover	0.13 (13)
Distance to the nearest village	0.09 (9)	Distance to the nearest village	**0.12 (12)**
Distance to the nearest water body	0.04 (4)	Size of forest patch	0.09 (9)
Tree density	0.03 (3)	Distance to the nearest water body	0.09 (9)
Size of forest patch	0.01 (1)	Tree density	0.03 (3)

$P<0.05$ are bold marked.

There were canonical (species-environment) correlations registered between species axes and environmental axes (Table 3). Based on the analysis of the ordination diagram it is possible to see that abundance of *P. pygmaeus*, *P. pipistrellus*, *P nathusii*, *N. noctula/leisleri* and *M. mystacinus/brandtii* were correlated with dead tree density and area of water cover in the forest model. Abundance of *E. serotinus* was negatively correlated with all environmental variables and other bat species (Fig. 4).

Abundance of *M. mystacinus/brandtii*, *N. noctula*, *P. pipistrellus*, *P. pygmaeus, P. nathusii, M. daubentonii* and *N. leisleri* were correlated with the amount of standing dead tree density and forest age in the water model. Besides, abundance of *E. serotinus* had positive correlation with the distance to the nearest village but negatively correlated with the other bat species and environmental variables (Fig. 5).

Three variables "distance to the nearest water body", "area of water cover" and "distance to the nearest village" in the forest model and three variables "size of forest patches", "distance to the nearest water body" and "area of water cover" in the water model were collinear with the other variables when performing RDA test (Table 1). Collinear environmental variables occurred possibly because of small size of species and/or environmental data sets (ter Braak & Smilauer 1998).

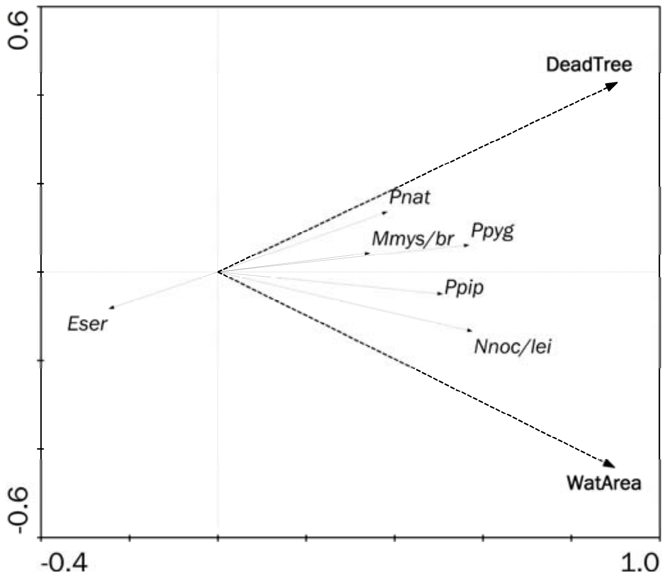

Fig. 4. Redundancy analysis ordination diagram with bats species (solid arrows) and environmental variables (dashed arrows) represents species-environmental relationships of bats registered in the forest habitat. The first axis ($p < 0.002$), and all four axes in the RDA ($p < 0.002$) were significant with the abundance of the analysed species. The species-environment correlations, canonical eigenvalues and explanatory power of variables are shown in Tables 3 & 4. For species and environmental abbreviations: see Tables 1 & 2.

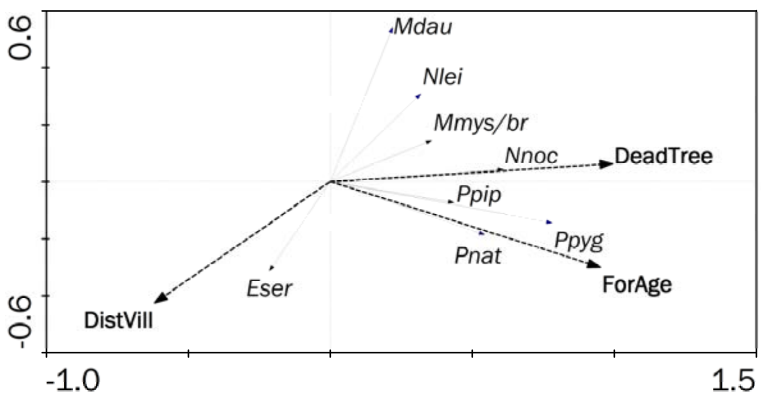

Fig. 5. Redundancy analysis ordination diagram with bats species (solid arrows) and environmental variables (dashed arrows) represents species-environmental relationships of bats registered near the water ecotone. The first axis ($p < 0.002$), and all four axes in the RDA ($p < 0.002$) were significant with the abundance of the analysed species. The species-environment correlations, canonical eigenvalues and explanatory power of variables see in Tables 3 & 4. Species and environmental abbreviations see in Tables 1 & 2.

Seasonal changes

The highest abundance of bats was registered in LT and GT forests. In general, the bat abundance decreased in the period September-October in the CM ($p<0.015$), CL ($p<0.015$), VM ($p<0.168$) and VT ($p<0.001$) sites for bats recorded in forest habitats and GT ($p<0.010$), LT ($p<0.001$), VT ($p<0.001$) and VM ($p<0.001$) sites for bats counted near the water bodies (Figs. 6 & 7). On the other hand there were no differences in abundance of bats registered in the forest habitat of LT ($p<0.443$) and GT ($p<0.957$) sites between the two seasons (Fig. 6).

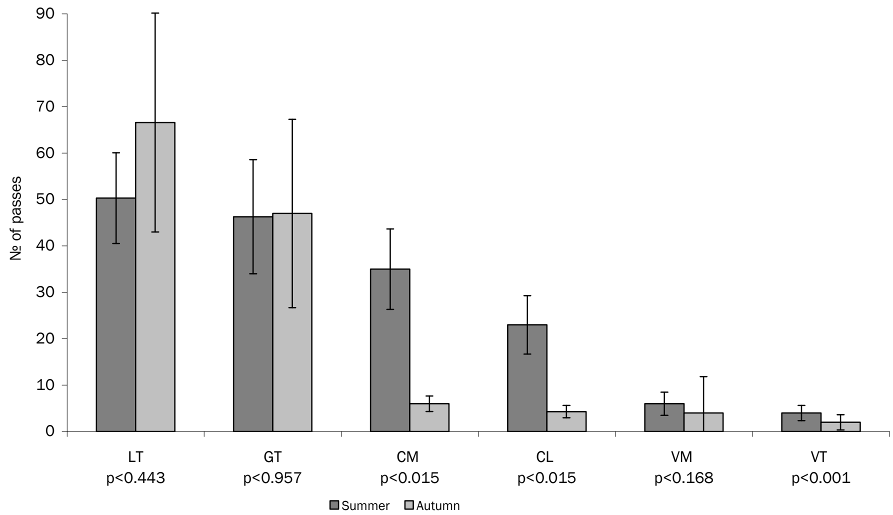

Fig. 6. Mean number of bat passes, standard deviation and p value showing differences in general abundance of bats between summer and autumn recorded for sample sites in the forest (based on line-transects).

In the LT and GT woodlands the abundance of *P. nathusii* ($p<0.023$) recorded near the water ecotone in GT site and *N. noctula/leisleri* ($p<0.043$) registered in the forest habitat of the LT site, increased (Tables 5 & 6).

The reason for the big differences between the numbers of passes recorded in the forest along line-transects and near the water ecotone at observation points are due to the different methods used for data collecting.

A Wilcoxon Signed Rank Test revealed statistically significant changes in abundance of some bat species between summer and autumn (Tables 5 & 6). Such species as *N. noctula* (in the VM and LT forests), *N. leisleri* (LT), and *E. serotinus* (GT, VM and VT) registered near the water ecotone and *P. pygmaeus*

(VM and CM) registered in the forest showed considerable changes in abundance between summer and autumn with large effect size.

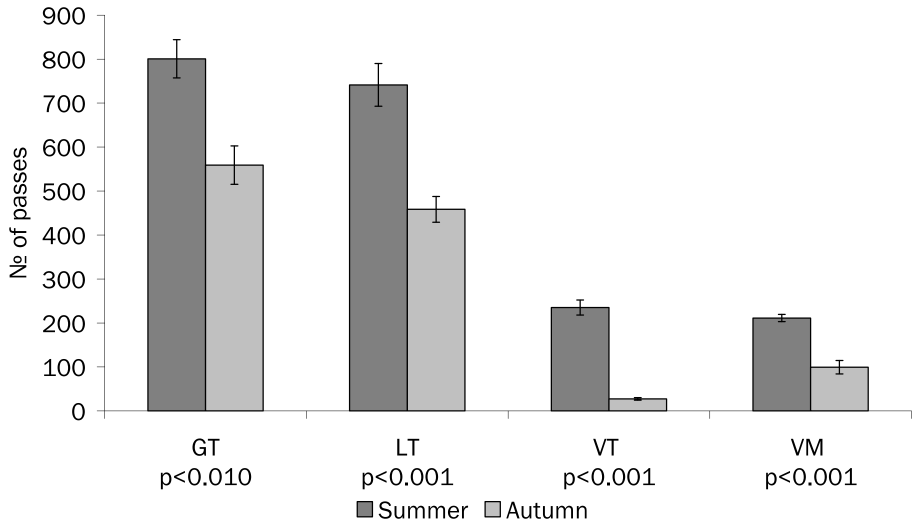

Fig. 7. Mean number of bat passes, standard deviation and p value showing differences in general abundance of bats between summer and autumn recorded for sample sites near the water habitat (based on observation points).

Table 5. Comparison of bat abundance between summer and autumn registered along the water bodies by Wilcoxon Signed Rank Test.

Plot	Indices	Species									
		Mdau	Mmys/ br	Nnoc	Nlei	Ppyg	Ppip	Pnat	Eser	Pkuh	Mdas
	z	-0.157	-0.577	-3.196	-1.265	-2.374	-0.284	-2.273	-3.73	-	-
GT	p	0.875↑	0.564	**0.001**	0.206	**0.018**	0.777↑	**0.023**↑	**0.001**	-	-
	r	-	-	0.533	-	0.396	-	0.379	0.622	-	-
	z	-2.507	-	-3.515	-	-2.575	-	-1.377	-3.58	-	-
VM	p	**0.012**	-	**0.001**	-	**0.01**	-	0.169↑	**0.001**	-	-
	r	0.418	-	0.586	-	0.429	-	-	0.597	-	-
	z	-2.641	-	-2.731	-	-2.265	-	-1.641	-3.724	-	-
VT	p	**0.008**	-	**0.006**	-	**0.024**	-	0.101	**0.001**	-	-
	r	0.440	-	0.455	-	0.378	-	-	0.621	-	-
	z	-2.937	-0.577	-3.681	-3.041	-1.198	-2.282	-1.765	-	-2.333	-2.449
LT	p	**0.003**	0.564	**0.001**	**0.002**	0.231	**0.022**	0.078↑	-	**0.02**	**0.014**
	r	0.490	-	0.614	0.507	-	0.380	-	-	0.389	0.408

z-value of Wilcoxon signed rank test; p-significance level; r-effect size. p<0.05 are bold marked. Blue arrows represent bat abundance that was increased in autumn. Species abbreviations see in Table 2.

Table 6. Comparison of bat abundance between summer and autumn registered in the forest habitat by Wilcoxon Signed Rank Test.

Plot	Indices	Species					
		Mmys/ br	Ppyg	Ppip	Pnat	Eser	Nnoc/ lei
	z	-1.3	-1.483	-1.604	-2.032	-1.342	-0.422
GT	p	0.194	0.138↑	0.109	**0.042**	0.18	0.673↑
	r	-	-	-	0.479	-	-
	z	-1.414	-2.032	-1.841	-2.06	-1.604	-1.633
CL	p	0.157	**0.042**	0.066	**0.039**	0.109	0.102
	r	-	0.479	-	0.486	-	-
	z	-1.633	-2.214	-2.06	-1.857	-0.272	-0.632
VM	p	0.102	**0.027**	**0.039**	0.063	0.785	0.527↑
	r	-	0.522	0.486	-	-	-
	z	-	-1.604	-	-0.828	-1.633	-2.264
VT	p	-	0.109	-	0.408	0.102	**0.024**
	r	-	-	-	-	-	0.479
	z	-1.604	-2.207	-1.342	-2.014	-	-1.753
CM	p	0.109	**0.027**	0.18	**0.044**	-	0.08
	r	-	0.521	-	0.475	-	-
	z	-0.378	-0.406	-2.06	-0.365	-	-2.023
LT	p	0.705↑	0.684	**0.039**	0.715	-	**0.043↑**
	r	-	-	0.486	-	-	0.479

z-value of Wilcoxon signed rank test; p-significance level; r-effect size. p<0.05 are bold marked. Blue arrows represent bat abundance that was increased in autumn. Species abbreviations see in Table 2.

M. daubentonii (VM, VT, and LT), *N. noctula* (VT), *P. pygmaeus* (GT, VM and VT), *P. pipistrellus* (LT), *P. nathusii* (GT), *P. kuhlii* (LT), *M. dasycneme* (LT) recorded near the water and *P. pygmaeus* (CL), *P. pipistrellus* (VM and LT), *P. nathusii* (GT, CL and CM) and *N. noctula/leisleri* (VT and LT) recorded in the forest showed small alterations in abundance with medium effect of size.

Movements

Five *P. pygmaeus* were radio tracked from August to November (Table 7; Fig. 8). The first bat was marked in August in the GT forest around two hours after sunset. The bat was hunting within the forest. In two days later, I tried to find the bat within the GT forest, but the bat disappeared from the area. One day later, I found the bat hunting near the catching place. Next days and nights, the bat was not registered at the research area, probably due to the bat moved to other area or malfunction of transmitter. However, this result also might indicate that the marked bat sometimes use the GT forest as foraging habitat (Table 7).

Table 7. The tracking details of the studied bats in the CL and GT forests.

Species	Bat ID (ring number)	Date of marking	Place	Sex	Days tracked	Distance* (m)	Comments
P. pygmaeus	MD000007	22 August 2008	GT	♀	4	?	Transmitter signal loss
P. pygmaeus	MD000025	04 September 2008	CL	♂	19	0	Did not change a roost
P. pygmaeus	MD000026	14 September 2008	CL	♂	17	400	Moved within the same habitat
P. pygmaeus	MD000028	27 September 2008	CL	♂	8	1 500-2 100	Moved to GT forest
P. pygmaeus	MD000029	21 October 2008	CL	♂	4	?	Transmitter signal loss

*Distance is the straight-line distance where the bat was recorded from the last roost.

Fig. 8. *Pipistrellus pygmaeus* marked with radio transmitter and ring with reflective tape in the CL forest.

Next two bats, which were marked in the CL forest, did not move from the habitat during all time of radio tracking. This data might indicate that during period of tracking (04 September-01 October) the conditions in the CL forest were good enough for living of bats.

Later in October, one bat marked in the CL area was observed in the GT area and on the next day, the bat was again found at the roost in the CL forest.

The last marked bat was roosting in the CL forest during four days then the signal was lost, probably because of the bat movement.

Discussion

Forest bat assemblages

Altogether 11 species of bats were found (Table 2). Of these nine were identified by ultrasound detectors and two species, *P. austriacus* and *M. mystacinus*, were identified by trapping. So far, *M. brandtii* has not been found in Moldova, and therefore it is more likely that species identified as *M. mystacinus/brandtii* by ultrasound detector is *M. mystacinus*. However, due to lack of studies, *Myotis brandtii* can not be excluded, therefore observations by ultrasound detectors are identified as *M. mystacinus/brandtii*.

P. pygmaeus was the most frequent species found in both forest and riparian habitats, and it was common at all research plots. The group of species *N. noctula/leisleri* and *P. nathusii* were common in the forest habitats. *M. daubentonii* was widely distributed in all research plots where ponds were present. However, frequency of occurrence of some species like *P. pipistrellus*, *M. mystacinus/brandtii* and *E. serotinus* registered in woodland sites and *P. nathusii*, *E. serotinus*, *P. pipistrellus*, *N. leisleri*, *M. mystacinus/brandti*, *P. kuhlii* and *M. dasycneme* counted in riparian habitats was low (Figs. 2 & 3).

In general, revealed patterns complement findings from other studies. For instance, *P. pygmaeus* is known to be associated with riparian areas, therefore this species is quite common in the area with high area of riparian woodlands (Vaughan *et al.*, 1997; Davidson-Watts & Jones 2006; Nicholls & Racey 2006a). *N. noctula*, *N. leisleri* and *P. nathusii* are mainly associated with woodlands and prefer to roost in tree cavities and cracks (Ahlén 1990; Ruczynski & Bogdanowicz 2005). *M. daubentonii* is often found foraging above the water surface (Ahlén 1990).

P. austriacus was caught in all research areas. It seems to be quite common at the research area but *Plecotus* species were not registered with acoustic and visual observations. These species usually hunt in the tree canopy and often use weak echolocation signals, which can be heard only within about 5 m that makes it difficult to find these bat species in the forest (Ahlén 1990).

Total species richness was relatively uniform across research sites. Two species *M. dasycneme* and *P. kuhlii* were found only at the LT forest. However, abundance of bats varied a lot between the study plots. The highest abundance of bats was registered in GT and LT forests during both summer and autumn periods (Figs. 6 & 7).

Based on the number of recorded bat passes, individuals and species of bats by using both methods (captures and bat detectors) it was found that bats mainly were aggregated at the GT and LT forests (Figs. 6 & 7). The analysis of the GT and LT habitats showed the high availability of standing dead trees (GT index=1.0, LT-0.93), presence of old-growth forest stands, presence of diverse pounds like rivers, lakes and swamps (Table 1). Thus, it is possible to assume that more diverse habitat conditions might reflect higher species richness and abundance of bats. Based on the high abundance of bats both during summer and autumn seasons, and high diversity of habitat composition revealed in the GT and LT forests these habitats can be identified as key habitats for bat in the research area, and all other studied habitats (CL, VM, VT and CM forests) can be identified as suboptimal habitats.

However, relatively uniform species richness found among research sites suggest that even small and monotones structure of habitat occasionally can support high diversity of bats (Shafer, 1995) but can not provide bats with all necessary resources during the whole activity period and thus, can not maintain high abundance of bat populations.

In general, surveys by ultrasound detectors have some limitations, which must be adjusted for when interpreting the results. Neither line-transects nor point counts give the true number of bat individuals, but give an index. In both methods, some individuals will be counted several times, and especially for point counts, this is obvious. However, if systematic methods are used it is possible to compare different sites. Observation point method was selected to study bats activity along the water coast since river and lake coasts were rushy and overgrown with different vegetation, that made it impossible to perform observations along the lake or river by using a linear transect. Another problem is that some species, especially species using weak sounds such as *P. austriacus* might be underestimated.

Habitat preferences

Most important environmental factor affecting bat abundance was standing dead tree density which had the highest explanatory power (27 percent) in both water and forest models (Figs. 4 & 5; Table 4). Abundance of all species, except *E. serotinus*, used in the redundancy analysis was positively correlated with availability of dead trees. That means that the more standing dead trees there are in a forest the more abundant is the bat fauna.

Another important factor affecting bat assemblages was forest age, which explains 25 percent of variability in the species data recorded in the water model. According to Fig. 5, the variable "average forest age" and "standing dead tree density" are positively correlated with each other. Indeed, the more mature is a forest the more dead woods can be found there.

The variable "area of water cover" is positively correlated with most bat species in the forest model, as well as positive correlated with the amount of standing dead trees (Fig. 4). This variable explains 18 percent in the variability of the counted bats that show the importance of this variable for bat populations. The correlation between "area of water cover" and "standing dead tree density" can be explained by old trees and dead woods, which were remained as water protection forest along water bodies.

This research showed the influence of occurrence of settlements on the abundance of *E. serotinus*. In this study, only the abundance of *E. serotinus* was positively correlated with the distance to the nearest village. Besides, the abundance of this species was negatively correlated with the other environmental factors and abundance of other species. *E. serotinus* is known to be synanthropic species prefers to roost, at least in Moldova, mostly in urban constrictions and forage in open agriculture landscape (Ahlén 1990; Andreev & Bondarenco 2006). Therefore, this species has no strong relationships with forest habitats and forest dwelling bat species.

All explanatory variables tested in this study might be important for bats. Availability of dead trees is important for bats since they provide suitable large cavities and areas of loose bark that provide roosting habitats and therefore support high abundance and species richness of bats (Sedgeley & O'Donnell 1999; Kunz & Lumsden 2003; Ruczynski & Bogdanowicz 2005; Yates & Muzika 2006). Presence of freshwater with a smooth surface are preferred foraging patches of several bat species (e.g. *M. daubentonii, M. dasycneme* and *P. pygmaeus*) and strongly influence the distribution of bats because of high prey availability (Kusch *et al.* 2004; Brooks & Ford 2005; Biscardi *et al.* 2007). Forest age is another factor influencing bat abundance. It has been shown by many authors that many bat species prefer old deciduous forest with high density of large-diameter snags because of food and roost availability. However, there are still some gaps in our understanding of the relationships between activity patterns of bats and age of forest. In some studies, it has been shown that young forest also could provide bats with necessary resources (Krusic *et al.* 1996; Crampton & Barclay 1998; Erickson & West 2003; Loeb & O'Keefe 2006; Perry *et al.* 2007).

The positive correlation of most bat species with amount of dead trees, forest age and area of water cover shows that the woodlands characterised by high availability of dead wood, old forest patches and water habitats preferred by bats. This supports results of the analysis of the forest bat assemblages. The highest abundance and species richness of bats was found in two study sites the LT and GT forests that are characterised by presence of mature forest stands, high density of dead trees and diverse riparian habitats.

However, since some collinear variables were detected during performing of the RDA analysis more estimates of bat populations and landscape are needed. For example, research should cover three seasons: spring, summer and autumn, other environmental factors like forest understory density, availability of linear landscape elements should also be tested.

Seasonal changes

The results of this study showed that species richness and abundance of bats decreased in the period September-October compared to the period of July-August at all study sites. Some species like *M. dasycneme* and *P. kuhlii* were not registered any more on the research territory. However, *P. pygmaeus* and *N. noctula* were found in all habitats during the second survey (Figs. 6 & 7; Tables 5 & 6).

There was an indication of general increased abundance of bats during the critical season in the GT and LT forests, but it was not significant. However, the abundance of *P. nathusii* registered in the riparian habitats of the GT site and *N. noctula/leisleri* counted in the forest habitat of the LT site increased significantly (Tables 5 & 6). This result might suggest that some individuals of *P. nathusii* and *N. noctula/leisleri* moved to the GT and LT forests from other areas due to seasonal changes in habitat conditions.

One possible factor, which varies during different seasons, is prey abundance. That prey abundance is influencing distribution pattern and activity of bats has been demonstrated in several studies (de Jong & Ahlén 1991; Rautenbach *et al.* 1996; Kalcounis *et al.* 1999; Carter *et al.* 2004; Kusch *et al.* 2004; Fukui *et al.* 2006). Thus, changes in prey availability may be the main reason of movements of *P. nathusii* and *N. noctula/leisleri* from some adjacent suboptimal habitats, which probably could not support high prey abundance at the critical period of time, to optimal habitats (GT and LT forests), which have more diverse habitat structure and could support high insect abundance during the critical season.

In general, the decrease in species richness and abundance can be explained by local migration of bats from summer roosts to hibernation places that is a common pattern for the most Moldovan bats in autumn (Andreev & Bondarenco 2006).

The decrease in the bat activity also can be due to the worst weather conditions and decrease of the night temperature during the period of September-October. The air temperature is known to affect the activity of flying insect prey, therefore changes in weather, decrease of air temperature can result decrease of activity of prey insects and bats activity respectively (Hayes 1997; Meyer *et al.* 2004).

Thereby, the results of this study showed that during critical period of time some bats can move from suboptimal habitats to key habitats (GT and LT forests) probably due to decreasing in insect abundance. This also supports the finding that the highest abundance of bats was registered in the GT and LT forest. It suggests that these two habitats are most important for bats in the study area and that these habitats can support bats with necessary conditions like food and roosts not only during the optimal period but also during the critical season.

Movements

The main purpose of using radio tracking was to register possible movement of bats between different habitats during the critical season (September-October).

The data show that there are movements of bats between different areas. In particular, I recorded that one bat which was roosting in the CL habitat was foraging in the GT forest. Probably, the GT area was better for foraging (occurrence of a river, older forest and more diverse habitat), while the CL area was good enough for roosting. Because of the higher bat abundance in the GT area, it might be preferable to roost somewhere else to avoid competition (Nicholls & Racey 2006 a, b).

The changes in abundance of bats and the results from radio tracking indicates that bats are moving between different areas and that only some habitats (key habitats) are used for foraging later on when insect abundance decreases. However, the data from radio tracking are very limited and it is not possible to conclude that this is a general pattern.

Conclusions

Bats are highly mobile animals, and therefore a landscape approach must to be used for management. During the nights, bats are able to visit different habitats. Within a single season bats can change their roosts several times in different habitats. Many species of bats migrate from their summer roosts to hibernation sites each year (Lacki *et al.* 2007). In general, mobile organisms that require combinations of different habitats are more sensitive to fragmentation and degradation of habitat, since several suitable habitats must be available within reasonable commuting distance (Swihart *et al.* 2003), and some species of bats have been shown to be sensitive to habitat fragmentation (Law *et al.* 1999; Bernard & Fenton 2007; Meyer *et al.* 2008).

The results indicate the importance of areas with old forest located near lakes and streams and with high density of dead trees for bat populations. These areas are important, not only for bats roosting here during summertime, but also for bat populations living in contiguous stands, especially during the critical seasons when availability of prey in general is low.

Conclusions about relationships between bats and habitats based on data received from acoustic survey have to be considered with caution since this method provide data only on relative habitat use and therefore can not be used for analysis of habitat preferences of individual species (Miller *et al.* 2003). Nevertheless, data received with acoustic methods can be used for analysis of habitat use and selection, and it can be tested with other techniques (Sherwin *et al.* 2000).

The results of this investigation suggest that future studies have to be more concentrated on habitat selection and movements of bats during critical periods. More studies on characterisation of optimal and suboptimal habitats are needed. Radio tracking methods should be used in future research since this method permits to derive detailed data about habitat preferences. Additionally, study of differences in fitness between bats roosting in suboptimal habitats and bats roosting in key habitats could provide more information on using key and suboptimal habitats.

From this study, the following can be concluded:

- the distribution pattern of bats in the landscape varies significantly during different seasons;
- the result showed that only some specific habitats in the landscape are used during more critical periods and that there are movements between these key habitats and suboptimal habitats;
- in this study the GT and LT forests were identified as key habitats;

- dead tree density is one of the most significant factor influencing bat communities. Thus, this factor should be considered when planning management activities on the protected area "Lower Dniester" Ramsar Site;
- more research is needed for better understanding of the movements of bats between optimal and suboptimal habitats during different seasons. It is also important to understand the function of key habitats and the factors affecting bat distribution.

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