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Source: Folia Zoologica, 68(1) : 21-28

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.040.2019

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Folia Zool. – 68 (1): 21–28 (2019) DOI: 10.25225/fozo.040.2019

Space use, habitat selection and daily activity of water voles *Arvicola amphibius* co-occurring with the invasive American mink *Neovison vison*

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Received 9 June 2018; Accepted 5 January 2019

Abstract. A water vole *Arvicola amphibius* population inhabiting midfield ponds was studied by live-trapping, radio-telemetry and with camera traps. Within the midfield ponds, water voles did not prefer any particular type of littoral vegetation and avoided open water areas within the ponds. The mean distance of daily movements was 118 m for males and 53 m for females. The maximum distance between two locations of a radio-tracked individual within its home range during the whole study period was 450 m. Water vole movements between the studied ponds were very limited. Most of the hiding places were located in the areas around ponds. Water voles were active mostly during the night.

Key words: home range, activity pattern, radio-tracking, camera traps, spatial activity

Introduction

The water vole *Arvicola amphibius* is a semi-aquatic rodent widespread in Eurasia. Its distribution and habitat selection are mostly determined by the presence of freshwater, food and vegetation cover (Bonesi et al. 2002). However, it is difficult to distinguish between suitable and non-suitable water vole habitat, as habitat suitability is affected by various meta-population processes (Telfer et al. 2001). For example, in suboptimal habitats, water vole presence may be positively influenced by the proximity of water vole colonies that form source populations, whereas optimal but isolated environmental patches may be less likely to be inhabited by water voles (Bonesi et al. 2002). One of the main factors explaining the avoidance of suitable habitats is high level of predation by the invasive American mink *Neovison vison* (Lawton & Woodroffe 1991, Barreto et al. 1998), and in aquatic ecosystems, the presence of mink can significantly affect water vole distributions and densities (Halliwell & Macdonald 1996, Brzeziński et al. 2018a).

Mink predation is a key factor determining the distribution of water voles in riparian habitats (Lawton & Woodroffe 1991, Barreto et al. 1998), as it decreases vole density by increasing their mortality (Woodroffe et al. 1990). Moreover, water voles respond to the mink's odour by avoiding areas where they detect mink presence and by migrating to safe refuges (Barreto & Macdonald 2000). Therefore, refuges with low risk of mink predation are considered to be important for the survival of water vole populations in areas invaded by mink (Barreto et al. 1998, Macdonald et al. 2002). The Mazurian Lakeland, NE Poland, is an area where the distribution of water voles is affected by the presence of the invasive American mink because the probability of water vole occurrence is significantly lower at sites inhabited by mink (Brzeziński et al. 2018a). In this region, midfield ponds are generally avoided by mink; they thus provide safe refuge for water voles and may be able to maintain their populations at the landscape scale. However, in the Mazurian Lakeland the probability of mink occurrence at the midfield ponds increases with a decreasing distance between the pond and lake. The results of a recent study showed that at small water bodies adjacent to a large lake, a water vole population may inhabit ponds inhabited by mink, reach densities up to nine individuals per 1 km of a pond shoreline and withstand the impact of this invasive predator (Brzeziński et al. 2018b). The aim of this study was to analyze space use, habitat

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selection and daily activity of water voles inhabiting small midfield ponds utilized by mink as foraging sites.

Study Area

The study was conducted on the eastern outskirts of Lake Łuknajno (53°49′ N, 21°38′ E) in Mazurian Lakeland, NE Poland. The landscape of Mazurian Lakeland was formed by the last glaciation and is characterized by a variety of landscape forms and habitats, such as lakes, marshes, bogs, sandy hills, deciduous and coniferous forests, fields, meadows, pastures and fallows (Kondracki 1998), and also by a high density of small inland water bodies (natural ponds) that can reach up to 30 per km^2 (Solarski & Nowicki 1990). The number of ponds was originally even higher, but over the 20th century various human activities led to the disappearance of many. Since the 1990s however, some opposite trends have been observed, as large areas of farmland in Mazurian Lakeland were abandoned after the collapse of many state farms. The drainage systems that maintained the outflow of water from fields, meadows and pastures were not maintained; thus, the level of the water table increased and many previously drained marshes and small ponds started to recover. This process has also been supported by the activity of the growing population of beavers *Castor fiber*.

The study took place on an area of approximately 1.2 km^2 (Fig. 1), comprising various types of habitats but mostly covered by fallows (fields that have not been cultivated since the beginning of the 1990s and which are undergoing natural plant succession). Over the course of succession, the abandoned fields have become overgrown with grasses, herbs and shrubs: mainly pear *Pyrus communis*, dog rose *Rosa canina* and common hawthorn *Crataegus monogyna*. In the hilly landscape of the study area there are numerous depressions that are permanently or temporary filled with water, creating a network of over 20 ponds ranging in size from 0.1 to over 6 ha, and with depths of up to about 2 m. The study was conducted at six selected ponds: Pond 1-6.6 ha, Pond 2-1.8 ha, Pond 3-3.0 ha, Pond 4-1.2 ha, Pond 5-0.5 ha, Pond 6-0.3 ha, which are overgrown by four main types of aquatic vegetation: common reed *Phragmites australis*, bulrush *Typha angustifolia*, grey willow *Salix* spp., sedge *Carex* spp. The proportion and range of plant communities vary significantly between the ponds

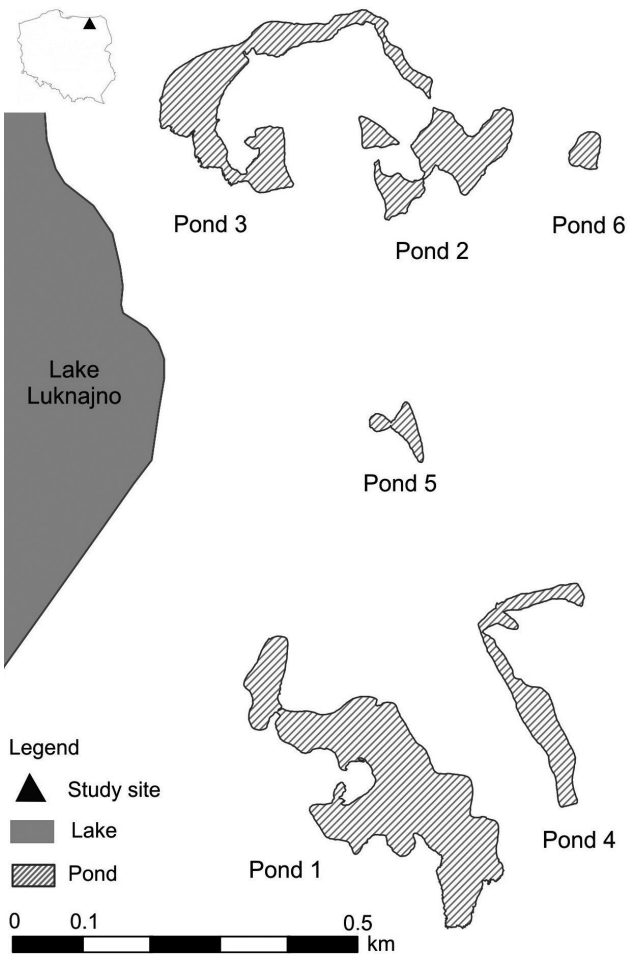

Fig. 1. Study site at Lake Łuknajno in Mazurian Lakeland, north-eastern Poland.

Table 1. Proportion and range of littoral vegetation types at the midfield ponds.

	Habitat								
Pond number	Common reed	Bulrush	Sedge	Grey willow	Forest (alderwood)	Other vegetation	Open water	Pond shoreline length [m]	Pond area [ha]
1	16 %	15 %	3 %	4 %	10 %	5 %	47 %	1966	6.58
2	6 %	24 %	38 %	24 %	0 %	4 %	4 %	788	1.82
3	20 %	53 %	6 %	16 %	4 %	0 %	1 %	1542	2.96
4	25 %	16 %	4 %	2 %	0 %	17 %	36 %	1096	1.17
5	0 %	40 %	13 %	6 %	0 %	9 %	32 %	513	0.53
6	0 %	21 %	3 %	8 %	0 %	9 %	59 %	224	0.34

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(Table 1). The boundaries of the study area are well defined by the shoreline of Lake Łuknajno in the west and a large mixed pine forest in the east. The midfield ponds are usually permanently frozen over winter. The fresh aquatic vegetation develops at the beginning of May, and prior to this period, old dead stands of reeds, bulrush, etc. build up in the littoral zone of the water bodies.

Material and Methods

Water vole radio-tracking

Radio-tracking was conducted to determine water vole home range sizes, daily movement distances, habitat preferences and daily activity patterns. In 2011, water voles were live-trapped along the shorelines of the three largest ponds (Ponds 1, 2, 3), while in 2012 and 2013 they were also trapped along three smaller ponds (Ponds 4, 5, 6). Wire mesh live traps (13 × 13 × 46 cm) were placed on wooden floating rafts (50 × 50 cm) in littoral vegetation, along shorelines (3-5 m from the bank), at about 50 m intervals. Traps were baited with chopped carrots and apples. All captured individuals were sexed and weighed with a precision of 1 g. Animals were marked by the implantation of subcutaneous chips (UNIQUE company, 2 × 11 mm size). In 2011 and 2012, thirty-four individuals (17 per year), all of which weighed over 100 g, were fitted with radio-telemetry collars (Biotrack, U.K.; weight ~ 2.9 g, battery duration up to three months). To install the transmitter, animals were anesthetized (Narkamon, at a dose of 0.01 ml/g body weight). In total, 26 males and eight females were radio-collared. All individuals were released at the place of capture. Animals were radio-tracked using the "home-in" telemetry method (White & Garrott 1990) with an estimated accuracy of up to 5 m. They were tracked on foot using Yagi antennae and R-1000 receivers (Communications Specialists, inc. U.S.A.). Each specimen was located from 1 to 11 times per day (both day and night), and the interval between successive fixes was a minimum of 1 hour. We assessed that this interval was enough for a water vole to freely traverse across its entire home range; thus, it provided independent locations and enabled us to avoid high autocorrelation of our data due to unnatural clumping of locations (White & Garrott 1990). In both years water voles were radio-tracked from mid-April until the end of June.

Home range analysis

Home range analysis was conducted using the computer software Ranges 8 (Kenward et al. 2008). In the first step we rejected all the specimens for which we obtained less than 30 locations, because this is the lowest number of locations required for the accurate calculation of a minimum convex polygon (Kenward 1987) and Kernel home range (Seaman et al. 1999). For the remaining individuals (from 30 to 149 locations), an incremental area analysis was used to determine the necessary number of fixes to establish a stable home range. The analysis showed that an average of 45 ± 21 fixes were required to reach the stable home range (calculated as a minimum convex polygon). Thus, to avoid inadequate sampling, only the stable ranges with ≥ 45 fixes (12 individuals) were used for further analysis. However, to enlarge the sample size, an additional estimation of the area of water vole home ranges was made, in which the 24 individuals with more than 25 fixes were taken into account.

To estimate home range size, we used a minimum convex polygon (Hayne 1949) and fixed Kernel density estimation (Worton 1989) with an adjusted smoothing factor (fixed multiplier of h_{ref} = 0.43), which was calculated as proposed by Wauters et al. (2007). To estimate core areas, only the fixed Kernel density estimation with the adjusted smoothing factor (fixed multiplier of h_{ref} = 0.43) was used. The home range size of each water vole was calculated as the 95 % minimum convex polygon (MCP_{95}), and 95 % Kernel density estimation (KDE_{95}). The core areas were calculated as the 80 % Kernel density (KDE_{80}), and 50 % Kernel density estimations (KDE_{50}). The 80 % isopleth was the mean core for all specimens (n = 12 ranges, mean ± SD = 80, 4 ± 4.5 %), selected by examining the utilization distribution curves (% of area plotted against % of locations; Powell 2000). The 50 % isopleth is widely used as a standard core area.

Habitat selection

In 2011 vegetation was mapped at six ponds in the study area using a handheld GPS receiver. Vegetation classes were defined by the dominant species or dominant group of species, such as common reed *Phragmites australis*, bulrush *Typha* sp., sedge *Carex* spp., and willow *Salix* spp. Other plants (*Phalaris* sp., *Juncus* sp., *Scirpus sylvaticus*, *Alisma plantago-aquatica*, *Hippuris vulgaris*), which covered 5.1 % of all ponds, were classified within a single group. All gaps without vegetation were classified as open water. The habitat around the ponds was mapped in ArcView 10.0 using satellite images as a background layer. Two more vegetation classes were defined: fallow and forest (alderwood or/and mixed pine forest). The habitat selection of water voles was analyzed using the

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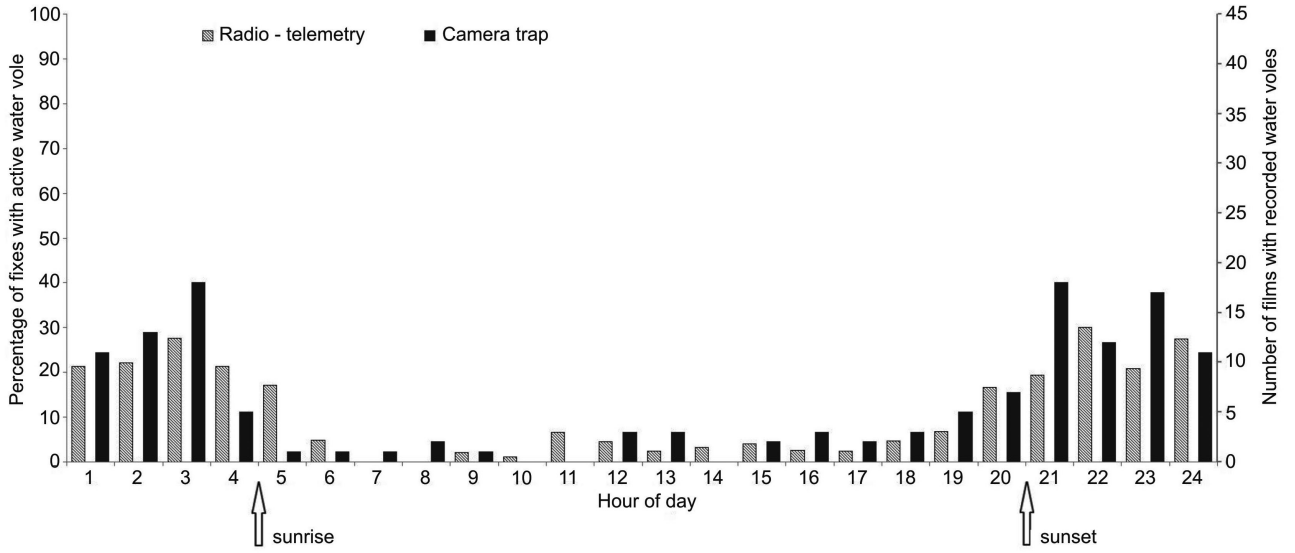

Fig. 2. Pattern of daily activity of water voles based on radio-telemetry and camera trap recordings.

Jacobs index (Jacobs 1974) according to the formula $D = (r - p)/(r + p - 2rp)$, where r is the proportion of habitat used by specimens and p is the proportion of available habitat. D values range from –1 (strong avoidance) to 1 (strong preference), and a value of 0 means that the habitat types are utilized proportionally to their availability. Habitat selection was evaluated by comparing the utilized and available habitats at two spatial levels: second-order selection (home range composition *vs.* available habitat composition) and third-order selection (core area composition *vs.* home-range composition; Johnson 1980). The habitat available for water voles was assessed using a 400 m wide buffer around all KDE_{95} home ranges. According to Stoddart (1970), 400 m is the minimum dispersal distance, and thus the area within this buffer was potentially available to and penetrated by water voles. In the third-order selection, the habitat type "forest" was excluded from the analysis because it did not occur in any core area or home ranges. Habitat selection was estimated for 12 water vole individuals that were radio-tracked with more than 45 fixes.

Daily activity estimation

Estimation of the pattern of daily activity from the radio-telemetry study was based on the number of taken fixes. A varied signal strength indicated the animal was moving, while a continuous signal showed it was still. Daily activity was estimated for 24 water vole individuals. All of them were radio-tracked for more than 13 days. In total, the pattern of daily activity of water voles was estimated on the basis of 363 fixes. Water vole activity in a given one hour period was then calculated as the proportion of the number of fixes with water vole activity relative to the total number of fixes.

Water vole camera-trapping

Camera-trapping was used (as an additional method) to estimate the daily patterns of water vole activity. In May 2012, 11 camera traps (HCO ScoutGuard SG580M and TV-6220M) were used to record the daily activity of water voles. They were deployed on wooden pegs in the littoral vegetation at three ponds (Ponds 1, 2 and 4). A wooden floating raft with a lure (carrots and apples) was installed in front of each camera trap. Camera traps were checked every 24 hours and the bait was supplied before each camera-trapping session. Each trap monitored for a different length of time, but they worked for a total of 95 days. The camera traps were activated by animal movements, both during the day and night, and recorded 1 min-long films with 10 s intervals. Water

Table 2. The mean home ranges of water voles. Only those individuals whose locations were fixed at least 45 times were included. Explanations: n, number of individuals; SD, standard deviation; MCP_{95}, 95 % minimum convex polygon; KDE_{95}, 95 % Kernel density estimation; KDE_{80}, 80 % Kernel density estimation; KDE_{50}, 50 % Kernel density estimation.

		Home range (ha)		Core area (ha)	
		MCP_{95}	KDE_{95}	KDE_{80}	KDE_{50}
Male (n = 10)	Mean	1.49	0.93	0.52	0.24
	SD	1.59	1.00	0.46	0.22
Female (n = 2)	Mean	0.11	0.06	0.04	0.02
	SD	0.02	0.02	0.01	0.01

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Table 3. Habitat selection of water voles calculated using Jacobs' index (Jacobs 1974). Explanations: MCP_{95}, 95 % minimum convex polygon; KDE_{95}, 95 % Kernel density estimation; KDE_{80}, 80 % Kernel density estimation; KDE_{50}, 50 % Kernel density estimation.

Habitat	Second order selection	
	MCP_{95}/Buffer	KDE_{95}/Buffer
Pond	0.88	0.87
Terrestrial habitat	–0.91	–0.91

Habitat	Third order selection			
	KDE_{80}/MCP_{95}	KDE_{80}/KDE_{95}	KDE_{50}/MCP_{95}	KDE_{50}/KDE_{95}
Common reed	0.16	–0.02	0.15	–0.03
Bulrush	0.10	0.05	0.18	0.13
Sedge	0.08	0.03	0.13	0.08
Grey willow	–0.02	0.04	–0.06	0.00
Other vegetation classes	0.15	0.12	0.26	0.23
Open water	–0.29	–0.12	–0.43	–0.27
Fallow	0.10	0.06	0.13	0.09
Forest	-	-	-	-

voles were recorded on 375 out of 1957 recordings (19.2 %). The duration of films with water vole presence (in minutes) relative to the total monitoring time of camera traps was 0.27 %. To calculate daily activity, we used 24 one-hour long periods starting and finishing in the middle of each hour (for example between 1:30 and 2:30). In the calculation, if there was more than one film with a water vole in a single one-hour period, it was counted as one record. This assumption was adopted to avoid overestimating water vole activity, because while active, the animals entered the rafts multiple times, which multiplied the numbers of recordings.

Results

Water vole home ranges and movements

The mean area of the male home range was 1.49 ha (Table 2), and it varied from 0.22 to 4.9 ha (MCP_{95}). If calculated with KDE_{95}, the mean area of male home range was 0.93 ha, and the core area covered 56 % (KDE_{80}) and 26 % (KDE_{50}) of the home range. The mean area of the female home range was much smaller and was 0.06 ha (KDE_{95}) or 0.11 ha (MCP_{95}). The analysis of home range sizes, which included more individuals (those with at least 25 fixes: 19 males and five females), showed slightly smaller but similar home ranges to those calculated for 12 individuals: the mean area of the male home range was 0.78 (KDE_{95})-1.33 ha (MCP_{95}), and the mean area of the female home range was 0.04 (KDE_{95})-0.09 ha (MCP_{95}).

Water vole movements between the studied ponds were very limited. We recorded one radio-tracked male that moved from one pond to another (from Pond 3 do Pond 2) and another that moved approximately 300 m between Pond 1 and the shore of Lake Łuknajno. Among the marked water voles, six individuals (only males) were recaptured at ponds other than the pond of first capture: in 2011 one male moved from Pond 3 to Pond 2, in 2012 two males moved from Pond 4 to Pond 1, and in 2013 two males moved from Pond 3 to Pond 2 and one male from Pond 6 to Pond 3. Among seven individuals recaptured the following year, we did not record movements between ponds. The maximum distance between two locations of a radio-tracked individual within its home range was 450 m. The distance of daily movements calculated for radio-tracked individuals with more than five fixes per day was 118 m (SD = 55, n = 9) for males and 53 m (SD = 15, n = 2) for females. In males, mean daily movements varied from 54 to 212 m per day and the furthest recorded daily movement was 862 m.

Water vole habitat selection

According to the second order selection, water voles exhibited a strong preference for ponds, and strongly avoided the forest and fallow (Table 3). The third order selection analysis showed much lower values of Jacobs' index, which indicates that habitat selection was weaker in the core area. Water voles did not prefer any particular type of littoral vegetation, and the strongest selection was that they avoided open water areas within ponds (Table 3).

Burrows and hiding places were identified for 16 radio-tracked water voles. In total, 16 burrows and six hiding places were found. Hiding places were located close to pond shorelines or in clumps of vegetation

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(mainly sedges) within pond areas, whereas burrows were situated at larger distances from the water's edge. All female burrows were no further than 5 m from the pond shoreline (five cases). On the other hand, male burrows were located both within 5 m of the water's edge (five cases) as well further away (six cases). The maximum distance between a burrow occupied by a male and the nearest pond was about 200 m.

Pattern of daily activity of water voles

Water voles were active mostly at night: 82 % of radio-telemetry fixes of active animals and 86 % of camera trap recordings (assigned to 1 h-long periods) took place between sunset and sunrise (Fig. 2). The activity of water voles at night was rather stable and was not characterized by any significant peaks, aside from a slight decrease in activity just after midnight. The decline in activity at dawn was more rapid than the increase in activity at dusk (Fig. 2).

Discussion

The mean size of home ranges of water voles inhabiting midfield ponds was over ten-fold larger in males than females, and the smallest male home range was larger than the largest female home range. Moreover, the recorded mean daily movements of males were at least twice as large as those of females. These results confirm that water vole females occupy small territories with well defined borders rather than home ranges, while males, which compete for females, are less territorial and have relatively large home ranges that overlap with the territories of females and ranges of other males (Strachan et al. 2011). Due to the small number of radio-tracked females, we were not able to confirm the stability of these territories. The observations of water vole males were more informative; some of the radio-tracked individuals displayed high spatial activity within their home ranges, with daily movements over 800 m. At rivers and streams, such long linear movements are often considered to be dispersal; however, at the studied ponds, males mostly moved along pond perimeters, and after long distance movements, returned to their core areas, which constituted relatively small parts of their home ranges.

It is difficult to compare the sizes of the two-dimensional home ranges evaluated at midfield ponds with those previously reported in the literature, because water vole home ranges are usually described linearly (Stoddart 1970, Moorhouse & Macdonald 2005, Strachan et al. 2011). The mean length of weekly home ranges recorded by Moorhouse & Macdonald (2005) ranged between about 100 and 150 m for males and between about 70 and 100 m for females; however, the total range lengths increased after longer periods of tracking. It has also been found that the length of water vole home ranges is inversely correlated with population density (Moorhouse & Macdonald 2008). Moreover, Moorhouse & Macdonald (2005) concluded that female water voles exhibit drifting territoriality, and the degree to which territories drifted was smaller at higher densities. Results of recent studies conducted in U.K. showed, similarly to our results, that activity of resident water vole males was about twofold higher than activity of resident females (Baker et al. 2018). Mean weekly distance between two locations was about 30 m in males and 15 m in females, and maximum weekly distance was about 315 m in males and 70 m in females. However, due to methodological differences (in the study conducted in U.K. water voles were located once per week) these values can not be directly compared to distances of daily movements recorded by us.

In the study area, water voles were associated mainly with aquatic habitat, their terrestrial activity far from the midfield ponds was limited, and most of their dens were located close to the bank. Within the pond area, water voles did not exhibit any significant preference or avoidance of any particular type of vegetation, and the most pronounced behaviour was their avoiding of the open water area and moving under the cover of littoral plants, which increased their security. During the study we confirmed mink presence at the midfield ponds near Lake Łuknajno on the basis of camera-trapping and the presence of mink dens and latrines. Despite the fact that ponds were utilized by mink as foraging sites, water voles inhabited the area; however, the effect of the mink presence on their distribution, habitat preferences and activity was not possible to determine and remains unknown. Several radio-tracked individuals disappeared from the inhabited ponds and we found evidence that at least some of them were depredated. One radio-tracked water vole was killed by a mink and three were killed by a fox *Vulpes vulpes*, as their transmitters were found in dens of the predators. In areas inhabited by mink, most water vole mortality has been ascribed to this invasive carnivore; however, other mustelids, foxes and herons are also responsible for killing water voles, and the total predation by native predators on water voles can be even higher than that of the American mink (Carter & Bright 2003, Forman 2005). When present in high densities, water voles can be hunted in big numbers by many predator species (Weber et al. 2002), including those that normally

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specialize in hunting other prey, for example badgers *Meles meles* (Weber & Aubry 1994).

Water voles inhabiting midfield ponds in the Mazurian Lakeland were mostly nocturnal, with activity peaks at dusk and dawn, and this finding contrasts with findings from Scotland, where water voles were active by both day and night, but with a marked daytime maximum (Stoddart 1969). Similar activity peaks to those observed in our study have been found in the water voles *Arvicola terrestris scherman* (Airoldi 1979) and *Arvicola sapidus* (Pita et al. 2011), but in neither of these studies did water voles have higher activity in the night than in the day. A nocturnal activity pattern may protect water voles from predation by diurnal raptors, such as marsh harriers *Circus aeruginosus*, buzzards *Buteo buteo* and lesser spotted eagles *Aquila pomarina*, which are abundant in the study area. However, it does not help in avoiding predation by carnivores, whose patterns of activity are similar to that of water voles: American mink and polecats *Mustela putorius* in the study area have been found to be most intensively active before dawn and after sunset (Brzeziński et al. 2010). To maximize hunting success, mink may synchronize their hunting activity patterns with the activity patterns of nocturnal rodents (Gerell 1969). On the other hand, the activity patterns of rodents may to some extent result from their densities and the abundance of their main carnivore predators. For example, root voles *Microtus oeconomus* have been found to be more nocturnally active in years of high abundances of weasels *Mustela nivalis*, which are mostly diurnal (Gliwicz & Dąbrowski 2008).

Conclusions

Water vole movements within and between ponds were limited; however, some individuals displayed high spatial activity within their home ranges, with daily movements over a few hundred meters. Males were more mobile than females and had larger home ranges. Water voles did not prefer any particular type of littoral vegetation, avoided open water areas within ponds, and were mostly active at night.

Acknowledgements

This research was a part of a scientific project realized in the years 2009-2012 and financed by funds from the National Science Centre of Poland, which were granted by decision number N N305 034637. We are grateful to T. Diserens for English correction.

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