Mammal Research (2023) 68:13–25
https://doi.org/10.1007/s13364-022-00656-0

ORIGINAL PAPER

Seasonal and diel activity patterns of small mammal guilds on the Pannonian Steppe: a step towards a better understanding of the ecology of the endangered Hungarian birch mouse (*Sicista trizona*) (Sminthidae, Rodentia)

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Received: 8 September 2022 / Accepted: 12 October 2022 / Published online: 28 October 2022

Abstract

Temporal activity differences facilitate species' coexistence by reducing interspecific competition. Such patterns can be studied via diel activity analysis, but obtaining data in cryptic mammals is difficult. We investigated the annual and diel activity pattern of such a small mammal, the endangered Hungarian birch mouse (*Sicista trizona trizona*), in its only known habitat. We employ trail cameras for the first time to reveal the diel and annual activity of a sminthid species. Data acquisition included the spring and summer seasons between 2019 and 2022 and was extended to detect the activity overlaps with other common coexisting rodents and shrews. The diel activity results rely on 581 detections of *S. trizona* over 5670 trap-nights of camera trap deployment characterising also activity pattern of the small mammal community in this Central European grassland ecosystem. *S. trizona* was not recorded during the day but was active at dawn and night, and in comparison with other coexisting species, its activity level was high. The presumed cold sensitivity was not confirmed as we detected activity at −6 °C. Diel activity peaked in early May in the mating season. Although the diel activity pattern of co-occurring small mammal species was also nocturnal, activity overlaps were relatively high suggesting that temporal niche partitioning is limited within the habitat. Our work provides the first insight into temporal overlaps within a small mammal community in a natural European grassland, moreover, also the first documented research on the activity pattern of a sminthid in its natural habitat.

Keywords Activity level · Grassland · Rodents · Soricidae · *Apodemus* · *Microtus*

Introduction

Birch mice (genus *Sicista*, family Sminthidae) are the master of hiding as they can remain unobserved for decades even in the vicinity of cities (Selyunina 2003; Cserkész and Gubányi 2008; Popov 2011; Rusev et al. 2012; Cserkész et al. 2015). Consequently, their behaviour and lifestyle are little known (Holden et al. 2017). The Hungarian birch mouse, *Sicista trizona* (Frivaldszky, 1865), STT hereinafter, is endemic to the Carpathian Basin, listed now as Endangered by the IUCN (Cserkész 2019) and is on Annex IV of the Habitats Directive (Council Directive 92/43/EEC). Moreover, it is a strictly protected species in Hungary, regarded as a "national treasure." It weighs 6–16 g, and it is restricted to grassland habitats with high, unmowed, dry vegetation. This cryptic, and increasingly rare, threatened species is seldom captured with usual box traps and can only be successfully sampled by pitfall trapping (Cserkész and Gubányi 2008). Quantitative data is still lacking on the activity pattern of any sminthid species, while exact knowledge of the seasonal and diel activity rhythms represents a key focus for species conservation and management (Brivio et al. 2016; Lashley et al. 2018), especially in the case of those species being targeted

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Communicated by: Karol Zub

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for captive breeding. It is essential to gain a more thorough insight into diel and seasonal activity rhythm, including the starting and ending of hibernation under natural conditions, for zoo keepers managing captive populations. STT captive breeding has recently been launched by the Budapest Zoo (Pivarcsi et al. 2021) utilizing the results presented in this paper with the aim, partially, to generate new information on the secret life of this unique rodent species. At the beginning of the last century, Vásárhelyi (1929) also kept STT in captivity for a short time, representing the only previously available information on STT's lifestyle, and characterised them as shy and cold-sensitive animals.

In this study, we deployed trail cameras in the field which were reported to be a reliable tool to evaluate activity patterns in a broad spectrum of wild animals (e.g., Ridout and Linkie 2009; O'Brien 2011; Burton et al. 2015; Rovero and Zimmermann 2016) if at least 30–50 detections are available (Ridout and Linkie 2009). Camera trap surveys have emerged as an increasingly cost-effective method for collecting presence/absence data (De Bondi et al. 2010; Meek et al. 2014). They provide substantially higher detection rates for some elusive species (Roberts 2011), detect a broader range of species (Paull et al. 2012), and are ethically preferable to prevailing survey methods (particularly against live- and kill-trapping) that require animals to be physically captured (Putman 1995). They offer non-invasive and economical alternatives for testing hypothesises relating to wildlife (Meek et al. 2014). Finally, some other advantages of using trail cameras are a reduction, but not the elimination, of human sampling error and an increase in geographic coverage of surveys (Burton et al. 2015).

One way to assess the temporal niche of a population is the diel activity pattern. Subsequently, temporal overlap of activities and the similarity between two activity patterns can also be calculated. These similarities are usually described by using activity levels (i.e., the number of hours in a day when a population is active) and activity peaks, the time of maximum activity (Rowcliffe et al. 2014). However, small mammals pose particular challenges for the implementation of camera trapping studies because with trail camera set conventionally, small mammals may be too small to reliably activate the thermal sensors and, if recorded, may be more challenging to identify on images than large-bodied mammals (e.g., carnivores and ungulates) are (Littlewood et al. 2021).

Our work provides the first insights into temporal pattern interactions within a small mammal community in natural European grassland; moreover, this study is also the first documented research on the activity pattern of a sminthid (*Sicista*) species in its natural habitat, but not the first one which used trail cameras to detect the presence of a sminthid species. In Sweden, Van der Kooij et al. (2016) proved the capability to detect Northern birch mice (*Sicista betulina*) with trail cameras. In Austria, Resch and Resch (2019) carried out a targeted survey using trail cameras in alpine pastures and detected *S. betulina* several times. Both studies underlined the suitability of trail cameras for examining the presence of sminthids, otherwise challenging to detect with classical field methodology.

We studied the activity of a terrestrial small mammal community including STT to determine seasonal differences and overlaps in diel activity patterns. During three consecutive years, conventional trail cameras were deployed at the Borsodi-Mezőség Landscape Protection Area (north-eastern Hungary), which is the only known habitat of STT and hosts several other terrestrial small mammal species. Our study focused on the most frequently camera-trapped small mammals in the habitats sampled.

The main objective of this study was to test the use of trail cameras to investigate seasonal and diel activity patterns and levels of STT. Additionally, we wanted to know whether STT can be detected and identified with an acceptable level of certainty by cameras in the presence of a similar-looking sympatric small mammal, *Apodemus agrarius*. A further objective of this study was to investigate the temporal niche partitioning process in a terrestrial small mammal community that inhabits a natural grassland ecosystem. Moreover, we aimed to characterise the temperature profile of the active period of STT, and test the "shy mouse" observation, whether STT avoids the activity peaks of other rodents and can mostly be observed when the others are less active. In summary, our study was driven by seeking answer for the following questions: (1) Can STT be distinguished from *A. agrarius* on trail camera images even in infrared light? (2) does the activity peak of STT shift to the inactive period of other rodents? Or (3) the activity pattern of nocturnal small mammals will be similar and only the diurnal species will differ.

Materials and methods

Study area

To fulfil the aims, we deployed 48 camera trap stations in Borsodi-Mezőség Landscape Protection Area (Natura2000 site code: HUBN20034) during 3 years. Data were collected from March 2019 to May 2022, and kept constantly active throughout the year except the winter season (December, January, February) when birch mice hibernate (Holden et al. 2017). Borsodi-Mezőség, the long-term monitoring site for STT, is the second largest grassland in Hungary with a continuous protected area of 18,470 ha under the management of the Bükk National Park Directorate since 1989. The mosaic grassland areas cover almost 65% of the surface, where *Agropyron repens* (L.) P.Beauv., *Poa angustifolia* L., *Festuca rubra* L., and *Alopecurus pratensis* L. are the most abundant species. Traditional human activities including livestock grazing are currently employed for conservation purposes. The Landscape Protection Area consists of landscapes with two distinct characteristics: a large part of the area is a grassland divided by winding marshes; the other, smaller part had been the floodplain of River Tisza until a large-scale dam construction in 1939. Its northern part is intersected by ancient riverbeds; a homogeneous alluvial plain prevails in the south levelled by the former floods of Tisza. Thus, although watercourses played the main role in forming the actual surface, human activity such as cultivation, flood control, and livestock grazing also played a key role in reshaping the landscape. Due to its remote location and the resulting relative isolation from development and exploitation, the vast majority of Borsodi-Mezőség is composed of pristine or secondary grasslands. Partly thanks to these circumstances, the Borsodi Mezőség is the only known, and most probably, the last habitat of STT. The area has a continental climate characterised by warm and dry summers with at least one month of drought in the summer and cold winters. The mean annual temperature is between 9.8–9.9 °C, and 17.2–17.6 °C in the vegetation period from March to November. The annual precipitation ranges between 540 and 560 mm, of which 320–330 mm falls in the vegetation period (Dövényi 2010).

Camera trapping

Camera trapping was conducted over 9 months per year from March to November for three consecutive years. During the winter of 2020–2021, the cameras were active till the 15th of January, and we were able to reach the study area and deploy the devices only in April. Data were recorded using 8 Uovision UV785 Full HD 12 MP trail cameras, randomly placed over the study area on a 9-hectare territory, positioned in open habitat patches (i.e., patches with low coverage of vegetation). This camera model does not operate with visible light only with infrared (IR) (wavelengths > 900 nm). They were set to “close objects” and operate 24 h a day, to take two photo bursts every time the sensor was triggered. The time lag between successive photo captures was set to high frequency: 20 s to obtain accurate photographed time. Cameras were placed at 50 to 60 cm above ground level and were checked twice monthly to download photos, check the battery status, renew the bait, and clean the vegetation to avoid false triggering when necessary. The eight camera trapping sites were always located at a minimum distance of 20–30 m from each other, a sufficient interval to theoretically assume independence among them. To prevent addiction to bait, we changed camera locations approximately every 3 to 4 months, but over the years, the sites were reused. These settings are resulting in a total number of 48 locations at the end of the study period. We used the clock time of a triggered camera photo as an activity record. Time stamps of events were recorded in Central European Time (CET) throughout the year (i.e., Daylight Saving Time was ignored). Cameras have integrated temperature sensor components enabling the collection of temperature data at the time of detection; however, these embedded sensors can be susceptible to errors when the device is exposed to direct sunlight (Meek et al. 2012a). Consequently, ambient air temperature measures using the camera stamp temperature were derived only from records during the night.

Identification

Species identification is difficult where similar species occur in sympatry (Meek et al. 2014; Burns et al. 2018), and this is especially true for small mammals (e.g., Claridge et al. 2010; Meek and Vernes 2016). Grasslands of Borsodi-Mezőség are home to six species of rodents and five species of shrews (Cserkész and Gubányi 2008), most of them occurring in sympatry, and all of them are uniquely identifiable by size and pelage. However, camera trapping relies on the identification of species from images alone and this can be challenging due to low image quality, and inappropriate camera settings (e.g., too much IR light). Co-occurrence with non-target similar-looking species can also lead to misidentification (Burns et al. 2018). *Apodemus agrarius*, particularly subadults, are similar in size and shape to STT, meaning that in infrared images, where colouration can hardly be used for identification, body shape may not be distinctive enough to allow identification. Both species have a characteristic black stripe on the back; however, this stripe is bordered by pale bands in STT which can be seen in most images facilitating the discrimination (Fig. 1).

In this study, STT, *Apodemus agrarius*, and *Microtus arvalis* pictures taken by camera traps were identified at the species level, but it was not possible for shrews (*Sorex araneus* and *minutus, Crocidura leucodon* and *suaveolens, Neomys anomalus*), in which species was not evident in most cases. Two further species of *Apodemus* used to be trapped in the grassland plots of the Borsodi Mezőség: *Apodemus uralensis* and *A. sylvaticus*. Owing to difficulties in differentiating between these species, all “unstripped” *Apodemus* photographic records were grouped at the genus level (i.e., *Apodemus*) for analyses. Consequently, these small mammals classified as low confidence were recorded within the categories “Apodemus” and “Soricidae,” which included also those images assigned with high confidence to the species level. Different individuals of the same species were not identified due to the absence of individual fur marks. When more than one individual of the same species was recorded in a picture, these were considered as single detections to facilitate the analyses.

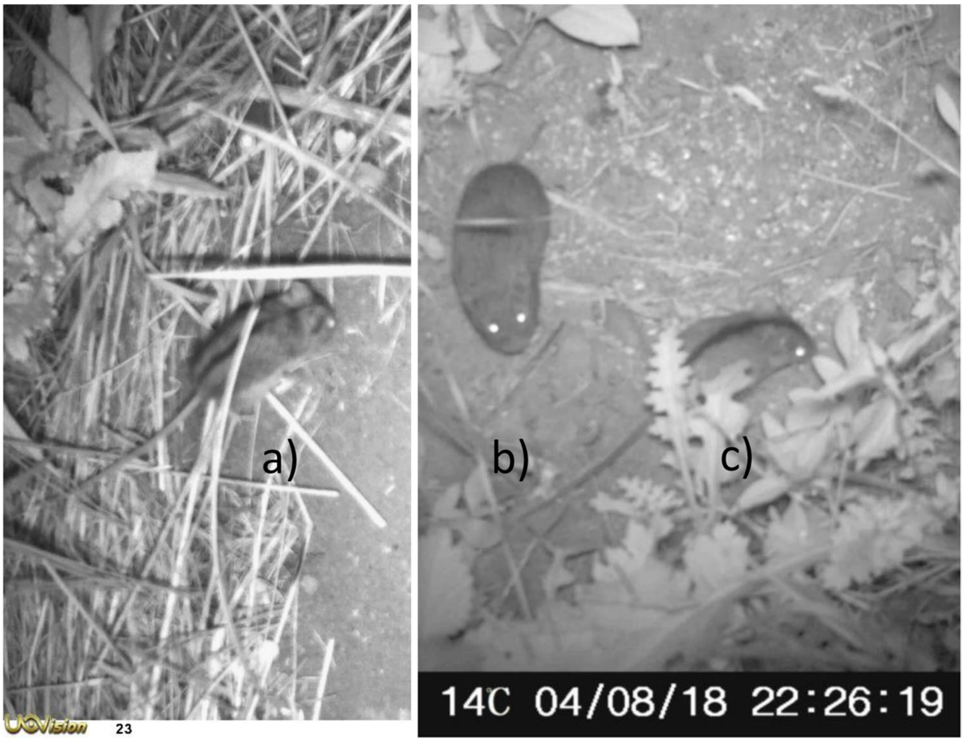

Fig. 1 Camera trap images of three rodent species delineating their distinct morphological features: **a** *Sicista trizona*, **b** *Microtus arvalis*, **c** *Apodemus agrarius*, and the latter two on the same image

Bait

Following Van der Kooij et al. (2016), the trail cameras were baited with flaxseed (*Linum usitatissimum*) to increase detection rates. Our intent was to make the animals spend more time in the detection zone of the cameras, thus increasing the probability of detection. To prevent the influence of a stable food source on the behaviour of the animals (i.e., the habituation of animals to the bait), observations should not be carried out for many days (Łopucki and Kiersztyn 2020). In our study, the bait was not available continuously under the cameras to prevent addiction to bait and alter the natural diet of the animals, but it was renewed only every 2–3 weeks, while the small mammals and other animals consumed it within approximately a single week. Moreover, to further reduce the “bait-effect,” the location of the cameras was changed every three months. The insectivorous shrews were not influenced by the bait effect.

Data analyses

As the first step of the analysis, we removed images of the same species recorded at the same location occurring in < 5 min from our image collection to reduce pseudo-replication bias (Meek et al. 2014; Meredith and Ridout 2014). This interval is commonly used in camera trapping studies (e.g., Diete et al. 2017; Randler and Kalb 2021) and enabled us to maximise the number of theoretically independent detections allowing more precise estimation of diel activity patterns (Ridout and Linkie 2009). Picture metadata were extracted with TotalCommander software and used to build a database including camera site, species, additional species, and date, and time of each image.

We included the effect of the season by dividing the information into two groups according to the calendar, or meteorological seasons in which it had been obtained. Spring was considered from the 1st of March to 31st of May, whereas summer was from the 1st of June to the 31st of August. Data from autumn and winter were not evaluated because only a few images were taken on STT; moreover, it hibernates during winter.

Data were pooled from independent detections of all camera sites to calculate diel activity patterns (input data: minute/hour) of all small mammals, and an annual one (input data: month/day) for STT using the R package “activity” (Rowcliffe 2016). A probability density function (PDF) was performed on the fits kernel density to the radian time-of-day data to generate graphical representations of the diel activity of species over a 24-h cycle (with 10.000 number of bootstrap iterations) (Rowcliffe et al. 2014). By comparing Gaussian kernel density functions in pairs, activity overlap indices were calculated of the species within a season (Silverman 1986). Activity overlap indices correspond to the area shared by the two functions compared. Patterns of temporal overlap of activity rhythms among the species were calculated using the R package “overlap” (Meredith and Ridout 2014). We estimate the coefficient of overlapping (Δ) of temporal activity patterns among species and its 95%

confidence intervals (hereafter, CI); particularly we used the Δ4 estimator when records were more than 75 for both species and the Δ1 estimator when records of at least one species were less than 75 (Meredith and Ridout 2014). Confidence intervals (95%) for overlap indices were estimated by bootstrapping 10,000 samples (following Havmøller et al. 2020) from the Kernel functions and calculating the overlap index for each iteration within each pairwise comparison by using the same R package "overlap" (Meredith and Ridout 2021). Coefficients of overlapping range between 0 — no overlap and 1 — total overlap (Meredith and Ridout 2014). A Wald test was performed for each species in each season to assess the statistical difference between two activity level estimates (Rowcliffe et al. 2014). All statistical analyses were performed in R using RStudio v. 2021.09.0+351 (R-Team 2015).

Results

Most cameras operated continuously for 4 years, excluding winters, yielding 5670 trapnights in total. The studied grassland possesses a highly diverse European small mammal community: we identified the presence of *Microtus arvalis*, *Apodemus agrarius*, *Sorex* spp., *Crocidura* spp., *Sicista trizona*, *Dryomis nitedula*, *Muscardinus avellanarius*, and *Micromys minutus* on the images. *Dryomis nitedula* proved to be a new record for the local fauna of Borsodi-Mezőség. We were able to identify 97.5% of small mammals to the species level in the photos. During the study period, 10,329 independent detections were obtained for the five studied groups (i.e., *S. trizona*, *M. arvalis*, *Apodemus*, *A. agrarius*, Soricidae). Each target species appeared in almost all the camera sites. In total, we recorded 603 *S. trizona* (STT), 1663 *A. agrarius*, 3102 *Apodemus*, 4756 *Microtus arvalis*, and 205 Soricidae detections. The number of STT detections was highest in 2020 with 275 events. There were seven detections when two STTs were recorded on the same images; *Apodemus* sp. was also detected six times, *Apodemus agrarius* three times, and *Microtus arvalis* twice together with STT.

Activity levels and diel activity patterns

We collected 237 photographs of STT in spring and 344 valid records for analyses in the summer season. 22 detections recorded during autumn were not evaluated here. We observed a very limited diurnal and crepuscular activity of STT as it was detected only three times in daylight. We recorded a lower temporal overlap in spring (mean $\Delta = 0.77$) and a higher one with the other studied species in summer (mean $\Delta = 0.86$).

Excepting STT, all of the studied small mammals exhibited a similar activity level in summer and spring (Fig. 2). STT's activity level differed significantly between the two seasons; however, the difference was quite minimal (difference = 0.04; SE = 0.02; $W = 4.91$; $p = 0.027$). Soricidae showed a higher activity during summer, but the difference was not significant (difference = 0.101; SE = 0.05; $W = 3.46$; $p = 0.063$). In both seasons, *Microtus arvalis* was the species with the largest activity level, while in summer, the STT's activity level was the second and in spring the third highest one. The activity level of *Apodemus agrarius* was one of the lowest in both seasons.

Main activity types were largely constant (Fig. 3; Online Resource 1 depicted probability density function (PDF) kernel activity densities by seasons). Rodent species had a regular activity pattern with two peaks in both seasons. Only shrews showed a unimodal pattern with an activity peak centred at midnight in spring and after midnight in summer, although the small sample size during spring might have partially affected the results (Fig. 3). Only *M. arvalis* showed slight but considerable diurnal activity in both seasons, while *A. agrarius* was active in the daytime during spring. Around noon and early afternoon, almost all small mammals were inactive in summer; some activity in the afternoon was detected typically in spring.

Regarding diel activity pattern variations, STT was the only group that showed statistically significant differences between the seasons; however, the patterns seem to be the same (Table 1; Online Resource 2 depicted kernel activity densities overlaps by seasons). The other groups did not show significant variability, the peaks in activity time were

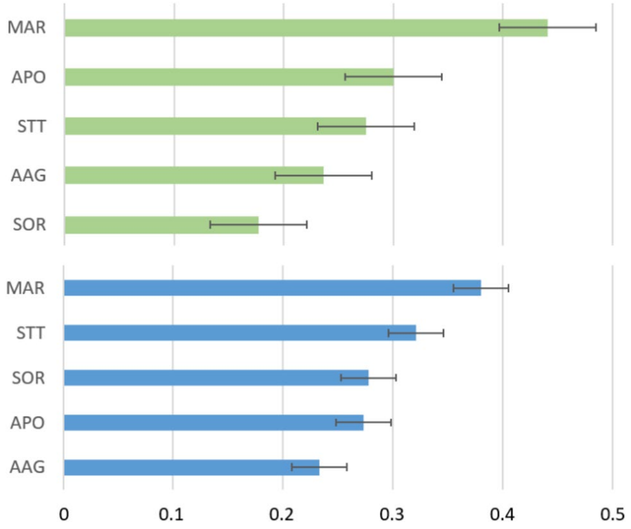

Fig. 2 Activity levels and standard deviations (*x*-axis) in spring (green bars) and summer (blue bars). Abbreviations (*y*-axis): MAR, *Microtus arvalis*; APO, *Apodemus* sp.; STT, *Sicista trizona*; AAG, *Apodemus agrarius*; SOR, Soricidae

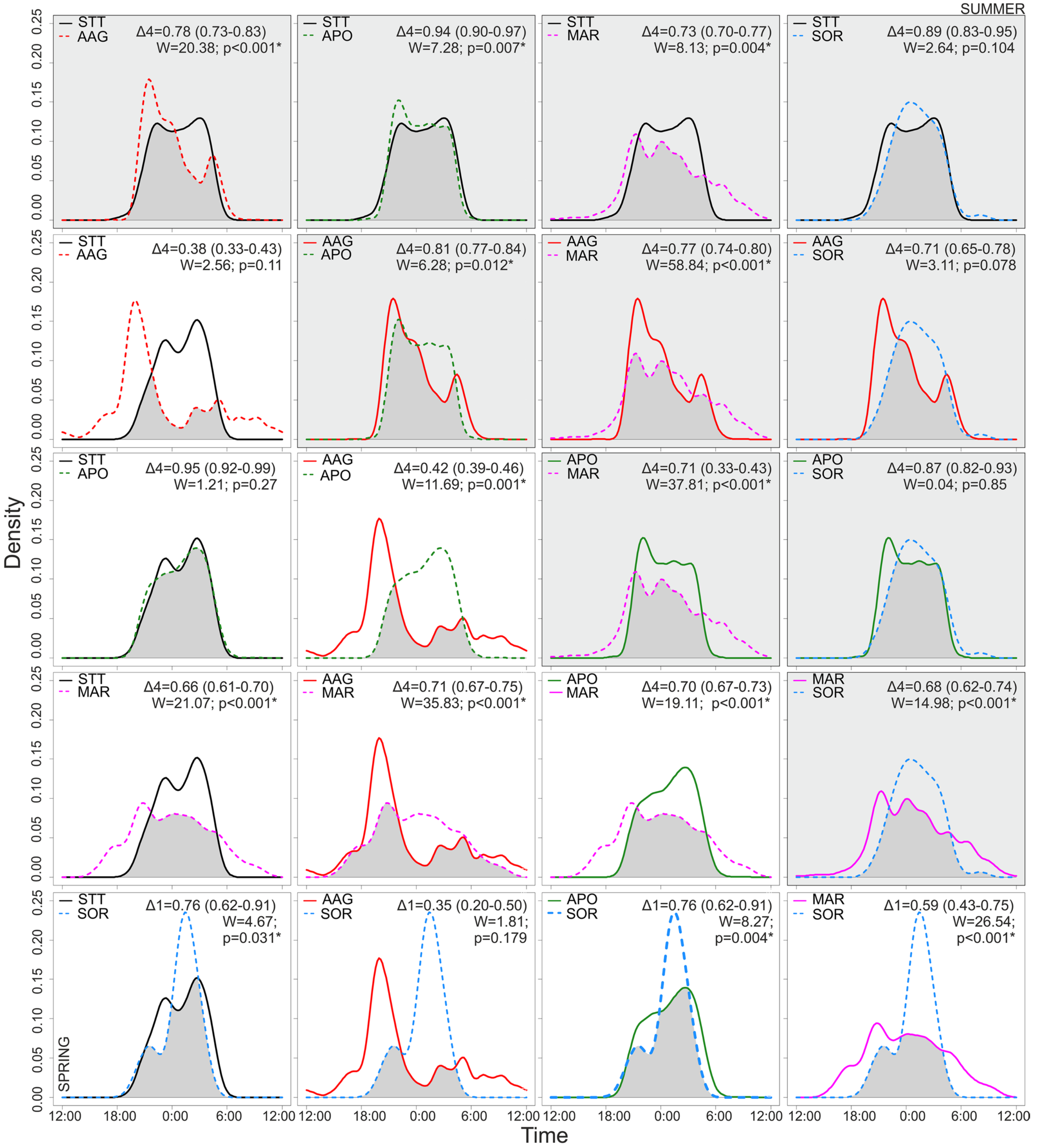

Fig. 3 Pairwise comparison of diel activity patterns between the studied small mammal species in spring and summer. Diagrams on white background (i.e., the lower left part) show spring, whereas diagrams on grey (i.e., upper right part) show summer activity curves; function colours follow species (cf. line colour on each draw). At the top of each graph: Δ4 (or Δ1 for shrews in spring) activity overlap coefficients obtained with the confidence interval, and Wald-coefficient (*W*) with the *p*-value

largely constant across seasons (Table 1; Online Resource 2). The pattern of *Microtus arvalis* and *Apodemus agrarius* was nearly exactly similar in both seasons; in the case of *A. agrarius*, a markedly high activation can be seen at dawn and a minor peak at dusk, and the peak downshifted a few hours later due to shorter summer nights. Despite not showing

Table 1 Daily activity pattern variations: summer *vs*. spring. Difference: differences between estimates of seasons; SE: Standard Errors of the differences; *W*: Wald statistics; *p*-values

	Difference	SE	*W*	*p*
Sicista trizona	−0.046	0.021	4.913	0.027
Apodemus agrarius	0.003	0.014	0.053	0.818
Apodemus sp.	0.026	0.017	2.186	0.139
Microtus arvalis	0.061	0.036	2.95	0.086
Soricidae	−0.101	0.054	3.459	0.063

significant differences, *Apodemus* also shifted peaks across seasons (Online Resource 2): its diel activity increased toward dusk in summer and peaked around dawn in spring.

The pairwise comparison of density estimates of daily activity patterns indicated various overlaps in the activity of the studied species. When comparing small mammals to one another, *A. agrarius* was the group that temporally overlapped the least with the other small mammals in spring (Fig. 3). Overlap indices also showed that all species temporally overlapped more in summer than in spring. Overlap values became more similar between the rodents in summer.

All comparisons between STT and the other small mammals, except for the *Apodemus* groups, resulted in significantly different activity patterns. On the other hand, STT and *Apodemus* were the groups with the most similar daily routines on average; their activity patterns were almost the same (Fig. 3) (Table 2).

Annual changes in total activity

Together with the diel activity, daily changes in the total activity of STT were also revealed from the images taken. In spring, the first individual was detected on the 11th of April, while the last one on the 19th of October. No photo of this species was recorded during winter. Activity levels of all other species were significantly reduced during early spring, except for STT in which the number of photos was the highest in spring, more precisely in early May (Fig. 4).

Identification problems?

Camera trapping may facilitate broad-scale surveys, but only if we are able to identify each species on the images. One of the objectives of this study was to test whether the STT could be identified with an acceptable level of certainty by images taken by trail cameras when a similar-looking sympatric rodent, *Apodemus agrarius* is present. We were able to identify 603 *S. trizona* and 1663 *A. agrarius*, and we were not able to decide which species (STT or *A. agrarius*) can be seen on the image in six cases. Consequently, the rate of successful identifications was almost 100%.

Table 2 Significance of overlap of diel activity between the studied species-pairs. Abbreviations: AAG, *Apodemus agrarius*; APO, *Apodemus* sp.; MAR, *Microtus arvalis*; SOR, Soricidae; STT, *Sicista trizona*. Delta (Δ): activity overlap coefficients; CI, bootstrap confidence interval; Difference: differences between estimates of species; SE, Standard Errors of the differences; *W*, Wald statistics; *p*-values

	Δ	CI	Difference	SE	*W*	*p*
Spring						
STT_AAG	0.38	0.33–0.43	0.039	0.024	2.561	0.110
STT_APO	0.95	0.92 –0.99	−0.024	0.022	1.210	0.271
STT_MAR	0.66	0.61–0.70	−0.166	0.036	21.072	<0.0001
STT_SOR	0.76	0.62–0.91	0.098	0.045	4.666	0.031
AAG_APO	0.42	0.39–0.46	−0.063	0.018	11.698	0.001
AAG_MAR	0.71	0.67–0.75	−0.205	0.034	35.827	<0.0001
AAG_SOR	0.35	0.2–0.5	0.059	0.044	1.809	0.179
APO_MAR	0.7	0.67–0.73	−0.142	0.033	19.114	<0.0001
APO_SOR	0.76	0.62–0.91	0.121	0.042	8.266	0.004
MAR_SOR	0.59	0.43–0.75	0.264	0.051	26.536	<0.0001
Summer						
STT_AAG	0.78	0.73–0.83	0.089	0.02	20.378	<0.0001
STT_APO	0.94	0.90–0.97	0.048	0.018	7.276	0.007
STT_MAR	0.73	0.70–0.77	−0.059	0.021	8.126	0.004
STT_SOR	0.89	0.83–0.95	0.043	0.027	2.637	0.104
AAG_APO	0.81	0.77–0.84	−0.04	0.016	6.281	0.012
AAG_MAR	0.77	0.74–0.80	−0.147	0.019	58.835	<0.0001
AAG_SOR	0.71	0.65–0.78	−0.045	0.026	3.111	0.078
APO_MAR	0.71	0.69–0.73	−0.107	0.017	37.809	<0.0001
APO_SOR	0.87	0.82 0.93	−0.005	0.024	0.038	0.845
MAR_SOR	0.68	0.62–0.74	0.102	0.026	14.988	<0.0001

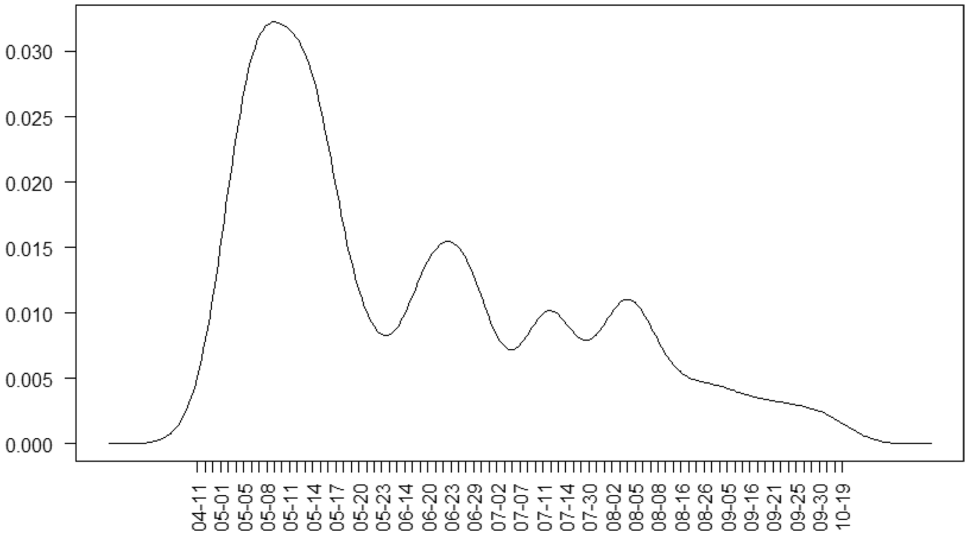

Fig. 4 Monthly variation in the average level of the birch mouse activity decreasing from the spring (beginning in May) through the fall (October), with a spring plateau centred in early May. *x*-axis: date (month-day), *y*-axis: density

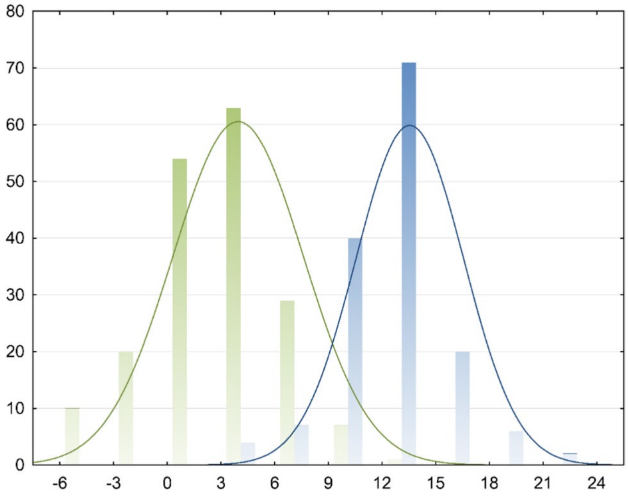

Fig. 5 Thermal characteristics of the active period of *Sicista trizona* in spring (green bars) and summer (blue bars). *x*-axis: temperature (°C), *y*-axis: number of observations

Thermal characteristics of the STT's active period

Activity peak was detected at around 4 °C in spring, and around 13°C in summer. Increases in detections were not associated with increases in ambient temperature (Fig. 5). In spring, we noted 29 STT detections when ambient temperatures were 0 °C or lower. On the 15th of May 2020 between 00:40 and 04:30, we observed an individual of STT three times when the air temperature was −6 °C. This is the thermal minimum recorded for this species in the study area. The thermal maximum is 24 °C, and it was measured on the 19th of August 2021 at 18:00.

Discussion

Mammals display a range of diurnal and nocturnal activity patterns. A remarkably high proportion of species have crepuscular or nocturnal lifestyles since the early evolutionary stage of mammals known as the "nocturnal bottleneck hypothesis" (reviewed by Gerkema et al. 2013). Diel activities are often endogenous and fluctuate on a light/dark scheme. Such cycles are referred to as "circadian" and are generally influenced by biotic and abiotic factors (Enright 1970; Benstaali et al. 2001). We investigated the diel and seasonal activity of *Sicista trizona* (STT) by using 24-h trail cameras in an undisturbed grassland plot of the Borsodi Mezőség Landscape Protected Area, NE Hungary, between 2019 and 2022. Cameras allowed collecting datasets that would be otherwise impossible by direct observation or trapping. Statistical modelling showed that STT exhibited a nocturnal activity pattern. The slightly bimodal pattern started at dusk and ended before dawn which is quite common in rodents (e.g., O'Farrell 1974; Meek et al. 2012b), and we also plotted a similar trend in three other co-occurring rodent species. The bimodal activity pattern enables an efficient selection of periods of the day with optimal temperatures for activity. It could be advantageous in areas with larger daily temperature fluctuations (Šklíba et al. 2007).

So far, information on STT's daily and seasonal activity patterns was limited to trapping results (Cserkész 2021) or observations in an ex situ population (Pivarcsi et al. 2021). Our study surveyed STT using non-invasive camera trapping continuously from March to November covering two seasons: spring and summer. Autumn was omitted due to the limited number of detections and so was winter when STT hibernates. As a basic assumption, we wanted to know whether the STT could be detected and identified with an acceptable level of precision by cameras when a similar-looking sympatric small mammal, the *Apodemus agrarius*, was present. Our study suggested that the two species are both reasonably identifiable in infrared black and white images. For both species, pelage colouration differs adequately to distinguish them (see Fig. 1).

Annual changes in total activity

The density of STT detections differed to a greater extent across months (Fig. 4). Low level of activity in April was followed by a peak in early May and a sharp decline until low levels were reached again in August and September. The high-level activity in early May must be connected to the mating season in this month. Pitfall trappings were also prominently successful in May; moreover, males were captured at a markedly higher rate indicating their main role in searching for a mating partner (own unpublished data). Low-level activity in summer may be the outcome of summer torpor periods which were observed in captive specimens (Cserkész 2011; Pivarcsi et al. 2021). STTs may stay in the nests, overall reducing their movement and energy expenditure during these days; however, some lower levels of activity may still be present. Vásárhelyi (1929) noted that STT stores food in its underground nest, even if it blocks the entrance, and stays in there until it runs out of food stock. However, this behaviour was not confirmed by the latest trials, and STT kept in terrarium never stored food (Cserkész 2011; Pivarcsi et al. 2021) although this can simply be the result of ease of availability of food under captive conditions.

As an alternative interpretation, the higher detection rate of STT in spring may be due to the lower number of other small mammals in this season. STT is the only obligatory hibernator within this small mammal community; its abundance is not decreasing significantly during winter. Populations of other species suffer sharp declines during winter; therefore, the initial population sizes are low in early spring. Later, thanks to their high reproductive rate, the population sizes are starting to increase sharply, and overwhelming the bait stations, diminishing the rate of STT.

Diel activity

There was no systematically collected dataset on activity patterns of a free-ranging sminthid species before. We observed no diurnal and crepuscular activity of STT; consequently, it can be regarded as a nocturnal species exhibiting bimodal activity peaks at dawn and dusk when temperatures were relatively cool. We found that its activity patterns also changed between spring and summer: during the year, the activity peak shifted from before midnight to after midnight. Our study systematically surveyed STT activity across both spring and summer; however, effort should be increased in autumn and early spring.

Thermal characteristics of the active period were also depicted: individuals were active between −6 and 24 °C, and definitely not sensitive to cold as it was predicted by earlier observations (Vásárhelyi 1929). We believe that cold temperature during the vegetation period is unlikely to be a factor limiting activity patterns of the STT.

Roll et al. (2006) reviewed the activity patterns of rodents worldwide and found that murids were predominately nocturnal. They found temperature and habitat to be the chief factors influencing whether rodents were diurnal or nocturnal with rodents in cold climates being more active in daylight. The diel activity pattern of all target small mammal species was dominantly nocturnal in this study; however, *M. arvalis* and *A. agrarius* showed slight diurnal activity; moreover, some activity pattern shifts occur throughout the seasons. These shifts fall mainly on activity peaks, such as in the case of *Apodemus*—its activity peak moves toward dusk from spring to summer. Around noon and early afternoon when the ambient temperature was the highest, almost all small mammals were inactive in summer; some activity in the afternoon was detected typically in spring when the temperature is cooler in Hungary.

In this study, the diel activity pattern of *M. arvalis* was also mainly nocturnal with low-level activity in the morning; however, other studies (e.g., Lehmann and Sommersberg 1980) and handbooks (e.g., Denys et al. 2017) mention it as a diurnal or crepuscular species with ultradian (i.e., active period in every 2–3 h) feeding rhythm (Gerkema et al. 1993). Briner et al. (2005) found a polyphasic activity pattern with a phase length of 1.7 h in the case of *M. arvalis* inhabiting wildflower strips can be considered high-quality habitat with a trend toward diurnal activity. Therefore, more activity phases could be expected in a high-quality habitat than in a poorer one. Also, predation pressure influences activity patterns in microtine rodents (Halle 1993; Jacob and Brown 2000). Daytime could be more dangerous than twilight or night when only the activity patterns of potential predators were considered (Randler and Kalb 2020). If protection from predators is sufficient, activity phases should be equally distributed over a given day. The Borsodi Mezőség, with its warm and continental climate, is home to a variety of diurnal birds of prey, which may explain the mainly nocturnal activity of all target small mammals. Inactivity at noon and early afternoon can be also explained by avoiding the part of the day when ambient temperature is the highest. Global clime change associated with drier and more hot summers in Central Europe (Göndöcs et al. 2018) can result in shifting to a more nocturnal activity of otherwise diurnal animals because nocturnal niches might be favoured in a warming world (Bonebrake et al. 2020; Buchholz et al. 2021). Possibly, mammals will be able to reduce heat stress associated with climate change and increased near-surface air temperature by limiting their activity during the hottest part of the day, shifting to eventually being active nocturnally (Levy et al. 2019; Fuller et al. 2021).

Apodemus agrarius was nocturnal and crepuscular in this survey, and this finding is supported by other studies in rural and natural habitats (Lee and Rhim 2016; Łopucki and Kiersztyn 2020); however, in urban habitat, Łopucki and Kiersztyn (2020) found significant activity in the daytime. *A. sylvaticus* and *A. uralensis*, grouped in *Apodemus*, were also evidently nocturnal which is consistent with other observations (Wolton 1983; Denys et al. 2017).

Shrews were also completely nocturnal with a typically unimodal activity pattern with no movements detected during daylight hours. Otherwise, *Sorex araneus*, the most frequent Soricidae in Borsodi Mezőség, was characterised by Merritt and Vessey (2000) and Ivanter and Makarov (2002) as a multiphasic type of daily activity with a peak of mobility at night.

Overlap in activity

Despite similar diet or habitat requirements, time partitioning could favour the coexistence of species that occupy the same guild. The number of studies focusing on the temporal niche of sympatric small mammals is quite limited yet (Di Cerbo and Biancardi 2013; Diete et al. 2017; Gracanin and Mikac 2022). Some studies could demonstrate that temporal avoidance can reduce competition and thus facilitate species coexistence (Meek et al. 2012b; Andreoni et al. 2020; Viviano et al. 2022). If we take into consideration the observations of Vásárhelyi (1929) on the shy behaviour of STT, we could suppose that STT would avoid other, dominant rodents (e.g., the murids). But we found no indication that STT try to keep out the other small mammal's way; even STT and *Apodemus* were the groups with the most similar daily routines on average (see Fig. 3). By comparing Kernel density functions in pairs, we found high overlaps indicating the lack of competitive interactions suggesting that the temporal niche partitioning was small among them. This is supported also by those images that depicted STT more times in company with murids and voles. Low-level overlaps were found only in the case of *M. arvalis*/*A. agrarius* vs. STT, and it is due to the crepuscular activity of these common rodents.

Limitations

Although our study can be regarded as pioneering in many respects, we also need to consider its potential limitations. Activity is only counted when animals visit fixed camera-trap stations, and no information of activity away from the camera traps (e.g., in or near burrows) was measured. As for all the target species in this study, *Microtus arvalis* was recorded as active mainly during the dark periods, even though this species, unlike the others, is known frequently to be active during the day (Briner et al. 2005). We also noted the diurnal activity of this species during pitfall trappings. It is possible that some diurnal activity of the target species was missed by the trail camera when the difference between body and ambient temperature is small (Meek et al. 2012a). However, the number of photographs missed is likely to be very few, as we did get many images of diurnal snails, passerines, and lizards. Moreover, we were not able to reliably distinguish between adults and juveniles and therefore did not compare the activity pattern between age groups.

Utilisation of baits and attractors is controversial. Baited camera traps are known to have an influence on species detection and measures of population demographics compared with non-baited traps (Mccoy et al. 2011; Randler et al. 2020) and mainly represent feeding activity (Di Cerbo and Biancardi 2013). Moreover, it was reported that baits and attractors can have different effects depending on individuals and species (Meek et al. 2014; Rovero and Zimmermann 2016; Stewart et al. 2019). Furthermore, bait preferences may vary between different populations (Morgan 1982) or may change seasonally depending on the availability of natural food resources (Bennett and Baxter 1989; Claridge et al. 1993). Despite all these disadvantages, 60% approximately of trail camera studies directed the devices at some form of attractant supplied with bait or lure 23% of the studies (Burton et al. 2015). Moreover, baiting can be particularly important for rare and elusive species that can be difficult to detect in the wild, especially when they are present in low local abundance (Diete et al. 2017). Overcoming "bait-effect," the negative consequence of the utilisation of baits, we want to take steps toward a survey running without baits in the future even if it is going to be at the expense of efficiency.

Implications for conservation

Reliable information about the occurrence and distribution of endangered, nocturnal small mammals is usually challenging and expensive to obtain but remains critical for developing effective species conservation plans and habitat management methods. In Central Europe, the species of greatest concern are mostly small mammals (e.g., *Nannospalax* species; see Csorba et al. (2015)), cryptic in behaviour or rare, making them difficult to detect. As a flagship species in Hungary, STT is a heavy focus of conservation efforts, listed as strictly protected and a target species of more LIFE projects financed by the European Union and the Hungarian government.

Our study offers insight into the diel activity patterns of a small mammal community that had not previously been investigated. This study could be valuable for field biologists to improve the schedule of live-trapping surveys, and for zookeepers for understanding the general ecology of this species. Indeed, one of the biggest challenges in the conservation of the declining STT is the lack of an effective and non-invasive survey method for monitoring its numbers. Developing survey protocols for the species is challenging because very little is known about the seasonal and diel activity patterns. Such information is difficult to obtain in the field by pitfalls, because the detectability of STT may be further reduced by disturbance and habitats may be hurt by the digging of field workers. Trail cameras are proved to be effective tools for unravelling activity patterns of the STT, and they will probably be useful for estimating abundance, too. Our survey and ecological observations are important for the survival of the last STT population, allowing the management of the protected area to plan rapid actions in favour of this endangered species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-022-00656-0.

Acknowledgements We are grateful to Jeroen van der Kooij for the inspiration and useful advice at the early stage of the survey and to the Bükk National Park Directorate and ZooBudapest for their cooperation. We appreciate the helpful comments of Emiliano Mori and an anonymous reviewer given during the peer-review process. We thank Dávid Ferge and Péter Balázsi for their help in the field activities.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Tamás Cserkész and Csaba Kiss. The first draft of the manuscript was written by Tamás Cserkész, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by University of Debrecen. This fieldwork was supported by the GRASSLAND-HU LIFE (LIFE17 IPE/HU/000018). The work of GS was supported by the OTKA Young Researcher grant (FK 137962).

Availability of data and material The datasets generated and/or analysed during the current study are available from the first author on reasonable request.

Code availability The code generated during the current study is available from the second authors on reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate All authors agreed to participate in this study and co-authorship.

Consent for publication All authors agreed with the content and that all gave explicit consent to submit

Conflict of interest The authors declare no competing interests.

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