Circadian and ultradian rhythms in free living bank voles (*Myodes glareolus*)

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Abstract: Data of 17,065 recordings in baited camera traps in the Netherlands revealed that bank voles (*Myodes glareolus*) expressed most activity between sunset and sunrise, with an exception for June-July. When corrected for the duration of respectively night and day the nocturnal bias was observed in all months, but was stronger when nights were longer. On top of the circadian rhythm, a rather distinct ultradian rhythm was superimposed, especially during the night. Activity peaked just after sunset in August-March, during sunset in April-May and before sunset in June-July, to be followed by a series of 1-4 distinct peaks and lows during the night. For full cycles (from peak to peak or low to low), mean duration was 224 minutes. Activity was highly synchronised between traps (individuals), areas separated by unsuitable habitat (populations) and years.

Keywords: bank vole, *Myodes glareolus*, activity, camera trap, circadian, ultradian, season, Struikrover.

Introduction

From August 2018 through January 2020 activity patterns of mustelids were studied in various habitats in and near a river valley in the northern Netherlands. The study used camera traps in baited tubes. Apart from mustelids, many other mammal species were recorded. Bank voles (*Myodes glareolus*) appeared to be one of the most frequent visitors of the tubes. In this paper, we present an analysis of the camera trap recordings of bank voles that were made over the study period. The aim was to increase our insight into their daily activity patterns across the year.

Methods

The camera traps were situated in a Struikrover®, a pvc tube painted in camouflage colours with a diameter of 20 cm, cut at an angle of 45° and covered by a lid at the other end. The longest length (along the bottom) amounts to 40 cm. The tube holds a trail camera in the back and bait at the other end. On top of the tube, just in front of the camera, is an opening with a diameter of 10 cm, covered by plexiglass. This opening provides the camera sensors with extra light, in order to avoid overexposure of pictures during sunny conditions. The camera lens is fitted with one of the lenses of a pair of reading glasses (for most camera types +3) in order to reduce the focal length to 35 cm. The cameras were set to make two or three pictures when triggered, followed by a one-minute pause. The Struikrovers were baited with a slightly opened sardine can. Bait was refreshed every 2-4 weeks.

The devices were placed in the half open landscape of the river valley of the Drentse Aa (6.64°E, 53.03°N; Province of Drenthe, the Netherlands). This area used to consist of wet meadows, hedgerows and woodlots, embedded in a small scale agricultural landscape

Table 1. Number of locations where bank voles were observed during two-monthly periods, the number of records and the proportion (%) of records for the top three sites, and the rest.

	Dec-Jan	Feb-Mar	Apr-May	Jun-Jul	Aug-Sep	Oct-Nov
n locations	14	7	11	11	13	16
n observations	2811	2554	1153	1049	3009	6489
% 1	41.7	57.7	46.7	54.7	25.3	31.0
% 2	27.9	30.5	39.2	18.2	22.7	18.7
% 3	10.9	7.8	6.9	10.6	19.2	15.5
% others	19.6	4.1	7.2	16.5	32.8	34.8

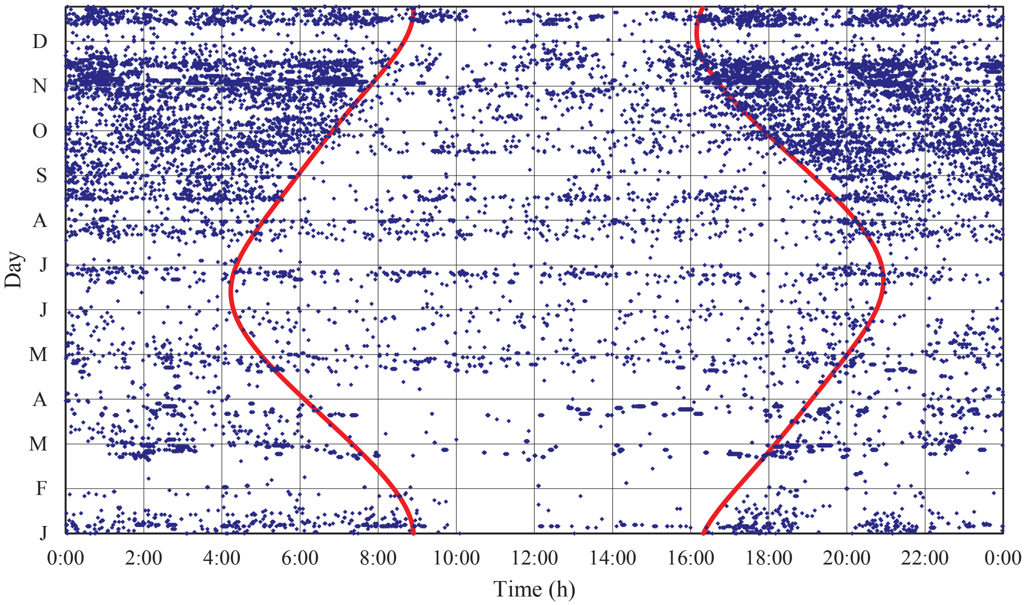


Figure 1. Monthly and diel distribution of bank vole observations via camera traps, relative to sunrise and sunset (red lines). Each dot represents one observation.

with fields, heaths and villages. From 1970 onwards the vicinity of the Drentsche Aa was drained, agriculture intensified and field sizes increased after land consolidation. Despite conservation measures, the river valley gradually desiccated. By the late 20th century ditches were filled in order to stop drainage, after which large sections of the river valley became very wet and partly changed into marshland. When possible, mowing takes place once a year in August-October (Spek et al. 2015). Several Struikrovers were deployed in other habitats like heaths and woodland. In most cases we placed the camera traps in linear vegetation elements or ecotones.

The data cover the period from 2 August 2018 through 19 January 2020. The Struikrovers were deployed at 42 locations and bait was refreshed 120 times (referred to as 'sessions'). Across all two-monthly periods, bank voles were identified at least at seven locations. In some periods the data were strongly biased by records from, possibly, single individuals at a single site (table 1). The nearest neighbour distances between devices where bank voles were observed varied between 59 en 4386 m (mean=526 m, sd=829, *n*=35). The cameras were triggered 57,657 times, 17,065 of

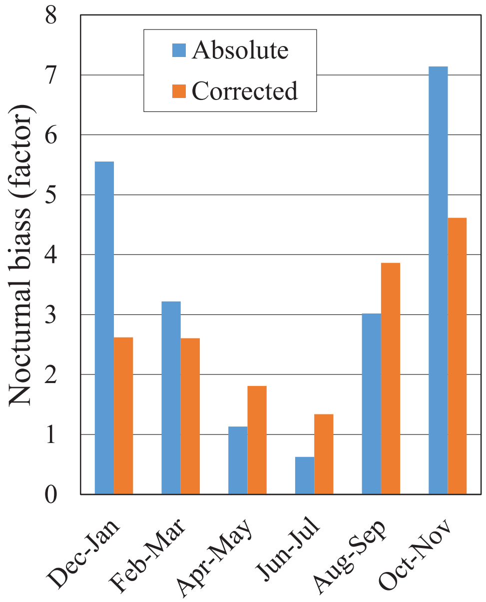


Figure 2. Intensity of nocturnal activity of bank voles, expressed as the proportion of observations between sunset and sunrise relative to the number observed between sunset and sunrise (1 = equal numbers during night and day; 2 = twice as many nocturnal observations etc.). Both the proportions in absolute numbers and in numbers corrected for the sum of day- and night-hours in the given periods are given. Based on data in table 1.

which referred to bank voles. All observations were registered in Central European winter time and related to local sunrise and sunset. Due to variable sample sizes, we used two-monthly periods: December-January, February-March, and so on. For the same reason we lumped data of different locations and years (see also Discussion). Calculations were made in Microsoft Excel.

It is possible that the sensitivity of the cameras was negatively influenced by high temperatures. This may have reduced the number of daytime observations during some very hot (>30°C) summer days. We assume this did not affect the general patterns as found in this study.

Results

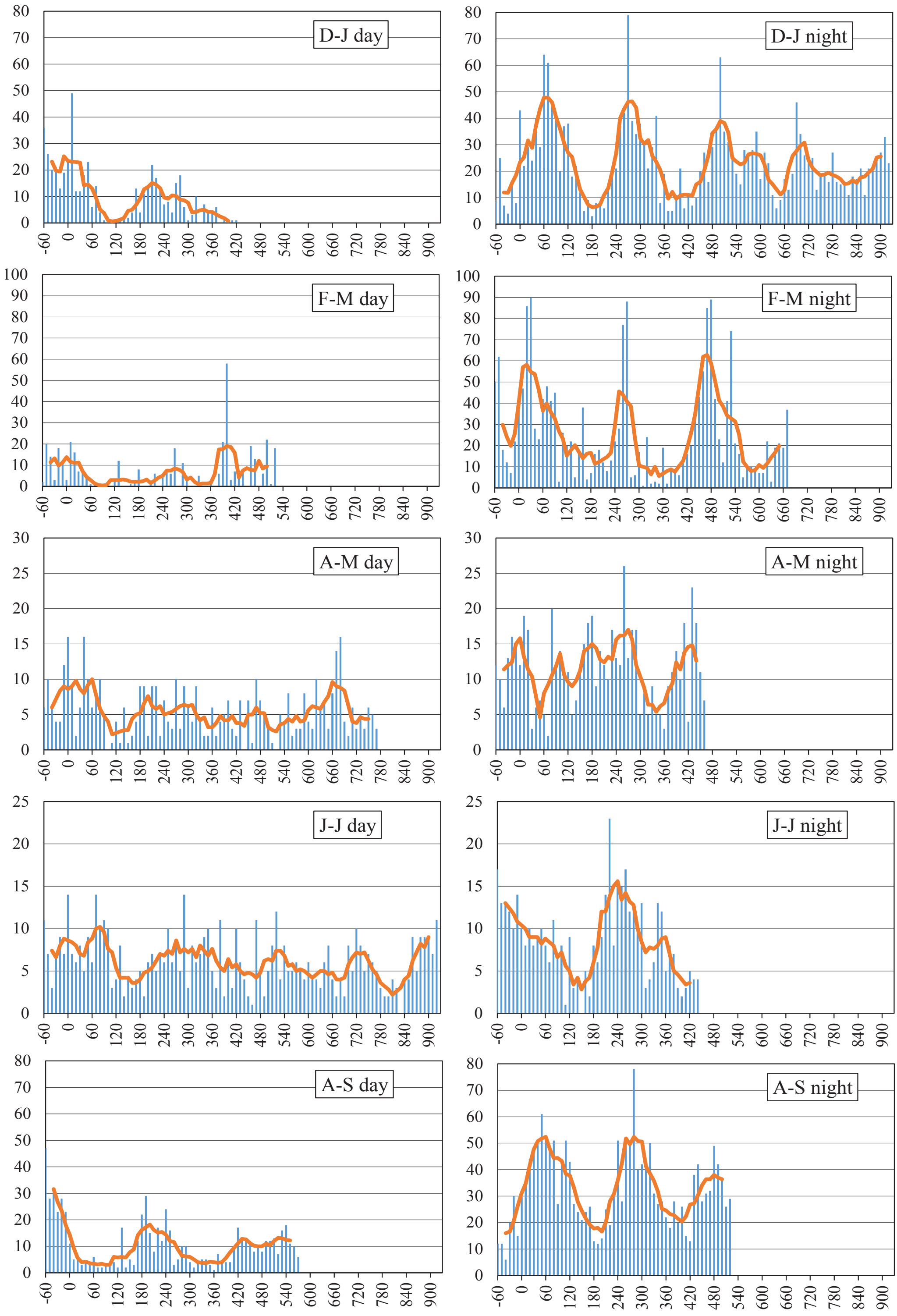
Circadian rhythm

Throughout the year, bank voles were mainly nocturnal, especially during September-April and least so during May-August (figure 1). On average bank voles were 2.8 times more frequently observed between sunset and sunrise (night) than between sunrise and sunset (day). Nocturnal activity was most outspoken in October-November. In contrast, in June-July most observations were recorded during daytime (figure 2), which mainly derives from the lengthy period of daylight in summer. When corrected for available day- and night-hours, bank vole activity was always biased towards the night but three times more so in October-November than in June-July.

Ultradian rhythm

On top of the circadian rhythm, a rather distinct ultradian rhythm was superimposed (figure 1), albeit with variable intensity across the year. An ultradian rhythm was especially evident during August-March (figure 3), with an activity peak just after sunset, normally within the hour, to be followed by a series of 2-4 distinct peaks and lows during the night. In April-July the activities started already about 1-2 hours before sunset and peaked at sunset during April-May and an hour before sunset in July and August. During April-May nocturnal activity was rather diffuse, but in June-July a distinct peak 4-5 hours after sunset was registered, fading away towards sunrise (figure 3). A diurnal activity peak at around 3-4 hours after sunrise was only evident in December-January and in August-September.

The mean interval between peaks and lows amounted to 115 minutes (sd=22.9, n=19) and between lows and peaks 109 minutes (sd=21.8, n=15), but the range was considerable. Cycles could theoretically be shortened by sunrise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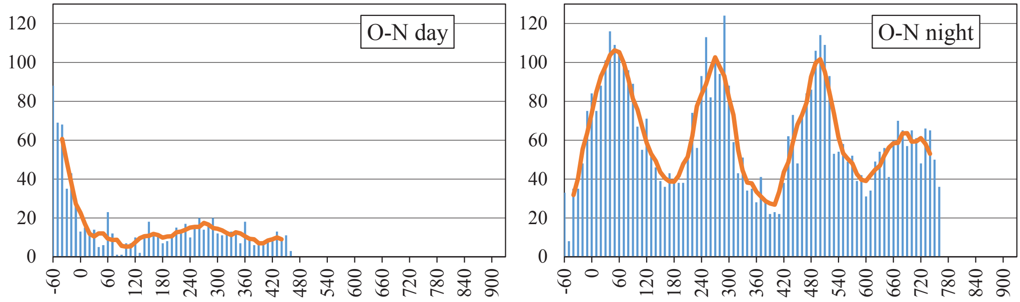

Figure 3. The number of bank voles recorded across the day per 10-minute periods relative to sunrise (left, one hour before sunrise to one hour before sunset) and sunset (right, one hour before sunset to one hour before sunrise), including running averages of five periods. Due to variable lengths of daylight periods and sample sizes, each time series is cut off at the shortest day or night.

or sunset, but cycles at the end of the day or end of the night were not shorter than other cycles. Since there may be some noise in the exact moment of a peak or a low (figure 3), we checked if very short cycles were followed by longer ones, but this was not clearly the case. The mean duration of full cycles (from peak to peak or low to low) was 224 minutes, ranging from 180-290 minutes (sd=27.7, *n*=22).

Discussion

Synchronized activity patterns between locations and years: a biased finding?

The activity patterns derived from the camera traps may have been biased given the fact that data of various locations have been lumped and sometimes more than 50% of the data in some months came from a single site. Generalising from meagre datasets may coincidentally produce synchronised activity patterns based on one or few individuals. The only validation possible came from October-November when a substantial number of locations provided data. The bank voles at these sites showed a highly synchronised activity pattern, in line with the finding reached for the entire dataset (figure 4). The autumn locations were sufficiently apart to exclude the possibility that the same individual was involved (Johnsen et al. 2019). Even the activity pattern at a location 2.7 km apart from the others and separated from these by unsuitable habitat (open arable fields) was mostly in line with the pattern in general. We therefore presume that ultradian rhythms in bank vole activities are synchronised over large areas when conditions are more or less similar. Therefore it is probable that the rhythms are caused by an individual internal instead of a social mechanism, in agreement with Halle (2000).

Interestingly, for December-January the data originated from December 2018 and 2019 and January 2019 and 2020, i.e. covering two separate years. The patterns in both years were highly synchronised at sunset, but at the end of the night the pattern in 2018/2019 had developed a delay of an hour towards the end of the night (figure 5). This may indicate that the ultradian rhythm is not ruled by an endogenous clock alone and that environmental factors may influence the pattern to a certain extent.

Circadian rhythm

The activity of bank voles is reported either as nocturnal (Bleicher et al. 2019), diurnal (Jędrzejewska & Jędrzejewski 1990) or variable according to season (Ylönen 1988). The choice of a predominantly diurnal or noctur-

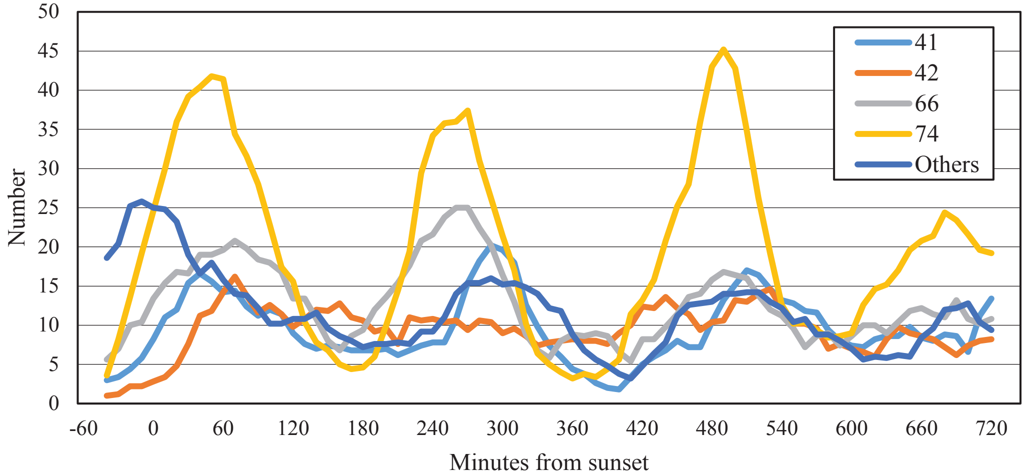

Figure 4. Number of registrations (moving averages per five ten-minute periods) of bank voles in the four most attended Struikrovers in October-November 2019. The category "Others" represents the summed observations in the other less attended Struikrovers. Nearest neighbour distances were 290 m (Struikrover 41), 371 m (42), 299 m (66) and 2750 m (74).

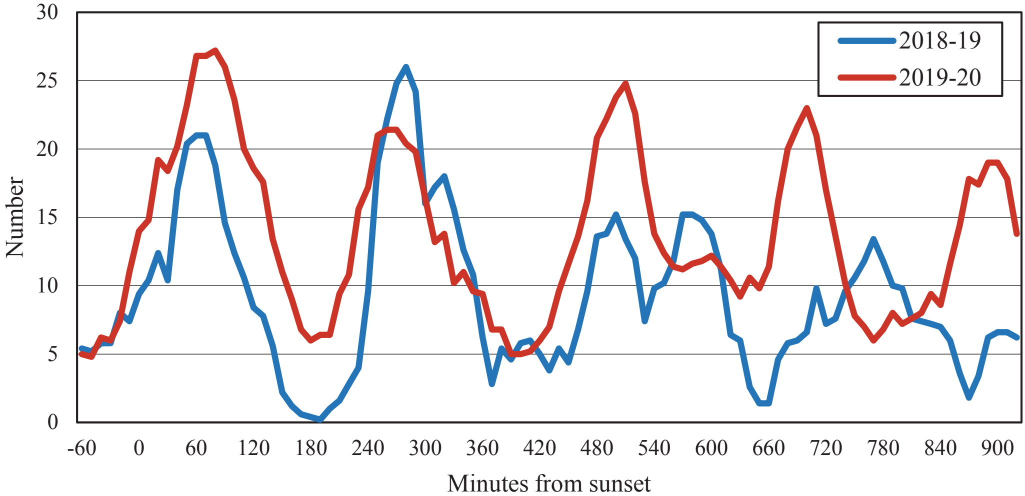

Figure 5. Number of registrations (moving averages per 5 ten-minute periods) of bank voles in December-January 2018-2019 and December-January 2019-2020 (different locations).

nal activity pattern is presumably a trade-off between energetic demands and the risk of predation. Foraging during the day could be more profitable due to better visibility of food items and higher ambient temperatures. In our study area, in the temperate climate zone, and under natural conditions, we more often encountered bank voles on foot under sunny conditions than when overcast, especially in spring when ambient temperatures are still rather low.

At night prey species may be better detectable due to – on average – lower wind speed and higher air humidity. Our study via camera traps revealed the presence of a number of (partially nocturnal) predators, i.e. pine marten (*Martes martes*) (97% of the images trig-

Bank vole smelling the small opening of a sardine can in a Struikrover. Taarlo, 15 May 2018. *Photo: Matthijs Smaal.*

gered by night, *n*=32), beech marten (*M. foina*) (96%, *n*=49), red fox (*Vulpes vulpes*) (80%, *n*=5), badger (*Meles meles* (75%, *n*=4), Western polecat (*Mustela putorius*) (35%, *n*=17), stoat (*M. erminea*) (33%, *n*=9) and weasels (*M. nivalis*) (26%, *n*=277). Numbers may be indicative of relative abundance. Aerial predators in the study area were represented by barn owl (*Tyto alba*) (nocturnal) and common buzzard (*Buteo buteo*) (diurnal), of which the latter has a local density of about one pair per 200 ha (van Manen, unpublished results). The barn owl is probably less common. The composition of the local predator guild suggests that the predation risk for bank voles may be highest during daytime due to the relative abundance of weasel and common buzzard. The predominantly nocturnal activity pattern of our bank voles may be a trade-off between two 'evils', of which nocturnal predators are the lesser. This is supported by an experimental study in Poland, where bank voles in semi-enclosures became more nocturnal in the presence of weasels (Jędrzejewska & Jędrzejewski 1990).

A nocturnal bias in activity was strongest during August-November and decreasing during December-July. This could be a result of maximum food availability in autumn, decreasing food availability in the course of the winter, the increasing daylength in the course of spring and summer and an increase in food demand due to reproduction, or a combination of several or all of these factors.

Ultradian Rhythm

Activity bouts in *Microtus* voles have been linked to a feeding pulse. In these species the duration of an above-ground activity bout takes about two hours. Activity cycles could depend on the time needed to digest meals, with on average longer cycles in larger species (Lehmann 1976, Daan & Slopsema 1978, Halle 2000). Relative to size, our bank voles had rather long activity bouts as compared to common voles of the same weight (Daan & Slopsema 1978). This difference might be related to differential diets.

As the observed ultradian rhythm was especially outspoken in periods when the voles were most nocturnal, a strongly synchronised ultradian rhythm might indicate high food availability. This is suggested by Grodzinski (1962), who found that activity patterns faded when animals were offered only nutrient-poor food, but contrasts with Halle (2000) who states that ultradian rhythms were not affected by deprivation of food.

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Samenvatting

Activiteitritme van vrijlevende rosse woelmuizen

Tussen 2 augustus 2018 en 19 januari 2020 hebben we in en rond het beekdal van de Drentsche Aa op 42 locaties onderzoek gedaan naar het voorkomen van kleine zoogdieren met behulp van Struikrovers®. Een Struikrover is een pvc-buis, met daarop een cameraval gemonteerd en een lek geprikt blikje sardine, dat als aas dient. Om een scherp beeld op 35 cm van de camera mogelijk te maken, werd een brillenglaasje voor de lens gemonteerd. De locaties van de Struikrovers bestonden in enkele gevallen uit bos, maar meest uit houtwallen en slootranden in halfopen gebied. Het systeem was in hoge mate aantrekkelijk voor rosse woelmuizen (*Myodes glareolus*), die op 17.065 afzonderlijke momenten als bezoeker van een Struikrover werden geregistreerd. Ze bleken daarbij in de meeste maanden voornamelijk nachtactief, alleen in de periode juni-juli waren er meer registraties overdag dan ’s nachts. Echter, wanneer werd gecorrigeerd voor het aantal beschikbare uren, bleek dat ook in juni-juli rosse woelmuizen ’s nachts vaker werden geregistreerd dan overdag. In zijn algemeenheid vertoonden ze minder activiteit overdag naarmate de nachten langer waren. Naast een dag-nacht ritme hielden de muizen er ook een kortere activiteitcyclus op na, waarvan de gemiddelde duur 224 minuten bedroeg. Dit ritme bestond uit een serie van 1-4 cycli die begonnen rond zonsopkomst en zonsondergang. Het aantal cycli hing samen met de duur van de dag of nacht en nachtcycli waren meer uitgesproken dan overdag. De cycli verliepen synchroon tussen plekken die van elkaar waren gescheiden door voor rosse woelmuizen ongeschikt habitat en eveneens in dezelfde periodes in opeenvolgende jaren (december-januari 2018-2019 en 2019-2020).

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