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Temporal behaviour profiles of *Mus musculus* in nature are affected by population activity

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HIGHLIGHTS

- This is the first field study on mice circadian rhythms without enclosure.
- Mice shift some of their activity to the day when population activity increases.
- Mice show seasonal rhythms in activity duration.
- Mice may estimate population density using olfactory cues.

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ABSTRACT

Animals have circadian clocks that govern their activity pattern, resulting in 24 h rhythms in physiology and behaviour. Under laboratory conditions, light is the major external signal that affects temporal patterns in behaviour, and *Mus musculus* is strictly nocturnal in its behaviour. In the present study we questioned whether under natural conditions, environmental factors other than light affect the temporal profile of mice. In order to test this, we investigated the activity patterns of free-ranging *M. musculus* in a natural habitat, using sensors and a camera integrated into a recording unit that the mice could freely enter and leave. Our data show that mice have seasonal fluctuations in activity duration (6.7 ± 0.82 h in summer, 11.3 ± 1.80 h in winter). Furthermore, although primarily nocturnal, wild mice also exhibit daytime activity from spring until late autumn. A multivariate analysis revealed that the major factor correlating with increased daytime activity was population activity, defined as the number of visits to the recording site. Day length had a small but significant effect. Further analysis revealed that the relative population activity (compared to the past couple of days) is a better predictor of daytime activity than absolute population activity. Light intensity and temperature did not have a significant effect on daytime activity. The amount of variance explained by external factors is 51.9%, leaving surprisingly little unexplained variance that might be attributed to the internal clock. Our data further indicate that mice determine population activity by comparing a given night with the preceding 2–7 nights, a time frame suggesting a role for olfactory cues. We conclude that relative population activity is a major factor controlling the temporal activity patterns of *M. musculus* in an unrestricted natural population.

1. Introduction

To anticipate environmental changes caused by the Earth's rotation around its axis, animals have developed an innate circadian clock. In mammals this clock is located in the suprachiasmatic nuclei (SCN), at the base of the hypothalamus. SCN neurons have a genetic ability to generate circadian rhythms. The rhythms generated by the SCN as a whole are entrained to outside factors – the so-called *Zeitgebers* – the most important of which is light. In the last decade, research has yielded considerable insight into the genetic properties of rhythm generation and the effects of light on the biological clock (e.g. [27,64]). Most of these studies were performed in a laboratory setting, where environmental conditions are controlled artificially. Under these conditions, mice, hamsters and rats are strictly nocturnal ([12,51,63,39,19]). In contrast, under more natural conditions these animals display activity patterns that deviate substantially from activity in the laboratory [32,34]. For example, hamsters in the wild have major activity peaks during dawn and dusk whereas in the laboratory they are exclusively nocturnal [19,63]. Attempts to study temporal patterns in animal behaviour under natural conditions have often been performed in outdoor enclosures, and although enclosure studies are closer to a natural situation than laboratory studies, they still miss many aspects of natural diversity in

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behaviour, physiology, genetics, ecology, etc. (see also [36,39,56,69,9,32]. Most importantly, dispersal, which is generally induced by social factors such as dominance/submission, aggression and/or the availability of mates cannot occur in an enclosure. We hypothesise that a number of external factors, not present under laboratory conditions, affect the temporal profile of *Mus musculus*.

Our recording equipment was installed around a food source, and could be freely accessed by any animal up to the size of a rat. We recorded the behavioural activity patterns of any visiting animal over a period of nearly two years, thus acquiring a multitude of video recordings of various animal species that visited our equipment. Among these animals, *M. Musculus* was the most commonly observed species. We then investigated the influence of seasonal changes in day length (photoperiod), temperature, variations in nocturnal light intensity, temperature, and population size on the behavioural activity pattern of these mice. Our study indicates that a high population activity affects temporal patterns in the behaviour of wild mice.

2. Methods

2.1. Recordings

A recording unit was built and installed in a natural environment (>20 m from the nearest house) in a spacious, green area on the outskirts of the city of Leiden, the Netherlands. The unit consisted of a cage-like structure (100 cm × 70 cm × 70 cm) with a running wheel and an infrared camera, motion detector, temperature sensor and light sensors installed in the roof (Fig. 1). Mice and other small animals could freely enter and leave the recording unit. To attract animals, a mixture of food (standard rodent chow and chocolate crumbs) was available ad libitum. Food was replenished before it ran out about once a week, at random times. When movement was detected by the passive infrared motion detection system (Panasonic EW AMN14112 PIR), the camera (Axis P1346 with a C70316–TS3V310 lens) automatically started a 20-second recording; this information was used to be

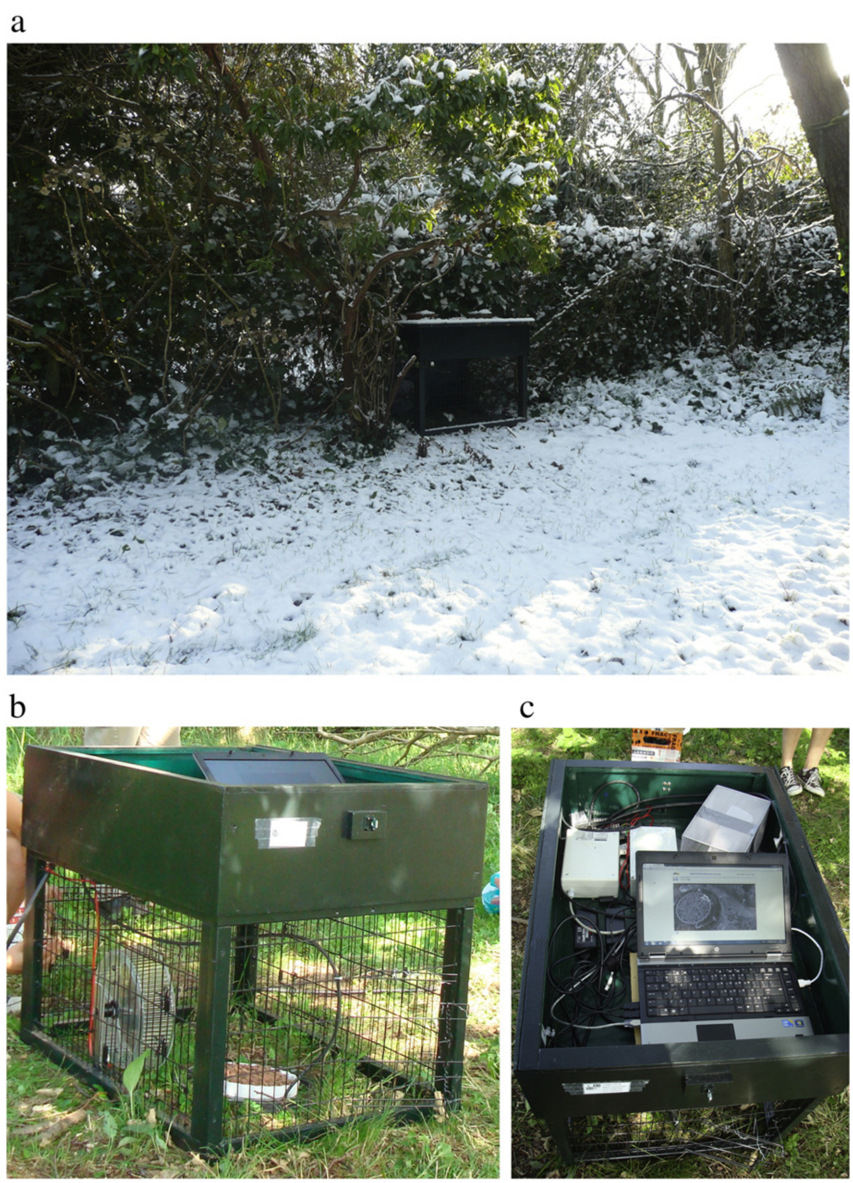

Fig. 1. Our experimental setup and its immediate surroundings. Panel a shows the setup as photographed during the experiment on 19 December 2009. Panel b shows a close-up of the setup. Note that even though the setup resembles a cage, small animals can freely enter and exit the recording area and food tray. Panel c shows the sensors, camera and laptop embedded in the roof of the cage.