



Original article

Nocturnal soil-surface behaviour of a giant earthworm in the Black Forest, SW Germany

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ABSTRACT

The behaviour of the large, deep burrowing earthworm *Lumbricus badensis*, endemic to the southern Black Forest, was studied in its natural beech and spruce dominated forest habitat. Using night vision cameras, nocturnal activities at the soil surface were recorded of adult individuals, over six consecutive nights in early summer. Behaviour consisted of sub-midden activity (near-surface, worm unseen), foraging, and mating, which accounted for 60, 34 and 6% of activity, respectively. Less than 1% of activity was over surface dispersal. Sub-midden activity, likely consisting of litter incorporation, feeding and casting, usually started before all others and continued throughout the night. This activity may relate to the role of the midden as an external rumen where the incorporated, initially recalcitrant, litter becomes more palatable. Foraging started later in the night, and apart from collection of and feeding on small litter items, it also involved displacement of large objects such as spruce cones. Surface litter samples collected from paired areas of high- and low-density *L. badensis* showed that higher density areas contained significantly less beech leaves and woody litter. The five recorded mating events all occurred after midnight and involved pre-copulatory exploratory behaviour. Mating itself was unlike that previously reported for earthworms and involved no mutual ventral alignment and long-lasting close contact. Instead, individuals attached in turns to the partner's clitellar region with anterior segments and only for a short period, with an equally short intervening period between the two attachments. This unexpected observation warrants further in-depth study. Rainfall was shown to interrupt aboveground activity, which may also be reduced on cloudless, moon-lit nights. With climate change already affecting Black Forest ecology and the indications of detrimental effects of increasing summer droughts on *L. badensis* juveniles, there is some urgency to better understand the environmental controls and conservation needs of this enigmatic ecosystem engineer.

1. Introduction

Earthworms (Annelida, Crassicitellata) are often the largest invertebrates in soil communities where they can form the major proportion of the soil faunal biomass. This is particularly so in rich, mull type soils that, to an important extent, result from their activities. The size variation of earthworm species is, however, large and in a community sample of adults can span an order of magnitude [1]. In Europe, particularly large earthworms are found among the so-called anecic or epi-anecic species [2]. The adults of these species inhabit vertical, deep penetrating home burrows which open at the soil surface, on to their nocturnal foraging and mating grounds. Of epi-anecic species, the dew

worm *Lumbricus terrestris* (Linnaeus, 1758), is perhaps most well-known. Over recent decades, observational studies of *L. terrestris*, using night vision video techniques, have provided new insights into the behaviour of epi-anecic earthworms which now appears richer than earlier thought. This involves findings on sexual behaviour as summarized by van Straalen [3] as well as homing [4] and foraging behaviour [5].

Among the European epi-anecic earthworms, there are exceptionally large species, where adult fresh mass is measured in tens of grams, whereas the mass of e.g., adult *L. terrestris* usually remains well below 10 g. An intriguing example is the giant earthworm of the Black Forest, the "Badischer Riesenregenwurm" *Lumbricus badensis* (Michaelsen, 1907) [6] (Suppl. Fig. 1). In a sample of field-collected individuals, their

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fresh mass reached 41 g, with a mean adult biomass of 25 g [7]. Endemic to the highlands of the southern Black Forest (Schwarzwald) of SW Germany [8], this species was thought to have recently evolved to local soil conditions from *Lumbricus friendi* (Cognetti de Martiis, 1904) [9]. However, recent DNA analysis suggests that *L. badensis* was part of a Central European *Lumbricus* species group which had their range fragmented during the last Ice Age and while others of this group may have become extinct, the ancestor of *L. badensis* survived in a refuge within or near the Black Forest [10]. Distribution of *L. badensis* is restricted to a relatively small geographical area, as it requires humid climatic conditions but can tolerate soils with low pH [11].

Lumbricus badensis was extensively investigated in the 1980s, producing novel information on its basic biology, ecology and ecosystem engineering role, particularly on its extensive impact on soil physical properties [11–15]. The soils inhabited by *L. badensis* are typically base-poor cambisols with a mull-type forest floor [13]. As with more closely studied epi-anecic species, such as *L. terrestris*, adult *L. badensis* gather materials from around their burrows on the soil surface to feed and to form middens – a collection of material interspersed with earthworm casting. Burrows, 14–16 mm in diameter, can reach depths of 2.5 m [13]. Cocoons are deposited below ground in chambers, which the adults excavate in the burrow walls at depths between 0.4 and 1.5 m and emerging hatchlings live an epi-endogeic lifestyle before becoming deep burrowers [13].

During a visit to the Black Forest in 2015, preliminary data was collected relating to the ecology and until then entirely unexplored soil surface behaviour of *L. badensis* [7]. The results included observations on co-occurring earthworm species, estimates of *L. badensis* density and for the first time, night vision video records of surface behaviours. Whilst providing novel information of *L. badensis* behaviours, the investigation left many nocturnal activities inadequately covered, and some field manipulations of the soil surface undertaken to enhance data collection may have influenced the behaviours. Therefore, a subsequent field study was undertaken with the aim of obtaining a more comprehensive and realistic view of *L. badensis* nocturnal activity. Specific objectives were to gather more information on the timing – and possibly also the controls – of activity and its allocation between different behaviours. Previous observations of sexual behaviour were especially deficient and required further data collection. Earlier field investigations had also suggested that *L. badensis* middens might have unique features, so special attention was given to midden-related activities. In addition, to evaluate the impact of *L. badensis* on its environment, data was collected on the population density of this species at the study site, and on the litter layer characteristics in areas with differing levels of occurrence.

2. Material and methods

2.1. Field site

At a location c. 1160 m asl, in the Belchen region of the Black Forest, a site was selected for field work (approximate location: 47°49'45"N, 7°51'36.0"E). Data (1981–2010) from a local meteorological station (Wieden; www.dwd.de) records a mean annual temperature and precipitation of 6.5 °C and 1822 mm, respectively. The field site was the same location as used in a preliminary study [7], within a forest dominated by European beech (*Fagus sylvatica* Linnaeus, 1758) and Norway spruce (*Picea abies* (L.) Karsten, 1881) on an east-facing, 20° sloping hillside, with little ground vegetation cover (see [Suppl. Fig. 2](#)). These conditions allowed for relatively easy observation of the soil surface, where signs of *L. badensis* presence could be discerned. These consisted of middens, somewhat less clearly defined than those of *L. terrestris* [16], and on closer examination often had gently ascending side branches from the main burrow, usually with associated earthworm casting and small scattered stones at the soil surface [13]. The forest had an understory vegetation of mountain ash (*Sorbus aucuparia* Linnaeus, 1758)

and saplings of the dominant tree species, with a sparse ground layer of *Vaccinium*, *Rubus* and some pteridophytes. Most of the leaf litter was from beech with scattered spruce needles and cones. Data of the earthworm community on site showed that, in addition to *L. badensis*, *Aporrectodea icterica* (Savigny, 1826), *Lumbricus rubellus* (Hoffmeister, 1843) and *Octolasion lacteum* (Örley, 1881) were present [7]. Even though mole (*Talpa europaea* Linnaeus, 1758), red fox (*Vulpes vulpes* Linnaeus, 1758) and wild boar (*Sus scrofa* Linnaeus, 1758) were reported locally and prey upon *L. badensis* (Franz Lamparski, pers. comm.), no signs of their predatory activity were observed at the study site.

2.2. Recording of surface behaviour

Within an area of approx. 12 m × 7 m, six positions with high levels of *L. badensis* presence, based on midden observations, were chosen for behavioural recording. At each position, an infrared outdoor security camera (F19803EP, Foscam, Houston, USA; 720p (HD): 1280 × 720 pixels), powered by an individual 6-V battery, was mounted on a lightweight tripod with the camera focused down, directly at the sloping soil surface (see [Suppl. Fig. 3a](#)). With each camera positioned 0.65 m above the surface soil, this allowed detailed and accurate behavioural observations to be made within an area of approx. 0.25 m² (see [Suppl. Fig. 3b](#)). All camera positions were physically marked with pegs beside tripod leg positions. The soil surfaces in view were not manipulated in any way, i.e., litter (leaves, twigs and cones) were not moved, and artificial watering of the focal areas did not occur, as had been the case in the previous study [7].

The behavioural recordings were made on six consecutive nights, 18–23 June 2019, from 21:00 to 06:00. With sunset and sunrise at c. 21:30 and 05:30 respectively, the recordings covered all 8 h of darkness from each night, plus the crepuscular periods before and after dark. Cameras were retrieved after sunrise and data from memory cards was downloaded each morning, with blank memory cards and recharged batteries used the following night to ensure no data loss.

2.3. Collation and classification of behavioural data

In the compilation of behavioural data, each nightly webcam recording from the six positions was viewed numerous times using a standard media player, so that all *L. badensis* activity could be codified and verified in as much detail as possible. As no other epi-anecic species were present, there was no risk of confusing the surfacing earthworms with other species. Each emergence and activity were recorded, the position marked on an acetate sheet attached to a monitor, and each earthworm given a specific night/camera/numerical reference. Individuals were determined as adult or juvenile, depending on clitellum presence. Even though the same six positions were filmed on sequential nights, new designations of individuals were applied each night, as certainty could not always be placed on individual recognition, because main burrows can have several openings on to the soil surface. Timing and duration of each activity across the filmed hours of darkness was noted.

Activities were codified as:

- Sub-midden activity: subsurface actions below a midden, when the individual was not seen, but movement of the midden surface could clearly be seen (behaviour was deemed to have stopped if no activity was recorded for a full 5 min). This was a sign of topsoil bioturbation and gave an indication of midden dimension;
- Foraging: movement beyond the burrow on the soil surface, but tail retained in burrow and often movement or collection of organic matter, with no behaviour associated with other individuals;
- Mating: pre-copulatory and copulatory interaction with another *L. badensis* individual on the soil surface with tail retained in own burrow;

- Dispersal: movement across the soil surface completely away from a burrow;
- Other activity: this included direct surface casting and “worm-waving” (orienting side-to-side movements of the raised anterior segments at emergence; as previously recorded by Butt et al. [17] for *L. terrestris*).

Recorded activity of other animals at the soil surface was also noted to determine if they had any interactions with the earthworms and if there was a response.

2.4. Sampling of litter layer and soil

To study the impact of *L. badensis* foraging on the litter layer, a further five positions of confirmed *L. badensis* presence (middens present) were located at 10–20 m distance from the area used for behavioural recordings. These were paired with five positions, at the same levels on the hillside and within 1.5 m distance, where there were no signs of *L. badensis* at the soil surface (middens absent). Each of the ten positions was sampled (0.1 m² quadrat), with all plant litter material from the soil surface collected into a plastic bag (excluding individual spruce needles), sealed and taken from site. Any living plants were also cut and collected, and a soil sample was taken to a depth of 5 cm from within each quadrat. In the laboratory each sample was sub-divided into beech leaves, woody debris, spruce cones and living plant material. These were oven-dried at 60 °C and dry masses were recorded. The soil was dried for moisture evaluation and organic matter content estimated by loss on ignition (LOI), and pH (in water) measured [18]. Further analyses examined macro nutrients of the soil using Inductively Coupled Plasma – Mass Spectrometry (ICP-OES) [19] plus analysis for % CHN and C:N ratio with a ThermoScientific CHNS Organic Elemental Analyser.

2.5. Weather conditions during the study

During filming at the study site, air temperature was recorded daily at 07:00 h and soil temperature at 5 cm depth every two days. Timing of nighttime rainfall events were obtained from the video footage observations. Daily and hourly meteorological data on temperature, precipitation and cloudiness were obtained from the Feldberg weather station (47°52'29.28"N, 8°0'13.68"E) through the open data services of Deutsche Wetterdienst (www.dwd.de). The station is situated at approximately 11.5 km distance from the study site in an open mountain environment and 330 m higher in elevation. The weather conditions at the station can therefore differ considerably from those at the forested study area. It was, however, considered that the data would provide a useful reference of the temporal variation in temperature while the rainfall and cloudiness conditions between the localities were likely to have been highly similar. Moon-phase data for the study period was obtained using the data service of the U.S. Naval Observatory's Astronomical Applications Department (<https://aa.usno.navy.mil/data/MoonFraction>) as moon-light possibly suppresses soil surface activity of epinecic earthworms [20].

2.6. Statistical analyses

Graphical presentation was used to summarise the number of *L. badensis* individuals involved in different activities (sub-midden activity, foraging, mating) during the six successive nights of recording. The variation of *L. badensis* surface activities (time in minutes of total, sub-midden, foraging and mating activity) over the six-nights was studied with a repeated measures GLM, after checking for normality and tests of sphericity with Mauchly's test. Observations on dispersal were not included in the analyses as they were very rare. Because of the limitations of the data, the covariation of different *L. badensis* surface activities with the meteorological variables were not analysed

statistically. The dry masses of total, leaf, woody litter and cones in quadrats with and without *L. badensis* middens, were compared with a paired samples Wilcoxon test. The statistical analyses were undertaken with *rstatix* and *Hmisc* packages of R [21]. Graphical presentations used *ggplot2* package [22].

3. Results

3.1. Weather conditions

During the nights of recordings, air temperature at the Feldberg weather station varied from slightly below 10 °C to slightly above 15 °C. Nights 1 and 6 were the warmest (Fig. 1a). During Night 2, a sharp drop of temperature from 15 °C occurred while on other nights the temperature remained more stable. Field measurements of nighttime air temperature were often close to 12 °C at the study site with the first and the last nights standing out as somewhat warmer, corresponding with the trend in Feldberg (Fig. 1a). Soil temperature remained between 11 and 11.5 °C throughout the recording period. Four main rainfall events were recorded at Feldberg, the heaviest during daytime on 23.6. (Fig. 1b). Two nighttime rain events occurred, the heavier on Night 2 and the lighter during Night 4 (Fig. 1b). Both rainfall events were observed at the study site. The rain on Night 2 lasted in the field for about 50 min (from 03:28 to 04:17). Nighttime cloudiness was often variable at Feldberg with Night 4 as the cloudiest and Night 6 with mostly bright sky (Fig. 1c). The moon was full on Night 1 (18.6.) and for the rest of the study period (19–23.6.), the fraction of illuminated Moon surface at midnight declined from 97% to 73%.

3.2. Records of *L. badensis* behaviours

All cameras recorded as programmed, resulting in a total of 324 h of footage. Activity of *L. badensis* at the soil surface was relatively easily seen as under infrared recording, the darkly pigmented earthworms appeared to be relatively light in colour (Suppl. Fig. 3b). A clitellum, if present, could also be clearly discerned. Altogether, 268 *L. badensis* individual records were followed from the video recordings, of which 157 were mature animals emerging from a midden sufficiently away from the edge of the camera view to allow for full coverage of their activities. Immature individuals, determined by size and no sign of a clitellum, and mature animals with middens at the edge of the camera view were excluded from behavioural analyses. Mean ($\pm$ se) density of all *L. badensis* and of clitellate individuals, based on numbers of individuals seen per camera per night, were 30 ± 1.8 m⁻² and 17 ± 1.1 m⁻², respectively.

Sub-midden activity and foraging: Over the six nights, the earliest indication of activity was at 21:05 h when subsurface movement was recorded. From all activity of mature *L. badensis*, sub-midden activity was the most frequent (60%) and the most often seen first for each earthworm (89%) (Fig. 2). Only 10% of nighttime activities began with foraging, with an individual extending its anterior out of a burrow entrance without prior subsurface activity. Supplementary Fig. 3b shows an adult extending to c. 20 cm from its burrow. At the earliest, foraging began at 21:47 h, and it accounted for 34% of recorded activities (Fig. 2). Foraging individuals appeared to collect small fragments of litter and on occasion, a beech leaf would be grasped with the proboscis and dragged into the burrow opening (see Suppl. Fig. 4). Some bouts of sub-midden activity and foraging were lengthy. For example, on Night 1, an individual *L. badensis* exhibited sub-midden activity for 251 min and then foraging for a further 69 min resulting in total activity of more than 6 h. On Night 3, another individual spent a total of 434 min (over a 7-h period) in two bouts of sub-midden activity separated by 11 min. The longest continuous foraging bout seen was also on Night 3 and lasted for 137 min.

Mating: Six records of mating or attempted mating were obtained and this accounted for 6% (by time) of surface-recorded activity. All

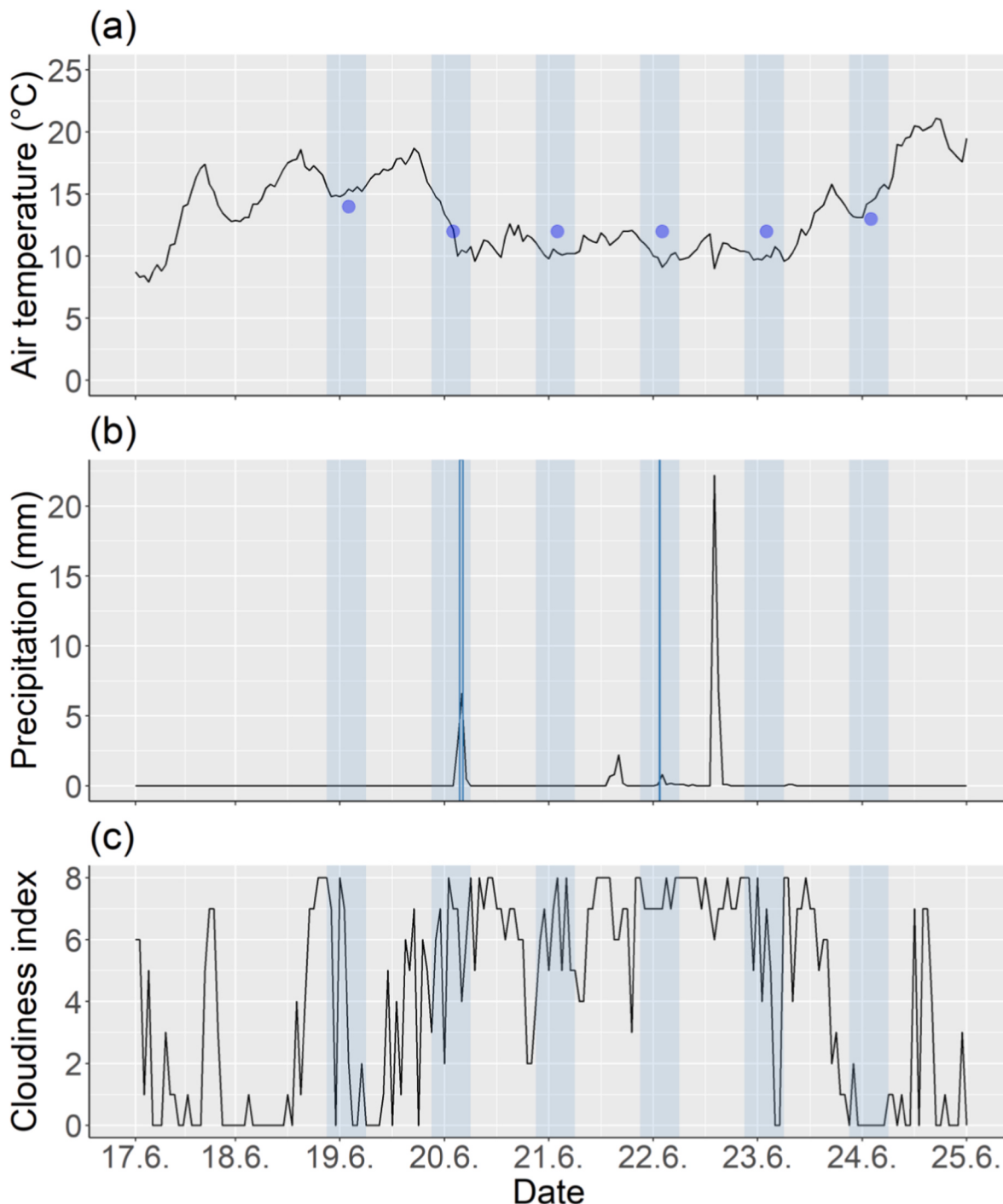


Fig. 1. Weather conditions during the study period (June 2019) at Feldberg weather station, situated 11.5 km distance from the study site: (a) air temperature (°C), (b) precipitation (mm) and (c) cloudiness (on a nine-grade scale from 0 (entirely bright sky) to 8 (complete overcast)). The shaded areas denote the six periods of nighttime behavioural field recordings. In (a) the blue dots show the air temperature measured at the study site, in (b) the blue vertical lines delineate the rainfall events recorded from webcam footage (Source of Feldberg data: Deutsche Wetterdienst open data (www.dwd.de)). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

occurred post-midnight on four recorded nights (Fig. 2). Mean duration of the mating sequences, including pre-mating behaviours, was 168 min (range 94–240 min) (Table 1). Two of the matings were partially obscured by leaf litter and one (on Night 2) was interrupted by rainfall, but these two adults successfully mated on Night 6. In all instances prior to mating, at least one burrow visit (insertion of anterior end into partner's burrow) took place and was usually reciprocal (mean number of visits 1.4; range 1–3; Table 1). Thereafter, the partners were seen to be touching each other on the soil surface between their burrows (mean

burrow separation distance was 14 cm), until mating commenced. In cases where the mating could clearly be seen, this involved two reciprocal bouts. First, one individual attached its anterior ventral segments to the ventral side of the clitellar region of the partner, which remained more passive. The attaching area of the active partner could not be determined exactly by segments. After a period of minutes, the more active worm extended its body from its burrow to form a “loop” and rolled the more passive partner over, which then led to separation, after contraction of extended body length back into the burrow. The two

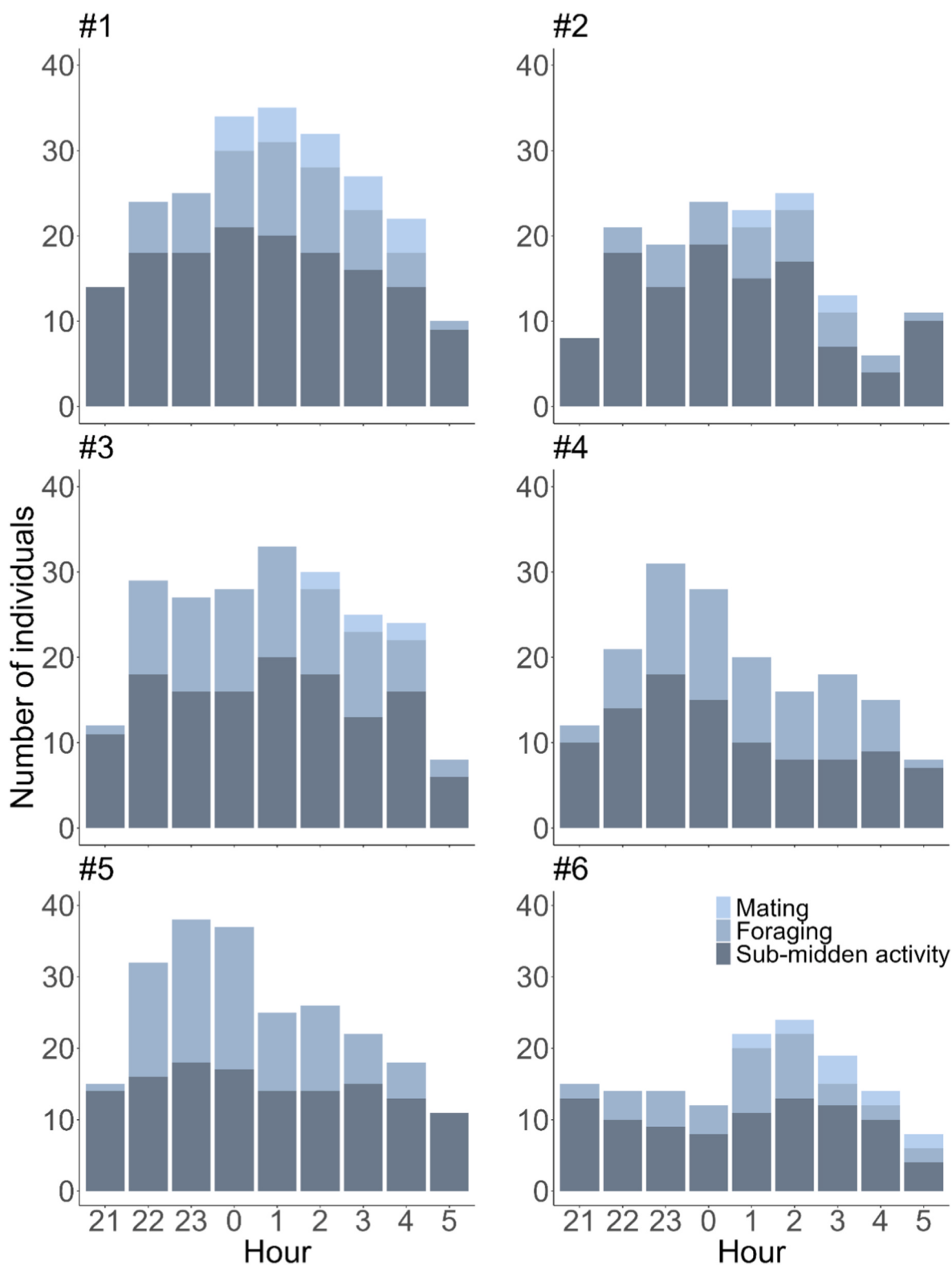


Fig. 2. Total number of adult *L. badensis* individuals engaged in sub-midden activity, foraging and mating activity from dusk to dawn during the six nights (#1 – #6) of behavioural recording.

earthworms then either stayed at the soil surface or briefly returned to their burrows. After an intervening period (mean duration c. 25 min) the partners encountered each other again and the attachment was repeated with roles reversed. Summary of the recorded matings (Table 1) shows that the average time of attachment was 15–16 min, occurring twice for each of the three clearly seen matings. Five complete matings of

L. badensis pairs were therefore recorded from a total of 324 h of webcam footage of a total soil surface area of approx. 1.5 m². This equates to 3.3 matings m⁻² in 324 h, which can also be summarized as 0.01 matings per hour per square metre.

Other activities: Movement of *L. badensis* away from burrows and over the soil surface was recorded five times. Only once was this seen for a

Table 1
Recorded *L. badensis* field matings in June 2019 at the Belchen study site.

Mating reference	Total duration (mins)	Burrow visits (n)	Attachment 1 (mins)	Attachment 2 (mins)	Mating interval (mins)	Notes
Night:Camera						
1. N1:C1	233	1	17	15	21	Good view
2. N1:C3	240	2	Not seen	Not seen	30	Obscured
3. N2:C2 ^a	138	3	na	na	na	Interrupted
4. N3:C4	130	3	16	17	31	Good view
5. N6:C2 ^a	175	3	13	14	17	Good view
6. N6:C6	94	Not seen	Not seen	Not seen	Not seen	Obscured
Mean ± se	168.3 ± 24.0	2.4 ± 0.4	15.3 ± 1.2	15.3 ± 0.9	24.8 ± 3.4	
Median	156.5	3	16	15	25.5	

^a Same pair of adults; na - not applicable.

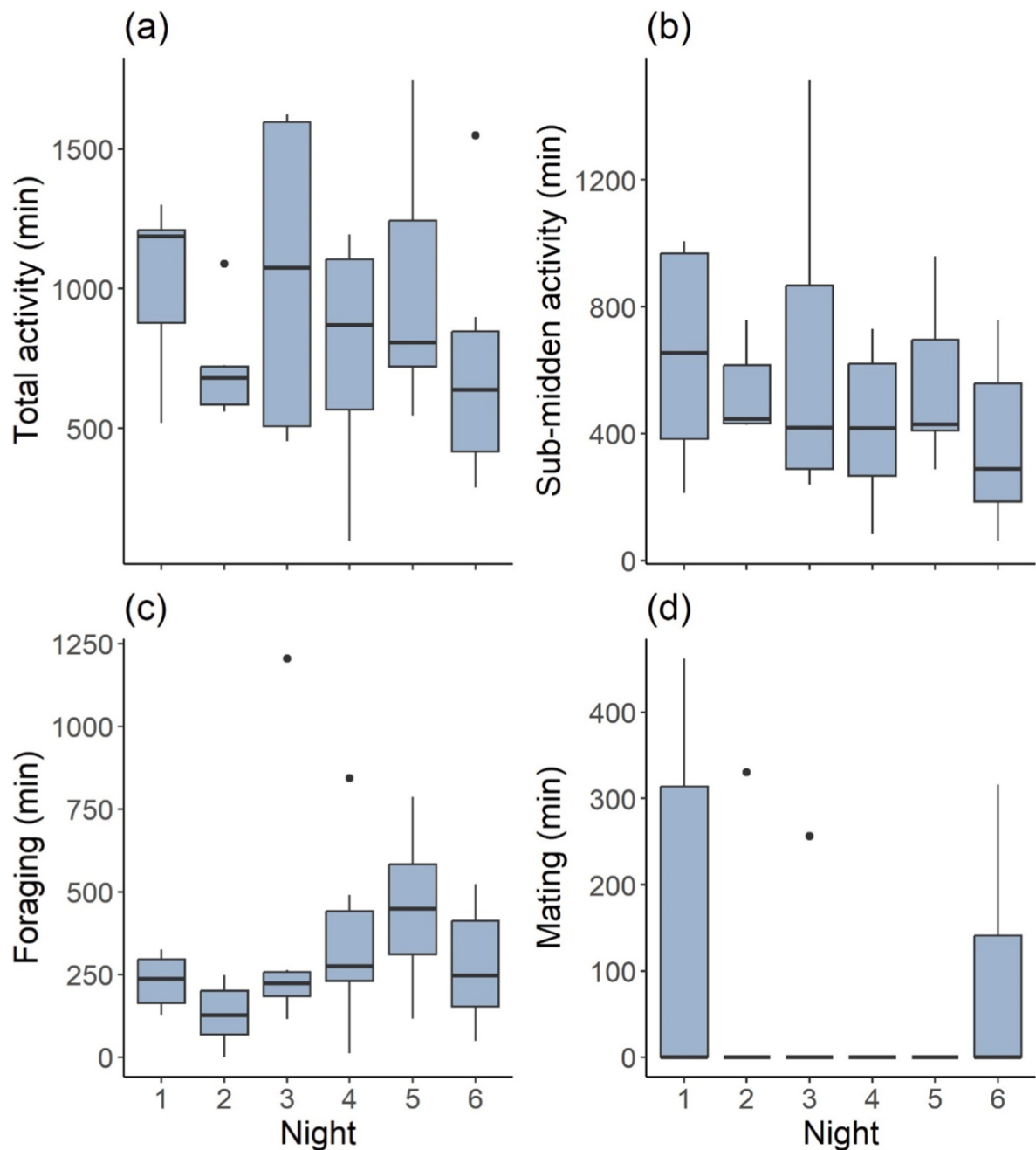


Fig. 3. Box-plots of the duration of *L. badensis* (a) total, (b) sub-midden, (c) foraging, and (d) mating activities during the six nights of behavioural observation (N = 6). Based on repeated measures GLMs, there were no statistically discernible differences between the nights for any of the four variables ($p > 0.05$).

mature animal, that crossed from top of view to bottom (04:05-04:09 h) towards the end of the rain event of Night 2. The other four movements involved immature worms which were in view for 1 – 3 min on three separate nights at a variety of times. Direct observation of casting by *L. badensis* on to the soil surface was recorded once on Night 3. Here a mature individual spent 4 min (22:17-22:21 h) producing a single set of casting above the burrow entrance. A series of circular, apparently orientating movements, by a mature individual with anterior held up from the soil surface was also seen to occur once. This “worm-waving” was after first emergence following heavy rain on Night 2 and lasted for 3 min. Overall, these other activities accounted for less than 1% of recorded surface activity.

3.3. Nightly patterns of activity

The number of individuals engaged in different activities typically increased towards midnight and beyond and then waned towards dawn (Fig. 2). There was, however, considerable variation in the nightly pattern from a bell-shaped change of activity of Night 1 to a rather level, low activity of Night 6. Sub-midden activity typically occupied the largest number of individuals throughout the night but with more foraging during the middle of the night. In terms of times spent in different activities, there was considerable variation in the levels of activity over the six nights (Fig. 3), with most devoted to sub-midden activity (Fig. 3b). The repeated measures GLM did not, however, find any statistically discernible differences between the nights in times spent in different activities (total activity: $F_{5,25} = 0.99$, $p = 0.445$; sub-midden activity: $F_{5,25} = 0.93$, $p = 0.476$; foraging: $F_{5,25} = 2.08$, $p =$

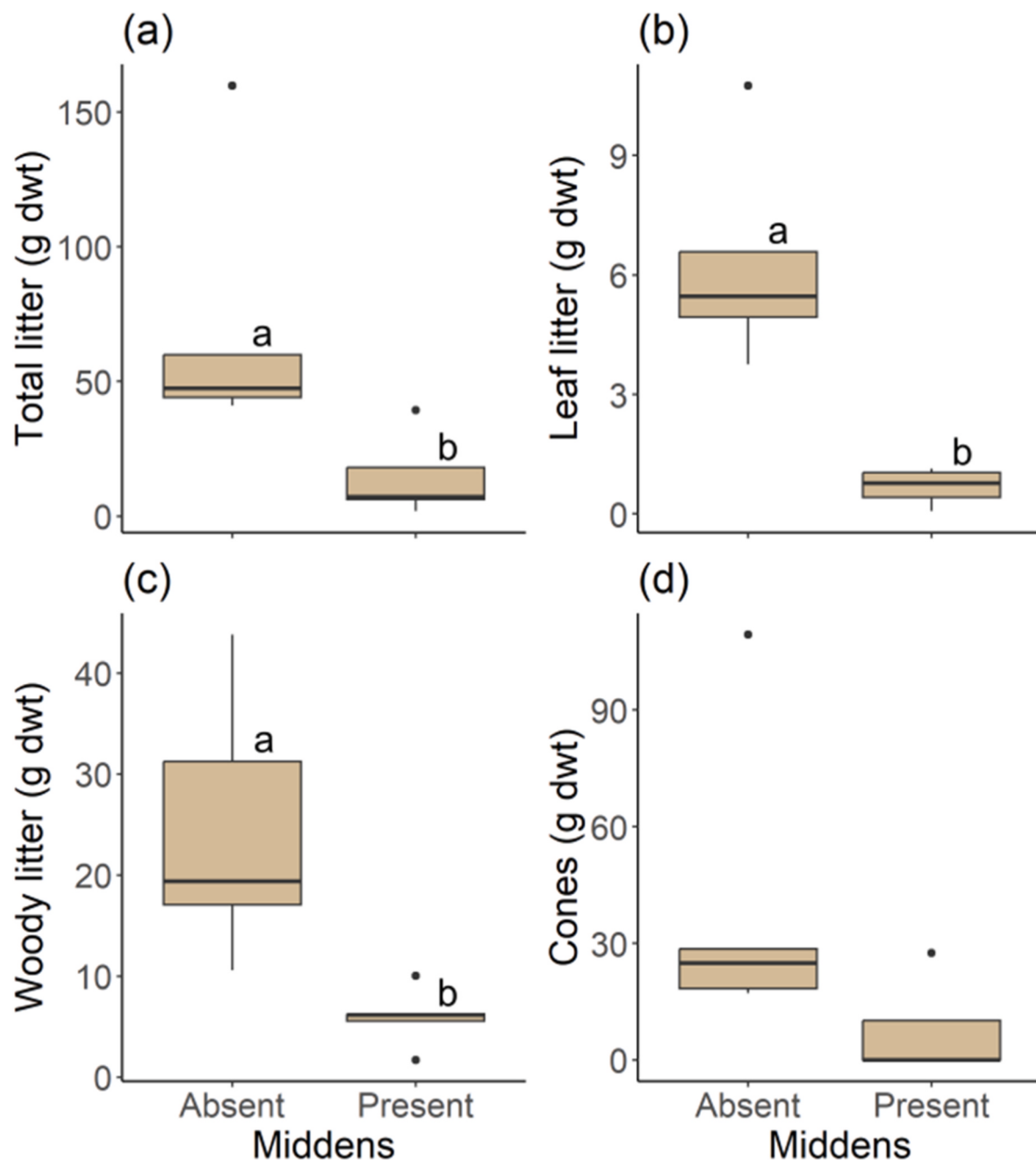


Fig. 4. Box-plots for the dry-mass of (a) total, (b) leaf, and (c) woody litter, and (d) cones, on the soil surface of plots with (Present) or without (Absent) *L. badensis* middens. Boxes marked with different letters differ statistically discernibly at 0.05 risk level (paired samples Wilcoxon test, $N = 5$).

0.175; mating; $F_{5,25} = 1.02$, $p = 0.427$). Qualitative comparison of activity levels, however, suggests that Night 2 had a reduced level of activity (Fig. 3), and this was likely related to the heavy rain which was seen to cause foraging individuals to retreat below the soil surface (Fig. 2; the activity dropping after 02:00 h).

3.4. Interactions with other animals

During filming, many other invertebrates such as insects and myriapods were observed moving across the soil surface and having no direct interaction with earthworms. On one occasion a large slug (*Arion* spp.) encountered a foraging *L. badensis*, at which point the latter withdrew into its burrow. On five occasions a wood mouse (*Apodemus sylvaticus* Linnaeus, 1758) came into view and on four of these times, the mouse disturbed a foraging adult which caused rapid retreat into its burrow. On two nights, between 21:00 and 21:30, a Ring ouzel (*Turdus torquatus* Linnaeus, 1758) was seen and appeared to be searching through the leaf litter, but this was before darkness and *L. badensis* emergence had not then occurred.

3.5. Presence of *L. badensis* and surface organic matter

Significantly less total litter was found on the surface within the 0.1 m² areas containing *L. badensis* middens compared with areas without middens (Fig. 4a). This was mirrored when total litter was sub-divided for leaf litter and woody litter (Fig. 4b and c, respectively). For cones, the mass was also lower when middens were present, but the difference with midden-free areas was not statistically significant (Fig. 4d). Two behavioural records showed that direct movement of cones (mean dry mass 11.81 g; $n = 20$) was possible by an adult *L. badensis* grasping the cone with its proboscis and pulling. The very few live plants collected from the quadrats were identified as recently germinated spruce.

3.6. Soil analyses

Sampling revealed an acidic soil with a pH of 4.36 ± 0.02 , a moisture content of $38.2 \pm 2.2\%$, and loss on ignition (LOI) of 18–20%. The LOI data and selected chemical analyses (including C and N content), comparing the areas of *L. badensis* middens present with paired middens absent areas are presented in Supplementary Table 1. No statistically significant differences were noted for all these measurements.

4. Discussion

4.1. Environmental setting and temporal patterns of activity

The video cameras employed in the field provided high quality footage of *L. badensis* behaviour, far superior, for instance, to older recordings of *L. terrestris* behaviour, even under laboratory conditions, see image in Butt et al. [5]. The current technology, linked with the large size of *L. badensis*, allowed much more detail of behaviours to be recorded, with individual segments of mature earthworms sometimes discernible.

The recording positions chosen proved suitable for the field work, the mean density of 17 adult *L. badensis* m⁻² being greater than that of 7–11 adults m⁻² reported by Kobel-Lamparski and Lamparski [13] and our similar estimate of 7 adults m⁻² in 2015 [7]. The abundance we observed is remarkably high considering that, using an adult mean biomass of 25 g [7], it would imply a total mass of more than 400 g m⁻² for adult *L. badensis* alone. The high abundance undoubtedly resulted from our deliberate targeting of positions with numerous middens, while previously reported densities are from more randomly placed sampling sites in the patchily distributed population. It is also possible that behavioural observations reveal higher numbers of adult individuals than the estimation methods, e.g., based on counts of large vertical burrows in subsoil associated with middens, used in earlier

studies. It could be thought that artifacts of video recording may have exaggerated the population density, in part due to the multiple burrow entrances of *L. badensis* individuals. However, repeated re-examination of all video footage, by the measurement of the separation distances of discrete middens and through records of simultaneous surface activity of very closely adjacent animals, allowed us to be certain that our estimates were not biased.

Environmental conditions during the field work were also favourable for *L. badensis* surface activity with nocturnal air temperature at the site remaining close to 12 °C. This temperature is known to be near the optimum for the activity of epi-anecic species of temperate and boreal regions, such as *L. terrestris* [23]. The filming took place some 6–8 weeks after snowmelt and this, plus high precipitation in May 2019, contributed to the high topsoil moisture content which will have further encouraged *L. badensis* activity close to the soil surface.

A thorough study of relationships between *L. badensis* surface activity and environmental conditions was not possible due to the short duration of the study, the fact that comprehensive weather data was not available from the site and because of the relatively stable nocturnal weather conditions during the study. However, qualitative observations showed that heavy rainfall interrupted *L. badensis* foraging and mating and lowered the overall activity during the night. Total surface activity was also markedly low during the night with mostly moonlit sky. Although the moon was then already at the waning gibbous phase and light is shaded by the forest canopy, moonlight may have suppressed *L. badensis* surface activity, as earlier suggested for *L. terrestris* [20].

4.2. Behaviours of *L. badensis*

Sub-midden activity. Accounting for 60% of the total activity recorded, this likely consisted of different, here inseparable activities such as incorporation of collected litter, feeding from the middens and subsurface casting. The middens of *L. badensis*, as observed during field work, had a notably different appearance from those of e.g., *L. terrestris*, with litter in *L. badensis* middens very highly mixed with soil and surface casts so that the middens had a semblance of soil patches [8]. The close incorporation of litter may have been a major component of the sub-midden behaviour, possibly necessitated by the nature of the plant litter in the living environment of *L. badensis*. The main tree litter types, beech leaves and coniferous needles, are both markedly recalcitrant against decomposition – beech leaves even more so than spruce needles [24] – and considered sub-optimal as earthworm nutrition [25]. For spruce needles, Lamparski [12] noticed that incorporation into middens makes the plant tissue decompose more rapidly while Hendriksen [26] noticed that pre-decomposition made beech leaf litter more acceptable for detritivorous earthworms. This impact renders the midden as an external rumen where microbial pre-decomposition can make initially poorly palatable material more suitable for earthworm consumption [12,27,28]. Casting is instrumental in producing the midden environment and can be important in the burial of litter [29]. This requires that the earthworm can readily turn in its burrow, which is accomplished by *L. badensis* individuals [12] and was seen from our single surface casting observation. One interesting question for further enquiries might be whether coprophagy, a possible component of the sub-midden activity, has a role in the feeding ecology of *L. badensis*.

Foraging. In earlier investigations at *L. badensis* living sites, it was noted that in spring, the major proportion of surface litter from the previous growing season had already been incorporated into the soil, largely by *L. badensis* foraging [12]. Accordingly, during our June field work, only a small proportion of leaf litter remained on the soil surface. However, *L. badensis* actively collected this, with foraging constituting 34% of the total recorded activity. Foraging leads to exposition of the soil surface and this predisposes the surface to splash erosion and downslope mass movement which is seen in the physical configuration of *L. badensis* middens in sloping terrain [30]. As an outcome of foraging, the amount of leaf and woody litter was significantly lower at sites of

activity compared with areas where middens of *L. badensis* were not observed. Indication for the collection of woody litter may seem unusual if not just for midden construction but it may have some nutritional function, as dead wood with associated microbiota can provide a food source for earthworms [31]. The notable force which *L. badensis* adults can exert upon objects was witnessed by their ability to move spruce cones. However, movement of such objects likely relates more to the covering of burrow entrances rather than for any nutritional purpose.

Dispersal. Departure from burrow and free over-surface movement of adult *L. badensis* was extremely rare with only one adult individual engaging in this activity during the heaviest nocturnal rain event of the study period. Such movement may not only be triggered by heavy rain and possibly temporary water logging of soil but also by local resource depletion at the living site which has been shown to increase the likelihood of surface dispersal in *L. terrestris* [5]. The rarity of departure from the burrow may be a general phenomenon in *L. badensis* and relate to the importance of the extensive burrow for the survival and reproduction of adult individuals, although mass migration has been witnessed during mild temperatures after rain (OE, personal observation). Earthworms are preyed upon by many vertebrates and leaving the burrow can be particularly risky for large individuals which are unlikely to achieve re-burrowing in virgin soil during a night. For them, a successful return belowground might require settling into another occupied or vacant burrow or homing to their own burrow, as has been observed in *L. terrestris* [4]. The areas where behavioural recordings were made also contained numerous juvenile *L. badensis*, and from these, four over-surface movements were recorded. With their more epigeic lifestyle [13] juveniles are possibly more prone to move on the soil surface, a behaviour that may also relate to movement away from parental living sites in search of less occupied areas. The data on dispersal was, however, limited and the behaviour we observed may be specific to the time of year of the study.

Mating. The low number of recorded matings suggests that they may be relatively infrequent in the population although the rate was more than twice as high than recorded from the same site in June 2015 [7]. The period of field work may, however, render the observations unrepresentative as it is possible that in June the strain of overwintering still lowers the mating readiness of individuals. The pre-mating behaviour of *L. badensis* bore close resemblance to that of *L. terrestris*, with intense touching of the partner, movement between burrow openings and mutual insertions of the body anterior into the partner's burrow, with both partners always keeping their posterior attached to their own burrow [32]. In hermaphrodite mating, insemination is regarded to be almost invariably reciprocal [33]. The prevailing conception is that in the mating of earthworms it is attained by the typical copulatory sequence described for *L. terrestris* long ago [34] viz: partners align themselves in close ventral contact, heads in opposite directions, and over a copulation which lasts for 2–3 h, simultaneously donate sperm which flows along the donor's external sperm tract to the partners spermatheca. Although our dataset is small, it consistently indicated that the mating is fundamentally different in *L. badensis*. Here individuals attached in turns – with an intervening period – into the partner's clitellar region for a relatively short period of time and invariably this reciprocal sequence occurred once. It is likely, that in our earlier research note we incorrectly interpreted an incomplete sequence of this behaviour as failed alignment for a *L. terrestris* type of copulation [7]. This new finding on the behaviour of *L. badensis* – and as far as we know on earthworm behaviour in general – raises many questions on its functions and implications. We will leave closer considerations of the subject to subsequent studies supported by additional biological information.

5. Concluding remarks

Current environmental issues have increased the awareness of earthworm conservation needs [35] and in those terms one can see some

urgency for the study of *L. badensis* ecology. As an endemic species evolved in highly specific environmental conditions, it can be particularly affected by climate change which has been predicted to influence the distribution and abundance of European earthworms [36]. The conservation status of *L. badensis* has not been assessed by the International Union for Conservation of Nature (IUCN), but its limited range suggests potential for vulnerability and the species is considered “data deficient” on the German Red List of earthworms [37]. It is known that climate change is already affecting the plant communities within the Black Forest [38,39] and there is reason to consider that the environment may be deteriorating for *L. badensis*. Specific future threats are increasing summer temperatures leading to periods of drought that may negatively affect the juveniles with their lifestyle close to soil surface [40]. It will be important to continue following the status of *L. badensis* in the Black Forest and consider whether conservation steps need to be, and indeed can be, taken to ensure its persistence.

Our observations provided a snapshot description of *L. badensis* behavioural ecology, and they complement knowledge on the biology of this still inadequately known earthworm species. The findings point to several questions for further enquiry. The importance of the extensive subsurface, midden-related behaviour in the feeding ecology of *L. badensis* warrants further investigation, particularly in relation to the idea of an external rumen and its potential importance in the maintenance of a high population density. Likewise, the importance of *L. badensis* soil modification activity as an ecosystem engineering impact in the forest environment and, on the other hand, as niche construction impacting *L. badensis* itself, could both provide fertile fields of research. The unexpected findings on mating behaviour in *L. badensis* will require closer study as they may indicate a need to re-evaluate mating behaviour variation and also sexual selection phenomena in earthworms.

CRediT authorship contribution statement

Kevin R. Butt: Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Friederike Lang:** Writing – review & editing, Investigation. **Otto Ehrmann:** Writing – review & editing, Investigation. **Rick Healey:** Writing – review & editing, Software, Resources. **Visa Nuutinen:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ejsobi.2026.103828>.

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