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Dew-worms in white nights: High-latitude light constrains earthworm (*Lumbricus terrestris*) behaviour at the soil surface

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ABSTRACT

Soil is an effective barrier to light penetration that limits the direct influence of light on belowground organisms. Variation in aboveground light conditions, however, is important to soil-dwelling animals that are periodically active on the soil surface. A prime example is the earthworm *Lumbricus terrestris* L. (the dew-worm), an ecosystem engineer that emerges nocturnally on the soil surface. In the summer, the northernmost populations of *L. terrestris* are exposed to a time interval with no daily dark period. During a two-week period preceding the summer solstice, we studied the constraints that boreal night illumination imposes on *L. terrestris* surface activity by comparing their behaviour under ambient light with artificially-induced darkness. Looking for evidence of geographical divergence in light response, we compared the behaviour of native *L. terrestris* (Jokioinen, S–W Finland; 60°48′N) with two markedly more southern populations, from Preston (Lancashire, UK; 53°47′N) and Coshocton (Ohio, USA; 40°22′N) where the nights have a period of darkness throughout the year (total latitudinal range ca. 2300 km). Under ambient light conditions, *L. terrestris* emergence on the soil surface was diminished by half compared with the darkened treatment and it peaked at the darkest period of the night. Also mating rate decreased considerably under ambient light. The native dew-worms were generally the most active under ambient light. They emerged earlier in the evening and ceased their activity later in the morning than dew-worms from the two more southerly populations. The differences in behaviour were, however, significant mainly between native and UK dew-worms. In the darkened treatment, the behaviour of the three earthworm origins did not differ. Under the experimental conditions light condition was the dominant environmental factor controlling surface activity, but elevated night-time air temperature and humidity also encouraged dew-worm emergence without discernible differences among geographical origins. Our results show, that in boreal summer, the high level of night illumination strongly limits soil-surface activity of dew-worms. Considering the important regulatory role of *L. terrestris* in many ecosystem processes, this can have significant corollaries in dew-worm impacts on the environment. Although evidence for geographical differentiation in behaviour was obtained, the results point to phenotypic flexibility in *L. terrestris* light response.

1. Introduction

Light is a great provider and pacemaker of life and adaptation to variation in the light environment is a central quest for all organisms (Gross, 2002; Bradshaw and Holzapfel, 2007). Soil is an efficient light barrier and, based on plant models, it has been asserted that ecologically and physiologically significant amounts of light rarely penetrate deeper than 4–5 mm into soil (Tester and Morris, 1987). The direct impact of light on the development of soil microbial community characteristics may even be limited to the surface 1 mm of soil (Jeffery et al., 2009). Therefore, direct impacts of light on belowground dwelling invertebrates, in general are likely to be small. Exceptions would be species residing permanently in the uppermost part of the soil or in habitats where the soil is too thin to allow escape from light (Wallwork, 1970).

Among soil invertebrates, there are also deep burrowing species that regularly visit the soil surface and become directly subjected to prevailing light conditions. A prime example is the anecic earthworm *Lumbricus terrestris* L. (the dew-worm), which as an adult

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lives in a deep (often > 1 m; e.g. Nuutinen and Butt, 2003), vertical burrow that opens at the soil surface below a midden, a mixture of collected organic and inorganic material and surface castings. The original authority for this species recognized the habit of *L. terrestris* to emerge nocturnally onto the soil surface to copulate (Linné, 1767) and Darwin (1881) realised that such emergence was important to foraging and midden construction.

Dew-worms display a diurnal vertical activity pattern, where individuals are nearest to the soil surface close to midnight and in the deepest position at noon (Joyner and Harmon, 1961). *L. terrestris* prefer moist and cool conditions and their emergence is known to be correlated with high air humidity, affected by air temperature and elapsed time from preceding rainfall events (Macdonald, 1983). Dew formation most certainly favours emergence but – remarkably – it seems that the importance of dew on *L. terrestris* activity has not been systematically investigated. While the nocturnal activity pattern relates to the prevalence of suitable moisture and temperature, avoidance of harmful daylight UV-radiation and the risks imposed by day-active predators are also likely to have affected the evolution of this behaviour (Edwards and Bohlen, 1996). The diurnal activity patterns of *L. terrestris* can also have an endogenous physiological component as the rhythms can persist under continuous darkness (Laverack, 1963).

L. terrestris senses light with photoreceptor cells that are mainly found in the first few anterior segments of the body, with greatest densities at the prostomium (Hess, 1925). Photoreceptors are found in other body regions too, chiefly within the posterior segments that are exposed to light when a dew-worm casts on the soil surface. The negative reaction of *L. terrestris* to light is well documented, as is its positive reaction to very weak illumination (Hess, 1924). Under artificial laboratory illumination and altered day–night cycles, *L. terrestris* strictly avoids light and adjusts its surface activity to the dark period (e.g. Butt et al., 2003; Field and Michiels, 2006). To our knowledge, the importance of light conditions on dew-worm emergence and mating activity has not been investigated under natural daily variation of illumination.

The geographical distribution of *L. terrestris* covers a wide latitudinal range and, consequently, a great variation in day-length and illumination conditions. In the Northern Hemisphere, it reaches beyond the Arctic Circle (66.56°N; e.g. Nieminen et al., 2011) where populations in summer are exposed to the polar day. Populations in the more southern parts of the boreal zone live in conditions where there is no dark period over a number of midsummer weeks, with twilight conditions prevailing throughout the night. The Global Biodiversity Information Facility (GBIF, 2013) records of *L. terrestris* distribution suggest that in the Northern Hemisphere the southern range extends to the northern parts of the Iberian Peninsula in Europe (41°N) and in North America still further south (37°N). A distribution map of Reynolds (1995) notes *L. terrestris* as far south as 33°N in North-America. In these southern latitudes the night always has a dark period which even at its minimum lasts for several hours.

Since soil-surface activity is critical for feeding, reproduction, and dispersal of *L. terrestris* (Mather and Christensen, 1988; Nuutinen and Butt, 1997; Butt et al., 2003) and thereby for the many ecological processes that this species regulates (Lee, 1985; Edwards and Bohlen, 1996; Borken et al., 2000; Shipitalo and Le Bayon, 2004; Milcu et al., 2006; Griffith et al., 2013), we investigated the constraints that a northern light environment imposes on dew-worm activity at the soil-surface. We hypothesized that boreal mid-summer white nights severely limit the time available for *L. terrestris* soil-surface activity, with temperature and humidity also playing an important, but secondary role. At the same time, we considered that populations residing in widely different environments could diverge in their behaviour (Foster and Endler, 1999; Hut et al., 2013). We predicted that a population from a northern area exposed to high illumination levels in midsummer, would show a higher level of activity under these conditions compared with more southerly populations with no previous exposure to white nights. Alternatively, phenotypic flexibility (*sensu* Piersma and van Gils, 2011) could lead to a similar response of populations, irrespective of their latitudinal origin.

2. Material and methods

2.1. Experimental animals

In mid-May 2009, we collected *L. terrestris* from three deciduous forests, selected to represent a wide latitudinal gradient with clear differences in day-length conditions during the Northern Hemisphere midsummer. The sites were, from north to south: Jokioinen (Finland ("FI"); 60°48′N, 23°28′E), Preston (Lancashire, United Kingdom ("UK"), 53°47′N, 2°41′W) and Coshocton (Ohio, USA ("US"), 40°22′N, 81°48′W). The set of locations represents a total latitudinal range of ca. 2300 km. The US site was chosen to represent the most southern conditions as we were not familiar with equally southern continental European populations of *L. terrestris* and the experimental animals could be readily obtained based on previous research collaborations. The differences among locations in length of darkness during midsummer 2009 are depicted in Fig. 1. In Preston, even the shortest midsummer night has 5 h 7 min of darkness and in Coshocton this is 7 h 51 min. In Jokioinen, there is a period of no darkness in midsummer, with civil twilight conditions prevailing at midnight. By definition, civil twilight begins in the morning (before sunrise) and ends in the evening (after sunset) when the centre of the Sun is geometrically 6° below the horizon (e.g. Forsythe et al., 1995). Under favourable weather conditions, illumination is then sufficient for terrestrial objects to be clearly distinguished and according to a traditional, although questionable definition, artificial light is not needed to perform outdoor activities (Leibowitz and Owens, 1991).

UK and US dew-worms were shipped to Jokioinen by express delivery lasting from 2 to 4 days. Prior to introduction into the experimental units, dew-worms from each origin were stored in

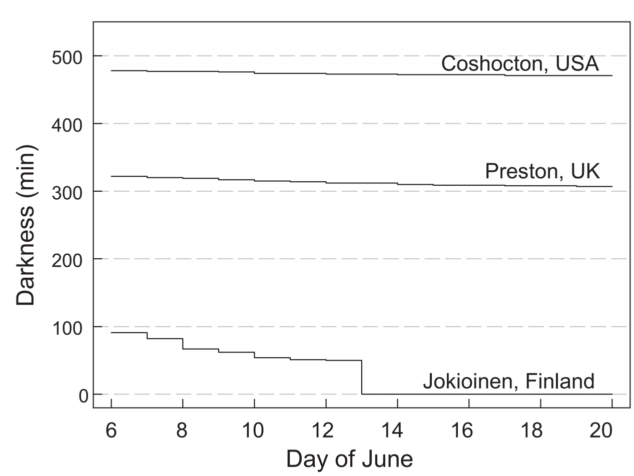

Fig. 1. Variation of nightly dark period (in minutes) during the experimental period in June 2009 over the three locations where the experimental *L. terrestris* were collected. The dark period shown represents the time between sunset and sunrise from which the civil twilight periods have been subtracted. The step down to zero dark period length in Jokioinen at 13 June results from the boundary value set for the Sun's position below the horizon in civil twilight definition (see text). U.S. Naval Observatory's astronomical data services were applied in the calculations (U.S. Naval Observatory, 2013).