Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands

Onrust, Jeroen; Wymenga, Eddy; Piersma, Theunis; Olff, Han

Published in:
Journal of Applied Ecology

DOI:
10.1111/1365-2664.13356

Publication date:
2019

Received: 28 February 2018 | Accepted: 14 January 2019
DOI: 10.1111/1365-2664.13356

RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands

Jeroen Onrust[1] | Eddy Wymenga[2] | Theunis Piersma[1,3] | Han Olff[1]

[1]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

[2]Altenburg and Wymenga Ecological Consultancy, Feanwâlden, The Netherlands

[3]NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, Utrecht University, Den Burg, Texel, The Netherlands

Correspondence
Jeroen Onrust
Email: j.onrust@rug.nl

Handling Editor: Marney Isaac

Abstract

1. Earthworms are an important prey for the endangered meadow birds of northwest Europe. Although intensive grassland management with high manure inputs generally promotes earthworm abundance, it may reduce the effective food availability for meadow birds through desiccation of the topsoil, which causes earthworms to remain deeper in the soil.
2. We studied the response of Red Worm *Lumbricus rubellus*, a detritivore, and Grey Worm *Aporrectodea caliginosa*, a geophage, to soil moisture profiles in the field and under experimental conditions. Surfacing earthworms were counted weekly in eight intensively managed grasslands (treated with high inputs of slurry by slit injection) with variable groundwater tables in the Netherlands. At each count, soil penetration resistance, soil moisture tension and groundwater level were measured, while air temperature and humidity were obtained from a nearby weather station. The response to variation in the vertical distribution of soil moisture was also experimentally studied in the two earthworm species.
3. In the field, earthworms' surfacing activity at night was negatively associated with soil moisture tension and positively by relative air humidity. Surprisingly, there was no effect of groundwater level; an important management variable in meadow bird conservation. Under experimental conditions, both *L. rubellus* and *A. caliginosa* moved to deeper soil layers (>20 cm) in drier soil moisture treatments, avoiding the upper layer when moisture levels dropped below 30%.
4. *Synthesis and applications*. We propose that in intensively managed grasslands with slurry application, topsoil desiccation reduces earthworm availability for meadow birds. This can be counteracted by keeping soil moisture tensions of the top soil above −15 kPa. We suggest that the late raising of groundwater tables in spring and the disturbance of the soil by slit injection of slurry increase topsoil desiccation. This decreases earthworm availability when it matters most for breeding meadow birds. Meadow bird conservation will benefit from revised manure application strategies that promote earthworm activity near or at the soil surface.

KEYWORDS
agricultural grasslands, agricultural intensification, dairy farming, earthworms, ecohydrology, food availability, meadow birds, soil desiccation

1 | INTRODUCTION

Most meadow bird species depend on earthworms as their main food source (Beintema, Moedt, & Ellinger, 1995). The currently high manure input in dairy farmland often promotes earthworm abundances (Atkinson et al., 2005; Curry, Doherty, Purvis, & Schmidt, 2008; Hansen & Engelstad, 1999). However, food availability for meadow birds is not only determined by the total abundance of earthworms in the soil but also by their vertical distribution in the soil profile and their activity on the surface (Onrust & Piersma, 2017). Tactile hunting meadow birds can only capture earthworms within reach of their bill in the upper, 0–10 cm deep, soil layer (e.g. for Black-tailed Godwits *Limosa limosa*, Lange, 1968), or when they can be seen at the surface for visually hunting meadow birds (e.g. Lapwing *Vanellus vanellus*, for Ruffs *Philomachus pugnax* see Onrust et al., 2017). Under desiccating conditions, earthworms might retreat deeper into the soil and stop their surfacing behaviour, which will negatively affect food availability for meadow birds.

Despite their name, and although common in many terrestrial habitats around the world, earthworms are evolutionary and functionally closely related to the oligochaete worms living in freshwater environments (Edwards & Bohlen, 1996; Turner, 2000). Their respiration and the maintenance of their hydrostatic pressure necessitate moist living conditions (Edwards & Bohlen, 1996; Turner, 2000). As their skin does not have the ability to prevent dehydration in dry conditions, lack of water is hazardous (Briones & Álvarez-Otero, 2018; Laverack, 1963). To avoid desiccation, earthworms spend most of their time below-ground. Under humid and not too cold conditions, the majority of earthworms are found near or at the soil surface (thus being available to meadow birds), while they migrate to lower depths at lower temperatures and when the topsoil is too dry (Gerard, 1967; Jiménez & Decaëns, 2000; Rundgren, 1975).

The capacity to cope with drier topsoil conditions differs between ecological groups (El-Duweini & Ghabbour, 1968; Roots, 1956). Generally, detritivorous, litter-eating, earthworms, are less tolerant to desiccation than geophagous, substrate-eating, earthworms, which go into diapause by curling into a small knotted ball in the soil and form a protective coating of secreted mucus (Edwards & Bohlen, 1996; Eggleton, Inward, Smith, Jones, & Sherlock, 2009; El-Duweini & Ghabbour, 1968; Ernst, Felten, Vohland, & Emmerling, 2009). Detritivores regularly surface at night to scavenge for food which is pulled into their burrows (Baldwin, 1917; Butt, Nuutinen, & Siren, 2003; Onrust & Piersma, 2019). These earthworms are therefore likely to be more sensitive to the microclimate above-ground. Although little is known about the conditions under which earthworms come to the surface, it has been noted that earthworms avoid dry surface conditions (Parker & Parshley, 1911) and high numbers of surfacing earthworms are usually counted during or after rainfall (Darwin, 1881; MacDonald, 1980).

Grasslands in north-west Europe are traditionally important for breeding and nonbreeding meadow birds (Newton, 2017). In order to maximize dairy production, they are now among the most intensively managed agricultural areas in the world (Bos, Smit, & Schröder, 2013). This involves two major agricultural practices: (a) the ongoing lowering of water-tables through landscape-level drainage, promoting longer growing seasons and higher grassland productivity through less water logging and (b) increased nutrient supply to grasslands, including the recent practice of slit injection of slurry (liquid manure). Although these grasslands have high densities of earthworms (Edwards & Lofty, 1982; Muldowney, Curry, O'Keeffe, & Schmidt, 2003; Rutgers et al., 2016), slit injection of slurry can affect earthworm abundances (de Goede, Brussaard, & Akkermans, 2003; Onrust & Piersma, 2019; van Vliet & de Goede, 2006). We expect that the activity of earthworms and their availability for meadow birds is reduced by the damage to soil structure and soil desiccation created by the slurry-based agricultural practices.

In this study, we investigated the influence of soil water conditions in intensively used grasslands on earthworm availability for meadow birds. In the field, we measured earthworm surface activity and correlated this with water conditions. Under controlled conditions we compared the vertical distribution of a detritivorous earthworm species the Red Worm *Lumbricus rubellus* and a geophagous earthworm species the Grey Worm *Aporrectodea caliginosa* under different soil moisture conditions. This shows how hydrological conditions influence surface activity and vertical movements of earthworms and hence food availability for meadow birds.

2 | MATERIALS AND METHODS

2.1 | Study site and observations in the field

The field study was conducted in a 10-km^2 area of dairy farming in south-west Friesland, the Netherlands (N 52°58′48, E 5°33′12). From 1990 until 2010, this area was subject to land 'rationalization' schemes which included drainage improvements and rearrangement and readjustment of grasslands to create efficient dairy farming systems, resulting in highly productive ryegrass (*Lolium* sp.) monocultures. We selected eight of these grasslands with similar management and history/age, but differences in groundwater level (ranging from 15 to 85 cm below surface level; see Table S1). All grasslands had a peat soil (80–160 cm thick) covered with a layer of clay (<40 cm). The size of the grasslands ranged from 1.92 to 6.97 ha (on average 4.02 ha; Table S1). The pH (H_2O) of similar managed grasslands within the study area measured in autumn 2013 was on average 6.03 (SD = 0.28, N = 16).

The management practices of these grasslands are targeted to harvest grass multiple times per year. Fertilization includes slit injection of slurry (liquid dairy cattle manure), for which the topsoil is cut (typically 3–5 cm deep with slits 15–25 cm apart) and filled with slurry manure (about 20 m^3 per ha). In the Netherlands this type of fertilizing became compulsory in 1994 and is allowed from 16 February until 1 September and occurs about three to four times a year. All grasslands were manured this way 2–4 weeks before the fieldwork started; mowing of the first sward occurred 1–2 weeks after the fieldwork ended.

The observation period took place from mid-March to late April 2015, coinciding with the period in which meadow birds are present and feed primarily on earthworms (Beintema et al., 1995). This is also the transition period in which the amount of evaporation becomes higher than the amount of precipitation in the Netherlands (Colenbrander, Blumenthal, Cramer, & Volker, 1989; Jacobs, Heusinkveld, & Holtslag, 2007). As March and April generally are the months with the lowest rainfall of the year (Colenbrander et al., 1989), we expected desiccating conditions during fieldwork.

In each grassland, all measurements were made along two transects of 25 m which were 25 m apart from each other. During an observation day all variables were measured on the same grassland and during the fieldwork period there were five observation days per grassland (approximately one per week). Prior to the observations (from 9 to 13 March 2015), earthworm abundance at each transect was determined by taking three soil samples of 20 × 20 × 20 cm which were cut in slices with a depth of 5 cm. Each slice was sorted by hand and number of detritivores and geophages were determined (Curry & Schmidt, 2007; Hendriksen, 1990). Earthworm activity was measured after sunset by counting surfacing earthworms from a height of 50 cm and within a width of 50 cm in front of the observer, making the total surface area that was observed 25 m^2 per grassland (for a description of this method, see Onrust & Piersma, 2017; Onrust et al., 2017). To measure groundwater level in centimetres below surface level (phreatic zone) during the moment of observation, a 100-cm-deep and 5-cm-wide 'well' was made in the middle of each transect.

Even at the same soil moisture content, soils can have different soil moisture tensions due to differences in physical properties such as texture, structure, pore size and organic matter content (Collis-George, 1959). Above a critical moisture tension, the soil will extract water from the body of earthworms causing first their diapause and then their mortality (Holmstrup, 2001). Soil moisture tension is thus a direct measure of what matters to earthworms, and probably a main determinant of their behaviour (Doube & Styan, 1996). Using a Quick draw tensiometer (Eijkelkamp, Giesbeek, 14.04.05.01) soil moisture tension of the soil was determined at three points on the transect (at 0, 12.5 and 25 m) at 10 cm depth. The tensiometer measures the suction pressure of the soil in KiloPascals (−kPa, negative as tension is a negative pressure).

Tactile hunting birds should be able to probe in the soil, therefore soil resistance to penetration was measured every 5 m along the transect using a penetrometer (Eijkelkamp, Giesbeek, 06.01.SA). The instrument measures the force in Newton per cm^2 that is required to push a probe through the soil at a constant velocity to a depth of 10 cm. Depending on the hardness of the soil, different cone diameters were used (1, 2 and 3⅓ cm^2) and soil resistance was calculated by dividing the measured value with the cone diameter, resulting in N/cm^2. The average soil resistance value per transect was used for further analysis. Hourly meteorological data were obtained from a weather station 15 km from the study area. We used air temperature in Celsius degrees at 10 cm above surface level and relative air humidity (%) measured during the times the earthworm surfacing observations were made.

2.2 | Laboratory experiment

To study the vertical distribution of detritivores and geophages under different soil moisture contents, we kept earthworms of both ecological groups for 24 days in 10-cm-diameter PVC tubes with a length of 30 cm. The tubes were split lengthwise, to allow us to open the tubes at the end of the experiment without disturbance causing the earthworms to redistribute. The two parts of the tube parts were held together by tie wraps; the lower opening was closed with a lid.

Each tube was filled with 25 cm of clean (no coarse or organic material and other earthworms) clay soil and 16–18 earthworms were then added on the surface. There were no plants growing in the top of the tubes and the soil contained no root structures. The wet bulk density in all tubes was on average 1.24 g/cm^3 (*SD* = 0.04, *N* = 36) at the beginning of the experiment. In 18 tubes we enclosed a geophagous species (*A. caliginosa*) and in 18 tubes a detritivorous species (*L. rubellus*). Prior to being added to the tubes, total earthworm fresh weight per tube was determined by rinsing the earthworms with tap water, carefully blotting them with absorbable paper and weighing them to the nearest 0.001 g. Both the earthworms and the soils were collected from the agricultural grasslands in southwest Friesland where we also carried out the field observations.

The tubes were placed in climate chambers with a constant temperature of 12°C, air humidity of 80% and light regime of 12/12 hr. The tubes were randomly assigned to either one of three treatments; wet, moist and dry. We used 12 tubes per treatment, divided over the species. Every day the tubes of the wet treatment received the amount of water that was equal to the evaporation in the chamber, which was 11 mm per day. The moist treatment received half of the evaporation, and the dry treatment received no water during the 24-day experiment. Water was applied at the soil surface. The earthworms were not fed.

When the tubes were opened, the soil column was immediately cut in five slices of 5 cm depth and the total number and fresh weight of the earthworms per slice was determined. Earthworm survival per tube was determined by calculating the proportion of earthworms that were still alive at the end of the experiment from the number at the beginning of the experiment. Furthermore, the average weight per earthworm in each tube was calculated by dividing the total fresh weight by the total number of earthworms. The soil moisture content of every slice was determined by oven-drying a weighted amount of soil at 70°C for 48 hr after it was weighed again. The relative change in weight was used as soil moisture content. Soil moisture tension was not measured in this experiment.

2.3 | Data analyses

We used GLMM in R version 3.1.2 (R Development Core Team, 2017) with package 'lme4' with the glmer function and family=poisson (Bates, Maechler, Bolker, & Walker, 2015). A binomial GLMM was built to analyse the data of the laboratory experiment. At the end of the experiment numbers of earthworms differed between tubes, so we used the proportion of earthworms at every depth. The response variable was entered as a matrix where the first column is the number of earthworms found and the second column is the number of earthworms not found. Species, treatment and depth were added as fixed effects with an interaction between treatment and depth. A random intercept term was added with depth nested in tube ID. In a similar analysis of survival data, species and treatment were the only fixed effects.

A GLMM was also used to analyse the number of surfacing earthworms per transect in the field. To account for differences between grasslands and transects, we added them as a random intercept in the model in which the factor transect was nested in the factor grassland. To control for temporal effects, we added observation day as a variable and as a random slope. We started the statistical analysis with a full model. We controlled for overdispersion by adding an observation level random factor (*X*). Explanatory variables (soil moisture tension, observation day, earthworm abundance, air temperature and air humidity) were rescaled to unity. A stepwise backward procedure was followed to find the minimal adequate model in which terms were removed in order of decreasing *p*-value (Quinn & Keough, 2005). We checked the normality of the residuals by visual inspecting the QQ plots (Miller, 1986).

3 | RESULTS

In the field, most earthworms occurred in the top 5 cm of the soil and no earthworms were found between 15 and 20 cm depth, with no difference between the vertical distributions of detritivores and geophages (Figure 1). Detritivorous species found were: *L. rubellus*, *Lumbricus terrestris* and *Lumbricus castaneus*. Geophagous species found were: *A. caliginosa*, *Aporrectodea rosea* and *Allolobophora chlorotica*. In the course of the study, grasslands

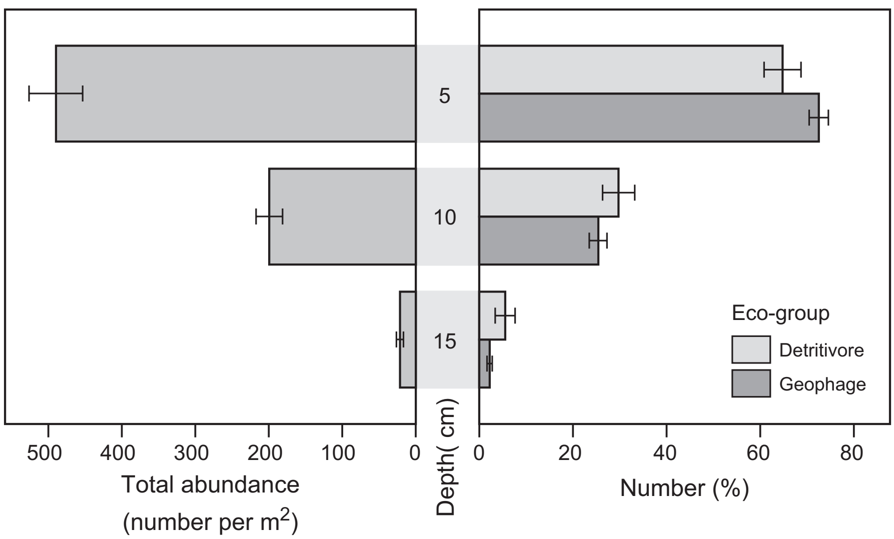

FIGURE 1 At the start of the fieldwork, the majority of earthworms in the field was found in the top 5 cm of the soil (left panel). No earthworms were found in the lowest layer of 15–20 cm depth and is therefore not presented. Proportionally there was no difference in the vertical distribution between detritivorous (*Lumbricus rubellus*) and geophagous (*Aporrectodea caliginosa*) earthworm species (right panel). *N* = 8 grasslands and error bars represent *SE*

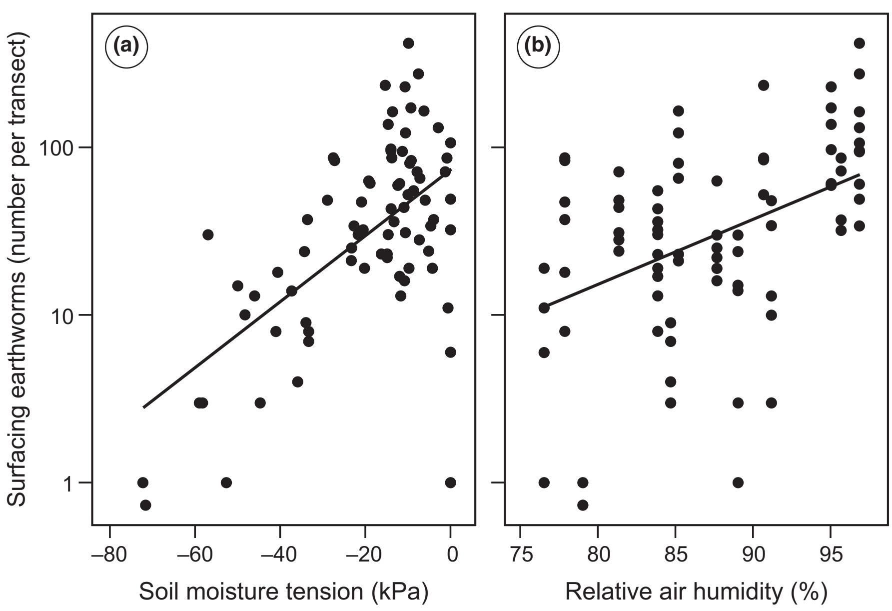

FIGURE 2 Surfacing earthworms (numbers per transect) as a function of (a) soil moisture tension (kPa) ($F_{1,78}$ = 52.04, R^2 = 0.400, p < 0.001) and (b) relative air humidity ($F_{1,78}$ = 20.52, R^2 = 0.208, p < 0.001) under field condtions. Note: the number of surfacing earthworms is plotted on a log-scale. *N* = 8 grasslands

became drier with groundwater levels declining from 10 to 85 cm (min–max) below surface level at the beginning to 42–90 cm below surface level at the end of sampling period. Soil moisture tension increased from −12.1 kPa (*SD* = −7.0) to -45.5 kPa (*SD* = −14.5) and soil resistance increased from 83.6 N/cm^2 (*SD* = 19.1) to 242.6 N/cm^2 (*SD* = 78.3).

Low soil moisture tension and high air humidity increased the number of surfacing earthworms at night (Figure 2 and Table 1). Air temperature at 10 cm above soil surface level ranged from 0.7 to 7.6°C. Temperature during observations, observation day and earthworm abundance did not explain the number of surfacing earthworms (Table 1). We found that more than 80% of the surfacing earthworms were counted on soils with a moisture tension value higher than −15 kPa.

In all three laboratory treatments, soil moisture content increased with depth (Figure 3). However, at every depth the soils in the wet treatment were wetter than the soils in the drier treatments. The wet bulk density at the end of the experiment for the wet treatment was 1.25 g/cm^3 (*SD* = 0.04, *N* = 12), for the moist treatment 1.19 g/cm^3 (*SD* = 0.04, *N* = 12) and 1.15 g/cm^3 (*SD* = 0.03, *N* = 12) for the dry treatment. In the wet treatment most earthworms were found in the upper layers ($F_{4,40}$ = 29.2, R^2 = 0.72, p < 0.001), while the earthworms retreated to greater depths in the dry treatment ($F_{4,40}$ = 9.235, R^2 = 0.43, p < 0.001) and were evenly distributed over the soil column ($F_{4,40}$ = 1.477, R^2 = 0.04, p = 0.227; Figure 3; Table 2). Perhaps surprisingly, but consistent with the similar depth profiles in the field (Figure 1), there were no differences in the depth response between the two ecological types of earthworm. In both species/eco-groups, earthworms mostly selected the soil layers with a soil moisture content of around 30%, irrespective of the moisture treatment (quartic polynomial: $F_{4,175}$ = 11.14, R^2 = 0.185, p < 0.001; Figure 4). The survival of geophages was significantly higher than that of detritivores (93% and 75% respectively; $F_{1,36}$ = 19.11, p < 0.001), irrespective of treatment ($F_{2,36}$ = 1.45, p = 0.250). Furthermore, although the geophages increased in weight (on average 37.0% increase), the detritivores lost weight in all treatments (on average −16.1% decrease).

TABLE 1 Coefficient estimates β, standard errors (*SE*) (β), associated Wald's *z*-score (=β/*SE*(β)) and significance level p for all predictors in the analysis derived from a Generalized Linear Mixed Model (GLMM) with number of surfacing earthworms at night as the response variable and soil moisture tension and air humidity during the observations as explanatory variables (fixed effects). Transect nested in grassland are the random effects and observation day is added as random slope. An observation level random factor (*X*) was added to the model to correct for overdispersion

Full model: AIC = 741.0				
Fixed effects	**Coef. β**	***SE* (β)**	***z*-value**	***p*-value**
(Intercept)	3.400	0.157	21.647	<0.001
Soil moisture tension	−0.847	0.158	−5.356	<0.001
Air humidity	0.450	0.078	5.767	<0.001
Temperature	0.111	0.097	1.155	0.248
Observation day	0.138	0.151	0.919	0.358
Abundance	0.226	0.143	1.573	0.116
Random effects	**Variance**	***SD***	**Cor**	
X	0.399	0.632		
Transect: Grassland	0.012	0.111		
Observation day	0.001	0.024	−1.00	
Grassland	0.144	0.379		
Observation day	0.038	0.195	0.63	
Minimal model: AIC = 751.8				
Fixed effects	**Coeff. β**	***SE* (β)**	***z*-value**	***p*-value**
(Intercept)	3.330	0.193	17.235	<0.001
Soil moisture tension	−0.814	0.119	−6.862	<0.001
Relative air humidity	0.448	0.079	5.694	<0.001
Random effects	**Variance**	***SD***	**Cor**	
X	4.052e-01	0.637		
Transect: Grassland	3.104e-05	0.006		
Observation day	2.982e-06	0.002	0.89	
Grassland	2.346e-01	0.484		
Observation day	8.073e-02	0.284	0.45	

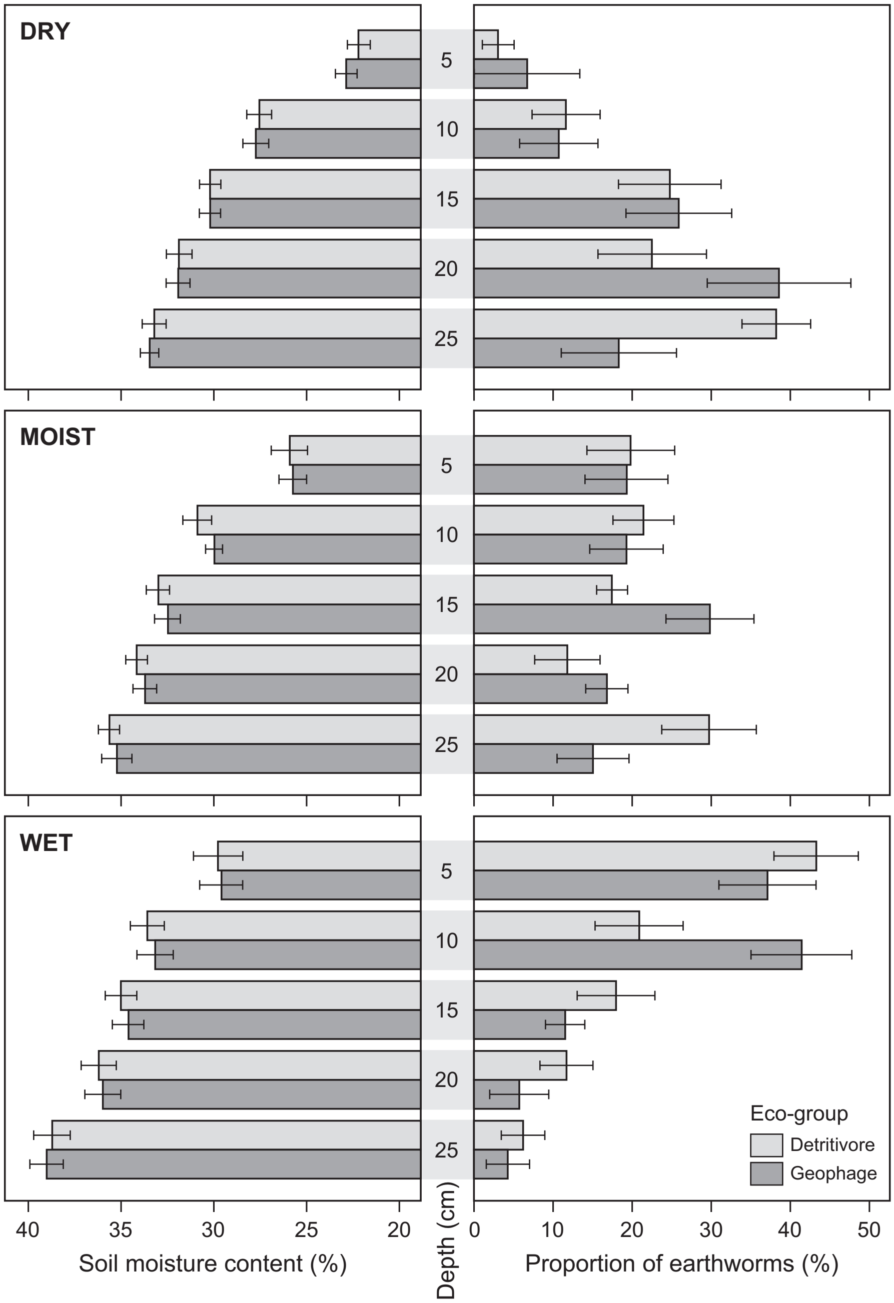

FIGURE 3 Changes in soil moisture content (%) and proportion of earthworms (%) with soil depth under dry, moist and wet experiment soil conditions. Per eco-group, 18 tubes divided over three treatments were used, each tube contained 16–18 earthworms. Error bars represent *SE*s

4 | DISCUSSION

The strong positive effect of soil moisture on earthworm vertical distribution and surface activity was implicated by earlier studies (Baker, Barrett, Grey-Gardner, & Buckerfield, 1992; Evans & Guild, 1947; Gerard, 1967; Nordström, 1975) and establishes a firm link between meadow bird food availability and the meadow-level hydrology. The novelty of this study is our demonstration of the link between soil moisture and the surface presence and activity of earthworms. Desiccation of the topsoil will thus directly negatively reduce food availability for earthworm predators.

Although being a freshwater oligochaete, soils fully saturated with water are avoided by earthworms (Figures 3 and 4) (Darwin, 1881; Laverack, 1963; Roots, 1956). In our experiment, both species moved to soil with a moisture content of about 30%–34% (Figure 4). Grant (1955) performed a similar experiment and found a soil moisture preference of 20%–30% in sandy loam soil for *A. caliginosa*. For another geophagous species, *A. tuberculata*, the optimum soil moisture for growth was also 25% (Wever, Lysyk, & Clapperton, 2001). Berry and Jordan (2001) found that *L. terrestris* in silty loam soils grow optimally with a soil moisture of 30%, but still grow in soils with a 20% soil moisture content when food was available *ad libitum*. Although most species in grasslands can survive up to 17–50 weeks submerged in water (Ausden, Sutherland, & James, 2001; Roots, 1956; Zorn, van Gestel, & Eijsackers, 2005), such survival depends on the oxygen level of the water and the ability to withstand prolonged starvation (Roots, 1956; Turner, 2000). In the field, earthworms vacate flooded soils, especially when the water is warm and

TABLE 2 Coefficient estimates β, standard errors (*SE*) (β), associated Wald's *z*-score (=β/*SE*(β)) and significance level *p* for all predictors in the analysis derived from a generalized linear mixed model (GLMM) with proportion of earthworms at different depths as the response variable and treatment (dry, medium, wet) and depth as explanatory variables (fixed effects). Depth is nested in tube ID and is added as random effects. Reference level for treatment is dry and for the interaction it is dry:depth

Predictor	Coeff. β	*SE* (β)	*z*-value	*p*-value
Fixed effects				
(Intercept)	−2.755	0.277	−9.961	<0.001
Treatment				
Medium	1.473	0.351	4.191	<0.001
Wet	3.008	0.353	8.519	<0.001
Depth	0.421	0.074	5.686	<0.001
Interaction				
Medium × depth	−0.456	0.099	−4.594	<0.001
Wet × depth	−1.041	0.111	−9.339	<0.001
Random effects	**Variance**	***SD***		
Depth: tube ID	0.000	0.000		
Tube ID	0.000	0.000		

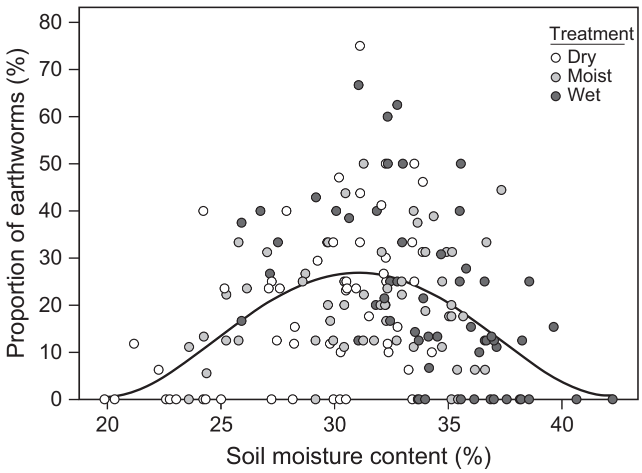

FIGURE 4 Proportion of earthworms (%) as a function of soil moisture content (%) under experimental conditions. Each data point represents a soil layer for both eco-group and all depths

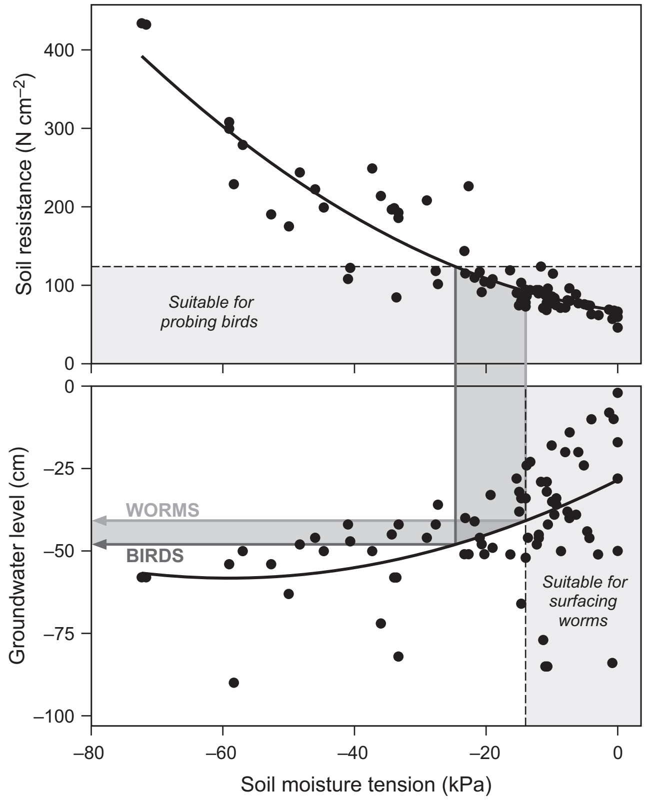

FIGURE 5 A soil should have a maximum soil resistance of 125 N/cm^2 (horizontal dashed line in upper box, Struwe-Juhl, 1995) to allow meadow birds to probe in the soil. Furthermore, the soil moisture tension should not be lower than −15 kPa as surfacing earthworms rapidly decline below this value (vertical dashed line in lower box). As soil resistance and groundwater table are strongly correlated with soil moisture tension (for soil resistance: $F_{3,76} = 25.87$, $R^2 = 0.505$, $p < 0.001$, for groundwater level: $F_{2,77} = 13.91$, $R^2 = 0.265$, $p < 0.001$), we plotted the maximum groundwater level that is required to allow meadow birds to probe in the soil (dark grey line) and earthworms to surface (light grey line). As soil moisture tension values are soil type specific, these values are specific for our studied grasslands (a clay-on-peat area in southwest Friesland)

contains decaying organic material resulting in low oxygen values (Plum & Filser, 2005; Zorn et al., 2005).

Although geophages are more drought tolerant than detritivores (El-Duweini & Ghabbour, 1968) and are therefore likely to show a slower response to drying soils, we did not find a difference in the vertical distribution between the detritivorous *L. rubellus* and the geophagous *A. caliginosa* in the field (Figure 1), nor in the experiment (Figure 3). However, in the experiment the survival of *L. rubellus* was significantly lower than *A. caliginosa*. As this effect was equal between the treatments, soil moisture was not the determining factor. We suggest that food availability caused *L. rubellus* to lose weight in all treatments, whereas *A. caliginosa* increased in weight. This makes sense as *L. rubellus* requires more fresh organic material, not present in the experimental tubes, whereas *A. caliginosa* obtains nutrients from more decomposed organic matter and the microbes living on it, still present in the soil as we only removed coarse organic material and other earthworms (Bouché, 1977; Curry & Schmidt, 2007; Onrust & Piersma, 2019). Earthworms may also lose weight by excreting body water in response to drought (Grant, 1955; Kretzschmar & Bruchou, 1991; Roots, 1956). As the weight response of the experimental earthworms was not correlated with treatment, the experimental soils must have been moist enough.

The studied grasslands with a high groundwater level (less than 25 cm below surface level) desiccated as quickly as grasslands with deeper water-tables (see Figure S1). An explanation may be found in the intensive management. The process of slit injection in late winter/early spring disturbs the topsoil and could therefore enhance the desiccation of the topsoil later in the season. In addition, by cutting through the soil, aggregates and fungal hyphae, which are both beneficial for the water binding capacity of a soil, are broken and therefore the drainage of water from the phreatic zone will increase (Beare, Hu, Coleman, & Hendrix, 1997; Bittman, Forge, & Kowalenko, 2005; Bronick & Lal, 2005; Franzluebbers, 2002; Pulleman, Jongmans, Marinissen, & Bouma, 2003). The timing of raising the groundwater table may have affected the seasonal drying of the soils too. In the Netherlands, ditchwater levels are usually kept higher in summer than in winter (Table S1). The switch from winter to summer level occurs mostly after the farmers have manured their land. However, in spring evaporation starts to become larger than precipitation, leading to desiccation in the top layer of the soil (Colenbrander et al., 1989; Jacobs et al., 2007). Raising the water level so late in spring probably does not have the desired effect of increasing soil moisture as the topsoil is already starting to desiccate, especially on clay soils (Armstrong, 1993).

Agricultural intensification is associated with strong declines of meadow bird numbers (Groen et al., 2012; Newton, 2017; Vickery et al., 2001). Protection measures often involve maintaining high groundwater levels or the creation of other wet features in grasslands (Armstrong, 2000; Ausden et al., 2001; Groen et al., 2012; Kleijn & van Zuijlen, 2004; Schmaltz, Vega, Verkuil, Hooijmeijer, & Piersma, 2016; Smart, Gill, Sutherland, & Watkinson, 2006). As a result of the higher soil moisture, the proportion of earthworms living in the topsoil within reach of tactile feeding birds is higher as well as the fraction of surfacing earthworms at night (this study). In addition, grass growth is retarded and this not only creates a less dense sward which is better for bird locomotion but is also likely to promote earthworm availability as evaporation of the slower growing vegetation is lower and therefore reduces soil desiccation (Atkinson et al., 2005; McCracken & Tallowin, 2004). Indeed, Verhulst, Kleijn, and Berendse (2007) found a positive relationship between groundwater table, prey density in the topsoil and meadow bird numbers.

To enable tactile earthworm hunters to probe, soil resistance should not exceed 125 N/cm^2 (Struwe-Juhl, 1995). For earthworms to surface, soil moisture tension should not be lower than −15 kPa (Figure 2). On this basis we predict that groundwater levels should not exceed −42 cm to maintain surfacing earthworms, and should not be lower than −46 cm to maintain a soil that is suitable for probing (Figure 5). Note that soil moisture tension values are specific to soil type (Collis-George, 1959), in our case to peat grasslands with a layer of clay.

We propose that the slurry- and slit injection-based management of the drained dairy grasslands of the Netherlands prevent earthworms to carry out their important ecological roles as this management promotes dry soil conditions during the season of growth. When earthworms are not active, they fail to perform their work as 'ecosystem engineers' in the grassland food web (Blouin et al., 2013; Lavelle, 1988). Maintaining moist soil conditions will therefore not only promote above- and below-ground biodiversity (Atkinson, Buckingham, & Morris, 2004; Milsom, Hart, Parkin, & Peel, 2002) but could also lead to more sustainable agricultural systems based on the positive effects of earthworms (Erisman et al., 2016; van Groenigen et al., 2014).

ACKNOWLEDGEMENTS

We thank the farmers for being so welcoming and helpful on the land under their care: Klaas Oevering, Sybren de Jong and Piet Visser. Special thanks goes to Ronald de Jong and Sytse Terpstra for providing the details of the water-tables in the study area and Jacob Hogendorf for help with the experiment. This work is part of the research programme which is financed by the Province of Fryslân (University of Groningen/Campus Fryslân support through the Waddenacademie), with additional financial support from the University of Groningen. We thank the anonymous reviewers and the editors for their constructive feedback.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; J.O. collected and analysed the data and together with T.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0gn43fr (Onrust, Wymenga, Piersma, & Olff, 2019).

ORCID

Jeroen Onrust https://orcid.org/0000-0001-7073-6214

REFERENCES

Armstrong, A. C. (1993). Modelling the response of in-field water tables to ditch levels imposed for ecological aims: A theoretical analysis. *Agriculture, Ecosystems and Environment*, *43*, 345–351. https://doi.org/10.1016/0167-8809(93)90097-9

Armstrong, A. C. (2000). DITCH: A model to simulate field conditions in response to ditch levels managed for environmental aims. *Agriculture Ecosystems and Environment*, *77*, 179–192. https://doi.org/10.1016/S0167-8809(99)00082-1

Atkinson, P. W., Buckingham, D., & Morris, A. J. (2004). What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? *Ibis*, *146*, 99–107. https://doi.org/10.1111/j.1474-919X.2004.00346.x

Atkinson, P. W., Fuller, R. J., Vickery, J. A., Conway, G. J., Tallowin, J. R. B., Smith, R. E. N., … Brown, V. K. (2005). Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *Journal of Applied Ecology*, *42*, 932–942. https://doi.org/10.1111/j.1365-2664.2005.01070.x

Ausden, M., Sutherland, W. J., & James, R. (2001). The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. *Journal of Applied Ecology*, *38*, 320–338. https://doi.org/10.1046/j.1365-2664.2001.00600.x

Baker, G. H., Barrett, V. J., Grey-Gardner, R., & Buckerfield, J. C. (1992). The life history and abundance of the introduced earthworms *Aporrectodea trapezoides* and *A. caliginosa* (Annelida: Lumbricidae) in pasture soils in the Mount Lofty Ranges, South Australia. *Australian Journal of Ecology*, *17*, 177–188. https://doi.org/10.1111/j.1442-9993.1992.tb00796.x
Baldwin, F. M. (1917). Diurnal activity of the earthworm. *Journal of Animal Behavior*, *7*, 187–190.
Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.
Beare, M. H., Hu, S., Coleman, D. C., & Hendrix, P. F. (1997). Influences of mycelial fungi on soil aggregation and organic matter storage in conventional and no-tillage soils. *Applied Soil Ecology*, *5*, 211–219. https://doi.org/10.1016/S0929-1393(96)00142-4
Beintema, A. J., Moedt, O., & Ellinger, D. (1995). *Ecologische Atlas Van De Nederlandse Weidevogels*. Haarlem, The Netherlands: Schuyt & Co.
Berry, E. C., & Jordan, D. (2001). Temperature and soil moisture content effects on the growth of *Lumbricus terrestris* (Oligochaeta: Lumbricidae) under laboratory conditions. *Soil Biology and Biochemistry*, *33*, 133–136. https://doi.org/10.1016/S0038-0717(00)00112-7
Bittman, S., Forge, T. A., & Kowalenko, C. G. (2005). Responses of the bacterial and fungal biomass in a grassland soil to multi-year applications of dairy manure slurry and fertilizer. *Soil Biology and Biochemistry*, *37*, 613–623. https://doi.org/10.1016/j.soilbio.2004.07.038
Blouin, M., Hodson, M. E., Delgado, E. A., Baker, G., Brussaard, L., Butt, K. R., … Brun, J.-J. (2013). A review of earthworm impact on soil function and ecosystem services. *European Journal of Soil Science*, *64*, 161–182. https://doi.org/10.1111/ejss.12025
Bos, J. F. F. P., Smit, A. L., & Schröder, J. (2013). Is agricultural intensification in the Netherlands running up to its limits? *NJAS - Wageningen Journal of Life Sciences*, *66*, 65–73. https://doi.org/10.1016/j.njas.2013.06.001
Bouché, M. B. (1977). Strategies lombriciennes. *Ecological Bulletins*, *25*, 122–132.
Briones, M. J. I., & Álvarez-Otero, R. (2018). Body wall thickness as a potential functional trait for assigning earthworm species to ecological categories. *Pedobiologia*, *67*, 26–34. https://doi.org/10.1016/j.pedobi.2018.02.001
Bronick, C. J., & Lal, R. (2005). Soil structure and management: A review. *Geoderma*, *124*, 3–22. https://doi.org/10.1016/j.geoderma.2004.03.005
Butt, K. R., Nuutinen, V., & Siren, T. (2003). Resource distribution and surface activity of adult *Lumbricus terrestris* L. in an experimental system. *Pedobiologia*, *47*, 548–553. https://doi.org/10.1016/S0031-4056(04)70236-X
Colenbrander, H. J., Blumenthal, K. P., Cramer, W., & Volker, A. (1989) *Water in the Netherlands. Proceedings and Information no. 37*. The Hague, The Netherlands: TNO Committee on Hydrological Research.
Collis-George, N. (1959). The physical environment of soil animals. *Ecology*, *40*, 550–557. https://doi.org/10.2307/1929807
Curry, J. P., Doherty, P., Purvis, G., & Schmidt, O. (2008). Relationships between earthworm populations and management intensity in cattle-grazed pastures in Ireland. *Applied Soil Ecology*, *39*, 58–64. https://doi.org/10.1016/j.apsoil.2007.11.005
Curry, J. P., & Schmidt, O. (2007). The feeding ecology of earthworms – A review. *Pedobiologia*, *50*, 463–477. https://doi.org/10.1016/j.pedobi.2006.09.001
Darwin, C. (1881). *The Formation of vegetable mould through the action of worms with observations on their habits*. London, UK: John Murray. https://doi.org/10.5962/bhl.title.107559
Doube, B. M., & Styan, C. (1996). The response of *Aporrectodea rosea* and *Aporrectodea trapezoides* (Oligochaeta: Lumbricidae) to moisture gradients in three soil types in the laboratory. *Biology and Fertility of Soils*, *23*, 166–172. https://doi.org/10.1007/BF00336058
Edwards, C. A., & Bohlen, P. J. (1996). *Biology and ecology of earthworms*. London: Chapmann & Hall.
Edwards, C. A., & Lofty, J. R. (1982). Nitrogenous fertilizers and earthworm populations in agricultural soils. *Soil Biology and Biochemistry*, *14*, 515–521. https://doi.org/10.1016/0038-0717(82)90112-2
Eggleton, P., Inward, K., Smith, J., Jones, D. T., & Sherlock, E. (2009). A six year study of earthworm (Lumbricidae) populations in pasture woodland in southern England shows their responses to soil temperature and soil moisture. *Soil Biology and Biochemistry*, *41*, 1857–1865. https://doi.org/10.1016/j.soilbio.2009.06.007
El-Duweini, A. K., & Ghabbour, S. I. (1968). Nephridial systems and water balance of three oligochaete genera. *Oikos*, *19*, 61–70. https://doi.org/10.2307/3564731
Erisman, J. W., van Eekeren, N., de Wit, J., Koopmans, C., Cuijpers, W., Oerlemans, N., & Koks, B. J. (2016). Agriculture and biodiversity: A better balance benefits both. *AIMS Agriculture and Food*, *1*, 157–174. https://doi.org/10.3934/agrfood.2016.2.157
Ernst, G., Felten, D., Vohland, M., & Emmerling, C. (2009). Impact of ecologically different earthworm species on soil water characteristics. *European Journal of Soil Biology*, *45*, 207–213. https://doi.org/10.1016/j.ejsobi.2009.01.001
Evans, A. C., & Guild, W. J. M. (1947). Studies on the relationships between earthworms and soil fertility. I. Biological studies in the field. *Annals of Applied Biology*, *34*, 307–330. https://doi.org/10.1111/j.1744-7348.1947.tb06367.x
Franzluebbers, A. J. (2002). Water infiltration and soil structure related to organic matter and its stratification with depth. *Soil and Tillage Research*, *66*, 197–205. https://doi.org/10.1016/S0167-1987(02)00027-2
Gerard, B. M. (1967). Factors affecting earthworms in pastures. *Journal of Animal Ecology*, *36*, 235–252. https://doi.org/10.2307/3024
de Goede, R. G. M., Brussaard, L., & Akkermans, A. D. L. (2003). On-farm impact of cattle slurry manure management on biological soil quality. *NJAS - Wageningen Journal of Life Sciences*, *51*, 103–133. https://doi.org/10.1016/S1573-5214(03)80029-5
Grant, W. C. (1955). Studies on moisture relationships in earthworms. *Ecology*, *36*, 400–407. https://doi.org/10.2307/1929574
Groen, N. M., Kentie, R., de Goeij, P., Verheijen, B., Hooijmeijer, J. C. E. W., & Piersma, T. (2012). A modern landscape ecology of Black-tailed Godwits: Habitat selection in southwest Friesland, The Netherlands. *Ardea*, *100*, 19–28. https://doi.org/10.5253/078.100.0105
van Groenigen, J. W., Lubbers, I. M., Vos, H. M. J., Brown, G. G., de Deyn, G. B., & van Groenigen, K. J. (2014). Earthworms increase plant production: A meta-analysis. *Scientific Reports*, *4*, 1–7. https://doi.org/10.1038/srep06365
Hansen, S., & Engelstad, F. (1999). Earthworm populations in a cool and wet district as affected by tractor traffic and fertilisation. *Applied Soil Ecology*, *13*, 237–250. https://doi.org/10.1016/S0929-1393(99)00037-2
Hendriksen, N. B. (1990). Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils*, *10*, 17–21.
Holmstrup, M. (2001). Sensitivity of life history parameters in the earthworm *Aporrectodea caliginosa* to small changes in soil water potential. *Soil Biology & Biochemistry*, *33*, 1217–1223. https://doi.org/10.1016/S0038-0717(01)00026-8
Jacobs, A. F. G., Heusinkveld, B. G., & Holtslag, A. A. M. (2007). Seasonal and interannual variability of carbon dioxide and water balances of a grassland. *Climatic Change*, *82*, 163–177. https://doi.org/10.1007/s10584-006-9182-7
Jiménez, J. J., & Decaëns, T. (2000). Vertical distribution of earthworms in grassland soils of the Colombian Llanos. *Biology and Fertility of Soils*, *32*, 463–473. https://doi.org/10.1007/s003740000277
Kleijn, D., & van Zuijlen, G. J. C. (2004). The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands,

in the period 1989–1995. *Biological Conservation*, *117*, 443–451. https://doi.org/10.1016/j.biocon.2003.08.012

Kretzschmar, A., & Bruchou, C. (1991). Weight response to the soil water potential of the *Aporrectodea longa*. *Biology and Fertility of Soils*, *12*, 209–212. https://doi.org/10.1007/BF00337204

Lange, G. (1968). Über Nahrung, Nahrungsaufnahme und Verdauungstrakt mitteleuropaischer Limikolen. *Beiträge zur Vogelkunde*, *13*, 225–334.

Lavelle, P. (1988). Earthworm activities and the soil system. *Biology and Fertility of Soils*, *6*, 237–251.

Laverack, M. S. (1963). *The physiology of earthworms*. Oxford, UK: Pergamon Press.

MacDonald, D. W. (1980). The Red Fox, *Vulpes vulpes*, as a predator upon Earthworms, *Lumbricus terrestris*. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology*, *52*, 171–200. https://doi.org/10.1111/j.1439-0310.1980.tb00710.x

McCracken, D. I., & Tallowin, J. R. (2004). Swards and structure: The interactions between farming practices and bird food resources in lowland grasslands. *Ibis*, *146*, 108–114. https://doi.org/10.1111/j.1474-919X.2004.00360.x

Miller, R.G. (1986) *Beyond ANOVA, basics of applied statistics*. New York, NY: John Wiley.

Milsom, T. P., Hart, J. D., Parkin, W. K., & Peel, S. (2002). Management of coastal grazing marshes for breeding waders: The importance of surface topography and wetness. *Biological Conservation*, *103*, 199–207. https://doi.org/10.1016/S0006-3207(01)00122-7

Muldowney, J., Curry, J. P., O'Keeffe, J., & Schmidt, O. (2003). Relationships between earthworm populations, grassland management and badger densities in County Kilkenny, Ireland. *Pedobiologia*, *47*, 913–919.

Newton, I. (2017). *Farming and birds* (Collins New Naturalist Library, Book 135). London, UK: HarperCollins Publishers.

Nordström, S. (1975). Seasonal activity of Lumbricids in southern Sweden. *Oikos*, *26*, 307–315. https://doi.org/10.2307/3543501

Onrust, J., Loonstra, A. H. J., Schmaltz, L. E., Verkuil, Y. I., Hooijmeijer, J. C. E. W., & Piersma, T. (2017). Detection of earthworm prey by Ruff *Philomachus pugnax*. *Ibis*, *159*, 647–656. https://doi.org/10.1111/ibi.12467

Onrust, J., & Piersma, T. (2017). The hungry worm feeds the bird. *Ardea*, *105*, 153–161. https://doi.org/10.5253/arde.v105i2.a4

Onrust, J., & Piersma, T. (2019). How dairy farmers manage the interactions between organic fertilizers and earthworm ecotypes and their predators. *Agriculture, Ecosystems and Environment*, *273*, 80–85. https://doi.org/10.1016/j.agee.2018.12.005

Onrust, J., Wymenga, E., Piersma, T., & Olff, H. (2019). Data from: Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.0gn43fr

Parker, G. H., & Parshley, H. M. (1911). The reactions of earthworms to dry and to moist surfaces. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *11*, 361–363. https://doi.org/10.1002/(ISSN)1097-010X

Plum, N. M., & Filser, J. (2005). Floods and drought: Response of earthworms and potworms (Oligochaeta: Lumbricidae, Enchytraeidae) to hydrological extremes in wet grassland. *Pedobiologia*, *49*, 443–453. https://doi.org/10.1016/j.pedobi.2005.05.004

Pulleman, M., Jongmans, A., Marinissen, J., & Bouma, J. (2003). Effects of organic versus conventional arable farming on soil structure and organic matter dynamics in a marine loam in the Netherlands. *Soil Use and Management*, *19*, 157–165. https://doi.org/10.1079/sum2003186

Quinn, G. P., & Keough, M. J. (2005). *Experimental design and data analyses for biologists*. Cambridge: Cambridge University Press.

R Development Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Roots, B. I. (1956). The water relations of earthworms. II. Resistance to desiccation and immersion, and behaviour when submerged and when allowed a choice of environment. *Journal of Experimental Biology*, *33*, 29–44.

Rundgren, S. (1975). Vertical distribution of lumbricids in southern Sweden. *Oikos*, *26*, 299–306. https://doi.org/10.2307/3543500

Rutgers, M., Orgiazzi, A., Gardi, C., Römbke, J., Jänsch, S., Keith, A. M., … Zwart, D. D. (2016). Mapping earthworm communities in Europe. *Applied Soil Ecology*, *97*, 98–111. https://doi.org/10.1016/j.apsoil.2015.08.015

Schmaltz, L. E., Vega, M. L., Verkuil, Y. I., Hooijmeijer, J. C. E. W., & Piersma, T. (2016). Use of agricultural fields by Ruffs staging in southwest Friesland in 2003–2013. *Ardea*, *104*, 23–32. https://doi.org/10.5253/arde.v104i1.a2

Smart, J., Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (2006). Grassland-breeding waders: Identifying key habitat requirements for management. *Journal of Applied Ecology*, *43*, 454–463. https://doi.org/10.1111/j.1365-2664.2006.01166.x

Struwe-Juhl, B. (1995). Effects of conservation measures in the Hohner See area on numbers, breeding success and feeding ecology of the Black-tailed Godwit (*L. limosa*). *Corax*, *16*, 153–172.

Turner, J. S. (2000). *The extended organism: The physiology of animal-built structures*. Cambridge, UK: Harvard University Press.

Verhulst, J., Kleijn, D., & Berendse, F. (2007). Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. *Journal of Applied Ecology*, *44*, 70–80.

Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J., & Brown, V. K. (2001). The management of lowland neutral grasslands in Britain: Effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, *38*, 647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x

van Vliet, P. C. J., & de Goede, R. G. M. (2006). Effects of slurry application methods on soil faunal communities in permanent grassland. *European Journal of Soil Biology*, *42*, S348–S353. https://doi.org/10.1016/j.ejsobi.2006.09.004

Wever, L., Lysyk, T., & Clapperton, M. (2001). The influence of soil moisture and temperature on the survival, aestivation, growth and development of juvenile *Aporrectodea tuberculata* (Eisen) (Lumbricidae). *Pedobiologia*, *133*, 121–133. https://doi.org/10.1078/0031-4056-00074

Zorn, M. I., van Gestel, C. A. M., & Eijsackers, H. (2005). Species-specific earthworm population responses in relation to flooding dynamics in a Dutch floodplain soil. *Pedobiologia*, *49*, 189–198. https://doi.org/10.1016/j.pedobi.2004.08.004

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Onrust J, Wymenga E, Piersma T, Olff H. Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands. *J Appl Ecol*. 2019;56:1333–1342. https://doi.org/10.1111/1365-2664.13356