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Determining the Availability of Earthworms for Visually Hunting Predators

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ABSTRACT Studies of interactions among earthworms as prey for visually foraging predators required a field method that measures earthworm availability (i.e., the density of surfacing earthworms). We present such a method by counting surfacing earthworms at night by an observer lying prone on a cart propelled by an observer across measured distances at constant low speed. The method was applied in dairy farmland grasslands in The Netherlands during October and November 2011. We quantified the numbers of surfacing earthworms as well as those measured during standard hand-sorting sampling (i.e., total abundance based on soil counts), distinguishing clay or peat soils and grasslands with either monocultures or species-rich vegetation. Managed grasslands with different soil types showed opposing correlations between surface availability and total abundance of earthworms. This emphasizes the importance of direct measurements of earthworm availability if the goal of the study is to explain the behavior of either visual earthworm predators or earthworms themselves.

KEY WORDS earthworm abundance, earthworm availability, foraging ecology, Lumbricidae, methodology.

Earthworms (Lumbricidae) play a critical role in soil ecology and nutrient cycling (Darwin 1881, Edwards and Bohlen 1996). At the same time, they are important as food for many animals (Macdonald 1983, Curry 1998, Onrust et al. 2017). These protein-rich prey are found in many ecosystems around the world and can be very abundant in fertile soils (Edwards and Bohlen 1996).

As soil-dwelling organisms, earthworms can be captured by predators that probe deeply in the soil (e.g., the long-billed sandpipers, Scolopacidae [Burton 1974]) and by pursuit predators that dig themselves through the soil (e.g., moles [*Talpa europaea;* Raw 1966]). Soil samples can be taken to measure the abundance of earthworms (Römbke et al. 2006, Coja et al. 2008). Such samples can then be subdivided in different depth layers to obtain measures of availability for a probing predator (Rundgren 1975). However, many predators only catch earthworms on the surface, especially reptiles and amphibians (Hamilton 1951, Macdonald 1983), some mammal species (e.g., badger [*Meles meles;* Kruuk and Parish 1981, Madsen et al. 2002]), and some bird species (e.g., little owls [*Athene noctua;* Hounsome et al. 2004, Romanowski et al. 2013], golden plovers [*Pluvialis apricaria;* Bengtson et al. 1978], and blackbirds [*Turdus merula;* Chamberlain et al. 1999]). Therefore, the abundance or biomass of earthworms derived from soil samples taken during the day will give a biased estimate of earthworm availability from the predator point of view at best, or perhaps no estimate at all (Duriez et al. 2006). In studies on the foraging ecology of visual earthworm predators, it would be important to directly measure the density of surfacing earthworms.

Earthworm availability is defined as the number of visible earthworms per unit surface area. Darwin (1881) already noted nocturnal activity of earthworms on the soil surface, and others showed that the highest activity is measured in the first hours after sunset (Baldwin 1917, Butt et al. 2003). Earthworms come to the surface to scavenge for living and decaying organic material (Edwards and Bohlen 1996). This behavior differs among species and is determined by their feeding ecology (Lowe and Butt 2002). Surface-dwelling earthworms mostly belong to the epigeic and anecic ecological group, which come to the surface to collect food, rather than the endogeic ecological group, which come to the surface in the reproductive period or during heavy rainfall events (Bouché 1977, Curry and Schmidt 2007).

Earthworm availability for visual predators has previously been assessed indirectly using climatic variables to calculate

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'worm nights' (including temperature, humidity and time since last rain; Macdonald 1980, Kruuk and Parish 1981, Baubet et al. 2003). A more direct method was used by Macdonald (1980), who counted surfacing earthworms on grids in gardens using a light fitted with a red filter. A similar method was employed by Dänhardt (2010), who measured earthworm availability for golden plovers in croplands in southern Sweden by walking transects of 30 m and counting the earthworms seen on the surface approximately 60–70 cm in front of the observer. However, we were interested in earthworm surface availability in grasslands, so an observer had to be close to the soil to discriminate earthworms from grasses. Furthermore, in studies aimed at understanding the feeding distribution of woodcock (*Scolopax rusticola*), Duriez et al. (2006) counted earthworms that were crawling on the surface at night. They noticed that earthworms were sensitive to vibrations and retreated in their burrows when a walking observer approached.

Here we describe a new method to measure surfacing earthworm densities directly in grassland habitats with a good visibility at the surface and without creating too much disturbance. We applied the method in 4 types of agricultural grasslands in an area of dairy farming in The Netherlands, a region commonly used by a wide variety of visually hunting earthworm predators such as red foxes (*Vulpes vulpes*), hedgehogs (*Erinaceus europaeus*), lapwings (*Vanellus vanellus*), and golden plovers. We compared the number of available earthworms with abundances in the soil. Although agricultural intensification of these grasslands might promote earthworm abundances (Muldowney et al. 2003, Atkinson et al. 2005, Curry et al. 2008), it is not clear whether earthworms would also become more available for predators. Indeed, less intensive agricultural practices are often used to promote habitat availability for the strongly declining meadow bird community (Vickery et al. 2001).

STUDY AREA

This study was performed on 48 grasslands throughout the province of Fryslân, The Netherlands, across an area spanning approximately 20 × 40 km. All grasslands were used for dairy farming and we selected them based on their soil type (clay or peat) and degree of agricultural use (monocultures vs. species-rich grasslands). Monocultures consisted predominantly of fast-growing rye grass species (*Lolium* spp.) and were mowed 5–6 times/year, in most turns followed by treatment with injected slurry. Furthermore, these grasslands have a relative low groundwater table (80–120 cm below surface level) and a monotonous vegetation (Groen et al. 2012, Howison et al. 2018). Species-rich grasslands had a management agreement to protect meadow birds, meaning that these grasslands were first mowed later in spring and less often (2–3 times) and fertilized with farmyard manure only, and therefore, tended to have a greater plant diversity. The annual average temperature for the study area was 9.7° C with average annual precipitation of 844.7 mm per year (data obtained from the nearest weather station for the period 1991–2011).

METHODS

We counted earthworms from a movable earthworm observation platform (the 'cart') that consisted of a robust rectangular metal frame with 4 fixed tires (100-mm width), with the frame being half-closed with a shelf (Fig. 1). In this way, while in prone position and with the head in front of the cart, the observer could touch the ground and move freely. The observer could then observe the soil surface from a height of 50 cm and to within a width of 50 cm in front of the observer. We could then estimate surfacing densities by dividing the surface (length of transect × 0.5 m) by the total numbers counted. At night, the observer used a headlamp (160 lumens) without any filter. We conducted all counts on grassland with a short sward height (<10 cm).

First, we examined activity patterns in the surfacing behavior of earthworms. In autumn 2010, we counted surfacing earthworms from 1600 CEST until 0800 CEST. Every hour, we counted the same transect of 100 m, but divided the counts in 3 periods of 4–5 hours over 3 days. This transect was in an agricultural grassland on clay soil near Akkrum, Friesland (N 53°3.367, E 5°52.012). The hourly counts were divided over 3 days, so we used the relative numbers of the maximum number counted per time period.

To test whether the management classification of the 48 grasslands resulted in distinct type of grasslands, we surveyed the vegetation composition of each managed

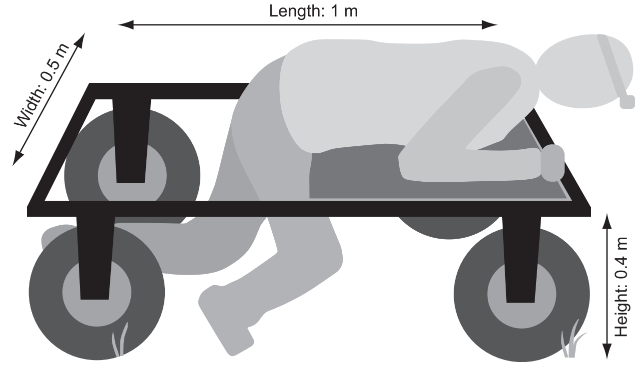

Figure 1. Graphical representation of the technique developed to count earthworms on the ground surface in The Netherlands during 2010 and 2011.

grassland field and determined a weighted Ellenberg's indicator value for soil fertility and moisture (Ellenberg et al. 1991). These values indicate the ecological preference of plants and are scored on a scale of 1–9 for fertility (9 represents extreme nutrient-rich situations) and on a scale of 1–12 for moisture (12 represents submerged conditions; Ellenberg et al. 1991). We surveyed vegetation in November 2011 by randomly placing a 1 × 1-m quadrat 5 times and determining the plant species (rosettes of most herbs still visible in this time of year) and abundance within that frame.

In October 2011, a single observer (JO) counted earthworms at 2 randomly placed transects of 50 m with a speed of about 0.3 m/second. We conducted counts during night time between 2100 and 2400 CEST because this is the period with the greatest surface activity (own observations; Butt et al. 2003). We considered every earthworm seen to be potential prey for an eye-hunting predator. Therefore, we counted all earthworms and made no distinctions among species, small and large earthworms, and earthworms that were either completely or partially out of their burrows. Over a period of 20 nights, we conducted counts on all managed grassland fields once. We also measured weather conditions during the observation period (Fig. 2).

In the morning after the night-time surveys, we excavated 4 soil samples of 20 × 20 × 20 cm at the transects (2/transect, 4 in total/grassland). We counted all earthworms by sorting out the samples by hand. There might be a sampling effect because some deeply burrowing anecics could be missed when hand-sorting soil samples, although this method generally yields the most individuals and greatest biomass of earthworms (Coja et al. 2008). We identified only adult earthworms to species level because this can only be done accurately when earthworms have a clitellum (Sherlock 2012). For the analysis, we classified species into 3 ecological groups according to Bouché (1977).

We obtained hourly weather conditions during observations from the nearest weather station in Leeuwarden (53°13′ N, 05°46′ E, www.knmi.nl). For analysis, we used the following average values for the 2100–2400 CEST period: temperature in °C at 10 cm above ground level, atmospheric humidity, total precipitation during the observations in mm, and total precipitation during daytime.

We performed statistical analyses using Program R (R Development Core Team 2016). We counted 2 transects/grassland in 2011; therefore, we were able to calculate repeatability of this method by estimating the Intraclass Correlation Coefficient (ICC) by using the R package 'ICC' (Wolak et al. 2012). For all analyses, we performed a linear mixed-effects analysis for nested data (transect or sample were nested within grassland) with the package 'nlme' (Pinheiro et al. 2016), because type of soil (clay or peat) and type of grassland (monocultures or herb-rich meadows) were fixed effects and grassland was the random effect. Data exploration for this multivariate dataset showed that earthworm availability and earthworm abundance contained outliers and violation of homogeneity. A log-transformation for availability and a square-root transformation for abundance solved these problems. For each model, we also built a random intercept model (with grassland as the random intercept) to account for differences between grasslands. Furthermore, we built a random slope model (with transect or sample nested in grassland as the random slope) to control for spatial effects. We then used the model with the lowest Akaike's Information Criterion (AIC) for further analysis. We obtained *P*-values by likelihood ratio test of the full model with the effect in question against the model without the effect in question. We checked the normality of the residuals by visual inspecting the QQ plots (Miller 1986). We made *post hoc* comparisons by using the R package 'lsmeans' (Lenth 2016).

RESULTS

Only in darkness did earthworms come to the surface, with numbers rising rapidly after sunset, remaining stable during the night, and declining equally rapidly before sunrise (Fig. 3). The Intraclass Correlation Coefficient for this method was 0.69 with 95% CI (0.36–0.85), which shows considerable agreement between the 2 transects in 2011.

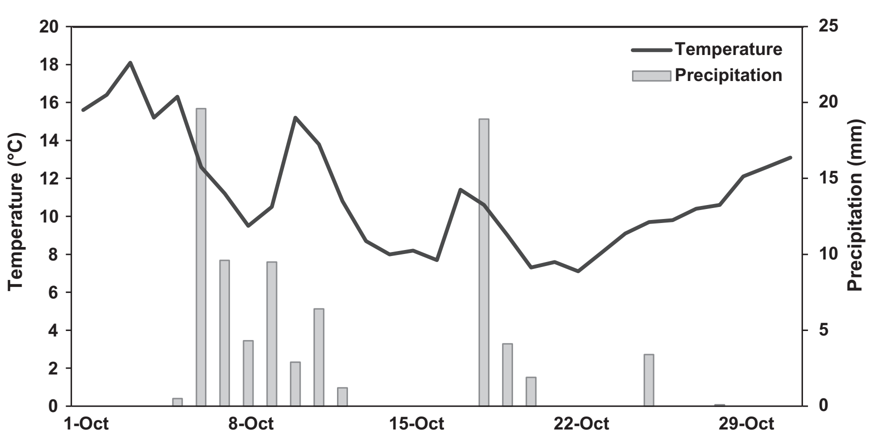

Figure 2. Meteorological conditions during period where we counted earthworms on the ground surface during October 2011. Data are from the nearest Royal Netherlands Meteorological Institute weather station in Leeuwarden, The Netherlands (53°13′N 5°45′E, all studied grassland were within a range of 30 km from weather station).

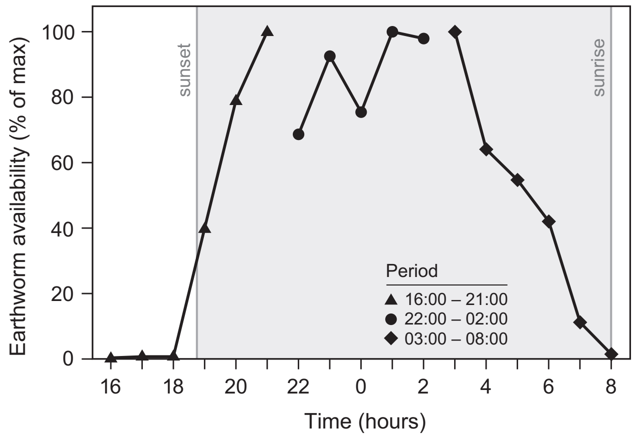

Figure 3. Earthworm availability at a single transect of 100 m in agricultural grassland from 3 counts at different time periods near Akkrum, Friesland, The Netherlands, during 2010–2011. The relative numbers of the maximum number counted in one time period is plotted as the counts were done on different days.

Grassland characteristics of the 48 studied grasslands are summarized (Table 1). Compared with monocultures, species-rich grasslands had a lower Ellenberg value for fertility ($\chi^2_1 = 61.54$, $P < 0.001$), but there was no effect of soil type ($\chi^2_1 = 0.58$, $P = 0.45$). In addition, species-rich grasslands had a greater value for moisture ($\chi^2_1 = 42.43$, $P < 0.001$), but the effect of soil type was also influential ($\chi^2_1 = 6.10$, $P = 0.014$). Nevertheless, during the fieldwork period, all grasslands did not flood and were moist enough to allow earthworms to surface. The pH of the soil, although greater on clay soils than on peat soils ($\chi^2_1 = 5.99$, $P = 0.014$), was well within earthworm tolerance levels (Edwards and Bohlen 1996). There was no effect of management type ($\chi^2_1 = 1.27$, $P = 0.26$). These results show that our classification distinguished grasslands based on management type rather than soil type.

In the period of observations, average sward height was short for all grasslands visited (7.5 cm, SD = 2.8, $n = 48$). Availability of earthworms varied between 0.12 and 3.66 earthworms/m^2, with an average density of available earthworms of 1.04 earthworms/m^2 (SD = 0.81, $n = 48$; Table 1). Most earthworms were only partially out of their burrow and in the process of collecting food items; others were mating or crawling around. There was no effect of soil type on earthworm availability ($\chi^2_1 = 3.09$, $P = 0.08$), but grassland type ($\chi^2_1 = 8.30$, $P = 0.004$) and the interaction between soil and grassland type were influential ($\chi^2_1 = 7.26$, $P = 0.007$). Nevertheless, a *post hoc* comparison revealed only a difference between species-rich grasslands on peat soil with all other grasslands at $P < 0.05$ (Fig. 4A).

There was large variation in number of earthworms collected from soil samples, with numbers ranging between 18.8 and 800.0 earthworms/m^2/grassland (Table 1). Although earthworm abundance was greatest in monocultures ($\chi^2_1 = 4.24$, $P = 0.04$) and in peat soils ($\chi^2_1 = 4.20$, $P = 0.04$; Fig. 4B), the interaction was not present ($\chi^2_1 = 0.40$, $P = 0.53$). A scatterplot of numbers of available earthworms on total abundance in the soil showed a lack of relationship for species-rich grasslands on both clay ($r^2 = 0.06$, $F_{1,11} = 0.34$, $P = 0.57$) and peat soil ($r^2 = 0.02$, $F_{1,11} = 1.22$, $P = 0.30$; Fig. 5). For monocultures, however, there was a positive relationship for clay soils ($r^2 = 0.49$, $F_{1,11} = 11.48$, $P = 0.007$), but a negative one for peat soils ($r^2 = 0.33$, $F_{1,11} = 5.86$, $P = 0.04$). None of the weather variables during observations explained earthworm availability ($F_{4,43} = 1.09$, $P = 0.37$).

In all grasslands, about half (46.8%) of the earthworms were adults and could thus be identified to species level.

Table 1. Grassland characteristics where we developed a technique to count earthworms on the ground surface, according to soil and vegetation type. Surface activity, abundance in soil sample, and number of species for grasses and forbs are all in numbers per m^2. Data were collected in October and November 2011, within the province of Fryslân, The Netherlands.

		Soil type							
		Clay				Peat			
		Species-rich		Monoculture		Species-rich		Monoculture	
Variable	Grassland	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Earthworm	Availability	1.22	0.85	1.10	0.49	0.44	0.21	1.76	1.60
	Abundance	264.06	132.91	353.65	187.85	371.35	220.83	543.23	305.76
Vegetation	Grasses	3.50	1.05	1.92	0.65	3.25	1.22	1.83	0.70
	Forbs	4.70	1.58	1.71	0.86	4.83	1.32	2.56	1.02
Ellenberg value	Fertility	6.10	0.35	7.11	0.46	6.05	0.40	7.03	0.37
	Moisture	6.17	0.64	5.34	0.35	6.47	0.79	5.42	0.36
pH		5.92	0.70	6.11	0.61	5.52	0.31	5.70	0.51

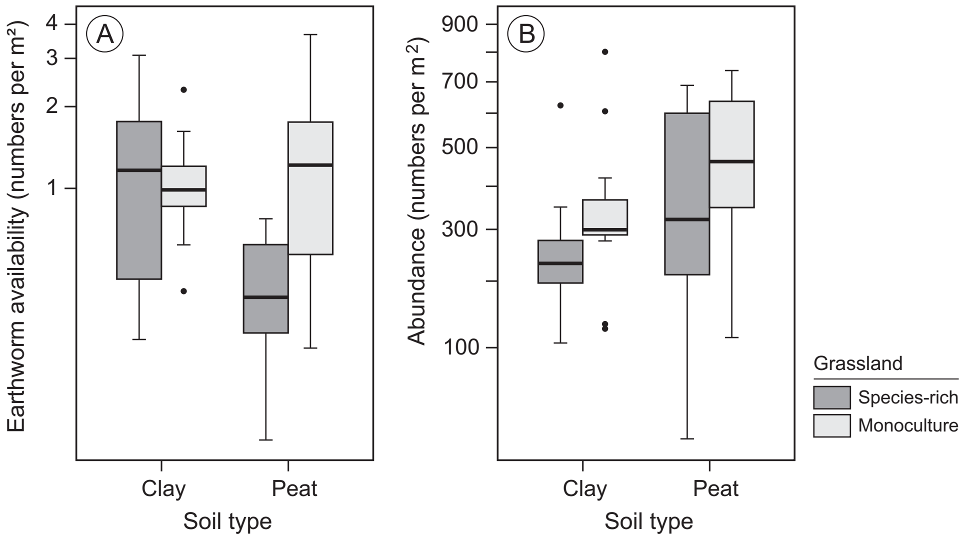

Figure 4. Boxplots of nocturnal counts with number of available earthworms per 100 m (A, in number per m^2) and earthworm abundances in the soil (B, in number per m^2), derived from soil samples taken from the same transects near Akkrum, Friesland, The Netherlands, during 2010–2011. Each boxplot represents 12 grasslands. Note that the *y*-axes are scaled to log (A) and square root (B).

From the identifiable individuals in the soil samples, only 15.3% were anecic (*Lumbricus terrestris*) or epigeic (*L. castaneus* and *L. rubellus*) species. There was no relationship between the abundance of this group (anecics and epigeics combined) of earthworms and the availability of earthworms ($r^2 = 0.02$, $F_{1,47} = 0.72$, $P = 0.40$). Endogeic species found were *Allolobophora chlorotica*, *Aporrectodea caliginosa*, and *A. rosea*.

DISCUSSION

We describe a new method that yields a direct measure of earthworm availability for visually hunting earthworm-eaters in grassland habitats. Earthworm abundance in the soil did not consistently predict the numbers of surfacing earthworms; therefore, direct measurement of the densities of surfacing earthworms is most definitely a requirement in studies in which prey availability for visual hunting predators is the key variable (Zwarts and Wanink 1993, Onrust et al. 2017).

During nocturnal counts, earthworms did react to the bright luminescence of the headlamp. This happened only after 2–3 seconds, which gave us enough time to spot and count them (Darwin 1881, Svendsen 1957). Using an infrared wildlife camera could overcome these problems. However, the camera should be close to the soil surface and, therefore, it will only observe a small patch. The densities of surfacing earthworms are rather low (on average 1 earthworm/m^2), so a larger surface should be scanned for a proper density estimation. However, Onrust et al. (2017) used the same method and in the same land-cover types, but scanned a larger surface per grassland (75 m^2), and also found low densities of surfacing earthworms (max. of

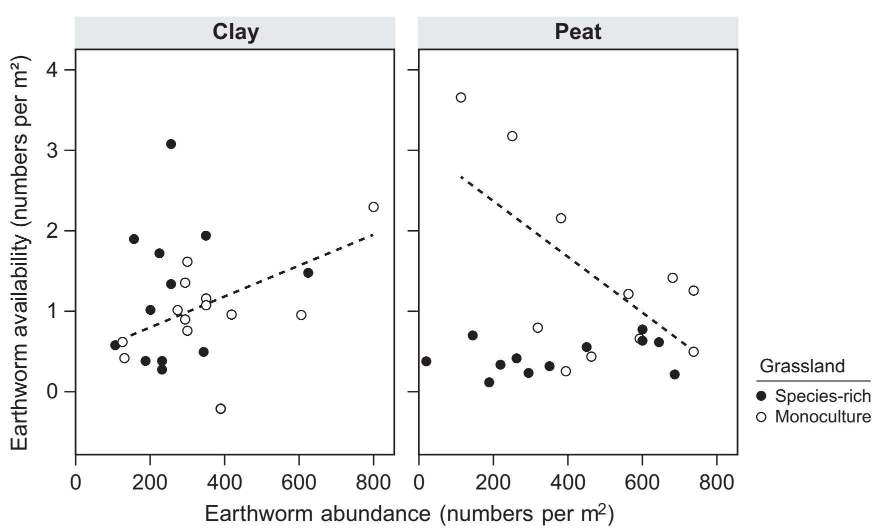

Figure 5. Earthworm availability at night as a function of the total abundance in the soil near Akkrum, Friesland, The Netherlands, during 2010–2011. For monoculture grasslands only (open dots), there is a positive relationship with clay soil ($r^2 = 0.49$, dashed line in left panel), but a negative relationship with peat soil ($r^2 = 0.33$, dashed line in right panel).

1.8 earthworms/m^2). Earthworms might come up or go down as a result of vibrations applied to the soil (Mitra et al. 2009). Only when the cart was close (within a few cm) to an earthworm would it retract in its burrow. An electrically powered cart might further reduce the vibrations. Further research is necessary to improve this method to come to an even more accurate measure of earthworm availability for visual earthworm predators.

The method of riding a self-propelled cart is useful in agricultural grasslands. Although tested in northwestern Europe, it should have worldwide applications. Agricultural grasslands are an increasingly widespread land-cover type generally containing large numbers of earthworms (Rutgers et al. 2016). In Europe, such grasslands host a unique 'meadow bird' community (BirdLife International 2017), which is a threatened group of birds that breed in this habitat and feed primarily on earthworms (Högstedt 1974, Baines 1990). The cart method can only be applied in fields with good visibility on the soil surface (i.e., with a short sward). Coincidentally, these are exactly the fields used by predators that are visually hunting earthworms (Mason and MacDonald 1999, Devereux et al. 2004).

The lack of relationship between earthworm abundance based on soil counts and earthworm availability based on counts of surfacing earthworms could be caused by species-specific surfacing behavior. Surfacing occurs most in epigeic and anecic species that scavenge for food on the soil surface (Svendsen 1957, Curry and Schmidt 2007). This explains why Cuendet (1983) found proportionally more epigeics than endogeics in the gut content of black-headed gulls (*Chroicocephalus ridibundus*), accounting for numerical presence in the soil. However, we did not find a relationship between the abundance of surfacing species and availability of earthworms. A large proportion of the collected earthworms could not be identified because they were immature and lacked a clitellum, and this might have obscured these data. Furthermore, deep burrowing anecic species could have been missed with our sampling design. Using an expellant solution might give a better estimation for these species (Lawrence and Bowers 2002). The surfacing behavior of earthworms is known to depend on soil moisture (Parker and Parshley 1911, Kretzschmar 1991), ambient light, and temperature (Darwin 1881, Baldwin 1917, Edwards and Bohlen 1996, Butt et al. 2003). Anecic and epigeic earthworms come to the surface to forage, so food conditions and state of hunger of the earthworm also affects this behavior (Onrust and Piersma 2017). The stock of earthworms in the soil thus will not give any information about the availability of earthworms for visually hunting predators. Using the cart method will provide new insights in the ecology of earthworms and their relationship with visually hunting nocturnal predators have come within reach (Onrust et al. 2017, Onrust and Piersma 2017).

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