The Hungry Worm Feeds the Bird

The hungry worm feeds the bird

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Earthworms (Lumbricidae) are important prey for many birds. Based on their own feeding ecology, earthworms can be separated into two ecotypes: the detritivores that feed on organic material and the geophages that feed on soil particles and organic matter. Detritivores collect their food on the surface during the night when they are exposed to nocturnal predators. Hungry animals tend to show more risk-prone behaviour and may therefore be more vulnerable to bird predation, so we expect well-fed detritivorous earthworms to visit the surface less frequently. In this study, we tested this hypothesis in dairy farmland in the province of Fryslân, The Netherlands. Two uniform grasslands were split, with each half receiving either an early (1 February 2014) or a late (14 March 2014) farmyard manure application. Every two weeks, nocturnal surface activity of earthworms was measured by counting surfacing earthworms from a slowly pushed cart. Furthermore, soil samples were taken for total abundances and to measure individual body conditions of earthworms. As predicted, the density of surfacing earthworms was on average 2.5 times higher in the fields before farmyard manure was applied. Immature detritivores had significantly lower body masses in fields not yet manured, suggesting that these growing earthworms were hungry. Differences in surfacing behaviour and body mass disappeared after all fields had been given farmyard manure. We conclude that hunger forces detritivorous earthworms to the surface. After manure application, they appear satisfied and avoid the risk of depredation by birds by staying away from the soil surface. To promote earthworm availability for meadow birds, spreading farmyard manure on the surface should occur as late in spring as possible. In this way, hungry earthworms are forced to the surface and are available as meadow bird prey for longer periods.

Key words: agriculture, foraging, grassland, Lumbricidae, meadow birds, predation risk, prey availability

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As places with highest food abundance are not necessarily the safest places, foraging animals must often trade off the rewards of feeding and the risks of becoming food themselves (Lima & Dill 1990, Sih 1992, Krebs & Davies 2007). During periods of shortage, eventually their increased need for food overrides the 'fear' of risk taking (Lima 1998). The tendency for hungry animals to show more risk-prone behaviour (Dill & Fraser 1984, Horat & Semlitsch 1994), may be relevant for the understanding of earthworm surfacing behaviour, with implications for their availability to avian predators.

Earthworms (Lumbricidae) are soil-dwelling organisms well known for their positive effects on soil functioning (Lavelle *et al.* 2006, Blouin *et al.* 2013). Earthworms feed on decaying organic material, e.g. farmyard manure, and derive nutrition by feeding directly on bacteria and fungi that grow upon these materials, but also on the mutualistic relationship with these micro-organisms in the earthworms' guts (Flack & Hartenstein 1984, Edwards & Fletcher 1988, Brown 1995). As most organic material is deposited onto the soil surface, earthworms need to visit the surface, or retrieve the food for ingestion in their burrows

(Photo 1). Earthworm species that mostly rely on food at the surface of soil, the surfacing species, are termed detritivores (Hendriksen 1990, Curry & Schmidt 2007). In contrast, earthworms that primarily feed on soil particles and humified organic matter are termed geophages (Svendsen 1957, Judas 1992, Neilson & Boag 2003). According to the widely used classification of Bouché (1977), who classified earthworms into three ecological groups, the anecic (e.g. *Lumbricus terrestris*) and epigeic species (e.g. *Lumbricus rubellus*) belong to the detritivores, whereas endogeic species (e.g. *Aporrectodea caliginosa*) belong to the geophages.

In turn, earthworms themselves are important food for many animals (MacDonald 1983, Curry 1998). By feeding or collecting food at the surface, detritivore earthworms expose themselves to their above-ground predators. An earthworm can effectively avoid predation by visually oriented diurnal predators by remaining in the soil, or by surfacing only at night. As earthworms do not rely on visual sensory cues for feeding, they can forage in darkness (Edwards & Bohlen 1996). Surfacing for feeding, moving or mating, not surprisingly, only occurs at night (Baldwin 1917, Svendsen 1957, Butt *et al.* 2003). Their night-time movements may explain to some degree why many earthworm-eating predators are also nocturnally active, e.g. Red Foxes *Vulpes vulpes* (MacDonald 1980), Badgers *Meles meles* (Kruuk & Parish 1981), adult Carabidae beetles (Jelaska & Symondson 2016), Little Owls *Athene noctua* (Hounsome *et al.* 2004) and Golden Plovers *Pluvialis apricaria* (Gillings *et al.* 2005, Piersma *et al.*

2014). Predation risk tends to be higher in moonlit nights (Galbraith 1989, Milsom 1990, Kirby 1997, Gillings & Sutherland 2007), which possibly explains why earthworm surface activity is lower around Full Moon (Ralph 1957, Michiels *et al.* 2001). Although the predation risk is higher when they are above ground, these soil-dwelling organisms need to come to the surface to acquire food. Surfacing activity by detritivores would best take place when food availability is high and when the need to collect food overrides the danger of being eaten.

In this study, we experimentally investigated the effect of increased food availability, in the form of surface-applied farmyard manure, on the surfacing activity of earthworms in an agricultural grassland. With this field experiment we aim to better understand how different manure application regimens may benefit earthworms as well as their key predators, meadow birds (Charadriiformes), in Dutch dairy farmland. Earthworms are staple food for these birds, especially during the pre-breeding period (February–April; Högstedt 1974, Galbraith 1989, Baines 1990, Beintema *et al.* 1995). We expect that earthworms will show more surfacing activity in areas without freshly supplied farmyard manure, as they are hungrier than earthworms in fields with freshly applied manure, and hunger will then force the earthworms to search for food on the surface. This would mean that the timing of manure applications would strongly affect the suitability of grasslands as feeding areas for meadow birds.

Photo 1. With its tail anchored in its burrow, a detritivorous earthworm (*Lumbricus rubellus*) is searching for food at night (Koudum, 17 April 2013).

METHODS

Study site

On the dairy farm of Murk Nijdam in Wommels, Fryslân, The Netherlands (53°5'35"N, 5°33'51"E), two adjacent grasslands (A: 100 × 350 m, B: 100 × 280 m) were selected for this study. Both grasslands have the same (low-intensive) management; the fields are fertilized once year at the end of March with farmyard manure and mowed in June, after which grazing occurs

until October/November. To create a homogenous sward, the two grasslands, separated by a path of concrete and surrounded by canals (Figure 1A), had been levelled in 1999, and there are no foot drains on the surface but buried drainage pipes. The plant community of the fields was dominated by *Agrostis stolonifera, Alopecurs geniculatus*, *Bromus hordaceus*, *Cardamine pratensis*, *Cerastium fontanum*, *Elytrigia repens*, *Lolium perenne*, *Poa trivialis*, *Ranunculus repens, Rumex acetosa* and *Taraxum officinale*. Farmyard manure consisted of straw mixed with cattle dung and urine, collected daily in the stable and then put on a heap outside. Here it is composted for up to a year before it is used as fertilizer. The carbon-to-nitrogen ratio at the time of application was 14.7 ($n = 3$, SD = 0.22), which was measured according to the DUMAS method which measures CO_2 and NO_x after combusting the sample at 1000°C.

Farmyard manure application experiment

For this experiment the two grasslands were each divided into a field with an early manure application (1 February) and a field with a late manure application (14 March), creating four rectangular experimental fields (Figure 1A, Photo 2). During an application, around 13 ton/ha farmyard manure was spread on the surface. Depending on the amount of farmyard manure available, most meadow bird reserves in The Netherlands are fertilized with 20 ton/ha once a year between 1 February and 1 April (van der Geld *et al.* 2013).

Surfacing earthworms were counted in each field every two weeks between 6 February and 3 April 2014. This was done by lying prone on a robust cart which was slowly moved forward by foot. In this way, only little vibrations are created and the observer can count surfacing earthworms from a height of 50 cm in a track 50 cm wide (Onrust *et al.* unpubl. data). Counts were conducted at night, as earthworms only surface then, and therefore a head torch (160 lumen) was used. The surfacing earthworms were counted on ten random transects per field, each transect had a length of 5 m.

When farmyard manure is put on the soil surface, it reduces the surface area on which surfacing earthworms can be detected by predators. To account for this 'shading' effect, we measured how much grass was covered by farmyard manure by randomly throwing a 1 × 1-m quadrat and estimating the percentage of manure cover within that quadrat. This was repeated 10 times per field for three days starting on 21 February, 21 March and 9 April 2014. One week after the application of manure, the farmyard manure covered 15% of the soil surface, with a rapid decline in
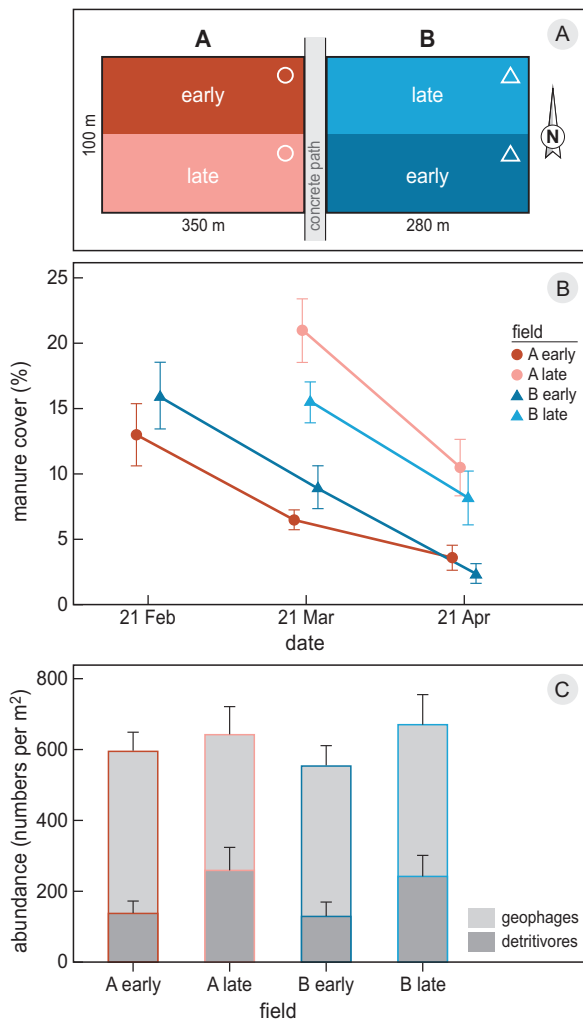

Figure 1. (A) Two adjacent agricultural grasslands (A in red and B in blue) were split into a field with an early (dark colour) and a field with a late (light colour) farmyard manure application. (B) Cover of farmyard manure on the surface was measured at three intervals during the fieldwork period in spring 2014. (C) Six hand-sorted 20 × 20 × 20-cm soil samples were used to determine earthworm abundances per field, bars represent stacked data for geophagous and detritivorous earthworms. Error bars represent SE.

the following weeks to 3% in the early fields and 9% in the late fields by the end of the experiment (Figure 1B). We used the interpolated percentages to correct the observed number of surfacing earthworms per square meter.

The overall densities of earthworms in the soil were measured on 6 March by randomly taking six soil samples of 20 × 20 × 20 cm per field. The samples were sorted by hand. As deep-burrowing anecic species could be missed, one litre of a spicy mustard solution was poured into the dig and for 15 min all emerging earthworms were collected (for a description of this method, see Lawrence & Bowers 2002).

To determine the mass of the individual earthworms in the different fields, we collected earthworms on two days. The first sampling day occurred 33 days after the early manure application treatment but before the late treatment was applied, and the second sampling day occurred 26 days after the late manure application treatment. All earthworms (detritivores and geophages) were collected and stored in 98% ethanol before being processed. From each individual earthworm, we measured ash-free dry mass (AFDM) in mg, later accounting for the length of the earthworm in mm. To do so, first dry mass was determined by drying

the worms in a stove at 70°C for 48 h after which they were weighed to the nearest 0.1 mg. The ash mass was determined by burning the earthworms in a muffle oven at 500°C for 4 h after they were weighed again to the nearest 0.1 mg. AFDM was then determined by subtracting the ash mass from the dry mass. As mature earthworms are heavier than immature individuals of the same length, we analysed these groups separately.

On the first sampling day, seven soil samples per field were taken randomly to determine the vertical distribution of both earthworm groups in the soil to a depth of 20 cm. We expect detritivores to be higher in the soil column when farmyard manure is applied. To measure this, a 20 × 20 × 20-cm soil sample was horizontally cut in four slices of 5 cm. Each slice was then sorted out by hand and the number of earthworms per group was determined. The vertical distribution was then calculated as the proportion of earthworms per slice and per group.

Statistical analyses

Earthworm abundances were analysed separately per earthworm ecotype using a Generalized Linear Mixed Model (GLMM) with grassland, sampling date and manure application as explanatory variables, soil

Photo 2. One of the experimental grasslands where the early field (left) has already received farmyard manure (Wommels, 6 March 2014).

sample as a random factor, and with a Poisson error distribution. For the vertical distribution of earthworms, we used proportion data and therefore the results were analysed using a binomial GLMM in which the response variable was entered as a matrix where the first column is the number of earthworms found at a certain depth ('successes') and the second column is the number of earthworms not found ('failures'). Earthworm ecotype and manure application were added as fixed effects and a random intercept term was added with depth nested in soil sample. A Generalized Linear Model (GLM) with Gaussian family structure was used to analyse the data on body condition of earthworms in all four fields. A Tukey HSD post hoc analysis was then performed to reveal differences between groups by using the lsmeans package (Lenth 2016). All statistical analyses were performed in R v. 3.1.2 (R Development Core Team 2017).

Because all fields were eventually fertilized with farmland manure, we analysed the data on surfacing earthworms according to two periods: period 1 is before the late manure application treatment and period 2 is afterwards. For both periods we used a GLMM with number of surfacing earthworms as response variable and grassland (A or B), manure application (early or late) and time (observation day) as explanatory variables. Transect number was added as a random factor. A stepwise backward procedure was followed to find the Minimal Adequate Model (MAM) in which terms were deleted in order of decreasing P-value (Quinn & Keough 2005).

RESULTS

The detritivorous earthworm species found were *Lumbricus castaneus*, *L. rubellus* and *L. terrestris*. Geophagous species were *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *A. rosea*. The abundance of detritivores was higher in the soil samples in grassland A than in B (GLMM: $F_{1,22} = 4.89$, $P < 0.05$) and in fields with late rather than early manure application (Figure 1C, $F_{1,19} = 412.36$, $P < 0.001$). The densities of geophagous earthworms was similar in the two grasslands ($F_{1,20} = 0.55$, $P = 0.46$), but the abundances were higher for the early manured fields than the late manured fields (Figure 1C, $F_{1,21} = 17.74$, $P < 0.001$).

One week after the farmyard manure was spread on the surface in the early fields, the total number of surfacing earthworms was significantly lower in the early than in the late application fields (Figure 2, $F_{1,116} = 191.3$, $P < 0.001$), with no significant differ-
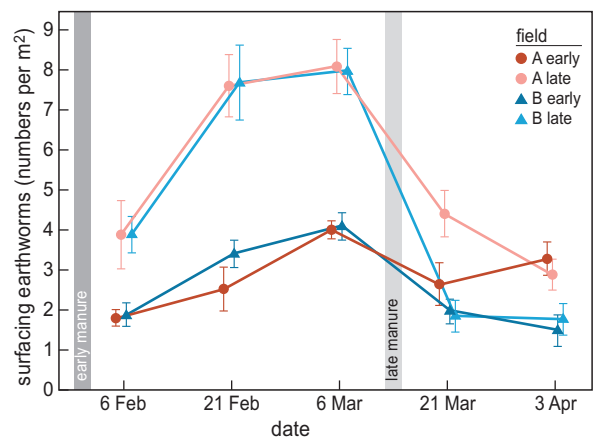
Figure 2. Number of surfacing earthworms in spring 2014 at two grasslands (A in red and B in blue) that were split into a field with an early (1 February, dark colour) and a field with a late (14 March, light colour) application with farmyard manure. Error bars represent SE. Application dates are indicated with vertical grey bars.

ences among the two grasslands ($F_{1,113} = 0.44$, $P = 0.51$). After the second application, there was no difference between early and late fields (Figure 2, $F_{1.77} = 2.84$, $P = 0.091$), although grassland A had a higher number of surfacing earthworms than grassland B ($F_{1,78} = 45.25$, $P < 0.001$).

The vertical distribution of earthworms in the soil column did not show significant differences between the two ecotypes of earthworm (Figure 3, $F_{3,162} = 0.31$, $P = 0.58$) and between fields with or without farmyard
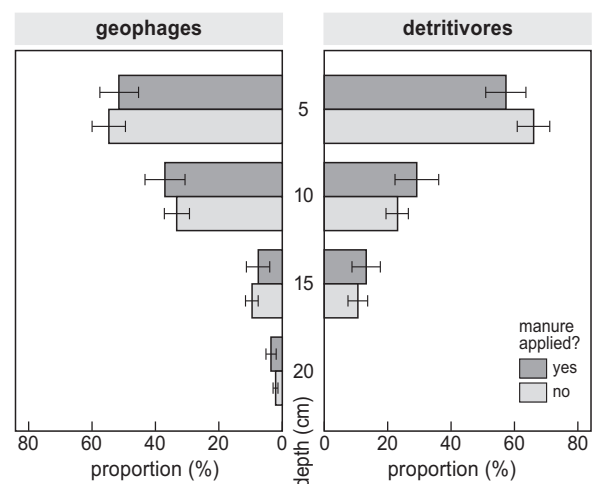
Figure 3. Vertical distribution of geophagous (left) and detritivorous (right) earthworms sampled 6 March 2014 in fields with (dark bars) and without (light bars) farmyard manure applied on the surface. In each field 14 soil samples were taken divided over two grasslands. Error bars represent SE.
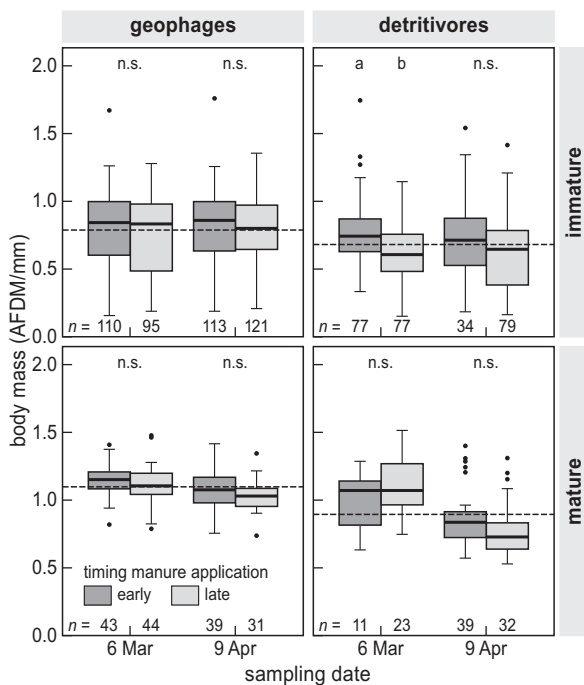
Figure 4. Body condition (expressed as ash-free dry mass (AFDM) in mg per mm length) of geophagous (left) and detritivorous (right) earthworms and for different age classes (immature top panels, mature lower panels). Earthworms were collected on two sampling days in spring (6 March and 9 April 2014). On 6 March, only the early fields had received an application of farmyard manure since 1 February. The late fields received manure on 14 March. Different letters denote statistical differences between timing of manure application (GLM: $P < 0.05$). Sample sizes are given below the boxplots and horizontal dashed lines show the average body mass per panel.

manure (Figure 3, $F_{3,162} < 0.01$, $P = 0.93$). Immature detritivores were significantly heavier in terms of AFDM per mm in the early application fields (Figure 4, Tukey post hoc analysis: $Z = 3.43$, $P < 0.05$) during the first sampling, but this effect disappeared during the second sampling (Figure 4, $Z = 1.09$, $P = 0.75$). In mature detritivores, mature geophages and immature geophages there was no significant difference between early and late farmyard manure application fields.

DISCUSSION

We found that earthworms come to the surface more frequently in the absence of fresh farmland manure, i.e. when food availability is expected to be low (Figure 2). Rapidly after the application of farmyard manure, detritivorous earthworms come to the surface to collect this and retrieve it into their burrows. They can then remain deep in the soil. Despite the mustard treatment, we may have missed the deepest detritivores; this would explain why the total abundances of detritivores were slightly higher in the late application fields than in the early application fields (Figure 1C). Indeed, only one individual of the deep-burrowing *L. terrestris* was found in the early fields compared to nine in the late fields. However, to our surprise, the manure application did not change the vertical distribution of detritivores and geophages in the soil (Figure 3). Although vertical

Photo 3. One week after the manure treatment was applied, blades of straw were partly incorporated in the soil and standing straight up in the grassland due to the action of detritivorous earthworms (Wommels, 13 March 2014).

distribution is mainly determined by soil moisture (Gerard 1967, Rundgren 1975, Jiménez & Decaëns 2000), we do not expect differences between the fields, with all probably being moist enough throughout the fieldwork period to keep earthworms actively surfacing (Onrust *et al.* unpubl. data).

Over a period of seven weeks, the availability of food in terms of manure cover sharply declined (Figure 1B). As earthworms actively collected food on the surface and pulled it into their burrows, they likely contributed to the decomposition of farmyard manure (Hendriksen 1990). This was illustrated by the observation that one week after the manure was applied, blades of straw were partly incorporated in the soil and standing straight up in the grassland (Photo 3). The collected manure is colonized and digested by microorganisms in the soil, forming a high-quality food source for earthworms (Wright 1972, Bonkowski *et al.* 2000). We found a small positive effect of manure application on the body mass of immature detritivores, probably the result of the relatively high energy requirements of this category of earthworms (Elvira *et al.* 1996). The time between application of manure and our sampling of the earthworms was probably too short to allow for any differences in mature detritivores. The absence of an effect in geophages is in line with the expectation that this group does not rely on organic surface material for feeding. In agreement with our hypothesis, we conclude that it is hunger that forces detritivores to come to the surface.

Detritivorous earthworms are known to also feed on living plant material (Cortez & Bouché 1992, Eisenhauer *et al.* 2010, Griffith *et al.* 2013). However, as earthworms depend on microorganisms for digestion and assimilation, decaying and decayed organic material is preferred (Curry & Schmidt 2007). Indeed, Griffith *et al.* (2013) only found earthworms grazing on living plants in locations with little plant litter on the surface. As earthworms do not have teeth, collecting living plant material takes more time than collecting decaying plant material. Furthermore, fresh organic material is colonized by microorganisms less than decaying material and might therefore be a less nutritious food source for earthworms. Surfacing frequency remains high only when no manure is applied. Thus, it is likely that earthworms will only feed on living organic material when they are hungry (Wright 1972). Food availability for earthworms will be low in early spring as plant growth has stopped during the winter. Furthermore, in The Netherlands, fertilizing is prohibited from 1 September until 1 February. Therefore, in the period before the first fertilization in spring, detri-

tivorous earthworms are likely to be hungry and feeding on living plant material to survive.

Feeding on living plant material of low nutritional quality for earthworms (Curry 1998) requires more surfacing. As we predicted, based on the literature on other animals (Lima 1998, Brown *et al.* 1999), hunger makes detritivorous earthworms more risk-prone and thus vulnerable to predation. Earthworms do indeed minimize their exposure at the surface by moving food into the safety of their burrows and feeding there. The main predators of earthworms in our study area are meadow birds, in particular Black-tailed Godwit *Limosa limosa*, Lapwing *Vanellus vanellus*, Oystercatcher *Heamatopus ostralegus* and Redshank *Tringa totanus*. These birds not only use these grasslands for foraging, but also for resting and breeding. During the fieldwork period in spring 2014, 164 nests of these meadow birds were found in the studied and surrounding grasslands (40 ha). Although earthworm abundances can decline due to predation by birds (Bengtson *et al.* 1976, Barnard & Thompson 1985), the number of surfacing earthworms did not show a one-to-one relationship with the total abundance in the soil (Onrust *et al.* unpubl. data) and therefore it is unlikely that depletion of earthworms in the soil also results in lower numbers on the surface.

As earthworms always live in the top 10 cm when the soil is moist, – confirmed by our study – earthworm availability for probing species such as the long-billed Black-tailed Godwits and Oystercatchers will not be greatly affected by the addition of farmyard manure. For visually hunting Lapwings, however, manure application does influence earthworm availability. High numbers of surfacing earthworms during the pre-breeding period are of special importance for female Lapwings as they need to build up reserves for egg production and incubation (Högstedt 1974, Galbraith 1989, Baines 1990). To promote food conditions for Lapwings and other visual hunters, spreading farmyard manure on the surface should occur as late in spring as possible. In this way, hungry earthworms are forced to surface and provide an easy prey for hungry birds.

The timing of manure application is thus relevant for farming policies aimed to encourage and help meadow birds, birds which are currently in strong decline across Western Europe (Busche 1994, Donald *et al.* 2006, Vickery & Arlettaz 2012, Kentie *et al.* 2016). Indeed, protective measures that involve fertilizing with farmyard manure instead of injecting slurry manure (Kleijn *et al.* 2001, Groen *et al.* 2012) may need to be re-examined with respect to the timing of the farmyard manure applications.

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SAMENVATTING

Voor veel weidevogels zijn regenwormen belangrijke prooien. Op basis van hun voedselecologie kunnen regenwormen in twee ecotypen worden ingedeeld: wormen die van grof organisch materiaal leven (detrivore wormen) en wormen die van bodemdeeltjes en organische stof leven (geofage wormen). Detrivore wormen verzamelen 's nachts hun voedsel aan het bodemoppervlak en stellen zich daarmee bloot aan nachtelijke predatie. Hongerige dieren zijn geneigd om meer risico's te nemen en zijn daardoor extra kwetsbaar voor predatie. We verwachten dan ook dat goed doorvoede detrivore wormen zich niet (of minder) aan het bodemoppervlak zullen begeven dan minder goed doorvoede wormen. In dit onderzoek hebben we deze hypothese getoetst op het melkveebedrijf van Murk Nijdam in Fryslân. Twee uniforme graslanden werden beide opgesplitst in een perceel dat op een vroege datum (1 februari 2014) ruige stalmest kreeg toegediend en een perceel waarop dat op een late datum (14 maart 2014) gebeurde. Elke twee weken werden 's nachts op alle percelen de regenwormen geteld die aan het oppervlak kwamen. Tevens werden er bodemmonsters genomen om de regenwormdichtheid, de diepte waarop de wormen zaten en de lichaamsconditie van de wormen te bepalen. Zoals verwacht, waren de aantallen regenwormen die 's nachts aan het oppervlak kwamen in de percelen die nog niet waren bemest veel hoger (namelijk 2,5 keer zo hoog) dan in de percelen die wel waren bemest. In de nog niet bemeste percelen waren bovendien onvolwassen detrivore wormen significant lager in lichaamsgewicht dan in bemeste percelen (geen verschillen tussen volwassen detrivore wormen en tussen beide groepen geofage wormen). Op percelen met een late bemesting was de dichtheid aan detrivore wormen hoger en die van geofage wormen lager dan op de percelen met een vroege bemesting. Er werden geen verschillen gevonden in de diepte waarop de wormen verbleven. De verschillen tussen de percelen verdwenen nadat alle percelen waren bemest. We concluderen hieruit dat de oppervlakteactiviteit van detrivore regenwormen vooral bepaald wordt door honger. Na bemesting is er geen noodzaak meer om aan het oppervlak te komen en daarmee voorkomen ze om zelf opgegeten te worden. Dat betekent dat de beschikbaarheid van regenwormen voor weidevogels vergroot kan worden door bemesting in het voorjaar zo lang mogelijk uit te stellen om zo de regenwormen hongerig te houden en op die manier aan het oppervlak te krijgen.