Chapter 1

GENERAL INTRODUCTION

Earth, worms & birds

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From a bird’s eye view, the rural area of The Netherlands looks open, wet and green. Being a delta of three large rivers, The Netherlands has fertile soils and combined with good climatic conditions (temperate maritime) (Berendsen 1997), the right setting for agriculture. However, being a low-lying country, groundwater levels are relatively high and this facilitates grazing by cattle. In contrast to arable farming, dairy farming works at high groundwater levels. The Netherlands is a perfect country for dairy farming after the loss of the extensive peatlands during a long history of cultivation; grasslands for dairy farming became the most widespread habitat (de Vries 1953). This man-made habitat was often, especially on clay and clay-on-peat soils, forming vast open spaces without trees or other vertical obstructions. This formed a perfect habitat for a community of birds that we nowadays we call by the name ‘meadow birds’ (Beintema et al. 1995, van der Geld et al. 2013).

A closer look at these agricultural grasslands today reveals, however, that the majority of these grasslands are no longer suitable for meadow birds. Although still quite open and very green, the intensification of agriculture converted wet and herb-rich meadows into dry rye-grass monocultures. In association, numbers of meadow birds have declined dramatically during the last decades (Vickery et al. 2001, Donald et al. 2006, Kentie et al. 2016). Although lots of research have resulted in a better understanding of the problems meadow birds are facing nowadays (Benton et al. 2003, Kentie et al. 2013, Kentie et al. 2015), there is still little understanding of how modern agriculture affected the staple food of meadow birds: earthworms.

This research project aims to investigate the relationship between dairy farm management (earth), earthworms (worms) and their availability for meadow birds (birds). We have done this by studying earthworms from a meadow bird’s perspective in differently managed dairy farmlands. By focusing on different ecotypes of earthworms, we hope to identify which group of earthworms are of importance for meadow birds and whether dairy farm management acts differently on different ecotypes (species and niche) of earthworm. To place our work in context, we first present a short history of the intensification of Dutch dairy farming and how this impacted on the whole dairy farm ecosystem.

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**A short history of the Dutch dairy farm ecosystem**

A wide variety of bird species belong to meadow birds, from passerines (e.g. Skylark *Alauda arvensis*) to ducks (e.g. Northern Shoveler *Anas clypeata*), but generally, as well in this thesis, it is about wader species (Beintema et al. 1995, Dekker 2009). The ‘big five’ of meadow birds are: Black-tailed Godwit *Limosa limosa*, Northern Lapwing *Vanellus vanellus*, Common Redshank *Tringa totanus*, Oystercatcher *Haematopus ostralegus* and Ruff *Philomachus pugnax*. For some species, The
Netherlands is home to a large proportion of the total population, for example 85% of the East-Atlantic flyway population of Black-tailed Godwits breeds here (Kentie et al. 2016). However, this group of birds acquired this status recently as most meadow birds originated from natural open habitats (Voous 1965), and shifted more and more to the agricultural landscape when their natural habitats rapidly disappeared and man started to intensify its farming practices (Beintema et al. 1995). Although these fields had an agricultural function, they had a high natural value as they were home to a large number of different species.

An impression of what the food web of dairy farmland looked like around 1950 is given in figure 1.1. The first trophic level consists of primary producers (plants)
and showed a high diversity with besides grasses, also forbs and legumes. Every part of a plant can be differently used by a primary consumer, for example flowers provide pollen and nectar for bees and butterflies, seeds are consumed by graminivores, stems and leaves by herbivores and litter is eaten by detritivores. These primary consumers are eaten by secondary consumers, which are then eaten by tertiary consumers etc. These biodiverse grasslands were manually mown only once a year, mostly in July when grass had set seed. Furthermore, as a fertilizer they received little manure and probably only the fields closest to the farm received farmyard manure. Together with differences in groundwater levels and soil moistures, this heterogeneity in abiotic conditions resulted in a large biodiversity. With higher number of plant species and more diversity in vegetation structure, there are more niches resulting in a higher trophic diversity. It is estimated that most meadow bird species reached their highest numbers in mid twentieth century (Schekkerman 2008, Kentie et al. 2016). The yield of such fields was by contrast very low, but this changed rapidly in the second half of the twentieth century.

Dairy farming, and agriculture as a whole, mechanized and switched from a locally-focused production towards an efficient internationally-oriented business since 1950 (Reinders & Vernooij 2013). The European Community stimulated farmers to increase their production by giving subsidies in the form of a guaranteed minimum price for their milk. Within decades, the number of dairy cows and the production of milk increased tremendously (Fig. 1.2A) and The Netherlands became one of the world leading producers of dairy products (van Grinsven & Kooman 2017). The production was even higher than the market demands, creating ‘milk lakes’ and ‘butter mountains’ in the 1970s. To solve this problem, in 1984 the European Community introduced the milk quota, which limited the production of milk to a certain level (van Grinsven & Kooman 2017). This had the desired effect and the number of cows declined as well as the milk production (Fig. 1.2A).

Although the lakes of milk evaporated, another flood still washed over The Netherlands. The increasing livestock, including pigs and chickens, created an enormous amount of animal manures which became one of the most severe environmental problems (Heij & Schneider 1991). High input of nutrients through the use or fertilizers and manure make it possible to reach high levels of agricultural production. However, a large proportion of the applied manure in dairy farmland was not absorbed by grasses, but washed away and ended up in surface water and groundwater. Another part of the nitrogen from the manure was released in the air in the form of ammonia (NH\textsubscript{3}). This not only caused eutrophication and eventually biodiversity loss of nearby areas, but also of natural areas further away (Heij & Schneider 1991, Bobbink et al. 1998, Erisman et al. 2015). Already in the 1970s, this problem was known, but it was not until 1987 that stricter legislation was introduced; since 1994 animal manures has to be applied to the land with supposedly low-emission
methods (Neeteson 2000, Stoate et al. 2009). This includes no fertilization in autumn and winter, and the manure has to be injected into the soil or into the sward. Only farmyard and other green manures are allowed to be applied on the surface.

Traditionally, dairy farmland was fertilized with farmyard manure as the cows were kept in stables with bedding material. This material, mixed with faeces, was collected and stored on a muck heap outside or a new layer of bedding material was added in the stable. After some months of composting, this farmyard manure was then applied on the surface. In modern stables, cows are kept in stables with cubicles for resting and alleys for feeding, walking and defecating (Remmelink et al. 2016). The slotted floors enable their dung and urine to fall through to be collected as slurry manure. This type of manure is much more liquid than farmyard manure. From the total dairy cattle manure that is produced nowadays, only 0.2% is farmyard manure, which also declined with more than 80% since 1990, whereas in the same period slurry manure increased with 31% (CBS 2017a).

Although still quite open and very glossy green nowadays, dairy farmland went through a huge metamorphosis. Large scale land re-allotments turned the landscape upside down, led to the disappearance of many smaller landscape elements (ditches, hedgerows, road verges etc.) and natural dynamics disappeared step by step. Intensive water management ensure nowadays that dairy farmland does not flood anymore and groundwater tables are manually kept low. With the help of new pumping-stations and the closing of the Zuiderzee and Lauwerszee in 1932 and 1969 respectively, outlet waterways in the Dutch province of Fryslân are kept at a constant level of −0.52 m NAP (Normal Amsterdam Water Level) (Claassen 2008). The original seasonal rhythm of higher groundwater tables in winter and lower in summer turned around, with now relatively higher groundwater tables in summer. These changes had a great impact on the functioning of grasslands. Grassland ecosystems changed from a groundwater (lithocline) dependent system towards a rainwater (athmoscline) dependent system as groundwater was drained away artificially (Schotsman 1988). This affected nutrient flow and soil pH (Paulissen et al. 2007). The original vegetation (and likely soil fauna) of these flooded grasslands almost completely disappeared (Grootjans 1985, Schotsman 1988). Although sustained winter flooding can be detrimental for some groups of soil fauna (as earthworms), it helps to keep the sward short and open enough for meadow birds to feed and probe in the soil (Ausden et al. 2001). Furthermore, it retards the growth of grass and therefore the timing of mowing, promoting plant and insect diversity.

Ploughing and reseeding subsequently converted species rich grasslands into dense, homogeneous Perennial Ryegrass *Lolium perenne* monocultures (Vickery et al. 2001). This grass species grows fast and is a competitive dominant under nutrient-rich and frequently mown conditions, circumstances which are detrimental for many natural grassland plant species. As nitrogen is an important limiting nutrient
for plant growth in many temperate grasslands, nitrogen enrichment through intensive agriculture reduces plant species richness by favouring the few species best adapted to high nutrient levels (Stevens et al. 2004, Erisman et al. 2015); it encourages the growth of such competitive, fast growing species at the expense of slower growing species (Vickery et al. 2001). Insect diversity and abundance strongly declines with increasing nutrient inputs (Zahn et al. 2010), and increasing grazing

**Figure 1.2:** Dairy farmland in The Netherlands from 1960 to 2017. (A) Milk production in billion kg (black line) and number of dairy cows (grey line) (CBS 2017b). (B) Percentage of permanent (at least five years no crop rotation, light grey) and temporary grassland (younger than five years old, dark grey) of the total area of grassland used for dairy farming (CBS 2017b). (C). Number of pairs of Lapwing *Vanellus vanellus* breeding in the whole of The Netherlands. ©Dutch Centre for Field Ornithology (SOVON) 2017.
pressure (van Klink et al. 2015). Especially large insect species become rare. Under intense cutting or grazing, large insects may have difficulties completing their life-cycles (Schekkerman & Beintema 2007). With an addition of 50 kg of nitrogen per hectares per year, the dry-weight of an insect is about 1 mg. With 400 kg N ha$^{-1}$ yr$^{-1}$, the average weight declines to less than a third (Siepel 1990). Everything else being equal for meadow bird chicks this would mean that they have to consume a three-fold of insects in numbers. Also food conditions for adults are affected as larger-sized soil biota (earthworms, enchytraeids, microarthropods, and nematodes) are more sensitive to agricultural intensification than smaller-sized soil biota (protozoans, bacteria, and fungi) resulting in loss of large and profitable earthworms in agricultural lands (Wardle 1995, Postma-Blaauw et al. 2010). However, the increase in nitrogen content of the vegetation may promote the abundance of phytophagous and decomposing species (Andrzejewska 1979, Atkinson et al. 2005, Curry et al. 2008).

In general, however, addition of fertilizers tend to decrease the numbers and diversity of grassland invertebrates (Fenner & Palmer 1998, Zahn et al. 2010). This decline is also promoted by increasing regular disturbance of the soil and vegetation structure as grasslands are ploughed, graded and/or reseeded to maintain a high grass production. More often these grasslands are ploughed and tilled to create temporary arable land to grow maize for the increasing demand for energy-rich food for cattle. When dairy farmland is grassland for five consecutive years without crop rotation, it is termed as permanent grassland. The area of permanent grassland in The Netherlands has been stable for a long time at 97% of the total area of dairy farmland. When slit-injection of manure became compulsory, permanent grasslands declined to 74% at the expense of temporary grasslands (Fig. 1.2B). Nevertheless, true permanent grassland that has never been ploughed or killed by herbicides is likely to be much rarer as farmers ‘improve’ grassland when the botanical composition is poor (i.e. less than 50% Perennial Ryegrass cover), when the field is difficult to be worked on due to unevenness of the soil surface (e.g. ditches), or when the sward is heavily damaged, as by drought, machinery or Voles Microtus arvalis (Remmelink et al. 2016). Temporary grasslands are high-productive Perennial Ryegrass monocultures and often used for silage production. Silage is grass that after it is cut, is stored (without drying) in a large heap which is compressed to leave as little oxygen as possible in it and then covered with a plastic sheet. The resulting fermented grass is fed to the cows in the stable. Nowadays, 90% of the grass is harvested for silage production and only 3% is used for hay making. In 1960, this was 25% and 65% respectively (Klomp 1951, CBS 2017c). This is also illustrated by the fact that grass on average is mown 2.8 times per year (with a maximum of up to 6 times per year) whereas in 1960 this was 0.8 times per year on average (van der Geld et al. 2013, CBS 2017c).
The intensification of agriculture is affecting the dairy farmland food web at every trophic level. Efficient farming created large and monotonous monocultures where hardly anything is wasted and where very few species can survive. Increased frequency of mowing reduces flowering and seed set, and hence food availability for seed-eating animals (Vickery et al. 2001, Atkinson et al. 2005). Small mammals like rodents and shrews disappeared from the agricultural landscape (de la Pena et al. 2003). This group of species are also the main prey of farmland predators, such as Stoat *Mustela ermine*, Red Fox, and Barn Owl *Tyto alba*. With the loss of prey species, predators have to switch to other prey. This ‘apparent predation’ might have caused the increased predation risk on meadow bird chicks (Roodbergen et al. 2012, Kentie et al. 2015). Furthermore, the landscape have become more enclosed, with roads, wood lots, tree lines and scattered trees. Predators, may use these elements as a breeding site, perching opportunity or hiding place (van der Vliet et al. 2010). Together with low water tables and the absence of winter flooding (ground predators can make burrows), these changes make the meadow bird habitat more accessible for predators. Furthermore, farming practices like cutting grass during the breeding season is not only altering the protective cover for the chicks, but also the feeding conditions, resulting in chicks that are in low condition and thus an easy prey for predators (Schekkerman et al. 2009). Within a few decades, farmland species have declined enormously (Busche 1994, Donald et al. 2001, Vickery et al. 2001, Donald et al. 2006, Kentie et al. 2016) (Fig. 1.2C).

The ongoing intensification was still continuing when on 1 April 2015 the European regulations for a limit on milk production per farm (milk quota) came to an end. Heralded by the dairy industry as ‘liberation day’ and in anticipation of the promising long-term developments across the global dairy market, dairy farms and companies invested in capacity by increasing the number of cows (PBL 2016, van Grinsven & Kooman 2017). Already in the first year, the record of 13.2 billion kg milk in 1983 was broken (to 13.3 billion kg milk) and even increased further in 2016 (to 14.3 billion kg milk) (CBS 2017b). This production was reached with almost one million cows fewer than in 1984 (Fig. 1.2A), which illustrates how efficient dairy farming has become.

This has come at a cost, though. The impoverished food web of today’s dairy farm is represented in figure 1.3. Although many species disappeared, new species entered the food web, mostly predator species (which recovered after persecution and pollution) or competitive species. Agricultural intensification changed and simplified the food web (Tsiafouli et al. 2015). This is not only detrimental for organisms depending on this habitat, but it makes this habitat also more susceptible for pest and insect outbreaks. It is shown that high plant diversity in grasslands increased the stability of a diverse arthropod community across trophic levels (Haddad et al. 2011). The same is true for the diversity of microorganisms below-
ground and ecosystem functioning (Tsiafouli et al. 2015, Bender et al. 2016). Furthermore, the ratio between bacteria and fungi may change towards a more bacterial dominated system as intensification increases (Wardle et al. 2004). In grasslands, arbuscular mycorrhizal (AM) fungi is an important symbiont for plants as facilitates nutrient acquisition (especially phosphorous), and protects the plant against diseases and drought (van der Heijden et al. 2008). Furthermore AM fungi can suppress aggressive agricultural weeds (Rinaudo et al. 2010). As already mentioned, the intensification did not have a great impact on macrodetritivores as earthworms, probably because artificial high litter input (via slurry or farmyard manure) replaced the role of dung depositions by cows in the field (Leroy et al. 2008).

**Figure 1.3:** Schematic of the dairy farmland food web in the Netherlands in 2017. It represents a monoculture of *Lolium perenne* where only litter and leaves are the primary food class. Compared to figure 1, grazing cows are replaced by the tractor that mows the grass and bring it to the cows in the stable. Furthermore, geese have entered the food web as primary consumers. Most of the tertiary consumers (predators) are replaced by other species.
What worms want

Although most organisms cannot cope with agricultural intensification, it does not seem to harm overall earthworm densities (Edwards & Lofty 1982, Hansen & Engelstad 1999, Muldowney et al. 2003, Atkinson et al. 2005, Curry et al. 2008). Highest densities of earthworms in northwestern Europe are found in The Netherlands (Rutgers et al. 2016), with Fryslân as the most earthworm rich province (Rutgers & Dirven-van Breemen 2012) (Fig. 1.4). Food conditions for adult meadow birds or other earthworm predators should therefore at first sight not be a limiting factor. However, as is generally true (Zwarts & Wanink 1993), for any earthworm predator it is not about how many earthworm are found in the soil (total abundance), but about how many it can catch (availability to predators).

Some meadow birds use their long bill to probe in the soil to catch earthworms by touch (Green 1988, Smart et al. 2006, Duckworth et al. 2010). Earthworms which are in top layer of the soil that matches the probing depth of a bird’s bill, are available to that bird. Furthermore, depending on the strength of the bill, a bird cannot probe in soil that is too hard, for example when it is too dry. Struwe-Juhl (1995) observed that Black-tailed Godwits are unable to probe in the soil when the soil resistance exceeds the limit of $125 \text{ N/cm}^2$. Earthworm depth and soil resistance are thus limiting factors for a tactile hunting earthworm predator. There are also predators that catch earthworms which are visible to them. An earthworm is thus only available for this group of predators when it is, partly or completely, on the soil.

![Earthworm abundances in Northwest Europa (Rutgers et al. 2016) and in The Netherlands (Rutgers & Dirven-van Breemen 2012).](image)

**Figure 1.4**: Earthworm abundances in Northwest Europa (Rutgers et al. 2016) and in The Netherlands (Rutgers & Dirven-van Breemen 2012).
Throughout the thesis, a discrimination is made between these two earthworm hunting strategies. A bird probing in the soil (e.g. Black-tailed Godwits, Oyster catcher) could potentially catch all earthworms that are in reach of their bill, which includes non-active earthworms. A bird using visual cues (e.g. Lapwing, Ruff), can only catch earthworm which are active on the surface. It is thus likely that earthworm availability differs between these groups (Fig. 1.5).

Since Charles Darwin wrote his last book about earthworms (Darwin 1881), the importance of these organisms is recognized, especially in agriculture. More and more agricultural scientists became interested in these ‘low creatures’ and with every published paper, the recognition of the importance of earthworms increased. Earthworms break down organic material and make nutrients again available to plants, they bioturbate the soil by burrowing and increase water infiltration (Lavelle 1988, Lavelle et al. 2006, Blouin et al. 2013). By performing all these ecosystem functions, they are even termed as ‘ecosystem engineers’ (Lavelle 1997).

Earthworm (family Lumbricidae) belong to the class of Oligochaeta (worms with few setae), which are part, together with other worm-groups, of the phylum Annelida (ringed worms) (Edwards & Bohlen 1996). They are thus worms with setea, or bristles, on each segment. Although in The Netherlands it is estimated that around 23 species of earthworms occur (van Rhee 1970), most of them are only
known by their scientific name. However, various species are functionally similar, which led Bouché (1977) to classify earthworms species in three ecological groups based on their vertical distribution in the soil and their feeding preferences. Anecic species form long permanent vertical burrows and emerge on the soil surface to feed or collect food which is pulled into their burrow. This group includes *Lumbricus terrestris*, the largest European earthworm species and also named as ‘Nightcrawler’ which reflects their nocturnal surfacing behaviour. Epigeic species typically live mainly in the top layer of the soil or in the litter layer and endogeic species inhabit the mineral soil and consume more soil than the other groups. This classification is now widely used in ecological studies of earthworms. In this work, however, we use a different and even simpler classification by dividing the species in only two groups; detritivores and geophages. Detritivores rely on surface foods and therefore show surfacing behaviour (Hendriksen 1990, Curry & Schmidt 2007). In contrast, geophages primarily feed on soil particles and humified organic matter and rarely come to the surface (Svendsen 1957, Judas 1992, Neilson & Boag 2003). According classification of Bouché (1977), the anecic and epigeic species belong to the detritivores, whereas endogeic species belong to the geophages. For earthworm predators that hunt by using visual cues, only surfacing detritivores are available to them. Tactile hunters can feed on both groups as long as they are in reach of their bill.

Earthworm availability for an earthworm predator is of course also determined by the behaviour of earthworms themselves. Moist conditions are of vital importance for earthworms as they lack lungs and gaseous exchange with their environment requires a moist skin (Laverack 1963, Edwards & Bohlen 1996). As a response, earthworms will retreat deeper into the soil to avoid dry conditions (Gerard 1967, Rundgren 1975, Jiménez & Decaëns 2000). Therefore, earthworms are not available when the soil is frozen (winter) or desiccated (summer). Interestingly, earthworms are hermaphrodite with testes as well as ovaries that can function simultaneously, but they do need a partner for copulation and fertilization (Edwards & Bohlen 1996). *Lumbricus terrestris* mates on the surface, and copulation can take more than three hours (Nuutinen & Butt 1997), making them vulnerable for predation. By lacking lungs, a skeleton, a skin that prevent them from dehydration, and a physiology that is comparable to marine animals (Laverack 1963, Turner 2000), it is remarkable that earthworms live in the earth and not in water. Their success on earth, is mainly determined by living belowground. By digging through the soil, and excreting mucus that cements their burrows and form aggregates that increase the water binding capacity of the soil (Edwards & Bohlen 1996, Lavelle 1997, Blouin *et al.* 2013), they can create their own damp environment. Furthermore, they collect litter to form middens over the mouth of their burrows or incorporate it, which also beneficial to maintain moist conditions (Ernst *et al.* 2009). And by doing so, they have become, according to Lloyd (2009), the most influential species on earth.
However, the tragedy of earthworms is that they also encompass the whole gamut of behaviours attributed to ‘advanced’ organisms (Darwin (1881) even played piano to them!), but that in the literature they have been ‘kidnapped’ by agricultural biologists because of their role in soil functioning, rather than them being interesting organisms in their own right (there are no ‘earthworm journals’, for example) (Ghilarov 1983, Scheu 2003, Gross 2016). Also in ecology, however, earthworms are often regarded as bulk prey for other organisms where even large conservation programs are for (badgers, meadow birds, kiwi’s etc.). To understand these animals in their environment and to be able to protect them, it is of paramount importance to understand how earthworms themselves respond to their environment, specific food abundance or to the risk of being fed upon (Laidlaw et al. 2013), so their behavioural ecology.

Inspired by intensive research on the declining shellfish food of foraging Red Knots Calidris canutus in the Wadden Sea during a period of intensive cockle dredging (van Gils et al. 2006, Kraan et al. 2009), we will explore earthworms in Frisian dairy farmland to understand what determines their distribution and availability for the strongly declining meadow birds. The research is conducted mainly in the province of Fryslân in the northwest of The Netherlands. Here, 90% of the cultivated land is used for dairy farming and the highest earthworm and meadow bird densities of The Netherlands have been traditionally found there (van Dijk et al. 1989, Altenburg & Wymenga 2000, Rutgers & Dirven-van Breemen 2012, Nijland & Postma 2016). Furthermore, it is this group of birds that are part of the Frisian culture, with rich traditions linked with both breeding and migrating meadow birds (e.g. egg collecting (Breuker 2012) and ‘wilsterflappen’ (Jukema et al. 2001)).

Outline of thesis

We started this research endeavour by developing new methods to measure earthworm surface availability properly. Especially for visually hunting predators, this was a challenge as surfacing earthworms retreat quickly into their burrows before they could be observed when they notice vibrations. Duriez et al. (2006) and Dänhardt (2010) counted the earthworms that were crawling on the surface in grasslands and arable fields at night by walking transects whilst illumination the soil with a torch. Walking observers still created vibrations and only large retreating earthworms can then be measured. Furthermore, in grasslands an observer have to be close to the soil to discriminate earthworms from grasses. In chapter 2 we describe how this hurdle is circumvented by building a robust cart which is pushed slowly across the field by a prone observer. In this way, number of surfacing earthworm could be counted without disturbing them. We test this method during day
and night and in different managed grasslands and compare number of surfacing earthworm with total abundances in the soil.

After we had a good method to measure earthworm availability for visually hunting earthworm predators, we apply this method in a study to understand how Ruffs use Frisian dairy farmland during spring migration. However, we did not know how this peculiar bird find its prey exactly. Therefore, in chapter 3 we perform an indoor feeding experiment with captive male Ruffs to study which cues they use in finding earthworms. In the field on different grasslands, intake rates of Ruffs feeding on earthworms during the day were scored as well as the number of surfacing earthworms at night. Together with transmitter data of Verkuil et al. (2010), we ask the question why Ruffs do not feed at night when food availability is much higher.

In chapter 4 we study what the short-term effect of fertilizing with farmyard manure is on the availability for visually hunting earthworm predators. This type of fertilizing was common in the heydays of meadow birds halfway the 20th century, but has become rare as modern stables only produce slurry manure instead of farmyard manure. As earthworms come to the surface to collect food, we expected well-fed earthworms to present themselves on surface least to avoid the risk of being eaten by a predator. Two uniform grasslands were split with either the two halves to receive an early (1 February 2014) or a late (14 March 2014) farmyard manure application. Every two weeks, nocturnal surface activity of earthworms was measured. Furthermore, soil samples were taken for total abundances and to measure individual body conditions of earthworms.

To understand food availability for meadow birds, we also had to understand how food of determines the surfacing behaviour of earthworms, and thus availability for meadow birds. Therefore, in chapter 5 we investigate the effect of different types of dairy manure on two earthworm ecotypes, the detritivores and the geophages. Detritivores rely on manure as a food source more than geophages and therefore the type of manure may determine the relative abundances of the two ecotypes. As detritivores come to the surface to collect food, they are an important prey for birds and mammals. We test the prediction that dairy farmland fertilized with slurry manure will contain fewer detritivorous earthworms (thereby becoming less attractive for earthworm predators) by quantifying the abundance of the two earthworm ecotypes in grasslands fertilized with either slurry manure, farmyard manure, or both. To determine the importance of detritivores for earthworm predators, we quantified earthworm surface availability by counting surfacing earthworms in the field and compared these numbers with abundances belowground. Furthermore, growth rates of the two ecotypes were measured under controlled conditions using either one of the two manure types.

Besides food, water is probably even more important for the moisture-loving earthworms. Dry conditions are avoided by going in diapause or by retreating
deeper into the soil. This would negatively influence earthworm availability for meadow birds. It is interesting to know, when earthworm surfacing behaviour stops in dairy farmland. In chapter 6, we study this by measuring weekly the number of surfacing earthworms, as well as hydrological conditions of eight intensive managed grasslands with different groundwater tables. The sensitivity of a detritivorous and a geophagous earthworm species to variation in the vertical distribution of soil moisture was experimentally studied.

Finally, I will synthesize the results in chapter 7 by placing them in the broader context. To do so, I use data collected in Flevoland, where we studied the role of earthworms in a natural grassland, as well as on a conventional intensive dairy farm and a dynamic-organic dairy farm. With a controlled indoor experiment, complete sods were collected in the three areas and received either earthworms (Lumbricus rubellus), cow dung, both or nothing and for three months, grass production was measured. This experiment showed the importance of earthworms, not only as a prey, but also as an ecosystem engineer.

Figure 1.6: Outline of the thesis “Earth, worms & birds”: How does dairy farm management (earth) affects earthworms (worms) and their availability for meadow birds (birds)? In the synthesis chapter 7, we study the role of earthworms (worms) in the dairy farmland ecosystem and how dairy farm management (earth) is affecting this.