Foraging for Farmers?
An evolutionary perspective on the process of Neolithisation in NW Europe – A case study from the Low Countries

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Abstract
Recent studies emphasise the mosaic character of the process of neolithisation in northwestern Europe. However, some overarching motives influencing the uptake of farming can be identified across regions. We model the importance of evolutionary processes underlying neolithisation. We focus on the southern part of the Low Countries, where the uptake of agriculture takes distinct trajectories in different biomes. We analyse the transition in terms of fitness benefits that foraging and agriculture bestow on the actors involved. We suggest that different substrates offer different fitness benefits with regard to the uptake of farming and that these benefits differed between the sexes, leading to differing "optimal" strategies for males and females regarding whether and how to adopt Neolithic novelties.

Keywords
Neolithic, Mesolithic, neolithisation, gender, Linearbandkeramik, Swifterbant, human behavioural ecology

Introduction

The reasons for the uptake of farming by hunter-gatherer societies have been debated in archaeology from a variety of perspectives[1]. We think that archaeological studies should take evolutionary processes into account, both in the domain of cultural and genetic evolution[2]. We argue that although trajectories of neolithisation were diverse, they can be understood in terms of a concise set of underlying principles: the interaction of different selection pressures with the social and environmental contexts of the hunter-gatherers who came into contact with agriculture.

The uptake of a Neolithic way of life entails both advantages and disadvantages. Advantages associated with the uptake of farming are increased food production and security[3]. However, a farming existence is generally also associated with increased mortality, decreased health and a higher workload[4]. For the successful adoption of farming, the associated negative consequences must be offset. However, the advantages associated with farming differ between different areas, e.g. because of differences in soil fertility, and this is

1 Thorpe 1996; Price 2000; Kienlin 2006.
2 Hawks *et al.* 2007; Patin/Quintana-Murci 2008; Mesoudi 2011; Shennan 2012.
3 Hayden 1990; Meiklejohn/Zvelebil 1991; Winterhalder/Kennett 2006.
4 Sahlins 1972; Larsen 1995; Groube 1996; Diamond 2002; Bocquet-Appel 2008; Smits/Van der Plicht 2009; Bowles 2011.

an important reason for the diverse trajectories of neolithisation. The advantages of farming also differ between the sexes, because reproductive success is dependent on different factors between the sexes.

Male fertility is limited only by the number of mates acquired during a lifetime. Female fertility is limited by the number of completed pregnancies over a lifetime. However, in contrast to males, females have certainty of parenthood. The maximisation of reproductive success stimulates different mating strategies in males and females. Female reproductive success is maximised by investing resources in the rearing of her offspring, maximising the chances of them reaching adulthood. Males may benefit more by investing resources in acquiring mates instead of provisioning offspring, especially because they do not have absolute certainty of paternity. If some children do not reach adulthood, this is compensated by a male's potential to sire larger numbers of offspring by maximising his mating opportunities. In hunter-gatherers, these differences result in differing foraging strategies between the sexes[5]. Females generally forage for reliable foods, mostly plant foods, and they share their returns mainly within the nuclear family[6]. Males try to acquire highly valued foods, most importantly meat. Moreover, these resources are sometimes shared widely to increase their societal standing and to acquire mating opportunities[7]. The increased reliability of food production associated with farming may thus initially have greater benefits for females than for males.

The different magnitude of advantages and disadvantages associated with a Neolithic way of life between the sexes influences the process of the uptake of farming. We focus on the neolithisation of the southern Low Countries (FIG. 1). This area comprises three different biomes providing different opportunities for hunter-gatherers and farmers. We examine how the application of evolutionary principles illuminates the different trajectories of neolithisation in this area. We suggest that the best strategies in transitional circumstances may have differed between the sexes and that female mate choice may have been an additional process influencing the trajectories of neolithisation.

Our interpretation of the role of evolutionary forces in explaining the long-term process of neolithisation does not mean that we see people constantly weighing different behavioural options in terms of their fitness benefits. Individuals in our scenario made choices based on their ideas and desires about whether to adopt new behaviours. However, the choices made by agents in this process often had unforeseen consequences over longer timescales, such as increasing population densities and the concomitant fissioning of communities, leading to population packing. Such developments over centuries may have made it increasingly necessary for hunter-gatherer populations to adopt agricultural subsistence methods to increase the yield of subsistence activities from territories of decreasing size.[8]

Setting the stage

The southern Netherlands form part of the Lower Rhine Area (LRA), which can be divided into three environmental zones differing in their suitability for foraging and farming subsistence economies.

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5 *E.g.* Kelly 1995; Bird 1999; Marlowe 2007.
6 *E.g.* Hawkes 1993; Marlowe 2007.
7 Kaplan/Hill 1985; Hawkes 1993; Bird 1999.
8 See for similar suggestions from a different perspective Robb 2013.

Figure 1

The southern part of the study region is part of the loess belt stretching from Central Europe to France. The area is covered by thick deposits of Pleistocene aeolian loess[9], which are dissected by large river basins (Meuse, Scheldt, and Rhine). During the Atlantic (~8000 – 4000 cal BC), the natural fertility of the substrate led to the formation of dense forests. Large parts of the area were covered by lime forest with restricted undergrowth, while a more varied arboreal assemblage, including shrubs and open pastures characterised the valleys[10]. The subsoil in this zone is extremely suitable for agriculture. The river basins provided an ecologically rich pendant with diverse resources. Because of the dense forest cover, most biomass was inaccessible to hunter-gatherers[11].

To the North of the loess belt lies a flat coversand landscape, consisting of Quaternary fluvial deposits, covered by aeolian sand during the Weichselian. Dunes and ridges of limited height are dissected by small brooks and scattered fens. Vegetation on these acidic sandy soils was patchy, consisting of forests with oak, hazel, elm and ash, and open spaces with shrubs, herbs and grasses[12]. The forests in this area were more open than those in the loess zone[13]. This is shown by the increased representation of hazel (*Corylus*) and oak (*Quercus*), which are moderately light demanding[14]. Because the forest cover in this area was less dense than on the loess, biomass suitable for human consumption was more abundant here during the Mesolithic[15]. However, the subsoil, being poorer in nutrients, is less suitable for agriculture than the loess.

To the North and West the coversand area is bordered by a wetland zone. In this zone the Meuse and several channels of the Rhine run East-West to the coast. This area was under continuous influence from the rising sea-level during the Holocene[16]. The western part of this area was a coastal environment consisting of beach barriers with low dunes and estuaries. East of the coastal zone was an area with tidal flats, salt marshes and low dunes intersected by creeks in brackish to fresh environments. In the central part of the riverine area, and the Scheldt Basin, freshwater wetlands consisted of streams, lakes and peat swamps. Dry inhabitable space was formed by an archipelago of riverdunes or 'donken' of various sizes[17], as well as the wetland margins. Further North, the IJsselmeer basin was also characterised by wetlands. Vegetation in the wetland area ranged from alder carr and reed marsh inland, to coastal vegetation including shrubs and small stands of trees further west, while riverdunes contained deciduous vegetation. This zone was rich in game, fowl, and aquatic resources[18]. Vegetable resources also provided important foraging opportunities. Due to the smaller importance of woodland vegetation, more edible shrubs were present in this zone. Moreover starch-rich plants like cattail (*Typha latifolia*) and arrow head or swamp potato (*Sagittaria sagittifolia*) were available[19].

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9 Bakels 2009.
10 Bakels 1978; Berendsen 1997.
11 Kelly 1983.
12 Munaut 1967; Svenning 2002.
13 *E.g.* Svenning 2002; Bradshaw/Hannon/Lister 2003.
14 *E.g.* Bakels 1978; Svenning 2002.
15 Arts 1989, fig. 5; Niekus 2005/2006, 43.
16 Vos/Kiden 2005.
17 Verbruggen 1992.
18 *E.g.* Zeiler 1997; Louwe Kooijmans 2003.
19 Bakels 2005; Hardy 2010.

Introducing the actors

The archaeology of the inhabitants of the three zones differs. These differences are caused mainly by taphonomic factors. Figure 2 shows a graphic representation of the current consensus about the cultural sequence of the region.

Figure 2

The loess zone

Mesolithic communities occupying the loess zone are poorly documented. As in much of Central and Western Europe[20], Late Mesolithic sites are virtually absent. This confirms the unattractive nature of loess plateaus to hunter-gatherers due to the limited amount of edible biomass[21].

The Neolithic Linearbandkeramik Culture (LBK) expanded from Central Europe to reach Dutch Limburg around 5250 cal BC. Prior to the arrival of the LBK in the study area, there is evidence for contact between the Dutch loess region and early farmers further East; and such contacts continue after the LBK arrives in the study area[22]. There were too few hunter-gatherers present to account for the full LBK population by a process of adoption/enculturation[23]. Hence, the spread of the LBK entailed colonisation by groups of farmers. The LBK settlement clusters in the study area include, from East to West, the Aldenhovener Platte in Germany, the Graetheide Plateau in the Netherlands, the Hezerwatercluster on the border with Belgium and the eastern Hesbaye region (see FIG. 1). LBK occupation lasts until *c.* 4900 cal BC and then disappears suddenly. The subsistence economy is characterised by a reliance on a narrow set of resources: emmer (*Triticum dicoccom*) and einkorn (*Triticum monococcum*) are the most important crops[24]. Bone material is not preserved in the study area, but in general LBK faunal assemblages are dominated by cattle, followed by sheep, goat and pig. The importance of wild game is usually small, always accounting for less than 30% of bone assemblages, and generally significantly less[25].

Quasi-contemporaneous with the LBK, three enigmatic phenomena are found in the loess zone, Limburg (LB), La Hoguette (LH) and *Begleitkeramik* (BL) pottery. These three types of pottery are distinct from the "normal" LBK ceramics. They have been found both at LBK sites and outside of the LBK settlement areas[26]. The interpretation of these types of pottery is contested. It has been proposed that LH pottery was produced by hunter-gatherer-pastoralists[27]. The similarities between LH and Cardial pottery have prompted the view that LH pottery represents a northward extension of the Mediterranean neolithisation process[28]. It was suggested that LB and BL pottery were associated with Late Mesolithic groups in the LRA[29]. Another possibility is that LB pottery was LBK pottery, but associated with a specific

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20 *e.g.* Bocquet-Appel *et al.* 2009.
21 Gronenborn 1999; Verhart 2003.
22 Vanmontfort 2008, 157-159; De Grooth 2014.
23 Kienlin 2006; Louwe Kooijmans 2007, 295; Vanmontfort 2008, 159.
24 Bakels 2005.
25 Marciniak 2005; see also Bedault 2009; Manning *et al*. 2013.
26 Lüning/Kloos/Albert 1989; Van Berg 1990; Jeunesse 1994; Manen/Mazurié de Keroualin 2003; Gronenborn 2007; Brounen/Hauzeur 2010.
27 See Kalis *et al*. 2001; Jeunesse 2003; Tinner/Nielsen/Lotter 2007; but also see Behre 2007.
28 Lüning/Kloos/Albert 1989; Gronenborn 1998; 1999.
29 Heinen 2006.

activity, possibly a transhumance component[30].

The occupation history on the loess after the end of the LBK is unclear. The chronological distribution of radiocarbon dates in the western parts of the LBK settlement area suggests a sparse Neolithic occupation in the early part of the 5th millennium, possibly as a result of a population collapse[31]. In the study region, the LBK disappears suddenly[32], yet for some LBK settlement clusters there is evidence for continuity of occupation. Subsequent Grossgartach (~4900 – 4600 cal BC) settlements are rapidly distributed from the Neckar region northwards,[33] followed by Rössen (4790 – 4550 cal BC) occupation[34]. In our study region, only a late Rössen site is known at Randwijck[35]. In the West the Groupe de Blicquy/Villeneuve-Saint-Germain replaces the LBK. This group suddenly disappears around 4800 cal BC[36].

From c. 4300 cal BC the study region sees substantial occupation by the Michelsberg culture (MK). This culture has a different character than the LBK. The MK-Neolithic shows a homogenous distribution of often small-scale sites. There is little evidence for large dwelling structures. Settlements are also found outside the loess. Sites are often recognized by extensive surface scatters of artefacts, but flint mines and enclosures also form part of the settlement system. The latter may have functioned as central places. Many, largely undiagnostic, surface scatters indicate a different type of exploitation on the sandy soils[37]. Changes also occur in the subsistence economy, resulting in a more flexible farming economy[38]. New crop plants such as naked barley (*Hordeum vulgare var. nudum*) and durum wheat (*Triticum durum*) are added to the repertoire. These crops are more resilient varieties of grain than emmer and einkorn[39]. It appears that hunting and gathering also increased in importance during the MK[40].

Various scholars have proposed that the genesis of the MK was the result of interaction between hunter-gatherers and farmers, resulting in the combination of subsistence elements of farming and foraging societies[41]. Unfortunately, taphonomic factors and archaeologically less visible building traditions prevent a more precise analysis of the role and input of the post-Danubian indigenous groups in the formation of this 'second Neolithic'.

The coversand zone

The Late Mesolithic communities in the coversand zone are better understood than those living on the loess, because more sites are known. Due to less dense forest, this area was more productive for hunter-gatherers. Some groups also spent time in the larger river valleys where more food resources were available. However, most streams crossing the coversand area are small, the only large rivers being the Meuse and Scheldt.

Most Late Mesolithic sites in the area consist of surface scatters, where site-formation

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30 Brounen *et al*. 2014.
31 Shennan/Edinborough 2007; Shennan *et al.* 2013.
32 Modderman 1988.
33 Jeunesse 2011.
34 Denaire 2009.
35 Louwe Kooijmans 1988.
36 Jadin 2003.
37 Vanmontfort 2004, 329-332.
38 Raemaekers 1999; Vanmontfort 2004; Louwe Kooijmans 2007.
39 Bakels 2005.
40 Verhart 2000, 232; Scheurs 2005, 317.
41 *e.g.* Verhart 2000; Vanmontfort 2004; 2007; Crombé/Vanmontfort 2007; Louwe Kooijmans 2007.

processes and repeated occupations have led to palimpsests yielding limited chronological and spatial information[42]. Late Mesolithic sites are mainly characterised by the production of regular blades in Montbani-style and the appearance of trapezoid arrowheads. Sites are generally located on the slopes of dunes and ridges. The lithic assemblages underline the importance of hunting and in combination with the *ad hoc* spatial structure of the sites, indicate a considerable degree of mobility[43].

There is some evidence for interaction with LBK farmers. Unfortunately, artefacts are often found together on the surface, so provide an open spatial association[44]. Some sites in the coversand zone contain BL, LH, and LB pottery[45]. The presence of large numbers of Rössen *Breitkeile* on the coversand attests to more intensive contact between hunter-gatherers living on the coversand and farmers on the loess than during the LBK[46]. From 4300 cal BC, the MK extends into the coversand zone. MK farmers lived in small dispersed settlements, perhaps consisting of single, mobile housesteads[47]. Unfortunately, MK settlements are usually preserved as surface scatters only[48].

The wetland zone

The meagre evidence available for the Late Mesolithic in the upland regions is contrasted by the situation in the wetland area. A number of well-preserved sites is known[49]. Site occupation was likely seasonal and lasted up to several months. Many sites show long-term constancy in occupation[50]. This occupation suggests that the degree of residential mobility in the wetland zone was lower than on the sandy soils[51]. This is supported by the occurrence of (semi)permanent features at Late Mesolithic sites in the form of postholes and interments[52]. Several sites yielded evidence for forager-farmer interaction. This is illustrated by the presence of a flint nodule from primary (chalk) context from Limburg (about 175km away), an LBK arrowhead at Hardinxveld Polderweg and ceramic finds of early Neolithic affinity, including Blicquy sherds at Hardinxveld[53].

A broad range of food sources was exploited. Small game is well-represented at many sites. It is generally present in higher population densities than large game and has a higher rate of reproduction[54]. Due to their high population densities, small mammal and bird species represent a large amount of available biomass. Their rapid rate of reproduction means that they can withstand intensive exploitation, enabling large human population sizes. Ethnographically, small animal exploitation is often practised by females to supplement foraging for plant foods[55]. A wide variety of plants is present at Mesolithic and Neolithic sites in this area and this variety appears to remain stable through time[56]. Many sites also yielded an abundance of fish remains and remnants of fish traps have also been found. This also

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42 Crombé 1999; Vermeersch 2006; Crombé/Vanmontfort 2007, 271.
43 Amkreutz 2009; 2013.
44 Amkreutz/Vanmontfort/Verhart 2009.
45 Modderman 1974; Verhart 2000; Brounen/Hauzeur 2010.
46 *e.g.* Verhart 2000; 2013; Klassen 2004.
47 *e.g.* Louwe Kooijmans 1998; Verhart 2000; Vanmontfort 2007.
48 See Verhart 2000; Vanmontfort 2004.
49 Louwe Kooijmans 2003; Crombé/Vanmontfort 2007; Peeters 2007.
50 *e.g.* Louwe Kooijmans 2003; 2007; Amkreutz 2013a.
51 Amkreutz 2009; 2013.
52 Louwe Kooijmans 2003; Peeters 2007.
53 *e.g.* Louwe Kooijmans 2003; Vanmontfort 2007.
54 *e.g.* Stiner *et al.* 1999; Stiner/Munro/Surovell 2000
55 Kelly 1995; Ugan 2005; Kuhn/Stiner 2006.
56 Out 2008a,b.

indicates low residential mobility. To exploit fish efficiently, it has to be mass-collected, but the technologies to do this, such as fish traps, require high investment. Producing them is only worthwhile in systems of logistical mobility[57]. At Hardinxveld-De Bruin, the tail end of a fish trap dated to about 5100 cal BC was excavated. Older fish traps are known from Mesolithic sites elsewhere[58].

In the wetlands, Late Mesolithic communities adopted elements of a farming existence over a long period[59]. These elements were integrated into the existing hunter-gatherer subsistence economy and mobility system. Most of the novelties were adopted from (post-) Danubian farming communities to the South and East[60]. Ultimately, post-Danubian methods of agriculture also found their way North[61]. Although "Neolithic" elements are found in the wetlands from at least 4700 cal BC, it is not until the Late Neolithic Single Grave Culture (from c. 2900 cal BC onwards) that agriculture becomes the main aspect of subsistence and most societies start living sedentary lives[62].

Evolutionary processes

We analyse the regionally diverse process of neolithisation in the LRA from an evolutionary perspective. Evolutionary explanations for changing human behaviour need to take into account that genetic inheritance is not the only way in which behaviour is transmitted across generations. Culture is also a mechanism of inheritance, as processes of selection also operate on cultural variants[63]. We focus on differential reproductive success associated with different reproductive strategies and on mechanisms of transmission of cultural skills that favour one behavioural variant over others[64]. Obviously, this does not mean that genetic evolution did not play a role in the period under consideration[65].

The introduction of farming in northwestern Europe is associated with a population increase[66]. Farming is considered a more productive way to extract energy from the environment than hunting and gathering, and is assumed to bring reproductive advantages[67]. However, while yielding a larger production of nutrients per spatial unit, in terms of labour productivity, farming in small scale societies appears to be a less efficient strategy of food production than foraging[68]. Moreover, severe disadvantages are associated with this way of life.

First, hunter-gatherers do not possess perfect knowledge of farming methods, making initial adoption a risky venture[69]. Secondly, farming and its associated sedentary lifestyle have negative health consequences, resulting in an increase in mortality compared to hunter-gatherers, especially in young children (<5 years of age)[70]. The decreased health of Neolithic populations is also signalled by an increase in markers of stress, compared to the preceding

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57 Cf. Ugan 2005.
58 McQuade/O'Donnell 2007.
59 Louwe Kooijmans 1998
60 Raemaekers 1999; Verhart 2000; De Grooth 2008; Van de Velde 2008.
61 Schrier 2009, 35-37.
62 Louwe Kooijmans 1993a; 2007; Amkreutz 2013a.
63 *E.g.* Shennan 2000; Richerson/Boyd 2005; Mesoudi 2011; Riede 2011.
64 See for reviews of cultural evolution: Richerson/Boyd 2005; Mesoudi 2011.
65 Hawks *et al.* 2007; Patin/Quintana-Murci 2008; Pickrell *et al.* 2009.
66 Shennan 2000; Shennan *et al.* 2013.
67 Meiklejohn/Zvelebil 1991; Gkiasta 2003; Gurven 2006; Shennan/Edinborough 2007.
68 Bowles 2011.
69 *E.g.* Gremillion 1996, 199.
70 Groube 1996; Bocquet-Appel 2008; 2011a; Smits/Van der Plicht 2009.

Mesolithic ones[71]. Thirdly, Sahlins[72] has argued that farmers work more hours per day than hunter-gatherers. Although this view has been nuanced[73], on average, early farming strategies appear to be less productive than foraging[74]. Fourth, adopting a farming lifestyle by moving from a hunter-gatherer community to a farming community leaves individuals with severely diminished alliance networks, due to the fact that they lose their own kin-based support networks and can therefore only depend on the alliance network of their spouse. This often results in lower evolutionary fitness[75]. Finally there is evidence for increased inter and intragroup violent conflict in European Neolithic societies[76]. The disadvantages associated with a farming way of life must thus be outweighed by the advantages. However, these factors are not static, but dependent on the ecological context in which people lived and developments in both foraging and farming methods.

The most important factor in the increase in fertility is not the increased provision of food, but the cessation of residential mobility, since the lower energetic demands placed on sedentary populations decreases the female birth interval. Cemetery analysis suggests that on average this led to an increase of two births during a female's lifetime[77]. The lower energetic demands allowed earlier weaning of infants[78]. In hunter-gatherers, weaning is often delayed, also because suitable weaning foods are often seasonally available[79]. Early weaning may have been further facilitated for farmers by their more reliable food supply and the use of pottery to produce weaning foods[80].

Cultural transmission mechanisms may favour one behavioural variant over others, resulting in the spread of specific behaviours even if they are not correlated with increased reproductive success. Biased cultural transmission concerns the preferential copying of behaviours. The factors influencing the decisions which variant to copy can be wide-ranging. When people have similar goals (e.g. the production of as much food as possible), this will lead to the preferential copying of the most successful behaviours. However, in many situations, the advantages associated with different behavioural variants are so small that they are very difficult to determine for individuals. In such situations, other forms of biased cultural transmission may take place. Prestige bias results in preferentially copying behaviours from prestigious individuals. Conformity bias entails copying the behaviours that are exhibited by the majority of the population[81].

Cultural transmission mechanisms

Although biased cultural transmission can be a very important factor in promoting behavioural change[82], ethnographic research shows that cultural transmission of subsistence methods often occurs primarily vertically between parents and offspring[83]. Since teaching of

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71 Larsen 1995, 189-194.
72 Sahlins 1972, 32-39.
73 Hill *et al.* 1985.
74 Bowles 2011.
75 O'Connell 2009, 49.
76 Wahl/König 1987; Golitko/Keeley 2007.
77 Bocquet-Appel 2011a; 2011b.
78 Bocquet-Appel 2002.
79 Clayton/Sealy/Pfeiffer 2006.
80 Bentley/Paine/Boldsen 2001.
81 Soltis/Boyd/Richerson 1995; Henrich 2001; Richerson/Boyd 2005; Mesoudi 2011.
82 Henrich 2001.
83 Guglielmino *et al.* 1995; Shennan 2000.

complicated subsistence technologies is costly to the teacher[84] parents will do most teaching[85], making similar subsistence strategies of parents and offspring likely. In a situation where a new behavioural variant is obviously much more successful than existing ones, biased transmission may be an important mechanism. However, if differing subsistence methods do not differ very obviously in productivity (i.e. calories produced per unit of time), as appears to be the case for early farming methods compared with foraging strategies[86], transmission is expected to remain mostly vertical, leading at most to a slow spread of new subsistence methods. In the case of conformity bias, hunter-gatherers may be discouraged from taking up farming.

People are more likely to copy behaviour from individuals of the same cultural entity[87]. This may inhibit the transmission of information across groups in contact situations. The physical distance between groups of farmers and groups of hunter-gatherers and hence the frequency and intensity of contact is also important in understanding the uptake of new behavioural strategies. If information on farming strategies was not observed directly, this would inhibit the likelihood of hunter-gatherers to experiment with the new subsistence methods.

One additional factor may be of importance regarding the transmission of farming and foraging subsistence methods, namely direct bias. Some ideas may, by their very nature, be more attractive to people than others, and hence be more readily transmitted[88]. Related to this, in our opinion, is the learning required in order to become proficient at skills. Foraging skills, both in the hunting and the gathering domains, may take until adulthood to fully master[89]. Although some decisions regarding the management of farming activities (*e.g.* when to plant, when to harvest, which animals to slaughter) are very complex, it appears that a number of menial farming skills are mastered more quickly. In villages with a mixed economy, where both agriculture and foraging are practiced, children from households relying more on farming work more regularly at subsistence tasks. Children from households relying more on foraging spend more time at play, producing deferred benefits of greater skill later in life[90]. This suggests that, although the productivity of fully skilled foragers may be higher than that of farmers, the easier learning of farming skills means that total productivity of a farming life history may be larger. Although people may not have been conscious of the overall productivity during a lifetime, this would make farming individuals and groups more productive, giving them a potential advantage in terms of food security. On the level of individual choice, foraging parents may have witnessed farming children starting to contribute to subsistence tasks at a young age, potentially increasing the attractivity of farming subsistence methods.

Gender specific strategies; Female agency

The appeal of different subsistence strategies varies between individuals. In spite of individual variation, some general patterns can be seen among hunter-gatherers, such as a division of

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84 Bock 2002.
85 MacDonald 2007.
86 Cf. Bowles 2011.
87 *E.g.* Richerson/Boyd 2005.
88 Mesoudi 2011.
89 Kaplan *et al.* 2000.
90 Bock 2004, 276.

labour along gender lines.[91] It appears that this division is caused by contrasting reproductive strategies between men and women. Although, foraging decisions were made at family or household level and based on cultural norms and the imitation of related or successful individuals, evolutionary successful decisions appear to have been perpetuated. We think the universal division of labour along gender lines also suggests divergent attitudes of men and women towards the uptake of Neolithic elements into their way of life.

Reproductive strategies

The investment put into the production of offspring varies across the sexes. Generally, females invest more time and energy than males to raise children. A human population's reproductive potential is limited by the number of females[92]. Female reproductive success is limited by the number of pregnancies completed during lifetime, while male reproductive success is limited by the number of mates acquired. For males, mating represents a very small investment, for females the potential repercussions in case of conception are immense. After all, pregnancy is a lengthy and energetically costly process and the resulting offspring will be dependent on adults for its survival for more than a decade. Female selection of mates that invest in offspring will thus increase reproductive success[93]. Since males never have absolute certainty of parenthood, their interests may be better served in maximising mating opportunities than in provisioning offspring[94]. Over time, these differing interests appear to have resulted in a universal division of labour among hunter-gatherers.

Women generally collect resources such as plant foods, shellfish and small fauna. These gathered resources are generally characterised by high reliability but relatively low return rates and they are consumed mainly within households[95]. Males generally collect honey and fish and hunt large game[96]. Especially large game hunting is associated with high return rates, but it is also an unreliable activity; up to 97% of hunting expeditions can be unsuccessful[97]. The spoils of males' foraging are more widely shared. This has led to the view that men share meat of large mammals beyond their own households to increase political power and mating opportunities[98].

This suggests that female reproductive strategies may initially profit most from the adoption of farming. Both males and females profit from the increased amount of food that can be produced with farming. For females additional benefits are associated with the increased reliability of the food supply associated with the uptake of farming. A female's reproductive success is determined to a large degree by the length of the interbirth interval. This is lowered by the cessation of mobility. The availability of grains and pottery to prepare weaning foods allow earlier weaning, lowering the inter-birth interval further[99]. Since females have certainty of parenthood and each pregnancy represents a significant investment, their priority is to minimise child mortality. Males generally use a lower investment strategy, by acquiring as many mating opportunities as possible[100]. In this strategy, the death of infants is

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91 Gurven/Kaplan 2006; Marlowe 2007.
92 Hawkes 1996.
93 Ebd.
94 Hawkes 1993.
95 Marlowe 2007.
96 Ebd.
97 Hawkes *et al.* 1991.
98 Hawkes 1993; Smith 2004.
99 Bentley/Paine/Boldsen 2001.
100 *E.g.* Heath/Hadley 1998; Bird 1999.

not as disadvantageous to their reproductive success as to that of females. For hunter-gatherer males moving into farming groups, the sharing of hunting products may become less potent in increasing mating opportunities[101]. Mating opportunities in farming societies are generally dependent on material possessions, often in the form of livestock, and accumulating large herds may take decades[102], thus limiting male potential to increase mating opportunities.

In this situation, mate choice of forager women may become a significant selective force. Cross-cultural analysis shows that males and females value different characteristics when choosing a partner, with women preferring mates with a high potential for resource acquisition[103]. Male parental investment and investment by paternal kin is beneficial for the survival of offspring. However, on choosing a mate, women cannot easily predict how much investment males and their kin will actually provide. Generally, the contribution of fathers and their kin to a child's survival are smaller than that of mothers and maternal kin. However, the influence of wealth in the paternal lineage may modify that pattern[104]. Hence, selection may focus on men that have access to resources, so there is at least the potential of male parental investment[105]. Ethnographic studies show that successful hunters enjoy higher reproductive success and more extramarital affairs than unsuccessful hunters[106]. Moreover, Hadza women show a much stronger preference for men who are successful foragers than vice versa[107]. Securing such investment is so important that, for instance in the case of the Ache, where due to high rates of violence males are scarce, females appear to nominate co-fathers (generally related to biological fathers) to secure added investment[108]. In at least 53 other societies, polyandrous unions are occasionally used to ensure male parental investment[109]. This suggests that in contact situations, a female preference for farming mates could ensue.

Mate choice may not have been solely determined by the prospective mates themselves, but may have been influenced, or even determined, by kin. Another factor in play is the distance between farming and foraging societies. If females ranged less widely in their mobility, which appears likely,[110] they may not have been as involved in contact between societies as males, and their mate choice would be constrained. In most hunter-gatherer societies, marriage practices are tightly regulated[111]. However, a cross-cultural study suggests the encroachment of agriculturalists may result in the simplification or deregulation of marriage systems[112]. As such, the arrival of farmers in the vicinity may have acted to increase women's influence on partner choice. Where partner choice is determined by parents, the interests of parents and children may overlap at least partly; cross-cultural analysis suggests that parents generally prefer successful hunters and good providers[113]. Another way for females to exercise partner choice is by divorce, which is common in many hunter-gatherer

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101 Alvard/Kuznar 2001
102 Kaplan/Hill 1985; O'Connell 2006; Gurven/Hill 2009.
103 Buss 1989.
104 Sear/Mace 2008.
105 Buss 1989; Sefcek *et al.* 2007.
106 *E.g.* Kaplan/Hill 1985; Smith 2004.
107 Marlowe 2004.
108 Ellsworth *et al.* 2014.
109 Starkweather/Hames 2012.
110 *E.g.* Ruff 1987.
111 Walker *et al.* 2011.
112 Ebd.
113 Apostolou 2007.

societies[114].

If farmers were seen as good providers, hunter-gatherer families may have favoured marrying daughters into the colonising farming societies. They may also have been motivated to do so to gain access to farming networks and associated prestigious items, such as adzes[115]. It has also been observed that intermarriage with farming societies may lead to inflation of bride-prices, leading to the acquisition of livestock by foragers in order to be able to marry[116]. However, if females moved between groups as marriage partners[117], and family ties were not severed in such situations, this could result in a conduit for the uptake of farming methods by hunter-gatherer societies.

In Mesolithic hunter-gatherer societies, female reproductive success would benefit from mates who through their foraging contribution to the household's energy budget are able to lower the degree of residential mobility needed and increase the food security in times of scarcity. This does not mean that women are presumed to be constantly aware of reproductive fitness considerations. However, in all studied hunter-gatherer societies, females appear to value good males, suggesting a male's provisioning potential is an important consideration[118]. If hunter-gatherer females married into farming societies with some regularity this would alter the ratio of reproductive males to reproductive females in hunter-gatherer groups. It appears that in situations with a shortage of women, mate choice leads to increased monogamy and increased male provisioning[119]. The question whether females were likely to preferentially choose farming mates is difficult to settle. Hunter-gatherer groups and farming communities were likely exogamous. It is well documented that choices of successful individuals are often copied preferentially[120]. Anthropologically, it seems that often farming males may marry hunter-gatherer wives, but hunter-gatherer males rarely marry farmer wives[121].

The transitions

The loess zone

The LBK settlement of the loess area of Dutch Limburg involved colonisation by incoming people. Here, farming radically improved the quantity and reliability of the food supply. Therefore, a Neolithic way of life was an evolutionarily attractive strategy for hunter-gatherers of both sexes. Due to the cessation of mobility, interbirth intervals decreased, increasing fertility. The small hunter-gatherer populations were crowded out by larger and faster reproducing incoming groups[122]. The unequal balance of power, coupled with increases in food availability under a farming regime, would lead many resident hunter-gatherers to adopt the Neolithic way of life[123]. This may be supported by isotopic evidence from southwestern Germany. Stable isotope analysis from human remains from early LBK occupations in Germany and the Czech Republic shows a mix of people with indigenous and non-local isotopic signatures. This suggests indigenous populations mixed with colonising

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114 Ebd.
115 *E.g.* Verhart 2013.
116 Cronk 1989; Zvelebil 1998.
117 Cf. Verhart 2000; 2013.
118 Smith 2004.
119 Cashdan 1996, 140.
120 Richerson/Boyd 2005.
121 Grinker 1994; O'Connell 2006; Quintana-Murci *et al.* 2008.
122 Bocquet-Appel *et al.* 2009.
123 *Sensu* Zvelebil 1986.

farmers to form the founding populations of LBK settlements[124]. It is likely that not all hunter-gatherers adopted farming. Part of the hunter-gatherer population probably adjusted their territory in relation to the new LBK villages to avoid conflicts over resources[125]. This may have started extended periods of co-existence in some regions[126]. Part of the hunter-gatherer population may also have been killed by incoming farmers[127].

In the study region, the LBK colonisation of the loess zone was followed by a period of co-existence of farming communities on the loess and hunter-gatherer groups in adjacent areas. Contact between the societies in the study region is difficult to ascertain[128]. However, it is indicated by the presence of LBK artefacts outside their settlement zones and transport of raw materials from Mesolithic settlement areas to LBK settlements[129]. The presence of Banholt-type flint from Dutch Limburg in the earliest LBK at Friedberg-Bruchenbrücken (i.e. prior to the LBK settlement of Limburg) suggests foragers in the loess zone were aware of the LBK phenomenon before it expanded into the Dutch loess area[130]. These contacts continued after the LBK entered the study area, as illustrated by Neolithic objects at Hardinxveld[131]. In this phase, marrying into the LBK would represent a reproductively smart choice for hunter-gatherer females. The cessation of mobility, as well as the more reliable food supply would dramatically increase their reproductive success. The access to farming networks and goods that was afforded by having family ties with Neolithic households may also have held appeal for families of hunter-gatherer women marrying into the LBK. A continued influx of women from outside may have increased the reproductive capacity of the LBK, although sampled LBK skeletons from Saxony-Anhalt in Central Germany shows that here, hunter-gatherer mtDNA haplogroups are rare (~2.9%) in LBK contexts.[132] There are archaeological reasons to suggest a larger influx of Mesolithic individuals in the LBK of the Low Countries and Western Germany, but these regions have so far not yielded aDNA from the LBK[133]. Moreover, there are taphonomic arguments to suggest that not all individuals with a hunter-gatherer background may be visible in LBK. So far interred individuals have been sampled, but part of the population was treated differently (i.e. cremated, or subjected to archaeologically invisible disposal methods).[134] More importantly though, the relatively low percentage of individuals with a hunter-gatherer background measured against a Neolithic population may represent a more substantial of their population of origin, as hunter-gatherer populations are generally characterised by much lower population densities than farmers, especially in continental settings at temperate latitudes.[135]

The LBK was likely patrilocal[136], this would discourage hunter-gatherer males from marrying into farming societies. They would lose much kin-based support and may have encountered difficulties in acquiring skills and land. They would thus be unable to increase

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124 *E.g.* Kienlin 2006, 146; Nehlich *et al.* 2009; Zvelebil *et al*. 2012, 143.
125 Cf. Vanmontfort 2008.
126 Bollongino *et al.* 2013; Stäuble/Wolfram 2013
127 Golitko/Keeley 2007.
128 Amkreutz/Vanmontfort/Verhart 2009.
129 Gronenborn 1998; 1999.
130 De Grooth 2014.
131 Louwe Kooijmans 2003.
132 Brandt *et al.* 2013.
133 Hofmann 2014.
134 Ebd.
135 Binford 2001; Johnson 2014.
136 *E.g.* Bentley *et al.* 2008.

their reproductive success. This may be supported by stable isotope analyses from southwestern Germany. Here, Sr isotope ratios have been interpreted to suggest that non-locals continued to enter Neolithic villages after the pioneer phase, but that most of the non-locals in later phases of the LBK are women. This could mean that only female hunter-gatherers married into LBK villages[137].

In the long term, the transition to agricultural subsistence in the loess zone was not successful everywhere. The near-absence of Neolithic occupation in the study area and adjacent Belgium after the demise of the LBK has been interpreted as evidence for a collapse of the Neolithic way of life in the region[138]. The short-term evolutionary advantages of the Neolithic may in the longer term have led to unsustainable population sizes and overexploitation of farmland, leading to a collapse of this way of life[139].

The coversand area

Phase I

After the establishment of the LBK on the Limburgian loess, the spread of the Neolithic way of life ceases in that part of the LRA[140]. For the hunter-gatherers in the coversand area, the new way of life held limited appeal. The coversand area is better suited to hunting and gathering than the loess. This is demonstrated by the larger number of Late Mesolithic sites in the coversand area. Moreover, LBK farming practices were less effective in the coversand zone because of its lower soil fertility[141]. Hence, no wholesale adoption of the LBK system would be expected for societies living outside the loess.

Evidence from the LBK elsewhere suggests that foraging was of limited importance to the subsistence economy, although there are exceptions, with wild animals accounting for around 20% of the bone assemblage at Cuiry les Chaudardes[142]. This made the new way of life economically unappealing for well-established hunter-gatherers who may have been able to forage with equal or even higher return rates[143]. The unimportance of foraging to the LBK is probably a result of the fact that its spread of farming in these cases was the result of colonization of unfamiliar landscapes, of which the foraging opportunities were initially poorly understood[144].

In this situation, the different fitness benefits associated with farming could lead to different evolutionarily successful strategies for the sexes. Although the coversand zone provided better foraging opportunities than the loess, much of the available biomass was still locked in trees[145]. Women's foraging will have concentrated on seasonally available plant resources such as nuts and berries. Storage is assumed to have been unimportant, as is often the case in residentially mobile groups[146]. This resulted in low productivity of women's foraging for plant foods. In addition, females may have exploited small game to supplement

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137 *E.g.* Price *et al.* 2001; Bentley *et al.* 2002, 802; 2003.
138 Crombé/Vanmontfort 2007.
139 Cf. Shennan *et al.* 2013.
140 Cf. Louwe Kooijmans 1998.
141 Bakels 1978; Bogaard 2004.
142 Lamys 2001; Marciniak 2005; Manning *et al.* 2013.
143 Bowles 2011.
144 Kelly 2003.
145 Svenning 2002.
146 *E.g.* Binford 1980; Kelly 1995; Amkreutz 2013a. The Effective Temperature for Eindhoven, centrally located in the coversand zone is 13, which is only very slightly above the storage threshold of 12,75 defined in Johnson 2014.

their foraging returns[147]. This is most profitably done using traps, nets or snares. However, the return rates for these activities are generally lower than the return rates for large game hunting[148]. This suggests an important role for large game hunting and thus male activities for the wellbeing of the group. This is supported by the faunal spectra of several sites in the Meuse valley[149] as well as by the dominance of arrowheads in the toolspectra of Late Mesolithic coversand sites[150]. Finally, the aquatic resources available in the river valleys bordering the coversand plateau would have been at least seasonally important[151].

Upon adopting agriculture, the reduced importance of men's foraging activities might result in a loss of opportunities to increase their political power and access to mates that farming would not remedy, since developing farming proficiency and the accumulation of large, productive herds would take time[152]. In addition, the less healthy circumstances of Neolithic life were not immediately compensated. Mesolithic males in the coversand zone are thus expected to favour the continuation of a hunting and gathering existence. For females, the disadvantages of a Neolithic lifestyle were negated by the lower residential mobility, lowering the inter-birth interval[153], and by the more reliable food supply. In this situation, young females could increase their reproductive success by marrying into farming societies.

Within hunter-gatherer groups, small differences in degree of parental investment and small differences in the degree of residential mobility between males would have weak effects on reproductive success. These effects might be easily negated by other factors such as cultural drift or male preferences to increase their social capital by focussing on large game hunting. The arrival of Neolithic communities in adjacent areas increased the reproductive options for women. Women may have married into farming communities for various reasons, either on instigation of their kin, or of their own accord. A consequence of such marriages would be to dramatically increase the reproductive success of women compared to those marrying inside hunter-gatherer societies. Females probably moved into the agricultural societies in the South with some regularity, lowering the total reproductive potential of the coversand communities.

Since the hunter-gatherers on the coversand co-existed with farmers in neighbouring areas for a prolonged period, this cannot have been so common that women became rare in Mesolithic societies. However, in a situation with a lack of females, mate choice becomes more influential and can lead to increased male provisioning[154]. Increased male investment in a female partner and children increases fertility[155]. The increased selective effects of female mate choice favoured males who pursued strategies that increased female reproductive success. This may have led foraging strategies geared to lower mobility and increased stability of food supply to become more. Selective pressures would then favour males that were prepared to experiment with elements of the Neolithic way of life.

Societal changes are reflected in the material culture of the coversand hunter/gatherers. BL and LH pottery have been found in Late Mesolithic settlement areas off

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147 Kelly 1995; Ugan 2005; Kuhn/Stiner 2006.
148 Webster/Webster 2005; Ugan 2005.
149 Mees *et al.* 1994.
150 Amkreutz 2009; 2013.
151 Nicholas 1998.
152 Alvard/Kuznar 2001; Bowles 2011.
153 Cf. Bocquet-Appel 2002; 2011a.
154 Cashdan 1996.
155 *E.g.* Marlowe 2001.

the loess[156]. The use of ceramics could increase female reproductive success by increasing the yield of their foraging activities by allowing cooking of starchy foods, facilitating the production of weaning foods and potentially lowering mobility through increasing storage.

Hunter-gatherers (especially males) were probably more attracted to the use of livestock than planting crops. Tending livestock can be incorporated relatively easily in hunter-gatherer mobility patterns[157]. LBK transhumance could bring hunter-gatherers in contact with livestock herding seasonally. In the study area, clusters of LBK finds near Roermond in the coversand zone have been interpreted as evidence of transhumance by LBK farmers[158]. Outside the study region, LBK transhumance has been demonstrated. $^{87}Sr/^{86}Sr$ isotopic signatures at different stages of tooth formation of a cow from the site of Vaihingen suggest that it was born in the settlement, moved to an upland area during the summer of its first year of life, and returned to the settlement afterwards[159]. Although the distances involved in transhumance may be small, the increased area used by farming societies in this way increases the likelihood of encounters of hunter-gatherers with farming methods. Ethnographic studies suggest that some farming societies employ hunter-gatherers on a seasonal basis to herd livestock during episodes of transhumance[160]. The presence of LBK materials on the coversand area shows there was contact between farming and foraging societies. The practice of transhumance allowed hunter-gatherers to encounter agricultural methods in the coversand area. Whether hunter-gatherers were employed as herders is impossible to determine at present. Based on ethnographic parallels it is not an unlikely scenario, which may have facilitated the adoption of herding further.

Phase II

From 4300 cal BC the MK culture is present in the loess area. It is argued in the study region, the MK occupation resulted from the interplay between farming and hunter-gatherer societies[161]. This is based in part on perceived continuities between Mesolithic and MK flint-working in the study region.[162] Also, the settlement system appears to be the result of a more mobile way of life.[163] Finally, the subsistence repertoire of the MK was better suited to the coversand area. New crop plants and different methods (e.g. swidden cultivation or *Brandfeldbau*) were adopted[164]. Moreover, livestock and hunted foods appear to have played a larger role in the MK than in the LBK[165]. In the resulting mixed economy, exploiting low-ranked wild resources was foregone in favour of farming, allowing higher overall productivity[166], which may have been essential for the successful adoption of a subsistence economy incorporating agricultural methods on the less fertile coversand.

The increased yields are expected to favour biased transmission of agricultural subsistence methods, leading to the adoption of farming methods by hunter-gatherers. This was facilitated by the long-term habituation of hunter-gatherers with the new subsistence

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156 Brounen/Hauzeur 2010.
157 Ingold 1996; Whittle 2003.
158 Louwe Kooijmans 1993b; Brounen *et al.* 2014.
159 Bentley/Knipper 2005; Bentley 2007.
160 Gregg 1988; Gronenborn 2004.
161 Vanmontfort 2004; Amkreutz 2013a.
162 Verhart 2000; Vanmontfort 2004.
163 Ebd.
164 Schrier 2009, 34; Amkreutz 2013a, 41.
165 Scheurs 2005.
166 Cf. Bowles 2011.

methods, with LBK materials and Roessen objects such as *breitkeile* being widely distributed across the coversand zone[167]. Female mate choice also favoured marrying into farming communities or marrying hunter-gatherer males experimenting with farming subsistence methods. The marrying of females into farming communities would lead to a relatively low ratio of females to males. This would have favoured males investing in increased provisioning of the nuclear family and may have stimulated males to adopt experimenting with farming subsistence methods[168]. The availability of prestige items from farming societies, such as *Breitkeile* and livestock, may have led to inflation of bride-prices, similarly stimulating men to experiment with elements of a Neolithic lifestyle[169].

The increased reproductive success of farming families led to population growth on the coversand. This had consequences for the suitability of the landscape for hunting and gathering[170]. Since part of the land was now geared towards farming, the area available for hunting and gathering decreased. Moreover, hunting and gathering methods were also practised by farming households. The increased population densities led to the depletion of the wild resources. Hence over time, biased transmission, combined with the effects of population increase, probably led to resource stress and necessitated the use of farming subsistence methods at least to a degree by the entire coversand population. This is illustrated by the presence of farming settlements of the MK spreading in the coversand area. The joining of hunter-gatherer and farmer lifestyles continues during the subsequent Stein/Vlaardingen phase, with settlements represented across the coversand area and in the coastal and wetland zone. The wetland sites from this phase show that the exploitation of wild resources remained of considerable importance, due to taphonomic factors, this is unclear for the coversand settlements, although burnt hazelnut shells have been recovered there[171].

The wetlands

In the wetlands, there was less inclination to adopt farming, since the advantages of that way of life were smaller than in the uplands. This was a productive environment where food was available year-round. Both males and females intensively exploited a broad spectrum of resources, realising relatively high population densities. Late Mesolithic mobility here was likely organised logistically[172]. Large areas in this zone are near the groundwater table and are regularly flooded, and much of the area is covered by heavy clay soils in which drainage is poor, hence too humid to grow plant crops. To grow crops in these soils, ploughing or hoeing are indispensable. Higher lying dunes or donken would be more suitable for agriculture, yet their surface area is limited. Therefore, researchers doubt whether sufficient food could be grown in this area to feed a band of people[173]. Adopting farming was a risky option in the wetlands since knowledge how to farm successfully in this environment had to be developed.

Due to the high productivity of this area, male provisioning was less important to ensure the survival of offspring. Furthermore, residential mobility was already low, while farming had less immediate advantages. The risks of marrying into a farming community and

167 Raemaekers 1999.
168 Cashdan 1996.
169 See for an ethnographic instance Cronk 1989.
170 Cf. the relationship between the Hadza and Datoga described in O'Connell 2006.
171 See Amkreutz 2013a,b; Van den Brink/Van Kampen 2013.
172 Louwe Kooijmans 2003; Amkreutz 2009; 2013.
173 Bakels 1986; Out 2008b.

losing much kin-based support probably outweighed the advantages[174]. This situation resulted in different fitness effects regarding the adoption of agriculture compared to the other regions. Males' access to mating opportunities was not reduced by women marrying into farming communities, as it probably was for hunter-gatherer males living in the uplands. This was reinforced by the fact that the distance to farming communities was considerable. This means there was less direct contact and competition over resources between wetland hunter-gatherers and farmers. As a result, the arrival of farmers in the South starts a long trajectory during which hunter-gatherers in the wetlands co-opted selected behaviours at different points in time.

Rituals, such as deposition, and certain prestige or symbolic objects were taken over first (from at least 5300 cal BC)[175]. This may have had powerful may have had perceived beneficial effects. Moreover, the adoption of similar spiritual practices may have stimulated exchange relations between societies and may even have helped hunter-gatherers acquire farming products[176].

From around 5100 cal BC, the occupants of the wetlands start producing ceramics. Although the knowledge on producing ceramics was probably derived from LBK farmers, the produced pottery was of a characteristic local style, reminiscent of basketry[177]. The pottery was fired at low temperatures, resulting in brittle, fragile vessels of a different character from LBK pottery, named Swifterbant pottery. The adoption of pottery was advantageous for both sexes. The pottery was used for cooking, as attested by charring on many sherds[178]. Analysis of cooking residues suggests that Mesolithic meals consisted mainly of meat and fish, but starch-rich plants were also cooked[179].

From c. 4500 cal BC, remains of domesticated animals appear at Swifterbant sites[180]. Herding livestock may be more easily adopted by hunter-gatherers than crop agriculture, and some degree of habituation may have taken place due to contact with farming societies. However, it is difficult to gauge whether the early livestock remains at wetland sites represent animals herded by the occupants, or individual animals, or their meat, acquired by trade. The minimum herd size required to successfully tend livestock is large and it is unclear when wetland hunter-gatherers acquired sufficient animals of breeding age to tend viable herds. The eventual adoption of herding was a valuable addition to the subsistence spectrum. Meat is a highly regarded food in the human family, as attested by both ethnography and primatology. Large game is generally rare. Moreover, large animals have a slow rate of reproduction. Intensification of hunting large game results in the depletion of this resource.[181] Livestock herding may have allowed males to effectively increase the productivity of their foraging behaviour. This must have significantly increased the political and reproductive clout of individuals that were able to procure the animals.

Game, both large and small, continues to be well represented at sites from 4700 cal BC onwards. The amount of domesticated livestock accounts for between c. 3 % and 39 % of

174 Cf. O'Connell 2006.
175 Verhart 2000; 2013; Louwe Kooijmans 2003; 2007, 297; Peeters 2007; Amkreutz 2013a.
176 See for historically documented cases Hall 1986.
177 Louwe Kooijmans 2007, 297.
178 De Roever 2004.
179 Raemaekers/Kubiak-Martens/Oudemans 2013.
180 Louwe Kooijmans 2003; 2007.
181 Stiner *et al.* 1999; see also Dusseldorp 2009; 2012.

the faunal spectra at sites from this phase of the Swifterbant culture (see FIG. 3)[182]. Livestock was thus added to the way of life in the wetlands, but did not replace traditional subsistence methods. Livestock herding increased the reliability of the food supply. This increased reliability may have enabled hunter-gatherers to schedule their land-use in such a way that specific places in the landscape could be used at specific times. This development probably paved the way for the adoption of crop agriculture[183].

Figure 3

From 4100 cal BC, remains of crop plants have been recovered at sites from the wetland area. The oldest remains were found at levee sites at Swifterbant[184]. Other sites with remains of crop plants are the Hazendonk (from c. 4000 cal BC onwards) and P14[185]. The wetland societies in this period were still residentially mobile[186]. Until recently, most researchers thought the wetlands were unsuitable for crop farming and the donken too small in size. Since residential mobility combined with crop agriculture has also been documented ethnographically[187], it was argued that grain was farmed in the coversand zones and transported in the ear to the wetland sites[188]. Evidence for an agricultural field recently came to light at Swifterbant S4, showing that limited crop cultivation did take place in the wetland zone[189].

The adoption of crop agriculture does not signify a wholesale "conversion" to a Neolithic way of life. Wild game and gathered plant foods continue to be important and many sites still function in a system of residential mobility. Sedentary settlements and domestic resources only became dominant during the Single Grave Culture[190].

The rich array of available resources probably resulted in farming methods not being obviously more productive than foraging in the wetlands. This suggests that the effects of biased cultural transmission did not result in the uptake of farming methods in this zone. The small size of the area available for agricultural fields likely made a logistically mobile way of life more productive than becoming sedentary, which would lead to the depletion of wild resources in the vicinity of sites. Moreover, the increased reproductive success of a less mobile way of life may have been offset in the wetlands by the fact that exploiting a wide array of resources results in lowered infant mortality and increased life expectancy[191].

However, the selected addition of pottery and livestock to the way of life practised in the wetlands over time would have led to certain advantages, such as a population increase. Pottery allows increased yields from (starchy) foods by cooking, increased storage and the preparation of weaning foods. Livestock may have buffered periods of shortage arising from hunting and gathering, not only by slaughtering animals, but possibly also by the consumption of blood and dairy. The timing of the spread of lactase persistence through European

182 Also see Louwe Kooijmans 2007.
183 Schrier 2009, 24.
184 Cappers/Raemaekers 2008; Out 2009.
185 Ebd.
186 Cappers/Raemaekers 2008; Amkreutz 2013a.
187 *E.g.* Gregg 1988; Politis 1996; Barlow 2006.
188 Bakels 1988.
189 Van Berg 1990; Huisman/Raemaekers 2014.
190 Louwe Kooijmans 1993a; 2007; Amkreutz 2013a.
191 *E.g.* Ludvico/Bennett/Beckerman 1991; Bird/Smith 2005; Hockett/Haws 2005.

Neolithic populations is debated[192]. However, there are indications of cheese-making during the LBK in Central Europe, suggesting that methods to make dairy digestible for non-lactose-tolerant populations were known[193]. During the early phases of neolithisation, these effects would have increased the reproductive success of families using these elements compared to households that did not. This would slowly increase the proportion of the societies that was sympathetic towards adopting Neolithic elements. Over time people in the wetlands also adopted the growing of crops. This was co-opted into what was still in many ways a hunting and gathering way of life, where an "extended broad spectrum economy" was practised[194].

During the process of neolithisation in the wetlands, the security and success of the traditional way of life was an important reason for wetland hunter-gatherers not to adopt a fully Neolithic way of life. The eventual changes in the subsistence economy resulted in increased reproductive success. Populations in the wetlands would have grown steadily throughout the transition of hunting and gathering to farming. Building from these processes, this in turn may have speeded up the process as increased population densities would lead to "packing"[195], and may have led to fissioning of communities[196] and decreasing territory size. This may have led to intensification of the exploitation of wild resources, thus depressing their availability, leading to increased reliance on agricultural subsistence methods. As such the importance of mobility slowly decreased. Sedentary settlements appeared after several centuries of incorporating farming practices. However, the exploitation of wild resources remains an important element of the wetland way of life. Stable isotope analysis of the skeletons of the site of Schipluiden (~3600 cal BC) for example shows that here marine foods accounted for a large proportion of the diet[197]. Moreover, faunal spectra continuing into the Bronze Age illustrate the continuing exploitation of game animals[198].

Supporting evidence

Some supporting evidence from other sources for the proposed scenario is available. aDNA analyses of interments at LBK cemeteries and interments from Mesolithic contexts have increasingly been performed. Although these studies yield much new information, integration with material culture studies is often still limited.[199] So far, the available data shows a significant influx of non-local individuals in the earliest phase of the LBK[200]. However, both the Mesolithic and the LBK lineages appear to be less frequent in modern Europeans than in the ancient samples, suggesting that later population movements altered the European genetic make-up[201].

We argue that females receive greater fitness benefits from adopting farming than males and would more readily marry into farming communities. This appears to be supported by DNA analysis. In modern Europeans, the frequency of Near Eastern lineages, associated with LBK-colonists, differs between the mitochondrial and the Y chromosomal DNA. Mitochondrial DNA is inherited through the female line exclusively, while the Y-

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192 Compare Itan *et al.* 2009 and Burger *et al.* 2007.
193 Salque *et al*. 2013.
194 *Sensu* Louwe Kooijmans 2007.
195 Cf. Binford 1983; 2001.
196 Cf. Soltis/Boyd/Richerson 1995; Shennan 2000.
197 Smits/Van der Plicht 2009.
198 Zeiler 1997.
199 Hofmann 2014.
200 Haak *et al.* 2005; 2010; Bramanti 2009; Deguilloux 2013.
201 Bramanti *et al.* 2009.

chromosome is only transmitted from males to males. In the Y chromosomes of modern Europeans, Near Eastern variants are more common than in the mitochondrial DNA. This suggests that hunter-gatherer females had more reproductive success than hunter-gatherer males[202]. The timing of this development in the study region is difficult to pinpoint, because no local aDNA studies are available. It appears that admixture of hunter-gatherers into central European LBK populations may have been relatively limited[203]. However, mtDNA analysis from later Neolithic sites suggests that hunter-gatherer females had entered Neolithic societies[204]. Finally, mtDNA analysis from modern Europeans suggests that over time the populations fused and hunter-gatherer and farmer haplogroups expand similarly from 4000 BP, suggesting fusion was achieved by then[205]. This is consistent with the model proposed here for areas outside the LBK core-settlement area, which was limited to the loess belt. After transitional phases, such as described for the coversand and the wetland zones of our study region, hunter-gatherers here were able to adopt farming practices on their own terms, without suffering periods of serious constraints on their reproductive success.

Stable isotope analyses of German and Czech sites have also been interpreted to show the assimilation of indigenous hunter/gatherers by incoming farmers in the loess zone. However, they do not allow for a ready distinction between non-local farmers migrating into the analysed settlement and non-local hunter-gatherers doing the same. Moreover, they show that in later phases, non-local women continue to enter LBK societies. This supports the hypothesis that hunter-gatherer women regularly married into the farming communities. In addition, isotopic evidence from a comprehensive study of Belgian Mesolithic and Neolithic skeletons suggests that by the Middle Neolithic the age of weaning had dropped compared to the situation in the Mesolithic[206]. This suggests that the interbirth interval had decreased. Unfortunately, no Late Mesolithic/Early Neolithic skeletons were available for study, so the exact timing of this development remains unclear.

Conclusion

We suggest that the long-term dynamics of the spread of farming can be explained as the result of evolutionary processes. Our contribution specifically introduces the role of mate choice on the part of females and/or their kin as a strong transforming force in specific situations, such as the situation presented by the southern coversand region in the study area.

The uptake of farming has different socio-political and reproductive consequences for hunter-gatherer males and females. Females are expected to prefer partners spending a lot of energy on provisioning the nuclear family. Males on the other hand are expected to prefer expending effort on maximising socio-political power and access to mating opportunities. When faced with farming societies, asymmetric migration of males and females normally ensues. Some females will marry into the farming society, while hunter-gatherer males generally do not, and farming females usually do not intermarry with hunter-gatherers. Within hunter-gatherer communities, female mate choice is expected to favour males expending effort in provisioning. This can act as a powerful stimulus for the uptake of agricultural subsistence methods. In situations where subsistence methods are transmitted vertically, small

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202 Chikhi *et al.* 2002; Richards/Schulting/Hedges 2003; Dupanloup *et al*. 2004; Balter 2005; Balaresque *et al.* 2010; Rasteiro/Chikhi 2013.
203 Brandt *et al.* 2013**.**
204 Bollongino *et al.* 2013, 481.
205 Fu *et al.* 2012.
206 Bocherens/Polet/Toussaint 2007, 20.

differences in the reproductive success associated with farming and foraging may lead to the gradual increase of farming populations relative to foraging populations.

In our study area, the contrast between the subsistence strategies favoured by males and females was largest in the coversand area. Females marrying males prepared to experiment with taking up agricultural subsistence methods would be reproductively more successful than females marrying males favouring big game hunting. In the wetlands, adopting novelties such as livestock herding increased reproductive success of the adopters. However, due to the resource rich environment the wetlands offered, the differences in reproductive success would be much smaller. This led to a much longer period of transitional economies. The loess zone is more unsuitable for hunter-gatherers and very suitable to LBK farming methods. Both males and females are thus expected to favour the adoption of farming over continued foraging. Differential reproductive success would then lead to the crowding out of remaining hunter-gatherers.

The arguments presented here do not discount explanations on changing behaviour offered by models based on individual choice or agency. The explanation we propose is an explanation focussing on the ultimate, evolutionary causes of behaviour. These explanations do not exclude each other, but are explanations of the same phenomena at different levels[207]. The decisions to take up new subsistence methods, or to marry into a farming community were not always made with fitness benefits in mind. However, choices with positive effects on reproductive fitness are more likely to be repeated in following generations. The predominantly vertical transmission of subsistence methods would lead to increased size of farming populations in areas where farming methods and the geological substrate led to increased productivity of farming versus foraging. Similarly, the decision to marry into farming societies by hunter-gatherer females (or their families) may have been made to gain access to Neolithic resources or material culture items[208]. However, in the long term such decisions increased the reproductive potential of farming societies, while those of foraging societies decreased, leading to incentives for forager males to experiment with food production. The demographic consequences of individual choices were probably unforeseen. Nevertheless, increasing population size and concomitant fissioning of societies, may have stimulated the adoption of farming subsistence methods by ever more people as a way to ensure sufficient returns from subsistence activities. Similarly, the increasing use of the environment for agricultural purposes may have had a self-reinforcing effect, diminishing the returns of hunter-gatherer subsistence methods, thereby stimulating the increased use of the environment for agricultural purposes.

The combination of archaeological, ethnographic and genetic evidence examined using evolutionary theory suggests that female sexual selection was an important factor driving the process of neolithisation. We propose an evolutionary approach, considering the specific configuration of geological, social and historic circumstances, can be used productively to explain different neolithisation trajectories in different areas. Therefore, reproduction and the female role therein seem a crucial factor in determining whether societies decide to hunt or to plough.

Acknowledgements

207 See Tinbergen 1963.
208 See Schulting/Richards 2001, 336-337 for a hypothesis on neolithisation based on marriages between hunter-gatherers and farmers to form alliance networks.

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