



## Review

# A Time to Sow, a Time to Reap: Modifications to Biological and Economic Rhythms in Southwest Asian Plant and Animal Domestication

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**Abstract:** This paper reviews changes to lifecycle temporality in Southwest Asian plant and animal domestication, exploring their relationship to long-term processes associated with ancient and contemporary globalization. We survey changes under domestication to the timing of seed dispersal, germination, vegetative growth, flowering and maturation in wheat and barley and to birth, reproduction, lactation, wool production and death in sheep, goats and cattle. Changes in biological temporality among domesticates are ultimately related to globally increasing production intensity, geographic diffusion, and agricultural diversity associated with cultivar/breed evolution. Recently, however, increasing crop production intensity and geographic diffusion are accompanied by declining agricultural diversity worldwide. Similar processes are apparent in contemporary economic and cultural globalization, suggesting that long-term agricultural developments might be viewed as a subset of globalization. Moreover, the origin of certain features of contemporary globalization may be traced back to the beginnings of plant and animal domestication. Thus, while biologists since Darwin considered domestication as a model for the study of evolution, we suggest that domestication may also offer a model for the study of globalization.

**Keywords:** domestication; globalization; phenology; seasonality; archaeobotany; archaeozoology



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## 1. Introduction

Timing is everything. That this is true of agriculture may be obvious, but not trivial. Changes in human subsistence modes and methods since the origins of agriculture have significantly affected biological rhythms in human ecosystems. One profound illustration of this point is research demonstrating that human gut microbiome composition is significantly more seasonal among contemporary hunter-gatherers than residents of industrialized regions [1]. Biological rhythms of domesticated plants and animals have also been undergoing modifications since the onset of plant cultivation and animal management. We highlight this aspect of domestication by reviewing changes in plant and animal biological rhythms under domestication, focusing on the best-studied and most intensively farmed and herded of Southwest Asian domesticates: wheat and barley, sheep, goats and cattle. As a means to reflect on their relevance to contemporary life in long-term perspective, we relate these plant and animal lifecycle changes to the ‘domestication as globalization’ paradigm [2]. This approach views plant and animal domestication as initiating a path of intensification leading up to globalization. In focusing on a few Southwest Asian domesticated cereal and livestock species, we inevitably leave out entire classes of domesticates from across the globe. In some cases, such as tree-fruit domesticates in this region, profound

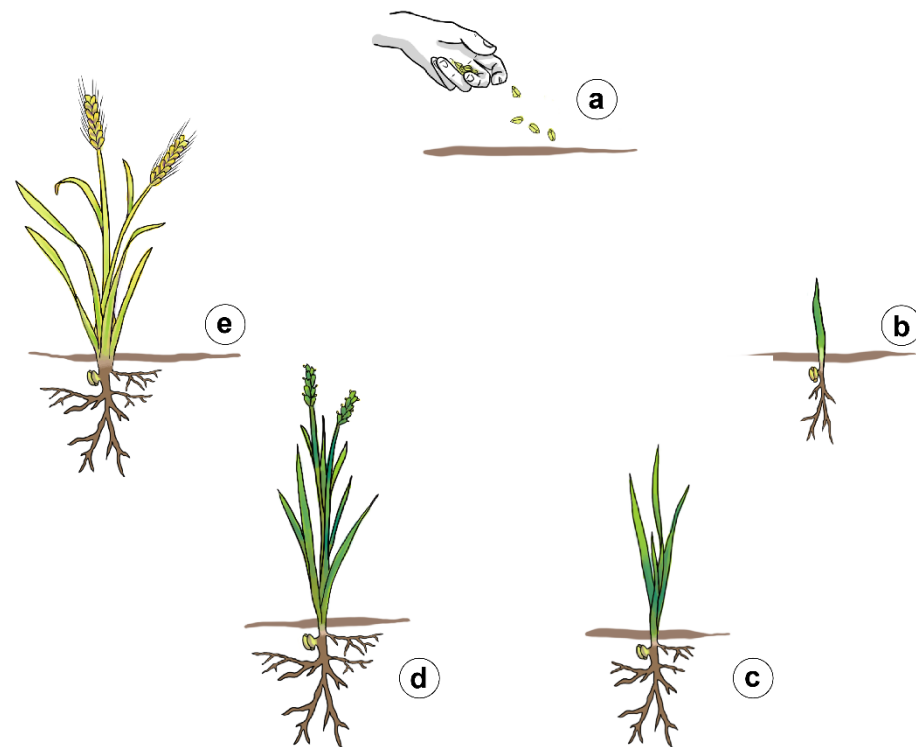
life cycle changes under domestication may be viewed as part of the same historic path of agricultural intensification. In other cases, crop histories may challenge this reconstruction. Indeed, the diversity of economic and social systems in the ethnographic and archaeological record argues against a straightforward directional trajectory leading to globalization as we know it today. Yet, in long-term perspective, certain globalizing processes associated with production intensification, geographic diffusion, and their effects on agricultural diversity have also affected timing in the lifecycles of domesticated plants and animals. We offer a window on such processes using some of the most successful domesticates as our test case.

In order to discuss domestication, biological rhythms, globalization and their interrelationships, defining basic terms is necessary. *Domestication* is a process that produces genetic changes in some plant and animal species resulting from their close relationship with humans, including increasing reliance on humans for survival and reproductive success, and adaptation to new, human-mediated habitats [3,4]. Changes to reproduction and dispersal, reductions in toxins and changes to organism or organ size are examples of traits often associated with domestication, or the ‘domestication syndrome’ [5,6]. We adopt the view that domestication is an ongoing process [7], which includes initial domestication and subsequent crop/stock improvement of plant and animal domesticates. Historically, genetic improvement was accomplished through selective breeding, while today genetic engineering is also part of this process. *Intensification* is an even broader process, leading to increased economically desired output over a required and otherwise limiting input, often at the expense of other inputs. Thus, intensification of agricultural production generally refers to the increase in yield per unit of land—and it is usually accomplished by additional energy input in labor and technology. Intensification of certain plant and animal species’ exploitation is a precursor to domestication, as is *management* of such species or their ecosystems by corralling animals or burning forest cover to encourage growth of wild annuals, for example. To distinguish between the raising of domesticated plants and animals, we use the terms *agriculture* and *pastoralism*, respectively, although we also use *agriculture* and its derivatives in collective reference to both. Through agriculture and pastoralism, domestication has enabled significant intensification in the production of food, fiber, and other useful goods worldwide. It has also led to the wide diffusion of domesticated plants and animals, also known as *domesticates*, across multifarious habitats, resulting in wide global *diversity* of crop varieties and animal breeds. This includes both phenotypic diversity of character traits long appreciated by farmers and breeders, and genetic diversity, which research is still beginning to reveal and exploit. For ease of exposition and brevity, we do not classify humans as domesticates. Characteristics of domesticates’ life cycles—including birth and germination, growth, reproduction, and death—display agriculturally meaningful diversity exploited by farmers and herders. Our focus is on changes to the timing of lifecycle activities, or biological rhythms, at the population level, the study of which is *phenology*. Our goal is to explore how changes to biological rhythms following domestication are related to production intensity, geographic diffusion and diversity—which we identify as key aspects of globalization [2]. Our discussion of agricultural diversity makes use of the concept of *landraces*; *landrace* has been defined as a “dynamic population or populations of a cultivated plant that has historical origin, distinct identity and lacks formal crop improvement, as well as often being genetically diverse, locally adapted and associated with traditional farming systems” [8]. Finally, *globalization* is widely conceived as a process of increasing worldwide interconnectedness in economic, cultural, political, and environmental spheres [9].

## 2. Cereals

As densely growing annuals, cereal populations can undergo genetic changes rapidly via selection. Thus, it has been estimated that following deliberate cultivation of wild wheat, full morphological domestication, i.e., spikelet non-shattering, could have evolved within 20–200 years [3]. However, the current archaeobotanical consensus view is that this process actually took millennia [10–17]; but see [18–20]. Over this time scale, various other

traits related to seasonality have been selected for, affecting different stages of the plant life cycle (Figure 1).



**Figure 1.** Key stages of the cereal lifecycle: (a) dispersal, (b) germination, (c) vegetative growth, (d) flowering, and (e) maturation.

### 2.1. Dispersal

At a very basic level, the primary domestication trait of cereals, non-brittle rachises, profoundly affected timing in the life cycle of both these plants and their human consumers. In wheat and barley, among other grasses of the Triticeae tribe, grains are held by a spikelet, which contains the grain encased in bracts (lemma and palea) and glumes. The spikelet base is a rachis segment that attaches to other rachis segments along a central spine-like axis, i.e., rachis, comprising the spike or ear. In wild cereals, such as wild wheats (*Triticum turgidum* subsp. *dicoccoides*; *T. monococcum* ssp. *boeoticum*) and barley (*Hordeum vulgare* ssp. *spontaneum*), spikelets detach or disarticulate from the central rachis, forming distribution units, which disperse sequentially after ripening, from top to bottom. In domesticated wheats (e.g., *Triticum turgidum* ssp. *durum*; *T. aestivum*) and barley (*Hordeum vulgare* ssp. *vulgare*), spikelets do not disarticulate upon ripening and may be broken by threshing [2,21]. Non-brittleness is conferred by mutations in one gene in einkorn wheat (*Btr1*), one of two genes in barley (either *Btr1* or *Btr2*), and two genes in emmer wheat (*Btr1-A* and *Btr1-B*) [22–25].

Pre-domestication wild cereal gatherers would have had to arrive at wild stands just before dispersal, prior to full ripening, in order to harvest intact ears [3], whereas ground collectors [26,27] would have had to arrive between the time of dispersal and consumption by other species such as insects and fungi. Non-brittle rachises enabled collection of the entire ear and field, after full ripening and in one go, thereby transforming the timing of harvesting. As a result, human labor must have replaced dispersal and competition with other organisms as the primary limiting factor affecting harvest season length. This also conferred greater flexibility of harvest time since a field of non-dispersing grains is a type of storage in regions without summer rain. Thus, in Israel today, the primary limiting factor affecting the timing of harvesting is the availability of combine harvesters, whose work is

spread over several months. The combined efficiency and flexibility of reaping time must have had significant implications for production intensity and surplus generation, as has long been appreciated [28].

## 2.2. Germination

Alongside the loss of rachis fragility, the loss of seed dormancy—during which seeds will not germinate even under ideal conditions—is considered a defining trait of domesticated plants [3,29,30]. This is because loss of seed dormancy directly increases dependence on humans for the continuation of the life cycle. In modern agriculture, germination rates of 95% of seeds sown are common [30]. Incidentally, uniform germination is also important for malting, enabling efficient production of malt-based products such as beer and whiskey. In the wild, germination rates are significantly lower as wild species have evolved to overcome multi-annual anomalies in environmental conditions. For example, in wild emmer wheat, for every pair of grains in a spikelet (dispersal unit), only one, the thicker upper grain, will germinate during the first rainy season following maturation [31]. Moreover, this is not simply physical dormancy resulting from seed coat and glume structure (which also exists in cereals) but is genetically determined physiological dormancy evolved as a complex bet-hedging mechanism [31–33]. No such mechanism exists in domesticated cereals. Dormancy would have been selected against by shifting cultivation because non-germinating plants would not be harvested [29], providing an example of genetic changes to phenology brought about by domestication. Genetic studies identifying the *QGD-4BL* locus of the wheat genome are consistent with the expectation that loss of seed dormancy was selected for relatively early in wheat's domestication history [33] (see also Fuller and Allaby 2009 on the *VP1* gene [29]), as are studies of the *Qsd1* gene in barley [34]. Yet, this is not the end of the story, as selective pressure for more rapid and uniform germination increases susceptibility to pre-harvest sprouting. In the absence of delayed germination mechanisms, pre-harvest sprouting may occur among grains still on the mother plant, usually in response to rain and causing substantial economic loss [35]. Therefore, modern wheat and barley crop improvement is seeking to selectively re-introduce seed dormancy [36]. Thus, human activities affecting the timing of germination and maturation continue to be a part of the long-term domestication history of cereals.

Human activities are also key to making the most of phenological genetic and environmental limitations, as exemplified by decision-making concerning when to sow. In traditional southern Levantine dry farming, cereals are usually planted after the first soil-drenching rain. This helps ensure that planted grains have sufficient moisture for germination and the initial stages of vegetative growth. If grains are sown earlier, a light rain followed by a dry spell could induce germination and subsequent plant death. However, in modern mechanized farming in the region, sowing is performed on dry fields because they are more tractor friendly. These examples represent different responses under different farming regimes to the relationship between cereal sowing time and water uptake efficiency [37].

Interestingly, grain size in wild barley (*H. vulgare* ssp. *spontaneum*) has been shown to correlate with time of germination and seedling growth rate, as well as number of seeds produced and drought tolerance [38–40]. Grain size also varies according to position along the cereal ear, such that the upper and lower 'tail grains' are smallest and 'prime grains' in the middle of the ear are largest [41]. However, there is ample evidence for increased mean wheat and barley grain size, particularly thickness, following domestication [21,42,43]. It stands to reason that the trend to increased grain size could have also affected uniformity of germination and plant growth. Indeed, a genetic locus in wheat has been identified (*QGD-4BL*) which favors spikelets with seeds of uniform size and synchronous germination [33].

## 2.3. Vegetative Growth

Germination culminates with the development of the first root (from the radicle) and leaf (from the coleoptile), followed by tillering, which is the growth of side leaves,

or tillers. It co-occurs with the development of side or axile roots [44] and is followed by stem extension in which plant height increases significantly but the number of tillers (side shoots) does not. Stem elongation culminates in heading, when the ears form and become visible and which is considered part of the reproductive stage in some phenological classifications [45]. Together, these pre-flowering stages make up the greater part of the wheat and barley life cycle.

According to Harlan et al. [46], more determinate growth of individuals in a wheat population (field) is an adaptation to the cycle of harvesting and planting harvested seeds; this includes synchronous tillering and uniform whole-plant maturation. According to Evans [47], shortening these stages through crop improvement is a method of increasing the number of croppings in the tropics, attaining, for example, 3–4 rice croppings per year. In wheat and barley, spring-habit cultivars (see below, *Flowering*) are marked by a shorter duration from germination to flowering and are therefore often preferred in intensive farming systems to hasten field turnover. As with the loss of seed dormancy, this manipulation of lifecycle length can sometimes be too much of a good thing. From the onset of stem elongation, and especially heading, cereals become progressively more sensitive to weather damage, such as frost [48] (see also the Biblical example regarding the plague of hail, Exodus 9:31–32). Interestingly, speeding up the vegetative growth stage, as in spring-habit cereals, may increase the risk of frost damage in temperate regions because heading occurs earlier in the season [49]. Delayed sowing can reduce this risk, but with potentially adverse effects for grain filling, ripening and yield [50].

In many traditional farming regimes, stem elongation is more than an intermediary stage leading to grain formation; it directly affects straw as a secondary product of cereals. Traditional uses of long straw range from roof thatching to basketry. Increased plant height is also conducive to weed suppression, which is especially important in pre-modern and organic cultivation [51]. However, modern high-grain yield cultivars developed over the past 150 years, alongside modern development of herbicides, tend to be short [52]. The short stature of semi-dwarf wheat cultivars is mainly controlled by ‘reduced height’ (*Rht*) genes—particularly *Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*)—which decrease the plant’s ability to respond to gibberellic acid. Selection for these alleles in modern crop improvement is part of a wider effort to prevent lodging and increase harvest index (i.e., the proportion of grain yield to above-ground biomass), which also targets flowering time among other traits [37]. Although *Rht* genes had yet to be identified at the time, they were selected for in the breeding programs which developed high-yielding semi-dwarf cultivars adapted to Latin American and South and Southeast Asian climates, for which Norman Borlaug won the Nobel Peace Prize in 1970 [53]. The history of these genes’ global trajectory is fascinating. Apparently, early semi-dwarf varieties were cultivated in Korea by the 3rd–4th centuries CE, reaching Japan in the Korean–Japanese war of the 16th century [54,55]. From Japan, they were targeted by Italian wheat breeders in the early 20th century. After World War II, these high-yielding cultivars were exported to the former Yugoslavia and central Europe. Around the same time, Japanese dwarf-wheat samples reached the U.S. and were incorporated into the breeding program behind the modern ‘Green Revolution’. By the late 1990s, the original *Rht* genes are estimated to have been incorporated in over 70% of global cultivars [56].

In ancient and traditional agriculture, the main activity involving human labor during vegetative growth is secondary tillage, such as hoeing, to reduce weed growth during the tillering stage. Tillage appears to affect the composition of weed flora even in the archaeobotanical record, as does crop lifecycle timing [57,58]. However, as far as we are aware, secondary tillage has not been a significant source of selective pressure on cereal phenology in the way that harvesting and sowing have been. The length of the pre-flowering crop cycle appears to be governed genetically and physiologically by the timing of the onset of flowering.



#### 2.4. Flowering

Flowering at the right time is critical for a plant to complete its lifecycle and for maximizing yield and quality in agronomically important plants such as cereal crops. The optimal flowering window in cereals is determined by a balance between the water required during vegetative development and that required during grain formation and filling, as well as the declining severity and frequency of frosts in middle latitude temperate zones [59]. If a cereal plant flowers too early, flowers may be at risk of frost damage. If flowering occurs too late, higher temperatures and a water deficit may mean that grain formation and filling will be restricted [60]. In wheat and barley, flowering occurs at the optimal time primarily through its regulation by genes involved in vernalization requirement (*VRN* genes), governing response to a period of cold, and photoperiod response (*PPD* genes), associated with changes in daylength (reviewed by Distelfeld et al. [61]). This tight regulation determines the initiation of flowering at the switching of the shoot apex from producing leaf primordium to spike primordium. A third class of genes known as earliness per se (*EPS*) genes affects relatively minor variations in flowering time once requirements of vernalization and photoperiod are satisfied [62].

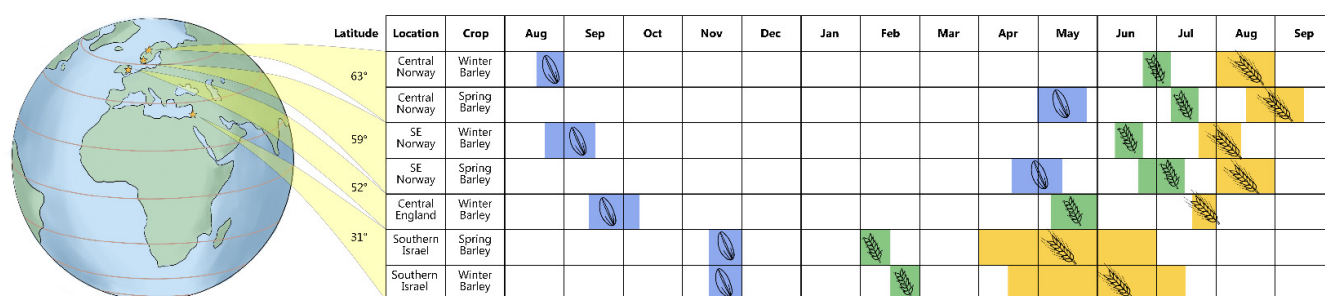
As agriculture spread out of Southwest Asia, alterations in flowering time pathways enabled cereals to be successfully cultivated in novel environments [63,64]. Southwest Asia typically has hot, dry summers and cooler, wetter winters. Flowering in wild wheat and barley is primarily triggered by a period of cold (vernalization requirement) in combination with days lengthening in the spring (photoperiod sensitivity)—traits which apparently reflect the ancestral condition [65]. Such controls of flowering time in winter cereals help protect sensitive floral tissues from freezing temperatures and enable flowering and seed set to occur before the summer drought. However, these flowering time triggers became increasingly maladaptive to domesticated cereals as farmers brought their cultivation out of Southwest Asia further north [63]. The evolution of ‘spring’ cereals, produced as a result of variation in *VRN* genes, and photoperiod sensitive/insensitive variants of *PPD* genes, has aided the worldwide spread of wheat and barley cultivation and their expansion into new areas, especially northerly latitudes [66] and higher altitudes [63]. Delayed flowering of spring-sown varieties is an advantage in higher latitudes, as it allows the plants to build biomass during the long moist summer and to flower later in the growing season, leading to better yields. Variants of the photoperiod response gene *PPD-H1* in barley [67], for example, show a marked latitudinal distribution of the photoperiod responsive and non-responsive alleles of *PPD-H1*, illustrating the importance of this gene in environmental adaptation [68,69]. Analysis of allelic variants of the *PPD-H1* gene in wild and cultivated barley demonstrated that the mutated forms of these genes exist in some wild barley populations [68]. This indicates that these wild progenitors may have been the source of cultivars with these mutations rather than the mutations being selected for in cultivated populations outside the range of wild barley.

It must also be noted that the genetic control of flowering time in cereals is complex and that the traditional classification of winter versus spring cereals has been oversimplified. Different genetic systems interact with each other and the environment. In modern crop improvement, flowering time is increasingly seen as a continuum, as local breeding programs select for cultivars optimally adapted to their growing environment (Figure 2). Such breeding programs also seek to produce varieties with differential flowering times that are resilient to future climate change [70].

Flowering is preceded by heading, in which flower heads form and become visible. Extending the length of the heading stage—which determines the number of fertile florets, directly affecting the final number of grains—has been proposed to increase yield potential so long as flowering is not delayed [71,72]. The timing of heading is under strong but complex genetic control associated with a variety of genes on different chromosomes [72]. Targeting these genes in modern crop improvement is still in its infancy.

Meanwhile, the agency of prehistoric farmers should also be recognized as contributing to the success of cereals’ expansion into harsher latitudes and altitudes. For example,

prehistoric garden beds showing evidence of ridge and furrow maize cultivation in the Great Lakes region of the USA are at the northern limits of maize cultivation in an area in which a short growing season was a constraint. The beds are thought to have served as a frost-avoidance mechanism to protect young seedlings from a late spring frost or an almost ripe crop from an early autumn cold spell [73]. This example suggests ancient manipulation of growing conditions by changing the local environment, while indicating the complex interplay of human agency and environmental conditions influencing crop evolution under domestication.



**Figure 2.** Spring and winter barley phenology at different latitudes: sowing, flowering and post-maturation harvesting. Under modern cultivation in high latitudes, winter habit cereal varieties are sown and germinated before the frost of winter, completing their lifecycle in spring and summer; spring habit varieties are sown after the frost of winter and rapidly complete their lifecycle slightly later than winter varieties. In lower latitudes, where winter frosts pose little concern, the offset between winter and spring varieties is minimal; indeed, spring varieties are often preferred for their shorter lifecycle. In ancient cultivation, spring habit varieties evolved together with the spread of barley (and wheat) to higher latitudes and altitudes. Approximate timings listed here represent a typical year in each locale but are often offset by 2–3 weeks depending on the timing of rainfall.

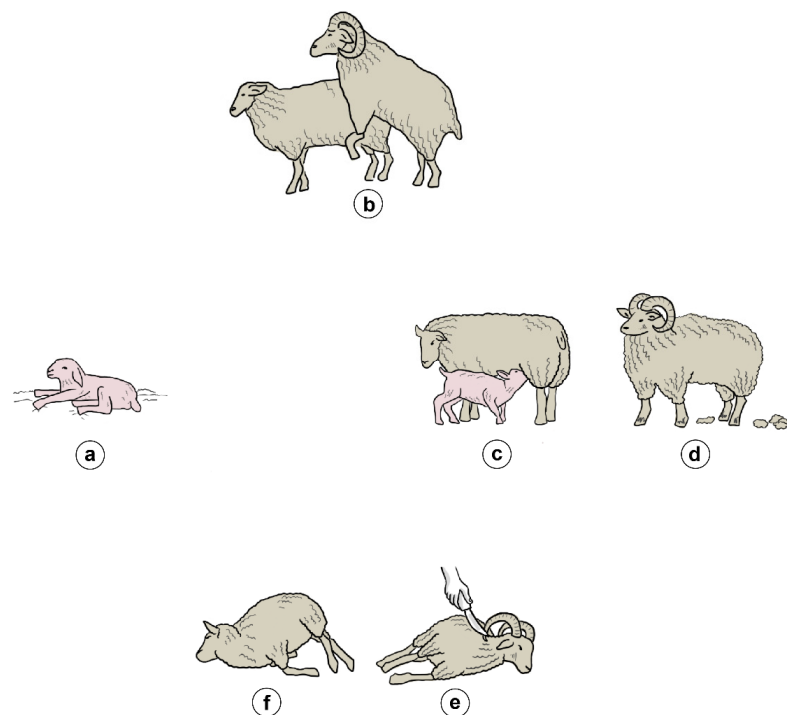
### 2.5. Maturation

Grain filling is the stage in which nutrients from the plant are remobilized into the developing grain. Grain filling is followed by ripening, which is part of senescence, when the entire plant turns from green to amber and dries out [74]. Uniformity of grain ripening is considered a key domestication trait as it improves harvest efficiency and would have been selected for by early sickle harvesting [21,46,75]. Uniform ripening followed by timely harvesting is especially important in regions experiencing rain in the harvest season and has been increasingly selected for in mechanized farming regimes. Unfortunately, current knowledge of the genetics governing maturation is relatively limited. The trend in modern crop improvement has been to delay senescence for better grain fill [47,76]. The delayed senescence of modern wheat is caused by fixation of a null mutant of the *Gpc-B1* = *NAM-B1* gene, with adverse effects on protein, iron and zinc content [76–78]. Asplund et al. [79] studied this gene in ca. 150-year-old specimens of historic cultivars. They discovered the ancestral allele in only some historic specimens, indicating that fixation of the null mutant was not ubiquitous 150 years ago. This suggests that delayed senescence might constitute a genetic lifecycle change brought about only in modern times.

### 3. Livestock

Sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos taurus*) were among the earliest Southwest Asian domesticates, as well as the most historically utilized in the region up to the present day. A major functional difference between caprines (also known as ovicaprids or sheep/goats) and cattle in their post-domestication history in Southwest Asia is that the former were bred for their meat, milk, and fleece, while the latter contributed more to agricultural production as work animals. In Southwest Asia, cattle are characteristic of agricultural society and rarely herded by nomads of the region owing to high water requirements and low tolerance of saline vegetation; in African savanna regions by contrast,

cattle pastoral nomadism geared at milk and meat is common [80]. Sheep and goats were the main animals herded by pastoral nomads of the Ancient Near East. Sheep produce more marketable goods but require higher-quality pasture, more water, and larger herds as risk-buffering to account for slower rates of reproduction. As a result, seasonal transhumant cycles are more closely linked with intensive sheep breeding, which, in turn, is motivated by market demand. Goats, on the other hand, can exist in smaller numbers on circumscribed territories and with low-quality food, and therefore were typically kept by farmers who did not synchronize maximally productive pastoral and agricultural activities. Nonetheless, sheep and goats are often herded together in mixed herds which enables some diversification of products (e.g., goat hair and sheep's wool), buffering their differential susceptibility to climatic anomalies and natural disasters, and use of 'lead goats' to set the pace in a primarily sheep flock [81]. Pastoral nomads tend to follow organized seasonal migratory patterns, based on availability of rangeland resources [80,82]. Seasonal availability of pasture affects more than nomadic migratory patterns, however, and sedentary livestock production may also be highly seasonal. Ultimately, biological rhythms in domesticated livestock are influenced by the interaction of environmental constraints and human economic motives. Economically significant aspects of livestock phenology include the timing of birth and reproduction, lactation, wool production, and death (Figure 3).



**Figure 3.** Key stages of the sheep lifecycle: (a) birth, (b) reproduction, (c) lactation, (d) wool growth and (e,f) death.

### 3.1. Reproduction and Birth

The timing of livestock reproduction is governed by the period of sexual receptivity and fertility known as *estrus* with respect to females, the *rut* or *rutting period* more generally, and *tupping* in sheep. This timing of mating directly determines the timing of birth and the onset of lactation. Although mating throughout the year does not always translate to continuous birthing [83], we discuss the two together since reproduction is a prerequisite to birthing. The very act of herd management introduces the possibility of controlling livestock reproduction by humans, intentionally or not, by influencing access to food and mates. Higher selectivity of mates is created by castration and culling. Human population migrations introduced livestock to regions with photoperiodicity different from



their wild progenitors' natural range, which would have affected the sheep and goats' reproductive rhythms. Seasonal fluctuations in the availability of pasture—which are marked in Mediterranean climate zones—directly affect optimal lambing seasons both in the wild and under domestication.

Observations of wild, primitive and modern domesticated sheep and goat breeds indicate that domestication has led to the expansion of livestock reproduction seasons, which are still somewhat restricted [84,85]. Sheep and goats are 'short-day breeders'; they become sexually active in response to decreasing day length in the fall and become sexually inactive in response to increasing day length in the spring. This indicates that rutting is a photoperiod response, albeit triggered by additional factors [84,86,87]. The photoperiod response is governed by melatonin secretion regulated by the pineal gland [88]. Breeding seasonality varies not only by climate and photoperiod regime, but also with nutrition, heredity and breed [84].

Cattle reproductive seasonality, by contrast, appears to be mainly associated with nutrition. Feral cattle have been observed exhibiting calving patterns corresponding to the seasonal availability of food on Amsterdam Island in the Indian Ocean [89]. The same is true for Scottish Highland cattle kept in the Rhine Taunus Nature Park, Germany [90] among other feral populations in Europe [91]. This singles out as exceptional the feral herd of Chillingham, England, which does not exhibit calving seasonality but which inhabits well-endowed pasture year-round [92]. Regardless, a wide variety of factors other than nutrition have been observed to affect cow estrus onset and mating. These include social interactions—social rank, estrous synchronization, social facilitation and sexual stimulation; management conditions—hormone treatment, corralling and animal density, noise, stable flooring quality and ceiling height, expectation of feeding and milking; environmental factors—weather, ambient temperature, day length and photoperiod; age and physiological status; genetic factors associated with different breeds; and presence of a bull [93].

In ancient and traditional Southwest Asian sheep and goat herding, late autumn and winter comprise the ideal birthing seasons, as this period synchronizes economic needs with ecological availability of rangeland resources. In a meat-oriented or multi-purpose flock, culling is desirable once males reach peak weight relative to food intake, generally at about 4–6 months. Additionally, where grazing resources are scarce, culling at or just after the peak season of rangeland productivity may be necessary to ensure herd survival during the low season. In Southwest Asia, these two needs may be synchronized by late autumn–winter births and spring culling (on culling see below, *Death*). One advantage to this timing scheme is that lambs born in autumn will have grown enough wool to be sheared (or plucked, see below, *Wool growth*) by the spring shearing, as indicated in Ancient Near Eastern texts [94]. Moreover, under this regime pastoralists' peak rangeland needs—for herds with cohorts of large juvenile (3–6-month-old) kids and lambs—will conveniently coincide with peak rangeland productivity in February–April. The challenge becomes surviving the 'hunger gap' of late autumn and early winter when rangeland food resources are at their lowest, which can be met by foddering.

Traditional pastoralists may actively control mating times to ensure lambing in the preferred season [95]. Traditional pastoralists in Cyprus reported that most sheep and goat births occurred in autumn and early winter, particularly October–January [96]. Among traditional Negev Bedouin, the preferred lambing season is October–November. Known as *badria*, meaning 'early', it can extend through December [97,98]. Among the Jabaliyah tribe of Sinai, whose flocks are dominated by goats grazing on poorer and higher-altitude rangelands, births are planned for late December to February, so that goat kid growth coincides with increasing rangeland biomass [99,100]. Among traditional Shahsevan pastoral nomads of northwestern Iran, the main lambing season was from November to February [101], and among the Lurs of Luristan, from late December to early March [102], (see also [103,104]). The combined range of primary lambing seasons in traditional Southwest Asian pastoralism (October–March) reflects regional microenvironmental climatic differences, including those related to latitude and altitude [105]. Similar considerations relating

pasture availability to lambing season apply in other regions despite different climatic regimes, such as in parts of Sudan where the rainy season is March–August [106].

Ancient Near Eastern herding contracts suggest that most births occurred in winter [107]. Nuzi documents from the later 3rd millennium BCE, Mesopotamia, indicate that peak lambing season was in autumn, equivalent to October–November [94]. Nearly contemporary Ur III administrative texts from the Puzriš-Dagan livestock center also exhibit highly seasonal reproduction and birth, which apparently peaked in August–October and January–March, respectively [104].

An expanding database of stable oxygen isotope ratios ( $\delta^{18}\text{O}$ ) incrementally measured from archaeological livestock tooth enamel hints at a process of expanding birthing seasons. Concerning sheep and goats, this research indicates a restricted lambing season for 8th millennium BCE Neolithic (PPNB) Tell Halula in the middle Euphrates Valley, modern Syria [105]. The identified 2.5-month lambing season at Tell Halula is similar to that of wild mouflon, and some traditional pastoralists' sheep populations in the region still maintain a restricted season [105]. In roughly contemporary Cyprus (8th millennium BCE, PPNB), a wider lambing season was deduced from enamel isotope data, in which the main period roughly corresponds to late autumn–winter as is still preferred by traditional Cypriot pastoralists. By contrast, sheep/goat enamel isotopic analysis from 8th–7th millennium (7400–6200 BCE) Çatalhöyük, Anatolia, indicates maintenance of the same restricted birthing season as local wild mouflon [108]. Full-fledged lambing de-seasoning is first evident by the 6th millennium BCE in southern France [109]. This contrasts with other European Neolithic sites, which generally exhibit a 3–4-month lambing season—longer than the wild mouflon but shorter than many traditional European breeds [110–115]. In later periods, tooth enamel isotope data indicate further expansion of birthing seasons to include, for instance, 80% of the annual cycle at Late Bronze Age (1500–1100 BCE) sites in the Tsaghkahovit Plain, Armenia [116].

The relative agreement between ancient and traditional Southwest Asian herds' primary lambing season contrasts to that of sheep and goats' wild progenitors. Spring is the primary birthing season of wild sheep (*Ovis orientalis*) and goats (*Capra aegagrus*) [117,118]. In the wild, concealed solitude, relative warmth, dryness, and abundant food are what post-partem ewes and does need most [118,119], making spring birthing ideal in Southwest Asia. Thus, human manipulation has modified the timing of life's beginning for domesticated livestock. Birthing seasons, reflecting different temperature, photoperiod and rangeland resource patterns, are often associated with latitude and altitude, as well as human cultural and economic variables [84]. As an example of the latter, synchronized lambing in meat-oriented production systems may lead to seasonal fluctuations of meat prices by affecting the seasonality of slaughter [120]. To take advantage of this situation, out-of-season lambing is a common strategy in modern livestock rearing [121], which employs techniques ranging from artificial lighting to gene editing in overcoming reproductive seasonality.

For cattle, the seasonality of reproduction and birth was conceivably overcome early on through foddering, but collecting empirical evidence for this process is still a work in progress. The latest incremental tooth enamel analyses suggest that seasonal calving was still the norm for domesticated cattle herds in prehistoric Europe, although notable exceptions include Linearbandkeramik (LBK) sites of the latter 6th millennium (ca. 5500–4900 BCE), and two Early Bronze Age (ca. 2000 BCE) sites in Britain [91,122,123]. Year-round calving was also identified at the 1st millennium CE British Iron Age site of Pool in Orkney [124]. Unfortunately, the available data do not enable disentangling climatic and cultural factors affecting calving aseasonality, but provisioning of winter foddering would likely have been necessary [91]. Such provisioning was apparently met through forest pasturing by LBK societies [125]. Year-round cattle breeding would have enabled a constant supply of raw milk.

An additional strategy associated with birthing temporality used by modern livestock breeders is to increase calving and lambing rates. In traditional pastoralism, female animals

did not usually give birth more than once a year. Biennial lambings have been observed in different regions, but some traditional pastoralists limit lambing to once a year to reduce mortality in preferred ewes [101,106]. However, modern ‘accelerated lambing systems’ employ environmental, nutritional, behavioral and hormonal interventions to increase lambing rates. The most common accelerated system involves lambing every eight months, or three times in two years, but four and five lambings in three years, and even twice in one year are well-documented (summarized by deNicolo 2007, pp. 13–14 [126]).

Yet another aspect of biological rhythms related to livestock birth is the age at which females first give birth. This may be governed by a combination of innate biological limits to sexual maturity, differences among breeds, herd size and structure, and human-induced preventive measures. This results in wide ranges observed among different pastoralist groups in the onset of mating and birth rates more generally [106]. In the Darfur region of western Sudan, a significant difference was reported between migratory and sedentary cattle herds in the proportion of heifers bearing calves by age four [106]. Meanwhile, cattle owners themselves claimed to have witnessed a rise in age at first calving from 3–4 years to 4–5 years in this region [106]. Calving in feral cattle under 2 years of age has been observed but is rare [92]. In 3rd millennium BCE Umma, Mesopotamia, cattle were classified by age brackets including 0–6 months, 6 months–1 year, 1–2 years, 2–3 years, and adult [127]. This must at least partially reflect the greater value associated with sexual maturity, in addition to differential foddering needs and traction power.

### 3.2. Lactation

Milk has long been an important secondary product of livestock in Southwest Asia—at least since the Neolithic period [128–133]. Preservation techniques such as fermentation, churning and cheesemaking allowed nutritional benefits to be enjoyed beyond immediate, direct consumption of whole milk, and to be more digestible to lactose intolerant people [134–136]. In milk production systems, the timing of lactation is a key issue, which includes the onset of lactation in individual cows or caprines and its duration—factors affecting the continuity of milk supply so central to intensive systems. Today, refrigeration has facilitated the demand for whole milk and dairy products while modern dairying has enabled supply to keep pace. Yet, seasonal fluctuations abound. For instance, Chemineau et al. [120] reported a threefold difference in France’s goat milk supply between November (10 million liters) and March (30 million liters).

At the individual livestock level, the onset of lactation is generally a direct consequence of birthing, whereas its duration and seasonal variability depend on environmental factors such as pasture, temperature and photoperiod, as well as breed, litter size and parity, i.e., the number of previous births [137–140]. Among traditional pastoralists in dryland Africa and the Middle East, the duration of lactation varies in cattle herds from three months to a year, with seven months as a common median [106]. In sheep, lactation is much shorter; Dahl and Hjort [106] assume 90 days when modeling African pastoralist milk production. Where a reliable milk supply is a herding goal, pastoralists must ensure that enough animals are lactating at any given time, but total milk production will still vary seasonally with rangeland resource availability [106,141].

The lactation curve describes milk yield over time following birthing [142]. As an illustration, data on Friesian cows in the UK during the 1950s and 1960s produced lactation curves with peaks a few weeks after calving and gradual decline until termination after about 10 months [143]. Milk protein and fat had different shaped curves from whole milk yield [144]. Yet, in all cases, strong seasonal fluctuations were observed, corresponding to the grazing cycle [143–146]. It follows that manipulating calving seasons for pastured herds is an effective strategy for optimizing milk yield [145], and this is practiced in modern commercial dairying [147].

Similar considerations abound for pasture-fed sheep and goats. For instance, traditional Sardinian dairy sheep management systems typically time lambing in autumn and winter to exploit seasonal availability of natural pasture [148]. Mating times are controlled

such that the more mature the ewe, the earlier the lambing will be in the season: yearling ewes receive optimal pasture early in their lactation cycle whereas mature ewes receive optimal pasture in an advanced stage of the cycle; all go dry in the summer. In this system, high seasonal variability of milk yield and content (fat, protein) is due primarily to pasture quality and availability—which includes the timing of peak pasture vis à vis pregnancy as well as lactation—but apparently also results from ambient temperature and photoperiod [137,148]. Different production systems give rise to different lactation curves. Hence, in a meat-focused system, lactation will decline more rapidly after birth and terminate sooner [138].

Regular milking in well-fed animals can prolong lactation, although a non-lactating dry period (optimally 50 days in cows) is necessary to restore mammary gland secretory tissue for the next cycle of milk production, ensuring milk quality and quantity while also promoting animal health and welfare [138,149,150]. High-yielding milk stock are targets of selection in both traditional and modern production systems. Additional methods for maximal exploitation of lactation well-documented in the ethnographic record include introducing an additional calf or kid, a fake calf or kid, insufflation (also known as cow blowing), and the application of herbs to the uterus [151]. Insufflation and related physical techniques to induce and/or maximize milk secretion in individual milkings are apparently attested to in the iconographic record of Egypt and Mesopotamia from at least 2500 BCE [151]. Traditional herbal techniques are perhaps not essentially different from modern hormonal treatments, although the latter may be used to induce lactation in the total absence of pregnancy [152,153]. The future of ruminant milk production might see effective elimination of dry periods without direct negative consequences for yield and animal health via hormonal and genetic treatments [154], although increased awareness of and concern for animal welfare may counterbalance this trend [150]. Individualized monitoring and management of herd animals is another direction contributing to the general goal of decreasing lactation seasonality, optimizing output and ensuring continuous milk supply [155–157].

Multi-annual milk output is correlated with age and parity. Among British and European cattle breeds, Brody et al. [158,159] observed a rise from the time of first calving at around 2 years of age, a rise directly related to increasing body weight, a peak at the attainment of maximum body weight around age 8, and a decline thereafter. Culling older cows (or ewes and does) is thus a means to optimize herd production, while culling calves (or lambs and kids) may be a means to maximize milk availability to the herder [160]. Debono Spiteri et al. [129] argue that there is a match between sites exhibiting early chemical residue evidence for dairying and mortality profiles consistent with dairying at Neolithic sites across the Mediterranean region. They conclude that “most communities began to exploit milk as soon as domesticates were introduced between 9,000 and 7,000 y ago” [129]. This is consistent with an archaeogenomic study of Neolithic goats, which identified changes following domestication to the *STAT1* gene involved in mammary gland development and linked to milk production [161]. These findings suggest that selection pressures on milk production were an early component of livestock evolution under domestication.

### 3.3. Wool Growth

The seasonality of wool growth has been dampened under domestication. The absence of highly seasonal spring molting found in wild and feral mouflon sheep is a defining feature of domesticated wool-sheep [162]. Wool also provides a particularly good test-case for the ‘domestication as globalization’ model since the intensification of wool production may be traced throughout several periods since the Neolithic. The historical development of wool production spans palatial, imperial and capitalistic economic systems through to its role in the onset of the Industrial Revolution in Britain and the global fine wool industry of today [163,164].

That breeds have been selected for based on their fleece characteristics is evident by observing the diversity of fleeces in living breeds. This includes the greater underwool

that gives Cashmere goats their special fibers, the longer, coarser mohair underwool in Angora goats, and super-fine Merino sheep wool [165]. Classification of wool breeds in both modern industry and archaeological textile analysis is based on measurements of fiber diameter and their distributions [166–168]. Thus, the ‘hairy’ coat of mouflon and some African sheep breeds consists of bristle-like thick outer fibers, or kemps, overlaying very thin underwool [134]. Both kemp and underwool are too short to be spun. By contrast, fine wool fleeces, as on Merino sheep, are characterized by only thin, spinnable fibers. Fine wool has been prized for millennia, but woolly fleeces have become increasingly spinnable and finer, shearable and heavier, and dyeable and whiter—all traits associated with its commodification and intensification of production.

Selective manipulation of caprine herds is evident from the mid-9th millennium BCE [169]. Spinnable wool might have evolved shortly after domestication in the Pre-Pottery Neolithic B (mid-9th–mid-7th mill. BCE), based on mortality profiles, spindle whorls apparently used for wool, and a couple of questionable textile finds [170–173]. More definitive evidence for spinnable wool production emerges in the 5th–4th millennium BCE Chalcolithic—a period of intensification in livestock exploitation for non-meat products like milk, animal fiber, and traction, originally conceived as the ‘Secondary Products Revolution’ [174–178]. Intensified wool production is well-attested by the late-4th millennium onset of the Early Bronze Age in Mesopotamia and is a component of agricultural intensification associated with Bronze Age urbanism in the Levant [179], Anatolia [180] and Mesopotamia proper [177,181–183]. Institutional palatial and priestly production systems organized much of this production from the mid-3rd millennium BCE in Mesopotamia, encouraging specialized flocks and breeds [127,184–187]. Among these breeds were woolly fleeced sheep, which evolved by selective thinning of the kemps and thickening of the inner wool, giving rise to ‘true’ fleece [188]. Insertion of an *EIF2S2* retrogene into an untranslated region of the *IRF2BP2* gene has been implicated as the genetic mechanism responsible for this switch [189].

In the 2nd millennium BCE, an active wool economy is also evident in the Aegean, as is the advent of woollen textiles in Europe, perhaps involving introduction of Ancient Near Eastern breeds [190]. It has been shown that primitive ‘hairy’ breeds in Europe represent a separate, probably Neolithic, diffusion of domesticated sheep from that of a subsequent, apparently 2nd millennium BCE, diffusion of ‘woolly’ breeds [191] (this confirms Ryder [192]; Deng et al. [193] suggest that a still later wave was responsible for the diffusion of fat-tailed sheep). In the 2nd millennium BCE, woolly sheep also apparently diffused into East Asia [194–196] (for Neolithic diffusion to Central Asia see Taylor et al. [197]), while dyed woollen textiles—facilitated by the evolution of white fleeces—were traded across the Mediterranean Sea [198]. Such movements of sheep and the commodification of wool have been considered a key component of the ‘Trans-Eurasian exchange’ and ‘Bronze Age globalization’ [199–202].

Among the key stages of fleece evolution, the most relevant to our discussion of biological rhythms is the evolution of continuous wool growth, as opposed to seasonal molting or shedding. Ryder [203] observed that goat hair shedding and growth are related to photoperiod. With regard to sheep fleece evolution, Ryder [134,166,188,192] postulated that continuous growth was associated with the invention of shears around 1000 BCE in Anatolia, which produced selective pressure for non-shedding; wool was previously harvested by plucking. Alternatively, it is possible that earlier selection for fleece weight led to continuous growth since fleece weight and shedding have been shown to be heritable and inversely related [173,204,205]. The timing of sheep shearing or, more generally, the wool harvest, has long been a landmark event in the annual cycle of Southwest Asian pastoralism. Spring shearing is attested to in Old-Babylonian shepherding contracts and marks the beginning and end of the contractual cycle [107]. The age at which individual sheep were able to be productively shorn also marks an important stage in the multi-annual shepherding cycle [107].



By the 1st millennium BCE, specialized breeds are well-attested in Ancient Near Eastern texts, including fat-tailed sheep and wool sheep [127,185]. From the 1st millennium CE, proliferation of breeds and their diffusion are sufficiently well-attested to allow scholars to surmise about the process by which the Merino breed evolved [206,207]. This might have involved the import of Italian fine wool breeds to the Iberian Peninsula, followed by crosses with North African berber breeds [163]. The Merino breed that emerged in the early 2nd millennium CE under the Spanish Mesta system was the basis for what became a major mercantile industry. Eventually, it was surpassed by the British woolen industry, which was central to textile mechanization associated with the industrial revolution, although cotton manufacture has been emphasized in the historiography [207–210]. Colonialism contributed to the spread of sheep and goats out of Afroeurasia and today a former British colony nearly as geographically distant as possible from the original center of sheep domestication, Australia, leads world wool production through local Merino breeds.

Yet, the evolution of wool breeds and manufacturing is not so straightforward. A ca. 1600-year-old sheep mummy from a Sasanian salt mine in Chehrābād, Iran, was shown to be of the ‘hairy’ type by genetic and morphological analysis of exceptionally preserved mummified fiber remains [211]. This suggests that woolly sheep did not become a universal norm even in 1st millennium CE Southwest Asia, and that hairy breeds may have been used at this time for specialized milk and meat production. However, in the context of wool production, the evolution of continuous growth was undoubtedly central to the long-term trend of production intensification, and it still is. Among domesticated sheep, wool diameter, staple length and fleece weight vary seasonally with photoperiod and temperature, although the extent of this variation depends on breed [212–217]. For instance, Merino sheep still exhibit seasonal fluctuations in fiber fineness [218], although similar variations are more pronounced in traditional Middle Eastern breeds [219]. Given the high financial stakes associated with optimizing production of Merino fine wool today, seasonal meteorological variables are perhaps more significant in pastured wool sheep than ever before [220].

### 3.4. Death

The timing of death can come at any stage in the livestock lifecycle, determined by both ‘natural’ innate and environmental causes, in addition to human motives. On one hand, environmental variables, including seasonal climatic fluctuations, affect mortality: drought or frost may lead to insufficient water and grazing, resulting in early death; anomalous weather events may increase the contraction of diseases or, in cold climates, cause animals to freeze [106]. On the other hand, human decisions on when and which to slaughter profoundly impact herd structure and selective processes.

Livestock death reflects livestock life in pastoralists’ herds because herd population structure—resulting from the timing of slaughtering, as well as additional manipulations such as castration and selective breeding—reflects herd function. Thus, in a specialized dairy herd, a disproportionately high proportion of newborns will be culled, whereas in a meat herd, most culling will target males in their first year, to optimize growth over grazing and fodder consumption. Herds focused on wool production will generally display the highest proportions of adults, especially of castrated males. Such differential age-at-death profiles are found in the ethnographic record, motivating analysis of mortality profiles in the archaeozoological record [160].

In practice, archaeozoological attempts to discriminate between highly specific herding regimes were shown to be overly optimistic, and statistically robust techniques for studying mortality profiles continue to be developed [221,222]. Identifying the scheduling of slaughter in archaeological livestock has been complicated by lack of accuracy in studies preceding the advent of microwear-based techniques. Moreover, the wide range of livestock mortality profiles reflects more than simplistic herding goals [223]; it includes diversity of breeds, environmental conditions and herders’ decisions [106]. The age at which pastoralists choose to cull varies from group to group and year to year [102,106].

As an illustration of this complexity, Arab pastoralists in Afghanistan distinguish three age categories of castrated Turki sheep, among which the 3–4-year-olds are twice the size of castrated 6-month–2-year-olds [224]. Although such a system might be challenging to reconstruct exclusively from bone remains, archaeozoological mortality profiles can nonetheless indicate cultural differences in slaughter practices [225]. Furthermore, while some herding and hunting profiles are indistinguishable, altered age and sex profiles in the archaeozoological record provide a key diagnostic for early herd management and domestication [226–229].

Sex profiles of herds are also related to function since relatively few males are needed in dairy and multifunctional herds—on the order of 1:10 in Ancient Near Eastern texts [127,230,231]. Given the seasonal nature of pasture availability and hence birthing described above, culling of males is needed to regulate livestock population within ecological boundaries. In many societies, concentrated ritual slaughter coincides with the need to regulate livestock populations (see Rappaport 1967 [232] for an example from a very different context). Large-scale ritual slaughter of sheep, goats and cattle is evident in Ancient Near Eastern archaeology and texts [233–237], including the Bible (e.g., Kings I 8:62–3; Chronicles II 7:5). The changing availability of pasture, and hence rangeland carrying capacity, gives rise to seasonal culling patterns, such as the Biblical yearling male Paschal lamb sacrificed in spring (Exodus 12:1–20).

One might expect that in periods and regions involved in intensive pastoral production, mortality profiles would closely follow the theoretical population structures expected by specified herd function. This would also entail a clear culling season since, given the seasonality of reproduction and birth, only certain age cohorts would be available for slaughter at any given time of year. Therefore, a peak of individuals of a certain age in an archaeozoological sample may represent a seasonal cull [238]. In practice however, such profiles are rare in the Southwest Asian archaeological record (but see Helmer et al. 2007 [239], noting that the statistical correction to mortality profiles that they offered has not been widely accepted). Rather than slaughtering males in their first year, after attaining maximal weight over consumption (a meat-production strategy) or keeping adult male herds (a wool-production strategy), the southern Levantine archaeozoological record attests to slaughtering males in young adulthood as typical, usually during the second to third years of life [240]. This is consistent with the idea that risk-averse stability, rather than production intensity, was the dominant long-term strategy. From a productivity perspective, culling during the peak rangeland productivity season (spring in Southwest Asia) is desirable for keeping herds within carrying capacity limits during the low rangeland productivity season (late autumn–early winter). However, this desirability may be offset by herd security considerations, i.e., to ensure a sufficient supply of males for breeding after juvenile natural deaths. Indeed, traditional pastoralists are loathe to slaughter at almost any time and gradual culling of male animals throughout the year could have afforded an easier, less risky solution even to the problem of supplying constant demand in large urban centers. Moreover, market fluctuations may offset seasonal ones in dictating culling patterns [238]. Finally, if pasture is effectively unlimited, i.e., herd populations do not approach carrying capacity limits, there will be much less impetus to cull. While the available mortality evidence does not generally support clear production-driven functional herding strategies, human timing of livestock death, i.e., culling, was a key source of selective pressure operating on livestock populations. Collating reliably constructed mortality profiles and determining the degree of seasonality in slaughter patterns may be goals for future archaeozoological research.

#### 4. Discussion

Having surveyed some of the changes to timing in plant and animal lifecycles following domestication, we consider more broadly their social and economic consequences, with reference to the ‘domestication as globalization’ model [2]. This model posits that heightening production intensity, widening geographic diffusion, and changes to world-

wide diversity of breeds and landraces are aspects of ancient globalization that follow from initial domestication. These are not inevitable developments that deterministically ensue from domestication, but they do demarcate long-term agricultural trajectories which can be understood with recourse to globalization. Here, we argue that phenological evolution under domestication fits well within a ‘domestication as globalization’ model, exploring insights gleaned from this long-term approach to economic phenology. We recognize that the species reviewed above represent but a small subset of global domesticates [6]. Nevertheless, wheat, barley, sheep, goats and cattle are some of the most successfully globalized domesticates and therefore offer an appropriate starting point for the ‘domestication as globalization’ model.

According to Balasse et al. [91]: “Artificial insemination combined with gene selection is the latest extension of the marked intensification of the artificial selection of animals, initiated in the eighteenth century.” A similar process holds for crop improvement and, more generally, intensification of agricultural selection is a feature of the long-term history of domestication. Practically all lifecycle traits targeted under domestication and reviewed above relate to the intensification of production or the diffusion of domesticates into regions removed from their wild progenitors’ regions of distribution. In cereals, these traits include spikelet non-shattering, seed non-dormancy, growth uniformity, adaptive flowering times, and delayed senescence. In livestock, they include synchronization of birth, reproduction and death with herding goals, extended lactation and continuous wool growth.

One result of these crop and livestock species’ geographic diffusion, combined with culturally varying production goals, is the diversity of extant landraces and breeds. This diversity, in turn, provides the genetic material from which further intensification of production and extension of geographic limits can be developed. Recent studies of prehistoric goat genomes suggest that Neolithic domestication resulted in lower genetic diversity at the population level [241], but subsequent stages of geographic diffusion and wild introgression led to increasing diversity at the global level. The possibility of increasing production by herding domesticated livestock and cultivating domesticated cereals in the Southwest Asian Neolithic contributed, directly or indirectly, to their geographic spread out of Southwest Asia. This eventually resulted in the evolution of breeds and landraces with phenological adaptations (different responses to photoperiod changes, germination requirements, etc.) suited to the new environments, especially at different latitudes and altitudes which presented different photoperiod and yearly temperature regimes. Not only could such adaptations facilitate still further geographic diffusion, but they have also contributed to increased production intensity. This is attained, for instance, by cultivating both spring and winter wheat in a single regime, or the cultivation of spring wheat in regions where winter wheat has been grown since the Neolithic, due to the former’s faster growth habit. This positive feedback loop between production intensity and geographic diffusion, in which phenological adaptations are part of the mechanism, is evident in millennial-scale perspective. A later-period example is the introduction of summer-season cultivars to the Levant during the 1st millennium CE—mostly crops domesticated in the Old-World tropics [242,243]. Unlike the evolution of spring wheat, this is not phenological evolution on the sub-species level, but rather a change to temporality in agricultural practice due to geographic crop diffusion. Moreover, by affecting agricultural work routines and crop rotation cycles, the introduction of summer cultivation to this region inevitably affected peoples’ perceptions of time and space—another basic characteristic of globalization [244].

We have seen that in certain cases lifecycle changes following domestication are governed by just a few genes, as with the non-brittle rachis in domesticated wheat and barley. In other cases, the changes directly result from environmental modifications associated with agropastoral production rather than specific genetic mutations, such as the loss of reproduction seasonality through year-round foddering in cattle. The latter example suggests that management, rather than domestication, was the prerequisite for some modifications in seasonality. It is therefore possible that lifecycle shifts in proto-domesticates co-evolved with humans over a long pre-Holocene period. Just as the human transitions from nomadic

to sedentary lifestyles and from foraging to farming are now generally considered to have been much more drawn out and less-directional processes [16,245–247] than originally conceived [28] or theoretically possible [3], it is plausible that some changes to seasonality in proto-domesticates likewise arose through very long processes of interaction with humans.

Nonetheless, initial and ongoing domestication have impacted plant and animal biological rhythms in unprecedented ways. This is true almost by definition, since domestication involves increasing dependence on humans for reproduction, which itself is highly seasonal. Yet, other targets of selective breeding, such as delayed senescence in cereals and continuous wool growth in sheep, exemplify non-reproductive changes to biological rhythms resulting from ongoing domestication. While our discussion has focused on population and biosphere levels of domesticates, it is also worth noting that the onset of agriculture and pastoralism entails a whole suite of ecological entanglements that affect biological rhythms in ways not discussed above. This includes the interrelated evolution and diffusion of weeds [248], pests [249], and seasonal agricultural tasks such as manuring, fallowing, and crop rotation [250–253]. For instance, following the initial introduction of agriculture to the Alpine Foreland in the European Neolithic, the seasonality of weed flora in archaeobotanical assemblages changed from a seasonally dispersed distribution to clustering around winter (einkorn, barley) and summer (flax) crop cultivation regimes [254].

Yet another change associated with seasonality that intensified through domestication with profound consequences for human history is the effect of storable wealth in the form of grains and managed herds [255–258]. Unlike the plant and animal lifecycle traits surveyed above, this phenomenon has to do with humans' lived experience of seasonality and is not directly related to domesticates' lifecycle changes. To be sure, hunter-gatherers store surplus food [259], while grain storage by humans in Southwest Asia preceded domestication [260,261], as did herd management [241] and sedentism [246,262]. Indeed, storage is a prerequisite for cultivating grains, which in turn is a precondition for cereal domestication [263], as is herding, in some form, a precondition for livestock domestication [241]. Yet, by gradually cementing human reliance on food production, domestication contributed to a long-term dampening of seasonality in human life. Although this brought about a replacement of one mode of seasonal subsistence (hunter-gathering) for another (agriculture) [264], the generation of surplus and storage enabled a dampening of seasonal fluctuations in food supply [265]. The extension of agricultural growing seasons and regions followed, of which spring wheat discussed above is just one example. Today, much effort is invested by agriculturalists to overcome temporal cycles, insofar as they pose limits on production or demands on resources. Thus, cattle breeding programs use insights from modern physiological research on phenology to guide selective breeding programs [266], while a major research project employs modern genomics to genetically engineer perennial barley [267,268]. In long-term perspective, there appear to be positive feedbacks between dampened seasonality in humans and domesticates.

We acknowledge that domestication today, i.e., modern crop improvement, is significantly different from that of ancient times—just as contemporary globalization is very different from ancient globalization. However, we see it as a difference in degree rather than in kind. Just as modern breeding programs employ novel techniques to attain age-old goals of intensifying production and trade worldwide, so too contemporary globalization sees new technologies employed in increasingly intensified production and connectivity. Moreover, domestication and globalization have had similar consequences for culturally defined diversity. The spread of domesticated plants worldwide led to a diversity of landraces, mimicking the diversity of cultural groups and sub-groups. Yet, in modern times, these types of diversity have come under threat, and traditional ways of life—including traditional agricultural varieties and breeds—are being abandoned under the forces of global markets. Ironically, the same intensification in global connectivity that has enabled us to appreciate this diversity is also leading to its decline. While gene banks attempt to preserve past agricultural diversity much as museums do for cultural diversity, modern

crop breeding employs genetic input from diverse germplasms from many areas of the world, and even from wild progenitors [269]. Thus, contemporary crop genomes attest to unprecedented connectivity associated with crop diffusion, while the diversity of landraces under cultivation declines, as does the diversity of livestock breeds being herded. These trends in diversity comprise one important way in which agricultural globalization may be considered a subset of cultural globalization. It emerges that the use of the term *hybridization* in global studies to signify “the mixing of different cultural forms and styles facilitated by global economic and cultural exchanges” (Steger 2009, p. 6 [244]) is a particularly apt case of terminological borrowing from biology.

This view of the relationship between ancient and contemporary domestication as different in degree rather than in kind is supported by a long-term view of agricultural phenology. We have seen that traits which originally evolved to meet specific agricultural needs are sometimes being used and developed in very different ways under modern agriculture. The modern cultivation of spring wheat in countries that traditionally grew winter wheat is an example. We have also seen how selection against dormancy has gone too far for some field conditions such that modern crop improvement is working on selectively reintroducing some dormancy. In addition, certain traits, such as delayed senescence, appear to have only recently been targeted, whereas others, such as those associated with dispersal, dormancy and flowering time, were subject to selective pressures relatively early in their domestication history. Meanwhile, modern crop improvement incorporates methods unprecedented in the long-term history of domestication [268]. Varying photoperiod cycles associated with the spread of cereals and livestock into diverse latitudes exemplify the introduction of new natural selection pressures affecting reproduction and growth following domestication. Human decisions about which animals to cull, and when, exemplify artificial selection pressures affecting the same. Contemporary use of artificial lighting or gene editing to influence photoperiod response represent new additions to herders’ and farmers’ repertoires. These phenological examples show that while historically unprecedented techniques are being employed to attain unprecedented levels of production, it is still the same basic process of increasing net yields via crop improvement and diffusion that is at least as old as domestication.

Moreover, this recognition of differences in intensity but not in kind between contemporary and ancient domestication adumbrates parallel developments of each. In their meta-analysis of over 200 domesticated crop histories worldwide, Meyer et al. [6] identified “an ongoing trend towards more rapid fixation of domestication traits.” This global domestication trend parallels the global economic trend toward increasingly rapid knowledge accumulation and technological innovation. Both lead to heightened production intensity. However, these trends are neither smooth nor inevitable. In the same study, Meyer et al. [6] conclude that: “Centers of domestication exhibit fluctuations in domestication activity over time, often corresponding with factors such as the expansions of major civilizations and increased trade.” Yet, although systems (social, political, economic) organizing production and land use rise and fall, there is a long-term pattern of increasing intensification [270–275].

The domestication as globalization model relates to an open question in global studies, namely, what is globalization and when did it begin [9,276–280]? Was it the Digital Revolution, particularly since the 1990s, coterminous with the application of genomics and genetic engineering to crop improvement; the post-World War II economic boom fueled in part by the Green Revolution of the 1950s–1960s; or the Industrial Revolution and the onset of modern scientific breeding programs? Globalization studies often stop there, tending to inhabit a post-Industrial timeline. By contrast, domestication research generally adopts a millennial temporal scale. This mismatch in timescales—which probably results from differences in the nature of the evidence and the disciplines usually involved in domestication research and global studies, respectively—presents a challenge to the ‘domestication as globalization’ model. Yet, Wallerstein’s influential World-System paradigm envisions a process of international economic integration going back five centuries [281], while some scholars envision world systems going back five millennia [278,282]. While



many archaeologists adopted and adapted the world systems framework (e.g., Woolf 1990 and references [283]), recent involvement of archaeologists in the globalization discourse has produced increasingly earlier and more diverse identifications of globalization, proto-globalization or globalizing developments [284–290]. At a minimum, such studies reinforce the sense that the question of globalization’s genesis remains unresolved.

An important component of the expanding archaeological discourse on globalization has been the interpretation of archaeobotanical data on crop diffusion in terms of ‘ancient globalization’ and ‘food globalization’ [63,291–296]. Some of these studies have identified ancient globalization in processes of crop diffusion across Eurasia as far back as the 2nd millennium BCE, which accords the views of some historians and theorists [280,282]. Our argument builds on these approaches and extends them further in time. We consider the beginnings of globalization to have been sown with the initial domestication of plants and animals, which set off the potential for significant intensification, geographical diffusion, and diversification of food production.

As we have seen, this potential has been manifested in changes to biological rhythms, among other classes of traits, and this drive is still ongoing. Contemporary crop and breed improvement are part of contemporary globalization; both involve novel methods and even unprecedented aspirations to ultimately increase production intensity and geographic diffusion, with complex effects on diversity. Ultimately, a long-term historical perspective on where we have come from in this regard may contribute to understanding where we are going. On that note, we close by acknowledging a primary driver of phenological change in domesticates today: climate change [297]. It is interesting to consider that manipulation of biological rhythms through domestication ultimately fueled the very process of intensification and globalization that is causing unintentional changes in phenology via anthropogenic climate change. Modern crop improvement efforts are responding with radical attempts at altering crop lifecycles [268]. Today, as global climate change affects a globally agricultural world, there has never been a better time for research and reflection on biological rhythms of domesticated crops and livestock.

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