Nutrition of Broodmares

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KEYWORDS

• Nutrition • Developmental origins of health and diseases (DOHaD) • Critical periods • Gestation • Broodmare

KEY POINTS

- Under normal conditions, forage availability can match mares' energy and protein needs but low forage quality or breeding out of season requires nutritional supplementation.
- Micronutrient availability, however, should be verified and often requires supplementation.
- Attention needs to be placed not only on the quantity of energy and nutrients, but also on their quality and characteristics.
- Mare nutrition and adiposity can influence the foal's long-term health and metabolism (developmental origins of health and disease); excess nutrition can be as deleterious as feed restriction.
- There is a need for more research on broodmare nutrition, taking into consideration genetics, breed, breeding conditions, and environment.

INTRODUCTION

Nutrition and reproduction are central facets of life, highlighting the critical importance of optimal nutrition for the broodmare. Our goal with this review is to provide the reader with a solid foundation of knowledge regarding:

1. Core broodmare and fetal physiology, as well as maternal nutritional requirements, and
2. The influence broodmare nutrition can have on the future health and performance of the foal.

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This review should enable readers to move beyond the basic dietary energy and nutrient requirements and consider a more precise formulation of diets for broodmares being kept in a wide range of different environments.

The first step in any nutritional evaluation should be to evaluate the mare and the performance sought. Once this point has been well-characterized, the diet and management best suited to that scenario can be formulated. Gestation and lactation result in substantial increases in nutritional requirements. Estimates of energy and nutrient requirements developed by equine nutritionists represent an excellent starting point for formulating a broodmare's diet.[1–3]

Nutrition, along with day length and ambient temperature, are important environment variables. Over tens of millions of years of evolution, horses have developed a seasonally polyestrous reproductive physiology that resulted in most foals being born in late spring and early summer, thereby synchronizing the nutrient requirements of late gestation and early lactation with environmental energy and nutrient availability.

Although those caring for broodmares can easily evaluate the mare and her environment (day length, ambient temperature, and forage and diet characteristics), it is more challenging to know the condition of the fetus or modify its environment. A primary histotrophic nutrition (based on uterine secretions) transitions to hemo (based on exchange between maternal and fetal bloods) and histotrophic nutrition after implantation.[4] The fetus progresses through various developmental stages, all of which may be influenced by the dam's nutrition. A growing body of research highlights the importance of the link between maternal nutrition and developmental programming of the fetus.

Nutrition is customarily evaluated as a balance between the requirements of the horse and the dietary supply. The objective is to find a balance that optimizes the long-term health and performance of the broodmare and her foal. Finding this balance requires an understanding of overnutrition and undernutrition, as well as the changes in requirements according to physiologic status. Furthermore, we now appreciate that optimal nutrition goes beyond simple quantities and requires consideration of the quality and form of the dietary energy and nutrients.

With the increasing incidence of obesity and the metabolic syndrome in horses, in addition to effects on mare fertility,[5] unforeseen effects may result, especially in terms of offspring health and metabolism. Conversely, under moderate maternal undernutrition, foal birth weight is not affected but long-term metabolic consequences may still be observed in offspring. There is a relatively clear connection between glucose and insulin homeostasis and metabolic consequences. However, other dietary components should also be considered, despite the fact that current knowledge is limited.

Key points

- Recommendations for dietary energy, protein, vitamins, minerals, and water are available, but these should be considered a starting point, from which the unique characteristics of each breeding operation should be further considered.
- Practitioners should consider the environment that a broodmares' physiology has been well adapted to as they make choices regarding diet and management during different stages of gestation.
- Knowledge of the negative implications of overnutrition and undernutrition, the metabolic and developmental impact of fiber, nonstructural carbohydrates, and fats as dietary energy sources, and the potential benefits of precision feeding using supplements or ration balancers is invaluable when formulating diets for broodmares.

CURRENT NUTRITION RECOMMENDATIONS

General Estimation of Broodmare Needs

Intake during gestation needs to meet mare plus fetal growth requirements. Studies on fetal growth, however, are limited. Fetal growth curve data are based on aborted or stillborn animals,[6–8] thus potentially underestimating fetal growth at the end of gestation.[1]

Historically, mare gestational nutritional requirements have been calculated based on the following assumptions:

- Accretion of uterine and placental tissues takes place in midgestation.[7,8] It is assumed that fetal adnexal tissue (placenta, amnion) and mammary development are linear to that of the fetus, as observed in the cow,[9] but this point has not been demonstrated in the horse.[10]
- Fetal growth is best represented by an exponential growth curve with rapid fetal development occurring from day 240 of gestation to parturition.[10]
- The foal's weight at birth is assumed to be approximately 10% of the dam's nonpregnant mature body weight.
- Uterine and placental tissues are metabolically more active (66.6 kcal/kg) than the rest of the body (33.3 kcal/kg body weight) and therefore have higher energy needs.[10]
- The efficiency of using digestible energy (DE) for depositing fetal and placental tissue during gestation is assumed to be 60%.[11]

Most of these factors are considered in the estimate of energy and nutrient requirements for pregnant broodmares that have been developed around the world. Differences between the various estimates are often owing to variation in interpretations of fetal, placental, and uterine growth data and estimates of changes in mare metabolism during gestation[12] (personal communication, Manfred Coenen, 2020).

Energy and Protein Requirements and Recommendations

Lactation and rapid fetal development in late gestation represent periods of high nutritional requirements for broodmares.[1,10] Nonlactating mares in early and even midgestation have energy and protein requirements either at or close to maintenance levels (**Fig. 1**). Estimated energy requirements in late gestation increase to between 1.3 and 1.5 times maintenance levels, and lactation can result in a doubling of energy requirements.

Horses obtain energy effectively from their environment, primarily from forages. Total dry matter intake (DMI) will likely range from 1.5% to 3.0% body weight, and in most cases at the higher end of this range in pregnant or lactating broodmares. Forages have most of their potential energy stored in the chemical bonds of structural and nonstructural carbohydrates and horses have evolved for the optimal use of this particular environmental dietary energy source. Therefore, caregivers should focus first on providing dietary energy from forages. Based on a host of published information, a rough approximation of the DE content of most forages is between 1.5 and 2.5 Mcal/kg, with more mature forages usually providing less DE.[1–3] For most mares, forages should make up at least 50% of their daily DMI, and in many cases may be close to 100%, if no energy rich concentrate/complementary feed or vitamin and mineral supplement is needed. Once dietary forage has been optimized, attention can shift to concentrates and/or vitamin and mineral supplements.

Mares in late gestation provided concentrates, in addition to grass forage, maintain body condition and weight better than those on forage alone.[13] Grains and

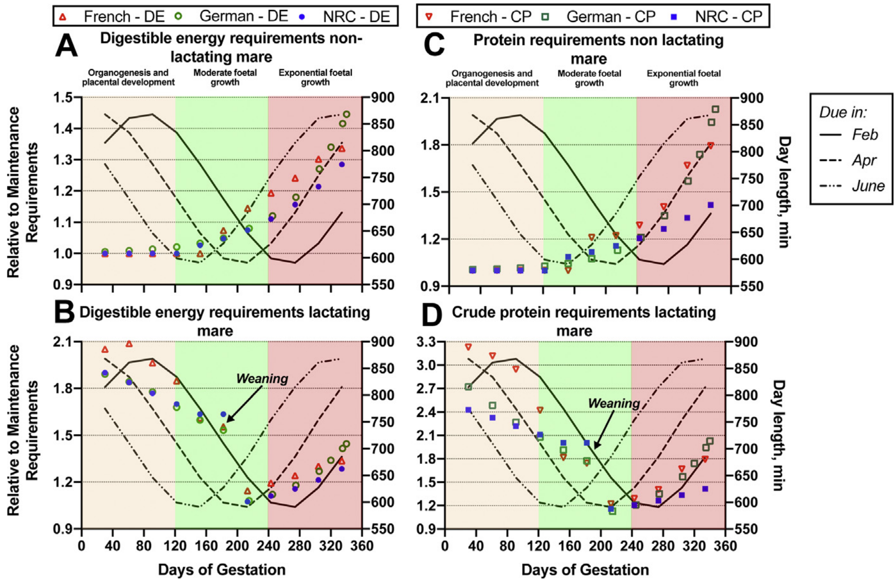


Fig. 1. Pregnant lactating and nonlactating mares' energy and protein requirements relative to maintenance, according to time of gestation and compared with day length. The symbols represent the DE (A, B) or CP (C, D) requirements relative to maintenance of broodmares with (B, D) or without (A, C) a foal at their side during gestation as determined using the French, German, and North American feeding standards for horses.[1–3] The lines represent the calculated day length at any point during gestation for foals due in February, April, or June for a north- ern latitude of 35, as an indicator of ambient temperature and forage availability. The colored regions represent important stages of gestation, represented by preimplantation, endometrial cups, and organogenesis (0–120 d), moderate fetal and organ growth (120– 240 d), and rapid fetal development (240–340 d). Those interpreting this figure should consider the synchrony between day length, a proxy for the broodmare's environment, and energy and nutrient requirements during gestation. (*Data from* Refs.[1–3])

concentrates should really be viewed as a complement or supplement to the energy and nutrients provided in the base forage diet (see Patricia Harris and Megan Shepherd's article, "What Would Be Good for All Veterinarians to Know About Equine Nutrition"; and Myriam Hesta and Megan Shepherd's article, "How to Perform a Nutritional Assessment in a First Line/General Practice"; and Nerida Richards and colleagues' article, "Nutritional and Non-Nutritional Aspects of Forage," in this issue). Grains contain high concentrations of starch, a nonstructural carbohydrate that can be a valuable dietary energy source for broodmares. An approximation of the DE content of grains is 2.5 to 3.8 Mcal/kg of DM,[1–3] with some high-fat grains providing even more. The DE in most commercial concentrates containing mixtures of nonstructural carbohydrates, fiber, and vegetable oil or fat will range from 3.0 to 3.8 Mcal/kg DM. In the vast majority of scenarios, grains and concentrates should not constitute more than 50% of the daily DMI. A range of 5% to 30% is probably appropriate in most cases, depending on the body condition score (BCS) of the mare, her health, and the quality and availability of the forage. More details on starch intake are developed in the section discussing the developmental origins of health and diseases.

Horses are somewhat unique as a grazing species owing to their gastrointestinal anatomy and their ability to digest and use dietary fats.[14] The location of the small intestine before the cecum and colon, allows the horse digestive and absorptive capabilities for fats before those fats reach the primary microbial populations in the cecum and colon. Adding dietary fat, therefore, can be an effective strategy to increase dietary calories for broodmares[15] while limiting the potential negative effects of excess starch on offspring health (see Part 3). Research indicates that horses are likely capable of digesting and absorbing dietary fat at concentrations of up to 200 g/kg DM density.[14] The increased energy density of added vegetable fat/oil provides several possible benefits, including flexibility to maximize fiber without sacrificing energy intake, especially when energy requirements are high and DMI may be limited, and potential improvements in fat soluble vitamin absorption[14,16] While horses may be capable of digesting and absorbing upwards of 15% to 20% dietary fat, forage contains only 2% to 4% fat/lipid. In the authors' opinion, the potential benefits of adding fat are more likely to be seen in the range of 5% to 10% dietary fat on a DM basis, calculated by evaluating both forage and concentrate fat intake. The quantity and ratio of dietary omega-6 and omega-3 fatty acids may influence inflammation, alter cell membrane fluidity, and gene expression but much more work is needed in this area.[17] Most forages are rich in omega-3 fatty acids (eg, alpha linolenic acid), so diets that contain at least 50% forage are more likely to have a relatively low omega-6-to-omega-3 ratio.[17] If additional omega-3 fatty acids are desired, flaxseed or flax oil would likely be the most practical to incorporate into the ration, but other sources such as fish and algae oils can also be used depending on the budget and the palatability of the oil for the individual animal.

The pattern of change in crude protein (CP) requirements during gestation is similar to that of DE (see **Fig. 1**). The CP requirements for nonlactating early gestation mares are near or at maintenance levels and increase exponentially in the last third of gestation, and then increase again during lactation. The estimated CP requirements vary around the world, likely owing to different assumptions of protein use for fetal, placental, and uterine development, as well as protein as an energy source in late gestation.

Of greater importance is protein quality, specifically its digestibility and amino acid composition. Under most circumstances, feeding the broodmare a higher quality protein will improve the mare's and developing fetus's ability to use amino acids for tissue development. The amount of available protein can be estimated by subtracting the acid detergent insoluble nitrogen and the nonprotein nitrogen from the CP to provide a better estimate of the protein available for absorption in the horse's small intestine.[1] This information can be provided on demand by most laboratories. The quality of the dietary protein is also improved by providing a composition of essential amino acids that most closely meets the requirements of tissue development.[18] More research is needed to uncover knowledge of broodmare's amino acid requirements, but it is assumed that lysine is the first limiting amino acid and its concentration is approximately 4.3% of the CP requirement.[1] Quality protein sources include soybean meal, alfalfa, and certain milk byproducts, owing to their amino acid composition.

Vitamins, Minerals, and Water Requirements and Recommendations

Essential vitamin and mineral requirements needed to support optimal embryo and fetal development are not clear. Vitamins A and E are normally high in fresh forages (**Table 1**).[19,20] Vitamin D requirements should be met by the horse having sunlight exposure; thus, mares maintained predominantly indoors may require additional vitamin D from the diet (see also Nerida Richards and colleagues' article, "Nutritional and Non-Nutritional Aspects of Forage," in this issue). Horses maintained in an environment where they have sufficient access to immature fresh forages during

Table 1
Ability of forage to meet broodmare fat soluble vitamin requirements

Vitamin	National Research Council Requirement (500 kg of Body Weight) 0–120 d Gestation	120–250 d Gestation	250–340 d Gestation	0–30 d Lactation	Fresh Forage Content (U/d)[a]	Hay Content (U/d)[a]	Is Forage Adequate?[b]
Vitamin A (kIU)	30	30	30	30	55–2418[c]	3.6–593.0[c]	Likely inadequate in preserved forage/hay
Vitamin D (IU)	3300	3300	3300	3300	341–19,800	990–61,160	Yes, if sun-exposure is not greatly limited. Higher values found in sun-dried forage/hay compared with fresh pasture.
Vitamin E (IU)	800	800	800	1000	147.5–6556[d]	164–3458[d]	Likely inadequate in preserved forage/hay

[a] Forage and hay calculations based on 500 kg body weight horse and 2% body weight (DM basis) consumption of forage only.
[b] For more information, see Nerida Richards and colleagues' article, "Nutritional and Non-Nutritional Aspects of Forage," in this issue (Forage).
[c] Calculated using the conversion 1 mg β-carotene = 333 IU vitamin A during pregnancy.[20]
[d] Calculated using the conversion 1 mg α-tocopherol = 1.49 IU vitamin E.[1]

late gestation and early lactation will likely be meeting their requirements. In contrast, dried hay (and especially hay that has been stored for a long time) will not be sufficient to maintain adequate vitamin A and E levels in pregnant mares when fed for several months.[21] Serum vitamins A and E concentrations are higher in summer when pregnant mares are in pasture, compared with in winter, when they are typically stabled and fed preserved forage.[19,22] Various B vitamins are found in forage and are also produced by microbes within the equine digestive tract. However, little is known regarding B vitamin requirements during gestation or their relative concentrations in forages.

Mineral supply from the pasture and hay is influenced by soil factors, plant species, state of vegetative growth, and fertilization and irrigation.[23,24] Therefore, specific recommendations regarding the need for mineral supplementation are difficult to state because they depend on the grass type, geographic location, and season of the year. Many fresh forages will meet the macromineral needs (see also Patricia Harris and Megan Shepherd's article, "What Would Be Good for All Veterinarians to Know About Equine Nutrition"; and Nerida Richards and colleagues' article, "Nutritional and Non-Nutritional Aspects of Forage," in this issue) of the mare during gestation for calcium (Ca), phosphorus (P), and potassium (K), but may be low in sodium (Na) and some trace minerals, including copper (Cu), zinc (Zn), and selenium (Se)[23,25–27] (**Table 2**).

Table 2
Ability of forage to meet broodmare mineral requirements

Mineral	National Research Council Requirement (500 kg) 0–120 d Gestation	120–250 d Gestation	250–340 d Gestation	0–30 d Lactation	Cool Season Grass Content (U/d)[a]	Warm Season Grass Content (U/d)[a]	Is Forage Adequate?[b]
Calcium (g)	20.0	28.0	36.0	59.1	20–86	24–89	Yes, although supplementation may be needed during early lactation.
Phosphorus (g)	14.0	20.0	26.3	38.3	12–31	15–98	Yes, although supplementation may be needed during late gestation or early lactation if consuming mature (seed heads present) cool season grass.
Potassium (g)	25.0	25.0	25.9	47.8	37–269	63–298	Yes
Sodium (g)	10.0	10.0	10.0	12.8	0–36.8[c]	Not reported	Supplementation is often needed.
Chloride (g)	40.0	40.0	40.0	45.5	19.6–144.0[c]	Not reported	May require supplementation.
Copper (mg)	100.0	100.0	125.0	125.0	39–87	43–143	Most cool season grasses are too low in Cu to meet the requirements throughout gestation. Some warm season grasses may provide adequate levels.
Zinc (mg)	400.0	400.0	400.0	500.0	149–273	196–634	Supplementation needed.
Selenium (mg)	1.0	1.0	1.0	1.25	0.5–0.7	0.3–4.0	Depends on geographic region.

[a] Grass value calculations based on 500 kg body weight horse and 2% body weight (DM basis) consumption of forage only.
[b] For more information, see Nerida Richards and colleagues' article, "Nutritional and Non-Nutritional Aspects of Forage," in this issue (Forage).
[c] Values for general grass pasture obtained from https://equi-analytical.com/common-feed-profiles/.

Water requirements during gestation seem to be similar to that of maintenance. Observed intakes range from 5.1 L/100 kg body weight[28] to 6.9 L/100 kg body weight[29] in pregnant mares and from 11.9 L/100 kg body weight to 13.9 L/100 kg body weight in lactating mares[1] and are influenced by several factors, including DMI and the environmental temperature. The availability of water is especially important for horses consuming dried preserved forage, such as during cold seasons and when stalled.[30,31] Water restriction during pregnancy results in decreased feed intake and loss of body weight.[29] Thus, water restriction should be avoided.

Key points

- Published energy and nutrient recommendations are best viewed as starting values, which can be tailored to meet individual scenarios.
- Mares' requirements are continuously changing based on stage of gestation and lactation.

NUTRITION OF THE BROODMARE: ADDITIONAL FACTORS TO CONSIDER

Gestation: A Unique Physiologic Status Affecting Metabolism

In early gestation, mares have more efficient glucose absorption, which results in a higher postprandial blood glucose.[32] They also have an enhanced endocrine pancreatic response, resulting in increased postprandial insulin secretion and basal hyperinsulinemia compared with nonpregnant mares.[32] Therefore, mares dedicate the first part of gestation to glucose storage as fat or glycogen in peripheral tissues (adipose tissue, muscles, and liver), to stock up for when fetal needs will increase. This is called "facilitated anabolism."[33] At the end of gestation, mares become more insulin resistant, have a decreased peripheral tissue glucose tolerance, and decreased pancreatic β-cell sensitivity, limiting the glucose storage in maternal tissues.[32,34–36] These changes are associated with a pronounced increase in glucose absorption after meals[32,36,37] (**Fig. 2**). These physiologic adaptations coincide with a strong increase in fetoplacental glucose requirements at the end of gestation; almost 75% of the circulating maternal glucose is used by the uterus and fetal tissues.[38]

Age and parity may alter these metabolic changes in mares. For instance, primiparous mares have been shown to have higher insulin responses to feeding compared with multiparous mares in late gestation, which could mean impaired metabolic adaptation to gestation in primiparous dams.[35]

In late gestation, mares have an increase in lipid mobilization, as observed through the following:

- Increased serum β-hydroxy-butyric acid[39] concentrations, a ketone that serves as an alternate adenosine triphosphate or energy substrate when glucose availability is low.[40]
- Some authors observed an increase in the plasma triglyceride concentration reaching a plateau from the seventh month of gestation onward[41,42]; however, not all investigators have observed such a change.[39,43]
- Plasma cholesterol concentrations are stable during gestation[44] and lower than in nonpregnant mares,[39] which may result from use of cholesterol for steroid synthesis.[45,46]

Nitrogen metabolism also adapts to the pregnant state. During gestation, the plasma total protein concentration varies,[39,41–43,47] although it remains lower than in nonpregnant mares.[39,42,43] Plasma urea concentrations are higher in late gestion

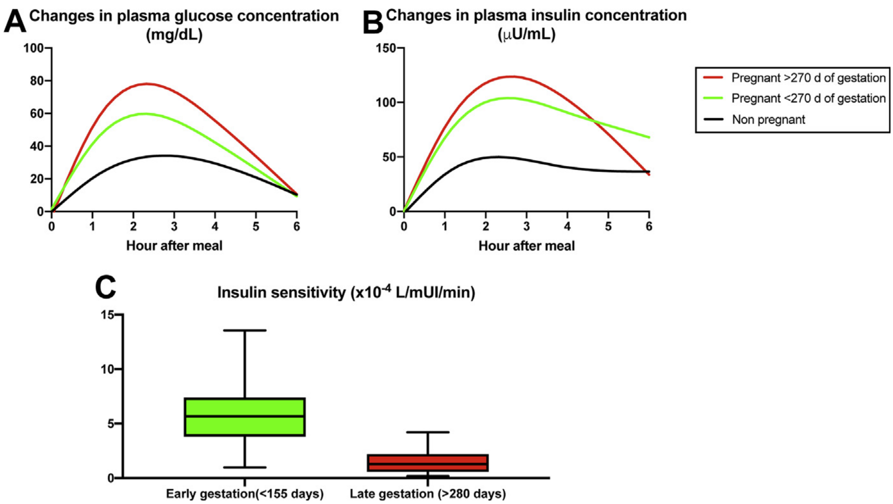


Fig. 2. Evolution of glucose metabolism during pregnancy in mares. (*A*) Changes in plasma glucose concentration after a meal in nonpregnant (*black*, n = 4) and pregnant mares at less than 270 days (*green*, n = 6) or greater than 270 days (*red*, n = 5) pregnancy. Pregnant and especially late pregnant mares are more efficient in absorbing sugar ingested. (*B*) Changes in plasma insulin concentration after a meal in nonpregnant (*black*) and pregnant mares at less than 270 days (*green*) or greater than 270 days (*red*) gestation. Pregnant mares produce more insulin in response to plasma glucose increase, but this response does not change between early and late gestation. (*C*) Insulin sensitivity in early (<155 days, n = 12) and late (>280 days, n = 37) gestation in French-Anglo Arabian mares. Insulin sensitivity decreases as gestation progresses. (Courtesy of Abigail L. Fowden, Development and Neuroscience University of Cambridge; with permission.)

mares than in nonpregnant mares, reflecting the increased need for amino acids to support anabolic processes during gestation.[39,43] Metabolic changes are summarized in **Fig. 3**.

Key points

- During the end of gestation, maternal metabolism allows for maximum glucose redirection to the fetus to meet its needs for full growth.
- The high use of glucose by the fetus leads the mare to use mainly her lipid reserves to meet both her own and fetal needs. This factor highlights the importance of the first months of gestation for the buildup of lipid reserves. A BCS of 5 (1–9 scale), however, should be targeted to avoid the detrimental effects of overweight and obesity on both maternal and fetal health.
- If there has been insufficient lipid storage earlier in pregnancy, the mare will need to also draw on her protein reserves to meet her own energy needs, as well as those of the fetus.

Considering the Season in Mare's Nutrition

Providing optimal nutrition for broodmares requires consideration of multiple factors, each likely to be changing daily over the approximately 340 days of gestation. Feral and semiferal horses manage excellent reproductive performance without human intervention,[48–50] even though body condition loss is often observed in late gestation.[48,49,51] Their success may be attributed to reproductive and feeding strategies

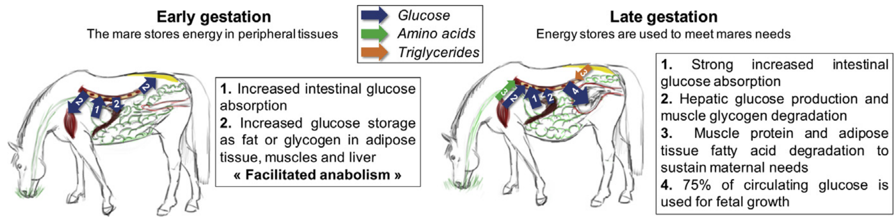


Fig. 3. Evolution of the mare's metabolism during gestation. Changes in carbohydrate, protein, and lipid metabolism allow the mare to provide for the needs of the fetus while having limited food availability in winter.

that evolved over 30 to 40 million years in temperate grassland environments, enabling adaptation to an environment that changed in a predictable manner with each season. Feral and semiferal horse herds today still foal and breed during some of the longest days of the year.[48,50] The connection of reproductive patterns with day length and nutrition are well-recognized,[52] with an evolutionary benefit to synchronizing reproduction, growth, and lactation needs with the environmentally available energy sources.

The diet is the primary source of energy, with adipose (and muscle) tissue serving as a supplementary source when the diet is limited. For domesticated broodmares, the responsibility for nutritional and reproductive management is that of the caregivers. In addition to gestational needs, changes in energy requirements owing to thermoregulation, feed acquisition, and disease in broodmares have been poorly studied. Optimal broodmare nutrition can be achieved by understanding and accounting for each of these factors.

In **Fig. 1**, the DE and CP requirements of broodmares during gestation are overlaid on day length, one of the primary environmental variables that leads to changes in ambient temperature and forage growth and availability. The day length curves represent day length experienced by mares that were due in mid to late winter (February), early to midspring (April), or early summer (June) in the northern hemisphere. Those feeding broodmares can examine this figure and not only consider what the broodmare's requirements are, but also the environmental energy and nutrient sources and sinks by which she is being influenced. Here are a few examples.

- A broodmare at 320 days of gestation and due in February has both high DE and CP requirements, yet day length is short, and ambient temperatures and fresh forage availability are low. Her caregiver should provide high-quality preserved forage and consider a complementary concentrate feed to provide the required DE and CP (including essential amino acids). Another broodmare at the same stage in gestation, but instead due in June has identical requirements, but is in an environment where day length is long, and the ambient temperatures and fresh forage availability are high. In this case, the caregiver can provide significantly less complementary feeds, based on what the mare's environment provides.
- A lactating broodmare at 40 days of gestation and due in February has high DE and CP requirements, primarily related to lactation. Day length is increasing, but the ambient temperature and fresh forage availability are just beginning to increase. To meet the nutritional demands of early lactation, she will require high-quality preserved forage and possibly a complementary concentrate. Another broodmare at the same stage in gestation, but instead due in June, has identical requirements, but is in an environment where day length has already

peaked, leading to higher ambient temperatures and likely plentiful fresh forage availability.

- Finally, Fig. 1 highlights a nutritional opportunity during early and midgestation to increase a broodmare's BCS when energy and nutrient requirements are low (in a natural environment, that is, if the mare is not overweight or obese). Obviously, this period is shorter for the lactating mare, extending from late lactation to the last third of gestation. An example would be a mare who foaled in midspring, was bred 1 month later, and her foal had been weaned at the end of the summer. She should be able to take advantage of good fall forage and relatively low energy and nutrient requirements of midgestation to increase her BCS. Another example would be a mare with no foal at her side, bred in March, taking advantage of spring forage to improve BCS. It will be much more challenging to increase BCS during early lactation, even with good spring forage, or in late gestation, because energy will be partitioned away from the mare and to the rapidly developing fetus.

The BCS is an indicator of energy balance. The BCS is a standardized subjective evaluation of subcutaneous fat stores. The evidence seems to indicate a moderate BCS of 5 (1–9 scale[53]) and 3 (1–5 scale[54,55]) in the broodmare as a target through gestation. Fat stores provide energy when the less predictable short-term environmental patterns of dietary energy result in a deficit. Maintaining sufficient energy savings can help to weather some of the unpredictability in other energy sources and sinks. The majority of evidence indicates that domesticated broodmares are best managed by maintaining a moderate BCS, but there remains some lack of clarity regarding how changing planes of nutrition, and even a changing BCS, may have positive or negative impacts on reproductive performance and progeny success.[5] Future work should focus on investigating how dietary energy and stored energy are communicated to the gonadotropic and somatotropic axes to influence reproduction and growth.[56] The knowledge uncovered here might allow for more precise and nuanced modifications of the diet through gestation to optimize health and performance of the offspring, but also the continued reproductive performance of the broodmare.

Key points

- Feral mares are bred and foal in the longest days, which coincides with increased nutrient availability from grazing. In midgestation (120–250 days of gestation), the fiber content of the forage increases and nutrient availability, as well as day length decrease. Late gestation (250–340 days of gestation) begins with low nutrient availability and short day lengths, but rapidly increasing nutrient availability coincides with exponential fetal growth.
- The body condition of the mare represents her energy savings, and hence her ability to provide for a rapidly developing fetus in late gestation and reproduce in the subsequent breeding season. In most situations it is prudent to maintain a moderate BCS (5/9) throughout gestation, with the understanding that, during lactation and late gestation, energy partitioning will first direct resources to milk and fetal development.

Fetal Nutrition During Pregnancy

Development and role of the placenta

During the first 40 days of the embryo's life, histotrophic secretions (endometrial glands secretions) are the main source of nutrients for the embryo.[4] Briefly, the embryo enters the uterus around 6 to 7 days after ovulation.[57] At this time and for the next 20 to 25 days, the embryo is surrounded by a capsule composed of glycoproteins, which regulates the assimilation of uterine secretions.[4,58] Between 20 and 30 days, the embryo capsule disintegrates so that the trophectoderm (precursor of placenta) is directly in contact with the endometrium.[59] Trophoblastic cells (placental epithelial cells involved in feto-maternal exchanges) develop and protrude into the endometrial glands, which facilitates histotrophic nutrition before implantation.[60,61] Thus, the embryo solely depends on the uterine environment for its development during this period.

The following nutrition and metabolic factors affect the uterine environment in the mare:

- Maternal obesity and excessively increased insulin resistance (knowing that insulin resistance is increased physiologically in response to gestation) in mares has been shown to increase the expression of genes and/or proteins involved in inflammation, lipid homeostasis, growth factors, and cell stress in uterine secretions, the endometrium, and embryos.[62,63] Moreover, alterations in the concentration of lipids involved in cell membrane integrity and signal transduction was observed in embryos of obese mares.[62]
- Conversely, supplementing the diet of overweight mares with omega-3 fatty acids–rich fat sources has been shown to increase the expression of genes involved in embryo and trophoblast development[64] and to decrease expression of proteins involved in inflammation.[63] Nevertheless, this has not been shown to overcome adverse effects of maternal obesity.

Although there is so far little knowledge on specific nutritional needs in early gestation in the mare, the quality of maternal nutrition should not be neglected at this stage.

The placenta is a complex organ involved in gestation maintenance, fetomaternal exchange, metabolism, hormones synthesis and immunity. In the mare, 2 different placentas develop during gestation (**Fig. 4**):

- A transient trophoblast (chorionic girdle) from 30 to 120 to 140 days of gestation.[4]
- A definitive noninvasive placenta that forms close interdigitations (microcotyledons) with the endometrium from 40 days. Two trophoblasts are involved in fetomaternal exchanges. The hemotrophic trophoblast lines the microcotyledons in close contact with the endometrium[65] and ensures exchanges between maternal and fetal bloods. The histotrophic trophoblast is located at the basis of microcotyledons and collects uterine gland secretions. Therefore, both hemotrophic and histotrophic nutrition play essential roles for fetal development.

Of interest is that the placental microvilli lengthen and branch out throughout gestation[66] and can adapt to a certain extent to adverse maternal nutritional conditions. For instance, in moderately undernourished mares, normal fetal growth was observed[67] thanks to placental adaptations:

- Increased volume of microcotyledonary vessels and
- Increased expression of genes involved in amino and fatty acids catabolism as well as vitamin transport.[68]

However, placental structural adaptations cannot overcome severe undernutrition.[69]

Developmental origins of health and diseases and critical periods of embryo and fetal development

The concept of developmental origins of health and diseases stipulates that fetal adaptations to an adverse in utero environment induce permanent changes in the fetus that are revealed as the individual ages or in the presence of an adverse postnatal

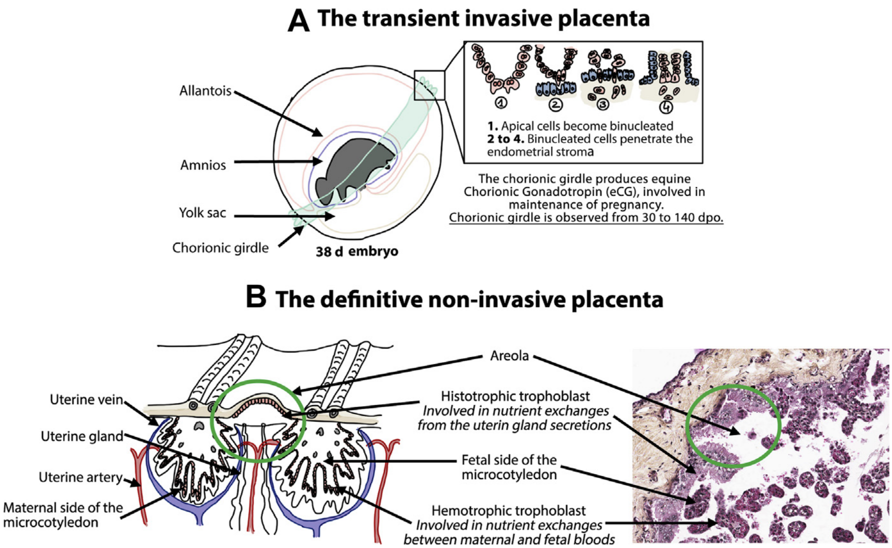


Fig. 4. Transient invasive and definitive noninvasive placentas. (*A*) Development and roles of the chorionic girdles. (*B*) Structure of the definitive chorioallantois. ([*A*] *Adapted from* Allen WR, Wilsher S. A Review of Implantation and Early Placentation in the Mare. *Placenta*. 2009;30(12):1005-1015; and Allen WR, Stewart F. Equine placentation. *Reproduction, Fertility and Development*. 2001;13(8):623-634; and Wooding FBP, Burton G. *Comparative Placentation: Structures, Functions and Evolution*., Springer, 2008; and [*B*] *From* Steven DH, Samuel CA. Anatomy of the placetal barrier in the mare. *J Reprod Fert*. 1975;Suppl. 23:579-582; with permission.)

environment. First demonstrated in humans,[70,71] this phenomenon has also been shown in animal models and domestic animals,[72,73] including horses.[74–77]

The adverse effects on fetal and postnatal development have been shown to differ, depending on the gestational stage at which they were applied.[71] This finding implies the existence of critical periods of development that are directly correlated with the timeline of fetal organ development and maturation. Mechanisms underlying these effects involve modification of gene expression without changing of DNA structure (epigenetic mechanisms[78]), which are sensitive to the environment and can persist until adulthood.

Critical periods of development can be defined depending on the organ concerned (**Fig. 5**). In the horse, by day 35, the embryo has completed most of its organogenesis[4,79] and is referred to as a fetus.[4] This time of gestation also coincides with the onset of placentation. These differences between organs have an important impact on fetal development in response to maternal feeding as the embryo and fetal organ development and maturation depend on the maternal environment (metabolism and nutrition). For more detailed information and references, see **Fig. 6**.

Although the developmental origins of health and diseases and the importance of critical periods have been well-described in animal models and some domestic species, so far, few data are available in horses. Nevertheless, maternal nutrition has been demonstrated to affect foal metabolism, onset of osteochondrosis, and the maturation of reproductive organs (**Fig. 7**).[77]

Key points

- The horse embryo depends solely on nutrients from uterine glands until 30 to 40 days after ovulation. Uterine environment may vary depending on maternal nutrition and metabolism.
- Obese mares may have a more inflammatory endometrial environment, which could impact embryo health and development in the first month of gestation.
- Organogenesis is largely completed at 40 days after ovulation, but organs continue to mature afterward, and critical periods of development vary between organs.
- Maternal environment (and nutrition) from early gestation has long term effects on offspring development.

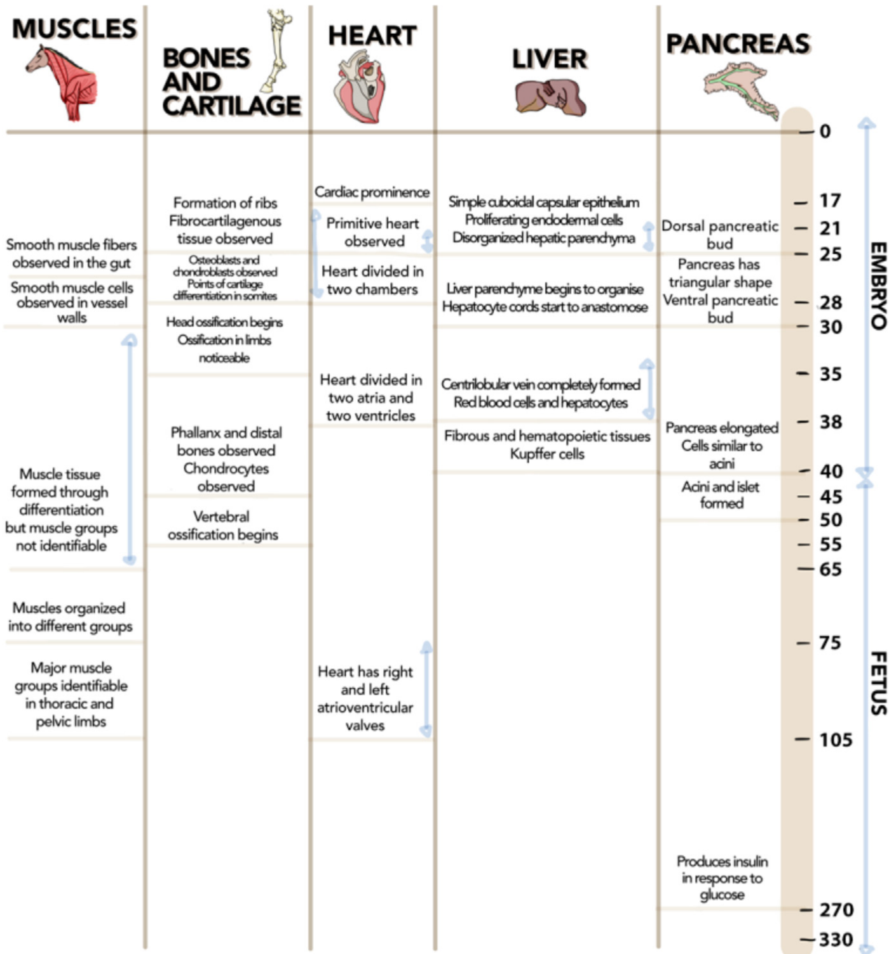
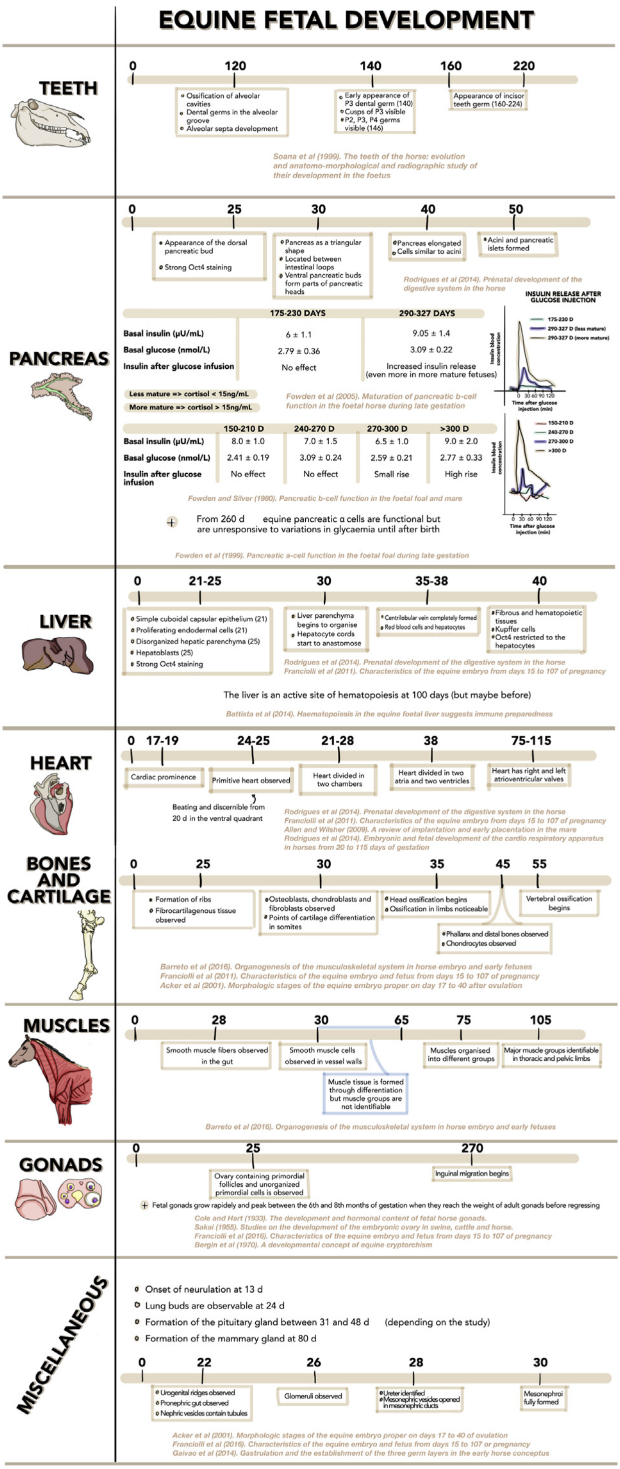


Fig. 5. The timing of organ development in the equine embryo and fetus. *Horizontal lines* indicate the specific day of gestation and *vertical arrows* indicate periods of gestation where observations were made.


EQUINE FETAL DEVELOPMENT
TEETH
0 120 140 160 220
Ossification of alveolar cavities
Dental germs in the alveolar groove
Alveolar septa development
Early appearance of P3 dental germ (140)
Cusps of P3 visible
P2, P3, P4 germs visible (146)
Appearance of incisor teeth germ (160-224)
Soana et al (1999). The teeth of the horse: evolution and anatomo-morphological and radiographic study of their development in the foetus
PANCREAS
0 25 30 40 50
Appearance of the dorsal pancreatic bud
Strong Oct4 staining
Pancreas as a triangular shape
Located between intestinal loops
Ventral pancreatic buds form parts of pancreatic heads
Pancreas elongated
Cells similar to acini
Acini and pancreatic islets formed
Rodrigues et al (2014). Prenatal development of the digestive system in the horse
175-230 DAYS 290-327 DAYS
Basal insulin (µU/mL) 6 ± 1.1 9.05 ± 1.4
Basal glucose (nmol/L) 2.79 ± 0.36 3.09 ± 0.22
Insulin after glucose infusion No effect Increased insulin release (even more in more mature fetuses)
Less mature => cortisol < 15ng/mL
More mature => cortisol > 15ng/mL
Fowden et al (2005). Maturation of pancreatic b-cell function in the foetal horse during late gestation
INSULIN RELEASE AFTER GLUCOSE INJECTION
175-230 D
290-327 D (less mature)
290-327 D (more mature)
Insulin blood concentration
0 30 60 90 120
Time after glucose injection (min)
150-210 D 240-270 D 270-300 D >300 D
Basal insulin (µU/mL) 8.0 ± 1.0 7.0 ± 1.5 6.5 ± 1.0 9.0 ± 2.0
Basal glucose (nmol/L) 2.41 ± 0.19 3.09 ± 0.24 2.59 ± 0.21 2.77 ± 0.33
Insulin after glucose infusion No effect No effect Small rise High rise
150-210 D
240-270 D
270-300 D
>300 D
Fowden and Silver (1980). Pancreatic b-cell function in the foetal foal and mare
From 260 d equine pancreatic α cells are functional but are unresponsive to variations in glycaemia until after birth
Fowden et al (1999). Pancreatic a-cell function in the foetal foal during late gestation
LIVER
0 21-25 30 35-38 40
Simple cuboidal capsular epithelium (21)
Proliferating endodermal cells (21)
Disorganized hepatic parenchyma (25)
Hepatoblasts (25)
Strong Oct4 staining
Liver parenchyma begins to organise
Hepatocyte cords start to anastomose
Centrilobular vein completely formed
Red blood cells and hepatocytes
Fibrous and hematopoietic tissues
Kupffer cells
Oct4 restricted to the hepatocytes
Rodrigues et al (2014). Prenatal development of the digestive system in the horse
Franciolli et al (2011). Characteristics of the equine embryo from days 15 to 107 of pregnancy
The liver is an active site of hematopoiesis at 100 days (but maybe before)
Battista et al (2014). Haematopoiesis in the equine foetal liver suggests immune preparedness
HEART
0 17-19 24-25 21-28 38 75-115
Cardiac prominence
Primitive heart observed
Heart divided in two chambers
Heart divided in two atria and two ventricles
Heart has right and left atrioventricular valves
Beating and discernible from 20 d in the ventral quadrant
Rodrigues et al (2014). Prenatal development of the digestive system in the horse
Franciolli et al (2011). Characteristics of the equine embryo from days 15 to 107 of pregnancy
Allen and Wilsher (2009). A review of implantation and early placentation in the mare
Rodrigues et al (2014). Embryonic and fetal development of the cardio respiratory apparatus in horses from 20 to 115 days of gestation
BONES AND CARTILAGE
0 25 30 35 45 55
Formation of ribs
Fibrocartilagenous tissue observed
Osteoblasts, chondroblasts and fibroblasts observed
Points of cartilage differentiation in somites
Head ossification begins
Ossification in limbs noticeable
Vertebral ossification begins
Phallanx and distal bones observed
Chondrocytes observed
Barreto et al (2016). Organogenesis of the musculoskeletal system in horse embryo and early fetuses
Franciolli et al (2011). Characteristics of the equine embryo and fetus from days 15 to 107 of pregnancy
Acker et al (2001). Morphologic stages of the equine embryo proper on day 17 to 40 after ovulation
MUSCLES
0 28 30 65 75 105
Smooth muscle fibers observed in the gut
Smooth muscle cells observed in vessel walls
Muscle tissue is formed through differentiation but muscle groups are not identifiable
Muscles organised into different groups
Major muscle groups identifiable in thoracic and pelvic limbs
Barreto et al (2016). Organogenesis of the musculoskeletal system in horse embryo and early fetuses
GONADS
0 25 270
Ovary containing primordial follicles and unorganized primordial cells is observed
Inguinal migration begins
Fetal gonads grow rapidely and peak between the 6th and 8th months of gestation when they reach the weight of adult gonads before regressing
Cole and Hart (1933). The development and hormonal content of fetal horse gonads.
Sakai (1955). Studies on the development of the embryonic ovary in swine, cattle and horse.
Franciolli et al (2016). Characteristics of the equine embryo and fetus from days 15 to 107 of pregnancy
Bergin et al (1970). A developmental concept of equine cryptorchism
MISCELLANEOUS
Onset of neurulation at 13 d
Lung buds are observable at 24 d
Formation of the pituitary gland between 31 and 48 d (depending on the study)
Formation of the mammary gland at 80 d
0 22 26 28 30
Urogenital ridges observed
Pronephric gut observed
Nephric vesicles contain tubules
Glomeruli observed
Ureter identified
Mesonephric vesicles opened in mesonephric ducts
Mesonephroi fully formed
Acker et al (2001). Morphologic stages of the equine embryo proper on days 17 to 40 of ovulation
Franciolli et al (2016). Characteristics of the equine embryo and fetus from days 15 to 107 or pregnancy
Gaivao et al (2014). Gastrulation and the establishment of the three germ layers in the early horse conceptus

DEVELOPMENTAL ORIGINS OF HEALTH AND DISEASE

The nutrition of the broodmare during gestation and lactation is not only important for her own health and fertility, but also for the development and health of her foal. The limited information available in horses is detailed here.

Maternal Energy Restriction

Moderate (70%–80% of energy requirements) undernutrition does not seem to affect in utero or preweaning postnatal growth of the foal.[67,80,81] Placental[68] (increased vascularization and nutrient transport) and maternal[67] (decreased insulin secretion following a glucose challenge, lipid mobilization) adaptive mechanisms seem to be sufficient to sustain fetal growth. However, moderate maternal undernutrition is associated with delayed testicular maturation at 12 months of age (beginning of puberty), decreased insulin sensitivity at 19 months of age, and decreased cannon width from 19 months of age.[82] Furthermore, severe undernutrition leads to in utero growth retardation.[69]

Energy Overfeeding and Obesity

Because horses are herbivorous, their body condition varies according to season and the nutritional availability of pasture.[51] A healthy horse in outdoor conditions will generally have a higher BCS in summer than in winter.[83] A horse is considered overweight when its BCS exceeds 6[53] (or 3.5 if using the 1–5 scale[54,55]) and obese when its BCS exceeds 7[84] (or 4 using the 1–5 scale). Obesity can also be chronic, as some horses maintain a high BCS throughout the year, with no seasonal variation[83]; see Megan Shepherd and colleagues' article, "Nutritional Considerations When Dealing with an Obese Adult Equine," in this issue.

A mare can be overweight owing to short-term overnutrition during pregnancy (or excess gestational fat deposition). Alternatively, obesity can result from long-term overnutrition and/or metabolic disease. These 2 scenarios may have different effects on foal health and development:

- *Obesity in late gestation*: Overnutrition during pregnancy, leading to obesity in late gestation, does not affect a foal's birthweight.[80,85] Nevertheless, decreased weight and thoracic perimeter at 2 months of age have been described when excess maternal nutrition is continuous from 2 months gestation.[86] This finding may be due to decreased milk production in overnourished mares during the first 2 months of lactation.[86] When overnutrition begins later (eighth month of gestation), a foal's growth between birth and 3 months of age was not affected[81] (later effects have not been studied).
- *Long-term obesity*: Maternal obesity from the time of insemination, together with decreased insulin sensitivity and increased plasma concentrations of

◀

Fig. 6. The timing of organ development in the equine embryo and fetus, detailed version. Each organ is separated by *horizontal lines* and represented by an icon. Part 1 features the teeth, pancreas, liver, and heart. Part 2 features the bones and cartilage, muscles, gonads, and a summary of neurons, lungs, pituitary gland, mammary glands, and kidneys. For each organ, a timeline expressed in days after ovulation presents the major developmental events, described in brown boxes. Detailed results in fetal insulin production are also provided for pancreas (tables and figures). For muscles, the *blue line* over the timeline highlights a period more than a set point. References are written directly in the figure for clarity.

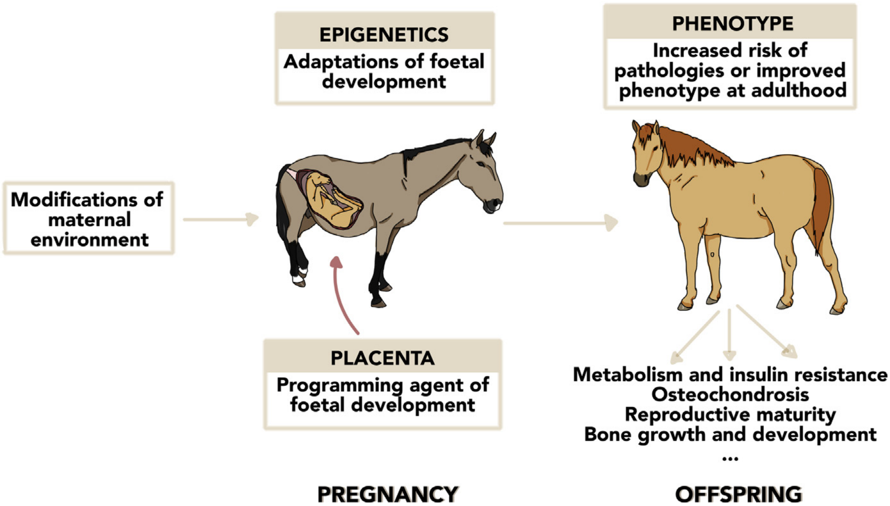


Fig. 7. The principles of the developmental origins of health and disease in the horse.

inflammatory biomarkers in late gestation, did not affect the birth weight or the growth of foals when monitored until at least 18 months of age.[87,88]

- Nevertheless, maternal obesity was associated with increased systemic inflammation, decreased insulin sensitivity, and an increased incidence of osteochondrosis in foals.[87] Maternal adiposity at the base of the tail, as measured by ultrasound assessment, has also been positively correlated to the same measurement in 4-month-old foals.[89]

The Source of Energy Matters

The use and effects of starch

Epidemiologic observations demonstrated that the risks for a foal to develop osteochondrosis were 11-fold higher when the broodmare's diet included "concentrated feeds" during gestation, compared with forage only.[90] This study, however, did not consider the quantity or the source of the concentrates given to the mares, albeit experimental studies performed using starch-rich barley as a concentrate validated this observation.[67] Nevertheless, in field conditions, forage is sometimes not available in sufficient quantity and quality to cover the mare's needs and the provision of an energy-rich concentrated feed remains a practical necessity. To decrease the potential detrimental effects of starch on foal development, starch quantity per meal and per day has to be closely monitored.

The results from several experimental studies, where the source of energy used was known can help to build these recommendations:

- *Study 1*[67]*:* Mares received 1.7 g of starch/kg body weight per meal as barley in addition to hay and haylage, or hay and haylage only during the last 4.5 months of gestation. Mares fed with barley produced more foals affected with osteochondrosis lesions at 6 months of age (45%) compared with mares fed with hay and haylage only (17%). This difference was not observed at 12 and 18 months of age, with some lesions spontaneously resolved and some new lesions in different individuals.[82]
- *Study 2 (MR, PCP personal communication):* Mares were fed with either a maximum of 0.75 g of starch/kg body weight per meal (range, 0.40–0.75,

n = 5) or a minimum of 1.1 g of starch/kg body weight per meal (range, 1.1–1.6, n = 5) during the last 2 months of gestation. Both groups received the same amount and type of forage during gestation. As a result, 12-month-old foals born to mares fed the high-starch meals experienced a higher incidence (80%) of osteochondrosis lesions, as compared with foals of mares fed low-starch meals (20%) (**Fig. 8**). Unfortunately, the foals were not monitored further.

These results indicate that excess starch provided to mares per meal has an impact on the osteoarticular development of foals. However, the role of starch source has not been fully investigated. Regardless, for now, the authors recommend that the starch plus sugar intake in pregnant mares should not exceed 1 g/kg of body weight per meal. Limits per day are currently unknown.

Feeding the broodmare with starch-rich concentrates may also affect colostrum quality; it has been shown to decrease the IgG colostrum concentration at birth, in comparison with mares fed with forage only.[12,91] A French epidemiologic study showed that mares producing foals with osteochondrosis lesions had colostrum that was poorer in IgG compared with mares that produced foals that remained healthy.[92]

The use and effects of fats

Because the diets richer in starch were also more energy dense in the previously mentioned studies, discrimination between the effect of starch and that of energy content per se on the foals' osteoarticular development is impossible. Feeding pregnant mares with a diet rich in starch (corn, >1 g starch/kg body weight per meal) was shown to alter the glucose metabolism of foals during preweaning growth compared with a diet rich in lipids (corn oil, <0.15 g starch/kg body weight per meal, 14% DM fat). These results indicate that vegetable oil or fat may be a good way to increase the energetic density of the diet of pregnant mares, without increasing the starch content, thus limiting detrimental effects on foal's development.[93]

The fatty acid composition may be important, because some fatty acids have immunomodulatory properties and could, therefore, affect the pathways involved not only in fertility, but also in inflammation. Essential fatty acids are also involved in fetal neuronal development. Thus, dietary fatty acids could affect maternal and uterine environment quality and, subsequently, embryo and fetal development. This point is particularly important for mares fed dry forage and concentrates, because the omega-3 to

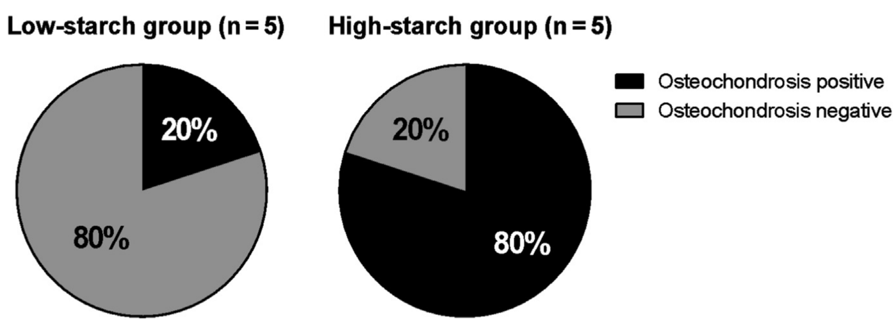


Fig. 8. The incidence of osteochondrosis at 12 months of age was higher in foals born to mares fed with high-starch meals (>110 g/100 kg body weight) compared with foals born to mares fed with low-starch meals (<75 g/100 kg body weight) (*MR, PCP personal communication*).

omega-6 ratios are low in dry forage and especially in cereals, in contrast with grass and fresh forage.[17,94,95] Because horses evolved grazing on fresh grass, the dietary omega-3 contents and omega-3 to omega-6 ratio are most probably important, especially around conception. However, there is little confirmed information regarding the exact quantities and ratios that might be optimal.

For now, supplementing mares with fat sources rich in omega-3 fatty acids has only been shown to increase the total omega-3 and docosahexaenoic acid transfer from the dam to the fetus at birth[96,97] and to increase lymphocyte proliferation in 7-day-old foals.[98] No other effects on colostrum quality or foal growth have been demonstrated.[96–98] The effects of maternal supplementation with omega-3 fatty acid during gestation on maternal and foal metabolism remain unknown. Both fish/algae and flaxseed oils have been studied independently, but more studies are needed to compare the efficiency of both sources. For now, we recommend flaxseed oil because it is more practical.

The use and effects of proteins

Protein needs are increased during gestation in mares. The quality of proteins, and especially the content of essential amino acids, such as lysine and threonine, is crucial for foal development.[1] It must be noted that, although the role of protein excess in foals in the development of osteochondrosis lesions has been ruled out,[99] to the best of our knowledge, no studies have been performed on the effect of overall protein quality fed to broodmares on the long-term health of the foals.

As an example, L-arginine is an essential amino acid during pregnancy and growth in the horse. The particular abundance of arginine in mare's milk seems to indicate that L-arginine may be needed in much greater proportions in foals than in the offspring of other species.[100] Supplementation with L-arginine (100 g/d) during the last 4 months of gestation to primiparous mares improved their glucose metabolism and increased the placental expression of genes involved in glucose and fatty acid transport, but did not affect placental and birth weights or the growth of foals monitored until 2 months of age.[47] In a study where mares' parity was not described, supplementation with 100 g of L-arginine/day from 21 days before foaling increased uterine arterial blood flow and shortened the gestational length by 12 days, without affecting the placental and foal weight at birth.[101] The effects on gestational duration were, however, not observed in another study supplementing 50 g of L-arginine per day in pregnant mares from 90 days before foaling.[102]

Further studies are needed to determine the effect of protein deficiency or excess, as well as the effect of protein quality during gestation, on foals' long-term health. Interestingly, alteration of protein intake in other species has been shown to affect the behavior, health and lifespan of the offspring.[103] Because some amino acids can affect absorption and cell use of other amino acids, dietary amino acid contents should be checked in accordance to the known optimal ratios, which may change between the different physiologic states.[1]

Key points

- Overnutrition and undernutrition of the mare are detrimental to foal's health. The energy content of the mare's feed should be considered according to mare's BCS and DMI.
- Forage should be the basis of a broodmare's diet.
- Broodmares should not receive more than 1 g of starch plus sugar/kg body weight per meal to limit the detrimental effects of nonstructural carbohydrates on a foal's metabolic and osteoarticular health.

- Vegetable oil or fat may be a good way to increase the energy content of the diet.
- The quantity (and ratio to omega-6 fatty acids) of omega-3 fatty acids may be important.

Feed Supplements: Useful for Improving the Health of the Future Foal?

As presented in section 1.3, the geographic location, season, soil factors, plant species, state of vegetative growth, and fertilization and irrigation can affect the amino acid and fatty acid profiles, as well as the vitamin and mineral content of the forage. Moreover, using cereal grains to provide additional energy can alter the balance between minerals. Depending on these factors, supplementation is not always needed and should be carefully thought out.

Some vitamins and minerals easily cross the placenta to be delivered to the fetus during gestation. In contrast, some are weakly transported through the placenta and their storage in colostrum is therefore essential for the newborn foal. For instance, vitamins A and E are poorly transferred through the placenta but are concentrated in colostrum,[104] whereas iodine is actively transferred through placenta and is also rich in colostrum and milk.[105] Some other nutrients, like copper, are stored in the fetal liver during gestation and used during fetal growth to compensate for low milk concentrations.[106]

Vitamins

Studies on the effects of vitamin excess and deficiency on the health of foals are lacking. In other species, it has been shown that maternal imbalance in D and B group vitamins could affect not only in utero growth, but also long-term growth, metabolism diseases and behavior of the offspring.[107] As presented in Section 1.3, vitamins E and D, as well as β-carotene, concentrations are high in fresh grass in spring and summer, implying that supplementation may not be needed if mares are kept in pasture and bred between spring and summer.[21] Conversely, mares bred out of season or fed dried forage would benefit from vitamin supplementation as observed in the following studies.

Natural vitamin E (RRR-α-tocopherol) oral supplementation, fed above the National Research Council (NRC) requirements (200%–300%)[1] has been shown to increase the concentration of vitamin E in the colostrum, milk, and plasma of neonatal foals as well as the immunoglobulin concentration in colostrum and plasma of 3-day-old foals, compared with mares fed a diet deficient in vitamin E (15%–30% of the NRC requirements).[108] Moreover, oral supplementation with β-carotene (1000 mg/d) to mares fed with hay and concentrates from 2 weeks before foaling, increased the concentration of β-carotene in colostrum and plasma of foals at 1 day of age.[109] To our knowledge, long-term effects of these supplements on foal health and development have not been studied yet. The observed increased insemination success with β-carotene supplementation, however, may imply an effect on the uterine environment, and then, on embryo and fetal development.[109]

Minerals and microminerals

Calcium and phosphorus. The effects of an inverse calcium:phosphorus ratio during pregnancy have not been studied, but may negatively impact the foal's bone and articular development. Mares consuming diets providing 80% of the NRC requirement for calcium (Ca:P = 1.1, lower limit) during late gestation gave birth to foals with thinner and weaker cannon bones, which persisted through the period of observation (10 months of age).[110]

Copper. Copper is a micromineral essential for the development of cartilage and bone. Although pregnant mare copper supplementation above NRC requirements (200%–300%) have been shown to decrease the prevalence of articular cartilage lesions in growing foals,[111,112] there is, so far, no substantial evidence that pregnant mares should be supplemented over the recommendations if the diet is correctly balanced (especially the Cu:Zn ratio).[1,113] Maternal copper supplementation does not affect milk copper concentration or foal plasma copper concentrations, but increases the foal's liver copper storage.[106] These results imply that fetal liver copper storage is essential for a foal's osteoarticular health, especially because supplementing the foal after birth will not counter the detrimental effects of in utero deficiencies.[112]

Selenium. Selenium deficiencies during gestation have been associated with white muscle disease in foals, a myodegenerative pathology, affecting skeletal and cardiac muscles and leading to the death of the foal in most cases.[114] The form of selenium distributed to pregnant mares is potentially important, as inorganic and organic selenium are not absorbed and incorporated into body tissues equally.[115,116] In fact, supplementing the mares with selenium yeast in the 2 last months of gestation increased the expression of genes involved in the proliferation and cellular immune response in lymphocytes of growing foals, compared with mares supplemented with sodium selenite,[117] which may imply improved foal immunity. Moreover, supplementation with selenium yeast (0.65 ppm vs. 0.35 ppm Se in total diet [650% vs. 350% of NRC requirements]) during the last 4 months of gestation has been shown to increase the selenium concentration in the plasma and muscle of foals, but without affecting the glutathione peroxidase activity in the foal's plasma.[118] Special caution must be paid to selenium excess because the optimal range is narrow, that is, the level of toxicity close to the recommended amounts (0.2 mg/100 kg body weight is recommended in pregnancy, and the safe upper limit is considered to be 1 mg/100 kg body weight[1]). Organic forms of selenium may have a stronger beneficial effect on foal development compared with inorganic selenium, but more studies are needed to confirm these effects.

Iodine. Thyroid function is involved in metabolism, bone development and growth. Foals have a very high iodine serum concentration at birth that slowly decreases during growth,[105] which correlates to tri-iodothyronine and thyroxine plasma concentrations.[87] Transplacental iodine transport may therefore be efficient. A strong excess or deficiency in iodine in the maternal diet have been linked to congenital hypothyroidism in foals, which can be characterized by thyroid gland hyperplasia and musculoskeletal abnormalities in foals, as well as an increased gestational duration.[119] More work is needed to study the effects of iodine intake on long-term foal development. Seaweed supplementation can cause iodine excess; therefore, iodine levels in seaweed supplements have to be carefully considered before feeding seaweed to pregnant mares.

Other minerals and microminerals. Other minerals and microminerals are also involved in metabolism regulation (chromium), inflammation and oxidation (iron), as well as bone and teeth development (fluorine), and their imbalances may also impact the long-term health of the offspring. Mineral supplementation should be developed in accordance with the balance between minerals and microminerals, because it can affect their absorption and cell use.[1] More work is needed to develop specific recommendations for pregnant mares.

The use of probiotics. The intestinal microbiota in early life can impact metabolic health, growth, and behavior of the individual.[120] The equine microbiota influences the risk of resistance to endoparasites,[118] colic[121] and metabolic syndrome.[122] However, few studies have focused on the effect of the mare's gut microbiota on foal health. Few prebiotics have been tested in pregnant mares so far, despite a large number of yeast and bacteria strains available on the market. Effects observed from one strain of probiotics cannot be extrapolated to other strains. Safety of strains and effective dosing are unknown, which calls for a cautious use of these nutraceuticals in mares (see also Ruth Bishop and David A. Dzanis' article, "Staying on the Right Side of the Regulatory Authorities"; and Ingrid Vervuert and Meri Stratton-Phelps' article, "The Safety and Efficacy in Horses of Certain Nutraceuticals that Claim to Have Health Benefits," in this issue).

Pregnant mare probiotic supplementation, however, has shown some beneficial effects on foal health and development. Pregnant mares were supplemented with live yeast (*Saccharomyces cerevisiae* CNCM-I1079, 7.10^{10} colony-forming units per day) from 8 days before to 4 days after foaling. Their foals had a decreased quantity of *Escherichia coli* and enterobacteria in the feces at 10 days of age, an increased proportion of normal-looking feces, and a tendency to an increase in the average daily gain from birth until 20 days of age.[123] In another study, the supplementation of pregnant mares with fermented feed products from 45 days before foaling until 60 days after did not affect the fecal pH of mares or the fecal concentration of culturable bacteria, but increased the maternal fecal proportion of acetate. Moreover, foals born to supplemented mares had an earlier establishment of gut microbiota and gut function, possibly leading to an increased weight between 19 and 60 days of age.[124]

In conclusion, studies on the long-term effect of probiotics during pregnancy and/or growth are needed to help develop recommendations on the use of these supplements in breeding horses. It is also worth noting that safety in pregnant animals has not been tested for most supplements. The effects of other nutritional supplements on other aspects, such as muscular and cardiovascular development as well as bone strength and resistance, remain to be studied in the horse.

Key points

- Supplementation must be carefully thought out because some supplements have not been tested for safety.
- Vitamins and minerals in excess can be as detrimental as deficiencies for the health of both the mare and the foal.
- Nutritional balance is important when supplementing amino acids, vitamins and minerals.
- More studies are needed to confirm beneficial effects of supplements in pregnant mares on long-term health of the foals.

SUMMARY

Although the basic recommendations for broodmare nutrition are known, as described in the first part of this article, there are many variations in the needs of mares according to season and possibly breed, age, or even parity. Combined with the discordant studies, more research is therefore needed. The mare's diet can positively or negatively affect her foal's health. Limiting the intake of starch and sugar rich concentrates especially and maximizing the intake of forage may help prevent nontransmittable diseases such as osteochondrosis and possibly, the in longer term, equine metabolic syndrome. Long-term studies are urgently needed to answer these questions.

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DISCLOSURE

The authors have nothing to disclose.

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