

# LINKS BETWEEN NUTRITION AND REPRODUCTION IN CATTLE

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## Abstract

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Situations in which nutrition modulates reproductive function, and targets involved, are identified, particularly in relation to initiation of cyclicity (at puberty, during the post-partum period or after induction of ovulation), fertility and induction of ovulation. The usefulness and pertinence of measurements of body weight variations, body condition score, nutritional balance or blood metabolites (glucose, ketone bodies, free fatty acids, cholesterol, urea and amino acids) to evaluate nutritional status in this context is considered. Leptin could play a central role in causal mechanisms linking nutrition and reproduction, in conjunction with somatotrophic axis, insulin, opioids, and neuropeptide Y.

## 1. INTRODUCTION

Nutrition is acknowledged as a modulator of reproductive function [1-4]. If the influence of quantitative variations of energy prevails, nitrogen [5, 6], vitamin [7] and mineral [7, 8] effects are also widely believed to be involved.

We shall identify here, situations in which such influences occur in cattle, and the target functions involved. Indicators which may reveal and quantify nutritional status of importance for reproduction will be explored and an attempt will be made to describe, on the basis of actual knowledge, mechanisms which could account for such effects.

Situations regarding females, especially energy metabolism, will be emphasised. But nutritional influences on male reproduction, which concern the onset of puberty as well as the components of the sexual activity of the adult (behaviour, semen production), underfeeding, overfeeding, protein deficiency, minerals and vitamins represent an important background for the management of animals for artificial insemination or natural service.

Practical situations in which nutrition affects female sexual activity are numerous, and differ as a function of production systems. In intensively managed dairy cows, the most frequently identified syndromes [9] concern too thin high producing dairy cows, primiparous females with high milk production, overfed dry cows with a fatty liver and developing ketosis, animals suffering from ration imbalance during the transition period and females with high blood urea concentrations in relation to excess protein intake and dietary energy shortage. Dairy cows, for whom conserved forage is an important part of the ration, and extensively managed cattle (e.g. European mountain-living breeds) face under-nutrition situations. It is the same for beef cows suffering both poor winter feeding, the consequences of suckling and difficult environmental factors. Flushing strategies can be used to override such energy-linked limiting conditions. In tropical *taurus* and zebu cows, underfeeding is generally very much marked in a seasonally-driven pattern, and in the context of suckling, pathological situations and environmental stresses.

## 2. FUNCTIONS RESPONSIVE TO NUTRITIONAL FACTORS

### 2.1. Cyclicity

#### 2.1.1 Puberty

Age at puberty determines the age at first calving and the productivity of the cow during all its lifetime. In certain systems, early mating is sought, and growth controlled consequently, in order to obtain calving at two years of age. In other cases, puberty is “abnormally” delayed due to environmental and nutritional factors and action can be taken to reduce the inactive period. The influence of feeding on puberty is definitely proved with a block on first ovulation after the prevention of LH secretion when feeding is severely restricted. Correcting nutrition allowed an increase of gonadotrophine secretion at a given weight of the animals, and, consequently, steroid and gamete production [10]. The wide range of mean age at puberty recorded by Mukasa-Mugerwa [11] in zebu cows (from 16 to 40 months according to the breed and environmental conditions) implies a negative effect of inadequate feeding conditions on this parameter. This has been confirmed by the demonstration of an influence of the regime on the age at puberty [12] in experimental conditions, or by values as low as 14 months when conditions are satisfactory [13].

#### 2.1.2. Post-partum

The post-partum resumption of ovarian cyclicity is a critical determinant of the calving interval and, therefore, of overall productivity in cattle, assuming that the one-calf-per-one-year postulation is valid in the economic circumstances of that environment. The occurrence of the first post-partum ovulation is the result of the removal of the negative feedback, and of the restoration of the positive feedback, of the oestrogens modulating the GnRH secretion, and, hence, ovarian activity. The interaction of nutrition, especially during energy restriction, with this system is well documented in the dairy cow [3, 14-17]. Under-nutrition during the post-partum period delays first ovulation and due to occurrence of a cyclic anoestrous period, the first oestrus [3, 18], while the most severe nutritional conditions produce true anoestrous situations.

In beef cows the post-partum period is longer due to low LH basal values and pulsatility, and weak oestradiol secretion by the follicles [19]. First ovulation tends to occur at the end of the third follicular wave, compared to the first wave for dairy cows [20]. Suckling and a low level of nutrition [21-26] prolong suppression of LH pulses: a 26-day difference was observed between low (0.7 x maintenance) and high (2 x maintenance) planes of nutrition [27]. In a field survey, Grimard [28] observed that cyclicity at 76 days post-partum was 15% for females with poor body condition score (BCS) (2.5) versus 25% for animals in better body condition; total controlled factors, including those relating to nutrition, accounted for 28% of the variability of post-partum cyclicity. In beef cows, suckling is not an absolute limiting factor,

provided feeding is sufficient. On the other hand, in zebu cattle, suckling has a deeper influence, and ovulation is more likely to occur after weaning, if the nutritional status is adequate [29].

#### 2.1.3. Response to the induction of ovulation

Grimard [28] observed that anoestrous primiparous Charolais cows losing body weight after calving did not respond to a treatment of induction of ovulation, while 56% of those in increasing condition ovulated. A 22-day long flushing period beginning 10 days before the induction treatment had a positive effect on the percentage of ovulations (75 vs 56%) [30] in

primiparous females. These responses can be explained by an action on the follicular development (number of follicles, maximal size) [31, 32].

## 2.2. Fertility

The success of mating or artificial insemination has been shown to be influenced as well by energy restriction (with variations of 12 to 25% between groups differing according to the extent of energy supplies [3]) and by protein imbalances: Diskin [33] showed that supplementation of dairy heifers by non rumen degradable protein during spring improved conception rate (76% vs 58%), believed at the time to be due to the negative effect of excess of degradable proteins and ammonia at the beginning of the grazing period.

## 2.3. Fecundity

The ability of the cow to produce multiple ovulations, spontaneously or after a super-ovulation treatment as practised for embryo transfer, is sensitive to nutrition. Lucy *et al* [34] observed that cows ovulating spontaneously two or more ovocytes during the post-partum period had a greater energy balance (7.58 Mcal/day) than cows with 1 (3.89 Mcal/day) or no (3.82 Mcal/day) ovulation. The response to a super-ovulation treatment [35, 36] is affected both by under-nutrition and by over-nutrition. We have shown that, in farms, nutritional parameters account for 30% of the variability of embryo collection [37]; where energy supplies were low (10 Forage Units (FU)/cow/day), total embryos ( $5.1 \pm 3.2$ ) and freezable embryos ( $2.5 \pm 2.4$ ) were significantly lower than when energy was high (16 FU) ( $8.9 \pm 5.7$  and  $5.6 \pm 3.3$  for total embryos and freezable embryos, respectively). On the other hand, overfeeding animals, which is frequent in intensive dairy cow production, based on maize silage rations, may have a depressive effect on embryo collection [38-41], which is in accordance to the positive effect of a transitory feed restriction ("negative flushing") in overfed beef heifers [42].

As mentioned above, underlying mechanisms of nutritional effects on reproductive functions are numerous and concern central as well as peripheral levels. Control of gonadotrophin secretion, particularly of LH, is obviously involved in a great proportion of these actions [17, 21, 43, 44]. Modulation of the sensitivity of hypothalamic nuclei to feedback of steroids is postulated. Response of the hypophysis to GnRH may also play a role. At the peripheral level, the capacity of steroid secretion by the follicles, the number and development of follicles have been reported to respond to nutritional factors [31, 32, 45-47]. It remains to be determined what metabolic signals are responsible for the interaction with these targets.

## 3. THE SEARCH FOR RELEVANT INDICATORS OF NUTRITIONAL STATUS

There is a need to evaluate the effect of feeding (resulting from management decisions, or dependence on pasture conditions) on the animal, first quantitatively and secondly qualitatively, to search for key elements taking part in the causal relationships.

### **3.1. Weight variations**

At puberty, a threshold value of weight, more than age, is assumed to explain the onset of sexual activity [10]. Conversely, cyclicity of heifers or of post-partum cows seems to be mostly associated with changes (gains or losses) in weight. According to Grimard [28], cyclicity of beef cows is affected when females loose more than 30 kg after calving. We observed, in post-partum dairy cows [18], that identical regimes had different impacts on the weight variations of cows from different breeds and on the resumption of sexual activity. Hence, weight variations may not be the best indicator of the level of nutrition. Its measure, even if easy, is not very precise, and concerns mainly long-term variations of the status of the animals.

### **3.2. Body condition**

Mean calving interval in beef cows is influenced by body reserves, estimated by BCS, as demonstrated by a large field study [48]. In dairy cows, [49], females with high (3.0) BCS at first breeding had 8.8 fewer days to first AI and 6.4 fewer days to conception than cows with lower BCS; Butler and Smith [15] observed that the loss of one unit of BCS resulted in 15 days more to first ovulation, and in a marked reduction of the conception rate (17% compared with 65% for cows losing less than 0.5 unit of BCS). Recent observations on zebu cows have shown that cows able to maintain their body condition through the early post-partum period had shorter interval to first oestrus [50], and that post-weaning supplementation could reduce the interval to first ovulation in poor condition females, as one unit loss (on a scale of 9) led to a 40 % increase of the time to return to cyclicity after weaning [29].

### **3.3. Nutritional balance**

In the post-partum dairy cow, a correlation has been observed ( $r = -0.60$ ) between the calving to ovulation interval and the mean energy balance for the first 20 days [51]. Energy balance affects the number of follicles per cow and the pattern of follicular distribution [34]. But, more than quantitative absolute values, it seems that the dynamics of energy balance during the post-partum period accounts for the induction of the first ovulation. Canfield and Butler [52] observed that the increase of LH pulsatile secretion preceding ovulation occurs in a close time-relationship with the minimal value of energy balance ( $r = 0.76$ ). Accordingly, this parameter appears to be of the utmost importance for the understanding of the relationships between nutrition and the central control of reproduction. The question arises as to how such information is transmitted to the nervous system. Calculation of a nutritional balance requires the knowledge of the inputs (i.e. individually controlled feeding of animals, and known nutritional value of feedstuffs), and of the requirements, according to genotypes and physiological situations, which is not yet achieved in all circumstances.

### **3.4. Blood metabolites**

Blood metabolic profiles have been developed, from the beginning of the 70's, to predict energy and nutrient intakes, milk production, and reproductive variables on an herd-basis [53, 54]. Basically, a negative energy balance induces hypoglycemia, hypoinsulinemia, and high cortisol, GH and epinephrine levels, which result in a mobilization of body reserves (lipids and proteins); lipolysis leading to an increase of free fatty acids and ketone bodies in the circulation [15, 55, 56]. Use of such profiles is however dependent on specific situations

(breed, production system, management), and the metabolic parameters may not always be indicative of reproductive status of the herd, as pointed out in dairy [57], or zebu [58] cows. Suitable reference values have to be considered for each given situation. Pertinent indicators to assess nutritional status would respond to alimentary imbalances, and would be associated with reproductive disorders.

#### 3.4.1. *Glucose*

Blood glucose (and also blood  $\beta$ -hydroxybutyrate) responds to both quantitative and qualitative variations of the ration in ruminants [27, 55, 59]. Clear associations with reproductive parameters have been demonstrated: in experimental herds, Miettinen [60] observed a positive relationship between blood glucose and reproductive performance (delay for uterine involution, onset of ovarian activity, interval to conception) in dairy cows; Whitaker [61] found a better prediction of the same parameters when glucose and  $\beta$ -hydroxybutyrate values measured at the beginning of the post-partum period were combined. In a survey involving 18 dairy herds in Sweden [62], high glucose values at the first insemination were found to be correlated with higher rates of pregnancy. In practice the collection of blood samples and analysis for glucose is quite difficult to achieve consistently. A direct action of glucose on the central nervous system can be suspected from experiments manipulating specifically blood glucose levels: the infusion of phlorizine, which inhibits renal reabsorption of glucose and induces hypoglycemia, lowers LH concentrations and pulse amplitude in cycling cows [63]. Similarly, 2-deoxy-glucose injections block ovulation in cattle [64]. While secondary effects of hypoglycemia cannot be excluded, the glucose availability as an energy fuel for the cells of the CNS could act as a signal for metabolic status on neuronal control of GnRH secretion.

#### 3.4.2. *Ketone bodies*

Elevated oxidation of free fatty acids in liver in case of an imbalance of energy metabolism gives rise to ketone bodies ( $\beta$ -hydroxybutyrate and aceto-acetate). Particularly, accumulation of reserves and excess fattening of cows during the dry period predisposes to ketosis (fat cow syndrome). In such cases, a negative effect on fertility has been established [60, 61]. A correlation ( $r = 0.51$ ) between  $\beta$ -hydroxybutyrate and interval between calving and first service have been observed in an experimental herd [65]. In a large field study conducted in 474 herds [66], ketosis, estimated by milk acetone, was associated with a lengthening of interval from calving to first service, a decrease of fertility and an increase of ovarian cysts.

#### 3.4.3. *Free fatty acids (FFA)*

High levels of FFA are the sign of lipomobilization and negative energy balance, and are well documented in underfed animals [15, 17, 27, 55, 56]. However, depletion of lipid reserves in extreme conditions leads to low levels of blood FFA, as shown by Yameogo [67] in N'Dama  $\times$  Zebu crossbred cattle during the dry season in Senegal. Whereas glycemia fell (from 0.55 to 0.35 g/L) from January to June, due to a shortage of feed, FFA values remained low (0.17 to 0.22 Eq/L) and increased only after the rainy season (0.35 Eq/L in October), probably after mobilization of reconstituted lipid reserves. We observed (unpublished data) similar low levels of FFA in food-deprived dairy heifers in negative growth (0.20 vs 0.38 Eq/L in control heifers), in association with small adipose cells size ( $65\mu$  vs  $142\mu$  in control).

Post-partum energy restriction of suckled beef cows [32] affected plasma concentrations of FFA (0.309 vs 0.168 Eq/L), with a significant negative correlation with LH pulse frequency

( $r = -0.61$ ) at 30 days post-partum. A direct effect of FFA on LH secretion has not been demonstrated after elevation of blood FFA by lipid infusion [17, 68].

#### 3.4.4. Cholesterol

As energy intake seems to have no effect on cholesterolemia, which is rather influenced by qualitative aspects of the composition of the ration [69], this parameter cannot be used as an indicator of the energy status. Nevertheless, a clear association has been demonstrated between post-partum cholesterol level and fertility (days-to-conception) in Holstein cows [70]. Elevated cholesterolemia consequence to a high-fat diet supplementation during the post-partum period in Brahman cows [71] or in beef heifers [68] was associated with increases in the number of medium-size follicles. Steroid synthesis by the follicle [71] or the corpus luteum [69, 72] are activated in such situations. As a consequence of these ovarian effects, high cholesterol levels result in better embryo collection in superovulated cows [73-75]. We observed similar effects in a field study [76]: in farms in which mean level of glycemia and cholesterolemia were simultaneously high, the number of transferable embryos ( $8.8 \pm 7.4$  vs  $4.9 \pm 2.7$ ,  $P < 0.15$ ) and of freezable embryos ( $6.5 \pm 5.4$  vs  $2.6 \pm 2.2$ ,  $P < 0.06$ ) were higher than in farms in which females had low levels of these two metabolites.

#### 3.4.5. Urea and Amino acids

The digestion of proteins results in ammonia, which is partly converted to urea in the liver. In this way, blood urea can be used as a marker of protein nutrition. Blood urea responds also to the protein/energy balance of the ration, and reflects the protein reserve use. On the basis of a large scale field study, Lee [53] confirmed the relationship between protein intake and blood urea. When the protein content of the ration was increased from 14 to 20% of CP [6], blood urea levels rose from 127 to 293 mg/ml. On the other hand, when the degradability of proteins were enhanced, uremia increased [43, 77]. High values of uremia are associated with an increase of calving to first service ( $r = 0.75$ ) and calving to fertilisation ( $r = 0.63$ ) intervals in dairy cows [65]. However, a review of the literature has failed to show evidence of direct causal links between high blood urea and poor fertility [Whitaker, personal communication]. Mobilization of body protein, which can be assessed by 3-methylhistidine blood levels, has not been found to be correlated with duration of post-partum anovulation in dairy cow [78].

## 4. CANDIDATE MECHANISMS

### 4.1. Growth hormone and insulin-like growth factors (GH-IGF1)

Growth promoting, galactopoietic, anabolic, lipolytic and diabetogenic effects of the somatotrophic axis are mediated by growth hormone (GH) and insulin-like growth factors

(IGF's) [79]. Their blood concentrations are influenced by nutrition: GH is elevated and IGF1 lowered during feed restriction in cattle [80], as in other species. The relationships between this system and reproduction can be suspected on the basis of observations and experimental interventions. Cows selected for high twinning frequency (29.8 vs 6.2% in controls) had greater IGF1 concentrations in their large follicles ( $327 \pm 28$  vs  $243 \pm 29$  ng/ml) and more large follicles than control animals [81]. Significant correlations have been calculated between IGF1 blood concentrations and luteal function [72], and between GH and IGF1 levels and follicular growth [82] in dairy cows. Chronically low IGF1 blood levels, caused by a GH receptor deficiency in cows, resulted in abnormal patterns of follicular waves, slow

development of corpora lutea, and low progesterone levels [83]. Conversely, the administration of exogenous GH to cows treated for super-ovulation significantly increased the number of fertilised oocytes ( $4.5 \pm 4.6$  vs  $2.2 \pm 3.1$ ) and of transferable embryos ( $3.8 \pm 4.3$  vs  $1.9 \pm 2.7$ ) collected [84].

#### **4.2. Insulin**

The pancreatic homeostatic hormone, insulin, plays a central role in the regulation of metabolism, and its peripheral concentrations are linked to the level of feed intake in ruminants [27, 85]. In these species, no direct effect of insulin on LH secretion has been demonstrated [17]. Peripheral actions are more likely, as insulin receptors have been demonstrated in the gonads, and as insulin induces *in vitro* proliferation of the granulosa cells and activation of steroid synthesis (either by a direct action, as on 3  $\beta$ -hydroxysteroid dehydrogenase, or in synergy with FSH, as on aromatase) [86]. Systemic administration of insulin in heifers treated for super-ovulation by FSH increased the diameter of the largest follicles [87], or the number of ovulations in underfed animals [88]. The question arises as to whether these effects are direct ones, or are mediated through IGF1, as insulin is known to induce IGF1 synthesis in ovarian follicles.

#### **4.3. Opioids**

The mediation of opioids in the regulation of LH secretion by nutrition have been intensively studied, particularly in the rodent model. Involvement of endogenous opioids in inhibition of LH secretion in post-partum suckled beef cows has been shown by the stimulation of LH secretion by naloxone, the opioid antagonist [89] in rat, pig and ewe. Opioids inhibit excitatory noradrenergic neurones controlling GnRH neurones. This action is exerted by enkephalin, outside the hypothalamus, or by endorphin in the basal hypothalamus [15]. In beef cows fed 70% of the maintenance needs, met-enkephaline concentrations in the pre-optic area was increased [90].

#### **4.4. Neuropeptide Y**

Neuropeptide Y (NPY), a neurotransmitter present in areas of the hypothalamus involved in food intake and neuroendocrine control, seems to be a major link between nutrition and reproduction. NPY administration stimulates feeding behaviour. NPY neurones are activated in negative energy balance conditions, and inhibited by insulin. In ewes [91], its concentration is increased in the cerebrospinal fluid of long-term food-restricted animals. Its intra-cerebroventricular administration to ovariectomized females led to significantly reduced blood levels of LH, as observed in other species. NPY is assumed to inhibit noradrenergic neurons involved in the pulsatile secretion of GnRH [92].

#### **4.5. Leptin**

The product of the gene OB, the mutation of which determines obesity in the mouse, is a protein synthesized by the adipocytes, and named leptin. It has been identified in 1994 [93-95]. When it is not secreted, as in the case of ob/ob animals, obesity and infertility are jointly observed: plasma levels of gonadotrophins and gonadal steroids are low, and cyclicity is blocked. The administration of leptin to such obese mice lowers feed intake, increases thermogenesis and oxidative metabolism, and restores gonadotrophin secretion. The leptin secretion is regulated positively by glucose, insulin, glucocorticoids, and negatively by

catecholamines. In normal situations, leptin parallels the mass of adipose tissue of the organism and plays the role of a lipostat, mainly by the way of inhibiting the secretion of neuropeptide Y in the hypothalamus. Such a direct action has been confirmed for the ewe by the effects of intra-cerebroventricular injections and by the localization of the leptin receptor in the hypothalamus [96]. Evidences of implication of such a mechanism in nutrition-reproduction interrelations are accumulating. The administration of leptin to female rats prevents the block of pulsatile LH secretion produced by fasting [97]. This effect is observed in the absence of oestrogens, in ovariectomized females, indicating that the mechanism does not involve the negative feed-back of these steroids on GnRH secretion. Similarly, the injection of leptin induces sexual maturity in food-restricted pre-pubertal rats [98]. The central effects of leptin on GnRH secretion has been confirmed by the observation of LH secretion after intra-cerebral injection of leptin and *in vitro*, by leptin-induced secretion of GnRH by median eminence and arcuate nucleus explants [92].

The hypophysis can also be a target for the leptin action on reproduction: leptin receptors have been identified in the pituitary [96], and leptin induces gonadotroph secretion by cultured pituitary cells [92]. Peripheral direct actions are also indicated by the existence of leptin receptors in the ovary, the adrenal and the pancreas, and the inhibitory effect of leptin administration on insulin and cortisol secretion [99], or induction of an insulin resistance [95]. Moreover, leptin attenuates insulin-induced steroidogenesis of thecal cells from bovine follicles cultured *in vitro* [100].

## 5. CONCLUSIONS

With the leptin hypothesis, a global comprehension of the nutrition-reproduction relationships appears possible. Leptin seems to be the missing link between nutrition (feed intake, regulation of body reserves) and reproduction (control of GnRH and LH secretions, peripheral actions), at least as far as energy metabolism is concerned (Figure 1). It remains to be determined what would be its respective role beside alternative or concurrent mechanisms. While this model has been developed in laboratory animals and primates, very few observations concern ruminants and none cattle. The gene for leptin has been recently cloned in the bovine species [101], and this will give rise to specific molecular tools and the opportunity to explore the validity of such mechanisms in cattle.

More generally, gaps in the knowledge of nutrition-reproduction relationships in cattle still exist: there is a need for comparative studies to come up to a finer understanding of the specificities of given situations (production systems, external conditions, etc.). African cattle have received too little attention in this respect. Tropical *taurus* and zebu cattle are models of adaptation to survival in harsh conditions of environment, nutrition, pathology and by their ability to serve as multipurpose (milk, meat, work) animals [102].



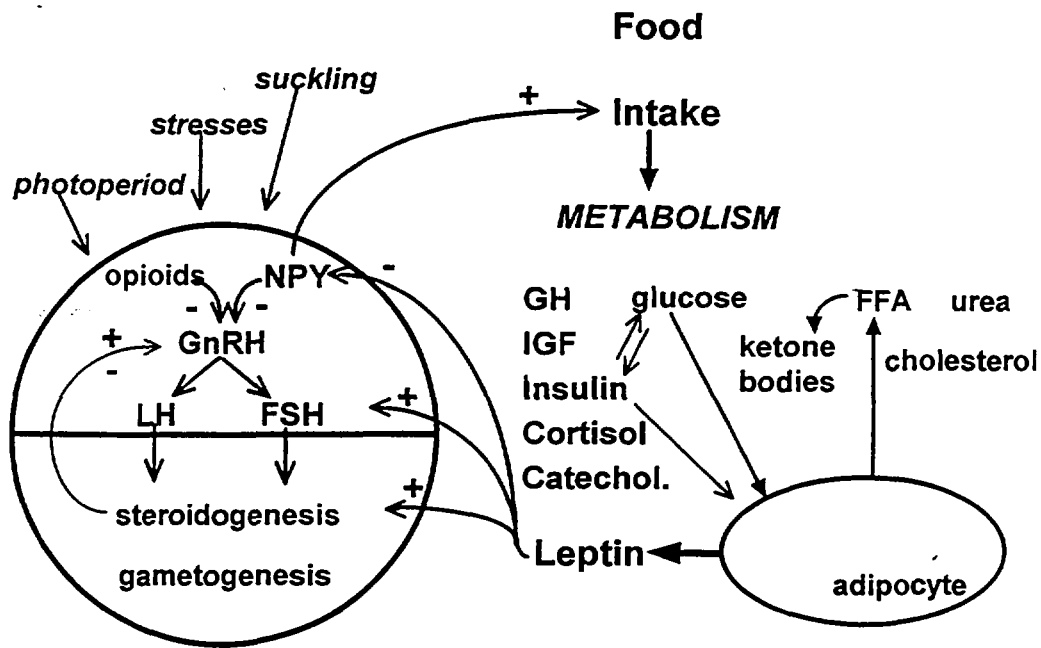


FIG.1. Nutrition-reproduction interactions in cattle with special reference to the putative role of leptin.

The determination of the physiological basis of these performances should certainly be profitable. From a practical point of view, understanding of nutrition-reproduction relationships is necessary to develop tools aimed at diagnosis of the causes and targets of nutritional effects, choosing adapted responses (providing supplementation strategies, adjusting management practices etc.) and assessing consequences of interventions on production systems.

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