RELATIONSHIPS BETWEEN NUTRITIONAL STATUS AND OESTRUS RESUMPTION IN *POST-PARTUM* CATTLE AND THEIR CONSEQUENCES IN AFRICAN LIVESTOCK PRODUCTION SYSTEMS

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1. INTRODUCTION

The importance of nutrition in determining the reproductive status and performance of ruminant livestock is well established (Robinson, 1990). A considerable body of evidence has accumulated to suggest that the ability of female cattle to rebreed successfully is severely compromised by inadequate nutrition resulting in a lengthy *post-partum* interval[1] (PPI) and, in consequence, extended calving intervals.

Prolonged PPI has been identified as a key characteristic associated with poor productivity observed in cattle management systems practised by small-holders in Africa (ILCA, 1987). Field observations suggest that periods in excess of 500 days between calving and subsequent conception are not uncommon (Pullan, 1979; Ward *et al*, 1988; Mukasa-Mugerwa *et al*, 1989; Osei and Effah-Baah, 1989). However, studies with *Bos indicus* breeds under improved management have indicated that they are capable of oestrus resumption within 120 days of calving (Alim, 1960; Swensson *et al*, 1981; Trail and Gregory, 1982). Clearly the genetic potential of these animals is not being achieved under field conditions.

The distribution of calving across the year may also be determined by nutritional restrictions which delay return to oestrus during periodic feed shortages arising because of seasonality in feed supply. In most small-holder livestock production systems, access of males to females is unrestricted. However, marked conception peaks are often observed in response to feed flushes at the onset of a rainy season or when crop residues are grazed. As many as 80% of conceptions may take place during seasonal feed flushes resulting in calvings, nine months later, which are clustered when feed supplies for supporting the increased nutritional demands of the dam during early lactation are extremely restricted. This lack of synchronization between supply of and demands for nutrients results in poor productivity. Furthermore, the mobilisation of nutrients from body reserves assimilated during periods of relative plenty, may be undesirable as the catabolism of body tissues represents, in biological terms at least, a less efficient path than the direct utilization of feed nutrients.

The pattern of irregular breeding with extended calving intervals observed in females limited by nutrient availability tends to reduce the number of growing animals available for domestic consumption or sale. It will also increase the reluctance of farmers to cull un-productive animals in their current holdings as they are unable to plan replacement strategies to maintain an acceptable herd size.

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[1] - *post-partum* interval may be defined as the interval between parturition and the first *post-partum* oestrus capable of initiating a pregnancy.

This review is intended to consider, in the context of the livestock production systems adopted in Africa, established knowledge of the relationships between nutritional status of female cattle and their *post-partum* reproductive performance. This information will be of use as a basis for suggesting improved management and feeding practices to promote a closer correspondence between the supply of nutrients to breeding cattle and varying nutrient requirements at different stages of their production cycles. The adoption of such systems by farmers could allow them to meet their production objectives more efficiently and give them more confidence in the making of herd management decisions.

2. THE PHYSIOLOGICAL BASIS OF THE *POST-PARTUM* INTERVAL

A number of recent, detailed reviews of the physiological processes which regulate PPI and their relationships with the nutritional status of the *post-partum* cow are available (Nett, 1987; Short and Adams, 1988; Short *et al*, 1990; Lishman and Inskeep, 1991). This subject is, therefore, summarised only briefly here.

2.1. **Components of the *Post-Partum* Interval**

Short *et al* (1990) have identified four principal components - general infertility, uterine involution, *post-partum* anoestrus and short oestrus cycles - which may determine the length of the PPI. General infertility refers to factors such as genetic abnormalities and pathogenic infection which affect reproductive function in general and do not act exclusively on PPI (Peters and Ball, 1987). The other factors all have functional effects which influence PPI directly.

2.1.1 *Uterine Involution*

The uterus becomes greatly modified in size and form during pregnancy and, *post-partum*, undergoes the process of uterine involution to return it to the physical condition associated with the non-pregnant animal. During the period between parturition and complete involution, the distorted uterus forms a physical impediment to the movement of spermatozoa towards the ovaries and the implantation of fertilized ova. Thus, time to involution is likely to be a significant component of the PPI during the early *post-partum* period and may represent a final limitation to the reduction of PPI in the absence of other limiting factors.

The time taken for involution of the uterus may be affected by season and the age of the dam but does not normally exceed 40 days in *Bos indicus* cattle (Mukasa-Mugerwa, 1989). Eduvie and Oyedipe (1991) quote a range of 16 to 35 days *post-partum* in published values for uterine involution in indigenous West African (*Bos indicus* and *Bos taurus*) cattle. The process is therefore unlikely to be of great significance in determining the lengthy PPIs exhibited in cattle under African conditions.

2.1.2. *Post-Partum Anoestrus*

Post-partum anoestrus is the interruption in the normally cyclical production of ova which occurs, to varying degrees, in all cattle following parturition. A continuing anoestrus state arises through suppression of the hormonal mechanisms which govern the development and maturation of the follicle. This appears to involve the hypothalamus-pituitary complex, the ovaries and a disruption of the feedback mechanisms between them (Short *et al*, 1990).

The most distinctive characteristics of anoestrus cattle are the low levels of circulating serum progesterone and luteinizing hormone (LH) and an associated decrease in the frequency of the episodic release of the latter (Richards *et al*, 1989; Canfield and Butler, 1990). These conditions imply a disfunction in the gonadotrophin releasing hormone (GnRH) pulse generator of the pituitary (Foster *et al*, 1989). This is supported by a number of studies conducted with anoestrus cattle in which artificial administration of pulsatile GnRH has initiated a pre-ovulatory LH surge leading to successful ovulation and development of the corpus luteum. However, it seems likely that GnRH pulses are first-limiting only in cattle in relatively shallow anoestrus. During the early *post-partum* period or in animals which are grossly underfed the exogenous administration of GnRH may fail to elicit a response (Rutter and Randel, 1984). Inhibition of LH synthesis by progesterone and oestradiol during pregnancy depletes pituitary LH stores in the *post-partum* animal. Thus, in deeper anoestrus, insufficient LH may be available to stimulate early follicle development even if GnRH pulses are generated artificially (Moss *et al*, 1985).

A feedback on the hypothalamus of oestradiol produced by the maturing follicle is responsible, under normal conditions of oestrus cyclicity, for the initiation of the pre-ovulatory LH surge. This feedback is also disrupted in the anoestrus animal. During deep anoestrus, levels of circulating LH are low, restricting follicular development and therefore the release of oestradiol to stimulate pulsatile GnRH secretion by the hypothalamus (Nett, 1987). There is also evidence that the hypothalamus becomes hyper-sensitive to oestradiol resulting in a negative feedback during deep anoestrus (Garcia-Winder *et al*, 1986).

Observations of oestrus behaviour and hormonal profiles in cattle in African livestock production systems suggest that an extended period of *Post-partum* anoestrus is the most important contributor to the length of the PPI (Dawuda *et al*, 1988; Mukasa-Mugerwa, 1991).

2.1.3. *Anomalous Oestrus Cycles*

It has been suggested that around 50% of cows returning to oestrus under the relatively intensive management systems of developed countries exhibit the phenomenon of short oestrus cycles (Peters and Ball, 1987). A short cycle is an abnormal first cycle characterised by a less pronounced rise in progesterone than is observed with the normal cycle. Short cycles may be followed by normal ovulations which can even result in fertilisation. However, pregnancy does not result due to the premature regression of the *corpus luteum* (Short *et al*, 1990). Other anomalous cycles include those which are associated with silent heats.

The majority of experimental observations of short cycles have been made in animals fed intensively. Under these conditions, only animals returning to oestrus activity within 40 days of parturition are likely to exhibit them (Short *et al*, 1990). However, silent heats associated with lower than normal rises in progesterone have been observed later than 100 days *post-partum* in cattle under farm conditions in Africa (Oyedipe *et al*, 1988; Mukasa-Mugerwa *et al*, 1991) prior to their return to normal oestrus cycling. It is therefore possible that, in some circumstances, anomalous cycles may be a significant component of extended PPIs.

3. NUTRITION AND THE *POST-PARTUM* INTERVAL

3.1. Effects of Nutritional Deficiencies on the Resumption of Oestrus Cycling

The hormonal interactions which determine the anoestrus state have been reasonably well defined. However, the means by which specific nutritional, and other, factors affecting *post-partum* anoestrus exert these effects on the hormonal system are relatively poorly understood. Nevertheless, pronounced effects of shortages of specific nutrients on oestrus resumption are clearly indicated in the literature. Shortages in current dietary intakes of energy and, to a lesser extent, protein and calcium may be compensated for by the mobilisation of body reserves. The relative importance of current and previous nutrition and the interactions between them will be considered later.

3.1.1. *Energy*

The relationships between energy balance and *post-partum* reproductive function in dairy cattle have been studied in detail and this work reviewed recently by Butler and Smith (1989).

High yielding cattle characteristically enter negative energy balance immediately *post-*

partum despite being fed to the constraints of their appetite limits. This is due to the increase in their nutrient requirements for milk production which is sudden while voluntary feed intake increases only gradually during the first few weeks of the lactation.

Significant correlations have been observed between the degree of the mean negative energy balance during the early *post-partum* period and the length of the PPI. Butler *et al* (1981) estimated an increase of 11 days in the PPI for each 1MJ of ME increment in negative energy balance. In this study, cattle were observed to return to oestrus while still in negative energy balance and the increases in serum progesterone levels appeared to correspond with the point at which energy deficit reached a maximum and started to recover. This is supported by Canfield and Butler (1990) who observed a significant positive correlation between the time to "energy balance nadir" and PPI. The inflection point was associated with increases in mean serum LH levels and LH pulse frequency.

Current appreciation of the relationships between energy status in cattle and the hormonal processes of the oestrus cycle is summarised in figure 1. The metabolism of glucose and insulin which are responsive to changes in energy balance appear to exert an effect on the resumption of oestrus cycling in dairy cattle *post-partum* (Short and Adams, 1988). Inhibition of GnRH secretion mediated by low insulin level (Harrison and Randel, 1986) and possibly the insulin-like growth factor, IGF-1 (Rutter *et al*, 1989) has been observed in studies with beef cows. In some studies, these relationships have not been apparent and changes in levels of plasma non-esterified fatty acids (NEFA) have appeared more likely to be involved in signalling the initiation of recovery from negative energy balance to the central nervous system (Canfield and Butler, 1990). Butler and Smith (1989) observed inhibition of LH release in dairy cattle in negative energy balance which was associated with increased levels of ß-endorphin which may inhibit GnRH pulse generation.

The significance of negative energy balance for the prolongation of PPIs in animals managed by small-holders is difficult to extrapolate from the information derived in more intensively managed animals and detailed studies of energy metabolism in the former do not appear to have been undertaken. It is unlikely that a clearly defined energy balance nadir occurs under these conditions and cattle calving during the earlier part of a feed flush may be seen to gain weight suggesting that they are in positive energy balance (Kidner, 1966; Holness *et al*, 1978; Djabakou *et al*, 1991). The fact that these animals do not return rapidly to oestrus may be due to the well documented inhibitory effects of lactation and suckling on return to oestrus cycling (Loudon, 1987; Williams, 1990).

3.1.2. *Protein*

The effects of protein nutrition on reproduction in dairy cows have been reviewed by

Ferguson and Chalupa (1989). The effects of changes in protein supply appear to be expressed mainly through secondary changes in energy balance. The stimulatory effect of rumen undegradable protein (UDP), mediated through increased amino acid absorbtion, on milk yield increases the energy demand of lactation tending to push the animal deeper into negative energy balance with increased body fat mobilisation. Under these circumstances, a limited degree of compensation may take place with the increased dietary UDP stimulating feed and consequently energy intakes (Roffler and Thacker, 1983) but hormonal profiles are generally consistent with an effect mediated by energy balance (Ferguson and Chalupa, 1989). Excessive rumen degradable protein (RDP) may lead to elevated levels of potentially toxic nitrogenous compounds such as ammonia and urea (Hibbitt, 1984). These do not appear to affect ovarian cycling directly, but might disrupt intermediary metabolism and the development of the *corpus luteum* (Ferguson and Chalupa, 1989) and uterine involution (Robinson, 1990).

The effects discussed above result from excessively wide protein to energy ratios which are unlikely in small-holder cattle. The proportion of crude protein in their feed intakes during the dry season may be as low as two to three *per cent*. Effects are therefore more likely to be due to protein limitation but the rôle of protein supply *per se* in mediating PPI in animals kept by small-holders has received little attention. Sasser *et al* (1988) observed a tendency towards delayed return to oestrus in beef heifers consuming adequate dietary energy but low protein between 50 days *pre-partum* and 110 days *post-partum*. Wiley *et al* (1991) demonstrated that supplementary UDP *post-partum* improved weight gain and reduced PPI in beef heifers irrespective of the plane of nutrition (low *vs* maintenance) *pre-partum*. These authors suggested that, supplying UDP *post-partum* may stimulate pancreatic insulin production, compensating for the adverse effects of low *pre-partum* plane of nutrition on insulin levels and, in consequence, promote oestrus resumption. These observations would suggest that, while energy may be the most important factor in governing breeding cycles in small-holder cattle, the importance of and possible modifying effects of quantity and quality of protein supplied should not be ignored when supplementation strategies are being considered.

3.1.3. *Fat*

It is difficult to draw conclusions on the specific rôle of dietary fat in mediating PPI due to the conflicting indications of different studies. There is some evidence that supplementary fat in early lactation may promote less severe negative energy balances but in other studies, cows responded to fat supplementation with increased milk yield and reduced dry matter intake rather than decreases in the length of the PPI (Grummer and Carroll, 1991).

Some components of dietary fats are important as precursors for reproductive hormones.

Animals supplemented with fat *post-partum* exhibit raised levels of serum cholesterol and progesterone (Grummer and Carroll, 1988) - of which cholesterol is a precursor - and improved follicle growth (Williams, 1989; Hightshoe *et al*, 1991). Linoleic acid appears to stimulate the secretion of prostaglandin $F_{2\alpha}$ (Lucy *et al*, 1990) which is involved in the promotion of follicular development and uterine involution and may therefore, under certain circumstances, affect PPI.

In view of the inconclusive nature of the evidence in this area and the lack of established causal relationships, possible interventions involving the use of fat supplementation to reduce PPIs should be considered with some care.

3.1.4. *Minerals*

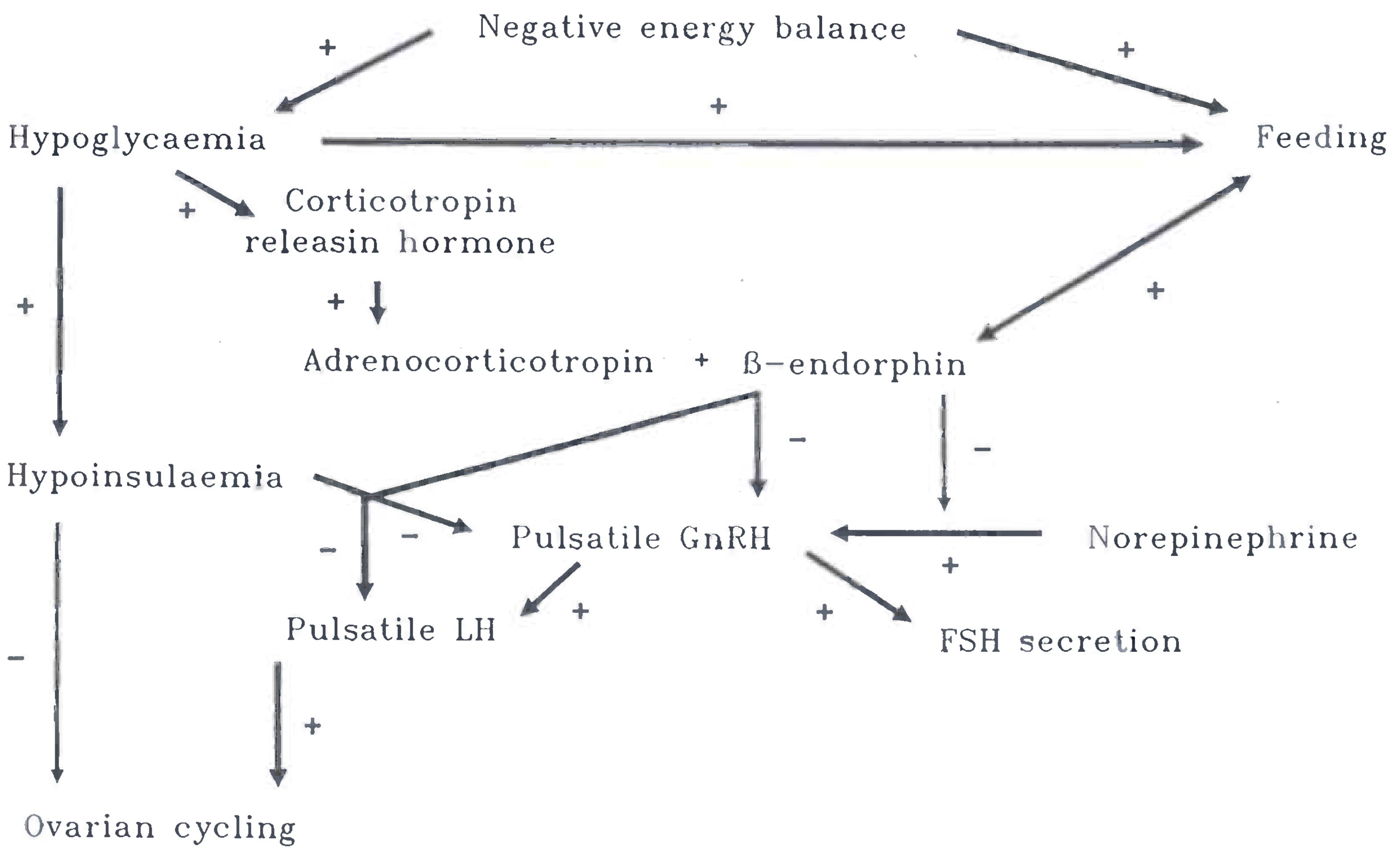
The effects of vitamins and minerals on the reproductive performance of dairy cattle have been reviewed by Hurley and Doane (1989). Borderline deficiencies in minerals and vitamins may result in impaired fertility before gross deficiency symptoms are observed. However, specific requirements for optimum reproductive function at different stages of the reproductive cycles of cattle have not been determined. Consequently, information on the effects of specific deficiencies in macro- or trace-minerals on the length of the PPI is limited.

A number of studies have observed positive responses in reproductive performance to mineral supplementation (Ca, P, Cu, Fe and I - Surendra Singh and Vadnere, 1987; Mn - Wilson, 1966). In others, similar responses have not been forthcoming (Cu - van Niekerk and van Niekerk, 1990). Minerals may exert adverse effects on *post-partum* interval when consumed in excess (e.g. Phillippo *et al*, 1989). However, this situation is probably unlikely to arise with the small-holder feeding systems practised in Africa. Mechanisms by which mineral deficiencies exert their effects on reproductive performance are unclear. Decreased serum insulin levels have been observed in hypo-calcaemic dairy cattle (Littledike *et al*, 1968) suggesting possible links with energy mobilisation.

Mineral status in breeding livestock is probably related to levels in feeds and consequently in the soils on which they are grown. However, the possibility of predicting reliably from soil mineral contents, instances in which reproductive performance might suffer, may not be easily practicable given the length of the pathway from soil to animal tissue. Attempts to supplement specific mineral deficiencies in the animal which are suggested by soil profiles may also be masked by more critical limitations imposed by other factors such as energy and protein.

Published information on the geographical distribution of specific mineral deficiencies in Africa has been reviewed by Schillhorn van Veen and Loeffler (1990). Deficiencies in phosphorous are widespread throughout the continent with more localised occurrences

Figure 1: Relationships Between Negative Energy Balance and Oestrus Cycling



Adapted from Butler and Smith (1989)

(Figure 2) of deficiencies in other minerals.

3.2. Nutritional Status and Post-Partum Intervals

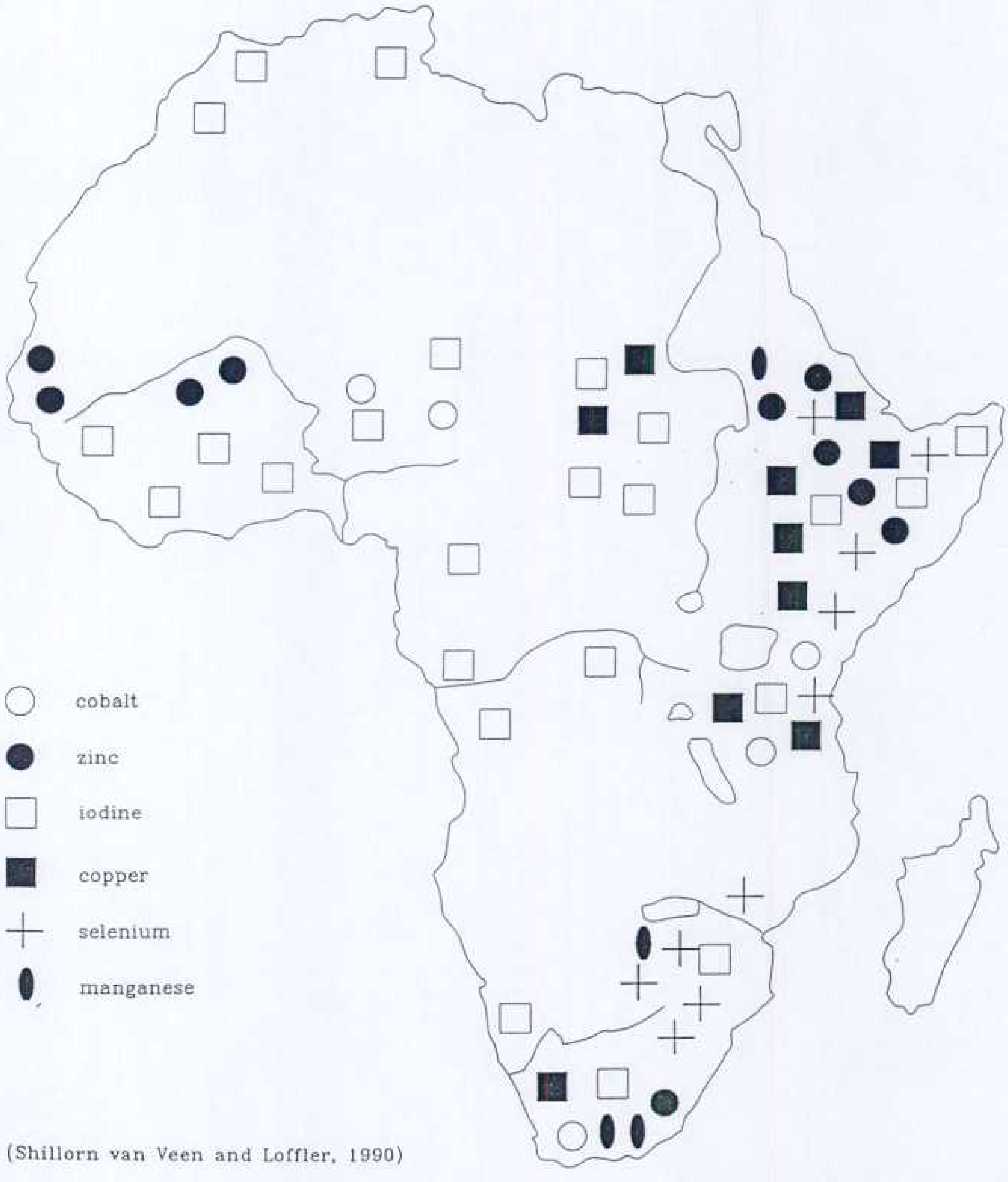
Numerous practical difficulties are likely in attempts to measure energy balance in smallholder cattle at different stages of their productive cycles. Therefore, most studies have relied on changes in body weight and body condition score to indicate changes in nutritional status over time. However, the interpretation of these changes as they relate to returns to oestrus may be complicated by the combined effects of a number of different factors. Where feed supply is seasonal, patterns of change in body weight or body condition tend to follow those in feed supply, usually with a lag period of around three to six weeks (Potter, 1985). This general seasonal pattern of changes in body weight and condition score is then modified by the varying demands of the animal for nutrients at different stages of its production cycle. For example, an animal calving during the dry season may utilise body reserves and, consequently, lose weight in early lactation in order to meet nutrient demands for milk production. Another animal, of similar initial body weight and condition, calving in the early wet season may be able to maintain these during the early part of its lactation but need to rely on catabolism of body reserves, thereby losing weight and condition, later in lactation as feed supplies dwindle during the post-rains period (Kidner, 1966; Djàbakou *et al*, 1991).

3.2.1. *Relationships Between Bodyweight and PPI*

Strong correlations have been observed in a number of studies between body weight immediately after parturition and the duration of the PPI (Steenkamp *et al*, 1975; Bellows and Short, 1978; Holness *et al*, 1978). Cows which are heavier at parturition return more quickly to oestrus than lighter ones. It seems likely, however, that current body weight would be more important in determining oestrus resumption and this is supported by Rudder *et al* (1985) who observed higher pregnancy rates in comparatively heavy cows exposed to a bull than in light cows. Nevertheless, animals which are heavier at calving are better able to maintain or lose less body weight and condition during lactation and will therefore achieve adequate condition to resume oestrus cycling earlier.

This is a manifestation of the common-sense concept of a target body weight at mating, adopted by Ward (1968) and popularised in a much quoted review of Lamond (1970) as a means of defining the likelihood of successful re-breeding on the basis of past and current nutritional status. The concept specifies that, for animals of a given breed under given conditions, there is a minimum body weight below which re-mating is unlikely to take place. This implies that a certain level of body reserves is necessary to support normal reproductive activity, whatever the level of current nutrition. Richards *et al*(1989)

Figure 2: *The Geographical Distribution of Certain Mineral Deficiencies in African Ruminants.*



(Shillorn van Veen and Loffler, 1990)

have demonstrated that oestrus cycling is an important component of the target weight concept by feeding normally cycling beef heifers to lose one *per cent* of their body weight per week. After thirty weeks of this regime, 91% of cows ceased cycling having lost approximately 24 *per cent* of their initial bodyweight. With increased feeding to restore bodyweight, oestrus cycling was re-initiated in around 9 weeks. A number of estimated target body weights are shown in table 1. However, the practical value of this approach for predicting the likelihood of an individual returning to oestrus is likely to be compromised by the confounding effects of other factors, particularly between-animal variability. (Richardson *et al*, 1975; Holness *et al*, 1978).

If the achievement of a target body weight is necessary for successful conception, it might be expected that the length of the PPI would be closely related to the rate of bodyweight recovery following parturition. However, information in the literature is contradictory.

Agyemang *et al* (1991) reported a study in which only 27.5% of cows which lost weight in the first four months *post-partum* calved again within 21 months compared with 50% of animals which gained weight during this period. Of the cattle which successfully conceived at 21 months, 71% were gaining weight in the three months prior to conception. However, in a number of other studies, cows which lost weight *post-partum* showed a faster return to oestrus (Steenkamp *et al*, 1975; Bellows and Short, 1978; Holness *et al*, 1978).

Table : *Quoted Values for Target Body Weights at Mating.*

target bodyweight (kg)	breed	reference
220	N'Dama	Agyemang *et al*, 1991
275	Mashona	Ward, 1968
<250	Mashona	Holness *et al*, 1978
318	Boran, East African Zebu and Hereford x	Odhuba and Carles, 1990

Of some use in resolving these apparent contradictions, is the suggestion of Short *et al*

(1990) that there is an approximate order of priorities for nutrient partitioning that may be attached the range of nutrient-demanding activities which the *post-partum* cow must or may potentially undertake (Table 2). The concept of a target weight for conception may be interpreted in terms of this order of priorities as the body weight reached when adequate additional energy reserves (priority seven) have been laid down.

Figure 3 presents a simple model, based on these priorities for nutrient partitioning, of how the same pattern of *post-partum* bodyweight change may occur in animals whose nutritional status is adequate *or* inadequate for the resumption of oestrus cycling. For example, animals which are below target weight, but increasing in body weight, may be regarded as laying down additional body reserves and therefore do not have adequate energy reserves to direct towards oestrus resumption. Conversely, an animal above the target weight, may also be losing weight but from excess body reserves and therefore still be able to direct available energy towards the resumption of oestrus cycling.

Perhaps the most important conclusion to be drawn is that *post-partum* body weight changes cannot be considered in isolation from the absolute body weight of the animal in relation to the breed average. This is underlined by correlations that have been observed between absolute bodyweight and *post-partum* body weight change. There is strong evidence that, under extensive management, lighter animals tend to gain weight between parturition and re-breeding in contrast to heavier animals of the same breed which tend to lose weight during this period (Steenkamp *et al*, 1975; Holness *et al*, 1978; Agyemang *et al*, 1991). Agyemang *et al*, 1991, reported that N'Dama cattle which were losing weight in the period before conception tended to be in higher weight class groups, in excess of the 220kg target body weight for conception estimated for this breed.

Table 2: *Priorities for the Partitioning of Nutrients in the Post-partum Cow (Short et al, 1990).*

1. Basal metabolism
2. Activity
3. Growth
4. Basic energy reserves
5. Pregnancy
6. Lactation
7. Additional energy reserves
8. Oestrus cycles and initiation of pregnancy
9. Excess reserves

If this scenario is accepted, it seems likely that *post-partum* body weight changes *per se* are not of particular significance for the length of the PPI unless the animals under consideration are light and need to regain a body weight in excess of the target body weight for conception. Body weight changes during this period merely reflect the combined effects of the nutrient mobilisation and utilization processes that are taking place in animals in particular metabolic states.

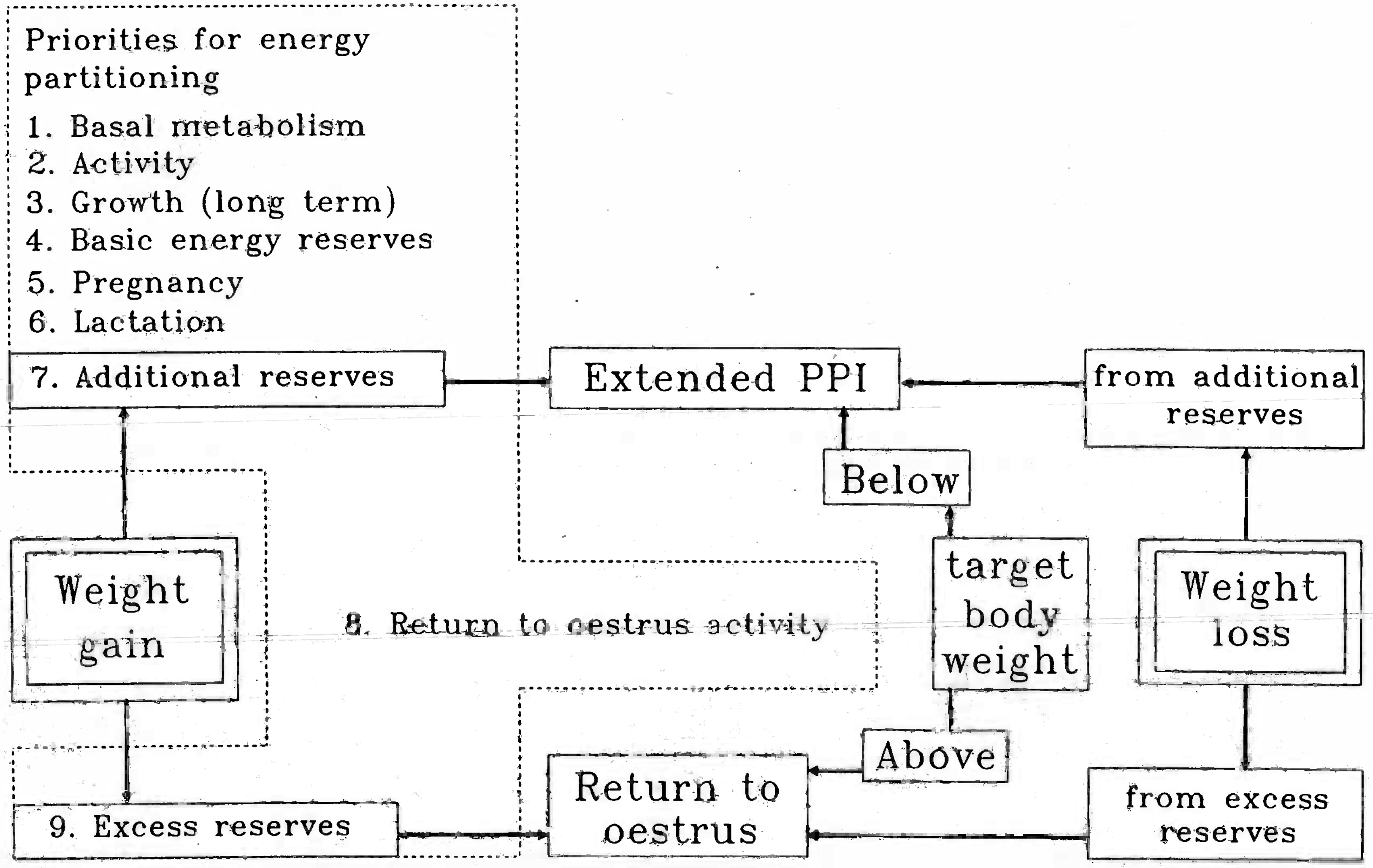
Within the framework of priorities for nutrient partitioning, the incidence in the *post-partum* animal under small-holder management in Africa of extended periods of anoestrus may be viewed as a consequence of the relatively low priority attached by the breeding cow to the resumption of breeding activity. This is clearly sound from an evolutionary point of view as the concentration of resources in other activities relating to the mother's own survival and that of current offspring which represent resources already invested is more likely to spread the animal's genetic material. Thus, a cow under nutrient stress after calving remains anoestrus until the additional energy reserves component of the animal's body reserves increases sufficiently to be able to support a concurrent pregnancy or until the demands of lactation cease at weaning. The incidence of extended periods of *post-partum* anoestrus might, therefore, be regarded as part of a breeding animal's general strategy for balancing, as far as possible, both short and long term nutrient requirements (for maintenance, lactation and pregnancy) with the supply available to it (from feed or body reserves).

Much of the difficulty in the interpretation of some earlier studies in this area may have arisen partly from too casual use of certain statistical methods for the interpretation of data on factors which affect return to oestrus. In view of the correlations between variables referred to above, relationships derived from multiple regression or least squares models need to be considered most carefully in the terms of the biological processes which may, *or may not be*, represented by the numbers.

3.2.2. *Body condition score*

Changes in body condition score (BCS) have been little used in studies of the relationships between nutritional status and return to oestrus in African cattle. However, in other parts of the world, BAS at calving has proved a useful indicator of nutritional status in studies of the effects of *pre-partum* nutrition on PPI as it represents a summation of the effects of the animals nutritional management up to the point of calving. It is particulary useful in this respect as it is, to an extent, independent of body weight and therefore avoids some of the problems of interpretation of data noted above. A clear negative relationship between body condition at calving and the length of the PPI has been observed in numerous studies (Bellows and Short, 1978; Holness *et al*, 1978; Richards *et al*, 1986; Wright *et al*, 1987; Richards *et al*, 1989; Houghton *et al*, 1990;

Figure 3: *Possible Relationships Between Energy Partitioning and Liveweight changes in the Post-partum Cow.*



Wright *et al,* 1992). In general, excessively fat animals at calving display a number of reproductive problems including extension of the PPI (Butler and Smith, 1989). This situation is normally seen in high yielding dairy cows and is unlikely to arise in the animals of small-holders. In thinner animals, changes in body condition score at calving exert a marked negative effect on the length of the PPI. The level of body reserves below which PPI begins to be adversely affected appears to be represented by BCSs slightly below the mid-point of the scales - between four and five on a scale of one to nine (Dzuik and Bellows, 1983; Richards *et al,* 1986) or 2.25 on a scale of one to five (Wright *et al,* 1987).

In an attempt to quantify the relationships between BCS at calving and the duration of *post-partum* anoestrus, Wright *et al* (1987, 1992) have estimated that, for European beef breeds under United Kingdom conditions, for each one point drop in BCS (on a one to five scale) at calving, there was a corresponding increase of 43 ±20 or 86 ±21.6 days respectively in PPI. In the latter study, the range of body weights was wider but that in body condition score narrower and there is clearly a considerable degree of between animal variability not accounted for by this simple regression approach.

The significance of BCS at calving as an indicator of PPI may be related to the importance of body reserves in maintaining adequate supplies of nutrients for the processes occurring during early lactation. These may often outstrip the nutrient restrictions imposed by limited feed availability of feed intake limitations to meet all the demand for nutrients.

As a general conclusion, it would appear that observations of changes in bodyweight are of little benefit in determining the likely reproductive path in a *post-partum* animal if the absolute bodyweight in relation to the target weight for conception or some idea of the body condition score is available.

4. CONSEQUENCES OF NUTRITIONALLY MEDIATED PPI IN AFRICAN CATTLE PRODUCTION SYSTEMS

Apart from lengthy PPIs, small-holder cattle in Africa usually display markedly seasonal conception peaks (Table 3) which are clearly related to seasonal infertility as males and females are generally kept together throughout the year. It has been suggested in a limited number of studies (Steinbach and Balogun, 1971) that this seasonality may be directly mediated by environmental factors such as temperature or photoperiod. However, in the majority of studies, the environmental stimulus appears to be indirect and expressed through seasonal changes in feed supply with conception peaks brought about by improvements in feed availability and possibly quality.

4.1. Timing of the Conception Peak

Commonly, a single conception peak appears to be associated with the onset of the rainy season which stimulates a pasture flush and presumably an associated increase in quantity and quality of feed consumed. In Northern Nigeria, a bimodal conception pattern has been observed (Pullan, 1979; Otchere, 1984) with a second peak coinciding with the locally adopted practice of crop residue grazing following the rainy season. In a study of N'dama cattle in the Gambia, Jeannin *et al* (1988) observed a pronounced peak, not in response to the rainy season but post rains. This may have been due to the fact that the mean body weights of the animals in this study were well below the target weight for the breed before the onset of the rains and therefore required the entire rainy season to regain adequate body weight.

4.2. Relationship Between PPI and Season of Calving

In some studies (Oyedipe *et al*, 1982; Mrode and Akinokun, 1986), there is little evidence of differences between the PPIs of cows which calve in the wet season in comparison with dry season calvers. This would appear to be due to the adoption of improved dry season feeding practices such as supplementation with oilseed cakes and forage conservation. In studies where feeding is restricted to grazing of pasture and crop residues, dry season calvers exhibit markedly longer PPIs than cows calving in the wet season. This is consistent with the observed negative correlation between body weight at calving and the length of the PPI in small-holder cattle which tend to be at their lowest body weights during the rainy season (Richardson *et al*, 1975; Fall *et al*, 1982; Wilson, 1986; Jeannin *et al*, 1988). With conceptions concentrated during the early to mid rainy season, the majority of calvings will be during the dry season so there is likely to be a self-reinforcing tendency towards long calving intervals.

Apart from poor productivity arising in this way, the concentration of calvings during the dry season has another disadvantage. The clustering of calvings during the dry season means that the accumulated nutrient demands of the herd, in which a majority of the mature females are at their peak in terms of demand for nutrients, coincide with the time at which feed supplies are at their most limited. Lactating cattle will therefore be reliant on the catabolism of any body reserves which may have been built up during the previous rainy season to support their lactations. In this situation, problems may arise from deficiencies in specific nutrients which are not readily mobilised from body reserves.

From the preceding, it would appear that, in principle, efficiency of feed utilization might be greatly improved if reproductive cycles could be manipulated for the calving peak to coincide with the rainy season. Wilson (1986) observed that cattle calving during and immediately after the rainy season had the highest body weight at calving and therefore

Table 3: *Observations of the Post-partum Interval and its Seasonality.*

Breed	Agro-ecological Zone / rainfall distribution	Timing of conception peak	Percentage of conceptions during peak	conception peak associated with...	*Post-partum* interval for cows calving in:			Feed management system	Reference
					wet	dry	mean		
Fulani	sub-humid Mar - Nov	a) Jun - Aug	a) 31	a) forage flush in rainy season	439	585	475	daytime grazing. crop residues available from Dec - Apr.	Otchere (1984)
		b) Dec - Feb	b) 48	b) crop residue grazing					
Fulani	sub-humid Apr - Oct	a) Jun - Aug	a) 46	a) forage flush in rainy season			542	rainy season grazing. crop residues in dec.	Pullan (1979; 1980)
		b) Jan - Feb	b) 28	b) crop residue grazing					
	sub-humid Oct - Apr				169	147	157	grazing during rains. hay/silage & crop residues in dry	Oyedipe *et al* (1982)
	sub-humid May - Oct	Mar - Jun	51	body reserves built up from crop residues			450	grazing. crop residues from Dec - Mar.	Voh and Otchere (1989)
Fulani	semi-arid Jul - Sep	Jul-Sep	56	forage flush in rainy season			383	grazing. limited crop residues.	Wilson (1986)
	sub-humid Mar - Oct				147	129	139	grazing. supplemented with oilseed residues during dry.	Mrode and Akinokun (1986)
Various Zebu types	semi-arid Jun - Sep	Jul - Oct	74	forage flush in rainy season			a) 279	a) transhumant	Wilson and Clarke (1975; 1976)
							b) 633	b) grazing with little supplementation	
N'Dama	sub-humid Jul - Sep	Nov - Mar	86	feeding of crop residues			448	grazing from Jul to Sep. Crop residues in early dry.	Jeannin *et al* (1988)
N'Dama	sub-humid Jul - Oct	Oct - Mar	80	Crop residues	364	317	620	daytime grazing on natural pasture	Agyemang *et al* (1991)
N'Dama	sub-humid Jul - Oct	Jul - Oct	48	forage flush in rainy season	129	283	213	grazing. supplemented with crop and oilseed residues during dry.	Fall *et al* (1982)
N'Dama	sub-humid Apr - Nov	Mar - Jun & Nov	46	forage flush in rainy season			220	grazing. supplemented with brewers grains during dry.	Tuah and Danso (1985)
N'Dama	sub-humid Apr - Nov				248	334	284	grazing. supplemented with brewers grains during dry.	Osei and Effah-Baah (1988)
N'Dama	sub-humid Mar - Nov	Dec - Jul	51	changes in photoperiod				grazing of improved and unimproved pasture.	Steinbach and Balogun (1971
West African Shorthorn	sub-humid Apr - Nov	Mar - Jun & Nov	43	forage flush in rainy season			181	grazing. supplemented with brewers grains during dry.	Tuah and Danso (1985)
West African Shorthorn	sub-humid Apr - Nov				265	351	284	grazing. supplemented with brewers grains during dry.	Osei and Effah-Baah (1988)
Nguni	highland Oct - Apr	Dec - Mar	58	forage flush in late rains				grazing. crop residues after harvest.	Butterworth (1983)

the highest level of body reserves to support lactation. These animals would also have access to a relatively abundant feed supply. Their comparatively high body weights at calving would also predispose them to a relatively early return to oestrus promoting improved overall herd productivity.

5. FEEDING STRATEGIES TO MANAGE REPRODUCTIVE CYCLES IN THE SMALL-HOLDER HERD

Feeding strategies to reduce PPIs and improve the convergence between seasonally varying demand for, and supply of, nutrients could be developed based on improving both *pre-* and *post-partum* plane of nutrition.

5.1. *Pre-Partum* Plane of Nutrition

Improved plane of nutrition *pre-partum* might be expected to increase weight at parturition and reduce PPI. This would improve the chances of an early conception to allow calving during or shortly after the next feed flush.

The effects of plane of nutrition during pregnancy on PPI have been studied by a number of workers (Randel, 1990) with the general conclusion that increasing the plane of nutrition during pregnancy is effective in reducing PPI. Bellows and Short (1978) observed that higher levels of feeding of cattle under feedlot conditions for 90 days *pre-partum* resulted in higher mean live weights (15%) and condition scores (64%) at calving relative to a group receiving a lower plane of nutrition. The former were in rising condition and body weight during the *pre-partum* period compared with the latter which maintained bodyweight but lost condition. The group on the higher plane of nutrition showed faster returns to oestrus and shorter PPIs. A high level of feeding *pre-partum* appears to be more effective in reducing PPI than high level *post-partum* due perhaps to the cow's inability to consume sufficient feed to meet the cumulative demands of maintenance, lactation and oestrus resumption *post-partum* (Bellows and Short, 1978).

5.2. *Post-Partum Plane of Nutrition*

Field observations of breeding female cattle in small-holder management systems suggest that the resumption of oestrus activity often occurs quite rapidly in response to improved plane of nutrition *post-partum* since conception peaks appear to be well established within two months of the identifiable onset of feed flushes. This observation raises the possibility of using short term supplementation of anoestrus animals outside the periods of relative feed abundance to stimulate return to oestrus and resumption of reproductive activity. Using this approach to induce calving at times of the year when feed availability is increasing and quality is better might allow improved lactation performance and calf survival and growth.

The efficacy of targeting the immediate *post-partum* period for supplementation to reduce the PPI has been demonstrated by Little *et al* (1991) who observed a doubling in the percentage of cattle conceiving again during the first 12 months *post-partum* when supplementary groundnut cake was offered for a five month period during the dry season. Experimental observations of the effects of plane of nutrition *post-partum* on PPI suggest that these are modified to a considerable extent by the level of body reserves accumulated *pre-partum*. This is usually expressed as a significant interaction between BCS at calving and *post-partum* feeding level with only cows in leaner body condition at calving responding with reduced PPI to increased plane of nutrition *post-partum* (Richards *et al*, 1986; Wright *et al*, 1987; Houghton *et al*, 1990; Wright *et al*, 1992).

Attempts to develop feeding systems which minimise re-breeding intervals should not lose sight of the value of extended post-partum anoestrus as an adaptation for ensuring the animal's well-being in times of nutrient stress. Possible interventions in feeding systems for breeding animals should, therefore, be assessed in the light of overall feed availability within production systems. If this is likely to be severely limiting, it may be better not to aim for an overall reduction in PPI but to use nutritional interventions only to retime conception and calving to coincide better with peak periods of nutrient supply.

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