Nutritional effects on puberty and lactational infertility in mammals: some interspecies considerations

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Nutrition and body condition are known to influence reproductive performance in a wide range of mammals, including marsupials, a large number of eutherians, both wild and domesticated, and man. Nutrition is known to influence reproduction on at least four levels. First, growth and the onset of puberty are clearly under nutritional control, and for a number of species, critical body-weights for ovulation or the onset of spermatogenesis have been described. Second, postpubertal ovulation rate is known to be profoundly influenced by both proximal nutrient intake and body condition in a number of species. Third, early embryonic wastage is frequently associated with plane of nutrition although even in some of the best studied mammals such as the sheep, the evidence remains equivocal (see Robinson, 1983). Finally, the return to oestrus post-partum is known to be regulated in many species by the sucking activity of the young. In many species with long periods of maternal dependence, plane of nutrition during lactation has a significant effect in delaying the onset of normal ovarian activity.

Currently, the level of understanding of how these four categories regulate fertility is very poor. A number of studies have shown that plane of nutrition can influence the pattern of pituitary luteinizing hormone (LH) release (Fitzgerald *et al.* 1982; Foster *et al.* 1985*a*; Piacsek, 1985; Steiner, 1987) and evidence is accumulating that undernutrition may directly modulate the operation of the gonadotrophin-releasing hormone (GnRH) pulse generator (Foster *et al.* 1985*a,b*; Steiner, 1987). Although similar models have been proposed to account for the effect of undernutrition in delaying puberty (Steiner, 1987), it is not yet established whether the physiological mechanisms mediating nutritional effects on puberty are identical to those regulating fertility in the postpubertal animal. Many of these topics have been reviewed and discussed elsewhere. Here, two specific aspects of nutritional effects on reproduction are considered. First, the interrelation between nutrition and season with respect to the onset of puberty in some seasonally breeding mammals is examined. Second, the role of nutrition in regulating fertility during lactation is examined, with particular emphasis as to the extent to which the sucking offspring may play an important role as part of a physiological feedback loop inhibiting ovarian activity.

Nutrition, photoperiod and puberty

In seasonally breeding mammals, the onset of puberty is a result of a complex interaction between photoperiodic stimulation and nutritional factors. Recent

work by Foster and his colleagues at the University of Michigan has provided important insights into the role of undernutrition in blocking the onset of the breeding season in ewe lambs. In the intact, well-nourished lamb, the onset of puberty is associated with a transition from negative to positive feedback action of oestradiol on gonadotrophin secretion (Foster & Ryan, 1980; Ryan & Foster, 1980). During early development in the pre-pubertal ewe lamb, the hypothalamic–hypophyseal axis is extremely sensitive to the suppressive effects of oestradiol, and post-castration rises in LH are blocked by levels of oestradiol which are ineffective in the adult (Foster & Ryan, 1979). The transition from the negative to the positive feedback action of oestradiol results in a shift from tonic secretion to a surge in LH and the first ovulation (Foster & Karsch, 1975).

It is well established in sheep that the impact of gonadal steroids is modified by the interaction of photoperiodic stimulation and nutritional factors. Ewe lambs reared on artificially long days (15 h light–9 h dark) or short days (9 h light–15 h dark) fail to achieve puberty at the normal time of year and either show short, non-sequential luteal phases or remain anovulatory (Yellon & Foster, 1985). In addition, 4 weeks of exposure to long days from birth followed by short days fails to induce normal puberty (Yellon & Foster, 1985). However, ewe lambs maintained on short days and subjected to a 7 d pulse of long days at week 22 of life achieve normal puberty some 12–15 weeks later (Yellon & Foster, 1985). From this it can be concluded that the developing lamb needs to experience long days followed by short days before it will ovulate but that exposure to long days in early life is ineffective, possibly because ewe lambs are born photorefractory to short days (Foster *et al.* 1985*b*).

In a series of experiments, Foster and his colleagues have investigated how nutritional factors influence the onset of puberty (Foster & Ryan, 1985; Foster *et al.* 1985*b*). Lambs raised on a high plane of nutrition can achieve puberty towards the beginning of the normal breeding season. Lambs with restricted intakes from birth which are subsequently given *ad lib.* feeding after different periods of restriction achieve puberty at later dates and lower body-weights than well-nourished controls (Foster & Ryan, 1985). Indeed, the critical threshold weight for puberty is extremely plastic in lambs, decreasing by a factor of 50% from the beginning to the end of the normal breeding season (Foster & Ryan, 1985).

It is by no means clear how undernutrition impairs the expression of a normal photoperiodic response in ewe lambs. It does appear, however, that the central photoperiodic time-measurement process may remain intact in the undernourished lamb. In one experiment to examine this question, feed-restricted, ovariectomized, oestradiol-implanted ewe lambs were exposed either to long or short days at 42 weeks of age (Foster & Yellon, 1985). After 6 weeks, lambs maintained on long days were exposed to short days and both groups given *ad lib.* feeding. Rapid catch-up growth occurred in both groups. However, lambs exposed to short days remained extremely sensitive to the inhibitory action of oestradiol while lambs maintained on long followed by short days showed a significant rise in LH,

characteristic of the onset of puberty (Foster & Yellon, 1985). These findings indicate that ewe lambs continue to accumulate photoperiodic information during a prolonged period of undernutrition and suggest strongly that critical levels of energy intake may be required before the lamb can express a normal photoperiodic response.

Although work on sheep has elegantly demonstrated the subtle interaction of nutritional factors and photoperiod within the 1st year of life, it is not possible to extend these observations directly to other short-day breeders. The red deer has a similar breeding season to that of the sheep (Guinness *et al.* 1971) and during the 1st year of life calves can achieve weights in excess of 65 kg (A. Loudon and J. A. Milne, unpublished results). Work on the adult red deer has established that ovulation normally occurs in hinds at weights in excess of 50–55 kg at the rut (Hamilton & Blaxter, 1980) and yet 6–9-month-old calves well in excess of this 'critical weight' during the breeding season fail to ovulate and breed (J. Robinson, personal communication; A. Loudon and J. A. Milne, unpublished results). Failure to breed in the first autumn of life may be a general feature of large, slow-maturing species such as red deer, since at this stage of development a proportionately greater increment of daily energy intake will be allocated towards growth.

One possible explanation for the seasonal decline in critical weights for the pubertal ewe (see Foster *et al.* 1985*b*) may be that as the breeding season advances, there is an associated photoperiodically mediated decline in metabolic rate and energy requirements. Such seasonal changes in metabolic rate have been described for deer (Silver *et al.* 1969) and sheep (Blaxter & Boyne, 1982). Blaxter & Boyne's (1982) study reported a sinusoidal change in metabolic rate with minimal metabolism in midwinter and maximal (30% greater) in midsummer. Substantial seasonal changes in appetite and growth occur in both growing and adult sheep and deer and are presumed to be a reflection of an underlying rhythm in metabolism (Wood *et al.* 1962; Pollock, 1975; Milne *et al.* 1978; Kay, 1979; Loudon & Milne, 1985; Suttie & Simpson, 1985). Although currently unsupported by results, it is intellectually attractive to propose that pubertal sheep may breed when the proportion of their total energy intake allocated to growth falls below a critical threshold. A seasonal decline in metabolic rate and growth rate may therefore permit puberty to occur at a lower weight. Such a hypothesis could be extended to larger, slower-maturing species, such as red deer, to explain why the rapidly growing calf may fail to breed in the 1st year of life despite achieving weights in excess of those required by yearlings and adults for the onset of ovarian activity. Thus, physiological maturity rather than absolute weight may be an important determinant of the onset of puberty.

Work on small mammals has confirmed that photoperiodic effects on metabolism and puberty are not confined to larger, seasonally breeding mammals (for review see Dark & Wade, 1985). In the meadow vole, photoperiodically induced reductions in body mass are associated with sizeable savings in energy requirements (Dark *et al.* 1983). Since gonadal steroids have profound effects on energy balance in most mammals (Wade & Gray, 1979), one possible explanation

for the photoperiodic effect on energy metabolism is that short days induce a suppression of gonadal activity with a concomitant effect on energy balance. However, recent work on the photoperiodic regulation of puberty in voles and hamsters indicates that seasonal changes in energy metabolism may be independent of gonadal influences. In a series of experiments, Horton (1984) examined some of the ways in which photoperiod and nutrition interact to regulate the timing of puberty in montane voles. Voles maintained throughout pregnancy on either 8 or 16 h light/d were transferred to an intermediate photoperiod of 14 h daylength. The young voles were weaned at 18 d of age and maintained on 14 h daylength until they were killed at 74 d of age. Male voles which had undergone gestation on 16 h of daylight had significantly smaller testes, weighed less than voles maintained on 8 h light during gestation, and were similar in form to wild voles born in the autumn on decreasing daylength (Horton, 1984).

These results show that some component of the prenatal photoperiodic environment determined the manner in which young voles would respond to a common treatment of 14 h of light after birth. Voles appeared to respond to the common photoperiod of 14 h light as a long or short day depending on the length of the day experienced during gestation. In subsequent experiments, Horton (1984) cross-fostered young on the day of birth and clearly demonstrated that the critical factor regulating growth and puberty was prenatal photoperiod and was not influenced by the foster mother during lactation (see Reppert *et al.* 1985). Recently, these experiments have been repeated in the Djungarian hamster (*Phodopus sungorus*) (Reppert *et al.* 1985) and, as with Horton's (1984) work on the montane vole, demonstrated that a photoperiodic message had been received by the fetus. In both species, photoperiod has a profound effect on growth and puberty.

The extent to which fetal programming with current photoperiodic information sets postnatal growth rates may vary considerably between species. There is currently a great paucity of information in this area, although it should be noted that in sheep, the ewe lamb is insensitive to the effects of short days on the reproductive axis for some considerable time after birth (Yellon & Foster, 1985). In this respect, larger long-lived species may differ in comparison with small mammals which have life expectancies in the wild of less than 1 year.

In one group of seasonally breeding mammals, the seasonal macropod marsupials (the Bennett's wallaby (*Macropus rufogriseus rufogriseus*) and the tammar wallaby (*Macropus eugenii*)), photoperiod is considered to be unimportant in determining the timing of puberty. The normal breeding season for these two species is from midsummer to midwinter and the termination of the breeding season is associated with the initiation of a period of quiescence by the corpus luteum which in turn prevents the activation and implantation of the blastocyst. In the tammar wallaby, young females commonly come into oestrus shortly after leaving the pouch at a time when their mothers are reproductively quiescent (Andrewartha & Barker, 1969; Tyndale-Biscoe & Hawkins, 1977). In this case, after conceiving, their corpora lutea become quiescent and their embryos enter

diapause (Tyndale-Biscoe & Hawkins, 1977); shortly after the summer solstice, the corpora lutea of both mothers and young reactivate, embryos spontaneously resume development and young are born. In the tammar wallaby, the growth of the pouch young is significantly correlated with milk yield (Green, 1984), while in the Bennett's, pouch-young growth velocity is significantly correlated with maternal prolactin level (see p. 213), presumably reflecting the overriding importance of this hormone for maintaining high milk yields. Thus, in these two species it is likely that puberty is primarily under the control of nutrition and growth, and is independent of photoperiod. Once puberty is achieved, the fate of the corpus luteum and blastocyst (quiescence or activity) is dependent on photoperiod. Although detailed information on the control of puberty in marsupials is currently unavailable, the previously described findings should caution against generalizations which link photoperiod, nutrition and growth and the onset of puberty in seasonally breeding mammals.

Lactation, nutrition and fertility

Demographic evidence. Lactation is unique insofar as it represents both an important nutritional process in which large amounts of energy are transferred to the young, and a reproductive process, since in many species the secretion of milk and sucking activity of the young are associated with the inhibition of ovarian function. The extent of transfer of nutrients to the young at peak milk yield varies enormously between species, being highest in carnivores and marine mammals and least in primates and great apes (Oftedal, 1984; Gittleman & Oftedal, 1987). The demographic evidence for the role of lactation as a birth-spacing mechanism is powerful. In man, a number of authors have drawn attention to the influence of breast-feeding in delaying a return to menses and most of these findings have been ably reviewed elsewhere (Howie & McNeilly, 1982; Hartmann *et al.* 1984; McNeilly *et al.* 1985; Ramachandran, 1985). A brief list of some demographic findings on the effects of breast-feeding is contained in Table 1.

Table 1. *Some demographic findings for the role of breast-feeding as a birth-spacing mechanism in women not using contraceptives*

Condition	Birth spacing	Reference
!Kung nomadic hunter–gatherers	3–4 years	Konner & Worthman (1980)
!Kung partial agricultural	Reduced interval	Kolata (1974); Konner & Worthman (1980)
Eskimo	1·5 years	Berman *et al.* (1972)
Rural Indian	>2 years	Potter *et al.* (1965)
Rural Rwandese	approximately 2 years	Bonte *et al.* (1974); Saxton & Serwadda (1969)
Urban Rwandese	9 months	Bonte *et al.* (1974)
Rural Gambian:		
Unsupplemented	50% menses by 80 weeks	Lunn *et al.* (1984)[*]
Supplemented	50% menses by 55 weeks	Lunn *et al.* (1984)[*]
Hutterites (1921–30)	24 months	Bongaarts (1980)
Bangladesh	37·4 months	Bongaarts (1980)

[*]Approximate values; information on interbirth interval not available.

Amongst non-domesticated mammals, lactation can have a profound effect on interbirth interval. For instance, in great apes such as the wild mountain gorilla, interbirth intervals between surviving offspring of just under 4 years have been reported (Harcourt *et al.* 1980) and, in the wild chimpanzee, intervals of approximately 4 years (Tutin, 1980). Generally, amongst primates, lactational infertility appears to be correlated with body size; the larger, slower-maturing species having a proportionately greater delay associated with lactation. In a laboratory study of two medium-sized primates, the rhesus monkey and crab-eating macaque (*Macaca mulatta* and *M. fascicularis* respectively), infertility has been reported to persist for the duration of lactation (Aso & Williams, 1985), although the seasonal nature of reproduction in these species complicates interpretation. In the smaller primates such as the common marmoset, lactation appears to be almost without effect on the resumption of fertility post-partum (McNeilly *et al.* 1981).

In ungulates, lactational effects on fertility have also been widely reported (see Lamming, 1978). Some demographic information from population studies of wild African ungulates are presented in Fig. 1. It can be seen that with increasing body size, there is associated with lactation an allometric increase in the length of time to the succeeding pregnancy. From such findings it might be estimated that an ungulate of less than 80 kg would be expected to have an immediate postpartum
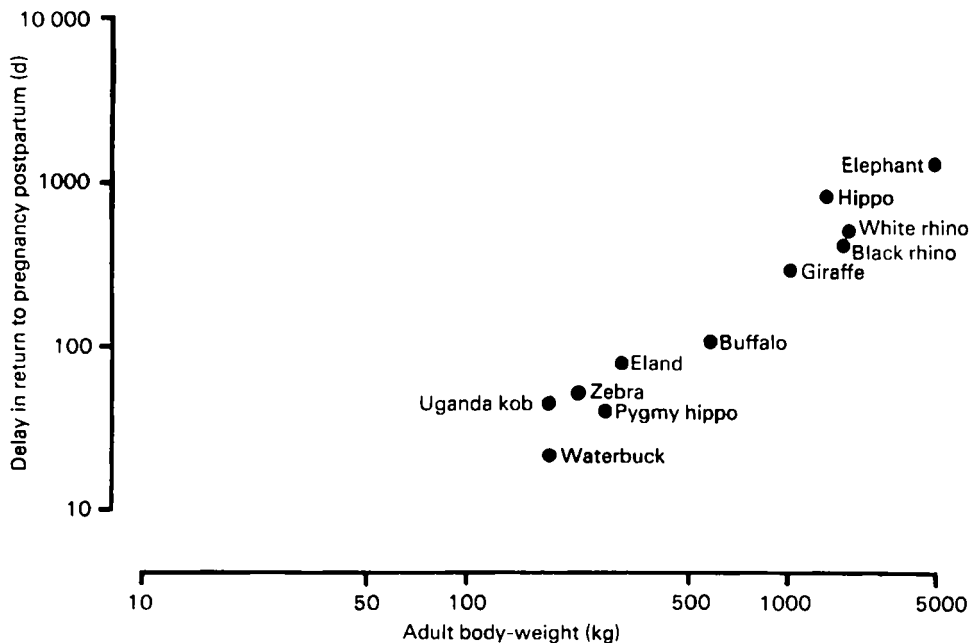

Fig. 1. The duration of postpartum anoestrus for a range of tropical African ungulates (values from: Klingel, 1969; Laws & Clough, 1966; Lawes & Parker, 1968; Laws, 1969; Skinner & Van Zyl, 1969; Morrison & Buechner, 1971; Mentis, 1972; Sinclair, 1974*a*, 1977; Laws *et al.* 1975; Skinner & Hall-Martin, 1975; Irby, 1979; Spinage, 1982).

oestrus, but by 200–300 kg a delay in return to oestrus would become a component part of the animal's biology. The elephant is the extreme example, with a delay of over 3 years between births, even in the best of habitats (Laws *et al.* 1975). The species shown in Fig. 1 differ in one important respect from ungulates of the temperate zones: they are aphotoperiodic and their reproduction is not governed by seasonal changes in daylength. When maintained in captivity in zoos in the temperate zones, tropical ungulates persist with an aseasonal pattern of reproduction (Zuckerman, 1952). However, even tropical species are exposed to marked seasonal changes in patterns of rainfall, but it would appear that many of these species lack the ability to predict environmental change and so time reproduction. For example, in the African buffalo, a period of gestation of 10 months is normally followed by a 5-month lactational anoestrus (Sinclair, 1974*a*, 1977). This combined interval of 15 months is 3 months out of phase with the yearly rainfall pattern and in consequence, wild buffalos frequently give birth close to the beginning of the dry season (Sinclair, 1974*b*). In such cases, the calf usually dies and the female enters anoestrus. Normally, African buffalo are only able to breed 2 or 3 years out of 4, presumably due to an inability to accurately track seasonal patterns in rainfall.

Sucking frequency, infertility and nutrition. Remarkably little is known of the physiological processes whereby lactation inhibits ovarian activity. Some of the best examples of the role of the sucking stimulus come from studies on marsupials. In many species of macropod marsupial, the quiescent blastocyst remains unimplanted in the uterus so long as the young joey remains in the pouch. In species such as the red kangaroo, reactivation of the blastocyst is closely associated with the permanent pouch exit of the joey (Sharman, 1963).

Sharman's (1963) classic studies of the red kangaroo provided one of the earliest and best demonstrations of the role of the sucking stimulus in controlling reproduction in a mammal. In the red kangaroo, the blastocyst normally resumes development about 30 d before the permanent exit of the joey and from this, Sharman (1963) concluded that it was the reduction in intensity of the sucking stimulus just before permanent pouch exit which triggered reactivation. Indeed, when the newborn offspring were removed from the teat (to which they are permanently attached for the first few months of lactation), the quiescent blastocyst reactivated and another newborn young appeared 31–32 d later (Sharman, 1965). From this, the conclusion can be drawn that it is the intense sucking stimulus of the permanently attached joey which blocks reactivation; the older joey which continues to suck much larger quantities of milk from outside the pouch is ineffective in blocking reactivation. In more recent experiments, the mammary glands of lactating tammar wallabies have been denervated. The joey continued to suck and grow but the sucking activity no longer blocked the development of the blastocyst (Renfree, 1979).

There are numerous examples from the literature covering domesticated livestock for the role of the sucking offspring in blocking or delaying resumed ovarian activity. In cattle, early weaning of calves is usually associated with a more

rapid return to oestrus (Laster *et al.* 1973), while the presence of a calf may interact in a complex manner with seasonal effects to delay oestrus (Jung, 1983). In experiments in which sucking frequency has been experimentally manipulated in sheep and cattle, reduced daily sucking frequency (one to two bouts per day) usually results in a more rapid return to oestrus by the dam (Randel, 1981; Dingwall *et al.* 1982; Bastidas *et al.* 1984*a*). In the case of sheep (Dingwall *et al.* 1982) and cattle (Bastidas *et al.* 1984*b*), such manipulations had no significant effect on the growth of the offspring or the yield of milk and from this one must conclude that the quantities of milk consumed by the offspring were similar, the essential difference being that this milk was obtained in one or two controlled bouts per d rather than *ad lib*.

One example of the interaction of nutrition, milk yield and sucking frequency comes from a study of the domesticated red deer (Loudon *et al.* 1983). In this study, two groups of lactating hinds were moved from a common treatment just before birth to either an impoverished pasture of indigenous hill vegetation or to an improved perennial ryegrass (*Lolium perenne*)–clover (*Trifolium repens*) sward. Hinds grazing the improved sward had significantly shorter daily grazing times and yielded approximately twice the quantity of milk of hinds on poor-quality pasture, as estimated by the calf-sucking technique (Loudon *et al.* 1984). Machine milking of hinds on the two treatments indicated that the rate of accretion of milk in the gland was significantly lower for animals maintained on hill pasture. Intriguingly, there were significant differences in the pattern of sucking activity of the calves on the two treatments. Calves from the low-yielding group sucked far more frequently per day and were more frequently rejected by their dams than those consuming larger quantities of milk on the improved swards (Loudon *et al.* 1983). These differences in sucking activity were associated with significant differences in plasma prolactin concentrations. In both treatments, prolactin declined seasonally but in the high-sucking-frequency group, levels were consistently higher (Loudon *et al.* 1983) and conception date in this latter group was significantly delayed by 6 d. In a more recent study, Milne & Sibbald (1986) weaned hinds in mid-September or mid-November. Early weaning had little effect on calf growth but did significantly advance the date of oestrus by 8 d when compared with a late-weaned group. Thus, studies on domesticated red deer hinds show that the pattern of sucking activity can serve to modify the date of oestrus, even in a species where the reproductive axis is so clearly under the overriding control of photoperiod.

These results should be considered together with the demonstration in sheep and cattle that artificial manipulations of sucking frequency do not influence milk yield but can affect the timing of oestrus (Bastidas *et al.* 1984*a,b*). One possible mechanism is set out in Fig. 2. In this model, the sucking offspring is an important part of the physiological feedback loop, whereby plane of nutrition, lactation and date of oestrus interact. On high planes of nutrition with copious milk production, sucking frequency may generally decline although total feeding time and milk consumption may be high. The reduced sucking frequency may release the GnRH
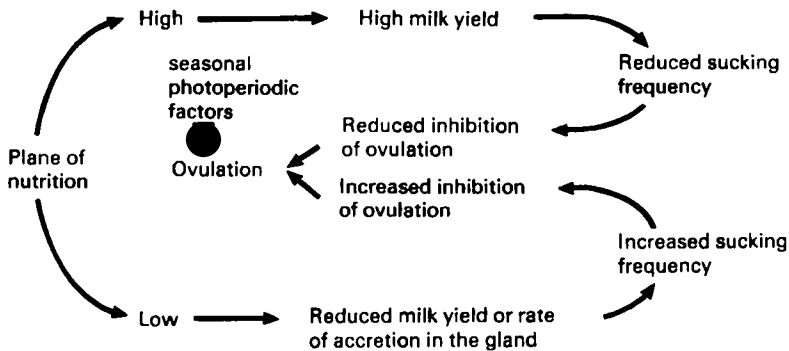
Fig. 2. A model for the interaction of plane of nutrition with milk yield, sucking frequency and inhibition of ovarian activity.

generator from inhibition and so permit pulsatile release of LH. In highly seasonal species such as sheep and red deer, photoperiod is a major overriding factor and the role of sucking may be limited to subtle but significant shifts in date of oestrus.

In nonphotoperiodic species such as man and tropical mammals, the intensity of the sucking stimulus may be the major factor which regulates the return to ovarian cyclicity. Some evidence which partly supports this hypothesis may be found in recent studies of nutrition and lactation in rural African women in The Gambia (Lunn *et al.* 1984). In the community studied, breast-feeding women normally experienced a delay of at least 76 weeks before the resumption of menses (as estimated from hormone indices) and 91 weeks before the first ovulation post-partum. Plasma prolactin levels were very high in this group, reaching a peak by weeks 10–12 and thereafter declining. At a later time, a large number of breast-feeding women were given a dietary supplement which effectively increased their daily energy intake by approximately 46% (Prentice *et al.* 1983). Plasma prolactin levels for the supplemented women were significantly lower at all stages in lactation and these women experienced a return to menses (as estimated from hormone indices) by week 55 and ovulation by week 70 (Lunn *et al.* 1984). In further experiments, women were supplemented during pregnancy as well as lactation and a further decline in prolactin levels occurred with earlier ovulation. Indeed, this latter group approached the levels of energy intake experienced by Western women breast-feeding on demand and had similar prolactin levels for any given stage of lactation (Howie & McNeilly, 1982). Interestingly, supplementation of the diet of Gambian women has been reported to have no effect on milk yield (Prentice *et al.* 1983). Although accurate information in suckling activity has not been obtained for the Gambian study, a small reduction in suckling frequency over a 12 h period did occur in supplemented women (Prentice *et al.* 1983). Lunn (1985) has suggested that the reported differences in prolactin levels were primarily a result of differences in suckling activity.

Detailed studies by Howie & McNeilly (1982) at Edinburgh provide further evidence for association of suckling frequency, plasma prolactin and lactational

infertility in breast-feeding women. Persistence of breast-feeding in a group of well-nourished Western women was associated with a postponement of ovulation for over 40 weeks, while the introduction of even small amounts of supplementary foods led to a decline in suckling frequency and duration, lower mean prolactin levels and earlier ovulation (Howie & McNeilly, 1982). From these findings, together with the studies of rural African women in The Gambia, it is possible to conclude that frequency of suckling may be a major factor regulating fertility in women and that the sucking behaviour of the offspring is a crucial component in the physiological feedback loop controlling fertility.

Prolactin, milk yield and fertility. In all mammals so far investigated, prolactin has been shown to have an important role in either the establishment or maintenance of milk yield (Cowie *et al.* 1980). High levels of prolactin during lactation have been reported for a large number of species and in these species, the sucking young are a major factor in maintaining maternal hyperprolactinaemia. In several studies, prolactin has been shown to provide a sensitive endocrine indicator of the probability of ovulation during lactation (e.g. Howie & McNeilly, 1982; Lunn *et al.* 1984). However, there is no clear evidence for the role of prolactin in directly maintaining the suppression of ovarian activity during lactation. The subject has been ably reviewed elsewhere (McNeilly, 1984; McNeilly *et al.* 1985). One of the major problems confronting most investigators has been that treatment with the dopamine agonist bromocriptine effectively lowers prolactin levels but also frequently causes a reduction or cessation of milk yield, with obvious effects on suckling activity. Thus, it is extremely difficult to disentangle the effects of suckling behaviour and prolactin release on the inhibition of ovarian activity.

In ruminants, several studies would suggest that prolactin has little or no role in the maintenance of anoestrus. In sheep and beef cattle, treatment with bromocriptine effectively suppresses prolactin levels but has little effect on the period of anoestrus (Williams & Ray, 1980; Fitzgerald & Cunningham, 1981). Furthermore, although many domesticated and wild ruminants breed in the autumn at a time of seasonally declining prolactin levels, species such as the roe deer and Pere David's deer (*Elaphunus davidianus*) breed in July. In the case of roe, prolactin levels are high at this time of year (Schams & Barth, 1982), probably reflecting the overriding influence of photoperiod in regulating prolactin release.

An example of the complex interaction of suckling activity, prolactin level and infertility comes from work on seasonally breeding wallabies. In the tammar and the Bennett's wallabies, the quiescent blastocyst remains in a state of diapause from midsummer to midwinter, due to the inhibitory effect of the sucking, pouched young (Tyndale-Biscoe *et al.* 1974; Fleming *et al.* 1983). During this period, removal of the pouched young in both species or treatment with bromocriptine effectively terminates diapause and birth follows approximately 28 d later. Such manipulations are without effect on circulating prolactin levels as measured by heterologous radioimmunoassay (Tyndale-Biscoe & Hinds, 1984; Curlewis *et al.* 1986). In the Bennett's wallaby, prolactin levels rise in late pouch life from midwinter to early summer. However, although treatment of lactating females

with bromocriptine or removal of pouched young has an immediate effect in substantially reducing prolactin levels, the quiescent blastocyst remains in a state of seasonal delay (see Curlewis *et al.* 1986). Prolactin is clearly of importance in maintaining milk yield in this species since in the previously-mentioned study, bromocriptine caused a weight loss in joeys comparable to complete removal from the pouch. Indeed, growth velocity in late pouch life is closely correlated with maternal prolactin levels, with peak growth velocity and prolactin levels occurring just before permanent pouch exit (see Fig. 3).

Finally, it should be observed that lactational infertility in many marsupials (including macropods) differs from eutherians in the form of the inhibitory mechanism. In eutherians, suckling is considered to act primarily on the secretion of LH, perhaps by interfering with the action of GnRH release (see McNeilly, 1984). In seasonal marsupials, on the other hand, there is no seasonal change in LH secretion. Lutectomy is followed by ovulation within 17 d in both seasonal and lactational induced diapause in the tammar wallaby (Tyndale-Biscoe & Hawkins, 1977; Tyndale-Biscoe & Hearn, 1981), indicating that gonadotropin secretion is not influenced by seasonal factors. More recently, Tyndale-Biscoe *et al.* (1986) have shown that LH shows no seasonal change in pulsatile activity. This contrasts greatly with the situation seen in seasonally breeding mammals such as sheep (see Legan *et al.* 1977). These differences should caution against generalizations concerning the operation of common central neuronal mechanisms whereby suckling induces a state of hyperprolactinaemia and also serves to maintain milk secretion and inhibit ovarian activity.
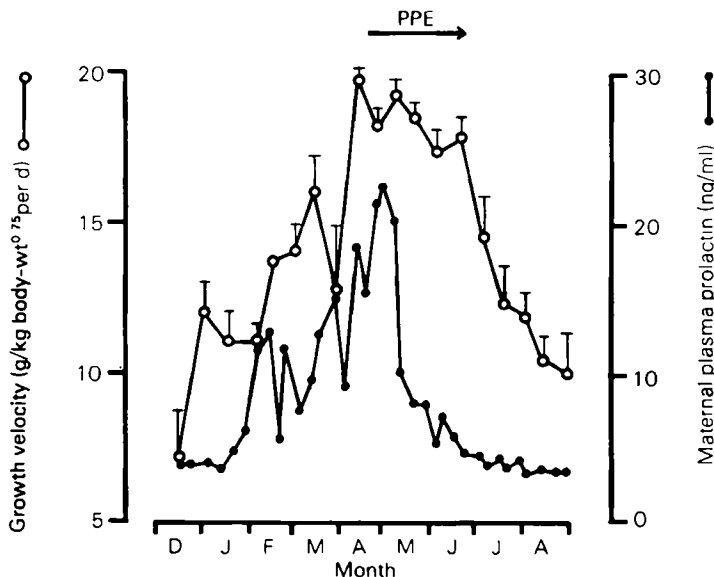

Fig. 3.   The growth velocity (O) of Bennett's wallaby (*Macropus rufogriseus rufogriseus*) joeys from mid-pouch life to pouch exit in relation to maternal plasma prolactin level (●). Findings on prolactin level from Curlewis *et al.* (1986). PPE, Permanent pouch exit. Mean values with their standard errors represented by vertical bars.

Conclusions

Nutrition clearly has a profound effect on the reproductive output of all mammals. Our knowledge, however, is currently confined to a few detailed studies of domesticated ruminants, laboratory rodents and some primates. Amongst seasonally breeding mammals, photoperiod influences not only the timing of reproduction but also has central effects on growth, appetite and metabolism. The way in which these factors interact is very poorly understood, particularly with respect to the onset of puberty. It is now clear that some of the recently developed models for the onset of puberty in the sheep cannot be directly applied to other seasonally breeding mammals. Information on nutritional effects on lactation and postpartum oestrus intervals indicate that the considerable between-species variation in the effect of the sucking stimulus in maintaining reproductive quiescence may be related to differences in body size and the growth and maturation rates of the neonate. There is currently only scant information on the great majority of mammals and for many phylogenetic groups, no information at all. The central question as to the physiological mechanisms involved in reproductive suppression during undernutrition remains one of the most exciting areas in current mammalian physiology.

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