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# Lactation under food constraints in Iberian red deer *Cervus elaphus hispanicus*

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The plane of nutrition in deer may affect body condition and lactation in hinds and calf growth both through long-term density-dependent effects and by short-term abiotically originated falls in food supply. Our study examines the effect of low nutrient availability after calving on lactation in captive Iberian red deer *Cervus elaphus hispanicus*. Twelve hinds and their calves were allotted to a food restricted (50-60% daily energy requirements) or a control group just after calving. Hinds in the food-restricted group showed a greater body mass loss, produced less milk and yield of milk fat, protein and lactose, and a different lactation curve shape, which resulted in reduced calf growth. However, the time course of lactation variables appeared to show a compensatory response up to week 4: a greater milk fat content in low-nutrition hinds than in the control group appeared to compensate for lower milk production, as neither calf nor hind mass differed from the control group, and lactation variables in both groups showed a standard lactation pattern. In contrast, as milk fat content fell below that of the control group after week 4, the low nutrition plane overcame a standard lactation pattern and groups differed in most variables (e.g. calf and hind mass and percentage of calf growth). Our results appear to show that deer mobilise body reserves in lactation to maintain offspring growth under temporary reductions in food intake, which may be a strategy of securing investment in current offspring at the expense of reproducing the following season.

*Key words: ecological constraints, food resources, Iberian red deer, lactation, milk composition, milk production, parental investment*

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Understanding how the plane of nutrition, maternal body condition, lactation and offspring behaviour interact to determine reproductive success is at the centre of understanding density-dependent effects in wild populations (White 1992). Particularly in monotocous species such as red deer *Cervus elaphus* (where investment in individual offspring is greater than in polytocous species), reproduction appears to be limited by availability of food resources rather than by predation (Bunnell 1987). Although ecological and epidemiological studies have shown relationships between nutritional status, population density, body condition and parasite load (Davidson & Doster 1997), little is known about compensatory responses by hinds to nutrition stresses during lactation. If occurring during late pregnancy, loss of mass due to poor nutrition results in lower birth masses and increased calf mortality (Thorne, Dean & Hepworth 1976), and reduced milk production during lactation (Rognmo, Markussen, Jacobsen & Blix 1983).

Most of the research published on the lactation responses to malnutrition involve cattle. However, responses in wild species are likely to be different and adaptive because, in contrast to cattle, which have been selected for a high production of milk of standard quality, lactation in wild mammals is shaped by allometrics and ecological adaptations (Martin 1984, Oftedal 1984a,b, 1985). In cattle, fine modifications of diet under standard nutrition affect mainly fat (which may change three percentage units), a rather small and controversial effect appears to be exerted on protein (which may change 0.5 percentage units), whereas lactose appears to change very little, or show no change at all (Sutton 1989).

Under standard nutrition in deer, milk composition is influenced by the nutritional requirements of the calf and not hind body size or her mass loss during lactation (Landete-Castillejos, García & Gallego 2001), a relationship not found in cattle. Milk protein is particularly related to calf birth mass and gain both within the same subspecies (Landete-Castillejos et al. 2001), as well as when comparing different deer subspecies controlling for social and diet conditions (Landete-Castillejos, Garcia, Gomez, Molina & Gallego in press). Thus, hinds are expected to keep milk protein content constant. Such a greater effort is often shown by a greater female mass loss during lactation both in cattle (Oldham & Friggens 1989) and in deer (Landete-Castillejos, García, Molina, Vergara, Garde & Gallego 2000b). Because mobilisation of body protein may not be possible for synthesis of milk protein (Reid, Mode & Tyrell 1966, Coppock, Tyrrell, Merrill & Reid 1968, Kaufmann 1979, White, Holleman & Tiplady 1989), deer hinds should seek maximum protein intake. That is what appears to happen: non-lactating yearlings forage to maximise protein intake (Wilmshurst, Fryxell & Hudson 1995), and lactating hinds also appear to select habitats which are richer in protein content than the habitats used by non-lactating hinds (Clutton-Brock, Iason, Albon & Guinness 1982b). Failure of hinds to keep milk protein constant, as in delayed births (Landete-Castillejos, García, Garde & Gallego 2000a), also results in a reduction in calf growth, particularly in the early stages of lactation (Landete-Castillejos et al. 2001) when calf growth is more dependent upon milk (Arman, Kay, Goodall & Sharman 1974).

Deer produce milk mainly from food ingested daily rather than from body reserves (Sadleir 1987). However, when protein is not severely limiting, fat reserves are mobilised when intake of metabolisable energy is reduced, to maximise milk production under such limiting conditions (White 1992). This is because body fat appears to be a more efficient fast-releasing source of milk fat than ruminal acetate (White 1992). Thus, hinds that are food-restricted during lactation are likely to show early symptoms of loss of body condition as they use body reserves to continue milk production. The impact of such a low nutrition plane may depend upon its timing and duration, as hinds are likely to compensate for the effects of short-term food restriction by using their own body reserves. However, it is not known how long such compensation may last.

Our study aims to assess the responses of hinds lactating at a low nutritional plane by comparing them with a control group with food *ad libitum*. The comparison involved milk production and composition, calf growth and hind mass change during lactation. Because it affected only lactation, the experiment simulated a drastic reduction in available food occurring precisely at lactation, rather than density-dependent reductions in nutrient plane also during gestation.

## Material and methods

Our subjects were 12 red deer hinds of the Iberian subspecies *Cervus elaphus hispanicus*. The mean age of hinds receiving restricted food during lactation was 5.0 ± 1.55 (SD) years of age, whereas the control group had a mean age of 5.5 ± 1.64 (SD) years. The first group had four male and two female calves, whereas all the calves in the control group were males.

The control group was kept in a 10,000 $m^2$ enclosure on an irrigated pasture dominated by tall fescue *Festuca arundinacea* (52.4%), cocksfoot *Dactylis glomerata* (28.6%), lucerne *Medicago sativa* (14.3%), and white clover *Trifolium repens* (4.8%). Furthermore, this group had access to a diet consisting of 1 kg $day^{-1}$ $individual^{-1}$ of barley straw and hay from barley, alfalfa, oat and sweet beetroot (16% CP) based on suggestions by Brelurut, Pingard & Thériez (1990). The food-restricted group was kept in a similar enclosure without pasture and had access to 1.5 kg $day^{-1}$ $indidual^{-1}$ of the previously mentioned diet (about 50-60% of the amount suggested for lactating hinds). Mean hind body masses at the start of the experiment (i.e. at calving) were 101.2 ± 14.2 (SD) and 103.7 ± 8.3 kg (SD) for the experimental and control group, respectively.

Hinds were milked in weeks 2, 3, 4 and 6, and then every four weeks up to week 18 in this and another simultaneous experiment involving two additional groups. This enabled us to best document early lactation when milk production changes most. However, for ethical reasons food restriction in the experimental group (and thus the results reported here) was stopped in week 10. Weaning was enforced simultaneously in all hinds within a group in order to keep social conditions constant throughout the experiment. Before each milking, hinds were separated from their calves for six hours (08:00 to 14:00) in a deer-handling facility. This was the only period of isolation of individuals of a group and is a standard period between sucklings (Arman et al. 1974, García, Landete-Castillejos, Molina, Abiñana, Fernández, Garde & Gallego 1999). Prior to this isolation period, no milking was conducted for ethical reasons fully explained in Landete-Castillejos et al. (2000a). Milking was carried out under anaesthesia with a milking machine set up to a 50/50 massage/milking ratio and 44 kPa of vacuum. The milking machine was turned off after 30-60 seconds whereafter the hind was hand milked to collect the remaining milk. Daily milk production was considered to be four times the amount collected in each milking. Milking frequency was therefore reduced to the minimum considered essential to prevent stress and potential damaging effects of the anaesthesia, which was achieved by using a low-dose combination of xylazine (0.5 mg/kg body mass) and ketamine (1 mg/kg) intravenously injected. Once anaesthesia was induced, 10 I.U. of oxytocin was injected into the right jugular vein one minute before the milking started. After the milking was finished, anaesthesia was reversed with a yohimbine injection of 0.25 mg/kg body mass. Hinds were weighed weekly in a ± 50 g electronic scale, whereas calves were weighed in a ± 5 g scale up to 35 kg of body mass, and then in the same scale as their mothers.

Two 30-ml samples of milk (replicates) were collected for chemical analysis. Milk analyses were carried out in an automatic milk analyser as described in Landete-Castillejos et al. (2000b).

## Statistical analysis

Differences between groups in age and mass variables of the hinds, body mass variables of the calves, and milk production and composition variables were tested for using one-way ANOVA. Because absolute body mass gain may depend on calf birth mass and a similar gain may, thus, not show a greater effort by lighter calves to grow faster, growth was also computed as rate of growth (percentage of body mass) for analysis. Pearson correlations (bilateral) were used to test the relationships between composition and mass variables of the hind and calf. Student's t-tests were used to test within-week differences for each of the variables monitored during lactation. Differences between groups per week consistently showed two phases in the pattern of most variables: from birth to week 4 and from week 4 until the end of experiment (week 10). Thus, we also analysed these two phases separately. Because of the small sample sizes involved, marginally significant tests ($P < 0.1$) are reported by their exact probability rather than as $P > 0.05$.

## Results

### Gross differences between groups

At the start of the experiment, i.e. after calving, hinds did not differ in age, body mass (see means in the Methods section), nor in calf birth mass ($P > 0.10$; Table 1). At the end of the experiment, hinds under low plane of nutrition had produced less milk than the control group ($P < 0.001$), and also less milk fat, protein and lactose ($P < 0.001$ for all components). In contrast, mean nutrient concentration was only marginally significant for fat ($P = 0.072$), but not for protein or lactose. The lower nutrient production in the food-restricted group also resulted in smaller gains both in absolute values ($P = 0.005$) and in rate of calf growth ($P = 0.014$). The smaller milk and nutrient production in the food-restricted group appeared to cost the hinds a greater effort, as they lost a larger amount and percentage of body mass during lactation ($P < 0.001$ in both cases) than hinds in the control group.

Because the sample size is very small and because there were only two female calves, the ANOVA was not powerful enough to detect sex bias. However, although the data are not shown, no detectable sex effect on

Table 1. Means (± SE) of total differences between food-restricted Iberian red deer hinds and control groups. Mean nutrient content was computed using data from all weeks to increase mean consistency, despite the greater influence of the first weeks on the total mean. Significant differences are indicated at: † = 0.1, * = 0.05, ** = 0.01 and *** = 0.001, and the variables are abbreviated in the following way: CBW: calf birth mass (in kg); CG: calf mass gained during lactation (in kg); PCG: percentage of calf mass gained during lactation (in %); HWC: hind mass change during lactation (in kg); PHWC: percentage of hind mass change during lactation (in %); TMY: total milk yield (in litres); TFY: total fat yield (in kg); TPY: total protein yield (in kg); TLY: total lactose yield (in kg); F: mean milk fat content (in %); P: mean milk protein content (in %); L: mean milk lactose content (in %).

| Variable | Restricted | Control | Mean |
|---|---|---|---|
| CBW | 8.2 ± 0.4 | 8.6 ± 0.4 | 8.4 ± 0.3 |
| CG** | 15.6 ± 1.9 | 22.4 ± 0.6 | 19.3 ± 1.4 |
| PCG* | 180 ± 59 | 262 ± 32 | 221 ± 62 |
| HWC*** | -12.9 ± 1.3 | -3.1 ± 1.8 | -8.0 ± 1.8 |
| PHWC*** | -12.6 ± 0.8 | -2.9 ± 1.7 | -7.7 ± 1.7 |
| TMY*** | 103.9 ± 13.2 | 180.4 ± 8.1 | 142.2 ± 13.7 |
| TFY*** | 16.4 ± 2.0 | 28.1 ± 1.2 | 22.3 ± 2.1 |
| TPY*** | 10.6 ± 1.4 | 18.9 ± 0.8 | 14.8 ± 1.5 |
| TLY*** | 10.1 ± 1.3 | 18.2 ± 0.7 | 14.2 ± 1.4 |
| F† | 9.2 ± 0.2 | 8.8 ± 0.2 | 9.0 ± 0.1 |
| P | 6.0 ± 0.1 | 5.9 ± 0.1 | 5.9 ± 0.1 |
| L | 5.7 ± 0.1 | 5.7 ± 0.1 | 5.7 ± 0.0 |

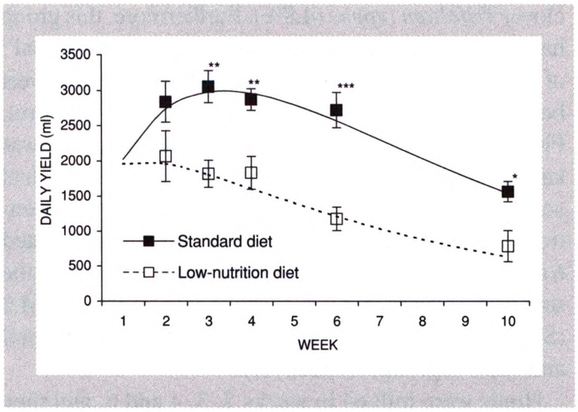


Figure 1. Lactation curves for milking data of two groups of hinds subjected to either a standard (■) or a low plane of nutrition (□). The fitting of the curve corresponds to the most widely used model in lactation: $Y(w) = a w^b e^{-cw}$, where w is yield at week w, and a, b and c are constants. Descending curves (type II) correspond to either those with a negative b coefficient, or a non-significant one. Within-week significant differences are indicated by asterisks.

pooled groups nor in the experimental group was found regarding mass at birth of calves or that of their mothers after calving. No detectable sex effect was found for gains in the experimental group either.

## Correlations among overall values

The correlations among variable values for the overall lactation (Table 2) showed that calf birth mass did not correlate with any variable. Calf gains showed a high correlation with total milk yield ($P < 0.001$). Regarding the production of each nutrient, absolute gains correlated most closely with total protein production, followed by lactose and fat ($P < 0.001$; see Table 2), whereas the difference between protein and fat was very small when the percentage of calf mass gained was considered. In contrast, it correlated marginally only with mean concentration of fat ($P = 0.057$), but not with protein or lactose. Gains also correlated marginally with hind mass at calving ($P = 0.056$) and with the percentage of body mass loss during lactation ($P = 0.063$).

The highest correlations between hind mass variables and milk production and composition were those of total fat yield and percentage and absolute mass lost during lactation ($P = 0.004$ and $P = 0.018$, respectively). A great deal of this effect appeared to have been due to the correlation with total milk yield ($P = 0.006$ and $P = 0.025$, respectively), as no correlation was significant between hind mass variables and fat, protein and lactose concentrations. The reduction in milk production appeared to increase only fat concentration ($P = 0.063$), but not the concentrations of protein and lactose.

Table 2. Correlation coefficients among overall lactation variable values in Iberian red deer (N = 12) kept under a low nutrition plane or a usual diet. Significant differences are indicated as: † = 0.1, * = 0.05, ** = 0.01 and *** = 0.001, and the abbreviations of variables are the same as in Table 1; HBW: hind body mass (in kg).

| Variable | CBW | CG | PAG | HBW | HC | PHWC | TMY |
|---|---|---|---|---|---|---|---|
| CG[a] | 0.145 | | | | | | |
| PCG | -0.226 | | | | | | |
| HBW | 0.400 | 0.589† | 0.276 | | | | |
| HWC | 0.194 | 0.465 | 0.290 | -0.133 | | | |
| PHWC | 0.267 | 0.577† | 0.310 | 0.037 | | | |
| TMY | 0.257 | 0.956*** | 0.809*** | 0.540† | 0.639* | 0.740** | |
| TFY | 0.244 | 0.941*** | 0.806** | 0.501† | 0.666* | 0.766** | |
| TPY | 0.280 | 0.968*** | 0.805** | 0.534† | 0.626* | 0.729** | |
| TLY | 0.280 | 0.959*** | 0.796** | 0.507† | 0.637* | 0.733** | |
| F | -0.445 | -0.587† | -0.258 | -0.419 | -0.242 | -0.291 | -0.552† |
| P | -0.285 | 0.081 | 0.236 | -0.149 | -0.036 | -0.045 | -0.034 |
| L | -0.102 | -0.236 | -0.239 | -0.276 | -0.159 | -0.225 | -0.278 |

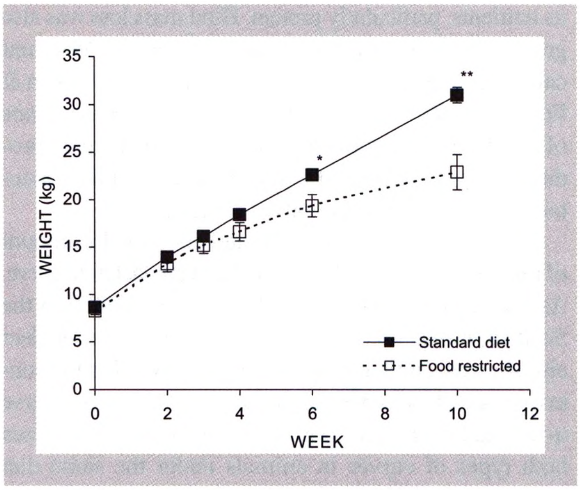


Figure 2. Mass (in kg) during lactation (weeks 0-10) of calves born to hinds either subjected to a standard (■) or a low plane of nutrition (□). Within-week significant differences are indicated by asterisks.

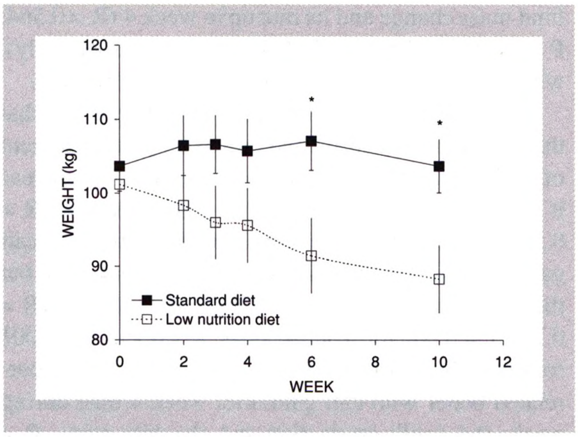


Figure 4. Mass (in kg) during lactation of hinds either subjected to a standard (■) or a low plane of nutrition (□). Within-week significant differences are indicated by asterisks.

## Lactation variables over time

The low plane of nutrition not only reduced the amount of milk produced, but it also changed the curve from a peaking curve (type I) in the control group to a continuously decreasing curve (type II) in the food-restricted group (Fig. 1). The effect of low nutrition plane appeared to show a cumulative pattern that exerted the greatest effect in most variables after week 4. Thus, calf growth in both groups started to differ after this time both in absolute mass of calves (Fig. 2), mean daily gains and rate of growth (Fig. 3). A similar effect was shown for hind mass (Fig. 4), although the effect of mass change was not as clear.

The reduction in milk production resulted in similar curve patterns for yields of fat, protein and lactose. In contrast, a less clear pattern was found for nutrient concentration (Fig. 5). Protein concentration remained constant, but hinds in a low plane of nutrition appeared to increase fat concentration in milk up to week 4, then it fell below the fat content in the control group. No difference was found for lactose.

## Correlations in weeks 0-4 and 4-10.

An analysis of correlations for early and late lactation showed patterns apparently similar to a standard lactation in weeks 0-4, but differing patterns, with food restriction exerting a great influence after week 4. The main differences were: calf birth mass correlated with

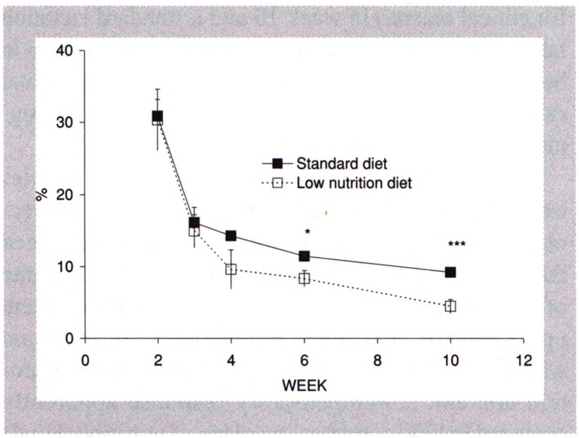


Figure 3. Percentage of growth (irrespective of birth mass) in calves born to hinds either subjected to a standard (■) or a low plane of nutrition (□). Within-week significant differences are indicated by asterisks.

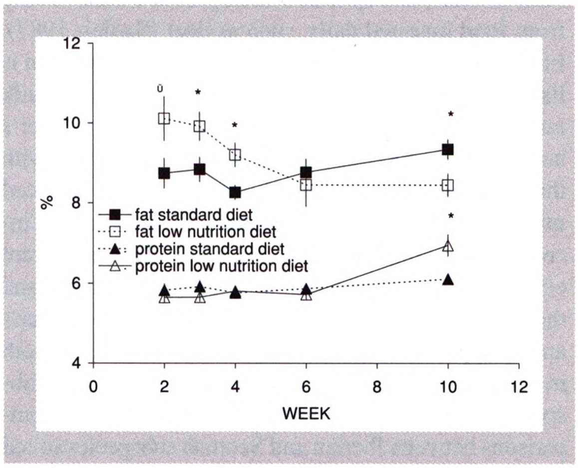


Figure 5. Milk fat and protein content (in %) during lactation of hinds either subjected to a standard (■, ▲) or a low nutrition plane (□, △). Lactose was not included as its concentration was constant and overlapping with that of protein. Within-week significant differences are indicated by asterisks.

hind mass change and its rate up to week 4 (R = 0.564, P = 0.056 and R = 0.584, P = 0.046, respectively), whereas no correlations were evident after week 4.

The most intriguing difference in calf gain was that the rate of growth correlated only with protein content of milk up to week 4 (R = 0.646, P = 0.023), whereas it correlated only with fat content after week 4 (R = 0.551, P = 0.064). There was no correlation between calf gains and mass change of the mother in weeks 0-4, but the relationship became significant after week 4 (R = 0.772, P = 0.003 for absolute gains; R = 0.932, P < 0.001 for rates). Similarly, milk and nutrient production correlated better with calf gain after week 4 than during weeks 0-4 (milk production and absolute gains; R = 0.912, P < 0.001 vs R = 0.653, P = 0.021, respectively; fat yield, R = 0.913, P < 0.001 vs R = 0.678, P = 0.014; protein yield: R = 0.912, P < 0.001 vs R = 0.669, P = 0.017; lactose yield: R = 0.912, P < 0.001 vs R = 0.710, R < 0.01, respectively; similar coefficients for rate of calf growth).

Another intriguing difference was that milk production correlated with fat, protein and lactose up to week 4 (R = -0.697, P = 0.012; R = 0.614, P = 0.034; and R = -0.703, P = 0.011, respectively), but not thereafter. Milk production correlated with hind mass and rate of mass change after week 4 (R = 0.642, P = 0.024 and R = 0.767, P = 0.004, respectively).

## Discussion

Lactation strategies fall broadly into two types: species which store reserves and produce milk mainly from these, such as seals, and species which produce milk mainly from food ingested daily, such as deer (Sadleir 1987). In the latter case a low plane of nutrition at lactation is likely to produce a great impact in the amount of milk nutrients produced, as well as both in the mother's body reserves and offspring growth. In agreement with this prediction, a low plane of nutrition greatly reduced milk and nutrient production and calf growth, and increased body mass losses in our study. This important effect overcame the pattern of a standard lactation and thus, no relationship was found between calf birth mass and milk production and composition. In contrast, both in comparisons between individuals of the Iberian subspecies (Landete-Castillejos et al. 2001) and in comparisons between Iberian and Scottish subspecies of red deer (Landete-Castillejos et al. in press) calf birth mass appears to influence milk composition, particularly protein contents.

Calf gain correlated strongly with the yield of milk and its nutrients, particularly protein. Hind mass loss was also greater the less milk they produced and the less their calves grew. This suggests, as pointed out by Oldham & Friggens (1989) that such hinds, mostly in a low plane of nutrition, were under a greater effort than higher producers to produce the little milk they could and to maintain the small gain their calves achieved.

A low plane of nutrition affected not only the amount of milk produced, but also the shape of the lactation curve. As found by Loudon, McNeilly & Milne (1983) in the Scottish subspecies of red deer *C. e. scoticus*, Iberian deer also showed a milk production curve of type I in the control group, whereas they displayed a type II lactation curve in the food-restricted group. Previous studies have shown both types of curves in animals under the same diet (Garcia et al. 1999, Landete-Castillejos et al. 2000a), although the general pattern for the milk production curve was a type II, and that for milk intake was a type I. Further experiments are needed to conclude the precise reason for such change of pattern, but the availability of irrigated pasture in the control group compared to both the food restricted and previous experiments without such pastures, or an overabundance of food in the control group with respect to a restricted or standard diet (Landete-Castillejos et al. 2000a) may be reasons for the type I milk production curve. Similarly, the group displaying a curve of type I in Loudon et al.'s (1983) study fed on fertilised high-production pastures, although the difference with the method to estimate milk production (calf weighing) does not allow direct comparisons of results.

The timing of several variables showed a cumulative effect of low plane of nutrition when lactation was divided into two stages: early lactation (up to week 4), and middle lactation (after week 4 - including presumably late lactation, although the experiment was stopped for ethical reasons in week 10 and a standard lactation lasts about 15 weeks). Thus, between-diet differences in both calf mass variables (calf mass, mean daily gain and rate of growth), and hind mass variables became significant after week 4.

During the first of the two stages most variables behaved as in a standard lactation, whereas in the second stage the effect of low nutrition plane overturned the relationships of a standard lactation. Thus, the rate of calf growth correlated only with milk protein content up to week 4, and hinds producing more milk and whose calves grew more also increased their milk protein content. A compensatory response apparently occurred in hinds under a low plane of nutrition. Hinds producing less milk concentrated milk fat above standard levels for the same weeks. Hinds in the restricted food group had a greater fat content in milk than the control group, which resulted in similar growth of calves in both groups. This appears to be consistent with White's (1992) hypothesis that under a low plane of nutrition fat reserves are mobilised to maximise milk production. Fat was the only nutrient that increased in concentration when less milk was produced and when a calf grew less. In addition, hind mass loss over the whole lactation was more closely related to the yield of fat than to any other nutrient.

The apparently compensatory response lasted four weeks under the restriction regime of this experiment. Not only did the ability of food-restricted hinds to keep fat concentration higher than in the control group fall after week 4, but calves of both groups started to diverge in mass at this point, and fat variables explained growth of calves and mass losses of hinds in this second stage of lactation. Thus, the rate of calf growth correlated only with milk fat content, as did the percentage of mass lost by hinds. As a result of this exhaustion of the compensatory response from body reserves, the cost of producing milk also increased sharply after week 4. Thus, whereas there was no correlation between hind milk production and mass or its percentage loss by hinds in early lactation, hinds producing less milk after week 4 lost more mass both in absolute and percentage terms. As a result of the exhaustion in the compensatory response, the relationship between calf gain and total milk yield, and that of their nutrients increased from low correlations during the first four weeks to very high coefficients after week 4.

Because the hinds started the experiment at similar body and mass conditions, this experiment may simulate sharp declines due to abiotic factors rather than malnutrition dependent on population overcrowding. In natural field conditions, the duration of the compensatory response based on body fat reserves will depend both on severity of food restriction, and on the existence of alternative sources of food. Lactating hinds on the island of Rhum fed predominantly on high-protein pastures (Clutton-Brock et al. 1982b), possibly to maximise milk production, as mobilisation of body protein may not be possible for synthesis of milk protein (Reid et al. 1966, Coppock et al. 1968, Kaufmann 1979, White et al. 1989), and volume of milk appeared to decrease in our food-restricted group to keep a protein content similar to that of the control group. It is likely that under sharp falls in food availability in the field, the hinds will seek to shift their diet so as to maximise intake of protein. If this is not possible, hinds may behave similarly to Alaskan free-ranging deer, which under low food availability shifted to a diet that increased rumen retention time and allowed them to extract similar amounts of metabolisable energy intake, but reduced protein intake by 50% (White & Trudell 1980).

Density-dependent reductions in food availability are more likely to affect both gestation and lactation. Longer-term reductions in food availability have a more drastic effect than short-term reductions (Albon, Clutton-Brock & Langvatn 1992). Rognmo et al. (1983) found that low nutrition affecting late gestation, when foetus growth is faster, results in lower birth masses, increased mortality and lower milk production. Because milk composition depends on calf birth mass (Landete-Castillejos et al. 2001), such low nutrition in late lactation may have an effect on milk composition. If it also affected maternal fat reserves prior to the start of lactation, this food reduction is likely to reduce the compensatory response based on fat found here.

We have not yet performed experiments on the effect of a low plane of nutrition during gestation on subsequent lactation variables. However, the effect might be similar to that of delayed births for which we do have data (Landete-Castillejos et al. 2000b, Landete-Castillejos et al. 2001). Deer show a seasonal pattern of voluntary food intake (Kay 1979, 1987, Kelly, Fennessy, Moore, Drew & Bray 1987) that is likely to cause a reduction of food intake affecting both gestation and lactation in late births. As found by Rognmo et al. (1983) under reduced nutrition during late gestation, late-calving hinds produced less milk (Landete-Castillejos et al. 2000b), and their calves also grew less than those of early calvers (Landete Castillejos et al. 2001). In contrast to the findings in the experiment reported here, late-calving hinds reduced the protein content of milk (Landete-Castillejos et al. 2000b), and the greatest differences with the control group occurred at the time of fastest calf growth, i.e. at early lactation (Landete-Castillejos et al. 2001). If the response under density-dependent reduction in food availability, or a similar abiotic effect occurring also during gestation was similar to late calving, thus it is possible that hinds may not have reserves to compensate for low milk production using fat.

For ethical reasons, we did not assess the consequences for both the mother and calf of continued malnutrition. We stopped the experiment in week 10 for fear that some of the calves would die and probably also some of the hinds, which suffered severe losses of body condition. It seems likely that continued malnutrition well over the compensatory period in early lactation may have ended in a sharp increase in calf mortality and probably also in hind mortality. Low body condition at the start of the mating season greatly reduces fertility (Clutton-Brock, Guinness & Albon 1982a, Sadleir 1987, Kelly et al. 1987) and the costs of lactation, even if they are not as high as in our case of undernutrition, increase hind mortality more than in non-lactating hinds (Clutton-Brock et al. 1982b). With such a sharp decline of food sources at lactation, hinds may forgo reproduction in the following season in order to secure the investment in current offspring.

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