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Food intake, diet selection and adaptation to protein deficiency in desert sheep

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SUMMARY - Voluntary food intake and diet selection, along with the food intake capacity of the animal, are important subjects as they control the amount of nutrients consumed by an animal relative to its requirements for maintenance and level of production. The basic and complex concepts underlying their regulation and integration are pointed out and briefly discussed. In desert animals, including sheep, these subjects are more complex and even more important because of the super-imposed direct and indirect effects of the environment, including food availability in quantity and quality. The practices undertaken by shepherds attempting to correct seasonal deficiencies on the one hand, and the animals' adaptive capacities on the other hand, among other factors, have or can exert modifying effects. Examples include concentrate supplementary feeding, the use of cultivated shrubs as forage reserve and water deprivation and salinity. In this context, long-term adaptation is of paramount importance. Sample experimental data are presented and discussed.

Key words: Food intake, diet selection, protein deficiency, desert sheep, review.

RESUME - *"Ingestion alimentaire, sélection du régime et adaptation au déficit en protéines chez les ovins du désert". L'ingestion alimentaire volontaire et la sélection du régime, de même que la capacité d'ingestion alimentaire de l'animal, sont des questions importantes car elles déterminent la quantité de nutriments consommés par un animal par rapport à ses besoins pour l'entretien et le niveau de production. Les concepts fondamentaux complexes qui constituent la base de cette régulation et cette intégration sont présentés et brièvement discutés. Chez les animaux du désert, y compris les ovins, ces questions sont plus complexes et encore plus importantes en raison des effets directs et indirects surimposés du milieu, y compris les disponibilités alimentaires en quantité et qualité. Les pratiques menées par les bergers visant à corriger les déficits saisonniers d'une part, et les capacités adaptatives de l'animal d'autre part, entre autres facteurs, ont ou peuvent exercer des effets modificateurs. Des exemples en sont la supplémentation en concentré, l'utilisation d'arbustes cultivés comme fourrage de réserve, le manque d'eau et la salinité. Dans ce contexte, l'adaptation à long terme est d'une importance capitale. Des données expérimentales échantillonnées sont présentées et discutées.*

Mots-clés : *Ingestion alimentaire, sélection du régime, déficit en protéines, ovins du désert, révision.*

The regulation of voluntary food intake

The concept

Food intake is an animal function concerned with the matching of different nutritional principles. It is concerned with matching intake with requirements for maintenance and production on the one hand, and matching diets with appetite, behaviour and learning on the other hand. The regulation of food intake is primarily a physiological function of the animal geared to satisfy its energy requirements for maintenance and production including continued fat deposition in the adult. Other nutrients such as proteins and amino acids may also play a role. On the other hand, the physical elements sometimes limiting the full expression of the physiological function involve the capacity of the digestive tract which is also an animal-related function, and the digestive capacity and rate of passage which are food-related functions. The recent book by Forbes (1995) is an excellent exhaustive and integrative review of the subject.

Classical theories

Classical theories attempting to explain the control of voluntary food intake are relatively recent. They originated as single factor hypothesis supported by experimental observations. Prominent among these are the 'glucostatic' theory proposed by Mayer (1953), the 'lipostatic' theory proposed by

Kennedy (1953), and there was the 'thermostatic' theory of Brobeck (1948). The physical limitation of the capacity of the digestive tract and the rate and extent of digestion of forages and the rate of passage of digesta were experimentally demonstrated as modifiers of the expression of the physiological mechanisms (Balch and Campling, 1962).

In the beginning it was the thermostatic theory which conceived that animals eat to maintain a constant body temperature. Later, this appeared to be an over simplification and it is now considered to be only a safety mechanism to guard against hyperthermia (Forbes, 1995). It is to be noted, however, that physiologically controlled hyperthermia is in itself an adaptation mechanism in certain species, the common example being the dromedary camel (Schmidt-Nielsen, 1964).

The glucostatic and lipostatic theories both centred around the concept that it is the maintenance of a stable energy status, monitored and controlled by the central nervous system (CNS), that the animal attempts to maintain through feeding. CNS centres in the hypothalamus monitor the levels of primary energy precursors and other metabolites circulating in the blood. This is glucose in monogastric animals, hence the term 'glucostatic' advanced by Mayer (1953). In ruminants it is the volatile fatty acids. Other metabolites and hormones may be involved as well. Monitoring is achieved through signal transmitted from receptors located at different sites an tissues as indicated below.

Fluctuations of the circulating levels of these metabolites and their effect on the initiation or termination of feeding represent the sort-term control of food intake related to and determining meal size and frequency. However, the actual matching of food (nutrient) intake with requirements is a different story. It represents the long-term adaptation of food intake and it is presumably related to the energy stored in the animal's fatty tissues and monitored by the CNS. Hence, the lipostatic theory of Kennedy (1953). Certain physiological states exert modifying effects on both the short- and long-term control of food intake. The classical examples are the increased energy requirements for maintenance and milk production, and the consequent increase of food intake in high yielding dairy cows.

Superimposed on both glucostatic and lipostatic mechanisms is the physical limit to intake. This was demonstrated experimentally by Balch and Campling (1962) as the positive relationship between the rate and extent of digestion, and the rate of passage, of a forage and its level of voluntary food intake. This lead to the development of the concept of physical-physiological regulation of voluntary food intake (Conrad *et al.*, 1964, Montgomery and Baumgardt, 1965, Jarrige *et al.*, 1986).

The integrative theories

The classical theories postulated that feeding is controlled by a single factor acting in a negative feedback manner. These include mainly stomach/rumen distention, osmotic pressure and titratable acidity, hypothalamic temperature, blood glucose/volatile fatty acids and amino acids concentrations, body fat stores, and others (Forbes, 1995). Nervous pathways from specialized receptors in the gastro-enteritis tract and other organs relay information to the brain. The hypothalamus responds with changes in signals controlling metabolic hormones, e.g., insulin, glucagon and growth hormone, and it also activates brain centres to initiate, continue or terminate feeding.

It was recently realized that the classical theories do not sufficiently explain how intake was controlled under many circumstances. The idea was expressed as follows: 'When eating increasing gastric fill and increasing hepatic delivery of calories both serve to reduce the likelihood that animals will continue to feed. Once they stop eating, they will remain satiated despite an empty stomach as long as the liver continues to get utilizable calories from the intestine' (Sticker and McCann, 1985, cited from Forbes, 1995).

This concept was the first step towards the development of the first integrative theory of the control of voluntary food intake, the 'energostatic' theory. Later, this was further developed to include the physical fill limits of the digestive tract and the digestion and sensory characteristics of the food as well. The question was then raised as to the integration of multiple feedbacks and whether it is additive or multiplicative. If multiplicative, then if any one feedback signal is missing the combined signal will be zero and intake will be uncontrolled. Accumulated evidence sufficiently confirm that some feedback signals combine additively in their effect on intake. One example came from experiments on sheep by Adams and Forbes (1981) infusing volatile fatty acids in the rumen and/or the portal vein and using a balloon to distend the rumen.

Later developments of the integrative concept of food intake regulation include several new aspects. Prominent is the presumed role of adipose tissue in long-term regulation (Forbes, 1995). The signals from the receptors and pathways described above, and others, must be integrated in the brain. Presumably, these rapidly fluctuating signals in relation to meals are added to the more constant signal coming from the adipose tissue. A relatively small change in the signal from adipose tissue will in the long-term play a significant part in controlling intake. Other theories presently in the process of development include the hypothesis that ruminants eat that amount of food per day at which net energy production per mole of oxygen is maximized (Tolkamp and Katelaars, 1992). Theoretical calculations based on ARC data (ARC, 1980) support this contention but experimental evidence is not available yet.

Aspects of long-term adaptations in sheep

The environment

Free grazing animals, and those in confinement in some intensive systems fed achoice, naturally feed *ad libitum* having food available almost all the time. They are general feeder as they feed from a wide range of foods. The herbage available to them varies in quantity and quality depending, among other factors, on the density of the pasture, dominant plant species, the season and time of the year, but it is rarely completely unavailable. This freedom of access to food, along with the capacity for diet selection, are some times seasonally conducive of over-eating leading to excessive deposition of fat and poor efficiency of food and energy utilization. In other times, animals may under-eat either because of seasonally partial or total inavailability of food or because of factors affecting their intake capacity, that is rumen fill and the bulk, slow digestion and delayed passage of poor herbage (Forbes, 1995).

In these environments characterized by seasonal and erratic rainfall and hot dry seasons, the annual feeding cycle of the grazing animal goes through several consecutive phases ranging from a relatively short period of abundant lush vegetation and practically no limitation on availability in quantity or quality, to periods of virtually total inavailability of herbage better than standing straw. These seasonal changes in herbage availability and the other direct and indirect environmental stresses are not abrupt. Rather, the transition in available food resources and consequently the nutritional state of the grazing animal is a gradual and slow process. Therefore, such grazing animals have a fair chance to adjust and adapt to the changing conditions whether improving or deproving, both behaviourally and at organ and tissue levels. Prominent among such adaptations in sheep, and in other grazing ruminants as well, is the long-term adaptation to protein deficiency, sometimes detrimental even to the mere survival of the animal. Other adaptations of importance under such conditions include the time necessary to attain stable voluntary intake from cultivated perennial shrubs to be used as a forage reserve, intake from ensiled and/or otherwise treated unpalatable shrubs conserved for dry season feeding, the effects of water deprivation and water salinity, and also shepherds' practices, namely concentrate supplementary feeding.

With this view in mind, our group started looking into some of these aspects of long-term adaptations in sheep and other ruminants. The following is a brief account of some findings from our laboratory and sample experimental results presented to illustrate the concept.

Long-term adaptation of sheep to low or decreasing protein intake

During dry season grazing sheep thrive better than expected. When shepherds resort to supplementary feeding, grains and other sources of fermentable carbohydrates are preferred. Experimentation indicated that this might enhance the utilization of nitrogen (urea) recycled to the rumen. Data from three experimental groups of local sheep, 3-4 animals each, fed diets with adequate energy for maintenance but with low (50-60% maintenance) or decreasing protein content were examined (Farid, 1985). The treatments extended over long periods ranging between 117 and 185 days with three or four digestion and balance trials during each to follow the course of adaptation in terms of nitrogen intake and balance, and of urinary nitrogen as a proportion of nitrogen intake (Fig. 1).

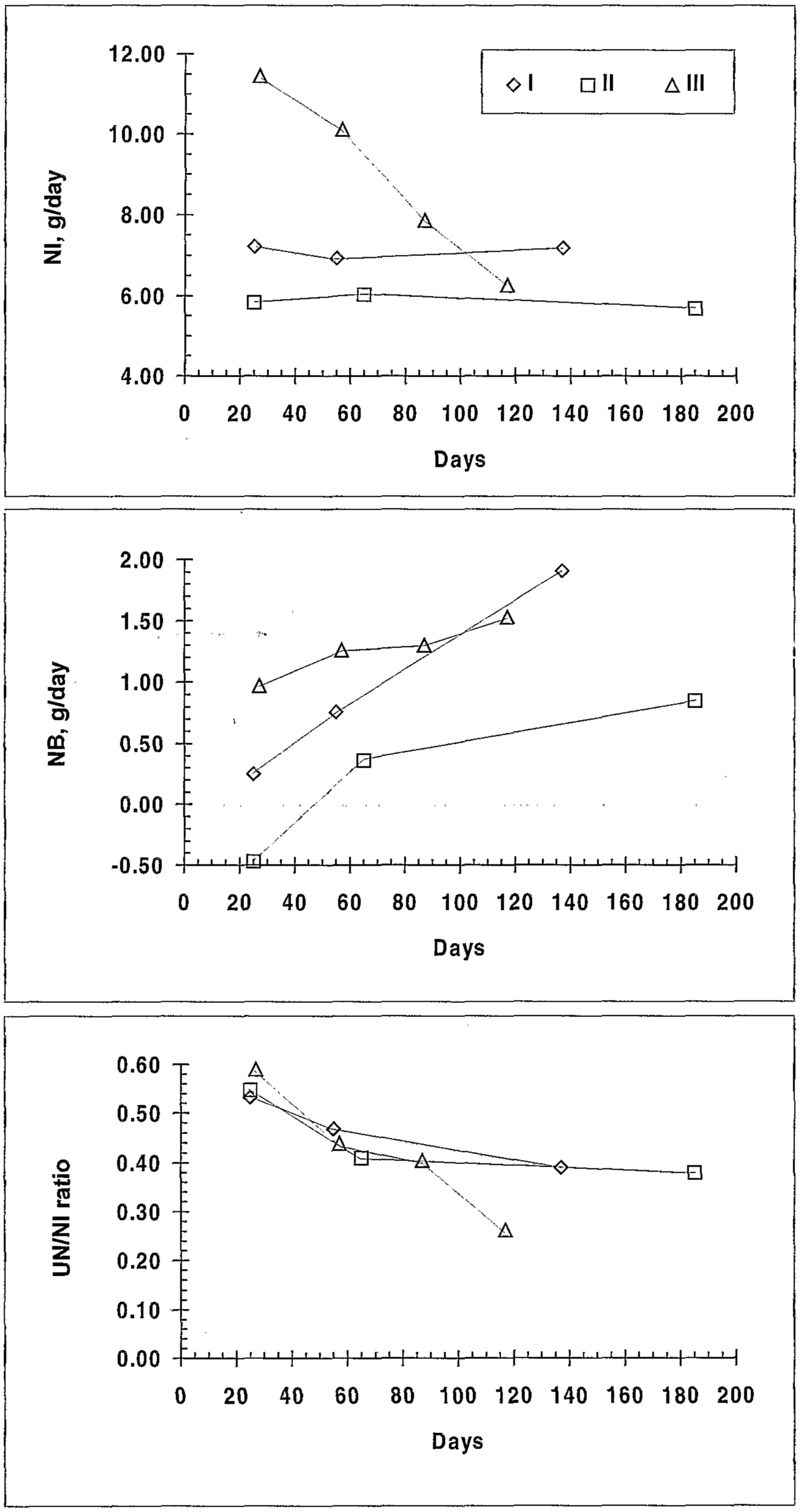

Fig. 1. Long-term adaptation of sheep to low (I and II) or decreasing (III) protein intake.

In the first two groups low nitrogen intake was maintained for 137 and 185 days. The stated days represent mid-collection periods. Nitrogen balance showed remarkable adaptation. In one group (group I) nitrogen balance was +0.25, +0.76 and +1.91 g/day at 25, 55 and 137 days. Group II sheep started with a negative nitrogen balance of -0.47 g/day after 25 days which improved to +0.31 and

+0.85 g/day at 65 and 185 days on the assumed protein deficient diet. These adaptations were brought about through reducing absolute urinary nitrogen excretion and urinary nitrogen as a proportion of either total or digested nitrogen intake. Faecal nitrogen excretion also decreased but to a lesser extent, and it was practically constant when expressed in terms of nitrogen excreted per unit faecal dry matter.

The average daily nitrogen intake of group III sheep decreased progressively from 11.45 to 6.36 g/day (-44%). Faecal nitrogen excretion was reduced only by 17%. Meanwhile, urinary nitrogen excretion decreased by 76%. On a relative basis, as a percentage of nitrogen intake, faecal nitrogen excretion increased from 32 to 49%, but urinary nitrogen excretion decreased from 59 to 26% (Fig. 1). The result from these transactions was a gradual improvement of nitrogen balance from +0.97 to +1.53 g/day (+58%) irrespective of the concurrent 44% reduction in nitrogen intake.

The results indicated that native sheep fed low protein but otherwise adequate diets were, if allowed a period of gradual adaptation, able to attain a better state of nitrogen balance, and sheep fed decreasing levels of protein intake responded similarly. This was achieved primarily through progressive reduction of urinary nitrogen excretion (g UN/g NI, Fig. 1). The initial phase of adaptation requires approximately 60 day in sheep fed low levels of protein intake. The decreasing protein intake treatment group resembles the conditions during the natural progression of dry grazing season in arid and semi-arid rangelands.

Long-term adaptation to protein deficiency: effects of water deprivation and water salinity

An experiment was carried out to investigate possible long-term adaptation to low protein intake in sheep watered intermittently and the effect of urea supplements given in the drinking water (Farid *et al.*, 1989). Three groups of rams, three animals each, were fed diets adequate in energy for maintenance but supplying only 50% of protein requirements. One group was watered once daily whereas the other two groups were watered intermittently once every third day. In one of the water-deprived groups, 0.25% urea was added to the drinking water along with 2.0% molasses and sulphur from sodium sulphate equivalent to a tenth of the urea nitrogen present in solution. The experiment lasted nine weeks. Nitrogen intake and urinary excretion were followed up five times, 3 days each, being reported as days 1, 15, 30, 45 and 60. Results from the water-deprived groups are averages of the three-day water deprivation cycle.

Nitrogen intake was similar both for daily watered sheep and their water-deprived mates not receiving urea supplements. Water-deprived sheep that received urea supplements had a greater total nitrogen intake of which 21 to 26% was from urea added to the drinking water. The effect of adaptation on urinary nitrogen excretion in the three groups is illustrated in Fig. 2. Immediately after the beginning of treatments (days 1-3), sheep in all groups lost nitrogen amounting to 136-157% of their total nitrogen intake, indicating a definite negative nitrogen balance. After the first 15 days, the nitrogen excreted in the urine decreased markedly in all groups. From days 30-33 until the end of the experiment, days 60-63, urinary nitrogen excretion in the three groups remained practically constant. The control and water-deprived sheep excreted nearly similar amounts of nitrogen, whereas the water-deprived urea-supplemented animals excreted significantly greater amounts, a reflection of their increased nitrogen intake. Urinary nitrogen excretion as a proportion of total nitrogen intake followed a similar pattern. It was concluded that long-term adaptation to protein deficiency in sheep was not adversely affected by water deprivation, which is the normal practice of pastoralists and is known to improve the efficiency of nitrogen conservation and energy utilization, nor was it lost by nitrogen (urea) supplementation.

Similar to water deprivation, increased salinity of water available for drinking is among the indirect environmental stresses on grazing animals during dry seasons. An experiment (Farid *et al.*, unpublished) was carried out to investigate in sheep possible interaction between decreasing protein intake and the salinity of the drinking water on long-term adaptation to protein deficiency. Nine native Barki ewes in three groups were fed diets adequate in energy for maintenance but with progressively decreasing protein content over a total period of 200 days. Ewes in the control (FW) group received tap water (283 ppm total dissolved salts, TDS), whereas animals in the other two groups were offered diluted sea water containing 7650 and 13535 ppm TDS, designated as low (LS) and high (HS) salinity groups. The experiment consisted of four protein treatments each lasting 40 days, and each ended with a digestion and nitrogen balance trial. Results of nitrogen intake, nitrogen balance and the ratio of urinary nitrogen excreted to digested nitrogen intake are reported in Fig. 3.

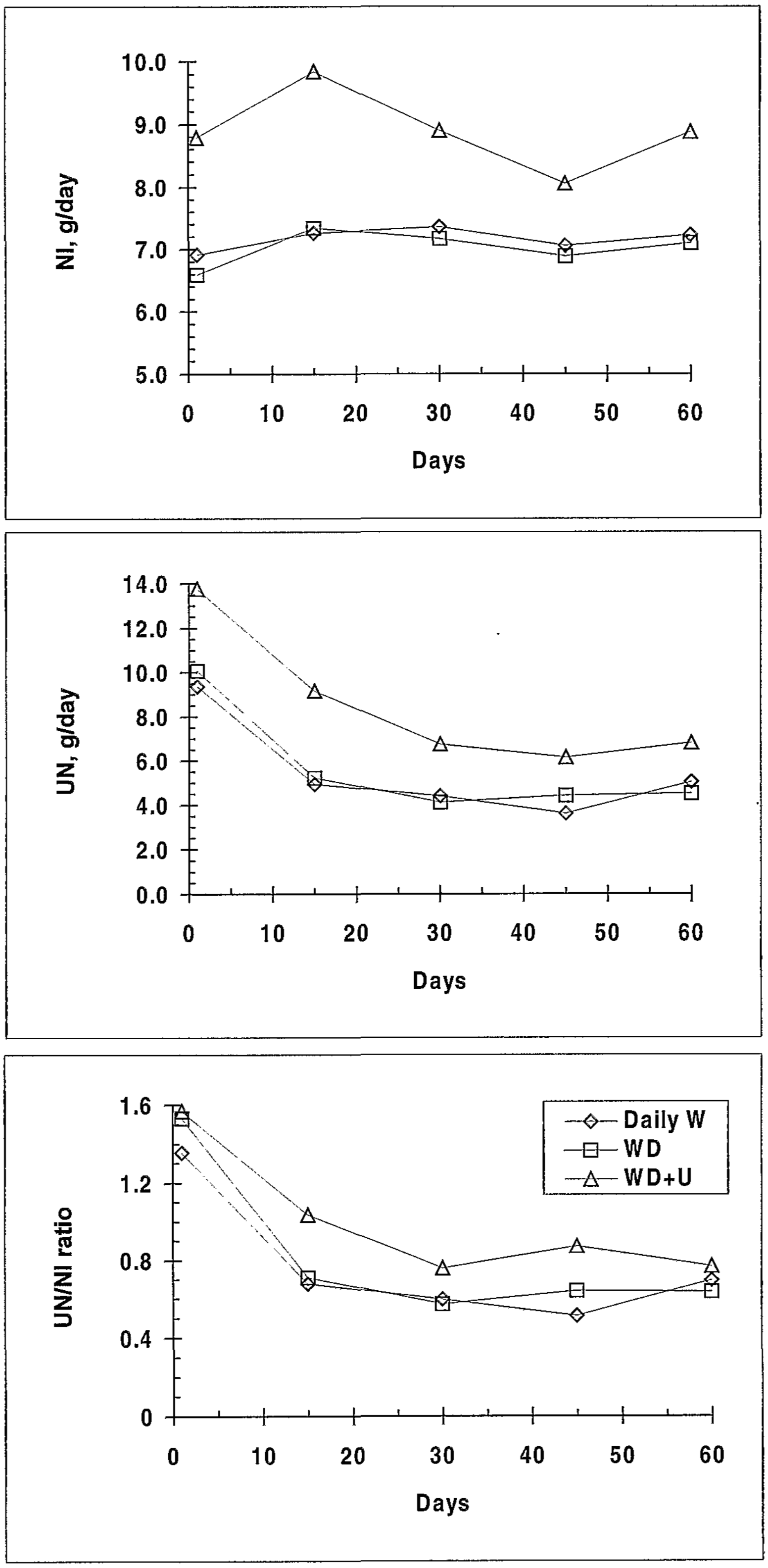

Fig. 2. Effects of water deprivation (WD) and urea supplementation in the drinking water (WD+U) on long-term adaptation of sheep to low protein intake.

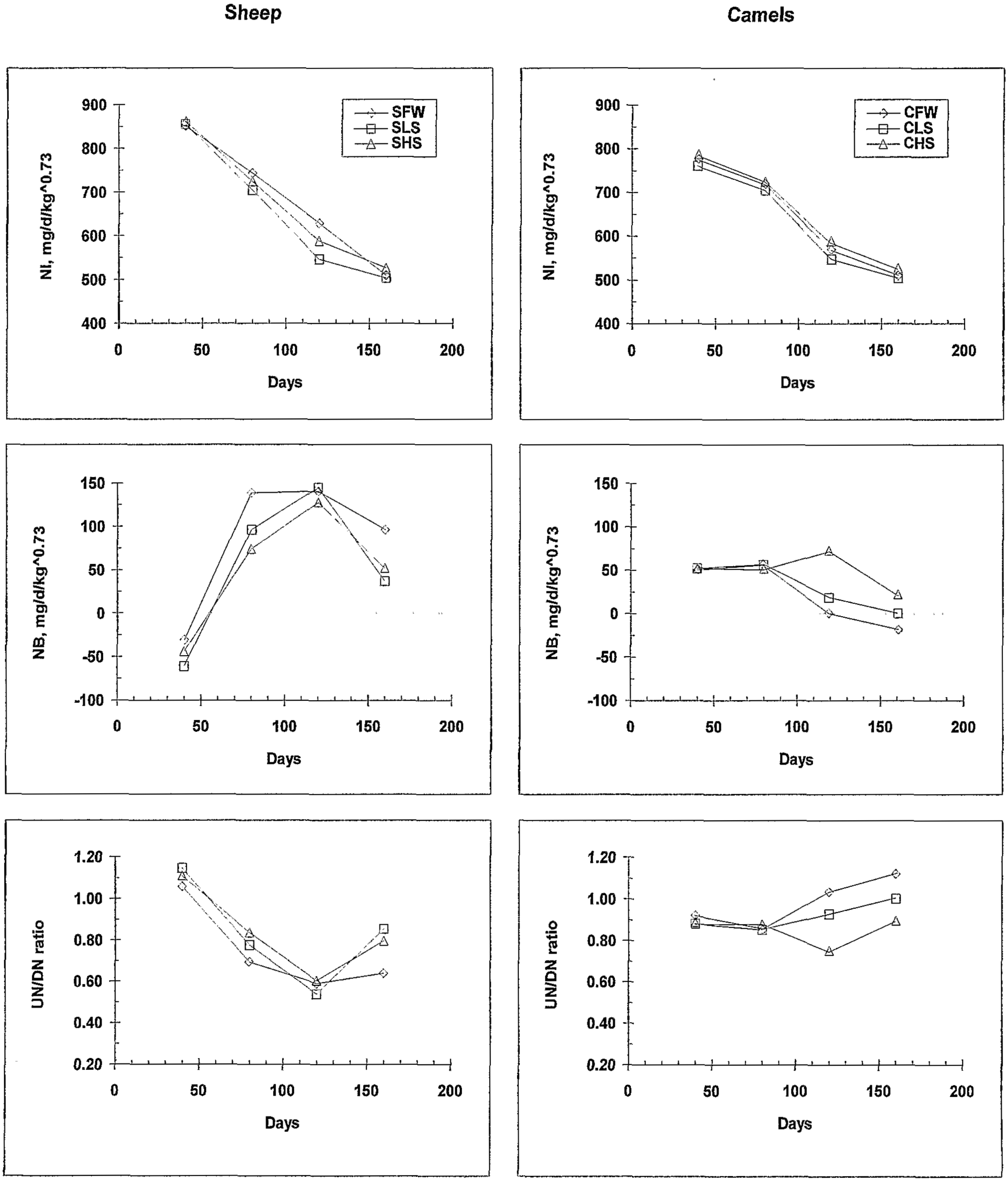

Fig. 3. Long-term adaptation of sheep and camels to decreasing protein intake and the effect of water salinity. (FW: fresh water, 283 ppm; LS: low salinity, 7650 ppm; HS: high salinity, 13535 ppm).

Nitrogen intake of sheep in all three water salinity treatments during the first period was approximately 120% of the maintenance requirements of native Barki sheep (Farid *et al.*, 1983). Surprisingly, all were in negative nitrogen balance and their urinary nitrogen excretion exceeded their apparent digested nitrogen intake. During the second and third periods adaptation to decreasing protein intake was evident. The ratio of urinary to digested nitrogen decreased and nitrogen balance markedly improved. However, During the fourth period nitrogen intake was only 70% of maintenance requirements and observed nitrogen balance values decreased, whereas urinary nitrogen as a proportion of digested nitrogen increased.

During the first three periods of the experiment, only minor differences in nitrogen utilization that could be attributed to water salinity were observed. In the fourth period, the controls maintained their low urinary nitrogen excretion and nitrogen retention decreased slightly. On the other hand, urinary nitrogen excretion increased in the two groups receiving the saline drinking water which resulted in a significant reduction in nitrogen retention. Whether this was a simple effect of water salinity at the lower level of protein intake or a result of cumulative response to long exposure to saline water cannot be ascertained at this point.

Results from a second experiment conducted concurrently on camels are also presented for comparison (Fig. 3). The observed differences between the two species were surprising. Results of nitrogen balance indicated that control camels offered fresh tap water performed better than sheep when nitrogen intake was not limiting, periods 1 and 2. As nitrogen intake decreased, the proportion of digested nitrogen excreted in the urine increased and nitrogen retention decreased, even becoming negative in the fourth period. These results are different from those reported earlier (e.g., Farid *et al.,* 1979).

Another major difference between camels and sheep was their response to water salinity. As salinity increased, digested nitrogen excretion in the urine increased and consequently nitrogen retention decreased but to a lesser extent than in the controls. The possible interactions observed between salinity of the drinking water and the animal's capacity to adapt to protein deficiency, and the categorical differences between animal species, warrant further investigations.

Adaptation and diet selection and voluntary intake

Adaptation to protein deficiency is not the only aspect of the long-term adaptation phenomenon in ruminants grazing arid and semi-arid rangelands. Diet selection and voluntary food intake are influenced by long-term adaptation as well. This is illustrated in the following two extracts of experimental data.

The first experiment (Khamis, 1988), attempted to render palatable some native perennial shrubs of known poor palatability to sheep and goats, *Atriplex halimus (Ah),* 12.6% CP and 25.7% CF, and *Zygophyllum album (Za)*, 7.0% CP and 11.4% CF, the latter is totally unpalatable in the fresh state. It was believed that such plants can provide a good forage reserve for the dry season if, through certain treatments, they become palatable. One such treatment was to ensile them with non-conventional foods, e.g., broiler litter. In this particular experiment, the silage was made of equal parts, dry matter basis, of the plant and the broiler litter with added 4% molasses and 1% salt. It was fed to entire male native sheep and goats, 12 each, over a period of 45 days, 30-day adaptation period followed by a 15-day digestion and nitrogen balance trial. Food intake was recorded daily (Fig. 4). Voluntary food intake, g DM/day/kg$^{0.75}$, of both goats and sheep from either plant silages with broiler litter increased throughout the adaptation period. Although it seemed to approach a plateau during the last five days or so, it had not by no means reached what can be considered a stable intake. A longer adaptation period would have been more appropriate.

In the second experiment (Shawket, Farid and Ahmed, unpublished), diet selection and voluntary food intake from three introduced perennial species intended as dry season forage reserve were investigated using sheep and goats. The three plants were *Acacia cyanophylla (Ac)*, *Atriplex nummularia (An)* and *Atriplex semibaccata (As)*. This was a cafeteria feeding experiment on freshly cut material offered *ad libitum*, with and without barley grains supplements equivalent to half their energy requirements for maintenance. The experiment consisted of a 35-day adaptation period followed by a 15-day digestion and nitrogen balance trial. Results from the adaptation period are illustrated in Fig. 5. Significant differences were observed between sheep and goats, between plant species and the effect of grain supplementation on both diet selection and voluntary food intake.

Differences in selection between sheep and goats were evident. Both species had little appetite, if any, for *An*. Goats preferred *Ac* and moderately consumed *As*. Sheep, on the other hand, consumed both *Ac* and *As* equally well. Total voluntary intake of sheep was more than that of goats. When barley grain supplements were offered, a different picture was observed. A similar pattern of preference was observed in goats but intake from *Ac* practically doubled and after four weeks there was a small but noticeable increase in *An* consumption. Sheep, on the other hand, consumed significantly more from *An* but less from *Ac* and *As*, and total intake from pasture plans was not much different from that of their mates not receiving the grain supplements.

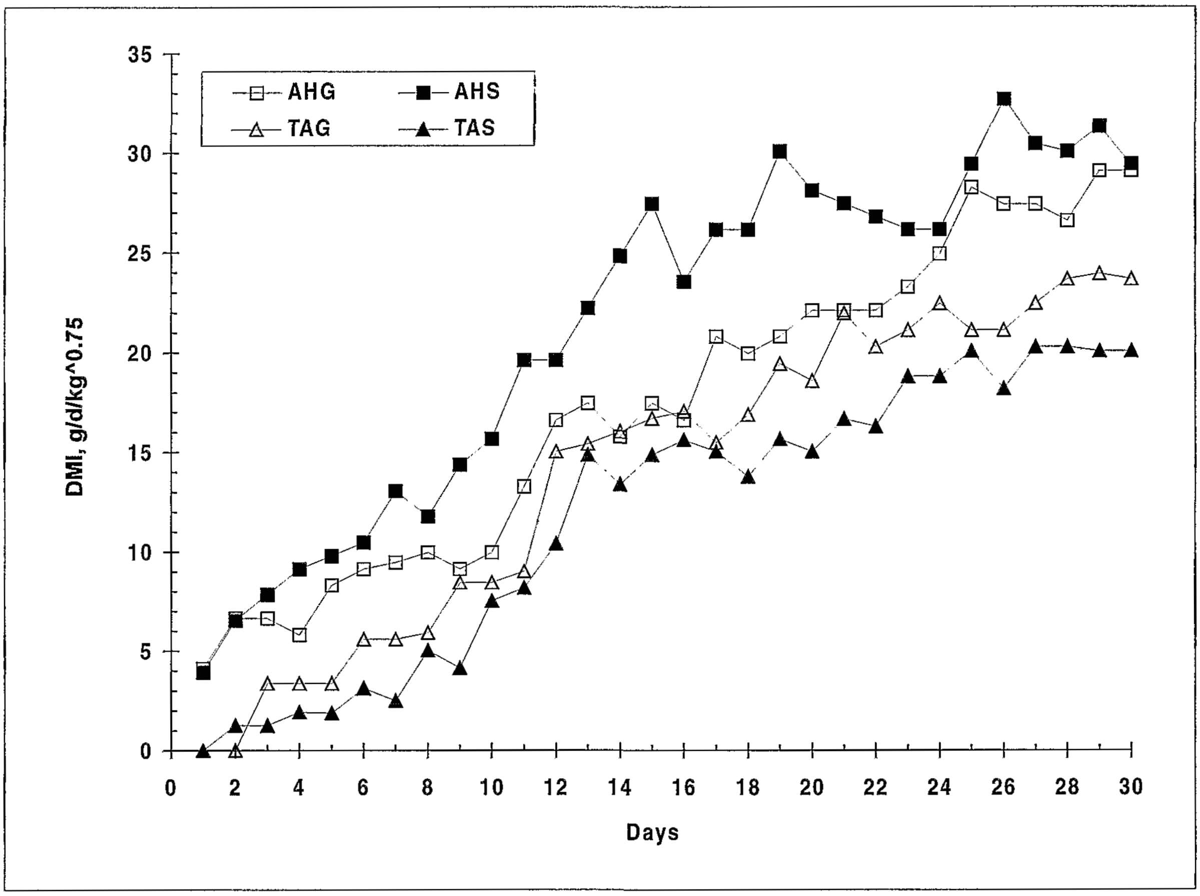

Fig. 4. Voluntary food intake and the adaptation of goats (G) and sheep (S) fed *Atriplex halimus (Ah)* or *Tamarix aphylla (Ta)* ensiled with broiler litter.

In general, voluntary intake of goats from pasture plants progressively increased during the 35-day adaptation period, but adaptation was apparently faster in sheep. Grain supplements appeared to enhance adaptation in both species. It was of interest to observe in sheep the inconsistent pattern of selection and intake from the three plants. For example, in sheep receiving grain supplements consumption during days 8 to 15 was, in decreasing order, *c-An-As*. It then went through s short period of transition and during days 20-27 the order was *As-Ac-An*, and so on. In goats, on the other hand, selection was more definite but intake from each plant had a wavy pattern.

These two examples, although not perfectly conclusive, point out the importance of taking into consideration long-term effects and adaptations in voluntary food intake when dealing with the physio-nutritional aspects, natural or imposed, of grazing ruminants in arid and semi-arid environments. The effects on diet selection is of paramount importance.

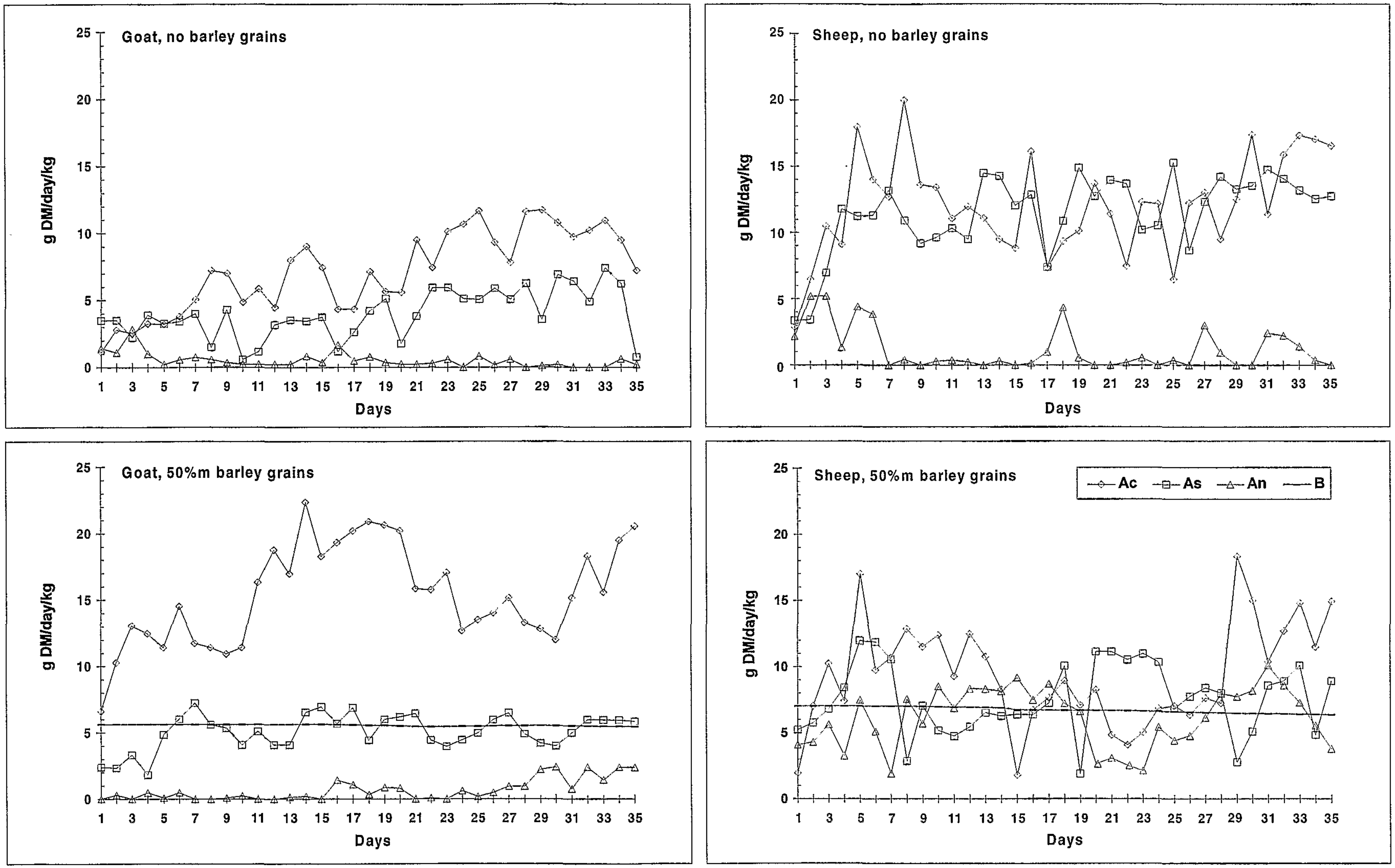

Fig. 5. Diet selection and voluntary food intake of goats and sheep offered freshly cut *Acacia cyanophylla (Ac)*, *Atriplex nummularia (An)* and *Atriplex semibaccata (As)* in a cafeteria feeding experiment.

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