GOAT PRODUCTION UNDER HARSH ENVIRONMENTAL CONDITIONS: THE PHYSIOLOGICAL BASIS AND THE CHALLENGE

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Abstract

Goats living in harsh environments represent a climax in the capacity of domestic ruminants to adjust to such areas. This ability is multifactorial. Low body mass and low metabolic requirements of goats can be regarded as important assets in minimising their maintenance and water requirements in areas where water sources are widely distributed and food sources are limited by their quantity and quality. An ability to reduce metabolism allows goats to survive even after prolonged periods of severe limited food availability. A skilful grazing behaviour and efficient digestive system enable goats to attain maximal food intake and maximal food utilisation in a given condition. There is a positive interaction between the better recycling rate of urea and a better digestion of such food in desert goats. The rumen plays an important role in the evolved adaptations by serving as a huge fermentation vat and water reservoir. The water stored in the rumen is utilised during dehydration, and the rumen serves as a container which accommodates the ingested water upon rehydration. The rumen, salivary glands and kidney coordinate functions in the regulation of water intake and water distribution following acute dehydration and rapid rehydration. Goats in the tropics base their diet when possible on tree-leaves and shrubs (browse) which ensure a reliable and steady supply of food all year around, albeit, of a low to medium quality. Some of the physiological features of ruminants defined as intermediate feeders are large salivary glands, large absorptive area of their rumen epithelium, and a capacity to rapidly change the volume of the foregut in response to environmental changes. These features are most likely responsible for the goat's superior digestion capacity. Although goats and sheep are mixed feeders, under mixed forage conditions goats consume a larger proportion of browse than sheep and use it more efficiently. Unlike sheep and cattle, which do not eat leafy material during the green season, browse constitutes at least 40% of the forage selected by goats at all times. This pattern of diet selection, however, is not compatible with maximizing milk yield. Indeed, selection of goats by men in harsh Mediterranean environments was most certainly based on breeding success and lifetime performance. Most browse species in the Mediterranean are dicotyledons that are high in tanninferous phenolic substances. Recent studies have shown that polyethylene glycol (PEG), a polymer that can bind tannins irreversibly over a wide range of pH, is very efficient in neutralising the negative effects of tannins in ruminant feedstuffs. PEG has improved the performance of grazing goats and sheep in a seemingly economic matter.

Introduction

The vast majority of the world's grazing land occurs in seasonal environments that are characterised by marked fluctuations in resource abundance. Among the most dynamic are the arid and semi-arid regions of the tropical belts, where extended periods of dryness (6 to 8 months) are punctuated by erratic rainfall and brief eruptions of forage production. The arid and semi-arid zones comprise 55% of the area of sub-Saharan Africa, and support 50-60% of the livestock and 40% of the people in that area. 88% of the world goat population (~ 610 million head) are located in Asia and Africa, mostly (80%) in the tropics and sub-tropics (Knight and Garcia, 1997). In the arid zone proper, goats are relatively much more numerous than cattle and frequently more

numerous than sheep; whereas cattle are more numerous than sheep and goats in semi-arid, sub-humid, humid zones, and highlands. Under desert and tropical environments where feed resources are restricted in quantity and quality, differences among ruminants in energy requirements and digestive efficiency reflect the efficiency of gross energy use for production. This is a very important criteria for the selection of the most appropriate type of animal to be grown in particular circumstances (Devendra, 1990).

It has been consistently shown in different countries and environmental conditions that goats indigenous to harsh environments perform better than other domesticated ruminants (Devendra, 1990; King, 1983; Shkolnik and Silanikove, 1981). The abundance of goats in the harsher environment of arid areas reflects most likely a better adaptation of this species to such environments. Goats suffer the least during successive years of drought which occur from time to time in the dry belts of the tropics and cause ecological catastrophes for livestock and human population that depend on them.

The purposes of the present review are to: 1) provide an integrative explanation of the ability of goats to survive and produce better than other ruminants in harsh environments, and 2) consider the importance of browse in goat diets and review recent approaches of increasing goat productivity under such conditions.

PART I: General Features of Adaptation to Harsh Environment

Ia. Small body size and widespread occurrence of dwarfism among goats in different adverse environments

Bergmann's rule (1847) is probably the best known in zoogeography. It states that "in warm-blooded animals, races from warm regions are smaller than races from cold regions" (Mayr, 1970). It is a purely empirical generalisation, describing a correlation between morphological variation and ambient temperature (Mayr, 1970). Correlation between size changes in fossil mammals from various parts of the world with paleoclimaticchanges is in accordance with this rule (Dayan et al., 1991). This rule was interpreted as adaptation to ambient temperature; the relatively larger body surface areas of the smaller races serving as efficient heat dissipaters in warm climates, while a small body surface area may help to conserve heat in cold climates (Searcy, 1980). Other scientists suggested that body size is better correlated with primary plant productivity (Rozenzweig, 1968), desiccation (James, 1970), type of food and its quality (Calder, 1984; McNab, 1971), than with temperature. However, it may be a combination of all these factors because in desert areas, these factors are highly interrelated.

In no other part of the world is hereditary dwarfism in goats so widespread as in equatorial Africa (Epstein, 1971). Three factors seem to account for that (Epstein, 1971): natural selection, artificial selection, and inbreeding. Selection is most likely the most important single factor: under unfavourable conditions dwarfed individuals are better adapted than the bulk of the ordinary stock. The pressure of selection brought a gradual alteration of the stock by the slightly higher survival and reproduction rate of small animals. Selection pressure toward a smaller size explains also the simultaneous widespread occurrence of dwarfism in domestic ruminants occupying the same niche (autochtonous development) in harsh environments (Epstein, 1971). In accordance with Bergmann's rule, even non-dwarfed breeds of goats in the desert and savannah areas of Africa are inmost cases much smaller than typical European breed of goats (Epstein, 1971).

Ib. Low metabolic requirements

The classical concept of Kleiber (1961) that energy requirements of a mammal is a simple function of body mass$^{0.75}$ implicates that the energy requirements per kg weight of body tissue in small mammals are relatively greater than in large mammals. Enhanced metabolic requirements of small ruminants cannot be met by diets rich in cellulosic matter because anaerobic fermentation is a relatively slow process and bioenergetically less efficient than other forms of digestion (Van Soest, 1982). Small ruminants, therefore, have to balance their comparatively higher energy requirements by eating more food of a higher nutritional value (Demment and Van Soest, 1985). The diet of extremely small (3-5 kg) wild ruminants like suni and dik dik is indeed composed of highly-digestible soft dicot leaves, fruits and flowers (Hofmann, 1989). However, small desert breeds such as the black Bedouin goat have been found tobe the most efficient exploiter of herbage high in low quality fibre among ruminants (Silanikove et al., 1980, 1993; Silanikove, 1986ab). In general, it appears that there is a contradiction between Bergmann's rule and the mass-metabolic requirement concept because body size is not explaining morpho-physiological feeding type in ruminants (Hoffman, 1989). The contradiction disappears if it is taken into account that the energy metabolism of desert goats is lower than predicted from their mass and in comparison to relatives from non-desert areas (Silanikove, 2000). As shown in Table 1 in Silanikove (2000) , the energy requirements of 5 desert goats weighing each 20 kg are at about the same level as those of goats from a European breed, weighing 100 kg. The ability to maintain a larger amount of animals on the same area provides an obvious advantage in terms of survival to the desert goats.

Ic. An ability to reduce metabolism

Most mammals are able to maintain steady body weights on energy intakes less than they would take voluntarily (Harvey and Tobin, 1982). However, whereas the capacity of non-desert Saanen goats to accomplish this is restricted to a level which is 20-30% below their voluntary intake on a high quality roughage; the Bedouin goats are able to do so with an intake that is 50-55% lower than their voluntary consumption. Similarly, their fasting heat production under food restriction was 53% lower than that predicted by the interspecies relationship (Silanikove, 1987). A similar capacity to adjust to a low energy intake by reducing energy metabolism was found also in other desert herbivores, such as zebu cattle and llama, which are annually exposed for long periods to severe nutritional conditions in their natural habitats (see Silanikove, 1987).

Although the visceral organs represent approximately 6-10% of body-weight, estimates indicate that tissues of the splanchnic bed (gastrointestinal tract and liver) account for 40-50% of whole-body protein synthesis, cardiac output and heat production (Johnson et al., 1990). The results of Burrin et al (1990) suggest that level of feed intake changes the relative proportion of visceral organs to body mass. Furthermore, the effect of visceral organs on whole-body metabolic rate appears to be primarily a result of differences in organ size rather than tissue-specific metabolic activity. In addition, several evidences from the work on Bedouin goat, suggest that redistribution of the blood flow between the visceral organs and the rest of the body under conditions of restricted feed intake may also affect the whole-body metabolism (Silanikove, 1987). Similarly, Eiseman and Nienaber (1990) suggested that food supply altered the partition of energy used as well as the total energy expenditure and that these changes were related to redistributed blood flow.

Id. Efficient use of water

Breeds of ruminants indigenous to arid lands are known for their capacity to withstand prolonged periods of water deprivation and graze far away from watering sites (Silanikove, 1994). Desert

goats seem to be the most efficient among ruminants concerning their ability to withstand dehydration (Silanikove, 1994). The black Bedouin goats and the Barmer goats, herded in the extreme deserts of Sinai (Middle East) and Rajasthan (India), often drink only once every 4 days (Khan et al., 1979a,b; Shkolnik and Silanikove, 1981). Camels, also, are famous for their capacity to undergo prolonged periods (as long as 15 days) of water deprivation (Macfarlane et al., 1963; Kay and Maloiy, 1989).The small black Moroccan goats use a low water turnover as a mechanism to economize on water (Hossaini-Hilali et al., 1993). The milk yield of the Moroccan goats is very low (~ 250 ml/day) even when fed a high quality diet (Hossaini-Hilali et al., 1993),and it drops quite rapidly following exposure to water deprivation (Hossaini-Hilali et al., 1994). The strategy adopted by the Moroccan goats resembles the one used by some wild herbivores (Maltz and Shkolnik, 1984a). This mechanism is characterized by a combination of maintaining a frugal water economy and a capacity to endure severe dehydration and rapid rehydration. The water economy of the ibex and of the bighorn sheep are typical examples of such strategy (Silanikove, 1994). However, the desert Bedouin goats are able to produce even 1 litter of milk per day while eating low-quality sparse desert pasture (Maltz and Shkolnik, 1984b). Unlike the Moroccan goats, when fed high quality food Bedouin goats are able to produce above 2 l milk/day (10% of their body weight). Total yields of milk and milk solids in Bedouin goats subjected to 4 days of dehydration followed by 2 days of rehydration were ~ 70% of normal yields and normal growth of the young was not disturbed (Maltz and Shkolnik, 1984b). The data presented by Knight and Garcia (1977) suggest that most goats breeds indigenous to the tropics and subtropics are able to do much better than the Moroccan goats.

It is obvious that a relatively high milk yield is associated with a significant burden on the water economy in lactating goats. The physiological mechanism that enables desert goats to cope with severe water deprivation is consistent with an unusual ability to withstand dehydration, and to minimize water losses via urine and feces. The water losses of Barmer and Bedouin goats by the fourth day of dehydration may exceed 40% of their body weight (Khan et al., 1979a,b; Shkolnik and Silanikove, 1981). However, when maintained under an intermittent or a partial watering regimen during the summer, the Barmer goats usually gain in body weight at the end of the season (Khan and Ghosh, 1981). Thus Barmer goats perform better than the Marwari sheep (Khan and Ghosh, 1981), which under similar water restriction conditions lost 6% of their body weight per day (Purchit et al., 1972; Ghosh et al., 1976). Silanikove (1994) concluded that the gut - and mostly the rumen - provides the major portion of the water lost during dehydration, which explains their capacity to withstand a higher level of weight loss during dehydration than most monogastric mammals. The role of the rumen as a water reservoir is more pronounced in desert species and breeds, particularly in desert goats (Silanikove, 2000).

The progress of dehydration in ruminants can be separated into two phases, phase 1 gradually grading into phase 2. In phase 1, food intake and salivation are still high enough to allow near-normal fermentation in the rumen. During the last stage of dehydration (phase 2), food intake, salivation and digesta content in the rumen fall severely (Brosh et al., 1988; Silanikove and Tadmor, 1989). The appearance of Phase 2 is delayed in desert adapted ruminants (e.g., after reduction of 30% of initial body weight in the Bedouin goats, Brosh et al., 1988) in comparison to non-desert ruminants (e.g., after reduction of 15% of initial body weight in European type of beef cows, Silanikove and Tadmor, 1989). Net absorption of water and Na+ at the last stage of dehydration was found to be slight in beef cows, despite the fact that the rumen contained considerable amount of fluid (more than 20l), which could supply the animals water requirements for additional 24 h (Silanikove and Tadmor, 1989). Under isotonic conditions, net absorption of water from the rumen to the blood depends on active absorption of Na+ (Dobson et al., 1970). Na+ absorption from the rumen is closely connected to the presence of volatile fatty acids (the major product of fermentation in the rumen) in rumen fluid (Holtenius, 1991). Food deprivation

in small ruminants indeed leads to hyponatremic hypovolemia (Dahlborn and Karlberg, 1986). It is reasonable to assume, therefore, that the reduction in Na+ and water absorption from the rumen at the last stage of dehydration is a consequence of severe reduction in food intake and volatile fatty acid production.

Desert adapted animals, such as the Bedouin goats, can continue to eat a significant amount of food (30% of ad libitum intake) even under the most severe stage of dehydration (Brosh et al., 1986). Etzion et al. (1984) reported that water-deprived Bedouin goats survived losing 50% of their initial mass after 6 days of dehydration in the desert (2 days more than allowed by the Bedouin herdsmen under the extreme situations). Since they survived, they must have utilized most of the water left in the rumen at the end of 4 days of dehydration and such utilization must also have involved the absorption of Na+ from the rumen. On rehydration, the goats imbibed the entire lost amount of water; however, all of them eventually died from haemolysis. The results of Etzion et al. (1984) are consistent with the conclusion of Silanikove (1994) that water is absorbed rapidly from the rumen following rehydration, and exemplifies the importance of sequestration of a critical amount of Na+ in the rumen at the end of dehydration. Induction of Na+ absorption upon rehydration increases the tonicity of the absorbate and prevents water intoxication (Silanikove, 1989). The advantage of desert goats in utilizing rumen fluid during dehydration relates on their large ruminal volume, a better capacity of the kidney to "desalt" the water absorbed from the gut and on the maintenance of a salivary flow to the rumen.

Following rehydration, ruminants can imbibe their entire water deficit in one drinking and the entire amount ingested is first retained in the rumen. The rumen volume at this stage may exceed the extracellular fluid volume and the sudden drop in rumen osmolality creates a huge osmotic gradient (200-300 mOsm/kg) between the rumen and systemic fluid. Ruminant animals are confronted at this stage by two opposing tasks, each of them of vital importance: (i) the need to prevent the osmotic hazard leading to water intoxication, and (ii) the need to retain the ingested water, or it will be lacking in the next dehydration cycle.

Gustatory-alimentary and hepatoportal signals regarding the presence of large amounts of water in the rumen and the absorption of water from the gut activate a range of homeostatic responses involved in fluid and sodium restitution (Silanikove, 1994). The efferent elements, presumably activated by the CNS, include: a dramatic increase in secretion of hypotonic saliva and, reciprocally, a dramatic drop in urine flow. The enhanced saliva secretion recycles a considerable portion of the water absorbed from the gut back to the rumen, which allows effective retention of water while avoiding the danger of osmotic threat to the red blood cells. The enhanced saliva secretion also drains large amounts of sodium and bicarbonate from the blood. Accompanying responses are marked retention of sodium and carbonic acid in the kidney. In addition to the effective retention of fluid, these responses allow the restoration of important functions such as appetite, digestion, and thermoregulation long before plasma osmolality is restored. These physiological responses are suited to animals that experience routinely intermittent availability of water (Silanikove, 1994). The capacity of desert goats to secrete large amounts of saliva allows them to achieve an efficient retention of water following rehydration.

Ie. An ability to economise the nitrogen requirements

Ie1. General introduction

Ruminants can use dietary or non-protein nitrogen (N) to meet protein requirements largely because of the symbiotic relationship between the host and its rumen microbes. However,

because of rumen fermentation, a substantial portion of N (16-80%) is absorbed as ammonia (Huntington, 1986). Net uptake of ammonia by the portal-drained viscera exceeds 0.4 to 6.5 times the uptake of amino N, with proportionally greater net uptake of ammonia with high-fibre forages than with low-fibre high-energy diets (Huntington, 1986). Ammonia is absorbed from the rumen by diffusion, and the rate of absorption depends largely on ammonia concentration and the pH in the chyme. Ammonia absorbed from the gut enhances formation of urea in the liver (Harmeyer and Mertens, 1980). In goats and other ruminants, urea functions as a source of N for biosynthesis of amino acids in the digestive tract by its recycling to the rumen (Harmeyer and Mertens, 1980). Urea recycles to the rumen by salivary secretion and via diffusion through the rumen wall; the latter was shown to be the principal route (Obara and Shimbayashi, 1980). Permeability of ruminal epithelium is related to fermentation products of rumen: ammonia is negatively related to urea influx, whereas carbon dioxide and volatile fatty acids are positively related (Harmeyer and Mertens, 1980). Urea N transfer to the lumen of the gut ranges from 10 to 42% of the total N absorbed when dietary N intake is above the maintenance requirements (Huntington, 1986).

Ie2. Urea recycling and nitrogen conservation in desert adapted goats

Nitrogen losses decrease in response to a decline in nitrogen intake due to sparing renal activities that are accompanied by increased urea recycling to the gut (Chilliard et al., 1998). However, Chilliard et al. (1998) concluded that ruminants do not seem to be able to compensate for a below maintenance level of intake by an increase in urea recycling and digestive efficiency. This conclusion, nevertheless, is not consistent with the results with desert herbivores, particularly desert goats and camels (Mousa et al., 1983; Silanikove et al., 1980). The higher efficiency of desert goats in terms of economising its nitrogen metabolism by recycled urea was not demonstrated on high protein rations (Choshniak and Arnon, 1985; Silanikove et al., 1980). When tested on wheat straw containing only 3% protein, the desert Bedouin goats recycled 87% of the urea-N entry rate, which was twice greater than N intake (Silanikove et al., 1980), and maintained a balanced N economy (Silanikove, 1986a). Wild goats (the Nubian Ibex) were also able to balance their nitrogen economy on wheat straw (Choshniak and Arnon, 1985). However, a nitrogen recycling rate at rate of ~ 90% of the intake has been demonstrated so far only in the camel (Mousa et al., 1983) and the Bedouin goats (Silanikove et al., 1980). It was established that digestion in the rumen of poor quality roughage such as straw is hampered by the shortage of nitrogen (Campling et al., 1962). It is also well established that adding urea to such diets increases the intake and digestibility of low quality food. Thus, there is a positive interaction between the better recycling rate and a better digestion of such food in desert goats. Interestingly, the greater utilisation of fibre by camels in comparison to sheep has been related to the higher cellulolytic activity of the rumen, the longer retention time of feed particles, and the greater buffering capacity of the rumen content against fermentation acids (Kayaouli et al., 1993). This analogy in the physiological basis for the superior digestive efficiency in desert goats and camels probably arose from their position as intermediate feeders.

Efficient recycling of urea requires first the retention of urea in the kidney instead of voiding it in the urine (Silanikove, 1984). Harmeyer and Martens (1980) concluded that the urea tubular reabsorption is ~ 50% for diets containing 8 to 20% protein. The glomerular filtration rate with such diets is relatively constant and urea filtration rate relates to urea concentration in the plasma. It seems therefore that under wide ranges of dietary protein concentration urea excretion is a function of protein intake with no special renal retention mechanism (MacIntyre and Williams, 1970). However, when a low protein food is being fed, a renal retention mechanism is clearly demonstrated in ruminants (Silanikove, 1984). The ability to avoid urea losses is more

pronounced in desert goats in comparison to goats from temperate areas (Silanikove, 1984), and in goats fed a high-tannin diet in comparison to sheep (Narjisse et al., 1995). Two mechanisms operate to reduce urea excretion in the kidney: (i) A fall in the filtration load as a consequence of a fall in the glomerular filtration rate, and (ii) a very high (87-95%) tubular reabsorption of urea (Silanikove, 1984). However, quantitatively the reduction in the glumerular filtration rate is by far more important than the increase in tubular reabsorption of urea (Silanikove, 1984).

The efficiency of urea retention in the kidney and recycling to the gut is increased under conditions that increase the strain on the animals. Water deprivation decreased nitrogen losses in urine, increased urea recycling to the gut and improved nitrogen balance of desert goats, sheep and camels (Brosh et al., 1987; Mousa et al., 1993). Thus for certain breeds of desert animals at near maintenance, nitrogen economy may in fact be improved by short periods of water deprivation. Sheep and goats decrease urea-N losses, and increase the efficiency of urea recycling to the gut during late pregnancy and lactation, consistent with the increased demand for N (BrunBellut, 1997; Benlamlih and de Pomyers, 1989; Maltz et al., 1981). The mechanism for the increased retention of urea in the kidney has been shown to increase tubular reabsorption of urea (BrunBellut, 1997; Benlamlih and de Pomyers, 1989; Maltz et al., 1981). The efficiency in the desert Bedouin goats (Maltz et al., 1981) appears to be higher than in non-desert goats (BrunBellut, 1997) or desert sheep (Benlamlih and de Pomyers, 1989).

If. Digestive Efficiency in relation to feeding strategies

Ruminants may be classified into a flexible system of three overlapping morphophysiological types: concentrate selectors, grass and roughage eaters and intermediate, opportunistic, mixed feeders (Hoffman, 1989). The evolution of different feeding strategies suggests that the digestive efficiencies of certain ruminant species or breeds within a species are optimal under forage conditions where their adaptive abilities can best be expressed. Grass and roughage eaters are considered to be the most efficient exploiters of lignocellulosic material. Concentrate selectors are the least efficient exploiters of lignocellulosic feed, and they are basing their diet on selection of low-fibre high-quality forage. The capacity of intermediate selectors to digest lignocellulosic material is intermediate between the two formerly mentioned extreme groups. Domestic goats are a classical example of an intermediate feeder with a strong preference for browse feeding (Hoffman, 1989).

There are two opposite views regarding the ability of goats to efficiently digest lignocellulosic material: (i) Goats are not truly efficient exploiters of cellulosic matter and their success in tropical areas relates to their ability to exploit forages with differentiated leaves, of less lignified material, and steams (Van Soest, 1982). Accordingly, goats have a smaller proportion of the gut in relation to body weight, resulting in rapid movement of digesta from the rumen and along the entire gastro-intestinal tract. (ii) With high-fibre, low-quality forages, goats have better digestive efficiency than other ruminants, and one of the main reasons is the longer mean retention time of digesta in the rumen (Devendra, 1990; Tisserand et al., 1991). Consequently, only evaluation of the results of comparative digestion studies in conjunction to evaluation of the quality of the diet available to goats under free ranging conditions might provide a solution to resolve this contradictory views. Numerous experimental results strongly suggest that in most grazing areas in which goats are raised, the forage available to them is relatively high in cell wall and lignin contents, and moderate to low in protein content. In addition, the forage available to goats frequently contains secondary metabolites like tannins, which further constrain food utilization (Kakabya, 1994; Lu, 1988; Mill, 1990). These situations are in accordance with reports that, in most cases, breeds of goats which are indigenous to semi-arid and arid areas are able to utilize

low quality, high-fiber food more efficiently than other types of indigenous ruminants or exotic breeds of goats (Tisserand et al., 1991; Silanikove et al., 1993).

Ig. Efficiency of utilisation of high-fibre forage

The digestive physiology of desert black Bedouin goats fed on roughage diets was investigated under controlled environmental conditions in comparison with Swiss Saanen goats (temperate) (Silanikove et al, 1980; 1983; Silanikove, 1986ab) and under conditions where these goats were exposed to the full impact of their respective natural environment: heat load and infrequent water regimens (Brosh et al., 1986a,b, 1988; Silanikove and Brosh, 1989). Digestibility in the desert goats was superior even when good quality hay (alfalfa) was fed. It was more pronounced when a medium quality hay and a poorer quality feed (wheat straw) were offered (Silanikove et al., 1980, 1986a,b). In parallel, the digestibility of the structural carbohydrates (cellulose and hemicellulose) and of nitrogen were also higher than in the Saanen goats. In fact, the level of digestibility of dry matter (53-55%) and structural carbohydrates (approximately 60% in hydrated animals and 70% in goats given water once every 4 days) found in Bedouin goats fed wheat straw has been observed in other ruminants only after chemical processing of the straw (Silanikove, 1986a; Silanikove and Brosh, 1989). Lignification of plant cell walls is the most important single factor that limits structural carbohydrates digestibility, while lignin itself is considered being indigestible (Van Soest, 1982). However, in Bedouin goats fed on low-quality roughage, lignin undergoes extensive modification, degradation and absorption during its passage through the gastrointestinal tract. This enhances the release and microbial fermentation of structural carbohydrates (Silanikove, 1986a; Silanikove and Brosh, 1989). Thus, delignification may possibly reduce the encrustation of structural carbohydrates by lignin and render them more susceptible to microbial degradation. In addition, formation and release of ligno-hemicellulose complexes to the water-soluble form would expose them to the influence of extracellular hemicellulases. Removal of hemicellulose and lignin may cause larger pores to be produced in the fibres wall, thereby rendering the remaining structural carbohydrates more accessible to the rather large molecule size of cellulase (Silanikove and Brosh, 1989).

Voluntary feed intake in the desert adapted Bedouin goats was less affected by a high-fibre diet than intake by Saanens and, consequently, breed differences in digestible energy intake were even larger than the differences in digestibility (Silanikove, 1986a). The main advantage of the Bedouin goats over the Saanen while digesting medium quality roughage may relate to their ability to maintain higher microbial density on the particulate matter, hence a higher total ruminal fermentation rate and higher volatile fatty acid formation (Silanikove, 1986b; Silanikove et al., 1993). Their ability to sustain higher microbial density on the particulate matter in the rumen was related to their superior urea recycling capacity (Maltz et al., 1981; Silanikove et al, 1980; Silanikove, 1984) and to their ability to prevent a fall of the rumen pH to below 6.5 (Silanikove, 1986b; Silanikove et al., 1993). In both breeds, rumen volume (approximately 20% of body-mass) considerably exceeds typical rumen volume of sheep under comparable conditions (Silanikove, 1986b; Silanikove et al., 1993). However, the mean retention time of particulate matter in the rumen was considerably higher (41 hours versus 32) in the Bedouin goats than in the Saanen goats. Thus, the combination of higher fermentation rate and longer retention of digesta in the rumen allows for greater feed intake and digestibility in comparison to less efficient non-desert goats (Silanikove, 1986b; Silanikove et al., 1993).

The digestive capacity of the Bedouin goats enables them to utilise efficiently high-fibre low nitrogen desert pastures. This characteristic is an important asset for their capacity to exist and produce in extreme arid areas. This capacity stands in sharp contrast to predictions from their size

(Demment and Van Soest, 1985) and with the views of Huston (1978), Brown and Johnson (1984), Van Soest (1982) and Hoffman (1989) regarding the digestive characteristic of goats.

Goats indigenous to woody areas are capable of consuming much more tannin-rich browse than sheep and digesting more efficiently (Kumar and Vaithiyanathan, 1990; Silanikove et al., 1994, 1996a,b; Wilson, 1977). The capacity of goats to eat browse species not consumed by sheep was utilised in many cases and in many parts of the world to open dense bush and to control noxious weeds. The advantage of the goats over other ruminants while consuming tannin-rich plants relates to their superior capacity to neutralise the negative effect of tannins on palatability and digestibility (Silanikove et al., 1996a). Because lignin and tannins are both complex phenolic compounds, there is analogy between the ability of goats to deal effectively with lignin and tannins.

PART II. Adaptation to Pastures Rich in Browse

IIa. Goats in ecosystems rich in browse

Trees and shrubs are an important source of fodder for livestock in tropical and dry environments (Devendra, 1990; Topps, 1992). Ecosystems where goats predominate often are characterised by an abundance of browse (woodland, scrubland, different bathas). In semiarid parts of theworld, such as African savannah (Rutagwenda et al. 1989), Texas (Bryant et al., 1980), and most circum-Mediterranean areas (Kababya, et al., 1998; Decandia et al. 1998), goats rely on browse most of the year. Thus, it is not surprising to find adaptations to browse - low CP availability and high toxins - at the basis of goat feeding behaviour. Goats are opportunistic feeders: time spent grazing species depends generally on the relative frequency of encounters, but this relationship depends on species of vegetation and habitat visited.

Goats that are adapted to exploit freely a Mediterranean environment consisting of scrubland and woodland organize their feeding behaviour to select dietary components in such a way that the concentration of available (non-linked to ADF) protein, NDF and condensed tannins (CT) in the total diet remains relatively constant throughout the year (Kababya et al., 1998). Thus, unlike sheep and cattle which do not eat leafy material during the green season, browse constitutes at least 40% of the forage selected by goats at all times (Kababya et al., 1998; Perevolotsky et al., 1998). Silanikove (1997) showed that adaptation of the microbial system in the rumen forms a very important element to utilize high-tannin foilage. Thus, maintaining intake of browse sufficient to preserve their adaptation to tannin-rich food is justified on the long run because this type of forage is available to them in large amounts all year around. This pattern of diet selection, however, is not compatible with milk yield maximization. Indeed, selection of goats by men in harsh Mediterranean environment was traditionally based on breeding success and lifetime performance (Santucci, 1984). In contrast to energy, protein cannot be stored over a long period in goats. Therefore, a decrease in protein intake in June is followed immediately by a drop in milk yield (Landau et al., 1993; Kababya et al., 1998). This pattern is preserved even if concentrate is supplemented (Landau et al., 1993), suggesting that the trigger is environmental (decreasing day length or ambient temperature). As energy intake remained steady, the drop in milk yield results in increased body weight and body conditioning score (Kababya et al., 1998). In August, at the onset of the oestrous season, goats are able to increase their protein intake from the summer depleted range (Kababya et al., 1998). It seems, therefore, that in June goats select a "self dry off-self fattening diet" in late spring and a reasonably good diet in late summer that improve the chance of reproductive success. This feature is consistent with the long-term genetic selection by

traditional farmers in the Mediterranean Basin, which focus on the maximization of reproductive performance in the face of low supplementation.

IIb Effect of tannins on the utilization of browse

Most browse species contain large amounts (up to 50% of the dry matter) of tannins (Leinmuller et al., 1991; Cabiddu et al., 1998). Tannins are complex phenolic compounds that contain sufficient hydroxyl and carboxyl groups to precipitate proteins and to bind carbohydrates under conditions that prevail in the digestive tract of mammals and birds. The negative effects of tannins on palatability and digestibility in ruminants are multiple (Kumar and Vaithiyanathan, 1990). They include: (i) reduction in protein availability due to binding of food proteins and inactivation of enzymes in the digestive tract, (ii) astringency caused by the interaction of tannins with salivary protein and oral mucosa, and (iii) gut irritation and systemic toxicity. All of the aversive effects can reduce forage palatability.

Immature vegetation in the Mediterranean region is high in protein (>14%) and in vitro and in vivo (cattle 70%, sheep 80%) digestibility. Unlike sheep and cattle raised in a similar environment that graze herbage in the spring (Rothman 1998), browse constitutes at least 50% of the forage selected by goats (Kababya, 1994; Kababya et al. 1998; Rothman 1998; Perevolotsky et al., 1998). Such behaviour may appear strange,particularly if considering that goats are characterised as opportunists (Hoffman, 1989). However, three strains of tannin-tolerant rumen bacteria were isolated from enrichment cultures of rumen microflora of sheep, goat, and antelope and established in medium containing high concentrations of crude tannin extract or tannic acid (Odenyo and Osuji, 1988). A strain of the anaerobe Selenomonas ruminantium subsp. ruminantium capable of growing on tannic acid or condensed tannin as a sole energy source has beenisolated from ruminal contents of feral goats browsing tannin-rich *Acacia* spp. (Skene and Brooker, 1995). Transferring these micro-organisms from feral goats to domestic goats and sheep fed tannin-rich foliage (*Acacia aneura*) increased feed intake and nitrogen retention in inoculated compared with uninoculated animals. Acclimation of microbes in the rumen of goats adapted to the Mediterranean scrubland enables goats to use high-tannin tree leaves (Silanikove, 2000). Spring in the Mediterranean is very short,and after three months the nutritional quality of the grass diminishes at an accelerated rate. Thus, much of the short-term advantage from switching foraging habits can be lost during the time necessary to regain the capacity required for digesting high-tannin browse sources. Though goats take advantage of the abundance of highly digestible grass (increasing its proportion from approximately 10% in the winter to 40-50% in spring), they also continue to eat sufficient browse to remain acclimated to tannin-rich food. Eating a variety of foods enables goats to meet nutrient needs, avoid toxins, and continually explore their environment. As discussed above, sensory-, nutrient-, and toxin-specific satieties cause decreases in the palatability of different foods and encourage animals to ingest a variety of foods. Goats eat only the most nutritious parts of a wide variety of plant species – evidently because they satiate quickly (i.e., they respond strongly to sensory-, nutrient-, and toxin-specific satieties).

In general, there is an inverse relationship between tannin concentration in browse sources and voluntary feed intake by herbivores (Kumar and Vaithiyanathan, 1990). Condense tannin contents above 3% may act as a feeding deterrent (Provenza, 1995), influence feed degradation in the rumen (Silanikove et al., 1996a,c) and the digestibility of the whole diet (MacNaughton, 1987; Silanikove et al., 1997a). Hence, when tannin-rich leaves are offered as a sole feed to sheep and goats they may not provide for adequate absorbed nutrients for maintenance despite their relatively high-protein and low-fibre contents (Silanikove et al., 1994, 1996a). They may also reduce animal productivity in terms of weight gain, milk yield and wool growth (Kumar and

Vaithiyanathan, 1990). Silanikove et al. (1996a) reported that tannin levels of approximately 20% of DM drastically reduced leaf intake of Pistacia lentiscus and goats fed such a diet were in marked negative nitrogen balance, and lost weight very rapidly (100 g/day).

Tannins can suppress intake by reducing digestibility or by causing illness. Tannins may bind to cell walls and cell solubles (Kumar and Vaithiyanathan, 1990; Reed, 1995) and in the process reduce the digestion of protein and yield of energy-rich byproducts of microbial fermentation such as volatile fatty acids (Makkar et al., 1995). This in turn may adversely affect preference of the feed containing the tannins (Villalba and Provenza, 1996, 1999). Tannins may also produce adverse postingestive effects that cannot be accounted for by digestion inhibition alone, primarily because they cause such rapid (within a few to 60 min) and dramatic decreases in food intake (Silanikove et al., 1997b; Landau et al., 2000). Silanikove et al. (1997b) in goats and Landau et al. (2000) in heifers have shown that feeding ruminants diets rich in condensed tannins was associated with lowered feed intake and shorter duration of eating bouts, mainly of the first eating bout, immediately after distribution of the diet. The data of Silanikove et al. (1997b) and Landau et al. (2000) suggest that: i) negative effects of condensed tannins derive from astringency and short-term post-ingestive malaise; ii) the increased number of eating bouts and their wider partition throughout the day are means to preserve the ruminal environment; iii) PEG has the potential to neutralize negative effects of condensed tannins. Adverse postingestive effects may be caused by lesions of the gut mucosa and direct toxicity (Reed, 1995; Dawson et al., 1999), which are likely to stimulate emetic mechanisms in the central nervous system (Provenza, 1995).

IIc Polyethylene-glycol (PEG) as means to neutralize the detrimental effects of tannins

Polyethylene glycol (PEG) is a polymer that can bind tannins irreversibly over a wide range of pH, and its presence reduces the formation of a protein-tannin complex (Jones and Mangan, 1977). PEG was supplied to grazing ruminants by: (i) spraying of tannin-rich browse (Kumar and Vaithiyanatan, 1990), (ii) mixing with tannin-rich harvested leaves (Kumar and Vaithiyanatan, 1990), and (iii) oral-drenching of animals grazing on tannin-rich pasture (Pritchard et al., 1992; Terrill et al., 1992). These procedures have been reported to increase feed intake and digestibility in goats and sheep, and wool growth in sheep; however, they are either impractical under field conditions (drenching) or uneconomical (spraying, harvesting and mixing). Recently, a new direction that is practical for field application has been proposed; that is, administration of PEG to sheep and goats once daily by its mixing with small amount of concentrates (Silanikove et al., 1994, 1996a; Decandia et al., 1998) or by mixing with the drinking water (Perevolotsky, unpublished data). The logic behind this approach relates to the finding that, as with monogastric animals, a considerable portion of the antinutritional effects of tannins is exerted in the intestine by depressing of the activity of the pancreatic enzymes (Silanikove et al., 1994, 1996a). Thus, despite the rapid washout of PEG from the rumen as a water-soluble molecule, the typical mean retention time of fluid in the entire gastrointestinal tract (approximately 40 h, Silanikove et al., 1993) allows effective neutralization of ruminal and postruminal effects of tannins by PEG. In fact, twice a day provision of PEG was not more effective than once-daily provision in terms of positive effects on intake and digestibility (Silanikove et al., 1994).

PEG binds to tannins and may thereby increase the availability of certain macronutrients, particularly of proteins. Supplemental PEG can cause increased intake of tannin-containing plants by animals as diverse as rats (Horigome et al., 1988), hoggets (Kumar and Vaithiyanathan, 1990), sheep and goats (Pritchard et al., 1988; Silanikove et al., 1994, 1996a; Titus et al., 2000a,b), and cattle (Landau et al., 2000). Recent results have shown that macronutrients, tannins, and PEG interacted along a continuum to affect food intake of ruminants (Titus et al., 2000a). In these

studies, lambs maintained intake of macronutrients when feeds were not too high in tannin and when alternative tannin-free feeds were available. Collectively, these finding indicate that lambs supplemented with PEG ingested more macronutrients and tannins than unsupplemented lambs, especially as the availability of low-tannin feeds diminished. Conditions where all alternative forages are nutritionally of the same quality (low to medium) and contain appreciable amounts of potential toxicological secondary metabolites often prevail in tropical and Mediterranean conditions (Khazaal et al., 1993; Reed, 1995). Sheep usually prefer old season blackbrush twigs over current season blackbrush, despite the higher protein content in the current season blackbrush twigs, because younger twigs contain much more tannins (Titus et al., 2000b). With PEG supplementation, sheep shifted their preference to the current season blackbrush, suggesting that PEG neutralised their negative effect (Titus et al., 2000b). Similar results were obtained in Israeli grazing studies in which PEG supplementation shifted the preference of grazing beef cows towards pistacia tree leaves (Perevolotski et al., unpublished data). This plant is widespread in Mediterranean areas, and is scarcely consumed by grazing ruminants because of its high tannin content (20%). Thus PEG supplementation emerged as a novel and powerful technique to control shrub encouragement.

Given the strong response of sheep and goats to supplemental PEG, we speculated that animals might self-regulate their intake of PEG when fed foods high in tannins, because animals can learn to consume foods and solutions that attenuate aversive effects of food ingestion (Phy and Provenza, 1998). Indeed, studies in the USA (Provenza et al, 2000) and Israel (Silanikove et al., unpublished results) have shown that sheep and goats self-regulate the intake of PEG. Positive interrelationships between tannin content and PEG intake, which in turn positively affected the amount of food consumed, were found in these studies. Supplementing PEG may be practical under many farm conditions (Silanikove et al., 1994; Gilboa et al., 2000). However, the labour required to supplement PEG is a disadvantage, particularly under extensive use of rangeland, where it is not possible to gather the animals everyday. The amount and frequency of dosing PEG depends on the tannin content of the diet, which varies with environment and season (Cooper et al., 1988). One solution to such problems is to let animals self-regulate intake of PEG. Since PEG is expensive, it may not be feasible to offer loose PEG as a supplement to free-ranging livestock. However, it may be possible to formulate "range" blocks that contain PEG, along with other compounds such as charcoal and macronutrient such as protein (Banner et al., 2000), which are known to increase use of forages rich in tannins and other secondary metabolites. PEG supplementation is costly because PEG must be administered to livestock daily prior to grazing, and it often is mixed with grain. The costs associated with PEG supplementation might be reduced if livestock would consume PEG without grain and if they would only consume as much PEG as needed to counter the tannins in their diet. This principle was exploited recently by Ben Salem et al., (2000). They used unmolassed feed blocks as supplement of tannin-rich *Acacia cyanophylla* Lindl. (acacia)-based diets. Inclusion of Quicklime (10.7%), urea (4.4%), and salt (4.4%) in the blocks constraint the block intake at levels of 15 to 20 g/kg $BW^{0.75}$. Nutrients were supplemented with relatively cheap local sources such as olive cake (42.2%), wheat bran (26.7%), and wheat flour (10.7%). The optimum responses of acacia intake, nitrogen retention, microbial N yield and daily gain were obtained in sheep given feed blocks with 18% of PEG, which correspond to a PEG consumption of about 23 g/day.

Experiments in which PEG was used to neutralise tannins have clearly shown that the major antinutritional effect of some tannins is reduction of protein availability and depression of digestive tract enzyme activities (Silanikove et al., 1994, 1996a, 1997a). These studies also supported previous findings that tannins may reduce cell wall digestibility by binding bacterial enzymes and(or) forming indigestible complexes with cell wall carbohydrates (Barry et al., 1986; Reed, 1986). Tannin-protein complexes formed in the digestive tract were determined as fecal

lignin (Reed, 1986), which led to apparent negative digestibility of lignin. Thus, the change from negative to positive apparent lignin digestibility in sheep fed tannin-rich carob leaves, following supplementation with 25 g/d PEG (or more) reflects the protein-sparing effect of PEG.

It was concluded that the protein-binding capacity of tannin-containing leaves might exceed considerably the protein content in the leaves (Silanikove et al., 1994). Thus, in range-fed animals tannins ingested with the browse may also affect the protein utilisation of any supplementary feed. Indeed, in goats fed tannin-rich foilage as their basal diet, supplementation with low protein concentrates depressed the basal diet intake whereas high-protein supplement stimulated basal diet intake (Silanikove et al., 1997a). Therefore, supplementing tannin-rich leaves with concentrate feed is recommended only if done in combination with PEG. Supplementation with protein increased leaf and digestible protein intake, but a considerable portion of the additional protein was wasted because of interaction with tannins (Silanikove et al., 1997a). PEG may enable farmers to economise in the use of such high-cost feeds due to the greater efficiency of protein utilisation (Silanikove et al., 1997a; Ben Salem et al., 2000). For example, when goats on tannin-rich oak leaves were supplemented with soybean meal, the addition of PEG increased digestible crude protein intake from 92 to 122 g/day from the supplementary feed and intake of the basal leaf diet from 844 to 1023 g/day (Silanikove et al., 1997a). Ben Salem et al. (1999a,b, 2000) have shown that PEG supplementation increased substantially the intake, digestibility and nitrogen balance of sheep fed a diet based on *Acacia cyanophylla* leaves, which was reflected in increased growth rate of yearling males. Notwithstanding, *Acacia cyanophylla* is a multipurpose tree widespread in Africa and the Mediterranean zone. However, its basic nutritional value is very low due to high tannins levels, which lead to poor performance of sheep and goats (Ben Salem et al., 1999a,b, 2000).

In animals on some tannin-rich diets, higher pH (~ 7) and lower VFA levels in the ruminal fluid suggest that the microbial activity was considerably depressed (Silanikove et al., 1996a, 1997a). The proportional increase in digestible OM and CP upon supplementation with PEG-, concentrate- or high-protein feedstuffs was much higher than the parallel increase in ruminal VFA, ammonia concentrations and microbial synthesis (Silanikove et al., 1996a, 1997a; Ben Salem et al., 2000). Two explanations are possible: (i) changes in feed intake resulted in higher inrumen DM and fluid contents, and therefore any increase in VFA production rate was not reflected by a proportional increase in their concentration; and (ii) part of the improved digestibility could be related to an increased proportion of feed digested in the intestine. This is consistent with findings in sheep, where some of the feed-protein that was bound to tannins passed the rumen undegraded (Barry et al., 1986). In goats supplemented with high-protein feeds, the larger increase in serum urea concentration as compared with that in rumen ammonia concentration, would suggest that the tannin-protein complex dissociated after leaving the rumen, and this caused increased the absorption of amino acids from the intestine (Silanikove et al., 1997a). However, in some cases the tannins, which probably were released before reaching the intestine greatly inhibited intestinal pancreatic enzyme activity in sheep (Silanikove et al., 1994) and goats (Silanikove et al., 1996a).

PEG is soluble in water and is not absorbed from the gastrointestinal tract. Once ingested, its content (and thus concentration) in the rumen decreases exponentially according to first order kinetics. Typical biological half-life and mean retention time of a soluble marker in the rumen are 7 and 10 h, respectively (e.g., Silanikove et al., 1993). The fact that no significant response was recorded when PEG was supplemented twice daily rather than once a day suggested that its tannin-binding activity is spread along the entire digestive tract. Condensed tannins in carob pods markedly depressed the intestinal activity of trypsin and amylase (as judged by their activity in fecal samples; Silanikove et al., 1994, 1996a), which agrees with findings that extracts from carob

pods inhibited the activity of digestive enzymes in vitro (Tamir and Alumot, 1969). The binding strengths between tannins and proteins appear to be weakened in the acidic environment of the abomasum (Jones and Mangan, 1977). Thus, the presence of PEG in the intestine may prevent tannins from binding tointestinal enzymes.

The effect of condensed tannins on the rumen content and passage rate of digesta along the gastrointestinal tract was studied in goats fed carob leaves with and without PEG (Silanikove et al., 2000). The main effects of tannins, as inferred from the neutralisation of tannins by PEG, are depression of the rumen fluid and particulate content of the rumen, acceleration of the passage of liquid from the abomasum, and delay of the passage of digesta in the intestine. The overall effect is a delay in the passage of fluid and particulate matter throughout the entire GI tract. It is hypothesised that these responses are largely the consequence of the interaction of tannins with digestive enzymes and the epithelium lining the digestive tract. According to this interpretation, changes in feed intake of a given fodder with a variable level of tannins are proportional to changes in the mass of digesta in the rumen. In accordance with this hypothesis, it was found that each increase or decrease in PEG intake in goats and sheep fed high-tannin foliage was accompanied by an abrupt (within 24 to 48 h) increase or decrease in feed intake and body weight (in the range of 300-1600 g), which probably related to changes in rumen contents. These abrupt changes were followed by stabilisation of feed intake at the new level, and gradual changes in body weight (within the range of -100 to +100 g/d), which were proportional to the metabolizable energy intake (Silanikove et al., 1994, 1996a). As a result, the ratio betweenrumen volume or mass and food intake was the same in the PEG treated and in the control goats.

IId Enhancing productivity by PEG supplementation

In ecosystems dominated by varieties of oak (ca. 10% condensed tannins), providing goats with a daily dose of 10 g PEG yielded the best cost-beneficial response in terms of improvements in intake and organic matter digestibility (Silanikove, 1996a). In woodland dominated by lentisk, in which the CT content reaches 20%, the daily dose of PEG needed by goats to neutralize the effects of CT amounts to 25 (Silanikove et al, 1996) or even 50 g (Decandia et al., 1998). In addition, PEG prevented the negative effect of concentrates rich in starch on browse intake, and allowed using expensive dietary protein from soybean meal without wasting it in tannin-linked complexes (Silanikove et al., 1997b). The cost of 10 g PEG (0.09 US $ under Israeli conditions) is cheap, when compared with the cost of increased digestible organic matter or protein that it allows. Consequently, it appears that the use of PEG under paddock conditions is potentially economically profitable. This aspect was tested with range-fed goats. Experiments were carried out in locations representing different types of management systems in Israel (see Landau et al., 1995 for review on the management systems, which are used for goat farming in Israel) and in Italy (Decandia et al., 1998). Most interestingly, PEG-supplemented Sarda goats spent more time foraging on tanniferous species, and less on herbaceous forage, ingested more dry matter and digested more protein than unsupplemented counterparts (Decandia et al., 1998). Although PEG-supplemented goats generally ingested more DM and digested more protein and energy from browse, production responses were different among breeds. In Mamber goats weight gain during pregnancy and higher birth weight of the kids were noted (Gilboa, 1996), whereas the most noticeable response was an increase in milk yield in Anglo-Nubian (Gilboa, et al., 2000) and Sarda goats (Decandia et al., 1998). Higher milk yield in Mamber goats supplemented with PEG was reflected in higher growth rate of kids, but this effect vanished after weaning (Gilboa, 1996). PEG-feeding was associated with lower content of lactose in milk, but this effect may be confounded with its effect on milk yield (Gilboa, 1996).

Although geographically coincident, Mamber and Anglo-Nubian (or their crosses with Damascus) goats are exploited in distinct production systems. Both breeds of goats are found where natural resources are scarce and seasonal fluctuations in resource quality are great. However, Mamber goats will usually receive little food supplementation, whereas Anglo-Nubian and Damascus goats will receive liberal supplementation (Landau et al., 1995). When PEG was given to Mamber goats, PEG was associated with more rapid growth of the litter (Gilboa et al., 2000), most likely resulting from increased milk yield at the onset of lactation. This effect on milk production ended shortly after weaning at 35 days post-partum, when milking was initiated. The production cycle of Mamber goats is characterized by relatively short lactation, moderate utilisation of body depots and rapid recovery of body condition in spring. This means that a time when high quality feed resources could be exploited to enhance lactation, they are directed, instead, to muscle and fat accretion. Mamber goats manage feed and body resources in a way that improves the probability of reproductive success, that prioritises embryo development and a milk production for a short period after parturition (Kababya et al., 1998). In Anglo-Nubian goats, a breed selected for milk production, which is able to utilise body depots for lactation to a great extent (Landau et al., 1993), PEG greatly enhanced milk production throughout a long lactation, independently of kid survival and growth.

Providing daily 10 g PEG (0.09 US $ under Israeli conditions) to Mamber goats was associated with an average of 26 and 22 g/d higher daily weight gain of kids in experiments 1 and 2, respectively (calculated from Tables 1 and 3 of Gilboa et al., 2000). Assuming that 1 g of gain is achieved by 1 g DM of milk (Gilboa et al., 2000), this is equivalent to 171 g of milk, worth 0.09 US $. In experiment 2 (Mamber goats), milk yield was 127 g/dhigher in PEG fed goats than in the controls. This relatively modest increase in milk yield is similar to that reported by Decandia et al. (1998), i.e., 110 g/d, for Sarda goats. This additional production of milk contributes 0.06 US $ during 35 days. It is clear that feeding PEG all year round for such a low return during 35 days is uneconomical. In contrast, in Anglo-Nubian goats, the difference in milk yield between PEG-fed and controls averaged 0.46 kg/d, priced 0.23 US $. Assessing an average lactation length of 210 days, the return on 365 days feeding PEG (cost 33 US$) is 48 US $. If an increase of milk yield is anticipated as a result of PEG-feeding, it is clear that the production system exploiting Mamber goats is more resilient to this new practice(as it is to concentrate supplementation; Landau et al., 1995) than the system that exploits Damascus or Anglo-Nubian goats.

To summarize, it seems that PEG-feeding, which improves the utilisation of Mediterranean browse, results in an elevation in milk production that parallels the production potential in goats. The more productive the goat, the more is PEG-feeding likely to be economical. However, PEG-feeding may improve the odds of successful reproduction of low productive goats on the long-term, maximising their career crop of kids, which has not been taken into account is the above brief calculation. In tropical and subtropical environments, PEG supplementation may increase the ability of ruminants to survive during successive periods of droughts.

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