Review

The physiological basis of adaptation in goats to harsh environments

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Abstract

Goat living in harsh environments represents 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 an important asset to them for it minimise 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 skillful 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, the salivary glands and the kidney coordinately function in the regulation of water intake and water distribution following acute dehydration and rapid rehydration. Goats in the tropics, when possible, eat a diet composed of tree-leaves and shrubs (browse), which ensure a reliable and steady supply of food all year around, albeit, from a low to medium quality food. Some of the physiological features of ruminants defined as intermediate feeders like large salivary gland, the large absorptive area of their rumen epithelium, and the capacity to change rapidly the volume of the foregut in response to environmental changes are most likely responsible for the goat's superior digestion capacity. © 2000 Elsevier Science B.V. All rights reserved.

1. Introduction

Under desert and tropical environments, where feed resources are restricted in quantity and quality, differences among ruminants in energy requirements and digestive efficiency, which are reflected in the efficiency of the use of gross energy for production, are very important criteria for the selection of the most

appropriate type of animal to be grown in particular circumstances (Devendra, 1990). 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 (6–8 months) are punctuated by erratic rainfall and brief eruption 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 goats population (∼610 million head) are located in Asia and Africa, mostly (80%) in the tropics and sub-tropics (Knight and Garcia, 1977). 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. For example, during the years 1961–1971 the number of goats in the entire desert of Rajasthan increased by almost 70% (from 3.42 to 5.81 million), whereas the number of sheep increased by almost 19% (from 4.35 to 5.16 million; Khan and Ghosh, 1981). In the natural environment of desert goats (Khan and Ghosh, 1981; Shkolnik and Silanikove, 1981), water sites are widely distributed and the herbage is extremely meager and mostly of low quality. Scattered thorny trees (e.g., Acacia's) and low desert scrub are relatively abundant only in wadi beds. In order to satisfy their needs for food, these goats must cover large grazing areas of barren desert. During bad years, watering once in every two days is very common and four days without water may occur in full lactation. Although milk production under such conditions drops, it is still sufficient to maintain normal growth of the single young (Shkolnik and Silanikove, 1981).

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 purpose of the present review is to provide an integrative explanation of the ability of goats to survive and produce better than other ruminants in harsh environments. First, the significance of small body size in adverse environment is considered. The contradiction between small body size, high digestive efficiency of goats and the widely held concept suggesting that the digestive efficiency of ruminants positively relates to body size is explained by low metabolic requirements, and the ability of goats to reduce meta-

bolism. Then, the physiological basis for the superior digestive capacity, efficient nitrogen economy, and efficient use of water in desert goats are considered. In the general discussion, we considered the grazing strategy of goats, and how this strategy in combination with the physiological adaptation to food and water scarcity contributed to drought resistance in goats.

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

The rule of Bergmann (1847) is probably the best known rule in zoogeography. It states: "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 paleoclimatic changes 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 (Rosenzweig, 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 towards a smaller size explains also the simultaneous widespread 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 in most cases much smaller than typical European breed of goats (Epstein, 1971).

3. 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 that in large mammals (Table 1). 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 to be the most efficient exploiter of high-fibre low quality

Table 1
Body weight (kg), metabolic body weights (BW$^{0.75}$), metabolic requirements (kJ (BW$^{0.75}$ day)$^{-1}$), and total requirements (kJ/day; product of number of animals × metabolic requirements × metabolic weight) of desert (dwarf Bedouin), and non-desert (large European; Saanen, Alpino, Anglo-Nubian; virtual goat having body weight of dwarf Bedouin goat and metabolic requirement of large European goat); in order to compare large and small animals the total weight of the total weight of dwarf goats was taken as a biological unity

Goat	Non-desert goat	Non-desert goats	Desert
Number of animals	1	5	5
Body weight	100	20	20
Total weight	100	100	100
Metabolic requirement[a]	657	657	418
Metabolic weight	31.6	9.45	9.45
Total requirements	20761	31043	19750

[a] According to Silanikove (1986a).

fibre among ruminants (Silanikove et al., 1980, 1993; Silanikove, 1986a, b). 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 (Hofmann, 1989). The contradiction disappears if it is taken into account that the energy metabolism of desert goats is lower than that predicted from their mass and in comparison to relatives from non-desert areas (Table 1). As shown in Table 1, the energy requirements of five 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.

4. 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 is restricted to a level which is 20–30% below their voluntary intake on 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 goats, 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 effect the whole-body metabolism (Silanikove, 1987). Similarly, Eisemann and Nienabar (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.

5. 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 (Hofmann, 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 intermediate feeder with a strong preference for browse feeding (Hofmann, 1989).

There are two opposite views regarding the ability of goats to digest efficiently 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 highly fibrous with a relatively high cell wall and lignin contents, and a moderate to low 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 situation are in accordance with the finding that in most cases breeds of goats which are indigenous to semi-arid and arid areas are able to utilize low quality high-fibre food more efficiently than other types of indigenous ruminants, or exotic breeds of goats (Tisserand et al., 1991; Silanikove et al., 1993).

6. 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 (temperate) Swiss Saanen goats (Silanikove et al., 1980, 1993; Silanikove 1986a, b) 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, 1996a, 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 in every four days) found in Bedouin goat 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

himself 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 it 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. In completion, the 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 were less affected by a high-fibre diet than in the Saanen's and consequently the breed's 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's 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 acids 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 h versus 32 h) in the Bedouin goats than in the Saanen goats. Thus, the combination of higher fermentation rate and longer passage rate allows maximising 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 (1985); Van Soest (1982); Hofmann (1989) regarding the digestive characteristic of goats.

Goats indigenous to woody areas are capable to consume much more tannin-rich browse sources than sheep and to digest it much more efficiently (Kumar and Vaithiyanathan, 1990; Silanikove et al., 1996b; Silanikove et al., 1994 vs. Silanikove et al., 1996a; 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.

7. Ability to economise the nitrogen requirements

7.1. 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 0.4–6.5 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).

7.2. Urea recycling and nitrogen conservation in desert adapted goats

Nitrogen losses decrease in response to decline in nitrogen intake due to sparing renal activities that are accompanied by increased urea recycling to the gut (Chilliard et al., 1988). However, Chilliard et al. (1988) 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, nitrogen recycling rate at rate of $\sim 90\%$ 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 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 Mertens (1980) concluded that the urea tubular reabsorption is $\sim 50\%$ for diets containing 8–20% 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 mechanism 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., 1983). 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, in consistence with the increased demand for N (BrunBellut, 1997; Benlamlih and de Pomyers, 1987; 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, 1987; 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, 1987).

8. 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 in every four days (Khan et al., 1979a, b, c; 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 ($\sim$ 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 the 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 l 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 per day (10% of their body weight) (Maltz et al., 1982). Total yields of milk and milk solids in Bedouin goats subjected to four days of dehydration followed by two days of rehydration were $\sim$ 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 (Purohit 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

Table 2
The contribution of rumen fluid to weight loss during dehydration in various ruminants

Species[a]	Dehydration, % of initial BW	Rumen contribution, % of dehydration
Cattle	18	49
Sheep	20	52
Mamber goats	30	58
Bedouin goats	40	68

[a] The cattle was of European type, the sheep — Merino (a semi-desert sheep), Mamber goats are semi-desert, and the Bedouin goats are desert one; See Silanikove (1994) for the source of data.

the rumen as a water reservoir is more pronounced in desert species and breeds, particularly in desert goats (Table 2).

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 20 l), 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., 1976). 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 the ad lib.) 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 six days of dehydration in the desert (two days more than allowed by the Bedouin herdsmen under the extreme situations). Since they survived, they must have utilised most of the water left in the rumen at the end of four 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 utilising 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 amount of saliva allows them to achieve an efficient retention of water following rehydration.

9. General discussion

9.1. Digestive adaptation

A key question that should be asked is: Are Bedouin goats outstanding in regard to the digestive characteristic of their species, or alternatively, do they represent the climax of successful evolutionary adaptations of many breeds of goats to semi-arid and arid environments? The answer provided in this review is that the Bedouin goats represent most likely a climax of evolutionary adaptation of ruminants in general and goats in particular to digest efficiently high-fibre low-nitrogen diets. The basis for this conclusion is: (i) the relatively large number of cases in which goats raised in harsh environments were found to be superior to other ruminants, and (ii) whenever goats were found superior to other ruminants, the digestive physiological basis was similar; namely, goats had an extended retention time of digesta in the gut, and higher cellulosic activity in the rumen which could be partially related to a more efficient recycling of urea from blood to the rumen (Devendra, 1990; Tisserand et al., 1991). The greater secretion of saliva in goats in comparison to sheep (Dominigue et al., 1991; Seth et al., 1976), and the larger surface area for absorption from the rumen (resulting from broad like leaves papillae compared to narrow like tongues papillae in sheep, Battacharya, 1980) is a general characteristic of intermediate feeders like goats, in comparison to grass eaters, like sheep. These characteristics may explain: (i) the more efficient recycling of urea to the rumen because urea recycling is mediated via saliva secretion and via diffusion through the rumen walls, and (ii) the prevention of fall in rumen pH even at pick fermentation, because: (1) salivary flow is the major contribution to rumen buffer capacity, and (2) efficient absorption of volatile fatty acids through the rumen wall enhanced the buffer capacity of the rumen (see Silanikove et al., 1993). A capacity to maintain a spacious rumen helps the Bedouin goats to quench against reduction in the quality of the diet (Silanikove

et al., 1993) and to maintain sufficient food intake under infrequent watering regimen (Silanikove, 1992, 1994)

9.2. Adaptation to the pasture

Fodder trees, fodder shrubs and herbaceous species are very important sources of food for livestock, particularly in desert and semi-desert areas (Devendra, 1990; Topps, 1992). It has been consistently shown in many semi-arid parts of the world, such as African savannah (Rutagwenda et al., 1989), northern Mexico (Mellado et al., 1991), and Texas (Bryant et al., 1980) that browse constitute most of the goats diet all year around. Goats are the principal ruminant in many scrublands surrounding the Mediterranean Basin, and are present in large number in Greece, Southern France (Provence) and Spain, and are parts of traditional extensive grazing systems in many other countries such as Morocco, Tunis, Israel, Jordan and Lebanon (Landau et al., 1999). Whenever comparative grazing studies were carried it was shown that goats consumed larger proportion of browse than sheep and cattle (Bryant et al., 1980; Rutagwenda et al., 1989).

Although the nutritional quality of pasture grazed by goats range from rather poor (Mellado et al., 1991) to medium quality (Landau et al., 1999) its nutritional quality did not fall very much during the dry season in savannah (Rutagwenda et al., 1989) and Mediterranean areas (Kakabya, 1994; Kababya et al., 1998). Such grazing strategy protects goats from fluctuations in resource abundance.

Most browse species are dicotyledons that contain large amount (up to 50% of the dry matter) of tanniferous compounds (Reed, 1986; Leinmuller et al., 1991). 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, the main effects being (Kumar and Vaithiyanathan, 1990): (i) reduction in protein availability due to binding of food proteins and inactivation of digestive tract enzymes, (ii) reduced palatability because of the astringency feeling caused by the interaction of tannins with salivary protein and oral mucosa, and (iii) gut irritation and systemic toxicity.

The Mediterranean spring green vegetation has a high protein content (>14%) and high in vitro and in vivo (Cattle, sheep) digestibility (70–80%). Unlike sheep and cattle which abundant grazing on leafy material during spring, browse constitutes at least 50% of the forage selected by goats (Kakabya, 1994; Kababya et al., 1998; Lu, 1988; Mill, 1990). Goats grazing desert pasture in northern Mexico maintained even higher (80%) proportion of browse all year around (Mellado et al., 1991). Such a non-opportunistic behaviour appears strange at first sight, particularly if considering that goats are characterised as opportunistic with regard to their feeding behaviour (Hofmann, 1989). 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 subspecies ruminantium that is capable of growing on tannic acid or condensed tannin as a sole energy source has been isolated from ruminal contents of feral goats browsing tannin-rich Acacia species (Skene and Brooker, 1995). Transferring these micro-organisms from feral goats to domestic goats and sheep fed tannin-rich foilage (Acacia aneura) increased feed intake and nitrogen retention in inoculated animals compared with uninoculated ones. Inoculation also improved N digestibility and reduced the rate of live weight loss in sheep and domestic goats (Miller, Brooker and Blackall, 1995). In accordance, in Table 3, it is shown that acclimatization of the microbial system in the rumen of goats adapted to the Mediterranean scrubland forms a very important element in the capacity of these goats to utilise efficiently high-tannin tree leaves (Table 3, from Gilboa, 1996). 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 the grazing habits can be lost during the time necessary to regain the capacity required for digesting high-tannin browse sources. It seems that although goats take advantage from the abundance of highly digestible grass (increasing its proportion from approximately 10% in winter to 40–50% in spring), they maintain the intake of browse sufficiently high to preserve their acclimatization to tannin-rich food. This maintains their specific advantage in digesting the food that is available to them in large amounts all the year around.

9.3. Adaptation to drought conditions

Whenever drought occurs the animals that suffer least are ruminant browsers like goats and camels, and non–ruminants like zebras and donkeys (Kay, 1997). This may be related to their capacity to survive on diet composed mostly of browse, which is least affected by the drought. If the drought persist, the herbivore biomass that the pasture can sustain will inevitably fall; however, it will support goats longer than other herbivores because of their ability to reduce metabolism. Cattle must frequently return to water and their grazing radius shrinks in the dry season (Silanikove, 1994; Kay, 1997). Consequently pasture near the settlements and watering points deteriorates while more distant grazing are under-used. On the other hand, the ability of goats to survive prolong periods of water deprivation allows them to graze far from the watering site and to exploit desert pasture evenly and efficiently. As a result, cattle are much more susceptible than goats to malnutrition, disease and death during severe droughts.

Table 3
Demonstration (based on % in situ organic matter degradation[a] of food samples in the rumen) that acclimatization is an important feature in the capacity of goats adapted to Mediterranean scrublands to exploit tannin-rich browse

Samples source[b]	Non-acclimatized	Acclimatized[b]	Significance
Ceratonia siliqua leaves	46.7	54.5	$P < 0.01$
Pistacia lentiscus leaves	40.9	50.2	$P < 0.01$

[a] Degradation of samples incubated for 36 h in the rumen of acclimatized and non-acclimatized goats.

[b] Acclimatized animals consumed the leaves under investigation as the sole feed + 10 g/day of polyethylene glycol (to maintain sufficient intake of leaves and steady body weight, Silanikove et al., 1996) for 30 days prior to measurements, whereas non-acclimatized animals consumed a diet composed of wheat hay for ad lib + 200 g of concentrate at the same time (16% crude protein); 4 goats per treatment.

9.4. Concluding remarks

Goats in the tropics, when possible, eat diets composed of tree-leaves and shrubs (browse), which ensure a reliable and steady supply of food all year around, albeit, a low to medium quality food. This grazing strategy in combination with the anatomical and physiological adaptations described in this review makes goats the most efficient desert-dwelling species among domestic ruminants. The most remarkable feature of the intermediate selector ruminant is characterised by short-term or seasonal anatomical acclimatizations to changes in forage quality (Hofmann, 1989). The corresponding morphophysiological adaptations are: (i) larger salivary glands, (ii) higher surface area of absorptive mucosa than in grass and roughage eaters, and (iii) a capacity to increase substantially the volume of the foregut when fed high-fibrous food. The results discussed in this review suggest that the general characteristics of intermediate feeders are probably important for the development of superior digestion and nitrogen conservation capacities and for the efficient use of water in goats.

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