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SUMMARY - Goats indigenous to tropical and subtropical environments generally performed better than other ruminants in terms of survival, reproduction and expression of their genetic potential for growth and milk yield. These advantages are emphasized in case of successive years of drought, a typical event in the dry belts of the subtropics. Low body weight (BW) and low metabolic rates per $BW^{0.75}$ allow desert goats to maintain a frugal energy and water economy. Some of the desert breeds, such as the Bedouin goats, are able to reduce their energy requirements by as much as 65% in response to reduction in feed availability. The digestibility of dry matter and structural carbohydrates found in some breeds of desert goats fed on highly-lignified diets exceeds considerably that observed in non-desert goats and other domesticated ruminants. The capacity of goats to consume high-tannin browse and to detoxify the tannin is higher than that found in sheep and cattle under comparable conditions. These advantages are probably related to the ability of goats to control effectively their rumen environment. Maintaining a spacious rumen allows a longer retention time of feed particles without negatively affecting feed intake. In addition, maintaining a steady pH in the rumen, and efficient recycling of key nutrients such as nitrogen and sulfur, enable goats to maintain a maximal ruminal fermentation rate at given conditions. In Mediterranean areas, goats exhibit a preference for browse even when plenty of green grass is available during spring. This behaviour is justified on the long run because plenty of browse is available all year around. Adaptation to high-tannin feed is a long-time process that allows goats to benefit from a steady supply of forage.

Key words: Animal performance, harsh environment, goats, review.

RESUME - *"Pourquoi les caprins élevés en milieu difficile ont de meilleures performances que d'autres animaux domestiques". Les caprins autochtones des environnements tropicaux et subtropicaux ont généralement de meilleures performances que d'autres ruminants en termes de survie, reproduction et expression de leur potentiel génétique pour la croissance et le rendement laitier. Ces avantages sont accentués dans le cas d'années successives de sécheresse, un événement typique dans les ceintures sèches subtropicales. Un faible poids corporel et des taux métaboliques faibles par poids corporel*^{0,75} *permettent aux caprins du désert de maintenir une économie frugale de l'énergie et de l'eau. Certaines des races du désert, comme les caprins des Bédouins, sont capables de réduire leurs besoins en énergie de jusqu'à 65% en réponse à la réduction des disponibilités en aliment. La digestibilité de la matière sèche et des hydrates de carbone structurels que l'on rencontre chez certaines races caprines du désert recevant des régimes hautement lignifiés, dépasse considérablement ce que l'on observe chez les caprins n'appartenant pas au désert et autres ruminants domestiques. La capacité des caprins de brouter des arbustes riches en tannins et de les détoxifier est bien plus grande que chez les ovins et bovins sous des conditions comparables. Ces avantages sont probablement liés à l'aptitude des caprins de contrôler effectivement leur environnement ruminal. Le fait d'entretenir un rumen spatieux permet un temps de rétention plus long des particules alimentaires sans affecter négativement l'ingestion alimentaire. En outre, le fait de maintenir un pH régulier dans le rumen, ainsi qu'un recyclage efficace des nutriments fondamentaux tels que l'azote et le soufre, permet aux caprins de maintenir un taux maximum de fermentation ruminale sous certaines conditions. Dans les zones méditerranéennes, les caprins montrent une préférence pour le broutage même si une herbe verte abondante est disponible pendant le printemps. Ce comportement est justifié à long terme car il y a abondance d'arbustes à brouter pendant toute l'année. L'adaptation à une alimentation riche en tannins est un processus de longue haleine qui permet aux caprins de bénéficier d'un approvisionnement régulier de fourrage.*

Mots-clés : *Performances animales, environnement difficile, caprins, révision.*

Introduction

Under desert and tropical environments, where feed resources are restricted in quantity and limited in quality, differences among ruminants in energy requirements and digestive efficiency, which are reflected in the efficiency in the overall use of energy for production, form a very important criterion for the selection of the most appropriate type to be bred in particular circumstances (Devendra, 1990). The vast majority of the world's grazing land is found in areas with seasonal environments that are characterized by marked fluctuations in resource abundance. Among the most dynamic, climatically, 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, where they support 50-60% of the livestock and 40% of the people. In the arid zone proper, goats are relatively much more numerous than cattle, and frequently more numerous than sheep, whereas cattle is more numerous than sheep and goats in semi-arid, sub-humid, humid, and highlands regions.

The abundance of goats in the harsher environment of the arid areas of the world most likely reflects a better adaptation of this species to such environments. Goats suffer the least during sequence of successive years of drought, which occur from time to time in the dry belts of the tropics, causing ecological catastrophes for livestock and the human populations that depend on them.

The purpose of the present review is to provide an integrative explanation for the ability of goats to survive and produce better than other ruminants in harsh environments.

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

Bergmann's rule (1847) is probably the best known rule 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 generalization, describing a correlation between morphological variation and ambient temperature (Mayr, 1970). Correlations between size changes in fossil mammals from various parts of the world and 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 dissipators in warm climates, while small body surface area may help in heat conservation in cold climates (Searcy, 1980). Other scientists suggested that body size is better correlated with primary plant productivity (Rozenzweig, 1968), desiccation (James, 1970), and type and quality of food (McNab, 1971; Calder, 1984), than with temperature. However, body size may be determined by a combination of all these factors which in desert areas 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 this (Epstein, 1971): natural selection, artificial selection, and inbreeding. Natural 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 in the size of the stock through the slightly higher survival and reproduction rates of small animals. Selection pressure toward a smaller size also explains the simultaneous wide spread of dwarfism in domestic ruminants occupying the same niche (*autochthonous* development) in harsh environments (Epstein, 1971). In accordance with Begmann's rule, even non-dwarfed breeds of goats, sheep and cattle in the desert and savanna areas of Africa are in most cases much smaller than their typical counterparts among European breeds (Epstein, 1971).

Low metabolic requirements

The classical concept of Kleiber (1961) that the energy requirements of a mammal is a simple function of 'body mass'$^{0.75}$ imply that the energy requirement per kg weight of body tissue in small mammals is relatively greater than that in large mammals (Table 1). The enhanced metabolic requirements of a small ruminant cannot be met by diets rich in cellulosic matter, because anaerobic fermentation is a relatively slow process and is bioenergetically less efficient than other forms of digestion (van Soest, 1982). Small ruminants, therefore, have to balance their relatively 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 such as the suni and the dik dik, is indeed composed of highly-digestible soft dicot leaves, fruits and flowers (Hofmann, 1989). However, small desert breeds like the black Bedouin goat have been found to be the most efficient utilizers of high-fiber, low-quality food, 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 does not explain 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 predicted from their mass, and in comparison with that of their relatives from non-desert areas (Table 1). As demonstrated in Table 1, the energy requirement of five desert goats, each weighing 20 kg, is the same as that of one goat of European breed weighing 100 kg. The ability to maintain a larger number of animals on the same area demonstrates an obvious advantage, in term of survival, for the desert goats.

Table 1. Lower metabolic requirement of desert goats in comparison with non-desert goats as a solution for the contradiction between Bergmann's rule (stating that animals in warm climates tend to be smaller than relatives in a temperate environment) and Demment and van Soest's concept (that small size ruminants have high metabolic requirement which cannot be satisfied by high-fibre, low-quality forage) in the light of the fact that the forage in desert areas is mostly of low quality

	European goat	Non-desert goats	Desert goat
Number	1	5	5
Weight[†] (kg)	100	20	20
Total weight (kg)	100	100	100
Requirement per metabolic weight[††] (kJ)	657	657	418
Metabolic weight ($W^{0.75}$)	31.6	9.45	9.45
Total requirements (kJ)	20761	31043	19750

[†]The weight of big goat of European breed (Saanen, Alpine, Anglo-Nubian), and of dwarf goats
[††]According to Silanikove (1986a)

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 in non-desert Saanen goats this ability is restricted to a level not more than 20-30% below their voluntary intake of high-quality roughage, the Bedouin goats were able to maintain body weight 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 from the interspecies relationship (Silanikove, 1987). A similar capacity to adjust to low energy intakes by reducing the energy metabolism has been found also in other desert herbivores, such as zebu cattle and the llama, which are annually exposed to severe nutritional conditions for long periods in their natural habitats (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 findings of Burrin *et al.* (1990) suggest that the level of feed intake changes the proportion of visceral organs relative to body mass. Furthermore, the contribution of visceral organs to the whole-body metabolic rate appears to be primarily a function of differences in organ size rather than of tissue-specific metabolic activity. In addition, evidence from several studies of Bedouin goats suggests 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 Nienabr (1990) suggested that food supply altered the partitioning of metabolizable energy, and that these changes are related to redistribution of blood flow.

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 are optimal under forage conditions in which their adaptive abilities can best be expressed. Grass and roughage eaters are considered to be the most efficient utilizers of lignocellulosic material. Concentrate selectors are the least efficient users of lignocellulosics, and they base their diet on selection of low-fibre high-quality forage. The capacity of intermediate selectors to digest lignocellulosic material is intermediate between those of the two extreme groups. Domestic goats are a classic example of an intermediate feeder, with a strong preference for browse feeding (Hofmann, 1989).

There are two opposite views regarding the ability of goats to digeste lignocellulosic material efficiently:

(i) Goats are not true utilizers of cellulosic matter and their success in tropical areas relates to their ability to exploit forages which have differentiated leaves of less lignified material, and stems (van Soest, 1982; Demment and van Soest, 1985). Accordingly, goats have smaller gut in proportion to body weight than other ruminants, resulting in rapid movement of digesta from the rumen and along the entire gastro-intestinal tract.

(ii) With high-fiber, low-quality forages, goats have better digestive efficiency than other ruminants, one of the main reason for this being their 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 with evaluation of the quality of the diet available to goats under free-ranging conditions might provide a resolution of this contradiction. 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 lignin content, ana a moderate to low protein content (see Ramirez, 1996 for a review). In addition, the forage available to goats frequently contains secondary metabolites, such as tannins, which further constrain food utilization (Lu, 1988; Mill, 1990; Kababya, 1994). This situation is 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 high-fibre low-quality, food more efficiently than other types of indigenous ruminants, or exotic breeds of goats (Tisserand *et al.*, 1991; Silanikove *et al.*, 1993).

The most remarkable feature of the intermediate selector ruminants is their short-term or seasonal anatomical adaptations to changes in forage quality (Hofmann, 1989). The corresponding morphophysiological adaptations are: (i) larger salivary glands, which ensure a higher capacity to secrete serosal buffered parotid saliva than that of grass and roughage eaters and (ii) a higher surface area of absorptive mucosa than is found in grass and roughage eaters. The result reviewed below suggest that these general characteristic of intermediate feeders are probably important for the development of the superior digestion capacity in goats.

Efficiency of utilization of high-fibre forage

The digestive physiology of the desert black Bedouin goat fed on roughage diets was investigated under controlled environmental conditions, in comparison with that of the temperate Swiss Saanen goats (Silanikove *et al.*, 1980, 1993; Silanikove, 1986a,b), under conditions in which these goats were exposed to the full impact of their natural environment: heat load and infrequent water replenishment (Brosh *et al.*, 1986a,b, 1988; Silanikove and Brosh, 1989). Digestion by the desert goats was superior even when good quality hay (alfalfa) was provided, and this 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 digestibility of dry matter (53-55%) and of structural carbohydrates found in Bedouin goats fed wheat straw (approximately 60% in hydrated animals and 70% in goats given water once every 4 days) 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 the digestibility of structural carbohydrates, while lignin itself is considered to be 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 with lignin and render them more susceptible to microbial degradation. In addition, formation and release of ligno-hemicellulose complexes in the water-soluble form would expose them to the influence of extracellular hemicellulases. Finally, the removal of hemicellulose and lignin may cause larger pores to be produced in the cell wall, thereby rendering the remaining structural carbohydrates more accessible to cellulose which has a rather large molecule size (Silanikove and Brosh, 1989).

Voluntary feed intake in the desert-adapted Bedouin goats was less affected by a high-fibre diet and consequently the differences between the breeds in digestible energy intake were even larger than the differences in digestibility (Silanikove, 1986a). The main advantage of the Bedouin goats over the Saanen in digesting medium-quality roughage may relate to their ability to maintain a higher microbial density on the particulate matter, and, therefore, a higher total ruminal fermentation rate and higher volatile fatty acids formation rate (Silanikove, 1986b; Silanikove *et al.*, 1993). The Bedouin goats' ability to sustain higher microbial density on the particulate matter in the rumen was related to their superior urea recycling capacity (Silanikove *et al.*, 1980; Maltz *et al.*, 1981; 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, the 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 longer (41 *vs* 32 h) in the Bedouin goats than in the Saanen goats. Thus, the combination of a higher fermentation rate and a longer passage time allows a maximizing of feed intake and digestibility in comparison with less efficient non-desert goats (Silanikove, 1986b; Silanikove *et al.*, 1993).

In the natural environment of the Bedouin goats, water sites are widely scattered and the herbage is extremely meagre and mostly of low quality. Scattered thorny acacia trees 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 every 2 days is very common and 4 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 may be concluded that the digestive capacity of the Bedouin goats enables them to utilize the high-fiber, low-nitrogen desert pastures efficiently and thus to produce in extremely arid areas. This capacity stand in sharp contrast to predictions based on their size (Demment and van Soest, 1985) and to the views of Huston (1978); Brown and Johnson (1985); van Soest (1982) and Hofmann (1989) regarding the digestive characteristics of goats.

A key question that should be ask is: Are Bedouin goats outstanding in regard to the digestive characteristics of the 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 proposed in the present review is that the Bedouin goats most likely represent a climax of evolutionary adaptation of goats to achieve efficient digestion of 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 to be superior to other ruminants, the digestive physiological basis was the same; that, goats had 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 the blood to the rumen (Devendra, 1990; Tisserand *et al.*, 1991). The greater secretion of saliva by goats than by sheep (Seth *et al.,* 1976; Dominigue *et al.,* 1991), and the larger surface area for absorption from the rumen (resulting from broad leaf-like papillae compared with narrow tongue-like papillae in sheep, Battacharya, 1980) is a general characteristic of intermediate feeders such as goats, in comparison with grass eaters, such as sheep. These characteristic may explain: (i) the more efficient recycling of urea to the rumen walls, because urea recycling is mediated via saliva secretion and via diffusion through the rumen walls and (ii) the prevention of a fall in rumen pH even at peak fermentation, because: salivary flow is the major contribution to rumen buffer capacity, and efficient absorption of volatile fatty acids through the rumen wall enhances the buffer capacity of the rumen (Silanikove *et al.,* 1993). The capacity to maintain a spacious rumen helps the Bedouin goats to remain unaffected by a reduction in the quality of their diet

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

Food intake and efficiency of utilization of high-tannin browse sources

Fodder trees, fodder shrubs and herbaceous species are very important source of food for livestock, particularly in desert and semi-desert areas (Devendra, 1990; Topps, 1992). Most browse species are *dicotyledons* that contain large amounts (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 tracts of mammals and birds. The negative effects of tannins on palatability and digestibility in ruminants are multi factorial (Kumar and Vaithiyanathan, 1990), the main effects being: (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.

Goats, the principal ruminant in many scrublands surrounding the Mediterranean Basin, are present in large numbers in Greece, southern France (Provence) and Spain, and are parts of extensive traditional grazing systems in many other countries such as Morocco, Tunisia, Israel, Jordan and Lebanon. Goats indigenous to woody areas are able to consume food from browse sources much richer in tannin than sheep can eat, and to digest it much more efficiently (Wilson, 1977; Kumar and Vaithiyanathan, 1990; Silanikove *et al.*, 1996a,b). The capacity of goats to browse species not consumed by sheep has been utilized in many cases and in many parts of the world to open dense bush and to control noxious weeds. The advantage of the goat over other ruminants' in consuming tannin-rich plants relates to its superior capacity to neutralize the negative effect of tannins on palatability and digestibility (Silanikove *et al.*, 1986a,b). The physiological basis for this capacity include a salivary defence mechanism (Silanikove *et al.*, 1996a,b). However, the major mechanism to detoxify tannins appears to be depended upon ruminal microbial degradation of phenolic compounds (Silanikove *et al.*, 1996b for a more detailed discussion; (Table 2). Because lignin and tannins are both complex phenolic compounds, there is an analogy between the abilities of goats to deal effectively with lignin and with tannins.

Table 2. Demonstration (based on % *in situ* organic matter degradation of food samples in the rumen) that adaptation is an important factor in the capacity of goats to exploit tannin-rich browse[†]

	Non-adapted	Adapted[††]	Significance
Ceratonia siliqua leaves	46.7	54.5	0.01
Pistacia lentiscus leaves	40.9	50.2	0.01

[†]Degradation of samples incubated for 36 h in the rumen of adapted and non-adapted goats
[††]Adapted 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 measurement, whereas non-adapted animals consumed a diet composed of wheat hay for *ad libitum* + 200 g of concentrate (16% crude protein); four goats per treatment (Gilboa, 1996)

Grazing behaviour of goats on scrublands

The ability of goats to stand on their rear legs, to move their upper lip, and to cover vast grazing areas allows them to attain a more versatile and efficient grazing behaviour than with sheep or cattle (see Lu, 1988; Mill, 1990; Kababya, 1994; Nastis, 1996 for reviews). A unique element in goats' grazing behaviour, which is considered below, is the maintenance of a high proportion of browse in their diet even when herbaceous spring herbage is available.

The Mediterranean spring green vegetation has a high protein content (>14%) and high digestibility (70 to 80%). Unlike sheep and cattle which do not eat leafy material during the spring, browse constitutes at least 50% of the forage selected by goats in the Mediterranean and other grazing areas (Lu, 1988; Mill, 1990; Kababya, 1994; Nastis, 1996). Such non-opportunistic behaviour appears strange at first sight, particularly when it considered that goats are characterized as opportunistic in regards to their feeding behaviour (Hofmann, 1989). Adaptation of the microbial system in the rumen forms a very important element in the capacity of goats to utilize high-tannin tree efficiently leaves (Table 2). Spring in the Mediterranean is very short, and after three months the nutritional quality of the grass diminishes at an accelerating rate. Thus, much of the short-term advantage gained from switching the grazing habits can be lost in regaining the adaptation required for digesting food from high-tannin browse sources. It seems that, although goats take advantage of the abundance of highly digestible grass (e.g., increasing its proportion in their diet from approximately 10% in the winter to 40-50% in the spring in Israel), they maintain intake of browse sufficient to preserve their adaptation to tannin-rich food. This maintains their specific advantage in digesting the food that is available to them in large amounts all year around.

Conclusions

Goats living in harsh environments represent a climax in the capacity of domestic ruminants to adjust to such areas. This ability is multi factorial. Low body mass and low metabolic requirements of goats can be regarded as important assets to them for they minimize their maintenance and water requirements, in areas where water sources are widely and sparsely scattered and food sources are limited in their quantity and quality. An ability to reduce metabolism allows goats to survive even after a prolonged period of severely limited food availability. Skilful grazing behaviour and efficient digestive system enable goats to attain maximal food intake and maximal food utilization under any a given conditions. Some of the physiological features of ruminants defined as intermediate feeders, such as large salivary gland, a large absorptive area of their rumen epithelium, and a capacity to change the volume of the foregut rapidly in response to environmental changes, are most likely responsible for the goat's superior digestion capacity.

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