Mat|ère
à débattre & décider

Livestock grazing systems and sustainable development in the Mediterranean and Tropical areas

Recent knowledge on their strenghts and weaknesses

Alexandre Ickowicz and Charles-Henri Moulin, editors

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Livestock robustness: physiological and behavioural levers of adaptation

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In Mediterranean and Tropical livestock production systems, animals are faced with sometimes drastic variations in the availability of food resources, for example during more or less predictable and extended droughts, leading to episodes of thermal, water and nutritional stress. In such conditions, grass and more generally biomass production is limited, either temporarily or over a longer period. In order to survive, ruminants, who are dependent on this resource must adapt either directly (individual physiological adaptation) or indirectly (with adjustments of management practices). By individual physiological adaptation, we are referring to the overall beneficial regulation of the physiological processes implemented by an individual subjected to new conditions and which allow it to respond in a more or less effective manner (dynamic process). Among the range of physiological adaptations, one of the main levers is the ability to adjust feeding behaviour, based on the implementation of mechanisms related to food choice and intake as well as spatial mobility. In conditions of extreme shortage, to compensate for the consequent negative energy balance, another physiological compensation mechanism on which ruminants rely is the mobilisation and reconstitution of body reserves. In addition to body condition, other traits such as the animals' reproductive performance are negatively affected by such food and nutrient deficiency events. Underfed females adapt their behaviour by changing the nature and frequency of estrus and mating. The reproductive behaviour of males is indirectly affected via the attractivity of females. Understanding the complex cascade of these physiological mechanisms (either singly or in combination), at both individual and herd levels, is an integral part of efforts to make good use of them in an adaptation strategy for these farming systems at various levels of organisation.

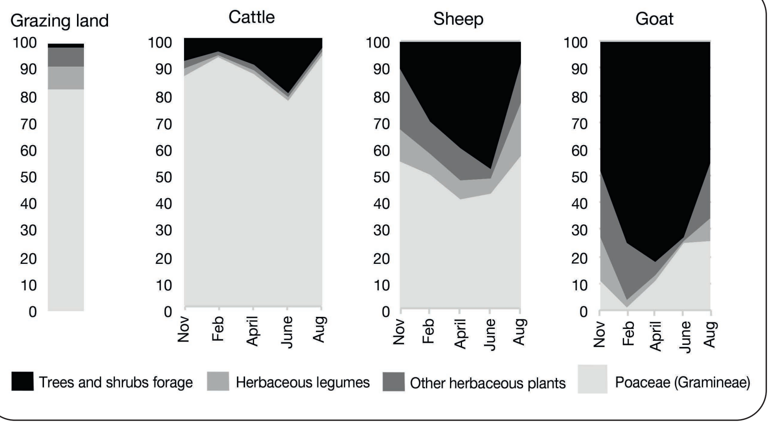
The feeding behaviour of grazing ruminants as an adaptation strategy

In grazing systems, the spatial and temporal variability of climatic conditions (mainly temperature and rainfall) results in a variable distribution of food resources for ruminants (quantity and quality of herbaceous and woody plant biomass). One of the primary adaptation levers for these livestock systems is the ability to adjust their feeding behaviour. This is based on three essential levers: food choice, food intake and mobility.

Selective feeding behaviour of ruminants on pasture

The selective feeding behaviour of ruminants is difficult to describe with precision, as these animals are freeranging, mobile and sometimes difficult to approach (Guérin *et al.*, 1988; Bonnet *et al.*, 2015). Studies show that it varies according to the ruminant species (Guérin *et al.*, 1988; Ickowicz, 1995) with a specific proportion of the diverse vegetation class contribution to the daily ration (figure 2.3).

Figure 2.3. Selective intake behaviour of three species of domestic ruminants (cattle, sheep, goats) on the same pasture in the Sahel depending on the season (in % of the botanical composition) (according to Guérin *et al.*, 1988; Ickowicz, 1995).



It should be noted that during the dry season or under conditions of low availability of herbaceous fodder, woody plants, in the form of leaves or fruit, can sometimes contribute even more to the diet, up to 50% of the biomass ingested by cattle for example, especially in the dry season (Ickowicz and Mbaye, 2001; Assouma *et al.*, 2018). These differences in selective ingestion behaviour of ruminants indicate complementarity between species that exert distinct grazing pressure on vegetation compartments and induce positive interactions for production at moderate grazing pressure. These differences advocate a mixed composition of herds, a regular practice in Mediterranean and Tropical arid zones (Guérin *et al.*, 1988). Consequently, the specific and adaptive behaviour of ruminants on grazing land is a significant lever for adapting to the spatial and temporal variability of resources on an intra- and interannual scale, but also over the longer term, for sustainable resource management. These mechanisms offer farmers the opportunity to adjust the specific composition of their herd in order to react to changes in climate and the environment while maintaining the productivity level of their herd by exploiting all plant diversity.

Adaptation of the ingestion capacity of ruminants

The ingestion capacity on rangeland (expressed in grams of plant dry matter intake per second, g DM/s) in part determines animal performance and is mainly a function of the animal species and its size (stature, bite or bite size), but also of the vegetation cover (Hodgson and Illius, 1996; Figure 2.4), and will be inversely proportional to the animal's speed of movement.

A recent study in a tropical environment (Chirat *et al.*, 2014) gives details on the model linking the ingestion capacity to the forage biomass available on the range (figure 2.5). We note here that below an availability of 1 tDM/ha, the animal is no longer able to compensate for the scarcity of resources by accelerating its forage intake, which exhausts the animal. Conversely, with offers above 3 tDM/ha, there is a reduction in the speed of ingestion linked to a vegetation structure that is too dense and bushy and often not very palatable. These interactions drastically reduce the daily intake capacity, especially in the dry season (Figure 2.6; Assouma *et al.*, 2018). Adapting to this dynamic may require the involvement of the farmer (or shepherd) for example by moving the grazing animal and offering a better density or quality of forage in order to avoid a drop in performance (Chirat *et al.*, 2014; Meuret, 2010).

Figure 2.4. Effect of available biomass (grass height in cm) on (A) bite weight (in mg) and on (B) intake rate (in bites/min) and (C) the resulting daily organic matter intake (kg OM ingested/day).

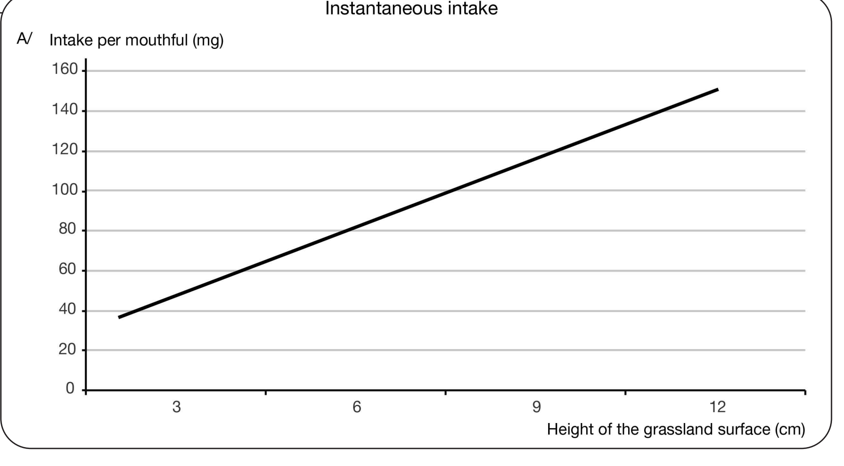
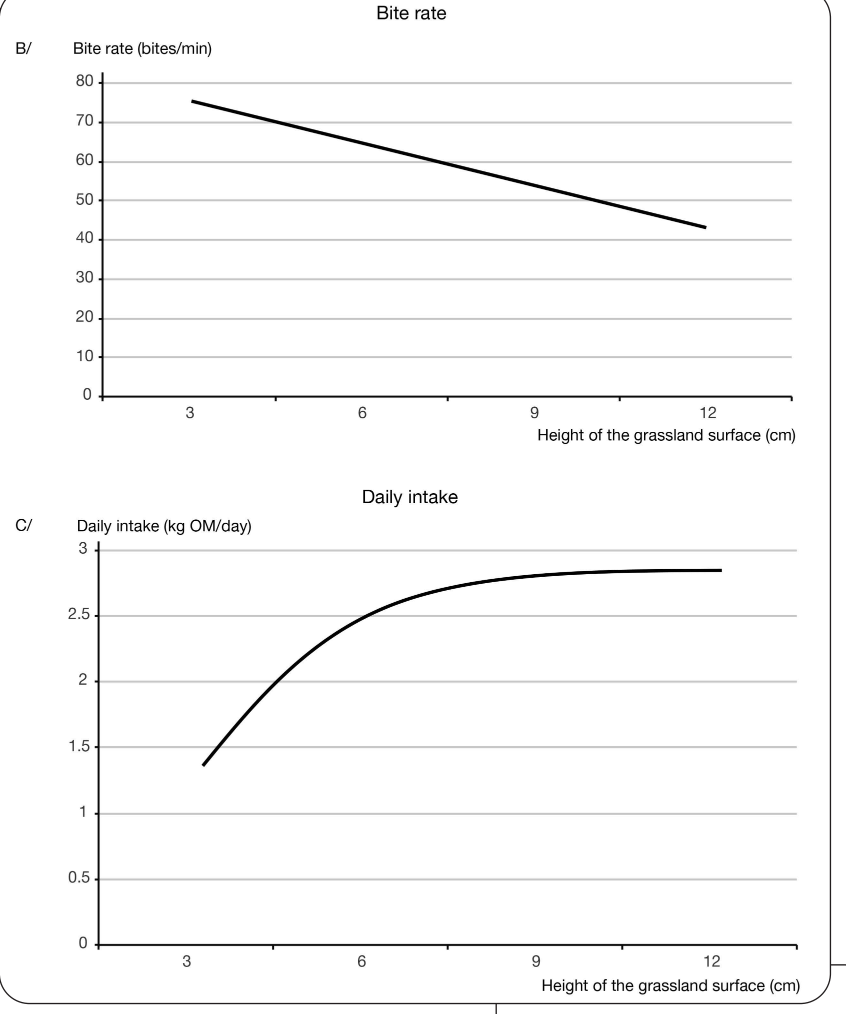
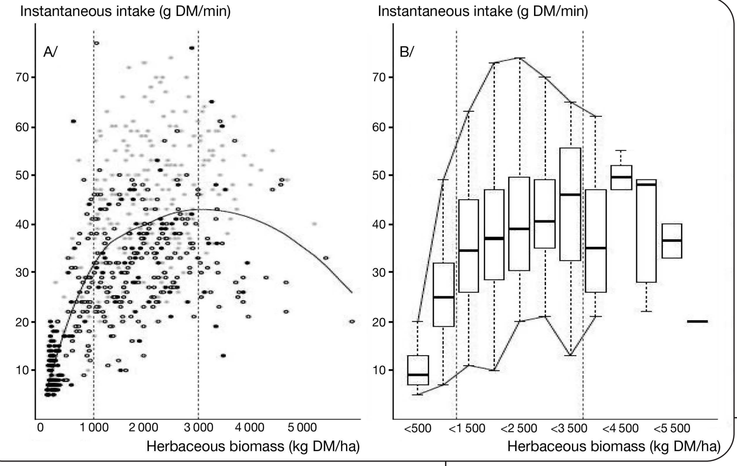


Figure 2.4. Next



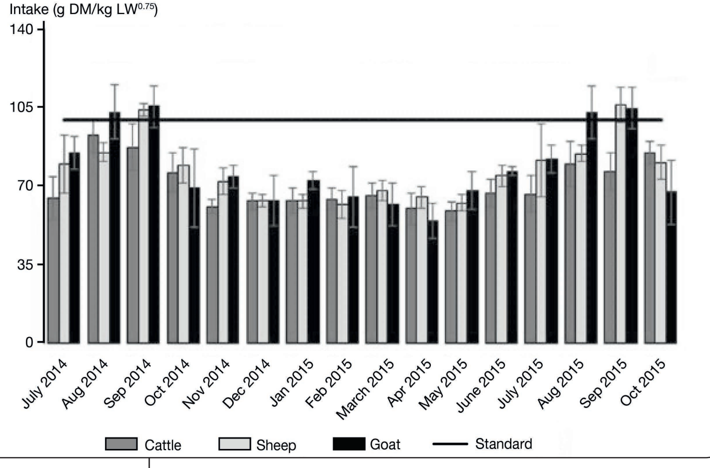
Adapted from Hodgson and Illius, 1996.

Figure 2.5. Adaptation of the ingestion capacity of ruminants on tropical rangelands (in g DM/min) as a function of the available plant biomass (in kg DM/ha). A. basic observed data and resulting intake curve. B. representation of observed means, standard deviations and extreme values for each biomass class.



Extracted from Chirat *et al.*, 2014.

Figure 2.6. Variations in daily intake of three ruminant species (bovine, ovine and caprine) (in g DM/kg metabolic weight) on rangeland in the Sahelian pastoral zone (Assouma *et al.*, 2018).



LW0.75: metabolic weight.
Significant reduction in the dry season when the availability of plant biomass is too low.

The role of mobility and the herder

The ingestion behaviour described above at the vegetation patch level can be significantly modified by the animal's mobility, with or without the intervention of a herder. The acceleration of food intake that the animal resorts to in order to compensate for the scarcity of fodder may be combined with an increase in the area of pasture prospection. The distances travelled lead to an increase in the energy expended in feeding, which may contribute to a decrease in performance. However, for adapted breeds, increased daily walking (within the distances reported) does not significantly increase weight loss due to lack of forage resources, but increases water requirements in situations where scarcity of water points may lead to animals having to drink every other day. The judicious intervention by the farmer in these situations is all the more essential as they know the space and the potential competition from other herds. For these two parameters, choice and ingestion capacity, the action of the farmer or the shepherd who accompanies the herd on the grazing land can be decisive in facilitating the organisation in time and space of food intake and ruminants getting used to new pastures (Meuret, 2010).

Body reserves as a characteristic trait in constrained conditions

The mobilisation-reconstitution dynamics of body reserves (BR) is an essential mechanism to compensate for all or part of the food and energy deficit incurred under stressful rearing conditions. This includes energy reserves stored in the form of lipids (adipose tissue) in subcutaneous regions or combined with internal organs. BRs are an essential asset especially for females that are accustomed to using them in late gestation and during early lactation to support milk production levels that induce adverse energy balances when their feed intake capacity is not at its maximum. These BRs are also mobilised when animals must compensate for energy deficits resulting from the time-varying quantity and quality of the grazing resource, as described above.

It is this component and its mobilisation-reconstitution processes that are studied in specific observed or induced situations using the breeding ewe as a model. The objective is to identify and understand the determinants that favour the functions related to the survival of the individual in short or longer periods after the disturbances undergone in conditions of undernourishment in Mediterranean and Tropical environments. The aim is to work on individual and collective scales (the herd), through the study of functional groups (e.g. according to physiological stages) and throughout the career. The phenotyping of individuals, in a dynamic perspective, is consistent with a detailed consideration of genotype × environment interactions, in time and space, and a hierarchical approach of adaptation processes. Finally, this approach enables the design of alternative feeding strategies while proceeding with genetic improvement of individual capacities identified as advantageous.

In combination with live weight (LW) and body condition score (BCS) monitoring, we use a set of plasma metabolites and hormones to characterise metabolic status involved in the adaptive mechanisms to negative energy balances. Studies of the robustness of ewes have been conducted in contrasting conditions at the INRAE experimental area of La Fage (Causse du Larzac, 800 m in altitude).

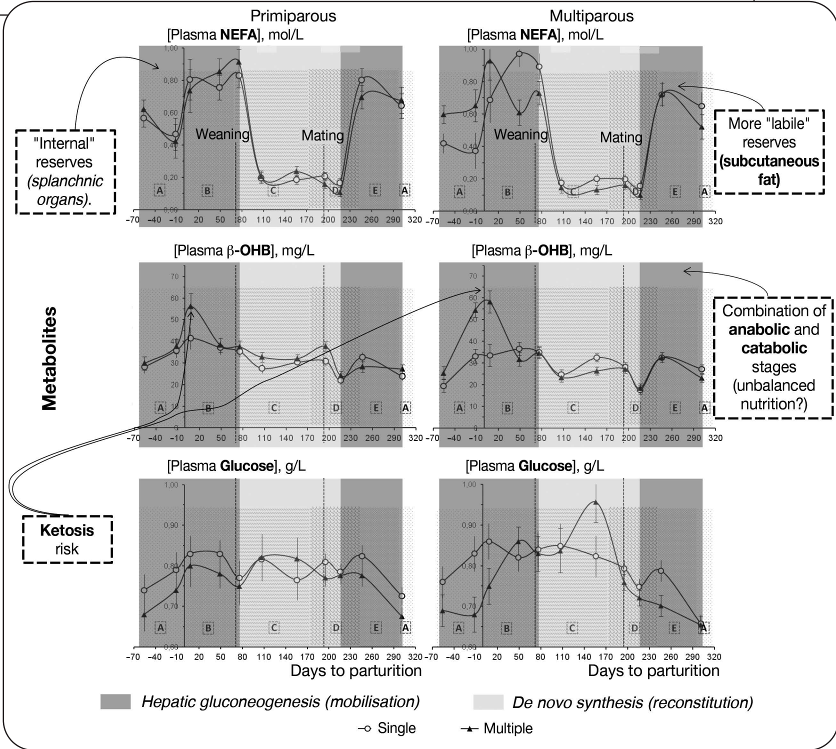
To illustrate, we monitored a batch of lactating Lacaune breed dairy ewes over several weeks with differing energy balances according to milking rhythm (standard or mono-milking) while voluntary intake (free choice offer with identical ingredients and rationing) remained unchanged (González-García *et al.*, 2015; Hassoun *et al.*, 2016). We also monitored suckling ewes of the Romane breed on rangeland for several months (González-García *et al.*, 2014). For each protocol, we monitored the trajectory of quantifiable biological parameters over the course of a full physiological year, such as LW, BCS and the concentration of plasma metabolites and hormones related to the mobilisation-reconstitution processes of BRs. The multiplicity of the chosen indicators enables understanding the diversity and complexity of the mechanisms and biological components inherent to adaptation to negative energy balance.

Our approach consists in subjecting the various genotypes to situations beyond the standards usually associated with the classical progression of successive physiological stages. In the case of dairy ewes, the experiment consisted in modifying the milking frequency (Once a day milking vs. Twice a day milking) in order to affect the energy request ("pull effect") related to milk production. For Romane ewes, the energy constraint was based on the combination of litter size (more energy demand in ewes with multiple litters compared to those with single litters) with the age of the female (priority or not to growth in primiparous or multiparous). These constraints were associated with a specific diet, representative of seasonal variations in rangeland forage and successive feeding regimes. The concentrations of metabolites and hormones then reflect the dynamics of metabolic energy flow in these conditions (figure 2.7).

Clear effects of parity, litter size, passage through a sequence of physiological states on metabolic profiles and milking frequency in the Lacaune breed and changes in biomass availability on the range in the Romane ewe were demonstrated. The combination of experimental factors taken into account reveals differences due to the age of the ewe (related to parity) and in the distribution of nutrients according to the biological priority at a given time (trade-offs or compromise). As a result, the changes observed during the post-weaning period are quite marginal when compared to the readjustments that occur at farrowing and up to weaning to compensate for the negative energy balance during this period.

Over and above the understanding of the mechanisms and dynamic processes implicitly mobilised during negative energy balance, all parameters evaluated enable us to detect sensitive and critical periods during an annual productive cycle for the two breeds in question in their rearing conditions. In this way, we have identified critical physiological states that are generally underestimated during early and mid-gestation, periods during which

Figure 2.7. Body reserve dynamics of Romane ewes (young or adult, with one or more lambs), raised in the open air on the La Fage range during a production year.



The graph illustrates two distinct phases of mobilisation (around farrowing and during gestation, as of the first month) and reconstitution of body reserves (from weaning to early gestation). Phenotyping of the metabolic profile of plasma non-esterified fatty acids (NEFA), ketone bodies (β-OHB), and plasma glucose provides an account of the energy balance of females.
The capital letters in the boxes represent the feeding regime of the farm: A, preserved feed (silage and hay) from the end of gestation up to calving; B, fertilized pasture and native rangeland during the lactation phase in spring; C, native rangeland grazing during drying off in the summer; D, native rangeland grazing during drying off in the autumn; E, cultivated grassland grazing (regrowth) during early and mid-gestation.

nutritional management could be improved. We have demonstrated the applicability of long-term studies on efficiency in the processes of mobilisation and replenishment of BR in ruminants. It is a component with a direct impact on the overall resilience of the herd under conditions where fluctuation in feed quantity and quality is one of the main constraints. A similar characterization of BR dynamics has been conducted with Arles Merino ewes subjected to varying energy balances (González-García *et al.*, 2020a).

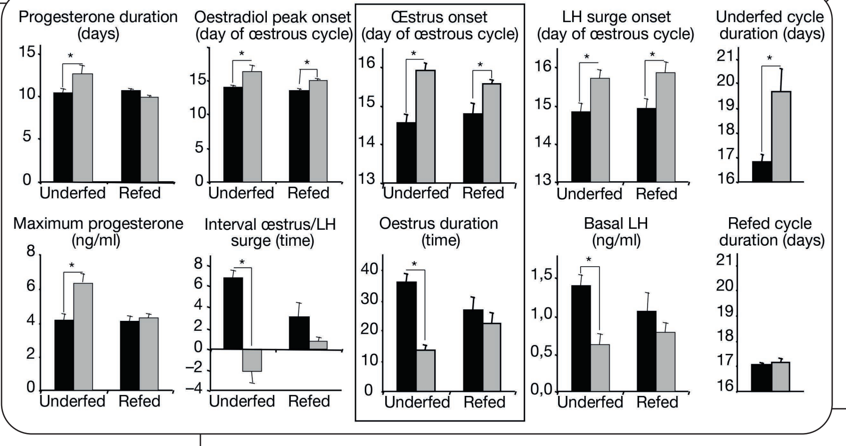
To understand the relationship between female growth rate and age at first breeding (early, 7 months vs. late, 19 months), a study with historical data from 1,359 females from the La Fage Romane herd born between 2002 and 2012 highlighted the effects of such a decision (early or late breeding) on the subsequent productive life of the female and the behaviour of her offspring (González-García and Hazard, 2016).

The adaptation of ovine reproductive behaviour in response to dietary constraints

By using sheep in a Mediterranean context as animal models, we focused on the behavioural adaptation of both females and males to ensure successful reproduction in situations of food constraint.

We assessed the static and dynamic effect of nutrition on the sexual behaviour and on the hormones of the estrous cycle of Merino d'Arles ewes. We demonstrated (Debus *et al.*, 2005; Blanc *et al.*, 2004) that a 50-day feed restriction (40% vs. 100% of energy maintenance requirements): 1) delays the time of estrus onset by 1.5 days and reduces the duration of estrus by almost 3 times, 2) increases plasma progesterone levels and delays their return to baseline, 3) delays the onset of the estradiol peak, 4) decreases luteinizing hormone (LH) baselines and delays the onset of its preovulatory peak, 5) greatly reduces the interval between the onset of estrus and the onset of the preovulatory LH peak, 6) extends the duration of the estrous cycle by 3 days (Figure 2.8).

Figure 2.8. Mean values ± standard error of the mean (n = 9) of 9 endocrine or behavioural reproductive parameters in restricted (grey bars) or well-fed (black bars) ewes.

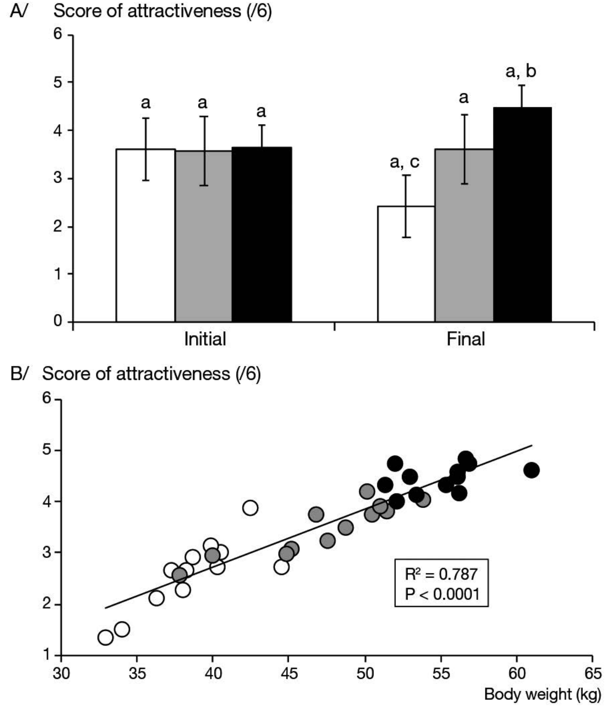


Underfed: Food restriction phase 100% or 40% of energy maintenance requierements. Refed: re-feeding phase. Statistically significant differences (Mann-Whitney U test) between batches are indicated by an asterisk (p < 0.05).

However, all ewes ovulated and exhibited cyclic variations in progesterone levels. Follicle stimulating hormone (FSH) secretions and ovulation rate were also unaffected by the feed restriction. Following this period of restriction, a re-feeding of 17 days was sufficient to restore parameters similar to those of control animals.

In the case of males, we observed the behaviour of 6 rams in relation to 36 Merino d'Arles ewes (12 ewes per batch) fed for 3 months with contrasting diets covering between 68 and 180% of maintenance requirements. We measured the attractiveness of the ewes to each male. After 3 months, we observed that ewe attractiveness was positively related to changes in body weight (Figure 2.9). Rams have a good

Figure 2.9. A. Mean attractiveness scores of ewes (white bars: batch with 68% of maintenance requirements; grey bars: batch with 113% of requirements; black bars: batch with 180% of requirements) before and after 3 months on a differentiated diet. B. prediction of the attractiveness score of Arles Merino ewes according to their live body weight. Attractiveness score measured with the Ovimate device (figure 4.4).



Bars with differing letters are statistically different ($p < 0.05$).

perception of the nutritional status of ewes and prefer ewes in good body condition to lean ewes. Moreover, they can discriminate ewes within a flock based on their body weight (Alhamada *et al.*, 2017b).

We demonstrate for the first time, the behavioural origin of the subfertility observed in undernourished ewes: the rams do not primarily seek lean ewes that are responsive for a shorter time than ewes in good condition. Underfed ewes with insufficient body reserves are therefore less likely to be mated. This means that they can replenish their body reserves and focus on survival rather than on completing a difficult pregnancy. This sub-fertility can be quickly overcome by re-feeding the animals. Our study demonstrates that ewes adapt individually to nutritional hazards in order to preserve their integrity and that at the flock level, male × female interactions favour the most productive females. From a practical point of view, these results indicate that a different breeding management is required (male/female ratio, batch management, *flushing*, etc.) depending on the nutritional status of the animals.

Genetic diversity and adaptation of local breeds to their breeding environment

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The use of animal genetic diversity is one of the main levers to be considered so as to improve the adaptation of livestock systems to the major current changes. Among domestic ruminants, there is a high intraspecific diversity, as illustrated by the high number of cattle breeds registered (more than 800) and classified as zebu (*Bos taurus indicus*), taurine (*Bos taurus taurus*) and zebu × taurine crossbreeds, or the more than 1,500 sheep breeds documented globally[4]. The main factors that have contributed to the generation of this diversity are domestication, the sometimes distant migration of ruminants from their domestication centers, and the different pressures of recent natural (such as exposure to new climatic conditions and pathogens, and the abundance or scarcity of food and water resources) and artificial selection (selection of animals by farmers based on morphological criteria, coat colouring, docility, or their performance, for example). Local hardy and heritage breeds, mainly considered in grazing systems, are the result of an evolutionary process that has determined their ability to live in a specific environment.

In order to conserve and make the best use of this genetic diversity within sustainable breeding systems, it is essential to characterise it well (for example at the population level or within the herd in relation to traits of interest such as feed efficiency or the dynamics of mobilisation-reconstitution of body reserves), to understand the demographic history of these breeds and to identify the genetic mechanisms underlying their

4. www.fao.org/dad-is/fr/