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Diversity in livestock resources in pastoral systems in Africa

B.A. Kaufmann*, M.A. Lelea & C.G. Hülsebusch

German Institute for Tropical and Subtropical Agriculture (DITSL), Steinstr. 19, 37213 Witzenhausen, Germany
*Corresponding author: b.kaufmann@ditsl.org

Summary

Pastoral systems are important producers and repositories of livestock diversity. Pastoralists use variability in their livestock resources to manage high levels of environmental variability in economically advantageous ways. In pastoral systems, human–animal–environment interactions are the basis of production and the key to higher productivity and efficiency. In other words, pastoralists manage a production system that exploits variability and keeps production costs low. When differentiating, characterising and evaluating pastoral breeds, this context-specific, functional dimension of diversity in livestock resources needs to be considered.

The interaction of animals with their environment is determined not only by morphological and physiological traits but also by experience and socially learned behaviour. This high proportion of non-genetic components determining the performance of livestock means that current models for analysing livestock diversity and performance, which are based on genetic inheritance, have limited ability to describe pastoral performance. There is a need for methodological innovations to evaluate pastoral breeds and animals, since comparisons based on performance 'under optimal conditions' are irrelevant within this production system. Such innovations must acknowledge that livestock or breed performance is governed by complex human–animal–environment interactions, and varies through time and space due to the mobile and seasonal nature of the pastoral system.

Pastoralists' breeding concepts and selection strategies seem to be geared towards improving their animals' capability to exploit variability, by – among other things – enhancing within-breed diversity. In-depth studies of these concepts and strategies could contribute considerably towards developing methodological innovations for the characterisation and evaluation of pastoral livestock resources.

Keywords

Animal – Breeding management – Characterisation – Contextual importance – Differentiation – Drylands – Environment interaction – Evaluation – Livestock resources – Local breeds – Molecular technologies – Pastoralism – Social–ecological system – Within-breed diversity.

Livestock resources in the context of pastoral systems in drylands

Contextual importance

Livestock resources in pastoral systems are usually referred to as 'local breeds', as opposed to 'exotic breeds'. A local breed can be defined as a livestock population which consists of animals whose affiliation to the breed has been determined by livestock keepers, rather than by formal actions taken by, for example, a breeding association or studbook (1). Referring to breeds as 'local' emphasises their contextual importance. As in 'local knowledge', it implies that the breed is important within a particular production system in a specific environment with its own climatic, ecological, economic, social and cultural conditions. While local breeds are important in their production systems of origin, where they were created by livestock breeders, they are mostly considered unimportant outside these systems.

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In contrast, the term 'exotic breed' is used to indicate that the breed originated far from the local area. It is commonly used for breeds that have been bred in, and for, input-intensive livestock systems and the livestock industry. These systems counteract the variability and heterogeneity of the natural environment by modifying and standardising the production environment, using external inputs at high capital and energy costs. They provide standardised feed rations, preventive veterinary treatments and shelter, so that animals can – as far as possible – express their full production potential. Livestock bred for such standardised production conditions have consequently become more homogeneous and uniform. If the required standardised production environment can be provided, these livestock resources can be kept in different regions, as the animals' interaction with the 'natural' environment is minimised.

Pastoral production systems and environmental conditions

Pastoral production systems produce by means of highly mobile exploitation of the resources in dryland areas. Drylands are largely considered unsuitable for alternative land uses, yet they contribute a considerable amount to national livestock sectors in many developing countries (2). The performance and output of a pastoral livestock system depend on how livestock keepers manage the relationship between their livestock and the environmental resources, so that the former transform the latter into a desired stream of goods and services. In recognition of the fact that pastoralists established this production system and continue to maintain it through their management, these systems are increasingly being regarded as social–ecological systems (e.g. 3, 4, 5, 6).

Pastoral livestock keepers have specialised in making use of the high temporal variability and spatial heterogeneity inherent to drylands (7, 8, 9). Natural dryland vegetation is usually sparse with low overall biomass yield and energy density per unit area. Vegetation growth and decay follows a pulsing rhythm of storage and release, typical of dryland systems (10). The land is very heterogeneous with regard to topographic, edaphic, ecological and climatic characteristics (e.g. 11). The resulting feed and water supply varies in space and time (seasonally, inter-annually), not only in amount but also in composition, nutritional value, and accessibility. Composition further varies by species and by nutritional value between species (and varieties), and between different phenological stages. As a consequence, dryland forage and water availability is comparatively low, highly variable in space and time, and the variability itself is unpredictable.

With increasing climatic variability and uncertainty, and since economic and infrastructural marginalisation are typical in pastoral areas, standardising production conditions is very costly, thereby increasing financial risk. A case study of peri-urban pastoral producers in Cameroon showed that intensification (through supplementation with cotton seed cake) led to increased production but reduced returns on capital investment, thereby lowering profitability, when compared to pastoral production (12). Pastoralists manage a production system that exploits variability and keeps production costs low. Providing animals with feed, water and minerals is not based on controlling conditions in a given place, but rather on strategically selecting suitable resources from what is available at any given time, e.g. through choosing grazing areas and watering places (7, 13, 14). Feed intake is hence a result of strategic human–animal–environment interaction, and management provides the framework for the animals' exploitation of the environment. Preventive management of diseases and parasites in dryland ecosystems likewise hinges on choice of grazing area, functional plant diversity and the animals' capability to self-medicate (15). Whether animals gain timely access to resources depends on the herders' knowledge of resource distribution in time and space, their herding competence, and their degree of mobility within a given area, a factor that depends on the political and administrative context (16, 17).

It becomes apparent that pastoral livestock's ability to make use of environmental resources and to produce depends on the characteristics of:

i) the dryland environment

ii) the production system, and

iii) the livestock keeper's management.

In other words, it relies on a set of factors much wider than the breed characteristics or even their genetic make-up.

This contextual nature of pastoral livestock's performance directly affects attempts to differentiate, characterise and evaluate breeds – or, more generally, livestock resources – with a view to their strategic use and improvement. Differentiating implies merely discerning that an animal population is perceived to be different from others, while characterising entails describing in detail the different properties and capabilities by which such populations are recognised. Evaluating further involves assigning a value to the characterised livestock resource.

Functions of livestock resources in pastoral systems

Pastoral systems are purposeful systems, in which livestock fulfil multiple functions to enable livestock keepers to achieve their production goals (4, 16, 18, 19). Pastoral systems worldwide rely on various livestock species (e.g. cattle, goats, sheep, donkeys, horses, yaks, camels, camelids and reindeer). In many pastoral systems, households keep herds of different livestock species that each have specific functions. Functions are further differentiated by class (e.g. by age, sex, physiological status) or type (e.g. by use) of animals in the herd, leading to a pronounced multi-functionality that increases livestock keepers' options. It is important to recognise that animals are self-reproducing assets, and that reproduction and maintenance of a viable herd are as important to the livestock keeper as their provision of products and services to the household. Selling livestock means that the pastoralists' only physical capital asset is exchanged for money. During past decades, pastoralists preferred livestock as a capital investment because: 'once in your hands, money is melting away all too easily while animals abide' (20). With banking services becoming more accessible in many pastoral areas, there are now more options for storing money. However, low interest rates can make a bank account less attractive than a herd of sheep or goats which, even under dryland conditions, can have an off-take of 20% and above (e.g. 21, 22).

Pastoral breeding management: selection for versatility

Through their breeding management, livestock keepers influence the characteristics of their animals and the composition of their herds so that the herd's ability to fulfil its functions within the production system is improved over time. Pastoral breeding management is thus directed towards increasing the herd's capability to productively interact with the environment. Diversity in livestock resources is the strategic answer to variability and heterogeneity, and the required multi-functionality. The pastoral herd must possess a versatility that can hardly be expected from a single type of animal but rather requires groups of individuals with different capabilities. Despite the challenge this poses with regard to breeding decisions, studies analysing pastoral breeding management are scarce, apart from two in-depth studies on cattle breeding in Niger (23) and one on camel breeding in Kenya (14). However, both of these point to similar functional properties of pastoral breeding management.

Krätli (23, 24, 25) studied the breeding management of Wodaabe pastoralists rearing Bororo cattle in Niger. The Wodaabe distinguish a variable number of matrilineal lineages in their cattle, each with distinct configurations of physiological and morphological traits, competences, skills, patterns of social interaction and learning abilities, i.e. their particular patterns of human–animal–environment interaction. Lineages that have remained in the herd for two or more human generations (through at least one major crisis) are regarded as particularly valuable ('the animals from the herd of my father and my grandfather…').

Likewise, in the Rendille and Gabra sheep and goat herds in Kenya, individual animals are identified and remembered by their matrilineal relationships (26, 27). Herders recall this relationship on a daily basis as they use it for the daily 'counting' of animals, which is conducted by checking whether families are complete (R. Gudere, personal communication). This regular management activity can also be seen as the basis for the recollection of pedigree and ancestry information. Pastoralists' knowledge of the ancestry and breeding history of their animals is retrievable and can be documented. More than 50 years of detailed genealogical knowledge of Wodaabe cattle in Niger have been documented (23, 25, 28). Tura (26) recorded ancestral information for four generations of local sheep and goat breeds of Rendille and Gabra pastoralists in northern Kenya, with 14 ancestors documented for each individual animal. Such mental records were found to be highly accurate when kinship relationships remembered by pastoral Ankole breeders were tested, using microsatellite DNA analysis (29).

Warui (27) found that 'being a member of a large family in the herd' is a preferential characteristic for breeding sheep and goats. For a family to become a large family in the herd, its females must have a comparatively better reproductive performance, good mothering ability, and high survivability of their offspring, demonstrating their ability to successfully interact with the environment to maintain themselves and reproduce.

Pastoralists base their breeding decisions on recalled ancestral and pedigree information. Breeding management consists of planned mating and consciously selecting and excluding (e.g. separation, castration, sale) animals for breeding. Selection for breeding can be made from within one's own herd or by sourcing animals from outside. Kaufmann (14) found that Rendille camel keepers use a step-by-step procedure to select and test their future breeding bulls. Young bulls are observed, 'first from when they are born up to 2–3 years of age; then when it [the selected bull] is serving the camels for the first time; and then when its calves are born and enter the herd [at the age of two years]'. In the first stage, the future bull is selected on the characteristics of its parents (e.g. sufficient milk production during the dry season, health, strength, performance of their calves) and on its own characteristics (e.g. strength and health). In the second phase, the bull might be excluded because of its own shortcomings (low sexual activity and fertility) and, in the third phase, because of shortcomings in its offspring (the health and survival of the calves).

Köhler-Rollefson (30, 31) conducted early studies on the differences between pastoral breeding management and conventional breeding systems by assembling information from different pastoral communities. Other authors have used structured questionnaires based on conventional breeding concepts to study pastoral breeding management (e.g. 32, 33, 34, 35, 36), but their contribution is limited, because the answers were confined to the underlying concept. Hence, there is both scope and need for more qualitative studies for insight into pastoral breeding management of different pastoral systems.

Breeding is a dynamic process and, as livestock keepers make strategic reproductive choices to improve their herds, breeds change over time. Mobile pastoralists have good opportunities to access 'new blood' for their herds (37). Upgrading is motivated by changing environmental conditions, societal needs (that influence production functions), and the economic environment (38). Fulbe pastoralists in Nigeria regularly explore new ecological zones and management strategies, to which they then adjust their herds (37, 39). Pastoralists have also been shown to consider market demand, such as in Sudan, where Hamari sheep breeders have adapted the colours of their animals to meet Saudi market demands (40). The Food and Agriculture Organization of the United Nations (FAO) (41) gives examples of pastoralists deliberately introducing animals from outside their systems into their breeding herds. However, empirical studies are scarce, so the extent of pure breeding, upgrading and crossbreeding, as well as actual breeding management practices and the concepts underlying the various systems, remains largely unknown. Nevertheless, pastoralists are recognised as having created different breeds through their breeding management (41).

Characterisation and evaluation of pastoral livestock resources

Differentiating breeds

To learn about the diversity of livestock resources created by pastoral societies, Scherf *et al.* (42) analysed Domestic Animal Diversity Information System (DAD-IS) data from 28 countries with considerable dryland regions in Africa, Latin America, Asia and the Near East. They found that about half of the documented breeds originated in drylands. About one-sixth of these are classified as 'regional transboundary', because they are also found in neighbouring countries, and one out of ten are considered as 'international transboundary', because they are present in several non-neighbouring countries (42), e.g. Boran cattle (43).

However, categorising animal populations into different breeds becomes controversial, due to the absence of a universally accepted concept of the term 'breed', and the existence of numerous – sometimes contradictory – definitions, each coined for specific purposes. Lush (44) takes the animal breeder's point of view, defining a breed as: 'a group of domestic animals, termed such by common consent of the breeders [...] for their own use, and no one is warranted in assigning to this word a scientific definition and in calling the breeders wrong when they deviate from the formulated definition. It is their word and the breeders' common usage is what we must accept as the correct definition.' This acknowledges the sovereignty of breeders and their formal or informal institutions for assigning animals to breeds. Cavalli-Sforza (45), from a geneticist's point of view, defines a breed as a group of individuals that is biologically different from other groups, and considers that, for that difference to be of practical relevance, it must be demonstrable at defined statistical levels of probability. This is driven by the aim of shedding light on how genetically different populations have developed, migrated and intermingled over time. Köhler-Rollefson (31) takes the livestock diversity conservationist angle, and defines a breed as a group of animals that:

i) are subjected to a common utilisation pattern

ii) share a common habitat/distribution area

iii) belong to a largely closed gene pool, and

iv) are regarded as distinct by their breeders.

This is an attempt to acknowledge the breeders' sovereignty over the genetic resources of their animals and to make reference to the gene pool.

Databases and literature usually identify breeds by names. Breeds kept by pastoralists are – more often than not – named by outsiders, i.e. within external constructs (38). The name assigned often refers to an ethnic group or a geographical location associated with the animals. Hence, being merely socio-geographic categories, these names are rarely used or even known by the breeders themselves (37). A breed name assigned in this way may group together animals considered distinct by their breeders, ignoring differences relevant to them, or it may distinguish between animals considered similar by their breeders. Such naming potentially prevents a deeper understanding of local breeding and production systems (38).

In the past two decades, numerous studies have advocated and employed molecular methods to identify and differentiate local livestock using mitochondrial DNA (e.g. 46), microsatellite DNA (e.g. 47, 48), and single nucleotide polymorphisms (SNPs) (e.g. 49, 50, 51, 52). These molecular methods are employed for different purposes, such as to determine phylogenetic relationships (e.g. 53), shed light on the history of livestock domestication and migration (54, 55), assign individuals to populations based on marker information, and inform decisions on breed conservation (48, 50, 52).

Microsatellite studies repeatedly reported difficulties in correctly assigning individual animals to their breeds (56, 57). Edea *et al.* (50) used SNPs on Korean and Ethiopian cattle and for five Ethiopian cattle populations and found a low degree of differentiation, which they considered indicative of a common origin and/or a high gene flow. However, differentiation was better for *Bos indicus* than for *B. taurus*- derived reference information (52). Breed assignment informed by molecular methods works better in comparatively homogeneous populations but proves more difficult in heterogeneous populations (58). Breed assignment studies usually attempt to assign sample animals to breeds reflecting socio-geographical categories (see above), rather than to populations with known phenotypic characteristics. The lack of sufficiently large, phenotypically described reference populations is a further reason for difficulties in correct breed assignment (59) and evaluation (60). Combining marker data on neutral diversity and functional diversity could improve differentiation and aid conservation decisions (61).

Characteristics of livestock resources

Considering the contextual importance of breeds kept in pastoral systems is a prerequisite for a meaningful description because many of an animal's characteristics depend on its ability to interact with their environment. The animal–environment interaction can be seen as a result of 'communication' between an animal and its environment. 'Communication' implies that the animal is equipped with senso-motoric features to observe and to act in order to source energy and material (nutrients) from the environment (62), and that it has further cognitive capabilities used for learning, i.e. for improving this communication. Animals which can interact well with their environment are those which perform particularly well with regard to the functions they fulfil in pastoral systems.

Much of the literature on breed characterisation emphasises morphological and physiological dimensions of animal–environment interaction. Hall (63) compiled traits of livestock found in hot drylands, including effective cooling mechanisms that do not expend much water, a high tolerance for dehydration so that other body functions are not affected, and a good ability to walk to distant locations with good pasture, which may also be far away from water (63). However, an animal's ability to interact with its environment is not only determined by morphological and physiological characteristics, but by cognitive characteristics which allow for purposeful behaviour and learning. Cognition and learning appear to be the foundation of many different animal capabilities, such as selective feeding, e.g. through choosing the most nutritious bites, combining different plants for a more rewarding diet, and circumventing plant defence mechanisms which would usually protect them from being eaten (i.e. thorns, high branches, toxicity). Further capabilities include managing health stress and orienting themselves in difficult terrains. A single animal's competence is enhanced within the production system, through its interactions with other animals and the strong social organisation within the herd (reducing stress from antagonistic behaviour), and through obedience and emotional attachment to the herder, which may invert the balance of stress during handling (e.g. 64, 65, 66, 67, 68; for a review, see 23).

Provenza and Balph (64) provide a comprehensive review on dietary learning and conclude that social learning in early life from experienced feeders (mothers, respected peers) in a herd has a large influence on the types of forage that animals utilise. Animals unfamiliar with an environment had 40% less feed intake than those which were familiar and these differences persisted for up to ten months (64). It has been shown that animals have the capacity to learn to eat plants of different species in certain sequences, so as to increase not only palatability and post-ingestive well-being, but also nutrient intake and yield (69). Animals do not only pass this knowledge from mother to young but can be trained.

This shows that – as in all systems – animal performance cannot be explained only by genetic make-up and further suggests that the more variable and heterogeneous the environment, and the more contextual the performance, the higher the share of non-genetic components (environment, management, and cognition) in determining the phenotypic expression.

Evaluating animal performance and determining breeding value

Performance recording

Breed evaluation means to assign a value to the characteristics of the breed. Evaluation of breed performance is mostly done comparatively, assuming that the production conditions under which the animals are kept can be abstracted. In high-input systems with standardised production conditions, the production potential of animals can be compared, i.e. performance is assessed and the animals' requirements are met under 'optimised' conditions. In pastoral systems, the production potential of a livestock breed is irrelevant, as optimisation of production conditions is not economically possible and therefore not the long-term aim for production improvements.

Performance and production outcomes of livestock in pastoral systems are the result of human management of animal–environment relationships, in a heterogeneous and highly seasonal environment. In these systems, performance data distributions are *not* monomodal and time-aggregated average values are *not* adequate to represent performance, which instead needs to be assessed at a higher temporal and/or spatial resolution. This has strong implications for:

i) determining animal performance

ii) comparatively evaluating breeds, and

iii) estimating breeding values.

Pastoral livestock keepers observe and evaluate trait expression in different seasons, e.g. milk production during rainy seasons versus milk production during dry seasons or droughts and these are regarded as two different characteristics of the animal. This assessment reflects the varying levels of access to feed during these seasons. For the same reason (different levels of feed access), performance in stationary, home-based herds and performance in very mobile satellite herds is also observed and assessed separately.

For reproduction parameters, the relationship to season and year becomes more complicated, as birth rates are influenced by the conditions that preceded the period of conception, so that, for instance, in a wet year, the birth rate can be low because of the preceding dry year(s).

If the aim is to compare performance parameters of different breeds kept in different pastoral systems, production data would need to be determined at each point in time, together with data on the production system and the environment (e.g. feed intake), to be able to mathematically control for the environmental effect. Relating performance (output) to the use of limited resources (input) would be a prerequisite to obtain meaningful values for comparison. Representatively estimating feed intake in pastoral systems is difficult, due to the mobility of the system, the heterogeneity of grazing resources, the herders' management effect and the animals' capabilities, such as for feeding selectivity.

Breeding values

These difficulties in determining the performance of pastoral livestock, i.e. describing their phenotypes, are reflected in the estimation of their breeding value. Here, average performance levels are not representative, since 'average' environmental conditions do not occur in reality. The more variable an environment, the more important it is to understand how animals interact with that environment (70). The great importance of 'environment' for the production outcome leads to the fact that heritability is generally lower in pastoral systems than in systems with 'controlled' environments.

The mathematical models used for calculating breeding values – i.e. estimated breeding values (EBVs) and expected progeny differences (EPDs) – usually employ a fixed-farm effect to control for systematic environmental effects, and the remaining unsystematic environmental effects – including variations due to animal–environment interactions – determine the prediction error. In pastoral systems, the farm effect is not fixed because the production conditions are not controlled and the herd is mobile. Consequently, the unsystematic environmental effects, including animal–environment interactions, are very great and cannot be controlled for in the model. Thus, the current methods of estimating breeding values appear ill adapted to livestock systems that do not attempt to standardise the production environment and so correct for environmental variation through their management practices.

Evaluating performance in pastoral systems therefore requires methodological innovations, so that results can produce representative data with necessary temporal and spatial determinants. Data collection would need to stretch over periods long enough to cover the different combinations of dry, wet and drought years, so that performance can be corrected for seasonal, annual and carry-over effects. For reproduction data, progeny history data can be used to cover ten or more years retrospectively. This tool can be usefully applied in pastoral herds because it makes use of the matrilineal organisation of the herds as well as herders' knowledge of reproductive data for managerial purposes (27, 71, 72, 73). Likewise, milk or growth performance could be recorded in different seasons cross-sectionally for large numbers of animals in different lactation or growth stages (which would permit regression at the population level), rather than longitudinally for smaller numbers. Spatial effects could be addressed by geo-referencing recorded values. Co-enquiry methods that engage pastoralists in data collection are a promising innovative approach, if they base their data collection concepts on the production and breeding management that characterises the system. In order to cover large areas and follow mobile herds, communication technology (mobile phones) can be used for data transmission, as has successfully been done for other purposes in pastoral systems (74). However, a real innovation challenge lies in the development of methods that are able to adequately address the contextuality of trait expressions.

For determination of breeding value, suggestions could also come from pastoralists' own evaluations of the breeding value of their breeding stock. For instance, Rendille pastoralists evaluate potential bull candidates with regard to the trait 'strength' by observing to what extent the animal loses body condition and whether it remains healthy during dry seasons. By assessing these trait expressions during dry seasons and especially during drought (and by comparing the different bull candidates within their own herd), Rendille pastoralists get close to the genetic foundation of the trait expression, i.e. they increase the 'heritability' of this trait (12).

Possible use of molecular technologies for evaluating pastoral livestock resources

The contemporary livestock industry employs molecular techniques for predicting genomic estimated breeding values (GEBVs) of animals as a basis for genomic selection (GS). SNP analyses currently allow the determination of an animal's genotype at 3,000, 7,000, 50,000, and 770,000 loci, using so-called 3 k – 700 k base chips (e.g. Illumina, San Diego, USA), at currently approximately US $40 (7 k), $140 (50 k), and $300 (770 k) per animal. Whole genome sequencing is also feasible at about US $1,000 per animal. GS requires clearly defined breeding goals and sufficiently large reference populations of known phenotypes and genotypes from which a prediction equation is derived. This equation uses the genotyping information of the selection candidates (sampled animals) to calculate their GEBV for a set of traits (60, 75). The accuracy of GEBV prediction is a function of:

i) the number of records in the reference population

ii) the heritability of the respective trait

iii) the length of chromosomes, and

iv) the effective population size (76).

It declines with the number of generations between the reference population and sample population (77), and is low for complex traits determined by multiple loci, no single one of which has a great effect (e.g. conformation or type) (78). More diverse livestock populations or across-breed analyses require a marker density of over 300 K for cattle, and a reference population including phenotypes from all populations under study for satisfactory predictions (79). In a pastoral setting in Ethiopia, Edea *et al.* (52) show that between 75 K and 150 K *Bos-indicus*-derived SNPs are necessary for satisfactory assignment of individuals to breeds. Where genetic relationships are pronounced between genotyped animals – as is the case with lineages within populations – accuracy of prediction decays quickly over generations (80).

Tier (81) concludes that GS, as it presently stands, 'will work where we do not really need it – for traits that are commonly recorded – but not for those where it would be most useful'. For GS to be relevant across different livestock industry branches, van Eenennaam *et al.* (60) identify the following as the most crucial issues:

i) determining and obtaining economically relevant phenotypes

ii) determining the optimal size of the reference population and the frequency of marker effect re-estimation

iii) cost-effective genotyping strategies

iv) the practicality of field implementation, and

v) the economic break-even point of adoption, i.e. the relative costs versus the benefits of the realised rate of genetic gain.

While the Holstein-dominated homogeneous US dairy industry profitably employs GS, its adoption is limited in the US beef industry, which uses about 30 breeds, has a less rigid breeding goal, and has only a few sufficiently large reference populations for economically relevant traits. Owing to the structure of the pastoral sector, the diversity of livestock resources, the genetic architecture of the traits considered by pastoral livestock breeders, and pastoral breeding management, the pastoral sector does not easily lend itself to economically profitable use of molecular techniques in livestock breeding at present. However, in scientific terms, these techniques could shed light on how breeding strategies have shaped the genetic architecture of pastoral livestock populations, and to what extent traits that are relevant in the pastoral context are anchored in the genome.

Breeders in pastoral systems select for and nurture all-round inheritable traits in their livestock population. Their breeding is poorly represented by the genetic inheritance model underlying molecular technologies for the determination of breeding values. Instead, it appears that pastoralists' breeding strategies converge with 'extended' or 'inclusive' inheritance models that have emerged in developmental biology and epigenetics (82, 83; see 84 for a review). This notion of inheritance embraces not only DNA sequences but all biological information transmitted from one generation to the next. In addition to DNA, this includes 'epigenetic inheritance' (phenotypic variations from environmentally induced changes in DNA expression); genetic and non-genetic parental effects (when the expression of parental genes or other biological information associated with parental behaviour becomes an environmental component affecting the development of offspring); ecological inheritance (the environmental 'niche' constructed by previous generations); and 'cultural inheritance' (e.g. socially transmitted variations in behaviour). Despite their current practical inadequacy in pastoral systems, molecular techniques may find a role in unravelling the functional genetic structure of pastoral livestock populations and lineages developed under the 'breeding for herd versatility and within-herd diversity' strategy.

Breeding for within-herd diversity

When studying the breeding management of Rendille and Gabra pastoralists in northern Kenya, it emerged that no uniform breeding aim is formulated but that three different types of animals can be distinguished in both camel and goat herds (27, 85). These types differ with regard to their ability

Table I
Adaptation and performance traits of dabakh (weak) and godaan (strong) camels (14)

Season	Traits	Dabakh	Godaan
Rainy season	Milk production	Highest volume of milk production Early and fast increase in milk production	Little milk, enough for family but not to sell
	Body condition	Good body condition, big hump, looks healthy, even healthier than others Early, fast and large increase in body weight	Full hump
Dry season	Milk production	Early, fast and steady decrease Small quantity, no milk for owner, might not even be enough milk for calf	Little milk for owner but still has milk
	Body condition	Early, fast and steady deterioration of body condition in comparison to other types Bony, thin, depressions in body, floppy hump	Retains body condition during dry season Very slow reduction in weight, does not lose body weight easily
Drought	Milk production	Lactation ceases	Lactation persists well into the drought
	Body condition	Extremely poor, animal might die	Strong, does not weaken, does not die easily during drought

to produce in different seasons. Based on their ability to produce during dry seasons, they are classified into 'strong', 'weak' and 'in-between' types. Both in camels and goats, the type which maintains body condition during the dry season and also produces milk – even though it may not be much – well into a drought is called *godaan* (literally, 'strong' in Rendille) and *bakhu* (in Gabra). The type which loses body condition quickly during the dry season and stops producing milk is called *dabakh* (literally, 'weak' in Rendille) and *milghisa* (in Gabra). However, during the rainy season, the latter has the highest milk production and responds best to the pulsing of energy in the environment. Note that the high-production type is classified as 'weak' and the low and steady production type is classified as 'strong' by these livestock keepers in this context. While the 'strong' type exhibits a high regulatory capacity with a rather constant and stable body condition and milk production throughout seasons, the 'weak' type has a low regulatory capacity in which a low input of energy leads to a low output, while a periodical high input leads to a high output (Table I).

The 'in-between' type (*aytimaasso* in Rendille; *masso khabto* in Gabra) combines features from both the highly drought-resistant type and the type with low drought resistance. It is regarded as best suited for supplying the household with milk when kept in homestead herds that cannot move away from the settlement and so have restricted access to vegetation. It has higher milk production than the 'strong' types, and a better capability to cope with the restricted feed supply near settlements than the 'weak' type. However, it is not regarded as 'ideal'. Rather, Rendille and Gabra livestock keepers prefer the presence of *all* types in the herd. This becomes understandable as each type has specific functions for different seasons (Table II).

Table II
The function of different types of Rendille camels and goats by season
(*Dabakh* – weak, *godaan* – strong, *aytimaassoo* – in-between)

Season	Production for sale	Production for the household	Reproduction of the herd
Rainy season	*Dabakh*	*Dabakh*	*Aytimaasso*
Dry season		*Aytimaasso*	*Godaan*
Drought		*Godaan*	*Godaan*

The emphasis on the different types shows that pastoralists recognise the interdependence between performance, metabolic function and the animals' capability to interact with the environment. The metabolism of high-performing animals requires high input, which, in drylands, is only available during the rainy season. Under the feed-restricted conditions in dry seasons, a metabolism with high regulatory capacity is required to maintain production output despite low input. Hence, pastoralists compose their herds of different animal types to sustain preferential performance during different seasons. This case also underpins the argument of Rege (38), that understanding livestock keepers' own naming and classification systems can provide insights into pastoral breeding systems that have shaped existing livestock diversity.

Conclusion

The authors conclude that, to cover livestock resources in pastoral systems in a meaningful and useful way, conventional methods of differentiating, characterising and evaluating livestock diversity need to be expanded and adapted. This process needs to be based on a sound understanding of local breeds in relation to their production context and its functional logic, and in relation to the role and objectives of the animals' breeders.

Mobile dryland pastoralism has developed according to a production logic that is not the same as that used in high-input stationary livestock operations. The latter aims at standardising the production environment in order to exploit genetically determined livestock production potential, using rigid breeding goals, and evaluating success based on return on capital investment. The former aims at advantageously engaging with a structurally variable environment by responding with a variable portfolio of livestock resources, involving a high proportion of non-genetic inheritance (such as learned capabilities); having multiple and adaptive breeding goals; and evaluating success based on a steady flow of goods and services from a highly pulsing ecosystem. Consequently, breeding strategies employed to constantly improve the livestock populations in these two systems also differ in their fundamental logic.

Such differences need to be reflected in methods used to analyse breeding strategies. Conventional methods for evaluating breeds and estimating breeding values, now supported by powerful molecular tools, have been designed around stationary, high-input systems in a standardised production environment. Their success rests on increased standardisation, and the research methods developed under these conditions are therefore ill adapted to systems that strategically exploit variability.

The considerable contribution of dryland pastoral systems to their national livestock sectors, as well as the nutritional, financial, cultural and ecological services they provide, calls for support systems for the pastoral livestock sectors operating in African drylands. These systems, however, require a much more context-specific analysis of their livestock biodiversity. The goals of such analysis should follow from the logic of production in pastoral systems, supporting pastoralist breeding strategies that aim to increase the capability of their livestock resources to actively turn environmental variability into a production advantage. Pastoral livestock keepers must be centre stage as the makers of their livestock resources and agents of change in their livelihood systems.

The development of relevant methodologies starts from a review of the qualitative assumptions underlying conventional mechanisms of data collection. Research should look at the complex processes that govern human–animal–environment interactions, working closely with pastoralists to develop ways of strengthening and expanding functional configurations. This could also provide insights for breeding in high-input livestock systems, now faced with the challenge of increasing variability on a global scale.

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■

Diversité des ressources de l'élevage dans les systèmes pastoraux africains

B.A. Kaufmann, M.A. Lelea & C.G. Hülsebusch

Résumé

Les systèmes pastoraux sont des facteurs importants de la production et la conservation de la diversité du bétail. La variabilité des ressources d'élevage est utilisée par les pasteurs pour s'adapter à la forte variabilité environnementale de manière économiquement rentable. Dans les systèmes pastoraux, les interactions humains–animaux–environnement constituent la base de la production et un facteur déterminant d'amélioration de la productivité et du rendement. En d'autres termes, le système de production pastoral exploite la variabilité et maintient les coûts de production à un niveau faible. Cette dimension à la fois dépendante du contexte et fonctionnelle de la diversité des ressources d'élevage doit être prise en compte au moment d'identifier, de caractériser et d'évaluer les races du cheptel pastoral.

L'interaction des animaux avec leur environnement n'est pas seulement déterminée par des caractéristiques morphologiques et physiologiques ; l'expérience et les comportements acquis par le groupe entrent aussi en ligne de compte. Étant donné qu'une grande partie des performances du bétail est déterminée par des composantes non génétiques, les modèles actuels d'analyse de la diversité et des performances du bétail, qui reposent sur le patrimoine génétique, sont peu pertinents pour décrire les performances du pastoralisme. Des méthodes innovantes d'évaluation du cheptel pastoral à l'échelle des races et des animaux individuels doivent être proposées, car les comparaisons classiques, basées sur les paramètres de production « dans des conditions optimales » sont peu pertinentes au regard de ce système de production. Ces innovations devront tenir compte du fait que les performances du bétail ou d'une race sont fonction d'interactions complexes animaux–humains–environnement et qu'elles varient dans le temps et l'espace en raison de la nature mobile et saisonnière du système pastoral.

Les stratégies et les concepts de sélection pastoraux semblent axés sur l'amélioration des capacités des animaux à exploiter la variabilité, notamment (mais non exclusivement) en améliorant la diversité au sein d'une même race. Des études approfondies de ces concepts et stratégies seraient utiles pour mettre au point des innovations méthodologiques permettant de caractériser et d'évaluer les ressources de l'élevage pastoral.

Mots-clés

Animal – Caractérisation – Différenciation – Diversité au sein d'une même race – Évaluation – Gestion des races – Importance de l'environnement – Interaction avec l'environnement – Pastoralisme – Race locale – Ressources d'élevage – Système socio-écologique – Technologies moléculaires – Terres arides.

■

Diversidad de los recursos ganaderos en los sistemas pastorales africanos

B.A. Kaufmann, M.A. Lelea & C.G. Hülsebusch

Resumen

Los sistemas pastorales son importantes generadores y depositarios de diversidad ganadera. Los pastores se sirven de la variabilidad de sus recursos ganaderos para lidiar con niveles elevados de variabilidad ambiental de manera económicamente provechosa. En los sistemas de pastoreo, las interacciones del ser humano, el animal y el medio natural constituyen la base de la producción y la clave para lograr mayores cotas de productividad y eficiencia. Dicho de otro modo: el pastoreo gestiona un sistema productivo que explota la variabilidad y mantiene bajos los costos de producción. A la hora de diferenciar, caracterizar y evaluar las razas pastorales hay que tener en cuenta esta dimensión funcional, y dependiente del contexto, de la diversidad de los recursos ganaderos.

La interacción de los animales con el medio natural viene dictada no solo por sus rasgos morfológicos y fisiológicos, sino también por la experiencia y el comportamiento socialmente adquirido. Esta elevada proporción de componentes no genéticos que determinan el rendimiento ganadero significa que los modelos actuales para analizar la diversidad y el rendimiento del ganado, basados en el patrimonio genético, resultan de poca utilidad para describir el funcionamiento del pastoreo. Hacen falta innovaciones metodológicas para evaluar las razas y ejemplares que son objeto de pastoreo, puesto que las comparaciones basadas en el rendimiento «en condiciones óptimas» no son aplicables a este tipo de sistema productivo. Tales innovaciones deben partir de la comprensión de que el rendimiento del ganado o de las razas se rige por complejas interacciones entre el hombre, los animales y el medio natural y varía en el tiempo y el espacio debido a la naturaleza itinerante y estacional que es propia del sistema pastoral.

Los conceptos de cría y los procedimientos de selección de razas de las sociedades de pastores parecen ir dirigidos a conferir a sus animales mayor capacidad para explotar la variabilidad, entre otras cosas mejorando la diversidad interna de las razas. El estudio pormenorizado de tales conceptos y procedimientos podría resultar considerablemente útil para alumbrar innovaciones metodológicas destinadas a caracterizar y evaluar los recursos ganaderos pastorales.

Palabras clave

Animal – Caracterización – Diferenciación – Diversidad interna de las razas – Evaluación – Gestión de razas – Importancia del contexto – Interacción con el medio – Pastoreo – Raza local – Recursos ganaderos – Sistema socioecológico – Técnicas moleculares – Tierras áridas.

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