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ANIMALES**

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**FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ORGANISATION DES NATIONS UNIES POUR L'ALIMENTATION ET L'AGRICULTURE
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**UNITED NATIONS ENVIRONMENT PROGRAMME
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Editorial

Research, Environment and Development. Interactions on Animal Production

Scientific advances and new methods of technology for food production, preservation and processing, transport and marketing force us to a fast change. Only time will show whether the present pace of rapid change will, on balance, have an overall positive or negative effect on the future state of the rural world. This change should be managed to prevent devastating effects not only on traditional animal production but also on the environment as a whole and allow for a planned evolutionary process so that humans and animals can adapt to the new socio-economic conditions they both must face.

Animal agriculture already contributes, to a greater or lesser extent, to the degradation and erosion of natural resources. If not well-managed, livestock production may specifically contribute to land degradation, the decline and pollution of water resources, the emission of greenhouse gases over and above the erosion of biodiversity. On the other hand, with good management, livestock production can make a positive contribution to the natural resources base by enhancing soil quality, increasing plant and animal biodiversity and substituting for scarce, non-renewable resources such as fossil fuels. Wherever possible these economically and environmentally attractive scenarios should be promoted, and policies and technologies which do so identified. However, as the expected increase in demand for food of animal origin must be met, it is likely that negative effects of livestock production,

resulting from not well thought out intensification and higher productivity, will continue to emerge. The challenge is to identify policies and technologies which mitigate any negative impact on the environment but which, at the same time, satisfy the considerable demand for livestock products and the social needs of the consumers and the producers. Additionally, an important factor is that present day popular interest is concentrating on the applicability of animal research results and the ethics that surround it. The hesitation and emotions existing at all levels and spheres of the population, with regard to such developments as transgenesis and its possible relevant applications, reflect the pace of scientific changes and are provoked by the growing interest and the puzzlement of the man in the street in genetically modified organisms and the possible medium- and long-term implications of modern biotechnology programmes.

Without necessarily promoting less progressive, conservation approaches and uneconomical environmental policies, it should be stressed that, regarding the livestock sector, today we run the risk of over-hastily accepting and applying new alternatives that might neglect the fundamental factors of adaptability and time which could lead to serious consequences especially in less benign environments.

The Editors

Editorial

Recherche, Développement et Environnement. Interactions avec la Production Animale

Les progrès scientifiques et les nouvelles méthodes technologiques utilisés pour la production, la conservation et la transformation des produits alimentaires, ainsi que pour leur transport et leur commercialisation, nous obligent à effectuer des changements rapides. Seul le temps pourra dire si cette situation de changements rapides aura un effet positif ou négatif sur le futur du monde rural. En outre, ce changement devrait être contrôlé pour pouvoir prévenir les effets néfastes, non seulement sur la production animale traditionnelle, mais aussi sur l'ensemble de l'environnement, et devrait, également, donné lieu à un processus d'évolution planifier qui permette aussi bien aux hommes qu'aux animaux de s'adapter et faire face aux nouvelles conditions socioéconomiques.

La production animale contribue, de toute façon et en différentes mesures, à la dégradation et à l'érosion des ressources naturelles. Si une bonne gestion n'est pas appliquée, la production animale peut contribuer de façon spécifique à la dégradation du territoire, au déclin et à la pollution des ressources hydriques, ainsi qu'à l'émission des gaz qui provoquent un effet de serre et à l'érosion de la biodiversité qui s'en suit. Avec une bonne gestion, la production animale peut par contre devenir un apport positif pour les ressources naturelles de base, ceci à travers l'amélioration de la qualité des sols, l'augmentation de la biodiversité végétale et animale et la substitution des ressources rares et non renouvelables, telles que les carburants fossils. Là où cela est possible, il serait nécessaire de mettre au point et promouvoir les mesures technologiques et politiques appropriées afin d'adopter ces propositions intéressantes. Cependant, si nous considérons la possibilité d'une augmentation de la demande

d'aliments d'origine animale, on peut supposer que les effets négatifs en provenance de ce secteur, et qui sont dus au manque de connaissances sur l'intensification et une majeure productivité, continueront à exister. Le défi posé consiste à identifier les politiques et les technologies qui puissent réduire tout impact négatif sur l'environnement mais qui, en même temps, puissent satisfaire la demande considérable de produits d'origine animale et les besoins sociaux des consommateurs et des producteurs. D'autre part, un autre facteur important est l'intérêt populaire actuel qui est centré sur la possibilité d'application des résultats de la recherche et toute la question d'éthique qui en dérive. Les doutes et le sentiment qui existent à tous les niveaux et dans les différentes sphères de la société en ce qui concerne ce genre d'études sur la transgénèse et ses possibles applications, reflètent la situation provoquée par les changements scientifiques et sont dus à l'intérêt croissant et à la perplexité générale vis-à-vis des organismes génétiquement modifiés et les conséquences à moyen et long terme des programmes modernes sur la biotechnologie.

Sans vouloir promouvoir des approches de conservation moins progressifs et prôner des politiques environnementales négatives, on devrait souligner que, en ce qui concerne le secteur de la production animale, aujourd'hui on risque d'accepter et d'appliquer hâtivement de nouvelles alternatives qui ne prennent pas en considération des facteurs fondamentaux d'adaptabilité et de temps, ce qui entraînerait de sérieuses conséquences, surtout pour les environnements les moins bénins.

Les Editeurs

Editorial

Investigación, Desarrollo y Ambiente. Interacciones con la Producción Animal

Los avances científicos y los nuevos métodos tecnológicos utilizados para la producción, conservación y transformación de los alimentos, así como para su transporte y comercialización, nos obligan a efectuar cambios muy rápidos. Sólo el tiempo podrá demostrar si el actual ritmo de cambio tendrá un efecto positivo o negativo sobre el futuro del mundo rural. Estos cambios deberían además estar controlados para prevenir los efectos perjudiciales no sólo sobre la producción animal tradicional, sino también sobre el medio ambiente en su conjunto, y deberían, a su vez, dar lugar a un proceso de evolución planificado que permitiera tanto a los hombres como a los animales adaptarse a las nuevas condiciones socioeconómicas a las que se enfrentan.

La producción animal contribuye ya, en mayor o menor medida, a la degradación y erosión de los recursos naturales. Si no se lleva a cabo una buena gestión, puede contribuir a la degradación del suelo, a la disminución y la contaminación de los recursos hídricos, a la emisión de gases que provocan el efecto invernadero y además a la erosión de la biodiversidad. Por otra parte, con una buena gestión, la producción animal puede contribuir positivamente al mantenimiento de los recursos naturales, mejorando la calidad de los suelos, incrementando la biodiversidad vegetal y animal y sustituyendo los recursos escasos y no renovables, como los carburantes fósiles. Siempre que sea posible, estas contribuciones positivas desde el punto de vista económico y medioambiental deberían promoverse, poniendo a punto las medidas tecnológicas y políticas necesarias. Sin embargo, teniendo en cuenta que se espera un incremento de la demanda de alimentos de origen animal, se supone que los efectos negativos

provenientes de la producción animal seguirán surgiendo, debido a la mal planificada intensificación y al aumento de productividad. El desafío está en identificar las políticas y tecnologías que puedan mitigar cualquier impacto negativo sobre el medio ambiente pero que, al mismo tiempo, puedan satisfacer la demanda considerable de productos de origen animal y las necesidades sociales de los consumidores y de los productores. Por otra parte, otro factor importante es que en la actualidad hay un mayor interés de la sociedad en las posibles aplicaciones de los resultados de la investigación y las cuestiones éticas que de ello se deriva. Las dudas y la preocupación existentes en todos los niveles y sectores de la población con respecto a novedades como la transgénesis y sus posibles aplicaciones, reflejan la situación provocada por los cambios científicos y se deben al interés creciente y a la perplejidad por parte de la gente corriente en todo lo referente a los organismos genéticamente modificados y las posibles consecuencias a medio y largo plazo de los modernos programas de biotecnología.

Sin querer con esto promover enfoques de conservación menos progresistas y políticas medioambientales ineficientes desde un punto de vista económico, hay que resaltar que, en lo referente a la producción animal, hoy en día se corre el riesgo de aceptar y aplicar apresuradamente nuevas alternativas que no tengan en consideración factores fundamentales de adaptabilidad y tiempo, lo que provocaría graves consecuencias, especialmente en los ambientes menos favorables.

Los Editores

Genetics of disease resistance in *Bos taurus* cattle

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Summary

This review summarises evidence for genetic variation of *Bos taurus* cattle to diseases encountered under temperate conditions, including internal and external parasitism, susceptibility to mycotoxic diseases (tall fescue toxicosis, facial eczema, ryegrass staggers), mastitis, ketosis, pasture bloat, leukosis, tuberculosis, foot and mouth, brucellosis and BSE. Averaging mean heritability estimates reviewed from 8 diseases (weighted equally) gave a value of 0.21, indicating that measurable genetic variation for disease traits in *Bos taurus* cattle is somewhat less than that for production traits, such as milk yield or body weight. Many estimates, however, have high standard errors, and there could be an upward bias resulting from non-reporting of zero or non-significant estimates.

Few single-trait selection experiments have been conducted to study the genetics of disease resistance traits in cattle. For the disease traits where selection is being applied extensively, index selection for improved disease resistance and increased production is more common than single-trait selection. Results from a long-term (25 year) divergent selection experiment with resistance/susceptibility to pasture bloat in cattle in New Zealand are reviewed. Four single-year experiments comparing progeny of 'high' versus 'low' sires for resistance to disease are also reviewed, one in Australia studying faecal nematode egg counts, one in the USA involving the mycotoxic disease, tall fescue toxicosis, a third in New Zealand

involving the mycotoxic disease, facial eczema, and a fourth in the USA involving *Brucella abortus*.

Resumen

Esta revisión resume la variedad genética evidente en *Bos taurus* a las enfermedades encontradas en condiciones templadas, incluido el parasitismo interno y externo, la susceptibilidad a las enfermedades micotóxicas (festuca cañosa, excema facial, tetania del raygras), la mastitis, la cetosis, el timpanismo pratense, la leucosis, la tuberculosis, la brucelosis y la BSE. La media de heredabilidad estimada sobre 8 enfermedades nos da un valor de 0,21, lo que indica que la variación genética medible en cuanto a enfermedades en el caso de *Bos taurus* es algo inferior con respecto a la producción, tal como el rendimiento en leche o rendimiento corporal. Varias estimaciones poseen sin embargo una elevada desviación estándar, y puede haber una ulterior desviación debida a la omisión del zero o de las estimaciones no significativas.

Algunos experimentos sobre selección de rasgos simples han conducido llevado a estudiar la genética de los rasgos de resistencia a enfermedades en bovinos. Para los caracteres sobre enfermedades, a los que se aplica una selección extensiva, el índice de selección para mejorar la resistencia a la enfermedad y aumentar la producción es más común que en el caso de la selección de un rasgo simple. Se analizan aquí los resultados obtenidos a largo plazo (25 años) y que muestran una divergencia entre el experimento de selección y la

resistencia/susceptibilidad al timpanismo pratense en los bovinos de Nueva Zelanda. Cuatro experimentos de un año comparan la descendencia de “arriba” hacia “abajo” de los machos en cuanto a la resistencia a enfermedades; uno en Australia realiza un conteo de las larvas de los nematodos fecales; uno en Estados Unidos sobre la enfermedad micotóxica, un tercero en Nueva Zelanda referido a enfermedad micotóxica y excema facial; y el cuarto en Estados Unidos sobre *Brucella abortus*.

Key words: *Cattle*, *Bos taurus*, *disease*, *resistance*, *genetics*

Introduction

Animals have always been subjected to assault by infectious and parasitic organisms and presumably the natural selection pressure in the wild is severe. In recent centuries, domestic animals have been subjected to artificial selection, particularly for visible traits and then for easily measurable traits such as live weight or height. For disease traits in cattle, however, studies of animal variation are less common than for live weight or height, so less is known about the potential to change animal susceptibility. In times when the use of antibiotics and drug therapy was common, cheap and acceptable, there seemed little incentive to select for disease resistance. The position has now changed because of increasing concerns over drug resistance by parasites, bacteria and viruses, increasing demands for residue-free animal products, and at the same time increasing concerns for animal welfare. Selection for disease resistance has been applied successfully in poultry, and opportunities are also being applied increasingly in pigs and sheep in some countries. This article reviews information on genetic variation in the susceptibility of cattle to disease, with the major emphasis on *Bos taurus* cattle, thereby restricting the review predominantly to temperate conditions.

Parasites

Internal parasites

Most genetic studies on the host resistance of farm animals to helminth parasites have been carried out in sheep, although the question of host resistance is also of interest in cattle and goats. There are numerous reviews of responses achieved to divergent selection for (sheep) host resistance to internal parasites (e.g. Woolaston & Eady, 1995; Morris *et al.* 1995b). These have concluded that selection has been successful in experimental flocks (e.g. Morris *et al.*, 1997b), with single-sample heritabilities for faecal egg count ranging from 0.2 to 0.3 (occasionally 0.4 or above), and the reviews have also described selection opportunities being applied in industry ram-breeding flocks. By following similar research techniques to those in sheep as described above, what has been found in cattle?

Barlow and Piper (1985) estimated heritabilities for single-sample faecal egg count in Australian Hereford and Hereford-cross cattle, with values of 0.04 ± 0.17 and 0.29 ± 0.19 for the two most common genera in the trial (*Cooperia* and *Haemonchus*, respectively), and with a value of 0.04 ± 0.18 for all genera combined. An estimate of 0.29 ± 0.18 was obtained for faecal egg count in Angus cattle in the USA (Leighton *et al.*, 1989).

By implication, responses similar to (or smaller than) those achieved in sheep could be achieved from selection applied to young cattle, although standard errors for heritability estimates are large in both cattle experiments cited here. Esdale *et al.* (1986) have described a single-year experiment with F_2 *et sequ.* Africander x Hereford cattle, where the progeny of 3 high and 3 low faecal-egg-count sires were compared, giving a realised heritability of 0.52 for the mean of 4 egg counts, a significant progeny group difference in faecal egg count ($P < 0.005$) and a single-sample repeatability of 0.20 ± 0.05 .

Data for (log) faecal egg count from Friesian-cross and Brahman-cross calves under temperate conditions in New Zealand (Morris *et al.*, 1992) have provided a further repeatability estimate of 0.21 ± 0.08 . From Barlow and Piper (1985), repeatabilities of egg counts for the two genera and for the total egg counts were 0.30 to 0.31. These indicate that, for individual assessments of an animal's phenotype for selection, it is useful to take more than one egg count record.

External parasites

Cattle ticks

Perhaps most work on host resistance to external parasites in *Bos taurus* cattle has been done by CSIRO at Rockhampton, with Hereford-Shorthorn and other crosses in investigations of resistance to the cattle tick (*Boophilus microplus*). A review of heritability estimates for host resistance to ticks in *B. taurus* and *indicus* breeds (Davis, 1993) led to an average of 0.34 ± 0.06 , or a value of about 0.30 for *B. taurus* alone.

Tick resistance was one of the traits monitored in the CSIRO Hereford-Shorthorn cattle selected for production (weight gain) under disease-challenge conditions. Extreme levels of resistance to ticks were found in one particular heifer, and subsequently in some of her relatives. As a result, matings were set up using likely carrier sires, and a two-allele major gene effect was identified (Frisch, 1994; Kerr *et al.*, 1994). The heterozygote mean was in between those of the two homozygotes, but the degree of dominance depended on the extent of tick challenge under which the animals were evaluated.

Bush ticks

Infestation levels of cattle to the bush tick, *Haemaphysalis longicornis*, have been compared in Herefords and their crosses in Grafton, New South Wales (Dicker and Barlow, 1979). The *Bos taurus* animals harboured twice as many ticks as *Bos indicus* crosses (Brahman x Hereford), but significant

differences amongst Hereford, Friesian x Hereford crosses and Simmental x Hereford crosses were not detected. Heritabilities were not estimated.

Mycotoxic Diseases

Tall fescue toxicosis

Tall fescue (*Festuca arundinacea*) is the most important cool-season forage grass in much of south-eastern and central regions of the USA (Stuedemann and Hoveland, 1988), being grown on about 14 million ha of land. Tall fescue toxicosis in cattle is caused by ergot alkaloids, predominantly ergovaline, from the fungal endophyte (*Acremonium coenophialum*), found in some tall fescues, and this leads to reduced intake in cattle, reduced weight gain, reduced milk production, reduced tolerance of heat stress and various metabolic, behavioural and physiological effects (Stuedemann and Hoveland, 1988). Breed differences in the depression of weight gains have been recorded (Morrison *et al.*, 1988), providing initial evidence of genetic differences in the host. Hohenboken and Blodgett (1997) have successfully selected for and against tall fescue toxicosis susceptibility in mice by selecting for and against a depression in growth whilst on an endophyte-infected fescue seed diet. In a subsequent study, Wagner and Hohenboken (1998) established that a toxin-containing diet had a larger detrimental impact on long-term reproduction of mated pairs of the susceptible than of the resistant line. The divergent selection lines of mice were shown to differ also in the activities of two liver detoxication enzymes.

These and other indirect measures of monitoring genetic susceptibility to fescue toxicosis or selecting against it could be tried in cattle. However, differences among aged Angus cows in lifetime production while grazing endophyte-infected fescue pastures could not be related to variation among them in physiological indicators of fescue toxicosis (Hohenboken *et al.*, 1991). Also, progeny of a presumed resistant bull and of a control bull

did not differ in physiological responses to fescue toxicosis (Gould and Hohenboken, 1993), although they did differ in rectal temperature whether on a diet of toxin-containing fescue or not. Apparent resistance to the condition may therefore be mediated by inherent differences in "basal" body temperature and liability to heat stress. Lipsey *et al.* (1992) progeny tested one susceptible and one tolerant bull for rectal-temperature response to heat stress at WC whilst on a diet containing ergovaline. Progeny of the susceptible bull were more temperature-sensitive to addition of dietary ergovaline ($P < 0.05$) than were those of the resistant bull. A simplified test might provide an opportunity for industry to begin to breed for resistance, if it was desirable within the prevailing cost structure.

Facial eczema

Facial eczema is caused by a toxin, sporidesmin, found in spores from the saprophytic fungus, *Pithomyces chartarum*. The fungus grows on the dead litter at the base of grasses in pastures during late summer/autumn in lower-lying areas of the North Island of New Zealand. The disease also occurs in Australia, Argentina, Uruguay, South Africa, USA and France, but the common and severe outbreaks seem to be in New Zealand for climatic and other reasons. Sporidesmin is a potent toxin that injures many body tissues, particularly the liver. The extent of liver injury in susceptible ruminants can be determined from analysis of serum gamma glutamyltransferase activity about 3 weeks after a toxic challenge. A long-term experiment selecting for high or low susceptibility to facial eczema (using the gamma glutamyltransferase indicator) in Romney sheep in New Zealand was established in 1975 and is still continuing (Morris *et al.*, 1995a).

From cattle studies set up in 1989 following a field challenge in Jersey cows (Morris *et al.*, 1990), the heritability of gamma glutamyltransferase activity was estimated to be 0.31 ± 0.10 . Studies in which calves were

dosed with sporidesmin have subsequently been carried out with male progeny groups of Friesian and Jersey sires (Morris *et al.*, 1998a), giving heritabilities of 0.29 ± 0.15 and 0.77 ± 0.13 respectively. Activities of this and other enzymes following sporidesmin challenge are closely correlated genetically (Morris *et al.*, 1998a), and they also have high between-animal repeatabilities under challenge conditions. A single-year progeny-test study with 5 highly susceptible and 5 resistant Jersey sires was also carried out, showing successful direct selection (Morris *et al.*, 1991b), so that selection for facial eczema resistance under commercial conditions would be practical if desired.

Studies are now underway in sheep to find the gene(s) responsible for facial eczema resistance, and to find a genetic marker close to (or on) the gene (Phua *et al.*, 1998). It is likely that these results would have direct relevance to cattle testing and selection. The availability of a genetic test would save the need for direct challenge with the toxin.

Ryegrass staggers

Ryegrass staggers (RGS) is a neurotoxic disease in ruminants caused by the mycotoxin, lolitrem B, found in endophyte-infected swards of perennial ryegrass (*Lolium perenne* L.). RGS can cause severe distress to animals and also management problems for farmers. Under summer/autumn grazing conditions, RGS can cause muscular incoordination in animals, and is most obvious in cattle or sheep when they are under the stress of being moved, mustered or driven by working dogs. Its effects are reversible, when the toxin and the stress are removed.

A selection experiment for resistance or susceptibility to RGS is underway in sheep in New Zealand (Morris *et al.*, 1998b). With a single-record heritability of 0.068 ± 0.028 and a between-animal repeatability of 0.24 ± 0.05 , an average divergence of 26 percentage points in RGS incidence has been achieved between the two lines after the first 5 years of selection (21 vs 47%).

A similar testing procedure using natural challenge could be applied in experimental cattle, given that RGS in cattle has also been recorded as having a significant between-animal repeatability, and that susceptibility to the disease runs in families (Morris, CA, unpublished data, 1998).

Mastitis

The inheritance of susceptibility of dairy cattle to mastitis has been studied for many years. Four early heritability estimates (1950-1972) reviewed by Spooner *et al.* (1975) had an average value of 0.25 (range 0.10 to 0.38), whilst recent estimates from regional or national databases are generally much smaller, e.g. 0.06 to 0.11 for records from 200 000 first lactations in Norway (Simianer *et al.*, 1991). There could be many reasons for the difference: improved statistical methodology, sire by environment interactions, natural and artificial selection having removed the most susceptible families of cows over the last 40 years, improved dairy-shed hygiene having altered the challenge, or the effects of altered milking machine technology and larger herd sizes. An extensive review by Miller (1982) gave separate heritability estimates for bacteriological measures of mastitis (average 0.10, n=3 studies), clinical treatment data (average 0.12, n=12) and somatic cell count (average 0.20, n=9). More recent heritability estimates for somatic cell count are still low, e.g. 0.09 to 0.11 in Canada and 0.10 in the USA (Powell *et al.*, 1997). Large-scale programmes have now been set up on a national basis (e.g. in Norway and Sweden) to rank bulls and select them on indices which include the milk traits and reduced mastitis, ketosis or 'any disease'.

Ketosis

Scandinavian dairy cattle selection programmes include records of (and selection against) ketosis, as mentioned above. The heritability estimates reported in Norway ranged from 0.08 to 0.11 (Simianer *et al.*, 1991). Consequently, large daughter group

sizes are required for accurate sire proofs, and this is part of the current Scandinavian progeny test design.

Bloat

"Foamy" or "pasture" bloat occurs in ruminants, especially cattle, when they are unable to disperse the gases of fermentation as quickly as these gases are produced. It is common in spring and autumn in New Zealand dairy cows. The conditions necessary for bloat to occur in susceptible animals are not known precisely. It is a metabolic problem which is more commonly encountered, but is not restricted to, animals grazing high white clover levels in white clover/ryegrass swards. Animal selection studies have been underway at Ruakura since 1972/73 (Morris *et al.*, 1991a), as described below. "Feedlot" bloat is a different syndrome, which was studied by Lindahl *et al.* (1957) who noted animal-to-animal variation in susceptibility, but no genetic factors were investigated.

Herds of Friesian-Jersey cross animals, selected at Ruakura for high or low susceptibility to pasture bloat, were established in 1972/73, and selection has continued since then. Outside sires were used for four years, and then the two herds were closed. Young stock have been scored for 2 to 3 weeks each year for susceptibility to bloat whilst grazing bloat-potent pasture. As reported by Morris *et al.* (1997a), after 23 years of divergent selection, herds differed by 1.2 phenotypic standard deviations for single-record (half-day) scores, the single-record heritability equalled 0.19 ± 0.04 and the repeatability equalled 0.44 ± 0.02 . Minimal response has been achieved since about 1984 in the low susceptibility herd, although the high susceptibility herd has continued to become more susceptible. The data are consistent with the presence of a major gene for bloat, recessive for susceptibility, which accounts for at least 78% of the genetic variance. A search for a linked genetic marker is underway, to provide a simple DNA test using blood, milk or semen,

obviating the need to score animals on potent pasture. A candidate gene has also been found, coding for a parotid salivary protein (bSP30). This protein has higher concentrations in the low susceptible herd than in the high susceptible herd (Rajan *et al.*, 1996). Thus, a secreted salivary protein and the genetic mechanism for its control are both under study here.

Leukosis

The aetiological agent of enzootic bovine leukosis is the bovine leukaemia virus (BLV), and B-cells are the principal target of BLV infection (Kenyon and Piper, 1977). Lewin and Bernoco (1986) investigated the role of the major histocompatibility complex in BLV infection in an infected Shorthorn herd, and found that specific bovine lymphocyte antigen types were associated with resistance or susceptibility to BLV. Resistance/susceptibility was shown to segregate in 33 offspring sired by a bull which was heterozygous at the appropriate locus. The authors concluded that "the bovine lymphocyte antigen system can be used to select for resistance to B-cell proliferation and the development of lymphocytosis in BLV-infected herds".

Analyses of data from Black and White cattle in Russia by Kulikova and Petukhov (1994) have provided a heritability estimate of 0.3 for incidence of leukosis.

Tuberculosis

The same Russian workers reported a heritability of 0.06 to 0.08 for resistance to tuberculosis in Black and White cattle, in a population showing a "morbidity" (? incidence) of 20.8%. Sire-offspring and daughter-dam relationships were analysed to obtain these estimates (Petukhov *et al.*, 1998). In a previous publication (Kulikova and Petukhov, 1994), the authors reported a positive genetic correlation between susceptibilities to tuberculosis and leukosis.

Foot and Mouth Disease

Templeton *et al.* (1988) quoted French data (Prat, 1952-53) showing that resistance to foot and mouth disease runs in families. All but one cow on a dairy farm contracted foot and mouth in 1938. Fourteen years later, after the herd had been re-established, another outbreak was experienced and there were then six resistant cows (three remaining healthy and three with only mild symptoms); all were descended from the original resistant cow.

Brucellosis

Templeton *et al.* (1990) described a study on natural resistance to brucellosis in cattle, in which they bred 11 resistant and 10 susceptible cows to a resistant bull, with the two groups of offspring being challenged with a discriminating dose of virulent *Brucella abortus*. Progeny were challenged as heifers in midgestation (16 to 24 months of age) or as bulls from 12 to 16 months of age. The percentage of animals resistant to brucellosis was three times higher (54%) in the offspring of resistant than susceptible dams. Also, the *in vitro* replication of *B. abortus* was controlled more effectively in macrophages from resistant-line animals than in those from susceptible-line animals, both before and after the animals were exposed to the disease challenge.

In more recent work (Adams *et al.*, 1996), the potential of the resistant herd was assessed and a positive genetic correlation between resistance to *Brucella abortus* and to *Mycobacterium bovis* was reported.

BSE

Intensive work on many aspects of bovine spongiform encephalopathy (BSE) in recent years has included a search for evidence of host variation in susceptibility. Different forms of the host-encoded prion protein have already been found in cattle (Goldmann *et al.*,

1991) which suggest that there are indeed host differences in susceptibility, as for scrapie in sheep.

Foot defects

An extensive review of the genetics of foot defects in cattle was published by Greenough (1991). There were various causes of foot defects, ranging from foot rot, lameness-producing lesions of the hind limb, claw disorders and laminitis, and he reported low heritabilities for most traits or their components. Overall in dairy cattle, a subjective score is usually given to 'feet and legs', which again is lowly heritable. Thus, selection could be applied to improve foot structure, if required.

In the future the consumer might decide to discriminate on animal welfare or food-safety grounds, because another supplier's product (or production system) is more desirable. In this context, 'desirable' could mean produced by cows under less stress (e.g. fewer lame or sick animals) or products from cows with fewer or no history of veterinary or prophylactic intervention (i.e. residue-free products).

Elements or metabolites in blood

Although genetic variation in trace element or metabolite concentrations in the blood does not demonstrate genetic variation in disease incidence *per se*, it could be a useful indicator of animals near a lower or upper threshold. For example, we have estimated a heritability of 0.15 ± 0.06 for Mg concentration in lactating Jersey cows which were the daughters of 65 sires (Morris *et al.*, 1990). It is not known if the genetic outliers for low Mg could be more prone to the clinical condition of grass staggers (hypomagnesaemia). In the same study, heritability estimates for Na and K concentrations were very close to zero. In a British study, Rowlands (1974) obtained heritability estimates (231 Hereford-Friesian calves, 12 sires) of 0.93 ± 0.36 , 0.74 ± 0.32 , 0.40 ± 0.23 , 0.28 ± 0.19 , 0.26 ± 0.18 and 0.09 ± 0.12 ,

for concentrations of haemoglobin, glucose, K, albumin, inorganic PO_4 and Na respectively.

Discussion

It is becoming clear that there is natural genetic variation in *Bos taurus* breeds for resistance to most of the diseases to which they are commonly or occasionally exposed. Over recent decades, however, we have been hiding this genetic variation (or not requiring expression of this genetic variation) because of the widespread use of drenches, vaccines, sprays etc., and because of the elimination of some diseases altogether (e.g. foot and mouth in some countries).

In this review, heritability estimates were obtained from the literature for 8 of the diseases considered. Averaging 8 mean heritability estimates (i.e. using one mean value for each disease) gave an overall mean of 0.21. Many of the separate heritability estimates had high standard errors, so the estimates for most traits are not very precise. However, it is encouraging to note that all the single-year selection studies described above, and the multi-generation study (on bloat), were successful in breeding divergent lines of cattle.

Some heritability estimates may not have been published because they were low or not significant, in which case there may be an upward bias to the overall value calculated here. However, if a disease trait has a heritability of 0.21 or greater, selection to change the mean incidence level is feasible although progress may not be as fast as for milk yield or live weight (other things being equal). For some traits (e.g. mastitis), where current heritability estimates are much lower, large progeny group sizes are now being generated in order to provide the accuracy required for continued sire selection. In other cases, e.g. ryegrass staggers or bloat, repeated records and restricted-maximum-likelihood analyses may be used to improve the accuracy of breeding value estimation above that possible with single-record phenotypic selection.

For the future in *Bos taurus* breeds, it seems that there will be some opportunities for following up candidate genes, ultimately to identify a major gene controlling host resistance to a disease. Use of a genetic marker on the gene, or very closely linked to it, will probably be the method of choice to select bulls and possibly cows for breeding. This may need to be repeated for a series of diseases, although the selection studies in mice by Biozzi *et al.* (1982) suggest that there should be opportunities for cross-resistance where antibodies play a dominant role.

A review (Morris, 1998) of selection responses for disease resistance achieved in 15 New Zealand and Australian single-trait experiments with sheep and cattle (mainly the former) showed that realised heritabilities averaged 0.28. It is to be hoped that research funding for selection studies on disease resistance will continue, so that we may learn more about how to breed for resistance. This would improve animal welfare and herd productivity, and would increase the availability of residue-free animal products.

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Indigenous cattle of Zanzibar: the need for conservation

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Summary

The indigenous cattle of Zanzibar commonly referred to as Zanzibar Zebu belong to the Small East African Zebu but with some influences of Boran and Somali cattle. The breed is under pressure from cross-breeding and from economic reforms that may lead to genetic erosion. This paper is an attempt to describe the characteristics and environment of these cattle as well as highlighting the implications of the prevailing conditions for conservation.

Resumen

El bovino indígena del Zanzibar normalmente se refiere al zebú de Zanzibar, descendiente del pequeño zebú del Este africano pero con algunas influencias del bovino del Boran y Somalia. La raza se encuentra bajo presión por los cruzamientos efectuados y por las distintas reformas económicas que han llevado a una erosión genética. Este artículo presenta una descripción de las características y del ambiente de estos bovinos, e intenta subrayar las implicaciones de las principales condiciones de conservación.

Key words: *Characteristics, In situ/ex situ conservation, Origin, Unguja, Pemba, Zebu.*

Introduction

Zanzibar comprises two main islands, Unguja (also called Zanzibar) and Pemba, with several islets adjacent thereto, off the coast of East Africa. Although administratively Zanzibar runs an autonomous government, it is part of the United Republic of Tanzania (URT). We can also speak of Tanzania as consisting of the mainland and the isles (Unguja and Pemba). Unguja island, covering a total land area of 1 464 km², is separated from the mainland of Tanzania by a channel which is at its narrowest 36 km across. It lies between latitudes 5°40' and 6°30' south; and longitude 39° east. Its sister island of Pemba has a total land area of about 864 km², and lies about 40 km NNE of Unguja, between latitudes 4°50' and 6°30' south and between longitudes 39° and 39°50' east.

Zanzibar is endowed with strains of cattle that have sustained the lives of thousands of people for centuries. The majority of these cattle are found in Pemba as the presence of tsetse is a limiting factor in Unguja (see table 1). The loss of genetic diversity in Zanzibar is imminent due to the artificial manoeuvres by man in an attempt to secure livelihood and extract more from its livestock. The existence of artificial insemination in cattle and extensive introduction of exotic breeds make this species most vulnerable to genetic erosion. The objective of this paper is therefore to describe the general characteristics of cattle in Zanzibar and highlight the need for their conservation.

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Origin

The cattle of Zanzibar have been described by Tidbury (1954), Griffin (1986), Mason (1988), and Felius (1995) as belonging to the Small East African Zebu, which is an indigenous type common in East Africa. Their origin has been a subject of many speculations. Payne (1970) and Epstein and Mason (1984) provided a general account of movements of thoracic-humped zebu cattle into the eastern horn of Africa by about A.D. 669. In addition, Payne (1970) suggested the direct sea route from India as the probable way by which these cattle entered Zanzibar in the earlier times. From these sources, zoological records (Moreau and Pakenham, 1941; Swynnerton and Hayman, 1951) plus records of the earlier explorers (Rigby, 1861; Burton, 1872), updated information on trade and people's movements (Sheriff, 1987), and recent records (Khan, 1921; Muir, 1941). It was found necessary to divide the influxes of cattle into the islands of Unguja and Pemba in three major historical epochs (Ali, 1997). Far back in history, cattle were introduced by migrating people from southern Arabia and India, either through the mainland of East Africa or directly via the sea route. In the middle centuries (1500-1700), slave and maritime trade were responsible for bringing in cattle from the mainland of East Africa. Lastly, in

the colonial era of the 19th century and the period that followed, cattle were imported for either experimental purposes, commercial production, or slaughter, and more so to Unguja than to Pemba. Although the origin of zebu cattle in Zanzibar can be traced to sources in India and southern Arabia, analysis based on past history, physical characteristics, and population data would tend to suggest greater similarities to small East African Zebras from the mainland of East Africa, with some noticeable features of Boran and Somali cattle.

Physical and Production Characteristics

The outcome of the different means by which cattle entered Zanzibar and the subsequent exposures to climatic and management features existing in the islands of Unguja and Pemba is the occurrence of a cattle population with some unique features. The Zanzibar Zebu, as cattle of these islands are called, show variability in colour patterns (Figure 1 and 3). The commonest colours are of the reddish type (light red, dun, roan, and brindle), black, and grey. Local Zebu cattle were described by Tidbury (1954) as being small, neat animals, whose height at hook bones is usually between 104 and 125 cm, with usually small and flat horns and with a pronounced hump. Adult bulls were reported to weigh on average about 320 kg and cows about 250 kg. Work carried out recently by the present author in Pemba from which also the cattle studied by Tidbury originated found lower values for both height at withers and estimated body weights (see table 2). Body weights in this study were estimated using the following regression equation: Body weight (kg) = -293 + 3.68 Heart girth (cm), developed after measurements were initially made on a sample of 37 zebu cattle at the Mtakata Dairy Farm where the weighing bridge could be obtained. An interesting observation of the recent work is the lower values of body measurements for bulls compared to cows. This could be explained by earlier off-take of bulls under field conditions

Table 1. Total number of cattle in Zanzibar.

Year	Unguja	Pemba	Total
1913	4 614	6 534	11 148
1938	6 908	30 061	36 969
1947	6 640	27 668	34 308
1951	9 662	32 969	42 631
1960	16 233	31 525	47 758
1966	19 599	30 179	49 778
1978	28 225	31 915	60 140
1985	28 365	48 000	76 365
1993*	45 750	65 943	111 693

*=1992/93 Zanzibar livestock census (preliminary report)

Source: Department of livestock.

and hence in such cases measurements would be made with younger animals (see age range in table 1).

It is generally believed that cattle in Unguja and Pemba are used for milk, beef and traction. But the work done recently by the author indicated cattle in Pemba serving more as living savings accounts to insure against unforeseen events. Pemba cattle are smaller than those found in Unguja, but are said to be relatively better milkers (Payne, 1970). Mean lactation yield for cows in Pemba (excluding milk taken by the calves) was estimated by Griffin (1986) to be 205 litres for a mean lactation length of 205 days. Mean weaning age for calves was estimated to be 13 months and calving percentage for cows of only 35% due to long periods of anoestrus. There is also some seasonality in occurrence of oestrus with peak observations in the months of October, November, December and January due to the relatively better condition of cattle than in other months. On average Zanzibar Zebu calve for the first time at

3.5 years of age and the average calving interval is about 20 months. Figure 2 shows a Zanzibar Zebu heifer. Figure 4 represents a grazing Zanzibar zebu cow.

Climate and Soils

In general the climate to which the cattle in Zanzibar are exposed is shaped very much by the trade winds of the tropical Monsoon system. The rainfall pattern is bimodal in nature, with a long rainy season (*Masika*) from mid March to the end of May, and short rains (*Vuli*) in the months of October to December. Comparing the two islands, Pemba, on average, receives more rainfall (1 900 mm) than Unguja (1 600 mm). The distribution of rainfall is such that there is more rainfall in the western sides than in the east. Temperatures in Zanzibar are high during the short dry season of January to February, with



Figure 1. Zanzibar Zebu. Various colour patterns.

maximum mean of 32°C, and low during the cool season lasting from May to September. The mean annual maximum and minimum temperatures are 29.3°C and 21.1°C, respectively. The relative humidity is high, with a monthly average ranging from 87% in April (*Masika*) to 76% in November (*Vuli*), and a minimum at 60% during the dry season.

According to earlier local classification based on physical characteristics, soils of Pemba can be categorized into upland soil types differentiated by geomorphology, and lowland soils whose parent material forms the basis for classification (CATAD, 1988). In general, soils of the western side of both Unguja and Pemba are deeper than those of the eastern side. This feature, together with the rainfall pattern described before, is associated with many differences of agricultural significance and actually forms the basis for the agroecological zonification of the two islands into the deep soil zone on the western side and coral rag zone to the eastern side.

Management

The management of cattle for most farmers in Zanzibar is rather traditional, involving limited use of shelters and veterinary inputs (Griffin, 1986; CATAD, 1988; Ali, 1997). Most farmers have no formal education and have acquired knowledge of livestock keeping through field experiences. Tethering is the dominant grazing system of feeding animals. This may be a response to limitations associated with raising livestock in crop producing areas where conflicts with crop farmers is a sensitive issue. Grazing is done on permanent crops, in fallow lands, and in the interseasonal crop lands in sophisticated systems of cattle movements. Fodder shortage is perceived by farmers as the most common problem of livestock keeping (Griffin, 1986; Ali, 1997). Field experiences point out the cyclical loss and recovery of condition among animals with seasons in Zanzibar. Diseases and insect disturbances are only secondary problems making the use of veterinary inputs a rare thought in the

minds of most livestock keepers. East Coast Fever is the primary health concern, particularly for young animals. Worms and other malaise become a health threat during the dry season when fodder is scarce and animal conditions are weak. Griffin (1986) observed morbidity and mortality rates of 53% and 7%, respectively, for cattle in Pemba. This implies that even though animals do suffer from various health problems, the majority recover and only few die.

Numbers

Data for total number of cattle in Zanzibar for the period from year 1913 to 1993 is presented in table 2 and table 3. It is evident from table 2, that the cattle population in the two islands has increased ten-fold from 1913 to 1993. Pemba has however comparatively more cattle than Unguja. This can be traced from 1913 onwards where the official records are available. Whereas for Unguja there was a slow growth at the beginning, for Pemba the period between 1950 and late 70's appears to have been very critical for the growth of the cattle population.

The Zanzibar Zebu is included in the World Watch List of domestic animal diversity as a breed at risk (FAO, 1995). It is unclear why such categorization is made to the Zanzibar Zebu if the name refers to all cattle in these islands, whose population is in the tune of many tens of thousands. The argument presented in this paper for the need to conserve Zanzibar Zebu is not based on its risk status as judged by the number of breeding individuals, but rather to genetic erosion due to widespread use of cross-breeding and to consequences emanating from the current economic reforms.

Implications for Conservation

Although livestock genetic resources in Zanzibar appear to be largely of similar origin to those found elsewhere in East Africa, the geographical and environmental features in the islands of Unguja and Pemba have

Table 2. Characteristics of Zanzibar Zebu.

Traits	Bulls (n = 33; age range 2-6 years)	Cows (n = 147; age range 2-18 years)
	Average±SE	Average±SE
Withers height (cm)	99.9±1.1	102.8±0.5
Heart girth (cm)	123.9±1.9	128.4±0.9
Body weight (kg)	162.9±7.1	179.4±3.4

Table 3. Total number of cattle in Zanzibar by class.

Class	Unguja	Pemba	Total
Bulls	5 699	10 513	16 212
Cows	20 391	26 143	46 534
Heifers	9 039	12 073	21 112
Male calves	5 203	8 686	13 889
Female calves	5 418	8 518	13 936
Total	45 750	65 943	111 693

Source: MALNR (1993). Zanzibar livestock census 1992/93 (preliminary report).



Figure 2. A Zanzibar Zebu heifer.

shaped livestock populations, particularly cattle, into unique types. The existence of tsetse flies in Unguja island is a factor that has disturbed cattle populations over many generations. Therefore, Pemba has historically served as refuge sanctuary for cattle in Zanzibar. The cattle of Pemba have, however, been exposed to the challenges of East Coast Fever (ECF) over many generations, and natural selection has probably favoured animals which are to some extent resistant to this disease. ECF is claimed to have wiped out a large number of cattle in the region from time to time. Both Unguja and Pemba are islands and are geographically isolated from the mainland of East Africa. For Pemba, the isolation has been strengthened by the fact that the channel separating it from the

mainland is wider (56 km) and deeper than that of Unguja. This isolation has made the cattle population of Pemba one of the most closed in the region. Inbreeding has probably prevailed for generations and loss of genes is probable.

Besides inbreeding, the threat due to extensive introduction of exotic breeds by means of artificial insemination demands close attention. Currently, artificial insemination is commonly carried out in cattle in the deep soil zone where demand for milk is high. Artificial insemination permits very rapid replacement of existing populations (Cunningham, 1992). Therefore, if cross-breeding is allowed to continue unchecked, chances of losing the indigenous cattle are very high. Another threat to the



Figure 3. Zanzibar Zebu. Various colour patterns.



Figure 4. A Zanzibar Zebu cow grazing using a tether.

cattle of Zanzibar is the growth of tourism and the hotel industry. It is possible that the demand for beef to supply the chain of hotels in these areas might tempt farmers to sell their cattle at numbers far beyond the reproductive rate of the population. Sales are even called for because the original grazing areas are now the important sites for hotel businesses. The eastern coast that includes most of the coral rag lands in Zanzibar were important cattle refuges for the country. The prices of beef in Zanzibar town on the Unguja island is very high compared to that of other parts in the country. This is currently causing a drain of cattle in large numbers from rural areas of Unguja and from Pemba into Zanzibar town for slaughter purposes.

Therefore, it can be concluded that the conservation of cattle in Zanzibar is of paramount importance. In this endeavour both *in situ* and *ex situ* methods should be adopted. However, before any steps for conservation are considered, it is important to

document genetic differences between cattle of Zanzibar and those found elsewhere in Tanzania. This work should be preceded by characterization work involving base-line surveys and monitoring of population status in the two islands. Efficient and effective conservation work may mean in the first place the need to review the legal and policy aspects associated with animal genetic resources. In this regard the commitment of the government is of utmost importance.

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The use of DNA markers in deciding conservation priorities in sheep and other livestock

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Summary

The genetic diversity of most livestock species is reducing and it is not possible to preserve all livestock breeds. In order to preserve as much of the genetic diversity as possible we must first have a robust method of measuring the genetic differences between breeds. The analysis of microsatellite allele frequency is now the method of choice. Using sheep as an example, this paper describes the methods used for both microsatellite amplification and the analysis of the data once it has been collected.

Resumen

La diversidad genética de muchas especies ganaderas ha quedado muy reducida y no es posible preservar todas las razas. Para poder preservar el mayor número posible de razas, debemos, en primer lugar, poseer un método riguroso de medida de las diferencias genéticas existentes entre razas. El análisis de la frecuencia alélica de microsatélites es hoy en día un método importante. Tomando como ejemplo los ovinos, este artículo describe los métodos utilizados para la amplificación de microsatélites y el análisis de datos una vez recogidos.

Key words: *Microsatellites, genome mapping, linkage, DNA, Genetic distance.*

Introduction

The aim of this article is to introduce the new methods that have become available recently to examine the genetic diversity within species. The new methods are based on the discovery in 1989 of microsatellites, a new type of DNA polymorphism (Weber and May 1989). Microsatellites, which are also known as STR's (simple tandem repeats) or SSR's (simple sequence repeats), are a new type of DNA marker that are not only informative but relatively easy to type and score. Microsatellites not only increase the ease of typing but also decrease the number of genotypes needed. This has made them the markers of choice in genetic linkage studies, including making maps and searching for genes affecting productive traits, auditing pedigree records, as well as what we will consider in this paper, estimating genetic diversity.

Genotyping Methods

At the heart of any microsatellite is a simple sequence, either a mono-, di-, tri- or tetra-nucleotide, that is repeated between 10 and 50 times. Virtually all of the microsatellites that have been found for sheep and other ruminants have the sequence (AC/GT) as the repeat unit. The reason for this is not that the other types do not exist but that this type is the most abundant within the ruminant genomes and hence it is much easier to find and characterize. The variation between

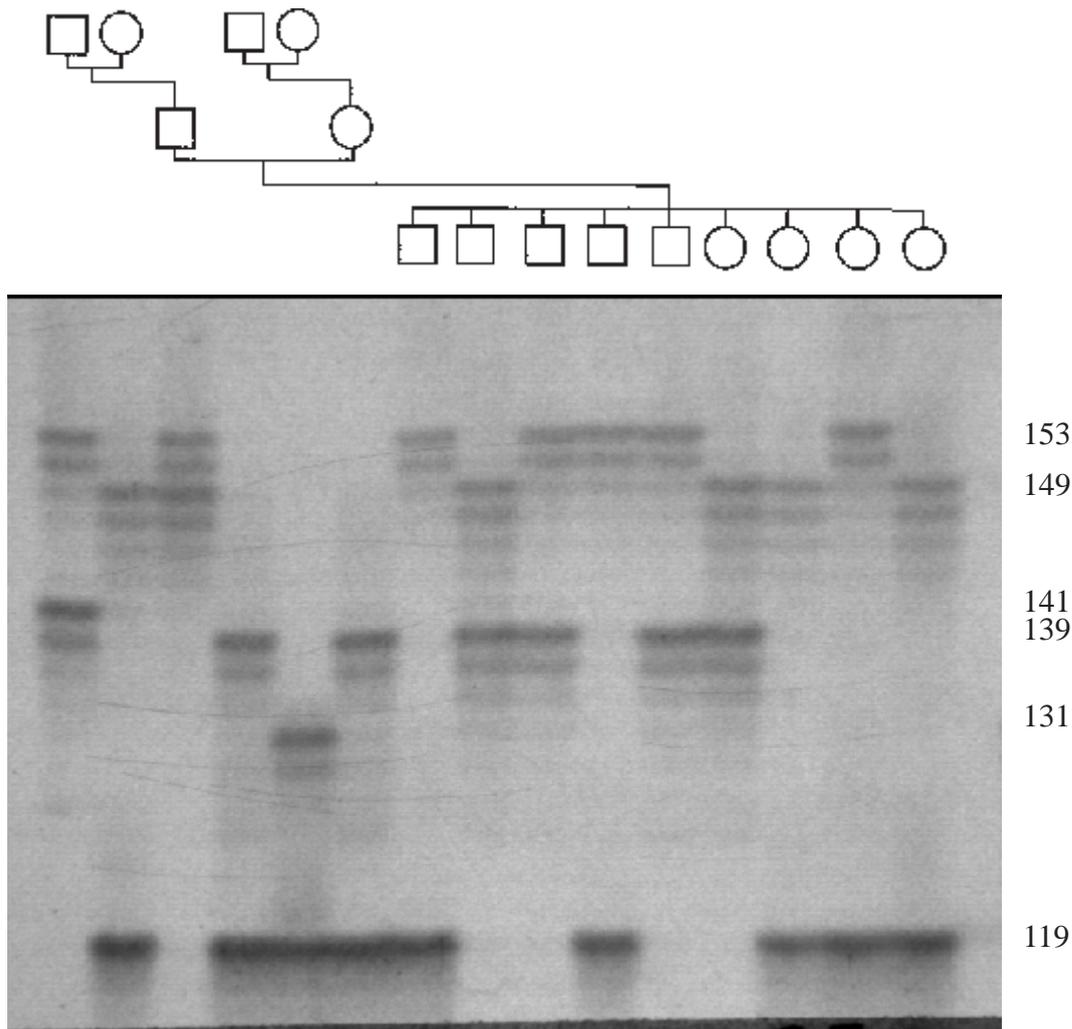


Figure 1. Analysis of a three generation pedigree of sheep with OarFCB226. A total of six different alleles can be identified in this family. The size of the different alleles which range from 119 to 153 basepairs is shown at the right side of the autoradiogram. The structure of the 3 generation pedigree is shown at the top of the figure.

alleles of the microsatellites is due to variation in the number of simple sequence repeats. The way microsatellites are typed is to design primers to the unique DNA sequences on either side of the repeat and, using PCR, amplify the region containing the repeat. The size of the PCR amplicon is then measured, usually by electrophoresis on a DNA sequencing gel, which resolves differences in DNA size.

A typical result from a microsatellite amplification is seen in figure 1. In this case the method of analysis uses radioactivity. One

of the primers used to amplify the microsatellite has been labelled at its 5' end with ^{32}P using T4 polynucleotide kinase. The products of the PCR reactions using the labelled primer are then run on a DNA sequencing gel which resolves length differences of only 1 base pair between PCR products. There are other ways of analysing the PCR products than by the use of radioactive markers. Increasingly one of the microsatellite markers is synthesized with a fluorescent dye attached to the 5' end and an

Table 1. List of microsatellite markers used by the AgResearch Molecular Biology Unit for examining genetic differences between sheep breeds.

Name	Primer sequences (5'→3')	Accession no.	Reference
BM6506	GCACGTGGTAAAGAGATGGC	G18455	Bishop <i>et al.</i> 1993
	AGCAACTTGAGCATGGCAC		
BM757	TGGAAACAATGTAAACCTGGG	G18473	Bishop <i>et al.</i> 1993
	TTGAGCCACCAAGGAACC		
BM1824	GAGCAAGGTGTTTTTCCAATC	G18394	Bishop <i>et al.</i> 1993
	CATTCTCCAAGTCTTCCTTG		
BM4621	CAAATTGACTTATCCTTGGCTG	G18529	Bishop <i>et al.</i> 1993
	TGTAACATATGGGCTGCATC		
BM6444	CTCTGGGTACAACACTGAGTCC	G18444	Bishop <i>et al.</i> 1993
	TAGAGAGTTTCCCTGTCCATCC		
McM357	ATCTCTTTGCTCACCAATTAAGCA	L34279	Hulme <i>et al.</i> 1994
	CCTGAGAAAACATTGAGTGTGCG		
OarFCB20	AAATGTGTTTTAAGATTCCATACAGTG	L20004	Buchanan <i>et al.</i> 1993
	GGAAAACCCCATATATACCTATAC		
OarFCB11	GGCCTGAACCTCACAGTTGATATATCTATCAC	L01531	Buchanan and Crawford 1993
	GCAAGCAGGTTCTTTACCACTAGCACC		
OarFCB128	CAGCTGAGCAACTAAGACATACATGCG	L01532	Buchanan <i>et al.</i> 1993
	ATTAAAGCATCTTCTTTTATTTCCCTCGC		
MAF23	GTGGAGGAATCTTGACTTGTGATAG	M38719	Swarbrick <i>et al.</i> 1990
	GGCTATAGTCCATGGAGTCGCAG		
McM218	GATCCTAGCATCAGTCTCCAGATG	L39828	Hulme <i>et al.</i> 1995
	CACTAAAAGCTTATGAAAGTTCCAGC		
OarHH64	CGTCCCTCACTATGGAAAGTTATATATGC	L12558	Henry <i>et al.</i> 1993
	CACTCTATTGTAAGAATTGAATGAGAGC		
MCM214	AAGCGACTCAGGAGCAGCAG	L38982	Hulme <i>et al.</i> 1995
	AATGCTTGCAATTTATCAAAAAGCC		
ETH225	GATCACCTTGCCACTATTTCT	Z14043	Steffen <i>et al.</i> 1993
	ACATGACAGCCAGCTGTAAT		
MAF209	TCATGCACTTAAGTATGTAGGATGCTG	M80358	Buchanan <i>et al.</i> 1992
	GATCACAAAAAGTTGGATACAACCGTGG		
OarFCB48	GAGTTAGTACAAGGATGACAAGAGGCAC	M82875	Buchanan <i>et al.</i> 1993
OarCP34	GCTGAACAATGTGATATGTTTCAGG	U15699	Ede <i>et al.</i> 1995
	GGGACAATACTGTCTTAGATGCTGC		
OarCP49	CAGACACGGCTTAGCAACTAAACGC	U15702	Ede <i>et al.</i> 1995
	GTGGGGATGAATAATCCTTCATAAGG		
OarFCB304	CCCTAGGAGCTTTCAATAAAGAATCGG	L01535	Buchanan <i>et al.</i> 1993
	CGCTGCTGTCAACTGGGTCAGGG		
OarCP20	GATCCCCTGGAGGAGGAAACGG	U15695	Ede <i>et al.</i> 1995
	GGCATTTCATGGCTTTAGCAGG		

automated DNA sequencing system (eg ABI 377) used to analyse the fragments. There are also some methods available which use ethidium bromide staining to detect and analyse the PCR fragments in non-denaturing polyacrylamide gels. An excellent Web site which describes in great detail the various methods used to isolate and conduct microsatellite analysis can be found at:

<http://www.inapg.inra.fr/dsa/microsat/microsat.htm>.

For most livestock species there are now many microsatellite markers to choose from, far more than is necessary to compare allele frequencies between breeds. We, therefore, have the luxury of choosing those markers that are highly variable and also are very

reliable and robust to use. The markers that we have chosen to use for the analysis of different sheep breeds are listed in table 1.

The mutation rate of microsatellites is very high by comparison with mutations that occur in other regions of the genome. Estimates in sheep are that a mutation, which is either the deletion or insertion of repeat units, occurs at a rate of $1.3 \pm 0.5 \times 10^{-4}$ mutations per gamete per generation (Crawford and Cuthbertson 1996). This rate is approximately 10 fold higher than the mutation rate for DNA sequence in the D-loop region of the mitochondrial genome and between 100 and 1 000 fold higher than the mutation rate of intronic genomic DNA. It is this high mutation rate which makes microsatellites ideal for examining genetic variation within a species.

For most studies of breed diversity it is recommended to type at least 20 animals at as many loci as practically possible with a minimum of 20 loci (Nei and Takezaki 1996). Assuming we are examining 20 loci, a mutation rate of 1×10^{-4} mutations/gamete/locus means that a new allele is likely to arise at any one of the 20 loci with every 250 animals born. Given the random nature of these mutations it is not hard to imagine that it would not take long for two populations that have been kept apart to begin to show different allele frequency differences. It is these allele frequency differences which are used to determine how long ago the populations studied have been apart.

Another important consideration when dealing with very rare breeds is that small population sizes will reduce one's ability to accurately estimate genetic differences as such things as founder effects will distort allele frequencies. Various statistical methods are available for analysing gene frequency data when the effective population size is small eg. (Wilson, 1980) but these lie beyond the scope of this article.

Statistical Methods

One intention of statistical methodology is to understand characteristics of the natural variation of populations, and to estimate these from subsamples of the population. The extent to which two (or more) comparable populations differ can then be assessed relative to the amount of variation within the populations.

A microsatellite from a sheep of a given breed provides a pair of alleles which are independent of each other and can be described in terms of the number of basepairs of DNA. These define categories, and so the distribution of counts within a population is multinomial. This assumes that individuals are independent of each other, and so must be unrelated, as well as randomly assigned. A standard way to compare the allelic composition of several populations, then, is to use a chi-squared contingency table, which can be analysed using a Poisson generalized linear model with log link function (McCullagh and Nelder, 1986). Terms are fitted for r alleles and c populations, and a test is given by the residual deviance, which has a $\chi^2_{(r-1)(c-1)}$ distribution. Often categories for rare alleles are combined, or merged with the common allele of the next smallest basepair number.

A widely-used measure of the difference in genetic composition of two populations is given by Nei's (bias corrected) genetic distance (Nei, 1978), denoted by D . If t is the time since the two populations diverged from a common ancestor population and μ is the mutation rate per generation, then the expected value of D is approximately $2\mu t$. So if the mutation rate is known, the time at which populations diverged can be estimated, or vice versa. This assumes that the ancestor population was in Hardy-Weinberg equilibrium, which can be tested using a likelihood ratio test (Weir, 1990). Standard errors can be calculated by resampling. Often calculated parameters can be compared with historically known dates (Buchanan *et al.*, 1994).

There are a number of more recent measures of genetic differentiation which relate specifically to microsatellites [see, for example, Goldstein *et al.* (1995), Slatkin (1995)]. A comparison of the various measures, focusing on their use in phylogenetic tree construction, (Takesaki and Nei 1997) found the D_A (Nei *et al.* 1983) and D_G (Cavalli-Sforza and Edwards 1967) are the most efficient in obtaining correct tree topology. The measures D_S (Shriver *et al.* 1995) and $(\delta m)^2$ (Goldstein *et al.* 1995a) were found to be the best at estimating the branch length of trees.

Further insights into population differences can be gained from resampling methods. For example, to determine the extent to which a set of alleles identifies the population of origin, the genotypes across all microsatellites of 1 000 individuals were simulated, assuming they belonged to a given population *a priori*, and each most likely population of origin *a posteriori* was calculated by Bayes' Theorem (Buchanan *et al.*, 1994). This approach has shown strong population identification based on 8 or more microsatellites.

Conclusion

Most of the endangered livestock breeds are found in regions far from the molecular genetics laboratories required for microsatellite analysis. This could be seen as a major problem for the widespread adoption of this technology. Fortunately only a small amount of animal tissue is required as a source of DNA to enable the analysis to be performed. DNA can be extracted from tissues which are easily collected, transported and stored, such as hair and wool follicles or small samples of ear tissue. In this way it should be possible to document the genetic diversity of rare breeds of livestock regardless of where they are found. Until we have information about the genetic relatedness of breeds no rational decisions can be made regarding which breeds should be preserved for future generations.

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