Feature Article

Breeds and lines of sheep suitable for production in challenging environments

Schalk W.P. Cloete,[†,‡] Johan C. Greeff,[ǁ,$] Cornelius L. Nel,[†,‡] and Ansie J. Scholtz[‡]

[†]Department of Animal Sciences, Stellenbosch University, Matieland 7602, South Africa
[‡]Department of Agriculture, Western Cape, Elsenburg 7607, South Africa
[ǁ]Department of Primary Industries and Regional Development, Perth, South Perth, WA 6151, Australia
[$]Institute of Agriculture, University of Western Australia, Crawley, WA 6009, Australia

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Implications

- The resistance of unimproved, indigenous fat-tailed sheep breeds and their composites to ticks and heat make them suitable when challenge conditions are high.
- Within-breed selection in Merinos resulted in lines resisting challenges from internal parasites, blowfly strike, and sheep lice.
- Lamb survival benefitted from selection for number of lambs weaned per ewe mated, being able to resist cold stress during a winter lambing season.
- Variation between breeds as well as between animals within breeds can thereby be exploited to allow the better adaptation of sheep to challenging environments.

Introduction

The adaptability and success of sheep are confirmed by the fact that they are the world's most diverse mammalian livestock species, contributing some 25% to the global number of farm animal breeds (Cottle, 2010). The latter author showed that the ovine species is indeed globally successful and present in farming landscapes throughout the world, ranging from arid to high rainfall areas and from sea level to the highest mountains. Sheep are often farmed in resource-poor and otherwise marginal regions, constrained by climate and soil type (Cloete and Olivier, 2010). There is also consensus that the global climate is highly likely to become more unstable in future (Rust and Rust, 2013). Droughts are expected to become more intense and persist longer, also leading to periods of prolonged heat stress (Van Wettere et al., 2021). Challenging environmental conditions are often characterized by further constraints, such as a variety of external and internal parasites (Karlsson and Greeff, 2012), as well as extremes in terms of climate, soil, and topography (Cloete and Olivier, 2010). Challenging climatic conditions at lambing also commonly compromise lamb survival (Pollard, 2006). Fighting and controlling endemic diseases and other stressors represent a considerable cost to livestock production, creating the need for more robust and easy-care animals being able to thrive in particularly challenging environments (Friggens et al., 2017).

This paper seeks to (1) explore the utilization of divergent genetic resources including unimproved, adapted indigenous resources to contribute to sustainable sheep farming in challenging environments; and (2) determine the role that lines of sheep, derived from directed genetic selection to resist such stressors, must play in such conditions.

Internal and External Parasites

Gastro-intestinal nematodes

Gastro-intestinal nematodes are major parasites of economic importance, infesting sheep in all producing areas (Kelly et al., 2010). These nematodes can be divided as hematophagous worms such as *Haemonchus contortus*, more commonly found in areas with summer rain, or irrigated pastures as opposed to non-hematophagous worms such as *Teladorsagia* spp., *Trichostrongylus* spp., and *Nematodirus* spp. in more temperate winter rainfall areas where irrigated pastures are uncommon (Besier et al., 2010). The acquisition of resistance to the major drenches used for chemical control is a problem in the sustainable management of these parasites (Kelly et al., 2010; Bath, 2014), and farming with resistant breeds or lines is considered as an alternative to relying on chemical drenches alone. In breeding programs, fecal worm egg count (FWEC) is commonly used as a proxy for nematode burdens (Colditz and Le Jambre, 2008).

Adapted Red Maasai sheep had lower values for FWEC than Dorpers under conditions of high challenge with *H. contortus*

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(Baker et al., 2003, 2004). Red Masaai sheep also outperformed Dorpers in terms of reproduction in the semi-humid region, but not in the semi-arid region (Baker et al., 2004). Good et al. (2006) similarly reported that Texel sheep were more resistant to gastro-intestinal nematodes than Suffolks, although reasons for this breed effect was not evident. Cloete et al. (2016) also reported that Dormer lambs had lower means for FWEC than South African Mutton Merino lambs during 6 of 8 yr studied. No direct selection for a low FWEC was practiced in either breed. Based on FAMACHA© eye scores, Dormer lambs were slightly less anemic than their SAMM contemporaries, with better condition scores. It might be that the improved energy reserves of Dormers relative to SAMM lambs contributed to the apparently greater resistance.

Many research groups have successfully bred sheep for lower FWEC (see Morris et al., 2005) within breeds. Karlsson and Greeff (2006) selected Merino sheep for low FWEC in a Mediterranean environment over a 15-yr period. FWEC genetically decreased on average by 2.1% per year. More importantly selection not only reduced FWEC in the selection line, but also significantly reduced the number of intestinal worms (immature and mature) and their egg laying ability in sheep that received a high or a maintenance level of nutrition (Greeff et al., 2019). The mean worm burden in the resistant line was only 7% of that in the control line (Kemper et al., 2010). However, there was a tendency for animals in the resistant line to become more prone to develop dags (Karlsson et al., 2005), particularly in a Mediterranean environment (Karlsson et al., 2004). It is therefore important to also select against dags in breeding programs to increase worm resistance based on FWEC.

Adapted indigenous and selected genotypes were better able to withstand the challenge from local parasites, even in more susceptible breeds such as the Merino and even on a low feeding level. It is thus not surprising that FWEC made its way to formal sheep recording schemes in Australia and New Zealand (Brown and Fogarty, 2017). Modelling studies indicated that breeding sheep for resistance to parasites should be more productive (Bishop, 2011). This prediction was supported by Greeff and Karlsson (2020) indicating that Merino sheep that were 21% to 25% more worm resistant than the progeny of the control sires were 1.6 kg heavier at weaning, received less anthelmintics during the experiment, and produced 0.3 μm finer wool at hogget shearing than progeny from control sires.

Breech strike by blowflies

Cutaneous myiasis, primarily caused by larvae of the Australian Sheep blowfly, *Lucilia cuprina* under humid and warm conditions, is a major source of production loss of wool sheep, while also having a marked impact on animal welfare (Horton et al., 2017). Flystrike of primarily the breech area was largely controlled by chemicals, as well as a surgical procedure referred to as the Mules' operation, where the folds on either side of the perineal area of lambs are surgically removed (Greeff et al., 2014; Horton et al., 2017). Chemical resistance of blowflies as well as welfare considerations regarding the Mules' operation necessitate other means of dealing with flystrike such as breeding for a lower incidence of flystrike (Horton et al., 2017).

One of the difficulties of breeding for a resistance trait is to provide all sheep with an equal challenge (Scholtz et al., 2010; Greeff et al., 2014, 2017). Moreover, the incidence of flystrike is dependent on a favorable climate, causing it to be transient and unpredictable. Therefore, through favorable genetic correlations with breech strike, several indicator traits were identified to serve as a proxy for the susceptibility of sheep to flystrike (Scholtz et al., 2010, 2011; Greeff et al., 2014, 2017). These traits are wrinkles in the breech area (Figure 1a), fecal soiling or dag formation (Figure 1b), urine stain, and larger bare areas around the breech and crutch. Neck wrinkle score also qualified as a significant indicator trait and is a particularly useful alternative trait where it is difficult to score breech wrinkle (Scholtz et al., 2010; Greeff et al., 2014). It is important to note that these traits are equally effective when an adequate blowfly challenge is absent and are therefore amenable for inclusion in formal evaluation schemes (Brown et al., 2010). However, skin wrinkle and fecal soiling only explains about 40% of the variation in breech strike in a Mediterranean environment (Greeff et al., 2017). In contrast, Smith et al. (2009) found that skin wrinkle was the dominant factor in a summer rainfall region. In a study on crossbred sheep, Scobie et al. (2008) found that dag score was negatively correlated with breech bareness score of sheep. This was in contrast with findings of Greeff et al. (2017) and Smith et al. (2009) who showed that bare breeches are not important in Merino sheep. Although the incidence of breech strike increased with an increase in skin wrinkle and dags (Greeff et al., 2014), a significant proportion of sheep with high skin wrinkle and dag scores were never struck. Large differences in breech strike were found between sire progeny groups, which were not entirely explained by breech wrinkle and dag scores (Greeff et al., 2018). None of the daughters of the two most resistant sires were struck over their lifetime, whereas a high proportion of the daughters of the two most susceptible sires were struck every year over their lifetime. The repeatable nature of breech strike implied that other factors, inherent to sheep, contribute to susceptibility of individual sheep. Further studies on breech moisture failed to conclusively account for the prevalence of breech strike when wrinkle and fecal soiling were considered (Greeff et al., 2022). However, Yan et al. (2019) demonstrated that the semiochemicals, octanal and nonanal, evoked an antennal and behavior response in gravid *L. cuprina* females, confirming the potential role as of these substances to attract *L. cuprina*. Greeff et al. (2021) found that odor profiles attracting blowflies are inherent to specific sheep and independent of the microbiome. Further studies on odor profiles of breech strike resistant and susceptible sheep are warranted.

Ticks

A variety of tick species across the world are hosted by sheep. The impact of these ectoparasites on their hosts is detailed by Cloete et al. (2016) and include the transmission of

Figure 1. Extremes in terms of breech skin wrinkles (a) and soiling by feces and urine (b) are conducive to flystrike under climate conditions favorable for blowfly activity.

disease, severe tissue damage and necrosis, the production of toxins that may cause paralysis, tissue damage on the udders and hooves of animals, blood loss at high infestations and "tick worry". All these factors combine to cause serious welfare issues in livestock at high tick loads (Porto Neto et al., 2011). Tick control in the past mostly centered on the usage of acaricides to curb the infestation. However, as for gastrointestinal nematodes and blowflies noted above, the major tick species became resistant to this line of defense (Porto Neto et al., 2011) and alternative measures of tick control are seriously needed.

As for other pathogens, ticks may also be controlled to an extent by farming with breeds expressing a higher level of resistance to the pathogen. An indigenous, unimproved fat-tailed breed, the Namaqua Afrikaner (Figure 2), had lower tick loads than those of internationally farmed commercial Dorper and SAMM ewes under extensive conditions, particularly in the sensitive loin and udder region (Cloete et al., 2016, 2017). Udder health scores were improved in the Namaqua Afrikaner when compared the other breeds (Cloete et al., 2016), with fewer Namaqua Afrikaner ewes being culled for udder problems than SAMM ewes (Cloete et al., 2016). A similar overall result was found when Namaqua Afrikaner lambs were compared to Dorper lambs (Cloete et al., 2021a). The cross of Namaqua Afrikaner rams with Dorper ewes produced lambs resembling the Namaqua Afrikaner regarding their lower tick loads and the Dorper regarding their higher weaning weights (Cloete et al., 2021a). Favorable hybrid vigor was thus suggested for both tick count and weaning weight, but this was not true for tick counts when crossing the commercial Dorper and SAMM breeds (Kao et al., 2022). It stands to reason that non-additive variation for a fitness trait such as tick load may not be present when two relatively susceptible commercial breeds are considered. Farming with a locally adapted indigenous breed may thus be advisable under conditions of severe tick challenge and general failure of chemical control. When contemplating breed substitution, however, it needs to be considered, though, that the Namaqua Afrikaner was generally inferior to the commercial breeds for carcass traits (Burger et al., 2013), mature live weight (Cloete et al., 2016), and weaning weight (Cloete et al., 2021a).

Limited other studies explored breed effects for tick burdens in sheep. Female *Ixodes ricinus* ticks were more likely to infest Scottish Blackface than Cheviot ewes (Macleod, 1932). Dorper and Merino sheep were also studied on Karoo shrub pasture (Fourie and Kok, 1996), with a lower burden of the tick species *Ixodes rubicundus* in Merinos. This result contrasts with the conclusions drawn above, as no differences were found between the Dorper and another wool breed (SAMM) in the study of Kao et al. (2022). In fact, autumn total tick counts were higher in SAMM than in Dorper ewes, whereas this breed difference was not recorded in spring (Cloete et al., 2017). The contrasting results between the South African studies may be associated with different tick species studied. Fourie and Kok (1996) related their results to different grazing habits in the breeds studied. Nevertheless, it is evident that further research is needed to inform industry on the putative benefit of breed substitution to alleviate the impact of ticks on extensive sheep.

Figure 2. The Namaqua Afrikaner breed carry lower tick loads than commercial breeds, while it also copes better with heat.

We could not find evidence on within-breed selection to establish ovine lines exhibiting a higher resistance to ticks. It is worth mentioning that worthwhile genetic variation in tick loads has been established in South Africa (Cloete et al., 2016, 2017) and Norway (Sae-Lim et al., 2017). These studies laid the foundation for within-breed selection, should it be desired.

Sheep mites and lice

Mange mites of small ruminants have an important impact on feed intake, while lesions caused by mite activity cause skin damage, resulting in rejections of skins by the leather industry (Asmare et al., 2016). Mange mites predominantly belong to three genera, namely: *Sarcoptes*, *Psoroptes*, and *Demodex*. Sheep scab, resulting from infestation by *Psoroptes ovis*, in particular, is an important condition of sheep, affecting welfare by causing restless and pruritic behavior and resulting in losses of wool and body condition due to an impaired intake (Van den Broek and Huntley, 2003). These authors suggest that breed differences indicate that it may be feasible to reduce the prevalence of sheep scab by genetic selection. It has indeed been demonstrated that scab lesions on Dorper meat sheep are smaller and more difficult to detect when compared to the Merino, as representative of wool sheep (Fourie et al., 2002). The authors, however, cautioned that the informal trade in Dorpers, combined with the difficulty to detect sheep scab in this breed, may contribute to the uncontrolled spread of the condition. No evidence to successful within-breed selection for a reduced susceptibility to sheep scab was found in the literature, and no heritability estimates could be sourced.

The sheep louse, *Bovicola ovis* (previously *Damalinia ovis*), is an important ectoparasite of sheep. It is an obligate parasite with no off-host stage and poor survival away from the host (James and Crawford, 2001). The chemical load of the Australian wool clip is markedly influenced by the pesticides used to control sheep lice (James, 2002), making it an important parasite from an economic perspective. Infestation with *B. ovis* results in mild to severe pruritis, thereby compromising sheep welfare while also reducing fleece weight by 0.12–0.22 kg per year (James et al., 2011). James and Nattrass (2001) reported an approximately tenfold higher lice count in Polypay ewes compared to Columbia ewes over a 2-yr period, using artificial challenge under housed conditions. James et al. (2002) also reported strain differences within the Merino breed in total lice counts, showing that strains within the more susceptible Merino breed may differ for their ability to withstand lice challenge. This indication of genetic variation between animals within a breed was supported by moderate levels of genetic variation for lice counts (Pfeffer et al., 2007).

Climatic Extremes

Climatic impacts on sheep are pertinent, as they are mostly farmed under extensive pastoral systems, or on modified agricultural landscapes, where they utilize crop residues and legumes forming part of ley-farming systems in cropping enterprises (Cloete & Olivier, 2010). Compared to other livestock, sheep are relatively resilient as far as heat stress is concerned (Rust and Rust, 2013). Nevertheless, the extensive settings and general lack of shelter common to most sheep enterprises commonly expose them to both heat and cold stress.

Figure 3. The Meatmaster was primarily descended from Dorper rams crossed to indigenous ewes (mostly the Damara). The breed copes well with heat when compared with commercial breeds.

Impact of heat

Extended exposure to heat stress can profoundly impact sheep performance, by impairing ewe conception, embryo survival, ram fertility and libido, and in utero lamb growth (Sawyer and Narayan, 2019; McManus et al., 2020; Van Wettere et al., 2021). Hopkins et al. (1980) showed that heat stress was associated with lower lamb birth weights and suggested that poor lamb survival of tropical Queensland Merinos was due to heat stress. In their review on the status and utility of indigenous genetic resources, Molotsi et al. (2020) listed tolerance to heat stress as one of the advantages of unimproved, indigenous breeds such as the Namaqua Afrikaner. This claim was supported by results from Cloete et al. (2021b), indicating that the respiration rate of Namaqua Afrikaners increased by only 84% from cool morning temperatures of 18.9 °C to hotter afternoons of 30.2 °C. In comparison, the respiration rate of Meatmasters (75% indigenous; see Figure 3) increased by 131%, that of Dorpers (50% indigenous) by 181%, and those of breeds from temperate regions (Dohne Merino, Dormer, Merino and SAMM) by between 203% and 278%. These results imply that the amount of work ewes need to do to maintain homeothermy was inversely proportional to the indigenous content of the respective breeds. Another breed, the Ile de France as a commercial temperate terminal sire breed, was added to these resources when a follow-up study was conducted by Steyn (2022). Rectal temperature (Figure 4) and geometric means for respiration rate (Figure 5) are provided for all breeds for cooler morning and hotter afternoon conditions. Note that the blue (mornings) and red (afternoons) lines on these graphs indicate mean values for the five temperate breeds, the Dorper (as a 50:50 temperate:heat adapted breed) and the Meatmaster and Namaqua Afrikaner as presumably more heat-tolerant breeds. The latter two breeds did not differ markedly and were combined. Morning respiration rates accordingly ranged from an average of 52.4 for the Meatmaster and the Namaqua Afrikaner to 59.9 for Dorpers and an average of 82.8 for the temperate breeds (ranging from 77 in the SAMM to 91 in the Merino; Figure 2). Corresponding averages in the afternoon were 133.3, 157.4, and 181.2 (ranging from 167 in the Dohne Merino to 192 in the Dormer and Ile de France). All breeds were generally able to maintain their rectal temperature in a relatively narrow band (Figure 1) but breeds from temperate regions depended on a higher respiration rate to maintain their core temperatures. If heat stress conditions persist, this additional energy need could compete with energy required for other production functions. Namaqua ewes also outperformed Dorper and SAMM ewes for number of lambs weaned (NLW) under marginal extensive conditions (Cloete et al., 2016). This difference was not seen for total weight of lamb weaned, as the commercial breeds weaned heavier lambs.

The advantage of adapted, indigenous sheep relative to temperate breeds was also seen in India and Egypt (see review

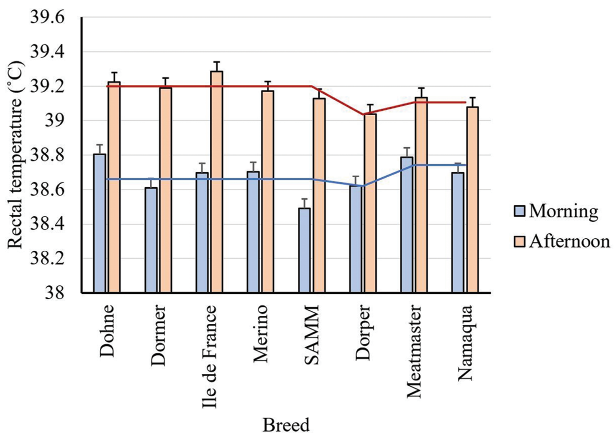

Figure 4. Rectal temperatures of eight sheep breeds during cooler mornings and hotter afternoons. The five breeds on the left of the graph are from temperate regions, the Dorper originated from a cross of a temperate breed with a heat adapted breed, and the two breeds right have a higher indigenous content. The lines are mean values according to the origin of the sheep breed for morning (light blue) and afternoon (red) recording sessions (adapted from Steyn, 2022).

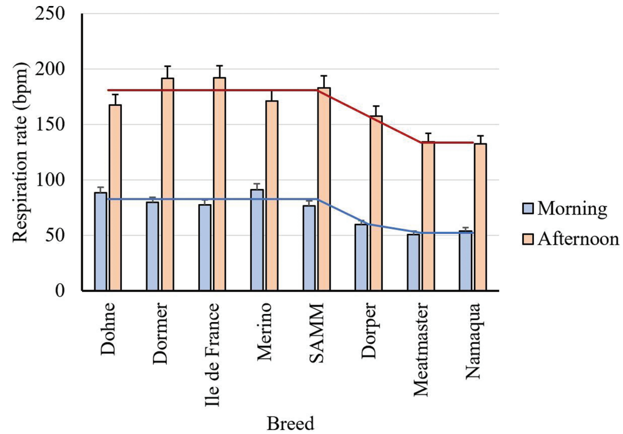

Figure 5. Respiration rates in breaths per minute (bpm) of eight sheep breeds during cooler mornings and hotter afternoons. The five breeds on the left of the graph are from temperate regions, the Dorper was derived from a cross of a temperate breed with a heat adapted breed and the two breeds right have a higher indigenous content. The lines are mean values according to the origin of the sheep breed for morning (light blue) and afternoon (red) recording sessions (adapted from Steyn, 2022).

by Cloete, 2012). In this respect, McManus et al. (2016) used broken stick regressions to determine inflection points for the temperature-humidity index above which values for respiration rate and eye temperature started to increase linearly. The input data included 1,071 repeated records for 80 ewes of 11 breeds, involving a range of breeds from temperate regions and local adapted breeds. These data were superimposed on climate data on a district basis to determine regions suitable for specific breeds. They concluded that the distribution of wool breeds would be limited to the south and southeast of Brazil, while a local adapted breed, the Santa Inés, could be farmed throughout the country. The Dorper could also be farmed widely. In a subsequent review, McManus et al. (2020) contended that the better adaptation of hair sheep to heat stress conditions was not determined by function (hair vs. wool) as such, but rather by adaptation to harsh environments. This contention is supported by results from Hopkins et al. (1980) that Queensland Merino sheep with lower rectal temperatures maintained lower respiration rates and were more likely to rear lambs in successive lambing seasons than those with higher rectal temperatures.

In the absence of heritability estimates for resistance to heat stress in the literature, repeatability (in theory the upper boundary for heritability) could be considered as a proxy. Moderately low repeatability estimates were reported for respiration rate (Cloete et al., 2021b; Steyn, 2022). Rectal temperatures showed very little variation, but were consistently repeatable (Hopkins et al., 1980; Steyn 2022), possibly leaving options for within-flock selection.

Impact of cold

Above-average rain, linked to other aspects such as foot problems, a high FWEC, low liveweight, and a poor condition can result in mortalities among adult sheep (Watt et al., 2021). Ewe mortality could be quite high on individual farms, with ranges per annum from 2.8% to 3.0% (Quinlivan and Martin, 1971), 2.0% to 2.8% (Fourie and Cloete, 1993), 5% to 8% (Morgan-Davies et al., 2008), and 3.7% to 4.4% (Watt et al., 2021). Campbell et al. (2009) accordingly reported that up to one in seven weaners may succumb during the first year after weaning, with low liveweight weaners being particularly at risk. Many of these deaths was not exclusively weather related.

Lamb mortality which may reach 16% to 23% in well-managed flocks is of greater importance, though (Haughey, 1991). Lamb mortality in extensive flocks in marginal areas may be as high as 22% to 40% (Kao et al., 2022). Apart from its direct impact on profitability, it is also considered as a major welfare issue (Brien et al., 2014). The bulk of lamb deaths are associated with birth difficulty and a complex presenting with the etiology of starvation, mismothering and exposure (SME; Haughey, 1991). Births stress is the single most important source of lamb mortality (Haughey, 1991), but SME-like deaths may also be associated with appreciable lamb deaths, especially for unsheltered flocks facing severe inclement weather (Pollard, 2006; Nel et al., 2021a, 2023). It is therefore important to consider the ability of lambs to resist cold stress caused by a combination of rain, wind, and a low ambient temperature.

There is marked variation between breeds in their ability to deal with cold stress, with Merino lambs generally performing worse than lambs of other breeds (Sykes et al., 1976; Slee, 1978). However, when the possibility of genetically improving lamb survival was considered, consensus among analysts was that genetic improvement was unlikely, owing to low heritability estimates that were derived (Brien et al., 2014). Haughey (1983) was probably the first reference to demonstrate that it is feasible to improve lamb survival by genetic selection. Similar results were later reported for New Zealand Marshall Romney lambs (Knight et al., 1988). Later, divergent genetic trends were reported for perinatal lamb survival in a Merino flock selected for and against NLW (Nel et al., 2021b). Selection resulted in a markedly improved lamb survival from birth to 3 d of age in these lines, in favor of the line selected for NLW (Nel et al., 2021a). Lambs from the line selected in the upwards direction were better able to maintain their rectal temperatures than those selected downwards under high levels of cold stress (Nel et al., 2021a). These results corroborate those reporting breed differences for the ability of lambs to resist cold stress, suggesting that the better survival in the upwards selected line stems from a greater adaptability to cold stress conditions. This has been supported on the genetic level by the so-called reaction norm analysis, showing a greater genetic difference in neonatal mortality between selection lines when cold stress levels were high (Nel at al., 2023). These findings lend support to the inclusion of lamb survival by considering ewe rearing ability in the recording and evaluation scheme provided by Sheep Genetics Australia (Bunter et al., 2021). Similarly, lamb survival is evaluated, and genetic trends provided in the scheme managed by Sheep Improvement Limited in New Zealand (Brien et al., 2014).

Conclusion

This study investigated the response of sheep to environmental challenges posed by parasites and the climate. Variation among breeds were occasionally available to allow producers a choice of genotypes that are better able to cope with environmental stressors peculiar to a specific environment. To add to this, within-breed selection was particularly successful in generating lines that are better able to handle environmental stress than the base population they were selected from. There is a need, though, to continue urgently with research on traits indicative of adaptation to adverse climatic conditions. There is also a need to urgently revisit the need for conserving unimproved, indigenous livestock, as they may contribute to understanding the underlying biology of some fitness traits.

Conflict of interest statement. None declared.

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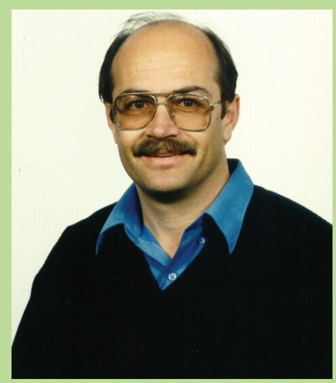
About the Authors

Schalk (SWP) Cloete

After retiring from a specialist scientist position at the Western Cape Department of Agriculture in March 2019, Schalk Cloete continued his career as an extra-ordinary professor at Stellenbosch University. He obtained his BSc (Animal Science and Animal Physiology), BSc Hons (Sheep and Wool Science), and MSc (Sheep and Wool Science) all from Stellenbosch University before obtaining a PhD in Animal Breeding and Genetics from the University of the Free State. He was employed by the Department of Cooperation and Development from February 1978 to February 1979, before joining the Winter Rainfall Region in January 1980. He was transferred to the Western Cape Department of Agriculture in April 1996, where he served until his retirement in March 2019. He specializes in Animal Breeding and Genetics with specific interests in Reproduction, Animal Behaviour, and Welfare. Most of his work is on sheep and ostriches.

Corresponding author: schalkc2@sun.ac.za

Johan (JC) Greeff



Dr Johan Greeff obtained his BSc Agric at the University of the Orange Free State in 1978, BSc Hons (Animal Breeding and Genetics) from Stellenbosch University, and MSc and PhD (Animal Breeding and Genetics) from the University of Pretoria. From 1977, he worked as a research scientist at the Animal and Dairy Science Research Institute at Irene, South Africa, where he undertook crossbreeding studies with the highly fertile Finnish Landrace and Romanov sheep breeds. He accepted a Geneticist position at the Department of Agriculture of Western Australia in 1993. In Western Australia, he specialized in breeding sheep for improved wool quality, and in breeding sheep that are resistant to gastro-intestinal helminths and blowflies. He retired in 2022.

Cornelius (CL) Nel

Dr Cornelius Nel is a scientist within the Department of Animal Science of the Western Cape Department of Agriculture, South Africa. He obtained his BSc, MSc, and PhD in Animal Science at the University of Stellenbosch and currently participates in research in quantitative genetics of farmed animals, mostly sheep. He has been the principal investigator of the first studies incorporating marker data into genetic prediction of South African Merino sheep but has also worked on lamb survival and cold stress resilience. His interests are in the genetic prediction of health and welfare traits, and the use of genomic information to enhance such breeding objectives.

Ansie (AJ) Scholtz

Dr Ansie Scholtz started her career at the Department Agricultural Technical Services (Pretoria) on 15 December 1980. She applied for a transfer to the Western Cape Province (formerly the Winter Rainfall Region) and has been working at the Western Cape Department of Agriculture since October 1989. In the beginning, she was involved in the Animal Feeds Laboratory, but subsequently became involved in Animal Behavioural studies and her own sheep research projects on Integrated Pest Management to control blowfly. She obtained her MTech (Sustainable Agriculture) in 2003 at the Nelson Mandela University of Technology and her PhD in 2010 at the University of the Free State (Centre for Sustainable Agriculture and Rural Development). She is a Production Scientist and has been involved in research projects in Sheep Breeding and Genetics with specific interests in Animal Welfare, Animal Behavior, and Sustainable Agriculture.