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Host resistance to ticks: a potential complementary and sustainable alternative to ticks and tick-borne disease control.

Stephen Mandara[1]*, Antony Maodzeka[2]

1. Department of Animal Production Sciences, Marondera University of Agricultural Sciences and Technology, Marondera. Zimbabwe. Emails: stevemandara@gmail.com ; smandara@muast.ac.zw. Phone: +263 773295080
2. Department of Crop Science and Post-Harvest Technology, Chinhoyi University of Technology, Chinhoyi. Zimbabwe. Email: antonymaodzeka@gmail.com. Phone: +263 786092514

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Corresponding Author
Stephen Mandara
E-mail: *stevemandara@ gmail.com; smandara@ muast.ac.zw*
Phone: *+263 773295080*

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ABSTRACT

Ticks and tick-borne diseases have caused huge losses to farmers due to control efforts and mortalities. The current review highlights the impacts of ticks and tickborne diseases, widespread conventional control methods currently in use, and explores advances in the use of breeding techniques in complementing other tick control methods. Ticks are widely distributed in the world including in Africa, affecting up to 80% of the world's cattle population. Tick-borne diseases cause enormous losses that are felt largely by poorly resourced farming communities. This has a big impact on the livelihoods of these communities. The traditional tick control methods of using chemicals called acaricide have proved unsustainable as evidenced by the continuous huge losses despite decades of usage. The resistance of the host animal to ticks has a huge bearing on the economics of tick control methods but it is often sidelined in control programs. The use of genome-wide association studies (GWAS) and regional heritability mapping (RHM) in identifying genetic regions of interest for cattle tick resistance has increased. Recent studies done across different countries, featuring different cattle breeds have indicated the potential use of genomic evaluation of breeds to tick resistance. Therefore it can be concluded that exploiting the animals' natural resistance to ticks offers another dimension, probably more sustainable, in the fight against ticks and their consequent effects.

List of Abbreviations

GWAS	Genome wide association studies	SNP	Single nucleotide polymorphism
RHM	Regional heritability mapping	QTL	Quantitative trace loci

INTRODUCTION

The major hindrance to profitable and sustainable livestock production in sub-Saharan Africa is the high prevalence of ticks and the diseases they transmit known as tick-borne diseases. The burden is also high in other tropical and subtropical areas outside of the African continent. The losses have been felt from way back into time, with reports of an estimated loss of US$186 million due to East Coast Fever alone in the year 1989 in over 10 countries in sub-Saharan Africa (Dolan 1999). As recent at 2021, Zimbabwe has seen increases in morbidity and mortalities of cattle, due to tickborne diseases, mainly theileriosis (Nhokwara et al., 2023).

Several methods of controlling ticks and consequently tickborne diseases have been used before. The main method used in sub-Saharan Africa is the use of chemicals called acaricides which kill the ticks. Other methods used in the control of ticks, albeit at a smaller scale are biological control methods, tick vaccines and pasture and grazing management. Pasture spelling has been done with fair results in some countries as the method only works against certain tick species such as *Rhipicephalus (Boophilus) microplus* which cattle are the exclusive host (Deken, et al. 2010). Anti-tick vaccines are still largely in the development phase, they gave satisfactory immunity but had to be administered a number of times in a year and needed to be combined with acaricide application for full efficacy. Furthermore they have not been widely adopted in the needy regions of East, Central and Southern Africa. (Kasaija, et al., 2023).

The traditional method of using acaricides to control ticks has become unsustainable due to the high costs of purchasing acaricides coupled with increasing reports of tick resistance to the chemicals. This presents a huge problem to the livestock sector as the high acaricide costs increase input costs in livestock production and also it takes time for new effective chemicals to be developed (Deken, et al. 2010). Furthermore, there is an important issue of the development of ticks that are resistant to these chemicals. These strains evolve at a faster rate than the development of any new chemical, (Kemp et al, 1999) leaving the farmer with chemicals that are increasingly becoming ineffective. All these challenges have an even greater negative effect on the livelihoods of communal farmers that depend on livestock.

Adding on to that, chemical control of ticks has always been criticized for its negative impact on the environment. Chemicals such as arsenic compounds and pyrethroids (which is now the predominant dipping chemical), have all been reported to have varying consequences such as arsenic poisoning of oxpeckers (*Buphagus* species) which threatens them with extinction (Livestock Production Program/Animal Health Program, 2003).

The best solution to the challenges of conventional tick control methods may lie in the identification and use of animal breeds that are naturally resistant to ticks. (Hayward 1981). Tick resistance can be defined as an animal's ability to limit the number of ticks that develop on it to maturity (Utech et al, 1978). Although the environment also plays a role, genetics still bear a significant part of an animal's disease resistance ability (Spickett et al., 1989; Rechav et., 1991). The numbers of ticks that infest cattle show a huge variation, largely believed to be due to the genetic makeup of the host. Several studies have demonstrated that even under the same ecological environment, some breeds of cattle are infested by fewer ticks than do others (Latif, et al., 1991; Marufu et al., 2011) with much of these differences due to the host animal's immunological response to infestation.

Impacts of ticks and tickborne diseases

Ticks are vectors of several major diseases of cattle and also cause other minor ailments, all leading to production losses. Bites from ticks irritate, sometimes leaving wounds that predispose the host animal to screw-worm myiasis, and expose it to other bacterial and fungal pathogens (Bram & George, 2000). In addition, livestock owners also lose due to the costs implicated in treatment, prevention and control efforts. Globally, tick-borne diseases are among the most important causes of production losses for beef and dairy cattle with estimated losses upwards of US$22 billion per year (Tabor, et al., 2017). The tropical and subtropical regions suffer the biggest losses from tickborne diseases than other regions of the world (Estrada-Pena & Salman, 2013). Although there are dozens of tickborne diseases, only a handful are of major economic importance. These diseases are caused by different etiological agents such as protozoa and bacteria, affecting different systems in the body such as the circulatory system and lymphatic system, but are all transmitted by ticks (Jongejan, 2004). The major tickborne diseases affecting tropical cattle will now be briefly discussed below.

Bovine Babesiosis

Babesiosis, also known as redwater or tick fever, is a disease of animals characterised by a fever, anaemia, haemoglobinuria and icterus. It is caused by intra-erythrocytic parasites of the Babesia species transmitted by a number of tick species (Taylor et al. 2004). In sub-Saharan Africa, the most important species are *Babesia bigemina* and B. *Bovis* transmitted by *Rhipicephalus (Boophilus) decoloratus* and *R.(B). microplus* respectively (Urquhart et al., 2007). The exotic European breeds of cattle are more susceptible, although the Zebu and Sanga are also affected. The acute disease manifests via a high fever (above 40°C), inappetance and a reluctance to move. Anaemia and haemoglobinuria (hence the name redwater) follow in prolonged cases with fatalities common as well. Cerebral babesiosis occurs in B. *bovis* infections, with additional signs such as hyperesthesia, head pressing, cycling and convulsions. Chemotherapy with a number of drugs is crucial in clinical cases of babesiosis, and the success thereof hinges on early diagnosis and prompt drug administration. The common prevention method is by controlling the tick vectors by regular dipping of cattle with acaricides at intervals, usually of two weeks or less (Vos et al. 1996).

Bovine anaplasmosis

Bovine anaplasmosis (or gall sickness) is an infectious, noncontagious arthropdod borne disease of cattle caused by the rickettsial organisms, *Anaplasma marginale* and A. *centrale*. The disease is widespread around the world and several tick species are known to biologically transmit the causative organism while some biting flies such as those of the Tabanidae family transmit mechanically (Urquhart, et al. 2007). Clinically, Anaplasmosis is characterized by fever, anaemia, weakness, constipation, icterus and laboured breathing. It also causes production losses due to reduced meat or milk production as animal's recover slowly if they survive acute infection (Drummond 1983) The disease is treated by a combination of drugs, and success also depends on prompt diagnosis and administration of the correct drugs. Prevention is largely by control of tick vectors although a vaccine made from the *A. centrale* isolates is available with varying results obtained around the world.

Heartwater

Heartwater is a septicaemic, often fatal, disease of ruminants. The causative organism is *Ehrlichia ruminantium*, a bacteria which is transmitted by ticks of the genus Amblyomma (Allsop, 2015). The disease is enzootic in sub-Saharan Africa, the areas corresponding to the distribution of the vector species. It has also been reported in the Carribean islands following cattle imports (Allsop, 2015). The perause forms of the disease cause sudden deaths and acute forms are characterized by central nervous system signs such as cycling, head pressing and ataxia. Treatment can result in recovery if given early. Vaccination with blood based vaccines is common in enzootic areas although control of the disease still mainly relies on dipping of cattle with acaricides (Meltzer, Perry, & Donachie, 1996).

Theilerioses

These are diseases caused by the tick-transmitted protozoa, Theileria parva in east and southern Africa. In North Africa, Asia and southern Europe, Theileria annulate is the causative agent. In its classical form, the disease causes severe clinical signs and fatalities. The tick vector is the brown ear tick, *Rhipicephalus appendiculatus*. The different disease syndromes caused by this parasite are East Coast fever, January disease (Zimbabwe Theileriosis) and Corridor disease. The clinical signs are typically fever, swelling of lymph nodes, laboured breathing, sometimes corneal opacity and bloody diarrhoea ending in death (Lawrence, Perry, & Williamson, 1996). Chemotherapy is used in clinical cases although success is largely dependent on early diagnosis and instituting treatment. The infection-treatment method has been used in vaccinations using a vaccine developed in East Africa, the so-called Muguga cocktail. However, acaricide application for tick control is still the main method for controlling the disease with application being done as frequently as less than seven days to control outbreaks.

Conventional tick control methods and their challenges.

Traditionally, ticks have been controlled by the application of chemicals, called acaricides, onto the host animal. The costs involved in this have been a huge burden on the livestock sector. These chemicals often have to be applied every week or every fortnight, depending on the strategy in use. There are also infrastructure development and equipment maintenance costs involved as well. Various methods of application of these chemicals have been used, from dipping tanks to spray-races and hand-dressing. They all have their own merits and demerits such as their efficacy in killing the ticks and the cost of setting up. Thus farmers have the choice to select a preferred method based on their farm circumstances (Deken, et al. 2010).

The use of dipping tanks is a very effective method in tick control as there is usually full immersion of the animal and all tick predilection sites are reached by the chemical. However, they have a high initial cost of setting up, making them out of favour by small-scale farmers unless it's a collective effort, usually led by a government agency. Hand spraying has become a common acaricide application method in the smallholder sector due to the high costs of building dipping tanks. The method has several disadvantages, mainly around inadequate application of chemicals and failure to reach the relatively inaccessible areas on the animal's body such as the ears and axilla. Spray races offer a cheaper alternative to the dipping tank (Deken, et al. 2010). They use many nozzles that try to reach as many parts of the animal as possible. Usually, they have a motor-driven pump that generates high pressure reaching the whole body. They also use smaller amounts of acaricide than the dipping tank. Hand dressing of acaricide is usually done as an emergency and/or complementary method to any of the above methods. It targets particular areas on the animal's body where particular ticks or tick stages are known to habitat. This is usually very effective in eliminating particular ticks.

To add onto the costs of setting up, running and maintaining an acaricide application program, there is another developing, more worrying challenge of acaricide resistance. The genetic selection of acaricide-resistant tick strains has become a major drawback to tick control by acaricides. Tick resistance to acaricides can be defined as a tick strain's ability to tolerate acaricide doses that normally kill the majority of the ticks in a population of that very species (Deken, et al. 2010). It is an evolutionary adaptation due to certain physiological mechanisms in the resistant ticks (Waldman, Klafke, & Jr, 2023). In any given population of ticks, there are always some individual ticks that can better withstand the effects of acaricides but this resistance is not always inherited by their offspring. However, survival against acaricide treatment by these individuals selects only them, and their reproduction increases the proportion of resistant individuals thus spreading the genetic acaricide resistance (Deken, et al. 2010). The acaricide acts as a selective screening process which leaves only the acaricide-resistant individuals that were already present in a population. Acaricide resistance is a process that takes several generations of ticks in a given population. Concentrations of acaricide that truly do not kill any ticks, do not select for resistance as all individuals will survive, and those that are lethal to all ticks do the same. So the development of resistance occurs at some point in between, where some individuals survive while others die as illustrated in Figure 1.

These resistant strains often evolve at a faster rate than any new chemical can be developed (Kemp et al, 1999). Wharlton & Roulston, (1970) reports that resistance of the tick species *Rhipicephalus (Boophilus) decoloratus* and *Rhipicephalus (Boophilus) microplus* can now be expected within a decade of the introduction of a new acaricide. The situation is dire especially with these species because they are one host tick that spend about 23 days of their life cycle attached to the animal's body (Wharlton & Roulston, 1970), exposing them and their offspring to many acaricide treatments when regularly done say every seven days. With three host ticks like the *Rhipicephalus appendiculatus* which only spends 5 days on the host, at each of its feeding stages, there is less acaricidal pressure.

Agricultural pesticides, including acaricides, have been associated with several environmental and ecosystem damage. Different chemical compounds have been used as acaricides, from organochlorines and arsenic to organophosphates and pyrethroids. One of the biggest impacts of cattle dips on the environment is soil contamination. This usually arises from the disposal of the waste liquid and sludge during dip tank emptying and refilling. Soil contamination also occurs when there is leakage from the dip tanks as well as at the chemical mixing areas should they spill (Livestock Production Program/Animal Health Program, 2003). The now more widely used pyrethroids have been reported to have negative impacts on pasture fauna due to their persistence in cattle dung (Vale and Grant, 2002). Mortalities and reduced reproduction of dung beetles and muscidae flies have been attributed to acaricide-treated cattle in Australia (Wardhaugh, et al., 1998) and Zimbabwe (Vale and Lovemore, 1999). Pyrethroids were detected in dung within days of application and there was no loss in their concentration in the dung, two months after use (Livestock Production Program/Animal Health Program, 2003).

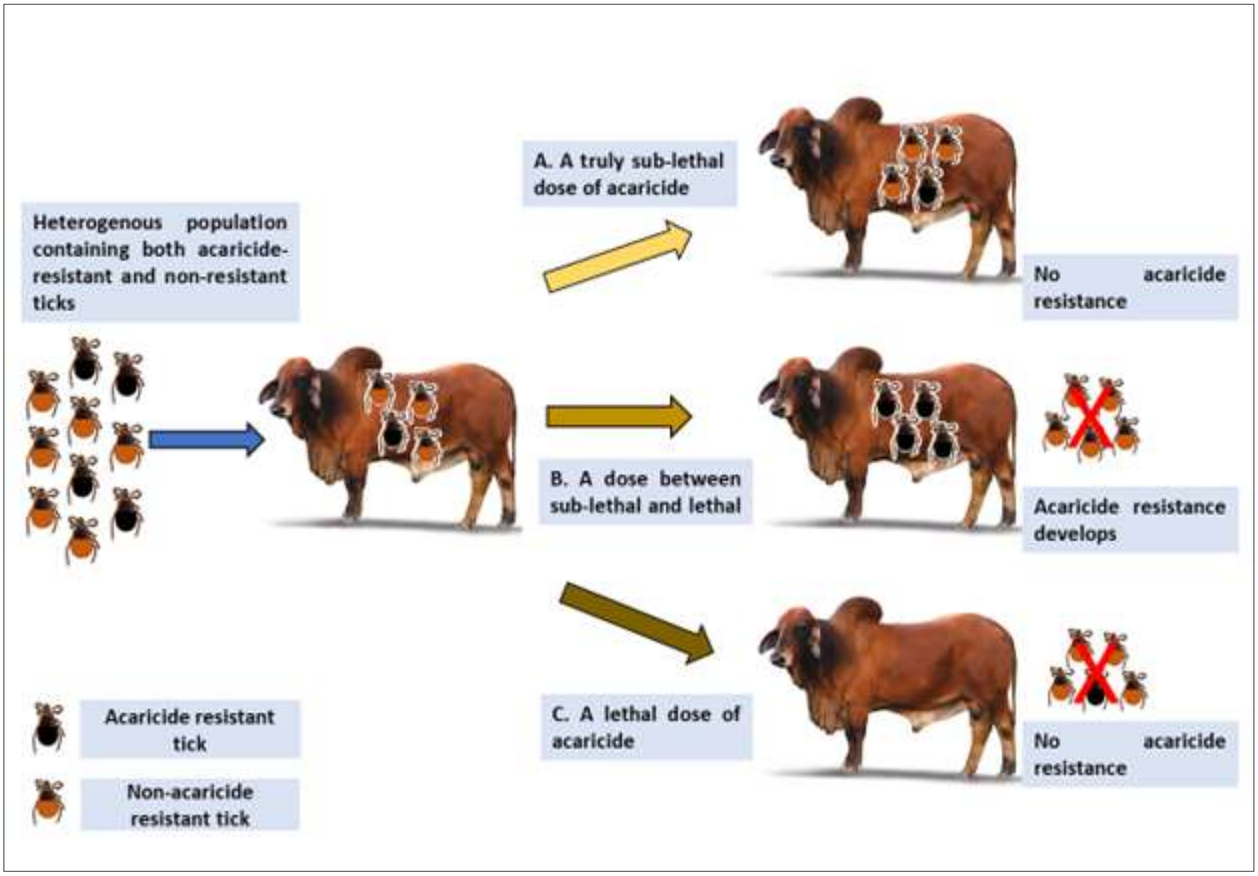

Figure 1: The development of acaricide resistance in tick populations: A- a truly sub-lethal dose of acaricide is applied, all ticks survive and the resistant ticks will be out-competed and there is no progression of acaricide resistance genes. B – a dose in between sub-lethal and lethal results in death of some ticks leaving the resistant ticks to pass on their genes. C – a lethal dose of acaricide kills all the ticks and no resistance develops.

Breeding for tick resistance

Sustainable control of ticks and their resultant effects on livestock production can be achieved by the selection of animals for increased resistance to ticks. This needs the use of animals that transfer the genes to their offspring, consequently making a population resistant. Anecdotal evidence indicates that livestock breeds indigenous to an environment where they are constantly challenged by disease or parasites have greater disease resistance (Shyma et al. 2013). The purity of these indigenous cattle breeds is now under threat due to breeding methods that select against them in support of imported breeds. This natural resistance has the potential to eventually reduce the need for the religious dipping of cattle, leading to reduced cost of purchasing acaricides. Crossbreeding has traditionally been used as a tick control method in many countries with reports that it is effective, coming from some countries like Australia (Sutherst, et al. 1979).

Genomic selection is often the best way to improve traits that are hard to measure such as tick resistance. The trait has often been avoided in many breeding programs because it is very expensive, mainly due to the difficulty in locating the individual animal variations. It is also laborious (Cardosso, et al., 2021). Furthermore, previously there was no pressing need to select animals for tick resistance (or disease resistance in general) as drug therapy and prophylaxis were cheap, widespread and the unquestionable *modus operandi.* However, the recent developments of increasing parasite resistance to chemicals, economic challenges resulting in exorbitant costs of drugs, and the new public preference for organically produced animal products, especially those in the upper-end market, now make it more imperative that the selection for tick resistance is taken seriously (Shyma et al. 2013).

Previous studies have reported low to high heritability for tick resistance depending on whether the method used natural or artificial tick challenge, the size of the population and the statistical method used (Regitano & Prayaga; 2010). This has given hope for the use of this strategy in helping tick control programs. The highly productive but disease and parasite-prone *Bos taurus* breeds have been crossbred with the *Bos indicus* which have lower productivity but high tolerance to ticks. These crossbreeding programs aim to have high production while keeping tick infestation minimal. Therefore genetic evaluation of tick resistance is important in gathering data and help to improve the tick resistance trait in cattle (Mkize, et al., 2021).

The genetic control of animal host's resistance to ticks has always been known to exist although it has been studied with a focus on the estimated breeding values from the phenotypic data and little attention to the genes behind the differences in the phenotypes (Goddard & Hayes, 2009). The use of molecular biology techniques and quantitative genetics has led to a better knowledge of the genetic mechanisms behind the host's tick resistance being obtained. One such approach is the use of genome-wide association studies (GWAS). This uses single nucleotide polymorphisms (SNPs) to identify genetic variants of traits that are complex (Mota et al., 2018). SNPs are widely distributed in the genome and are heritable which makes them ideal in studying and implementing genetic control strategies for improving tick resistance in cattle through utilising markers associated with low tick load in breeding schemes. GWAS tests each genetic marker independently for an association with the trait while at the same time controlling for any possible differences among animals caused by the breed (Neto, et al. 2010). Several quantitative trace loci (QTL) have been identified using linkage analysis (Mapholi, et al., 2014). However, successful application of this technique in developing countries is still hurdled by the high costs of sequencing (Mkize et al, 2021).

Although relatively few GWAS on tick resistance in cattle have been reported, especially in Africa, there have been some interesting findings such as in Australia where according to Barendse, 2007, several QTL associated with tick infestation were identified in dairy cattle and beef cattle of the Brahman breed (Patent No. WO2007051248-A1, 2007; Porto Neto et al., 2010; Turner et al., 2010). In Brazil, a study on F2 of Gir cross Holstein cattle identified QTLs associated with tick resistance on BTA 2, 10 and 23 during the dry season and BTA 5, 11, 23 and 27 during the wet season (Otto et al. 2018). Various genes were identified that were associated with tick count particularly *TREM1*, *TREM2* which are important regulators of immune response and CD83 which is an immunoglobulin superfamily protein. They used 23 microsatellite and 180 microsatellite markers ((Regitano & Prayaga, 2010; (Machado, et al., 2010). In South Africa, Mapholi et al. (2016), in a GWAS on tick resistance in Nguni cattle, identified several genomic regions containing QTL for different tick count traits. They identified three genome-wide significant regions on chromosomes 7 (for total tick count on the head), 10 (for total body *A*. *hebraeum* tick count) and 19 (total *A*. *hebraeum* on the perineum region). *A*. *hebraeum* is an important vector for heartwater disease in ruminants in southern Africa. Some of these studies are summarised in table 1.

It is to be noted that most of the GWA studies on cattle tick count data which have been done to date rely on SNP chips for genotyping individuals which particularly limits the discovery of novel markers as compared to other methods such as whole genome resequencing (Korte and Farlow 2013; Pavan et al. 2020). Since they only contain a subset of the SNPs, their low resolution typically may also provide for more room to miss other genetic variants or markers that might be of great significance.

An intergrated omic approach greatly boosts the resolving power in narrowing down to QTLs that are of the most significance in controlling specific phenotypes. In this regard, transcriptome studies are a valuable tool to support evidence from other techniques as GWAS that exploit genomic polymorphism. A study by Moré et al (2019) also showed the involvement of *TREM2* a key gene involved in regulation of immune responses as it was differentially expressed between the resistant and susceptible cattle supporting the work done by Otto et al. (2018). They also went on to identify other CD genes such as *CD4* and *CD14* that were coregulated in resistant hosts in response to tick infestation. In addition, they also revealed that defensive responses such as leukocyte chemotaxis and also skin degradation and remodelling were amongst some of the mechanisms that conferred tick resistance in Braford cattle.

Santos et al. (2022), conducted a post-GWAS analysis using the output from some of the studies mentioned earlier in combination with sequencing data where they detected genes that showed possible structural variants. They identified various genes that are involved in modulation of eosinophil chemotaxis, monocyte differentiation and also RIG-I signalling that included several genes that perform various immune functions were also identified that included *DAPK2*, *INPP5D*, *ACIN1* and *PUM1*. S. They also identified several transcriptional factor-gene networks that are key in modulating responses to tick infestation. These are shown in Figure 2.

In addition to GWAS, genomic regions of interest can also be identified using regional heritability mapping (RHM) (Nagamine et al., 2012; Riggio et al., 2013). RHM is a variance component-based approach for mapping genomic regions influencing complex traits, which combines information across contiguous SNPs**.** It is a more robust tool that can pick those genomic regions containing multiple alleles which each has little effect on variance such that they may not be detected by GWAS. It also provides heritability estimates that are caused by small genomic regions

The advent of GWAS and RHM should lead to a new era in studies on host resistance to ticks. Since there are many tick species affecting livestock in Africa, future studies may focus on finding whether host resistance pathways are similar or differ from one tick species to another. It can be safely argued that there is great potential in the use of genomics to identify genes responsible for tick resistance in cattle and in future provide a complementary method for tick and tickborne disease control for farmers (Penrith 2011).

Table 1. Recent genome-wide association studies carried out on identification of QTLs conferring tick resistance in cattle.

Reference	Population type/size	Genotyping platform/# of SNPs	QTLs or key genes identified in the study
Otto et al, 2018	Holstein X Gir F1 and F2 populations, 476 samples.	Illumina BovineSNP50BeadChip (Illumina Inc., San Diego, CA), SNPs used 40,283 (call rate >0.90 and minor allele frequency >0.03).	*TREM1, TREM2, CD83, TCF3, PAX5, TAL1, NFIL3, EGR1, SOX10,* and *REL*
Mapholi et al. 2016	586 randomly selected Nguni cattle (500 genotyped)	BovineSNP50 assay, SNPs used 40,436 (MAF > 0.02 and call rate >90%).	Chromosome 10 (SNP IDs rs420979558, rs43634842, rs41660143) Chromosome 1 (SNP ID rs1100893722)
Mota et al. 2018	928 Hereford and 3435 Braford cattle (Total - 4363 animals; 3591 genotyped)	Illumina BovineSNP50 BeadChip (Illumina Inc., San Diego, CA),	Chromosomes BTA 1,2,5,6,7,9,11,13,14,15,16,18,21,23,24,26 and 28
Sollero et al. 2017	Hereford and Braford cattle (3455 individuals genotyped)	Illumina BovineSNP50 BeadChip, 41,045 SNPs used (call rate >98%, and highest MAF or high correlation >98%)	SNP IDs ARS-BFGL-NGS-5811, ARS-BFGL-NGS-111179, Hapmap58695-rs29019899, BTB-00915241, BTB-02002785

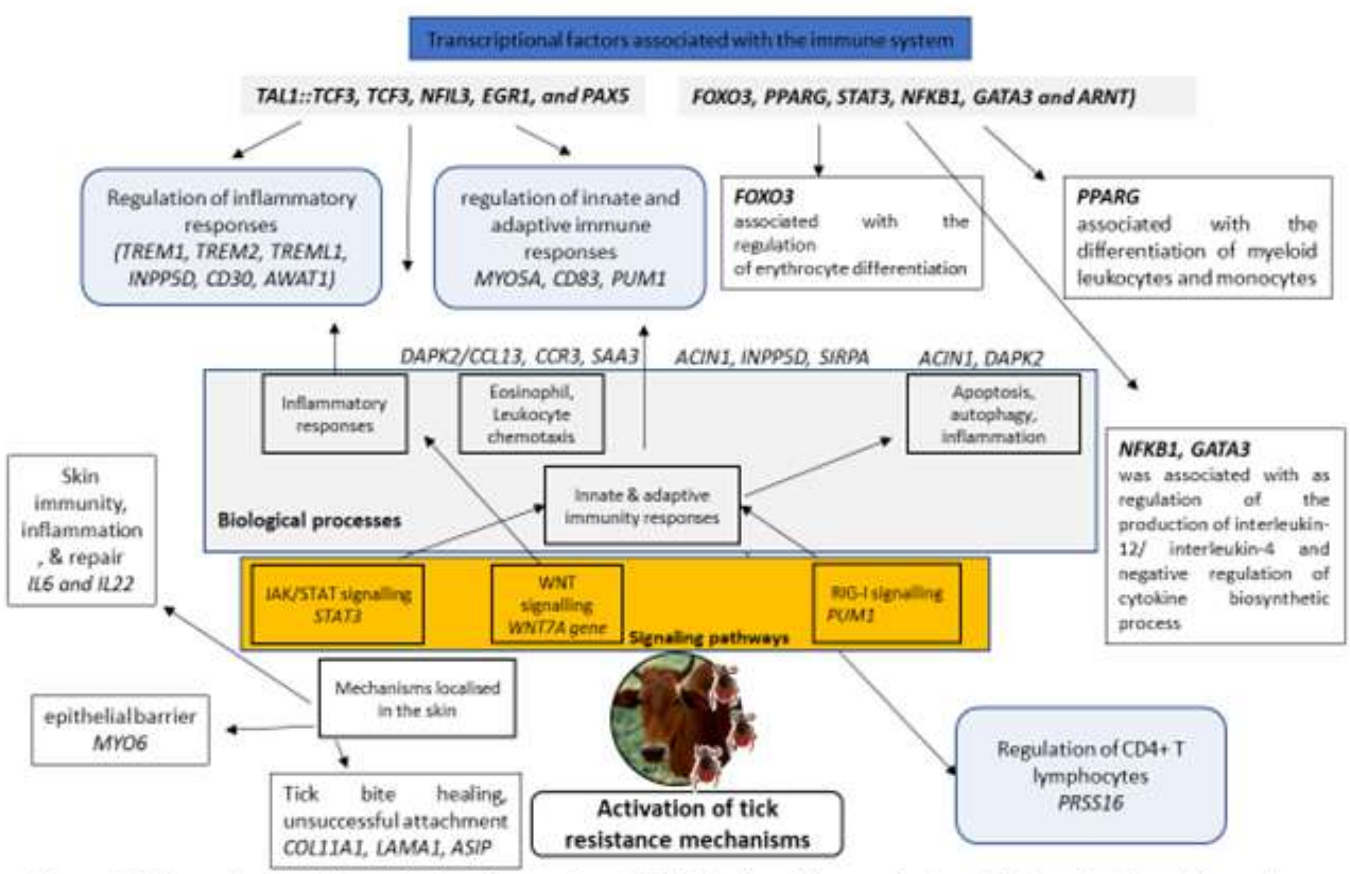

Figure 2. A theoretical model constructed from various GWAS studies of the mechanisms that confer tick resistance in cattle. The genes modulating the different biological processes are shown in italics with the transcriptional factors in bold.

CONCLUDING PERSPECTIVE

The impacts of ticks and the diseases they transmit have limited the development of the livestock sector for a long time. Control of ticks has remained mainly dependent on the use of acaricides. The modern era of environmentally sustainable solutions to agricultural problems call for more efforts to be placed on utilizing host resistance, and possibly anti-tick vaccines to reduce the overreliance on acaricides. New technologies in genomics offer hope for greater progress in the coming years. True potential exists that genetic resistance can help solve the environmental challenges created by use of chemicals. This will also add to the economic benefits of reduced cost of purchasing the chemicals, improving the productivity of and livelihoods in the semi-arid regions of the world that are mostly affected by ticks.

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Author's contribution:

Stephen Mandara: Conceptualisation, methodology, writing, review and editing.
Antony Maodzeka: Methodology, writing, review and editing.

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