

Genetic Study of Red Maasai Sheep and their Dorper Crossbred's Performance in Sub-Saharan Africa

Edwin Pancras Oyieng'

PhD DISSERTATION | JUSTUS - LIEBIG UNIVERSITY | 2025



Institute of Animal Breeding and Genetics
Justus-Liebig-University Gießen

**Genetic study of Red Maasai sheep and
their Dorper crossbred's performance in
sub-Saharan Africa**

DISSERTATION

For award of the doctoral degree (Dr. agr.)

in the Faculty of Agricultural Science, Nutritional Science and
Environmental Management at the Justus-Liebig University of Gießen

Submitted by
Edwin Pancras Oyieng'

From Nairobi, Kenya

Gießen, 2025

With the approval of the Faculty of Agricultural Sciences, Nutritional Science and
Environmental Management of the Justus-Liebig-University Gießen, Germany

Dean: Prof. Dr. Klaus Eder

Board of Examiners

1st reviewer: Prof. Dr. Sven König

2nd reviewer: Prof. Dr. Dr. Matthias Gauly

Examiner: Prof. Dr. Wehrend Axel

Examiner: Prof. Dr. Horst Brandt

Chairperson: Prof. Dr. Lühken Gesine

Date of Disputation: 8th July 2025

SUPERVISORY TEAM

Prof. Dr. Sven König

*Professor of Animal Breeding and Genetics, Institute of Animal Breeding and Genetics,
Justus-Liebig-University Gießen, Ludwigstraße 21 b, 35390 Gießen, Germany*

Prof. Dr. Dr. Matthias Gauly

*Professor of Animal and Veterinary Sciences, Faculty of Agricultural, Environmental and Food
Sciences, Free University of Bozen – Bolzano, Universitätsplatz 5, 39100 Bolzano, Italy*

Prof. Dr. Raphael Mrode

*Professor of Animal Breeding and Genetics, Scotland's Rural College, EH9 3JG Edinburgh,
United Kingdom.*

*Principal Scientist, Livestock Genetics Nutrition and Feed Resources Program, International
Livestock Research Institute, P. O Box 30709-00100 Nairobi, Kenya*

Dr. Julie Ojango

*Senior Scientist, Livestock Genetics Nutrition and Feed Resources Program, International
Livestock Research Institute, P. O Box 30709-00100 Nairobi, Kenya*

This thesis is dedicated to my sons (Edpancras and Pancras Oyieng'),

Parents (Vincent and Consolata Ochieng'),

Sisters (Nancy and Grace Ochieng'),

Niece (Arozie) and nephew (Jabari).

Thank you for your unconditional love, care and support during my PhD journey.

TABLE OF CONTENTS

LIST OF TABLES	x
LIST OF FIGURES	xii
LIST OF ABBREVIATIONS	xiv
Summary	xv
Zusammenfassung	xviii
CHAPTER 1: General Introduction	21
1.1 Livestock and livelihoods	21
1.2 Livestock and climate change	22
1.3 Livestock breeding for climate change	22
1.4 Small ruminant genetic resources in sub-Saharan Africa	23
1.5 Breeding strategies for sheep in sub-Saharan Africa	25
1.6 The Red Maasai sheep	26
1.7 The Dorper sheep	27
1.8 Objectives of this thesis	28
References	29
CHAPTER 2: Evaluating reproduction traits in a crossbreeding program between indigenous and exotic sheep in semi-arid lands	35
Abstract	36
2.1 Introduction	36
2.2 Material and Methods	38
2.2.1 Study area	38
2.2.2 Animal management and breeding	38
2.2.3 Data structure and traits studied	39
2.2.4 Data analysis	41
2.2.4.1 Genetic parameter estimation	41
2.2.4.2 Genetic gain	43

Table of Contents

2.2.4.3 Rainfall index	44
2.3 Results	44
2.3.1 Non-genetic factors.....	44
2.3.2 Genetic parameters	46
2.3.3 Genetic and phenotypic correlations.....	48
2.3.4 Genetic trends and gain	49
2.3.5 Phenotypic trends and rainfall pattern	51
2.4 Discussion.....	52
2.4.1 Non-genetic factors influencing reproduction of ewes	52
2.4.2 Genetic influence on ewe fertility.....	53
2.4.3 Phenotypic trends and genetic gain.....	54
2.5 Conclusion	55
Ethics approval	56
Data and model availability statement	56
Declaration of Generative AI and AI-assisted technologies in the writing process.....	56
Authors ORCIDs.....	56
Declaration of interest	56
Acknowledgement	56
Financial Support.....	57
References.....	57
CHAPTER 3: Lamb survival and ewe longevity in a crossbreeding program between indigenous and exotic sheep in semi-arid lands.....	63
Abstract.....	64
3.1 Introduction.....	64
3.2 Materials and Methods	65
3.2.1 Study area and flock management	65
3.2.2 Data structure	66

3.2.3 Data analysis	67
3.2.3.1 Survival analyses	67
3.2.3.2 Estimation of genetic parameters and genetic trends for lamb survival	70
3.3 Results	70
3.3.1 Lamb survival	70
3.3.2 Ewe longevity	75
3.3.3 Genetic parameters and genetic trends for lamb survival	77
3.4 Discussion	78
3.4.1 Factors affecting survival of lambs to yearling	78
3.4.2 Longevity of ewes	81
3.5 Conclusion	82
Ethics approval	83
Declaration of generative AI and AI-assisted technologies in the writing process	83
Authors ORCIDs	83
Declaration of interest	83
Data availability statement	83
Acknowledgement	83
Author contributions	84
Financial Support	84
References	84
CHAPTER 4: The impact of heat stress on growth and resilience phenotypes of sheep raised in a semi-arid environment of sub-Saharan Africa	89
Abstract	90
4.1 Introduction	90
4.2 Material and Methods	92
4.2.1 Study area and animal management	92
4.2.2 Animal and weather data	93

Table of Contents

4.2.3 Temperature-Humidity index (THI)	94
4.2.4 Factors of variation on live weight gain	95
4.2.5 Derivation of resilience phenotypes	95
4.2.6 Fixed effects factors of variation on resilience phenotypes	96
4.2.7 Genetic parameters of resilience indicators	97
4.3 Results	97
4.3.1 Fixed factors affecting growth	97
4.3.2 Threshold for heat stress on growth	98
4.3.3 Resilience phenotypes	100
4.3.4 Genetic parameters for resilience phenotypes	101
4.4 Discussion	102
4.5 Conclusion	106
Ethics approval	106
Declaration of generative AI and AI-assisted technologies in the writing process	106
Authors ORCIDs	106
Declaration of interest	107
Data availability statement	107
Acknowledgement	107
Author contributions	107
Financial Support	107
References	108
CHAPTER 5: GENERAL DISCUSSION	114
5.1 Reproduction efficiency	114
5.2 Pre- and post-weaning lamb survival	115
5.3 Ewe's length of productive life	116
5.4 Breeding for heat tolerance	116
5.5 Recommendations	118

5.6 Future considerations.....	119
5.7 Conclusions.....	120
References.....	121
LIST OF PUBLICATIONS.....	129
ACKNOWLEDGEMENTS	130
FORMAL DECLARATION	131

LIST OF TABLES

CHAPTER 2

Table 1: Descriptive statistics for the traits studied grouped by sheep breed.....	41
Table 2: Least square means (LSM) \pm SE for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) for the sheep population.....	45
Table 3: Overall and within breed variance components and heritability estimates for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) grouped by sheep breed	47
Table 4 Genetic and phenotypic \pm SE correlations for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) grouped by sheep breed.....	49
Table 5 Overall genetic gain \pm SE for age at first lambing (AFL), Lambing Interval (LI), birth weight (EBWT), weaning weight (EWWT), Lambing weight at birth (LWB) and lambing weight at weaning (LWWT) from 2003 to 2020 grouped by sheep breed.....	51

CHAPTER 3

Table 1 Summary statistics of lamb survival by breed	70
Table 2 Factors affecting lamb survival from birth to weaning and their risk ratio, mean age at failure (days) and Weibull parameter estimate (ρ) \pm Standard Error	72
Table 3 Factors affecting lamb survival from weaning to yearling and their risk ratio, mean age at failure (days) and Weibull parameter estimate (ρ) \pm Standard Error	74
Table 4 Summary of statistics of ewe longevity from first lambing to culling at 2,190 days ..	75
Table 5 Factors affecting ewe longevity and their risk ratio, mean culling age (days) and Weibull parameter estimate (ρ) \pm Standard Error	77
Table 6 Genetic variance and heritability estimates \pm standard error for lamb survival from birth to yearling by breed.....	77

CHAPTER 4

Table 1 Least square means (LSM) and SE (in parentheses) of fixed factors affecting growth	98
Table 2 Least square means and SE (in parenthesis) of resilience phenotypes expressed as change in growth per unit increase in temperature-humidity index	100
Table 3 Variance components and heritability estimates (SE in parenthesis) of resilience phenotypes and liver weight gain	101
Table 4 Genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) of the traits	102

LIST OF FIGURES

CHAPTER 1

Figure 1 Red Maasai ewe and its lamb.....26

Figure 2 Dorper ewe and its lamb.....27

CHAPTER 2

Figure 1 Genetic trends for age at first lambing by sheep breed from 2003 to 2020 (**AFL** = Age at first lambing, **EBV**=Estimated breeding values, **DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....50

Figure 2 Genetic trends for litter weight at weaning by sheep breed from 2003 to 2020 (**LWWT** = Litter weight at weaning, **EBV**=Estimated breeding values, **DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....50

Figure 3 Phenotypic trends for age at first lambing by sheep breed and rainfall patterns from 2003 to 2020 (**DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....52

Figure 4 Phenotypic trends for litter weight at weaning by sheep breed and rainfall patterns from 2003 to 2020 (**DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....52

CHAPTER 3

Figure 1 Pre-weaning and post-weaning Kaplan – Maier survivor curves for lambs of different breeds (**DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....75

Figure 2 Kaplan – Maier survivor curves of ewes from first lambing to culling for the different breeds (**DDDD**=pure dorper, **DDDR**=75%Dorper-25%Red Maasai, **DDRR**=50%Dorper-50%Red Maasai, **RRRR**=pure Red Maasai).....76

Figure 3 Genetic trends for pre-weaning lamb survival from 2003 to 2022 of different breeds (DDDD=pure dorper, DDDR=75%Dorper-25%Red Maasai, DRRR=50%Dorper-50%Red Maasai, RRRR=pure Red Maasai).....78

CHAPTER 4

Figure 1 The average monthly THI for each year in the study area.....99

Figure 2 Reaction norms for changes in weight in response to average temperature-humidity index for the population and each breed (DDDD=pure dorper, DDDR=75%Dorper-25%Red Maasai, DRRR=50%Dorper-50%Red Maasai, RRRR=pure Red Maasai).....100

LIST OF ABBREVIATIONS

AFL	Age at first lambing
ASAL	Arid and Semi-Arid Lands
CBBP	Community based breeding program
DDDD	Pure Dorper breed
DDDR	75% Dorper and 25% Red Maasai breed combination
DDRR	50% Dorper and 50% Red Maasai breeding combination or F1
EBV	Estimated breeding value
EBWT	Birth weight of the ewe
EWWT	Weaning weight of the ewe
GHG	Greenhouse gas
LBWT	Average birth weight in a litter for an ewe
LI	Lambing interval
LWG ¹	Pre-weaning live weight gain
LWG ²	Post-weaning live weight gain
LWWT	Average weaning weight for the litter of an ewe
RRRR	Pure Red Maasai breed
SRGR	Small ruminant genetic resources
SSA	sub-Saharan Africa
THI	Temperature-Humidity Index

Summary

The aim of this thesis was to study the performance of the Red Maasai sheep, the Dorper sheep and their crosses reared in a semi-arid environment. The study involved the analysis of reproduction parameters, survival of lambs and ewes length of productive life, the impact of heat stress on growth, and developed novel resilience phenotypes for the sheep population. The main breed groups in the breeding program comprised pure Dorper (**DDDD**), pure Red Maasai (**RRRR**), 75%Dorper-25%Red Maasai (**DDDR**) and 50%Dorper-50%Red Maasai – F1 (**DDRR**). R and ASReml-R software were used to evaluate reproduction parameters. Survival of lambs and the length of productive life of ewes were analysed using Cox and Weibull hazard models of the Survival Kit Version 6.12 software. Random regression models fitted with reaction norm functions were used to assess the impact of heat stress on growth and derive novel resilience phenotypes for growth in response to different levels of heat stress.

Information generated through studying the reproductive performance of the flock is presented in **Chapter 2**. The pure Red Maasai sheep had significantly lower values for average age at first lambing (AFL), ewe birth weight (EBWT), ewe weaning weight (EWWT), litter birth weight (LBWT) and litter weaning weight (LWWT) compared to other breeds studied. The birth type (single or twins), sex of the lamb and parity in which the lambs were born significantly affected ewes' birth and weaning weights. The overall heritability estimates of AFL (0.09 ± 0.04) and LI (0.00 ± 0.01) were not significant ($P>0.05$) while the heritability estimates for EBWT (0.38 ± 0.04), EWWT (0.23 ± 0.03), LBWT (0.19 ± 0.03) and LWWT (0.09 ± 0.02) were significant ($P<0.05$). The repeatability estimates were low for LBWT (0.25), LWWT (0.16) and that of lambing interval (LI) was near zero. Genetic and phenotypic correlations showed strong positive relationships between ewe and lamb weights. The Red Maasai had higher genetic and phenotypic correlations and genetic gains for the traits studied compared to the pure Dorper while the DDDR breed combination had a higher genetic gain among the crosses. LI had negative genetic correlations with LBWT and LWWT while AFL had positive genetic correlations with LBWT and LWWT. The phenotypic trends for AFL and LWWT showed a negative association with rainfall index over the years.

Chapter 3 presents the results of pre- and post-weaning lamb survival to yearling, and ewes length of productive life. The pure Red Maasai lambs and ewes had better pre-weaning lamb survival rates and better productive life compared to the other breeds. Overall, 95% and 83% of lambs survived to weaning (90 days) and yearling (365 days), respectively. The Red Maasai lambs had the lowest mortality rates (2%) while Dorper lambs had the highest post-weaning mortality (24%) among the breeds. Lamb survival was significantly influenced by the

season of birth, parity in which the lambs were born, birth type (single or twin) and birth weight. Single born lambs, those born during the wet season, offspring of multiparous ewes, and those having higher birth weights (>3kg) were associated with lower mortality risks. Ewe longevity was significantly affected by the breed, age at first lambing, parity and birth weight. Ewes of DDDR breed combination and those that had heavier birth weights (>3Kgs) had the highest risk of being culled, while ewes with a higher age at first lambing (>975 days old) and more than one lambing were less likely to be culled. Pre-weaning heritability estimates for survival (0.10–0.14) were higher than post-weaning estimates (0.01-0.05). The Red Maasai had the highest genetic gain for pre-weaning survival (-0.026) compared to DDDR (-0.018), F1 (-0.011), and Dorper (-0.012). General weakness, often due to poor nutrition, posed the highest risk for lambs dying post-weaning (12.99 risk ratio), followed by diseases like enterotoxemia and sheep pox (6.006 risk ratio).

The impact of heat stress on the growth of sheep and novel resilience phenotypes for growth are presented in **Chapter 4**. Heat stress, expressed as Temperature-Humidity Index (THI), significantly affected the growth of the sheep. The Red Maasai sheep had a higher tolerance for heat stress compared to the other breeds studied. The THI break points, when growth is affected by heat stress, were 78.75, 78.71, 78.42 and 77.93 for RRRR, DDDD, DDDR and DDDR respectively. At the THI break point, the growth rate declined at a rate of 0.06 Kgs, 0.09 Kgs, 0.05 Kgs and 0.15 in live weight gain per unit change in THI for RRRR, DDDD, DDDR and DDDR respectively. Random regression models fitted with reaction norm functions were used to develop two resilience phenotypes namely: Response and Stability. These resilience phenotypes were developed at THI 70 (representing low/no heat stress) and THI 85 (representing high heat stress). The breed, sex, type of birth, dams' parity and season of birth significantly affected the stability of growth at low and high heat stress. Genetic correlations of resilience phenotypes at THI 85 with pre-weaning live weight gain (LWG¹) were antagonistic and significant but not for post-weaning live weight gain (LWG²). Strong positive genetic and phenotypic correlations existed between response and its corresponding stability trait. The heritability estimates of resilience traits ranged from 0.12 for Response at THI 70 to 0.16 for Stability at THI 85.

The better lamb survival and ewe longevity, and high tolerance to heat stress of the Red Maasai breed are an indication of their suitability for the harsh environment. Crossbreeding of the Red Maasai with Dorper has the potential to optimize growth and reproductive efficiency in the semi-arid environment. The moderate heritability estimates for resilience phenotypes in the population studied highlight opportunities for selective breeding

to enhance resilience for growth under the changing climatic conditions. Context-specific improved animal management practices can increase the survival of lambs, improve their reproductive performance and reduce the impact of heat stress on growth.

Zusammenfassung

Das Ziel dieser Arbeit war die Untersuchung der Leistung von Roten Maasai-Schafen, Dorper-Schafen und ihren Kreuzungen, die in einer semi-ariden Umgebung gehalten werden. Die Studie umfasste die Analyse von Reproduktionsparametern, dem Überleben von Lämmern und Mutterschafen, der Länge des produktiven Lebens, dem Einfluss von Hitzestress auf das Wachstum und der Entwicklung neuartiger Resilienzphänotypen für die Schafpopulation. Die Hauptzuchtgruppen im Zuchtprogramm bestanden aus reinem Dorper (**DDDD**), reinem Roten Maasai (**RRRR**), 75% Dorper-25% Roten Maasai (**DDDR**) und 50% Dorper-50% Roten Maasai – F1 (**DDRR**). Die Software R und ASReml-R wurden zur Bewertung der Reproduktionsparameter verwendet. Das Überleben der Lämmer und die Länge des produktiven Lebens der Mutterschafe wurden mit Cox- und Weibull-Gefährdungsmodellen der Software Survival Kit Version 6.12 analysiert. Zufällige Regressionsmodelle, die mit Reaktionsnormfunktionen ausgestattet waren, wurden verwendet, um den Einfluss von Hitzestress auf das Wachstum zu bewerten und neue Resilienzphänotypen für das Wachstum als Reaktion auf unterschiedliche Hitzestressniveaus abzuleiten.

Informationen, die durch die Untersuchung der Reproduktionsleistung der Herde gewonnen wurden, sind in **Kapitel 2** dargestellt. Die reinen Roten Maasai-Schafe hatten signifikant niedrigere Werte für das durchschnittliche Alter beim ersten Lammen (AFL), das Geburtsgewicht der Mutterschafe (EBWT), das Absetzgewicht der Mutterschafe (EWWT), das Geburtsgewicht des Wurfs (LBWT) und das Absetzgewicht des Wurfs (LWWT) im Vergleich zu den anderen untersuchten Rassen. Der Geburtstyp (Einling oder Zwillinge), das Geschlecht des Lamms und die Parität, in der die Lämmer geboren wurden, beeinflussten die Geburts- und Absetzgewichte der Mutterschafe signifikant. Die Gesamtheritabilitätsschätzungen für AFL ($0,09 \pm 0,04$) und LI ($0,00 \pm 0,01$) waren nicht signifikant ($P > 0,05$), während die Heritabilitätsschätzungen für EBWT ($0,38 \pm 0,04$), EWWT ($0,23 \pm 0,03$), LBWT ($0,19 \pm 0,03$) und LWWT ($0,09 \pm 0,02$) signifikant waren ($P < 0,05$). Die Wiederholbarkeits-Schätzungen waren niedrig für LBWT (0,25), LWWT (0,16) und die des Lammintervalls (LI) war nahezu null. Genetische und phänotypische Korrelationen zeigten starke positive Beziehungen zwischen den Gewichten von Mutterschafen und Lämmern. Die Roten Maasai hatten höhere genetische und phänotypische Korrelationen und genetische Gewinne für die untersuchten Merkmale im Vergleich zu den reinen Dorper, während die DDRR-Rassenkombination den höchsten genetischen Gewinn unter den Kreuzungen aufwies. LI hatte negative genetische Korrelationen mit LBWT und LWWT, während AFL positive genetische Korrelationen mit LBWT

und LWWT aufwies. Die phänotypischen Trends für AFL und LWWT zeigten eine negative Assoziation mit dem Niederschlagsindex über die Jahre hinweg.

Kapitel 3 präsentiert die Ergebnisse des Überlebens von Lämmern vor und nach dem Absetzen bis zum Jährling sowie der Länge des produktiven Lebens der Mutterschafe. Die reinen Roten Maasai-Lämmer und Mutterschafe hatten bessere Überlebensraten vor dem Absetzen und eine bessere produktive Lebensdauer im Vergleich zu den anderen Rassen. Insgesamt überlebten 95% und 83% der Lämmer das Absetzen (90 Tage) bzw. das Jährlingsalter (365 Tage). Die Roten Maasai-Lämmer hatten die niedrigsten Mortalitätsraten (2%), während Dorper-Lämmer die höchste Mortalität nach dem Absetzen (24%) unter den Rassen aufwiesen. Das Überleben der Lämmer wurde signifikant durch die Geburtssaison, die Parität, in der die Lämmer geboren wurden, den Geburtstyp (Einling oder Zwilling) und das Geburtsgewicht beeinflusst. Einzelgeborene Lämmer, solche, die während der Regenzeit geboren wurden, Nachkommen von mehrgebärenden Mutterschafen und solche mit höheren Geburtsgewichten (>3 kg) waren mit geringeren Mortalitätsrisiken verbunden. Die Langlebigkeit der Mutterschafe wurde signifikant durch die Rasse, das Alter beim ersten Lammen, die Parität und das Geburtsgewicht beeinflusst. Mutterschafe der DDR-Rassenkombination und solche mit schwereren Geburtsgewichten (>3 kg) hatten das höchste Risiko, ausgesondert zu werden, während Mutterschafe mit einem höheren Alter beim ersten Lammen (>975 Tage) und mehr als einem Lammen weniger wahrscheinlich ausgesondert wurden. Die Heritabilitätsschätzungen für das Überleben vor dem Absetzen (0,10–0,14) waren höher als die Schätzungen nach dem Absetzen (0,01–0,05). Die Roten Maasai hatten den höchsten genetischen Gewinn für das Überleben vor dem Absetzen (-0,026) im Vergleich zu DDR (-0,018), F1 (-0,011) und Dorper (-0,012). Allgemeine Schwäche, oft aufgrund schlechter Ernährung, stellte das höchste Risiko für das Sterben von Lämmern nach dem Absetzen dar (12,99 Risikoverhältnis), gefolgt von Krankheiten wie Enterotoxämie und Schafpocken (6,006 Risikoverhältnis).

Der Einfluss von Hitzestress auf das Wachstum der Schafe und neue Resilienzphänotypen für das Wachstum sind in **Kapitel 4** dargestellt. Hitzestress, ausgedrückt als Temperatur-Feuchtigkeits-Index (THI), beeinflusste das Wachstum der Schafe signifikant. Die Roten Maasai-Schafe hatten eine höhere Toleranz gegenüber Hitzestress im Vergleich zu den anderen untersuchten Rassen. Die THI-Breakpoints, bei denen das Wachstum durch Hitzestress beeinflusst wird, lagen bei 78,75, 78,71, 78,42 und 77,93 für RRRR, DDDD, DDRR bzw. DDR. Am THI-Breakpoint nahm die Wachstumsrate um 0,06 kg, 0,09 kg, 0,05 kg und 0,15 kg an Lebendgewichtszunahme pro Einheit Änderung des THI für RRRR, DDDD, DDRR bzw.

DDDR ab. Zufällige Regressionsmodelle, die mit Reaktionsnormfunktionen ausgestattet waren, wurden verwendet, um zwei Resilienzphänotypen zu entwickeln, nämlich: Reaktion und Stabilität. Diese Resilienzphänotypen wurden bei THI 70 (geringer bis kein Hitzestress) und THI 85 (hoher Hitzestress) entwickelt. Die Rasse, das Geschlecht, der Geburtstyp, die Parität der Mutter und die Geburtssaison beeinflussten die Stabilität des Wachstums bei niedrigem und hohem Hitzestress signifikant. Genetische Korrelationen der Resilienzphänotypen bei THI 85 mit der Lebendgewichtszunahme vor dem Absetzen (LWG1) waren antagonistisch und signifikant, jedoch nicht für die Lebendgewichtszunahme nach dem Absetzen (LWG2). Starke positive genetische und phänotypische Korrelationen bestanden zwischen Reaktion und dem entsprechenden Stabilitätsmerkmal. Die Heritabilitätsschätzungen der Resilienzmerkmale reichten von 0,12 für Reaktion bei THI 70 bis 0,16 für Stabilität bei THI 85.

Das bessere Überleben der Lämmer und die Langlebigkeit der Mutterschafe sowie die hohe Toleranz gegenüber Hitzestress der Roten Maasai-Rasse deuten auf ihre Eignung für die raue Umgebung hin. Die Kreuzung der Roten Maasai mit Dorper hat das Potenzial, das Wachstum und die reproduktive Effizienz in der semi-ariden Umgebung zu optimieren. Die moderaten Heritabilitätsschätzungen für Resilienzphänotypen in der untersuchten Population heben Möglichkeiten für selektive Zucht hervor, um die Resilienz für das Wachstum unter sich ändernden klimatischen Bedingungen zu verbessern. Kontextspezifische verbesserte Tierhaltungspraktiken können das Überleben der Lämmer erhöhen, ihre reproduktive Leistung verbessern und den Einfluss von Hitzestress auf das Wachstum reduzieren.

CHAPTER 1: General Introduction

1.1 Livestock and livelihoods

Livestock are a key global commodity for the provision of food, income, employment and risk insurance to mankind. Globally, livestock products contribute 18% to the kilocalorie consumption and 25% to the protein consumption (FAO, 2021). The livestock system is a significant global asset with an estimated value of at least USD.1.4 trillion and occupying about 45% of the earth's surface area (Reid et al., 2008). The livestock systems in developing countries is rapidly changing as the demand for livestock products continues to increase due to increasing human population, rapid urbanization and increases in income (Thornton, 2010). In sub-Saharan Africa (SSA), livestock production contributes approximately 40% to the agricultural GDP (Enahoro et al., 2019; Sejian et al., 2015).

Approximately 20% of the world's cattle population, 25% of the world's sheep and goat populations are found in SSA kept by 300 million livestock keepers, mostly concentrated in East and West Africa, with fewer in Southern and Central Africa (FAO, 2021). These livestock are reared in different production systems that vary from region to region. The systems can be broadly categorised as small-scale and large-scale production systems. The small-scale production systems include pastoralism, agropastoral and mixed smallholder farming. The large-scale systems include ranching, large-scale commercial farming, co-operative farming and state farming. The large-scale system still accounts for a relatively small proportion of agricultural output in SSA since the bulk of production occurs in the traditional small-scale system found in rural areas and Arid and Semi-Arid Lands (ASAL) (FAO, 2021).

Majority of the rural households' livelihoods are dependent on livestock farming while they own less than 2 Tropical Livestock Unit (TLU) and practice mixed crop-livestock farming (Otte et al., 2012). Manure and traction from livestock, are usually a non-monetized livestock inputs into household farming systems. Savings / asset accumulation and insurance represent another category of non-monetized services provided by livestock in traditional smallholder settings (Kayigema and Rugege, 2014; Lwelamira et al., 2010; Pender et al., 2004). In rural settings, livestock also serve as financial instruments because of the persistent absence of credit and financial markets in rural areas of developing countries (Pell et al., 2010). Livestock are usually sold to provide income for investment in other ventures such as land or small businesses and provide a source of income to meet planned and unplanned household needs such as school fees and hospital bills.

1.2 Livestock and climate change

Climate change is primarily caused by greenhouse gas (GHG) emissions that result in warming of the atmosphere with the livestock sector contributing 14.5% of global GHG emissions (Gerber et al., 2013; Solomon, 2007). As the global demand for livestock products increases, climate change threatens livestock production due to its impact on quality of feed crop and forage, water availability, animal and milk production, livestock diseases, animal reproduction, and biodiversity. Heat stress caused by climate change causes physiological and metabolic adjustments in animals resulting from thermoregulatory responses causing negative consequences in animal productivity and health (Renaudeau et al., 2012). Increased stress due to climate change weakens the immune systems of animals, making them more susceptible to infections (Nardone et al., 2010) hence increases the risk of livestock diseases outbreaks. Heat stress has also been shown to have negative effects on milky tied and growth in sheep (Tsartsianidou et al., 2021; Sánchez-Molano et al., 2020) and in cattle (Oloo et al., 2024).

To cope with the challenge of climate change on livestock production, mitigation and adaptation strategies aimed at reducing the emission intensity of this sector are needed to meet the increasing demand for livestock products driven by population growth. One of the measures for mitigating GHG emissions is by improving feed and grazing management in ruminant animals since forage quality and digestibility affect enteric methane production. For example, harvesting forage (especially grass) for ensiling at an earlier stage to reduce lignification, chopping and grinding feeds (Hristov et al., 2013), addition of fats or fatty acids to the diets (Llonch et al., 2017a), adding feed additives such as electron receptors, ionophoric antibiotics and chemical inhibitors (Beauchemin et al., 2009), have shown a potential enteric methane reduction of about 5% per unit of fat protein corrected milk in dairy cattle (Knapp et al., 2014). Proper manure management can also help in mitigating the amount of GHG being emitted within the production system (Mohankumar Sajeew et al., 2018). The timing, quantity, and method of fertilizer applications are important factors which could help in optimizing biomass production and reduce soil greenhouse gas emissions (Grossi et al., 2019).

1.3 Livestock breeding for climate change

Selecting and breeding animals that are resilient and adapted to the changing climate is one of the important ways of mitigating and adapting to the effects of climate change on livestock. Well adapted animals are able to maintain their productivity within their environment with

little interventions. There is a direct link between greenhouse gas emission intensities and animal efficiency. The more productive the animal is, the lower the environmental impact will be per unit of product basis (Grossi et al., 2019). Both management quality and expression of full genetic potential are necessary to increase production efficiency. Genetic improvement is therefore an important tool to accumulate response to selection, and it can be used to reduce emissions (Cassandro, 2020). This can be done through breeding for improved efficiency which reduces the number of animals required to meet a given production level, improving functional traits such as fertility rates that can reduce wastage from the production system and selecting and breeding animals that are adaptable to the environment hence emitting less GHG.

Breeding for more productive animals can result in lower nutrient requirements to achieve the same level of production. This reduces GHG emissions by diluting nutrient requirements for upkeep, allowing a given amount of production to be reached with fewer animals (Bell et al., 2011). Additionally, a more efficient animal will retain more dietary nitrogen protein and there will be less nitrogen in faeces and urine (Gerber et al., 2013). However, unless balanced by selection pressure on functional traits, selective breeding for higher productivity can harm animal health and welfare and lead to numerous unexpected consequences (Fraser et al., 2013; de Vries et al., 2011), as shown by the association between high milk production and an increased incidence of fertility problems and metabolic disorders such as ketosis in dairy cattle (Walsh et al., 2011). Poor fertility requires more breeding animals in the herd to satisfy production requirements, as well as more replacements to keep the herd size stable, which increases GHG emissions. However, increasing reproductive pressure may increase the metabolic demands associated with pregnancy and breastfeeding, which could severely influence animal health and increase the risk of metabolic disorders, diminish immunological function, and thus reduce fertility (Llonch et al., 2017b). Therefore, developing selection indices that incorporate all traits of economic importance is necessary for breeding productive heat tolerant resilient livestock.

1.4 Small ruminant genetic resources in sub-Saharan Africa

Small ruminant genetic resources (SRGR), sheep and goats are widely spread in sub-Saharan Africa (SSA) and are an important source of food, income, saving and socio-cultural values. SRGR make up 62% of domesticated ruminant livestock in SSA, with goats contributing 34% and sheep 28%. Approximately 90% of these SRGR are native breeds in pastoral, agro-pastoral, mixed crop-livestock systems. These production systems are characterized by different

production goals, management strategies and constraints. The pastoral production system is mainly found in the ASALs where livestock is usually the main source of livelihood, breeds are mostly indigenous, and the animals are grazed. The agro-pastoral production system are found in semi-arid and in sub-humid areas. The production system is similar to the pastoral system however the pastoralists farm some crops to supplement their source of income and food. The mixed crop-livestock system is found in semi-arid, sub-humid and highlands areas. The systems has a densely populated a livestock population and are located near urban centres. The industrial system is a highly specialised system focusing on genetically improved and uniform genotypes. The animals are kept under intensive management system (Kosgey, 2004).

A larger proportion of goats (64%) and sheep (57%) are in the ASALs of SSA. Generally, goats out number sheep in most agro-ecological zones of SSA, except in the highlands where sheep are more prevalent. East and West Africa host the majority of SRGR, with East Africa leading in sheep numbers and West Africa in goats. Variations exist within regions; for instance, in southern Africa, South Africa has a higher sheep population than goats (FAO, 2021). SRGR in SSA are diverse consisting of about 61 sheep and 42 goat genotypes (Lebbie et al., 1996). It's important to recognize that, aside from exotic and synthetic or composite breeds, the true genetic uniqueness of most major genotypes and their varieties or strains—especially indigenous ones—remains unclear. As observed, indigenous SRGR are often named after specific ethnic groups (e.g., Red Maasai sheep) or regions (e.g., West African Dwarf). Likewise, the categorization of these primary types relies predominantly on their physical or morphological traits.

SRGR are particularly valued for their adaptability to harsh environments, rapid reproductive rates, and low maintenance requirements. For instance, indigenous breeds like the Red Maasai sheep and Small East African goats are well-suited to drought-prone areas due to their resistance to diseases and ability to thrive on low-quality forage (Mbuku et al., 2015; De Vries, 2008; Mugambi et al., 2005). The small ruminants are especially important to women who mostly manage them (Kariuki et al., 2022). Small ruminants also serve as a form of "insurance" for households, providing quick cash during emergencies or for social obligations such as weddings and school fees (Zonabend König et al., 2017). The small ruminants are known for their considerable ability to adapt and manage to survive and flourish in extremely hostile environments, including not only the arid zones but also the humid areas of West and central Africa. The weight and size of small ruminants in tropical Africa, are very much lower than in

temperate countries, tend to reduce steadily from the traditional, arid production areas towards the humid zones in which dwarf breeds have developed.

The domestic sheep (*Ovis aries*) is a very widespread small ruminant species raised primarily for its wool, meat, milk and hides. Sheep in Africa have been primarily a source of meat and much less important as milk and wool producers, than they are in Eurasia and Australasia (Da Silva et al., 2025). Africa hosts approximately a third of the world's 1.3 billion heads of sheep majority of which are classified as indigenous (FAO, 2021). The indigenous African sheep genetic resources have been classified into two main groups, fat-tailed and thin-tailed sheep. The fat-tailed sheep are the most widely distributed, being found in mostly in the Arid and Semi-Arid Lands (ASAL) of North Africa, Eastern and Southern Africa (Muigai and Hanotte, 2013).

1.5 Breeding strategies for sheep in sub-Saharan Africa

The main goal of animal breeding's is to genetically improve livestock populations so that they produce more and improved quality animal products as a lower input cost. Animal breeding is a long-term activity that needs long term planning and commitment for it to achieve its goal. Through a structured breeding program, the breeding goal is defined and a consistent increment in the hereditary potential of livestock populations can be accomplished by continuously and selectively choosing the parents from one generation to the next (Falconer, 1996). In the midst of climate change, the breeding strategies for indigenous breeds should be aimed at not only improving the breed but also conserving it to maintain genetic diversity. In SSA, the most common and effective way of conserving indigenous breeds is *in situ*, where farmers and their community maintain their farm animal genetic resources as part of their livelihoods (FAO, 2007). Given the nature of the sheep production system in SSA, the breeding structures and strategies are very different compared to other species such as dairy cattle. Most flocks kept by farmers are either highly inbred or indiscriminately crossbred which leads to loss of important genetic material. This is mainly due to farmers lacking knowledge on sound animal breeding practices, lack of animal breeding policies and lack of record keeping infrastructures to aid in selection and breeding.

The breeding strategies that have been adopted for sheep in SSA are nucleus breeding programs, importation of exotic breeds and community-based breeding programs (CBBP). A nucleus breeding program is centralized and only few farmers participate in the program thereby requiring long-term commitment. Recording keeping in this system is easy and the

genetic gain is higher (Kosgey and Okeyo, 2007). The recording keeping, genetic evaluation, delivery of genetic change breeding and selection happens at the centralised breeding. However, these breeding schemes has failed to sustainably provide the desired genetic improvement to small holders and engage the participation of the end users in the process (Haile et al., 2020). The importation of exotic or improved breeds is usually aimed at crossbreeding the indigenous breeds to upgrade them. However, this is mostly done without adequately assessing the viability and adaptability of these imported breeds and their consequent crosses to local production systems or conditions, and without a defined plan for determining the desired final genotype. Therefore, farmers end up practising indiscriminate crossbreeding with local populations resulting to genetic erosion of the local populations. Alternatively, in a CBBP, the selection and breeding is carried out by the farmers within the communities. The advantage of CBBP is that the farmer is actively involved throughout the process from inception through implementation. The success of CBBP is based upon proper consideration of farmers' breeding objectives, available infrastructure, participation and ownership (Mueller et al., 2015; Wurzinger et al., 2011; Sölkner et al., 1998). CBBP have been shown to achieve genetic improvement for indigenous sheep breeds in ASAL regions(Haile et al., 2019, 2020).

1.6 The Red Maasai sheep

The Red Maasai sheep breed is an indigenous breed native in East Africa (Figure 1). It is a fat-tailed transboundary indigenous breed mainly kept by Maasai pastoralists and neighbouring tribes in semi-arid and arid regions of Kenya and Tanzania. The breed is mainly used for meat, lard and other cultural practices for example, the fat of the Red Maasai is given after a woman has delivered a baby, after a cultural circumcision, and during sickness or injury. The breed is also used as a bride price where the Red Maasai is given to the mother-in-law (Liljestrand, 2012).



Figure 1 Red Maasai ewe and its lamb

The Red Maasai sheep is renowned for its adaptability to ASAL environments which are a low-input-output production system. The Red Maasai sheep is medium-sized, with a distinctive red-brown coat, polled head, and compact, resistance to gastrointestinal parasites,

particularly *Haemonchus contortus* (Kwallah et al., 2008; Baker et al., 2004). The actual population size of the purebred Red Maasai is currently not available, and thus its risk status remains unknown. However, there is evidence to show that the Red Maasai is threatened due to the indiscriminate crossbreeding with the Dorper sheep that was imported from South Africa in the 1970s (Zonabend et al., 2014; Gibson and Pullin, 2005). Very few populations of pure Red Maasai can be found in research stations and with few farmers.

In terms of production, the Red Maasai sheep has an average slaughter weight of 23.18 ± 0.20 kg at 9 months (Oyieng et al., 2022). A genetic analysis of reproduction and survival traits, and the effects of heat stress to the growth of the breed are yet to be studied and properly documented. Previous research on Red Maasai sheep has mainly been focusing on studying its resistance to *Haemonchus contortus* (Mugambi et al., 2005; Baker et al., 2004).

1.7 The Dorper sheep

The Dorper is a synsthetic breed developed in South Africa (Figure 2). It was developed through the selective crossbreeding of the Dorset Horn rams and the Black Headed Persian ewes resulting into two variants of the breed one with a characteristic black head and white body and the other that is entirely white in colour. The Dorset Horn sheep is known for its quality meat production while the Black Headed Persian sheep is well adapted to ASAL environments (Cloete et al., 2000; Milne, 2000). The Dorper is popularly known for its high-quality carcass and relatively early maturing, and this made it a main breed of choice for meat in other African countries (de Waal and Combrinck, 2000). The breed is currently widespread across the globe, and research both on production and reproduction traits have been



Figure 2 Dorper ewe and its lamb

carried out (Cloete et al., 2000, 2021; Zishiri et al., 2013)

When it was introduced to Kenya, no proper crossbreeding strategy was in place and farmers were not given instruction about how to maintain a continuous crossbreeding programme

resulting into indiscriminate crossbreeding with indigenous breeds especially the Red Maasai. Within the country, it is nearly impossible to find purebred indigenous sheep in the field since most sheep have been crossed with the Dorper.

The growth performance of the Dorper varies depending in the environment it is being reared with the highest birth weights of 4.19 ± 0.09 kgs reported in South Africa (Cloete et al., 2021), low birth weight of 3.33 ± 0.10 kgs reported in Ethiopia (Goshme et al., 2021) and better birth weights of 3.8 ± 0.02 kgs in Kenya (Oyieng et al., 2022). The age of first lambing for the ewes ranges from 346 in South Africa (Cloete et al., 2000) to 786 days in Ethiopia (Goshme et al., 2021) while lambing interval ranges from 198 days in South Africa (Cloete et al., 2000) to 422 days in Kenya (Wanjala et al., 2023). A 32.1% mortality rate of the Dorper lambs before yearling have been reported in Ethiopia (Tesema et al., 2020).

1.8 Objectives of this thesis

The overall objective of this thesis was to study the performance of the Red Maasai, Dorper and their crossbred combinations reared in an extensive production system in the semi-arid lands. The results of this study will not only help in informing the selection, breeding and conservation of the indigenous Red Maasai sheep but also in developing crossbreeding strategies between the Red Maasai and Dorper. More specifically, this thesis aims to:

- I. Evaluate the reproduction traits of the Red Maasai, Dorper and their crossbred combinations reared in an extensive production system in the semi-arid lands of Kenya.
- II. Assess the pre- and post-weaning to yearling survival of lambs and the length of productive life of ewes of the Red Maasai, Dorper and their crossbred combinations reared in an extensive production system in the semi-arid lands of Kenya
- III. Establish whether heat stress has an impact on the growth of Red Maasai, Dorper and their crossbred combinations reared in an extensive production system in the semi-arid lands of Kenya and develop novel resilience phenotypes for the sheep population.

References

- Baker, R.L., Mugambi, J.M., J.O., A., Carles, A.B., Thorpe, W., 2004. Genotype by environment interactions for productivity and resistance to gastro-intestinal nematode parasites in Red Maasai and Dorper sheep. *Animal Science* 79, 343–353.
- Beauchemin, K.A., McAllister, T.A., McGinn, S.M., 2009. Dietary mitigation of enteric methane from cattle. *CABI Reviews* 1–18. doi:10.1079/PAVSNNR20094035
- Bell, M.J., Wall, E., Simm, G., Russell, G., 2011. Effects of genetic line and feeding system on methane emissions from dairy systems. *Animal Feed Science and Technology* 166–167, 699–707. doi:https://doi.org/10.1016/j.anifeedsci.2011.04.049
- Cassandro, M., 2020. Animal breeding and climate change, mitigation and adaptation. *Journal of Animal Breeding and Genetics* 137, 121–122. doi:https://doi.org/10.1111/jbg.12469
- Cloete, S.W.P., Snyman, M.A., Herselman, M.J., 2000. Productive performance of Dorper sheep. *Small Ruminant Research* 36, 119–135. doi:https://doi.org/10.1016/S0921-4488(99)00156-X
- Cloete, S.W.P., Thutwa, K., Scholtz, A.J., Cloete, J.J.E., Dzama, K., Gilmour, A.R., van Wyk, J.B., 2021. Breed effects and heterosis for weight traits and tick count in a cross between an indigenous fat-tailed and a commercial sheep breed. *Tropical Animal Health and Production* 53, 165. doi:10.1007/s11250-021-02612-7
- Da Silva, A., Ahbara, A., Baazaoui, I., Jemaa, S. Ben, Cao, Y., Ciani, E., Dzomba, E.F., Evans, L., Gootwine, E., Hanotte, O., Harris, L., Li, M.-H., Mastrangelo, S., Missohou, A., Molotsi, A., Muchadeyi, F.C., Mwacharo, J.M., Tallet, G., Vernus, P., Hall, S.J.G., Lenstra, J.A., 2025. History and genetic diversity of African sheep: Contrasting phenotypic and genomic diversity. *Animal Genetics* 56, e13488. doi:https://doi.org/10.1111/age.13488
- De Vries, J., 2008. Goats for the poor: Some keys to successful promotion of goat production among the poor. *Small Ruminant Research* 77, 221–224. doi:10.1016/j.smallrumres.2008.03.006
- de Vries, M., Bokkers, E.A.M., Dijkstra, T., van Schaik, G., de Boer, I.J.M., 2011. Invited review: Associations between variables of routine herd data and dairy cattle welfare indicators. *Journal of Dairy Science* 94, 3213–3228. doi:https://doi.org/10.3168/jds.2011-4169
- de Waal, H.O., Combrinck, W.J., 2000. The development of the Dorper, its nutrition and a perspective of the grazing ruminant on veld. *Small Ruminant Research* 36, 103–117. doi:https://doi.org/10.1016/S0921-4488(99)00155-8
- Enahoro, D., Mason-D’Croz, D., Mul, M., Rich, K.M., Robinson, T.P., Thornton, P., Staal, S.S., 2019. Supporting sustainable expansion of livestock production in South Asia and Sub-

- Saharan Africa: Scenario analysis of investment options. *Global Food Security* 20, 114–121. doi:<https://doi.org/10.1016/j.gfs.2019.01.001>
- Falconer, D.S., 1996. *Introduction to quantitative genetics*, 4th Edition. ed. Longman.
- FAO, 2021. *Food and Agriculture Organization of the United Nations. FAOSTAT Statistical Database.*
- FAO, 2007. *The state of the world's animal genetic resources for foos and agriculture.* FAO, Rome.
- Fraser, D., Duncan, I.J.H., Edwards, S.A., Grandin, T., Gregory, N.G., Guyonnet, V., Hemsworth, P.H., Huertas, S.M., Huzzey, J.M., Mellor, D.J., Mench, J.A., Špinka, M., Whay, H.R., 2013. General Principles for the welfare of animals in production systems: The underlying science and its application. *The Veterinary Journal* 198, 19–27. doi:<https://doi.org/10.1016/j.tvjl.2013.06.028>
- Gerber, Steinfeld, H., Henderson, B., Mottet, A., Opio, C., Dijkman, J., Faluccci, A., Tempio, G., 2013. *Tackling climate change through livestock: a global assessment of emissions and mitigation opportunities.*
- Gibson, J.P., Pullin, R.S. V, 2005. *Conservation of Livestock and Fish Genetic Resources: Joint Report of Two Studies Commissioned by the CGIAR Science Council.* Rome, Italy.
- Goshme, S., Besufekad, S., Bisrat, A., Abebe, A., 2021. Reproductive and productive performance of Dorper sheep and their crossbreds with local highland sheep at Debre Birhan agricultural research center, Ethiopia. *Livestock Research for Rural Development* 33.
- Grossi, G., Goglio, P., Vitali, A., Williams, A.G., 2019. Livestock and climate change: impact of livestock on climate and mitigation strategies. *Animal Frontiers* 9, 69–76. doi:[10.1093/af/vfy034](https://doi.org/10.1093/af/vfy034)
- Haile, A., Getachew, T., Mirkena, T., Duguma, G., Gizaw, S., Wurzinger, M., Soelkner, J., Mwai, O., Dessie, T., Abebe, A., Abate, Z., Jembere, T., Rekik, M., Lobo, R.N.B., Mwacharo, J.M., Terfa, Z.G., Kassie, G.T., Mueller, J.P., Rischkowsky, B., 2020. Community-based sheep breeding programs generated substantial genetic gains and socioeconomic benefits. *Animal* 14, 1362–1370. doi:[10.1017/S1751731120000269](https://doi.org/10.1017/S1751731120000269)
- Haile, A., Gizaw, S., Getachew, T., Mueller, J.P., Amer, P., Rekik, M., Rischkowsky, B., 2019. Community-based breeding programmes are a viable solution for Ethiopian small ruminant genetic improvement but require public and private investments. *Journal of Animal Breeding and Genetics* 136, 319–328. doi:<https://doi.org/10.1111/jbg.12401>

- Hristov, A.N., Oh, J., Lee, C., Meinen, R., Montes, F., Ott, T., Firkins, J., Rotz, A., Dell, C., Adesogan, C., 2013. Mitigation of Greenhouse Gas Emissions in Livestock Production—A Review of Technical Options for Non-CO₂ Emissions. Food and Agriculture Organization of the United Nations (FAO): Rome, Italy,.
- Kariuki, J., Galie, A., Birner, R., Oyieng, E., Chagunda, M.G.G., Jakinda, S., Milia, D., Ojango, J.M.K., 2022. Does the gender of farmers matter for improving small ruminant productivity? A Kenyan case study. *Small Ruminant Research* 206. doi:10.1016/j.smallrumres.2021.106574
- Kayigema, V., Rugege, D., 2014. Women's perceptions of the Girinka (one cow per poor family) programme, poverty alleviation and climate resilience in Rwanda.
- Knapp, J.R., Laur, G.L., Vadas, P.A., Weiss, W.P., Tricarico, J.M., 2014. Invited review: Enteric methane in dairy cattle production: Quantifying the opportunities and impact of reducing emissions. *Journal of Dairy Science* 97, 3231–3261. doi:https://doi.org/10.3168/jds.2013-7234
- Kosgey, 2004. Breeding objectives and breeding strategies for small ruminants in the tropics. PhD Thesis, Wageningen University.
- Kosgey, I.S., Okeyo, A.M., 2007. Genetic improvement of small ruminants in low-input, smallholder production systems: Technical and infrastructural issues. *Small Ruminant Research* 70, 76–88. doi:10.1016/j.smallrumres.2007.01.007
- Kwallah, A.B.O., Okeyo, A.M., Mburu, D., Hanotte, O., 2008. Genetic Diversity and Relationships Of Sheep Breeds Of Kenya : Preliminary Results And Evidence of Dilution Of the Indigenous Red Maasai 7–10.
- Lebbie, S.H.B., Yapi-Gnoare, C. V, Rege, J.E.O., Baker, R.L., 1996. Current developments in the management of small ruminant genetic resources: Sub-Saharan Africa. In Of IGA/FAO Round Table On The Global Management of Small Ruminant Genetic Resources. International Goat Association, Beijing, China.
- Liljestrand, J., 2012. Breeding practices of Red Maasai sheep in Maasai pastoralist communities. Master Thesis, Swedish University of Agricultural Sciences., Uppsala, Sweden.
- Llonch, P., Haskell, M.J., Dewhurst, R.J., Turner, S.P., 2017a. Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective. *Animal* 11, 274–284. doi:https://doi.org/10.1017/S1751731116001440

- Llonch, P., Haskell, M.J., Dewhurst, R.J., Turner, S.P., 2017b. Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective. *Animal* 11, 274–284. doi:<https://doi.org/10.1017/S1751731116001440>
- Lwelamira, J., Binamungu, H.K., Njau, F.B., 2010. Contribution of small scale dairy farming under zero-grazing in improving household welfare in Kayanga ward, Karagwe District, Tanzania. *Livestock Research for Rural Development* 22.
- Mbuku, S.M., Okeyo, A.M., Kosgey, I.S., Kahi, A.K., 2015. Optimum crossbreeding systems for goats in low-input livestock production system in Kenya. *Small Ruminant Research* 123, 55–61. doi:10.1016/j.smallrumres.2014.10.001
- Milne, C., 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. doi:[https://doi.org/10.1016/S0921-4488\(99\)00154-6](https://doi.org/10.1016/S0921-4488(99)00154-6)
- Mohankumar Sajeev, E.P., Winiwarter, W., Amon, B., 2018. Greenhouse Gas and Ammonia Emissions from Different Stages of Liquid Manure Management Chains: Abatement Options and Emission Interactions. *Journal of Environmental Quality* 47, 30–41. doi:<https://doi.org/10.2134/jeq2017.05.0199>
- Mueller, J.P., Rischkowsky, B., Haile, A., Philipsson, J., Mwai, O., Besbes, B., Valle Zárate, A., Tibbo, M., Mirkena, T., Duguma, G., Sölkner, J., Wurzinger, M., 2015. Community-based livestock breeding programmes: essentials and examples. *Journal of Animal Breeding and Genetics* 132, 155–168. doi:<https://doi.org/10.1111/jbg.12136>
- Mugambi, J.M., Audho, J.O., Baker, R.L., 2005. Evaluation of the phenotypic performance of a Red Maasai and Dorper double backcross resource population: natural pasture challenge with gastro-intestinal nematode parasites. *Small Ruminant Research* 56, 239–251. doi:<https://doi.org/10.1016/j.smallrumres.2004.06.003>
- Muigai, A.W.T., Hanotte, O., 2013. The Origin of African Sheep: Archaeological and Genetic Perspectives. *African Archaeological Review* 30, 39–50. doi:10.1007/s10437-013-9129-0
- Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livestock Science* 130, 57–69. doi:<https://doi.org/10.1016/j.livsci.2010.02.011>
- Oloo, R.D., Ekine-Dzivenu, C.C., Mrode, R., Bennewitz, J., Ojango, J.M.K., Kipkosgei, G., Gebreyohanes, G., Okeyo, A.M., Chagunda, M.G.G., 2024. Genetic analysis of phenotypic indicators for heat tolerance in crossbred dairy cattle. *Animal* 18. doi:10.1016/j.animal.2024.101139
- Otte, J., A. Costales, J. Dijkman, U. Pica-Ciamarra, T. Robinson, V. Ahuja, C. Ly, D. Roland-Holst, 2012. *Livestock sector development for poverty reduction : an economic and policy*

- perspective : livestock's many virtues. Food and Agricultural Organization of the United Nations, Rome.
- Oyiang, E., Mrode, R., Ojango, J.M.K., Ekine-Dzivenu, C.C., Audho, J., Okeyo, A.M., 2022. Genetic parameters and genetic trends for growth traits of the Red Maasai sheep and its crosses to Dorper sheep under extensive production system in Kenya. *Small Ruminant Research* 206, 106588. doi:10.1016/j.smallrumres.2021.106588
- Pender, J., Nkonya, E., Jagger, P., Sserunkuuma, D., Ssali, H., 2004. Strategies to increase agricultural productivity and reduce land degradation: evidence from Uganda. *Agricultural Economics* 31, 181–195. doi:https://doi.org/10.1016/j.agecon.2004.09.006
- Reid, R.S., Galvin, K.A., Kruska, R.S., 2008. Global Significance of Extensive Grazing Lands and Pastoral Societies: An Introduction. In *Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems* (eds. Galvin, K.A., Reid, R.S., Jr, R.H.B., Hobbs, N.T.). Springer Netherlands, Dordrecht, pp. 1–24. doi:10.1007/978-1-4020-4906-4_1
- Renaudeau, D., Collin, A., Yahav, S., De Basilio, V., Gourdine, J.L., Collier, R.J., 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. In *Animal*. pp. 707–728. doi:10.1017/S1751731111002448
- Sánchez-Molano, E., Kapsona, V. V., Oikonomou, S., McLaren, A., Lambe, N., Conington, J., Banos, G., 2020. Breeding strategies for animal resilience to weather variation in meat sheep. *BMC Genetics* 21. doi:10.1186/s12863-020-00924-5
- Sejian, V., Hyder, I., Ezeji, T., Lakritz, J., Bhatta, R., Ravindra, J.P., Prasad, C.S., Lal, R., 2015. Global warming: role of livestock. *Climate change impact on livestock: Adaptation and mitigation* 141–169.
- Sölkner, J., Nakimbugwe, H.N., Zárate, A.V., 1998. Analysis of determinants for success and failure of village breeding programmes. In *In Proceedings of the 6th World Congress on Genetics Applied to Livestock Production*, 12–16 January 1998, Armidale, Australia.
- Solomon, S., 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Cambridge university press.
- Tesema, Z., Deribe, B., Kefale, A., Lakew, M., Tilahun, M., Shibesh, M., Belayneh, N., Zegeye, A., Worku, G., Yizengaw, L., 2020. Survival analysis and reproductive performance of Dorper x Tumele sheep. *Heliyon* 6, e03840. doi:https://doi.org/10.1016/j.heliyon.2020.e03840
- Thornton, P.K., 2010. Livestock production: Recent trends, future prospects. *Philosophical Transactions of the Royal Society B: Biological Sciences*. doi:10.1098/rstb.2010.0134

- Tsartsianidou, V., Kapsona, V.V., Sánchez-Molano, E., Basdagianni, Z., Carabaño, M.J., Chatziplis, D., Arsenos, G., Triantafyllidis, A., Banos, G., 2021. Understanding the seasonality of performance resilience to climate volatility in Mediterranean dairy sheep. *Scientific Reports* 11. doi:10.1038/s41598-021-81461-8
- Walsh, S.W., Williams, E.J., Evans, A.C.O., 2011. A review of the causes of poor fertility in high milk producing dairy cows. *Animal Reproduction Science* 123, 127–138. doi:https://doi.org/10.1016/j.anireprosci.2010.12.001
- Wanjala, G., Kichamu, N., Ciszter, L.T., Astuti, P.K., Kusza, S., 2023. An On-Station Analysis of Factors Affecting Growth Traits of Pure Red Maasai and Dorper Sheep Breeds under an Extensive Production System. *Animals* 13, 300. doi:https://doi.org/10.3390/ani13020300
- Wurzinger, M., Sölkner, J., Iñiguez, L., 2011. Important aspects and limitations in considering community-based breeding programs for low-input smallholder livestock systems. *Small Ruminant Research* 98, 170–175. doi:https://doi.org/10.1016/j.smallrumres.2011.03.035
- Zishiri, O.T., Cloete, S.W.P., Olivier, J.J., Dzama, K., 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. *Small Ruminant Research* 112, 39–48. doi:10.1016/J.SMALLRUMRES.2013.01.004
- Zonabend, E., Mirkena, T., Strandberg, E., Audho, J., Ojango, J., Malmfors, B., Okeyo, A.M., Philipsson, J., 2014. Breeding objectives for Red Maasai and Dorper sheep in Kenya – a participatory approach. In *10th World Congress on Genetics Applied to Livestock Production*. pp. 1–3.
- Zonabend König, E., Strandberg, E., Ojango, J.M.K., Mirkena, T., Okeyo, A.M., Philipsson, J., 2017. Purebreeding of Red Maasai and crossbreeding with Dorper sheep in different environments in Kenya. *Journal of Animal Breeding and Genetics* 134, 531–544. doi:https://doi.org/10.1111/jbg.12260

CHAPTER 2: Evaluating reproduction traits in a crossbreeding program between indigenous and exotic sheep in semi-arid lands

E.Oyieng^{a,b}, J.M.K Ojango^b, M.Gaulyc, R.Mrode^{b,d}, R.Dooso^{b,e}, A.M. Okeyo^b, C.Kalinda^{f,g}, S.König^a

^a Institute of Animal Breeding and Genetics, Justus-Liebig-University Gießen, Ludwigstraße 21 b, 35390 Gießen, Germany

^b Livestock Genetics Nutrition and Feed Resources Program, International Livestock Research Institute, P. O Box 30709-00100 Nairobi, Kenya

^c Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen – Bolzano, Universitätsplatz 5, 39100 Bolzano, Italy

^d Animal and Veterinary Science, Scotland's Rural College, EH9 3JG Edinburgh, United Kingdom

^e Animal Breeding and Husbandry in the Tropics and Subtropics, University of Hohenheim, Garbenstrasse 17, 70599 Stuttgart, Germany

^f Bill and Joyce Cummings Institute of Global Health, University of Global Health Equity, Kigali Heights, Plot 772 KG 7 Ave. P. O Box 6955, Kigali, Rwanda

^g School of Nursing and Public Health (SNPH), Discipline of Public Health Medicine, Howard College Campus, University of KwaZulu-Natal, Durban, South Africa

Published in

Animal, December 2024

<https://doi.org/10.1016/j.animal.2024.101391>

Abstract

Reproduction traits are important factors determining the efficiency of any sheep production system. This study evaluates the age at first lambing (AFL), lambing interval (LI), litter weight at birth (LBWT), litter weight at weaning (LWWT), birth weight of ewe (EBWT) and weaning weight of ewes (EWWT) in a crossbreeding program between the Red Maasai (RRRR) and Dorper sheep (DDDD) and their crosses, 75% Dorper (DDDR) and 50% Dorper (DDDR) breeds. All the traits significantly ($P<0.05$) differed across breeds and season of birth of the ewe. LBWT and LWWT were significantly affected by the sex of the lamb, type of birth of the lamb and parity in which the lambs were born in. AFL and LI had very high environment variances. Overall heritability estimates of AFL (0.09 ± 0.04) and LI (0.00 ± 0.01) were not significant from zero while the heritability estimates for EBWT (0.38 ± 0.04), EWWT (0.23 ± 0.03), LBWT (0.19 ± 0.03) and LWWT (0.09 ± 0.02) were significant ($P<0.05$). The RRRR had the highest genetic gain for all traits while the DDDR had a higher genetic gain among the crosses. LI had negative genetic correlations with LBWT (-0.53 ± 0.08) and LWWT (-0.28 ± 0.19) while AFL had positive genetic correlations with LBWT (0.27 ± 0.46) and LWWT (0.31 ± 0.34). The phenotypic trends for AFL and LWWT showed a negative and positive association, respectively, with the rainfall index over the years. With proper farm management, improved reproduction performance of ewes is possible by indirect selection using LBWT and LWWT for the Red Maasai, Dorper and their crosses within the semi-arid lands.

Keywords: Genetic parameters, Lambing, Weights, Red Maasai, Dorper

2.1 Introduction

Small ruminants can contribute to the efficient use of the semi-arid rangelands if harnessed for attributes that enable their optimal productivity and survival under the changing climates (Joy et al., 2020). Sheep and goats thrive through droughts more effectively than cattle, and flocks can be rebuilt more easily by the different communities following droughts (Haile et al., 2019; Muigai et al., 2017). The indigenous sheep and goat breeds raised by pastoral communities in the arid and semi-arid lands (ASAL) of East Africa are however reported to have low mature body weights and poor reproductive efficiency (Baker et al., 2004; Kosgey & Okeyo, 2007; Muigai et al., 2009; Wanjala et al., 2023) limiting their potential to adequately contribute to improving livelihoods of pastoralist households. Despite indigenous sheep breeds being well adapted to their environment due to natural selection over time, targeted

structured breeding programs to improve their productivity are limited (Haile et al., 2020). Their adaptability can be transferred through crossbreeding with exotic breeds, however without a comprehensive crossbreeding strategy that includes selective improvement and conservation of the indigenous breeds, their genetic variation can be rapidly eroded. Conservation of indigenous breeds in situ is best achieved through profitable use of their inherent traits.

When designing breeding programs for indigenous breeds, critical attention should be given to the reproductive performance of ewes as this influences the effectiveness and efficiency of sheep production (Tesema et al., 2020; Snyman et al., 1997). The ability of an ewe to regularly produce lambs over the years is considered a measure of the adaptability of the animal to the prevailing environmental conditions, and by extension, her long-term productivity (Kosgey et al., 2003). Since the 1970's, in Eastern Africa there has been indiscriminate crossbreeding between exotic and indigenous breeds in attempts to increase the productivity of pastoral production systems and mutton market preferences (Ojango et al., 2023; Getachew et al., 2016; Zonabend König et al., 2016). However, these efforts and strategies have not been accompanied by concerted and organized selection programs, aimed at improving productivity in the existing indigenous sheep populations on a long-term basis (Deribe et al., 2021; Getachew et al., 2016; Kosgey et al., 2008). This, together with frequent and severe droughts followed by seasons of excessive rainfall (Calvin et al., 2023) have resulted in a rapid decline in the number of pure-bred indigenous sheep breeds, despite their renown tolerance to the changing climate and certain diseases such as parasitosis (Wanjala et al., 2023). This underlines the need to selectively breed and conserve indigenous sheep populations while maintaining specific lines of their crossbreds

Since 2003, the International Livestock Research Institute (ILRI) has implemented a selective crossbreeding program for purebred indigenous Red Maasai and their crosses with the Dorper, a composite breed introduced from South Africa (C. Milne, 2000), targeting improved growth performance while maintaining the inherent resistance to *Haemonchus contortus* of the Red Maasai. Positive genetic gains have been achieved in growth performance as reported by Oyieng et al., (2022). This paper presents reproductive parameters and the genetic progress in reproductive performance of ewes of the Red-Maasai Sheep and their crosses with Dorper. The evaluation provides information on the fertility of the Red Maasai sheep and its crosses to guide crossbreeding strategies between indigenous and exotic breeds for optimum flock productivity in semi-arid areas.

2.2 Material and Methods

2.2.1 Study area

The study is part of a selection breeding program for sheep in an arid environment run at the Kapiti Research Station and Wildlife conservancy (formerly known as Kapiti Plains Estate) in Machakos County, Kenya (<https://www.ilri.org/research/facilities/kapiti-research-station-wildlife-conservancy>). The conservancy, owned by the International Livestock Research Institute (ILRI), is situated between 1,650 and 1,900 meters above sea level and at -1.6 latitude and 37.1 longitude. The area receives an average annual rainfall of around 552 mm, and the temperature ranges between 22 — 27 °C. It has four distinct seasons: the long-wet season (March to May), the short-dry season (January and February), the long-dry season (June to September), and the short-wet season (October to December). The conservancy mostly covered in grasses and shrubs is home to both wild and domestic animals. Grazing pasture supply is often limited during the prolonged dry seasons.

2.2.2 Animal management and breeding

The primary goals of the breeding program are to sustainably conserve the pure-bred Red Maasai sheep through within breed selection for growth, adaptability, and disease resistance and crossbreeding with the Dorper to increase the productivity and profitability of sheep raised in semi-arid and arid areas of Kenya. The Red Maasai sheep is characterized by thick red hair. Their growth characteristics have been described by (George Wanjala et al., 2023a; Oyieng et al., 2022). The crossbreeding program combines the faster growth rate and mutton-producing ability of the Dorper breed and the resilience of the Red Maasai breed to gastrointestinal parasites. The main breed groups in the breeding program comprise pure Dorper (DDDD), pure Red Maasai (RRRR), 75%Dorper-25%Red Maasai (DDDR) and 50%Dorper-50%Red Maasai (DDRR). The animals are reared in flocks comprising ewes that have lambed in the latest breeding cycle, and separate flocks of weaner and mature males, and weaner and mature females. The total flock size ranges from 1 300 to 1 500. This range is influenced by outflows due to culling and death, and inflows due to new births within the flock. Twice annually, in June and November, mating is conducted. The choice of the mating months is aligned to the rainfall seasons to enable lambing to take place at the best possible time of forage availability. When a lamb is three months old, it is weaned and separated from its mother. Every lamb born is weighed at birth, weaning (3 months), 6 months, 9 months, and one year of age. From nine months of age, when female lambs weigh at least 24 kgs, they are exposed to Rams for their first mating. Ewes are culled at the age of 6 years.

The selection of sires has a significant impact on mating and selection within the flock. Rams are chosen as sires based on three factors: their physical appearance, their dams' reproductive performance measured by the age at first lambing and intervals between lambings, and their genetic potential for growth to nine months using estimated breeding values. The number of Rams used is based on the number of female animals ready for mating and the desired number of offspring from each breed group required in the flock. The allocation of females to Rams in separate mating pens is managed to avoid inbreeding. Over a period of four weeks, each ram is given 20 to 30 ewes to mate. The performance of the Rams in the mating pens is monitored using coloured markers adhered to their underside that mark the rump of every ewe mounted. Inactive rams within a mating pen are replaced. Sires of the offsprings are recorded in line with the mating noted in each pen. To ensure genetic progress in the desired traits, 20% of the rams that were used in the previous mating season are replaced. The rams that have been culled but have good breeding values for growth and reproductive performance are sold to other sheep farmers as breeding animals while the rest are sold for mutton.

Water is provided *ad libitum* for all the animals when in the pens during the night, and before setting out for grazing. When animals are grazing in the open fields, water is provided twice in the day. Scheduled vaccination against blanthrax, enterotoxaemia, and foot and mouth disease are provided annually, bi-annually and every 5 months, respectively. Anthelmintic treatment is given to animals before and after the rainy season based on the age and body condition of the animals.

2.2.3 Data structure and traits studied

The pedigree used to construct the numerator relationship matrix of the animal models had 7 396 animals spanning 12 generations, including 206 sires and 2 591 dams. Lambing data of 2 056 ewes of the different breed types born between 2003 to 2020 was obtained for the analysis of reproduction of the sheep in an arid and semi-arid environment. The data was cleaned and boundaries determined based on the normal distribution for weight data. Weight records which were three standard deviations more or less from the mean were eliminated. Subsequently, only ewes with an age at first lambing between 330 and 1 080 days were included in the analyses. The lower limit was based on the possibility of including abortions that occurred in late pregnancy. The upper limit took care of the likelihood of a subsequent lambing event being misclassified as the first lambing due to an unrecorded first lambing. Lambing intervals below 240 days and above 600 days were also excluded. Following cleaning, records on 1 636 animals comprising 80% of the original data was used for the analyses. The traits evaluated were age at first lambing (AFL), lambing interval (LI), birth weight of the ewe

(EBWT), weaning weight of the ewe (EWWT), average birth weight in a litter for an ewe (LBWT) and average weaning weight for the litter of an ewe (LWWT). Descriptive statistics of the data used for the analysis of each trait is presented in Table 1.

Table 1: Descriptive statistics for the traits studied grouped by sheep breed

Trait	Breed group				Overall
	DDDD	DDDR	DDRR	RRRR	
Age of first lambing (AFL)					
N	327	428	473	408	1636
Mean	739.66	756.85	727.29	702.65	731.35
SD	165.45	182.97	172.97	164.36	173.08
CV%	22	24	24	23	24
Min	411	398	422	363	363
Max	1082	1087	1087	1080	1087
Lambing interval (LI)					
N	236	433	592	630	1891
Mean	425.60	407.02	431.10	425.87	423.16
SD	91.80	88.14	90.94	91.89	91.12
CV%	22	22	21	22	22
Min	211	208	211	209	208
Max	600	599	600	599	600
Birth weight of the ewe (EBWT)					
N	327	428	473	408	1636
Mean	3.67	3.63	3.38	3.06	3.42
SD	0.65	0.61	0.59	0.50	0.63
CV%	18	17	17	16	18
Min	1.8	1.9	1.7	1.3	1.3
Max	5.8	5.1	5.1	5.1	5.8
Weaning weight of the ewe (EWWT)					
N	327	428	473	408	1636
Mean	17.23	16.79	16.38	14.26	16.12
SD	4.00	4.23	3.99	3.05	4.00
CV%	23	25	24	21	25
Min	7.1	4.8	6	5.7	4.8
Max	27	30	28	23.5	30
Litter birth weight (LBWT)					
N	550	836	1053	975	3414
Mean	3.51	3.71	3.63	3.20	3.50
SD	0.71	0.66	0.67	0.57	0.68
CV%	20	18	19	18	19
Min	1.5	2	1.5	1.6	1.5
Max	5.5	5.6	5.3	5.2	5.6
Litter weaning weight (LWWT)					
N	444	719	964	829	2956
Mean	17.19	17.21	16.76	15.33	16.53
SD	4.82	4.38	4.18	3.78	4.29
CV%	28	25	25	25	26
Min	5.2	6.34	5.76	4.34	4.34
Max	37.45	38.4	31.91	27.98	38.4

Breed code: **DDDD**= pure dorper, **DDDR** = 75%Dorper-25%Red Maasai, **DDRR** = 50%Dorper-50%Red Maasai, **RRRR** = pure Red Maasai

2.2.4 Data analysis

2.2.4.1 Genetic parameter estimation

The Linear Model procedure of R (R Core Team, 2021) was used to evaluate the factors that influenced the AFL, LI, EBWT, EWWT, LBWT and LWWT. The fixed effects (that significantly influenced each trait ($P < 0.05$)) were included in the subsequent univariate and multivariate animal model analyses using ASReml-R 4.1 (Butler et al., 2018). Least-square means (LSM) of

different fixed effects groups for each model were calculated and contrasted using Tukey HSD Post Hoc test (Toothaker, 1993) at $P < 0.05$.

Different animal models were used to estimate the genetic parameters for the traits as the fixed factors affecting each trait differed. To analyse the AFL and LI, the model accounted for year-season of birth and breed effects. The breed, year of birth, season of birth and type of birth of the ewe were fitted to evaluate the EBWT and EWWT of the ewe. For LBWT and LWWT models, breed, sex of the lamb, type of birth of the lamb, year-season of lambing of the ewe, parity of the ewe, and age of the ewe nested within the parity were included as fixed effects. Additional effects included in the analyses of LBWT and LWWT were, type of birth, sex, and the breed of the lamb. Although 5 parities were represented in the data, parity effects were modelled with only four classes: parities 1, 2 and 3 separately, and parities 4 to 5 pooled into a fourth class. The effect of the Age of the ewe was fitted using a Legendre polynomial of order two.

The univariate animal model 1 was used to estimate the heritability, additive, phenotypic and residual variances for AFL, EBWT and EWWT.

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e} \quad \text{Model 1}$$

Where \mathbf{y} is the vector of observations on the specific trait of the animal; $\boldsymbol{\beta}$ and \mathbf{a} are vectors of fixed effects influencing the traits and direct additive genetic effects, respectively and \mathbf{e} is the vector of residual errors. \mathbf{X} is the incidence matrix relating observations to fixed effects; \mathbf{Z} is the incidence matrix relating records to random animal effects. The vectors of random animal effects \mathbf{a} and residual effects \mathbf{e} were assumed to be normally distributed with $\mathbf{a} \sim N(0; \mathbf{A}\sigma_a^2)$ and $\mathbf{e} \sim N(0; \mathbf{I}\sigma_e^2)$, where \mathbf{A} corresponds to the numerator relationship matrix, \mathbf{I} correspond to the identity matrix, σ_a^2 is the additive genetic variance, and σ_e^2 is the residual variance.

The repeatability animal Model 2 was fitted to estimate the heritability, additive, phenotypic and residual variances for LI, LBWT and LWWT.

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{pe} + \mathbf{e} \quad \text{Model 2}$$

where \mathbf{y} is a measurement of individual trait, $\boldsymbol{\beta}$ is the vector of the fixed effects in the model which included significant factors of variations for each in trait, \mathbf{a} is the solutions of random animal additive genetic effects, \mathbf{pe} is the vector of random permanent environmental effects

and non-additive genetic effects and \mathbf{e} is the vector of random residual effects. The vectors of random animal effects \mathbf{a} , random permanent maternal environmental effects \mathbf{pe} , and residual effects \mathbf{e} were assumed to be normally distributed with $\mathbf{a} \sim N(0; \mathbf{A}\sigma_a^2)$, $\mathbf{pe} \sim N(0; \mathbf{I}\sigma_{pe}^2)$ and $\mathbf{e} \sim N(0; \mathbf{I}\sigma_e^2)$, where \mathbf{A} corresponds to the numerator relationship matrix, \mathbf{I} correspond to the identity matrix, σ_a^2 is the additive genetic variance, σ_{pe}^2 is the permanent maternal environmental variance, and σ_e^2 is the residual variance. \mathbf{X} is the incidence matrix relating observations to fixed effects; \mathbf{Z} is the incidence matrix relating records to random animal effects. \mathbf{X} , \mathbf{Z} and \mathbf{W} are incidence matrices relating observations to fixed, random animal and permanent environmental effects, respectively.

Phenotypic and genetic correlations among traits were estimated using variances and covariances estimated from multivariate animal models. The following assumptions were made for the additive genetic effects in the multivariate models:

$$\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_n \end{bmatrix} \sim N \left[\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \mathbf{A} \otimes \begin{pmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} & \sigma_{a_1 a_n} \\ \sigma_{a_1 a_2} & \sigma_{a_2}^2 & \sigma_{a_2 a_n} \\ \sigma_{a_1 a_n} & \sigma_{a_2 a_n} & \sigma_{a_n}^2 \end{pmatrix} \right]$$

where \mathbf{a}_i is the vector with additive genetic effects for trait i , $\sigma_{a_i}^2$ is the additive genetic variance of trait i , and $\sigma_{a_i a_j}$ is the genetic covariance between trait i and j .

The residuals in the multivariate model were assumed to be:

$$\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_n \end{bmatrix} \sim N \left[\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \mathbf{I} \otimes \begin{pmatrix} \sigma_{e_1}^2 & \sigma_{e_1 e_2} & \sigma_{e_1 e_n} \\ \sigma_{e_1 e_2} & \sigma_{e_2}^2 & \sigma_{e_2 e_n} \\ \sigma_{e_1 e_n} & \sigma_{e_2 e_n} & \sigma_{e_n}^2 \end{pmatrix} \right]$$

where \mathbf{e}_i is the vector with residuals for trait i , $\sigma_{e_i}^2$ is the residual variance of trait i , and $\sigma_{e_i e_j}$ is the residual covariance between trait i and j .

The likelihood ratio test was used to test whether the heritability estimates differed significantly from zero by comparing the log likelihood of the tested model against a model without random animal genetic effects.

2.2.4.2 Genetic gain

The overall genetic gain was the regression coefficient of estimated breeding values. The EBVs were averaged over each of the traits within year of birth, and resultant values regressed across the year of birth, model 3:

$$y_a = b_0 + b_1 x_a \quad \text{Model 3}$$

where y_a is the average of EBV of a^{th} year of birth; x_a is the a^{th} year of birth; b_0 and b_1 , are the intercept and the linear regression coefficient, respectively.

2.2.4.3 Rainfall index

An annual rainfall index was developed to model the variation in rainfall from 2003 to 2020 experienced on the ranch using the monthly rainfall data collected at the ranch weather station. Equation 1 was used to calculate the annual rainfall index.

$$RI_i = \frac{X_i - \mu}{\sigma_\mu} \quad \text{Equation 1}$$

Where RI_i is the rainfall index for the i th year, X_i is the average rainfall for the i th year, μ is the overall mean rainfall for the period under study (2003-2020) and σ_μ is the standard deviation of the overall mean rainfall.

2.3 Results

2.3.1 Non-genetic factors

The least square means and their respective standard errors for significant ($P < 0.05$) fixed effects on the traits studied are presented in Table 2. The type of birth of the ewe and the season of birth of the lamb did not significantly affect the LBWT and LWWT. The pure Red Maasai had a significantly ($P < 0.05$) lower AFL, EBWT, EWWT, LBWT and LWWT compared to the other breeds. Among the crossbreds, the DRRR has significantly ($P < 0.05$) lower AFL, EBWT, EWWT, LBWT and LWWT compared to the DDDR breed. The DDDR breed had the lowest lambing interval across all breeds. Single born ewes were significantly ($P < 0.05$) heavier than ewes born as twins. Male and single birth lambs were also significantly ($P < 0.05$) heavier than female and twin lambs for both LBWT and LWWT. The LBWT increased significantly ($P < 0.05$) as the parity of the ewe increased. However, the difference in LWWT was only significant ($P < 0.05$) between litters born in parity one and those born in parity four.

Table 2: Least square means (LSM) \pm SE for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) for the sheep population

Fixed effects	AFL (days)	LI (days)	EBWT (kgs)	EWWT (kgs)	LBWT (kgs)	LWWT (kgs)
	(N) LSM \pm SE	(N) LSM \pm SE	(N) LSM \pm SE	(N) LSM \pm SE	(N) LSM \pm SE	(N) LSM \pm SE
Breed	***	**	***	***	***	***
DDDD	(327) 806.66 \pm 7.56 ^a	(236) 424.60 \pm 5.95 ^{ab}	(317) 3.32 \pm 0.04 ^a	(265) 15.01 \pm 0.26 ^a	(838) 3.51 \pm 0.03 ^a	(681) 16.30 \pm 0.25 ^a
DDDR	(428) 784.84 \pm 6.56 ^a	(433) 407.02 \pm 4.40 ^a	(428) 3.32 \pm 0.03 ^a	(413) 14.90 \pm 0.23 ^a	(1387) 3.56 \pm 0.03 ^a	(1138) 16.30 \pm 0.21 ^a
DDRR	(473) 752.65 \pm 6.52 ^b	(592) 428.10 \pm 3.95 ^b	(467) 3.10 \pm 0.03 ^b	(456) 14.12 \pm 0.23 ^b	(1736) 3.44 \pm 0.03 ^{ab}	(1508) 15.80 \pm 0.20 ^{ab}
RRRR	(408) 735.28 \pm 6.58 ^b	(630) 424.87 \pm 3.91 ^b	(411) 2.72 \pm 0.04 ^c	(378) 12.14 \pm 0.24 ^c	(1430) 3.03 \pm 0.03 ^b	(1232) 14.50 \pm 0.21 ^b
Type of birth (ewe)			***	***		
Single	-	-	(3340) 3.45 \pm 0.02 ^a	(3268) 15.51 \pm 0.10 ^a	-	-
Twin	-	-	(188) 2.78 \pm 0.06 ^b	(178) 12.50 \pm 0.35 ^b	-	-
Sex (lamb)					***	***
Male	-	-	-	-	(1644) 3.47 \pm 0.02 ^b	(1401) 16.30 \pm 0.18 ^a
Female	-	-	-	-	(1770) 3.30 \pm 0.02 ^b	(1555) 15.20 \pm 0.18 ^b
Type of birth (lamb)					***	***
Single	-	-	-	-	(3179) 3.68 \pm 0.01 ^a	(2763) 17.00 \pm 0.11 ^a
Twin	-	-	-	-	(235) 3.09 \pm 0.04 ^b	(1193) 4.50 \pm 0.30 ^b
Parity					***	***
One	-	-	-	-	(1602) 3.06 \pm 0.02 ^b	(1357) 14.50 \pm 0.19 ^a
Two	-	-	-	-	(895) 3.39 \pm 0.03 ^b	(793) 16.20 \pm 0.20 ^a
Three	-	-	-	-	(571) 3.49 \pm 0.03 ^c	(500) 16.50 \pm 0.23 ^a
Four	-	-	-	-	(346) 3.60 \pm 0.04 ^c	(306) 15.90 \pm 0.28 ^b
Season of birth (ewe)	***	***		***	***	*
Long wet	(446) 817.80 \pm 9.79 ^a	(633) 425.52 \pm 6.86 ^a		(498) 13.42 \pm 0.35 ^a	(509) 3.38 \pm 0.04 ^{ab}	(470) 14.80 \pm 0.32 ^a
Short wet	(640) 730.94 \pm 7.16 ^b	(731) 414.56 \pm 3.68 ^a		(585) 16.45 \pm 0.24 ^b	(667) 3.34 \pm 0.03 ^a	(606) 16.00 \pm 0.22 ^b
Long dry	(350) 783.23 \pm 8.94 ^a	(353) 407.62 \pm 4.85 ^{bc}		(378) 12.41 \pm 0.27 ^a	(384) 3.39 \pm 0.03 ^{ab}	(361) 16.10 \pm 0.25 ^b
Short dry	(200) 747.83 \pm 7.04 ^b	(174) 437.47 \pm 3.48 ^b		(233) 13.96 \pm 0.26 ^b	(229) 3.43 \pm 0.03 ^b	(167) 16.00 \pm 0.23 ^b

***, **, * means the fixed effect is significant at P<0.001, P<0.01 and P<0.05 respectively

Breed code: DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DDDR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai

2.3.2 Genetic parameters

The phenotypic, additive and residual variances, and heritability estimates for the traits by breed group and by population are presented in Table 3. The pure Dorper breed had higher heritability estimates for AFL, EBWT, and EWWT compared to the other breeds. Heritability estimates for LWWT were generally lower than that for LWB across all breeds. The heritability estimates for BWT, WWT and LBWT were all significant ($P < 0.05$) while the heritability estimates for lambing interval were not significant ($P > 0.05$). Overall, the heritability estimates for the ewe's birth weights were higher compared to that of their weaning weights, the same pattern also being observed between their corresponding lambing birth and weaning weights. The heritability estimates of EBWT and EWWT across the breeds were higher (ranging between 0.28 and 0.42) than those LBWT and LWWT (ranging between 0.00 to 0.18). The maternal effects on LBWT and LWWT was 0.19 and 9.05 respectively which accounted for 76% of the total residual variance. The overall repeatability estimates for LBWT and LWWT were 0.25 ± 0.03 and 0.16 ± 0.03 respectively. The repeatability estimate for LI was almost zero.

Table 3: Overall and within breed variance components and heritability estimates for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) grouped by sheep breed

Breed	σ_p^2	σ_a^2	σ_e^2	$h^2 \pm SE$	P Value
DDDD					
AFL	15619.60	3377.745	12241.85	0.22±0.16	0.15
LI	6835.09	0.02	6835.07	0.00±0.09	0.09
EBWT	0.33	0.14	0.19	0.42±0.03	0.00
EWWT	9.39	3.44	6.49	0.33±0.02	0.01
LBWT	0.36	0.05	0.231	0.13±0.04	0.03
LWWT	16.59	0.00	16.59	0.00±0.00	0.34
DDDR					
AFL	14424.75	1701.17	12723.58	0.12±0.14	0.14
LI	5936.84	198.80	5737.962	0.00±0.05	0.06
EBWT	0.28	0.09	0.19	0.34±0.03	0.00
EWWT	10.05	3.50	6.55	0.29±0.03	0.01
LBWT	0.35	0.06	0.29	0.18±0.06	0.03
LWWT	14.13	1.19	12.93	0.08±0.07	0.07
DDRR					
AFL	11756.65	1022.95	10733.71	0.09±0.11	0.41
LI	6152.05	0.99	6151.06	0.00±0.05	0.05
EBWT	0.29	0.11	0.18	0.39±0.02	0.00
EWWT	10.07	3.53	6.54	0.31±0.03	0.01
LBWT	0.31	0.06	0.25	0.18±0.06	0.01
LWWT	12.26	1.49	10.77	0.12±0.07	0.00
RRRR					
AFL	9665.58	690.82	8974.76	0.08±0.08	0.30
LI	6252.11	1.79	6250.31	0.03±0.03	0.07
EBWT	0.22	0.08	0.14	0.39±0.03	0.00
EWWT	6.61	2.52	3.98	0.28±0.08	0.01
LBWT	0.24	0.04	0.19	0.17±0.06	0.01
LWWT	10.07	0.26	9.81	0.03±0.03	0.00
Overall					
AFL	13604.58	1179.42	12425.16	0.09±0.04	0.30
LI	6262.51	0.0004.0	6262.51	0.00±0.00	0.18
EBWT	0.26	0.08	0.18	0.38±0.04	0.00
EWWT	10.04	3.50	6.54	0.23±0.03	0.01
LBWT	0.31	0.06	0.25	0.19±0.03	0.01
LWWT	13.16	1.25	11.91	0.09±0.02	0.00

σ_p^2 = Phenotypic variance; σ_a^2 = direct additive genetic variance; σ_e^2 = residual variance

h^2 = additive heritability of direct genetic effect

Breed code: **DDDD** = pure dorper, **DDDR** = 75%Dorper-25%Red Maasai, **DDRR** = 50%Dorper-50%Red Maasai, **RRRR** = pure Red Maasai.

2.3.3 Genetic and phenotypic correlations

The overall genetic and phenotypic correlations of the traits are presented in Table 4. A negative low genetic and phenotypic correlation between AFL and LI was observed (<0.05). LI had a moderate negative genetic and a weak phenotypic correlation with all the traits. AFL had a positive low genetic and phenotypic correlation with LBWT and LWWT. The genetic and phenotypic correlations between the weights of the ewe (EBWT and EWWT) and the lambing weights (LBWT and LWWT) were all positive and strong. The correlation between growth traits of the ewe and those of its lambs (EBWT and LBWT ; EWWT and LWWT) were positive and moderate. Generally, the pure Red Maasai sheep had higher genetic and phenotypic correlations between the traits than the pure Dorper sheep.

Table 4 Genetic and phenotypic \pm SE correlations for age at first lambing (AFL), Lambing Interval (LI), ewes' birth weight (EBWT), ewe's weaning weight (EWWT), Litter birth weight (LBWT) and litter weaning weight (LWWT) grouped by sheep breed

	Breed group				
	DDDD	DDDR	DDRR	RRRR	Overall
Genetic correlation					
AFL - LI	-0.11 \pm 1.47	-0.01 \pm 0.76	-0.07 \pm 0.95	-0.01 \pm 1.20	-0.04 \pm 0.82
EBWT - LI	-0.04 \pm 0.62	-0.32 \pm 0.25	-0.07 \pm 0.19	-0.30 \pm 0.49	-0.21 \pm 0.07
EBWT - AFL	0.11 \pm 0.30	0.02 \pm 0.21	0.06 \pm 0.21	0.20 \pm 0.19	0.21 \pm 0.53
EBWT - EWWT	0.12 \pm 0.13	0.39 \pm 0.06	0.42 \pm 0.04	0.45 \pm 0.04	0.85 \pm 0.28
EWWT - AFL	-0.03 \pm 0.24	-0.07 \pm 0.21	-0.02 \pm 0.21	-0.02 \pm 0.20	-0.10 \pm 0.13
EWWT - LI	-0.18 \pm 0.55	-0.21 \pm 0.23	-0.22 \pm 0.21	-0.29 \pm 0.48	-0.15 \pm 0.12
LBWT - AFL	0.09 \pm 0.55	0.06 \pm 0.37	0.24 \pm 0.45	0.25 \pm 0.38	0.27 \pm 0.46
LBWT - LI	-0.58 \pm 1.70	-0.19 \pm 0.37	-0.18 \pm 0.34	-0.22 \pm 0.66	-0.53 \pm 0.08
LBWT - LWWT	0.10 \pm 0.44	0.85 \pm 0.14	0.47 \pm 0.19	0.39 \pm 0.25	0.49 \pm 0.09
LBWT - EBWT	0.30 \pm 0.24	0.33 \pm 0.11	0.50 \pm 0.09	0.50 \pm 0.11	0.53 \pm 0.06
LBWT - EWWT	0.26 \pm 0.23	0.24 \pm 0.10	0.33 \pm 0.10	0.51 \pm 0.09	0.37 \pm 0.05
LWWT - AFL	0.04 \pm 0.65	0.13 \pm 0.43	0.02 \pm 0.56	0.08 \pm 0.54	0.31 \pm 0.34
LWWT - LI	-0.23 \pm 1.15	-0.07 \pm 0.40	-0.62 \pm 0.48	-0.16 \pm 0.92	-0.28 \pm 19.59
LWWT - EBWT	0.06 \pm 0.26	0.02 \pm 0.11	0.14 \pm 0.11	0.49 \pm 0.17	0.34 \pm 0.31
LWWT - EWWT	0.06 \pm 0.22	0.13 \pm 0.11	0.16 \pm 0.11	0.36 \pm 0.16	0.24 \pm 0.07
LWWT - LBWT	0.10 \pm 0.44	0.85 \pm 0.14	0.47 \pm 0.19	0.39 \pm 0.25	0.73 \pm 0.09
Phenotypic correlation					
AFL - LI	-0.12 \pm 0.09	-0.05 \pm 0.07	-0.02 \pm 0.07	-0.03 \pm 0.07	-0.01 \pm 0.03
EBWT - LI	-0.08 \pm 0.07	-0.09 \pm 0.06	-0.02 \pm 0.04	-0.04 \pm 0.04	-0.04 \pm 0.03
EBWT - AFL	-0.02 \pm 0.05	-0.00 \pm 0.050	-0.01 \pm 0.04	-0.05 \pm 0.04	-0.01 \pm 0.03
EBWT - EWWT	0.16 \pm 0.06	0.39 \pm 0.06	0.42 \pm 0.05	0.45 \pm 0.04	0.55 \pm 0.02
EWWT - AFL	-0.04 \pm 0.05	-0.02 \pm 0.05	0.00 \pm 0.04	-0.01 \pm 0.05	-0.02 \pm 0.03
EWWT - LI	-0.09 \pm 0.07	-0.06 \pm 0.06	-0.05 \pm 0.04	-0.04 \pm 0.05	-0.02 \pm 0.03
LBWT - AFL	0.01 \pm 0.06	0.03 \pm 0.05	0.06 \pm 0.04	0.00 \pm 0.05	0.02 \pm 0.02
LBWT - LI	-0.01 \pm 0.08	-0.01 \pm 0.05	-0.07 \pm 0.05	-0.06 \pm 0.05	-0.04 \pm 0.03
LBWT - LWWT	0.28 \pm 0.05	0.36 \pm 0.03	0.27 \pm 0.03	0.32 \pm 0.03	0.31 \pm 0.02
LBWT - EBWT	0.06 \pm 0.05	0.13 \pm 0.04	0.21 \pm 0.03	0.18 \pm 0.03	0.22 \pm 0.02
LBWT - EWWT	0.06 \pm 0.05	0.10 \pm 0.04	0.14 \pm 0.03	0.20 \pm 0.04	0.15 \pm 0.02
LWWT - AFL	0.04 \pm 0.07	0.11 \pm 0.05	0.01 \pm 0.05	0.01 \pm 0.06	0.07 \pm 0.03
LWWT - LI	-0.06 \pm 0.08	-0.03 \pm 0.06	-0.15 \pm 0.04	-0.04 \pm 0.05	-0.07 \pm 0.03
LWWT - EBWT	0.05 \pm 0.05	0.02 \pm 0.04	0.05 \pm 0.03	0.13 \pm 0.04	0.08 \pm 0.02
LWWT - EWWT	0.07 \pm 0.08	0.20 \pm 0.17	0.21 \pm 0.14	0.37 \pm 0.15	0.31 \pm 0.09
LWWT - LBWT	0.28 \pm 0.05	0.36 \pm 0.03	0.27 \pm 0.03	0.32 \pm 0.03	0.31 \pm 0.02

Breed code: DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DDRR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai

2.3.4 Genetic trends and gain

The traits of importance in the selective breeding program were age at first lambing (AFL) and average litter weaning weight (LWWT). Figure 1 and 2 shows the genetic trend for AFL and LWWT by breed group plotted against the year of birth of the ewes. The pure Dorper and pure Red Maasai ewes born in 2011 had the highest genetic gain for AFL. Among the crossbreds, the DDRR and DDDR born in 2017 and 2013 had the highest genetic gain for AFL. The ewes

born in 2008 and 2009 had the lowest genetic gain for LWWT across all breed groups (Figure 2). The pure Red Maasai ewes born from 2011 onwards had the highest genetic gain for LWWT compared to the other breed groups.

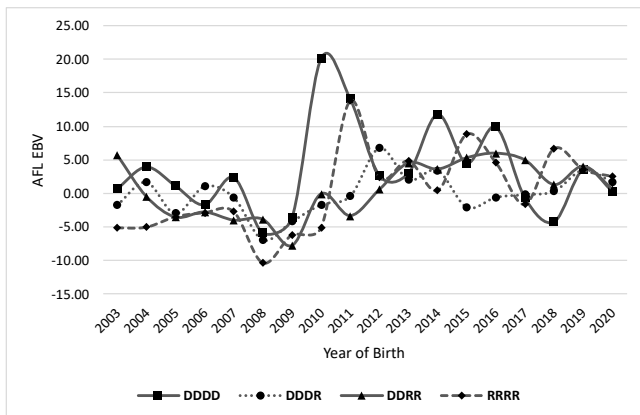


Figure 1 Genetic trends for age at first lambing by sheep breed from 2003 to 2020 (AFL = Age at first lambing, EBV=Estimated breeding values, DDDD= pure dorper, DDDR = 75% Dorper-25%Red Maasai, DDDR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai)

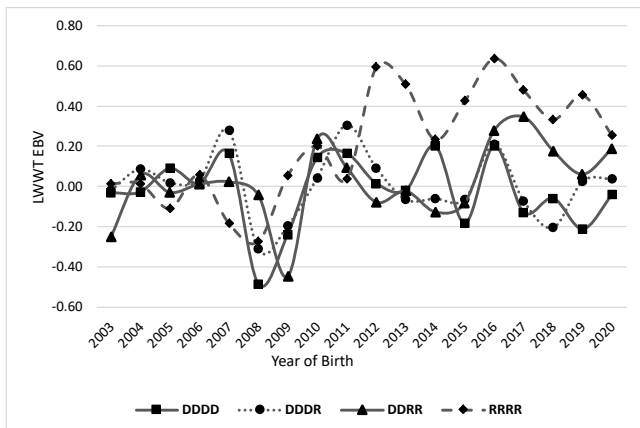


Figure 2 Genetic trends for litter weight at weaning by sheep breed from 2003 to 2020 (LWWT = Litter weight at weaning, EBV=Estimated breeding values, DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DDDR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai)

Table 5 presents the overall genetic gain achieved within each breed for the traits over 18 years (2003-2020). Among the pure breeds, the Red Maasai had the highest genetic gain for all the traits compared to the other breeds. Among the crossbreds, the DDDR had a higher

genetic gain for EBWT, EWWT and LWWT compared to DDDR. The genetic gain for LWWT was higher than LBWT for all breeds. An undesirable positive genetic gain was evident in AFL for all the breed combinations during the period under study.

Table 5 Overall genetic gain \pm SE for age at first lambing (AFL), Lambing Interval (LI), birth weight (EBWT), weaning weight (EWWT), Lambing weight at birth (LWB) and lambing weight at weaning (LWWT) from 2003 to 2020 grouped by sheep breed

Breed	AFL	EBWT	EWWT	LI	LBWT	LWWT
DDDD	0.09 \pm 0.03	0.01 \pm 0.00	0.05 \pm 0.03	0.05 \pm 0.07	0.01 \pm 0.01	0.01 \pm 0.03
DDDR	0.21 \pm 0.02	0.01 \pm 0.00	0.04 \pm 0.03	0.05 \pm 0.06	0.01 \pm 0.01	0.01 \pm 0.03
DDRR	0.37 \pm 0.02	0.02 \pm 0.01	0.10 \pm 0.03	0.01 \pm 0.05	0.01 \pm 0.01	0.03 \pm 0.01
RRRR	0.68 \pm 0.02	0.02 \pm 0.00	0.13 \pm 0.03	0.07 \pm 0.06	0.01 \pm 0.00	0.04 \pm 0.02

Breed code: **DDDD**= pure dorper, **DDDR** = 75%Dorper-25%Red Maasai, **DDRR** = 50%Dorper-50%Red Maasai, **RRRR** = pure Red Maasai

2.3.5 Phenotypic trends and rainfall pattern

The phenotypic trends for AFL and LWWT for the different breed combinations are plotted over the years against the annual rainfall index are presented in Figure 3 and Figure 4, respectively. The rainfall index is used to illustrate the semi-arid nature of the study environment where the sheep are raised. All the breeds had a similar trend for AFL. Generally, ewes born during years of low rainfall, 2007 to 2009 and 2013 to 2017, had higher AFL compared to those born during years of high rainfall reflecting a strong association between the annual rainfall and AFL (Figure 3). The below average precipitation of 2008, 2009, 2015 and 2016 did not negatively affect the average litter weaning weight of the different breeds (Figure 4).

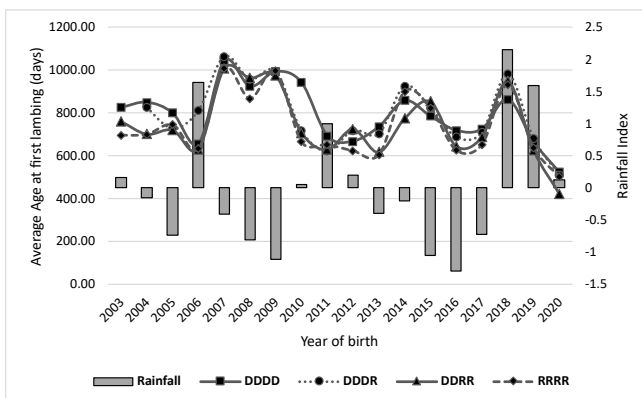


Figure 3 Phenotypic trends for age at first lambing by sheep breed and rainfall patterns from 2003 to 2020 (DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DRRR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai)

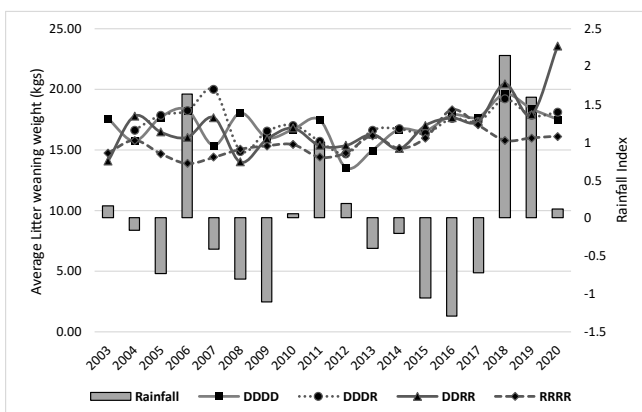


Figure 4 Phenotypic trends for litter weight at weaning by sheep breed and rainfall patterns from 2003 to 2020 (DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DRRR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai)

2.4 Discussion

2.4.1 Non-genetic factors influencing reproduction of ewes

The age at first lambing (AFL) is highly influenced by management decisions on when to mate the hoggets. AFL is an important indicator of the reproductive efficiency in a sheep flock therefore by delaying the AFL, the length of productive life and profitability of ewes in breeding lambs is negatively impacted(Abebe et al., 2023). The AFL of the Kapiti flock tended

to be higher for animals with a greater proportion of Dorper breed with the pure Red Maasai having the lowest AFL and the pure Dorper having a higher AFL. Among the crossbreds, the F1 had the lowest average AFL. This could be an indirect indication of an earlier onset of puberty or good conception rates in the Red Maasai compared to the Dorper within the semi-arid environment. Further research is required to confirm this hypothesis in order to optimize the AFL and improve the productivity of sheep in the arid environments. The AFL of 730 – 800 days reported in this study across all breeds was higher than that of 400 – 600 days reported in other studies on sheep raised under a similar extensive production system ((Abebe et al., 2023; Tera et al., 2020; Zishiri et al., 2013). Hoggets can be selected for breeding as early as 7 months hence optimizing the reproductive efficiency and lifetime performance of the sheep flocks (Abebe et al., 2023).

The lambing interval reflects the ability of ewes to regularly produce offspring and is a critical measure of the reproductive effectiveness of a sheep flock. Lambing intervals were variable across the different breeds of sheep in the flock analysed with the 75%Dorper-25%Red Maasai breed having on average, the lowest lambing interval. The lambing intervals were also longer (400 – 430 days) compared to other studies on sheep in tropical areas (240 – 300 days) (Asmare et al., 2021; Aragaw et al., 2011; Gbangboche et al., 2006). Improving farm management practices to enable early oestrus detection, exposing ewes to rams in shorter intervals following lambing, and improving their nutrition and health management should be adopted to reduce the lambing intervals.

As reported in studies on sheep production in other countries, the male lambs and singletons were heavier when compared to the females lambs and twins (Boujenane and Diallo, 2017; Abbasi et al., 2012). The significantly higher LBWT and LWWT of lambs born to older ewes compared to those of younger ewes was an indication of improved mothering ability with the increased age and parity of the ewe. A similar pattern in lamb growth was reported by Boujenane et al., 2013. The litter weight at weaning (LWWT) is an important indirect indicator of good mothering ability.

2.4.2 Genetic influence on ewe fertility

The overall heritability estimates for AFL was very low. Across breeds, the pure Dorper had the highest heritability estimate for AFL while the pure Red Maasai had the lowest heritability estimate indicating the large environmental effects on the expression of these traits. The heritability estimates among the crossbred groups were similar. These heritability estimates were similar to those reported in other populations (Abdoli et al., 2019; Rosati et al., 2002). Direct selection for improved AFL within breeds may not result in much genetic progress. The

AFL is notably an important reproductive trait as it has a strong influence on the profitability of the sheep enterprise. With the high influence of the environment on fertility, efforts to improve AFL should focus on farm management practices. Like AFL, LI is highly influenced by environment and that explains the overall heritability estimate of zero both at the population level and within breed groups.

The heritability estimates for LBWT and LWWT were in a similar range of those reported in other studies in tropical areas (Nabavi et al., 2014; Zishiri et al., 2013; Mohammadi et al., 2012). Across all breeds, the heritability estimates for LBWT was similar however the pure purebred (RRRR and DDDD) had lower heritability estimates for LWWT compared to the crossbreds. It was notable that growth rates were higher for lambs with a higher proportion of Dorper in the breed. The Dorper breed is known for its good genetic potential for growth which also has a higher heritability, making it a choice breed in many crossbreeding programs that want to improve growth rates (Charlotte Milne, 2000).

The overall and within breed genetic correlation between lambing interval and all the growth traits studied (EBWT, EWWT, LBWT and LWWT) was negative, indicating that shorter lambing intervals would not adversely affect the growth traits. The positive genetic and phenotypic correlations across all breeds between the weight of the ewes (EBWT and EWWT) with their litter weight at lambing (LBWT) and at weaning (LWWT) and the moderate heritability estimates indicates the opportunity for indirect selection of LBWT and LWWT using the birth weight or weaning weight of the ewe. Additionally, the high positive genetic correlation across all breeds between LBWT and LWWT indicates that selection for growth can be done using LWWT in line with results reported by (Bezerra et al., 2009). Generally, among the purebreds, the Red Maasai had higher genetic and phenotypic correlations across the traits while among the crossbreds, the F1 (DDRR) had higher correlations than the DDDR.

2.4.3 Phenotypic trends and genetic gain

The significantly high influence of the environment on AFL was reflected by the phenotypic trend and variation with annual rainfall. Adequate rainfall is crucial for maintaining pasture quality, which directly impacts the nutrition of breeding ewes. Semi-arid environments are generally characterized by low annual rainfall. The low annual rainfall leads to poor forage availability, affecting the body condition of ewes and delaying the age at which ewes reach reproductive maturity, suppress oestrus activity and reducing conception rates (George Wanjala et al., 2023b; Zhang et al., 2021; Ogotu et al., 2015). Despite the years that experienced low rainfall, the pure Red Maasai was able to maintain a slightly lower AFL compared to the other breeds. Indigenous sheep breeds are known to be well adapted to local

climatic conditions, which may influence their reproductive traits, including age at first lambing (Mengistu, 2008). The availability of pasture, which is influenced by amount of rainfall, also affects the quality and quantity of milk available for lambs up to weaning hence affecting the weaning weight of the lambs (Farrag, 2022; Gonzalez-Ronquillo et al., 2021). In this study area, the weaning weight of lambs was not adversely affected by low rainfall which could be an indication of adaptability of the flock to the environment for growth. The ability of ewes to consistently produce heavier lambs is a measure of their resilience within the environment in which they are raised. McLaren et al. (2023) found that ewes that were in good body condition between weaning and pre-mating had higher numbers of lambs weaned. Therefore, interventions in the semi-arid environments should focus on providing better pastures for lactating ewes and weaned females due to poor pasture which in turn influences the reproductive cycles of sheep, milk production and eventually the weaning weights of lambs.

The fluctuating genetic trend in AFL of this study indicated limited selection for the trait over the years. The Red Maasai was able to perform better even in years when there was below average rainfall compared to the other breeds hence had a highest genetic gain in EBWT, EWWT, LBWT and LWWT during the study period.

2.5 Conclusion

The Red Maasai breed is an indigenous breed in East Africa that is well adapted to its environment and is widely crossed by the Dorper breed for improved growth performance. Given the socio-economic and cultural importance of the Red Maasai sheep and the indiscriminate crossbreeding with the Dorper sheep among the pastoral communities, understanding the production parameters will enable the selective breeding and conservation within its natural environment while maintain the optimum level of crossbreds with the Dorper. Among the pure breeds, the pure Red Maasai ewes (RRRR) performed better than the pure Dorper (DDDD) for all the traits. Between the crossbreds, the 50%Dorper-50%Red Maasai ewes (DDRR) had a better response to selection compared to the 75%Dorper-25%Red Maasai ewes (DDDR) across all traits. Overall, under semi-arid conditions, the F1 (DDRR) would be a better breed when considering both growth and reproduction traits. This is more so given the increasing impact of climate change. This indicates the necessity to maintain the pure line of the Red Maasai both for conservation and sustainable utilization. However, to improve the performance of the ewes, a selection index should be developed for each breed group, using

the genetic parameters estimated, incorporating both growth and reproduction traits and improving farm management practices for optimal flock productivity.

Ethics approval

Not applicable

Data and model availability statement

None of the data or model were deposited in an official repository. This can be made available upon request to the corresponding author

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence assisted technologies in the writing process

Authors ORCIDs

E Oyieng: <https://orcid.org/0000-0002-5004-2060>

J M K Ojango: <https://orcid.org/0000-0003-0224-5370>

M Gaulty: <https://orcid.org/0000-0003-4212-5437>

R Mrode: <https://orcid.org/0000-0003-1964-5653>

R Dooso: <https://orcid.org/0000-0002-6004-3729>

A M Okeyo : <https://orcid.org/0000-0003-2379-7801>

C Kalinda: <https://orcid.org/0000-0002-8144-0248>

S König: <https://orcid.org/0000-0003-4226-3696>

Declaration of interest

None

Acknowledgement

The authors would like to thank the Kapiti Research Station and Wildlife conservancy of International Livestock Research Institute (ILRI) for providing the data. Our deepest gratitude goes to James Audho, Winfred Sila and Elias Mwarome Mwazonga who were responsible for managing the flock and ensuring timely and accurate data collection.

Financial Support

This study was supported by the CGIAR Research Initiative on Livestock and Climate Systems Resilience (LCSR) through the International Livestock Research Institute (Grant number: CGL002004). CGIAR research is supported by contributors to the CGIAR Trust Fund. CGIAR is a global research partnership for a food-secure future dedicated to transforming food, land, and water systems in a climate crisis (<https://www.cgiar.org>)

References

- Abbasi, M.A., Abdollahi-Arpanahi, R., Maghsoudi, A., Torshizi, R.V., Nejati-Javaremi, A., 2012. Evaluation of models for estimation of genetic parameters and maternal effects for early growth traits of Iranian Baluchi sheep. *Small Ruminant Research* 104, 62–69. doi:10.1016/j.smallrumres.2011.10.003
- Abdoli, R., Mirhoseini, S.Z., Ghavi Hossein-Zadeh, N., Zamani, P., Moradi, M.H., Ferdosi, M.H., Gondro, C., 2019. Genome-wide association study of first lambing age and lambing interval in sheep. *Small Ruminant Research* 178, 43–45. doi:<https://doi.org/10.1016/j.smallrumres.2019.07.014>
- Abebe, A., Berhane, G., Getachew, T., Gizaw, S., Haile, A., 2023. Reproductive performance and productivity of local and Dorper x local crossbred ewes under community-based management system, Ethiopia. *Heliyon* 9, e19906. doi:10.1016/J.HELIYON.2023.E19906
- Aragaw, K., Teferi, M., Haile, A., Tibbo, M., 2011. Effects of strategic helminthosis control on age at first lambing and lambing interval of communally grazed Menz ewes in Ethiopia. *Livestock Science* 135, 38–43. doi:10.1016/J.LIVSCI.2010.06.005
- Asmare, S., Alemayehu, K., Abegaz, S., Haile, A., 2021. On-farm evaluation of growth and reproductive performances of Washera and Gumuz sheep in northwestern Ethiopia: Basics for setting up breeding objectives/goals. *PLoS One* 16, 0254924. doi:<https://doi.org/10.1371/journal.pone.0254924>
- Baker, R.L., Mugambi, J.M., J.O, A., Carles, A.B., Thorpe, W., 2004. Genotype by environment interactions for productivity and resistance to gastro-intestinal nematode parasites in Red Maasai and Dorper sheep. *Animal Science* 79, 343–353.
- Bazerra, A.M., Lôbo, O., Nonato, R., Lôbo, B., Paiva, S.R., Pinheiro De Oliveira, S.M., Facó, O., 2009. Genetic parameters for growth, reproductive and maternal traits in a multibreed meat sheep population. *Genetics and Molecular Biology* 4, 761–770.

- Boujenane, I., Chikhi, A., Sylla, M., Ibnelbachyr, M., 2013. Estimation of genetic parameters and genetic gains for reproductive traits and body weight of D'man ewes. *Small Ruminant Research* 113, 40–46. doi:10.1016/J.SMALLRUMRES.2013.02.009
- Boujenane, I., Diallo, I.T., 2017. Estimates of genetic parameters and genetic trends for pre-weaning growth traits in Sardi sheep. *Small Ruminant Research* 146, 61–68. doi:10.1016/j.smallrumres.2016.12.002
- Butler, D.G., Cullis, B.R., Gilmour, A.R., Gogel, B.J., Thompson, R., 2018. ASReml-R Reference Manual Version 4.2. VSN International Ltd., Hemel Hempstead, HP2 4TP, UK.
- Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Jotzo, F., Krug, T., Lasco, R., Lee, Y.-Y., Masson-Delmotte, V., Meinshausen, M., Mintenbeck, K., Mokssit, A., Otto, F.E.L., Pathak, M., Pirani, A., Poloczanska, E., Pörtner, H.-O., Revi, A., Roberts, D.C., Roy, J., Ruane, A.C., Skea, J., Shukla, P.R., Slade, R., Slangen, A., Sokona, Y., Sörensson, A.A., Tignor, M., van Vuuren, D., Wei, Y.-M., Winkler, H., Zhai, P., Zommers, Z., Hourcade, J.-C., Johnson, F.X., Pachauri, S., Simpson, N.P., Singh, C., Thomas, A., Totin, E., Alegría, A., Armour, K., Bednar-Friedl, B., Blok, K., Cissé, G., Dentener, F., Eriksen, S., Fischer, E., Garner, G., Guivarch, C., Haasnoot, M., Hansen, G., Hauser, M., Hawkins, E., Hermans, T., Kopp, R., Leprince-Ringuet, N., Lewis, J., Ley, D., Ludden, C., Niamir, L., Nicholls, Z., Some, S., Szopa, S., Trewin, B., van der Wijst, K.-I., Winter, G., Witting, M., Birt, A., Ha, M., 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. doi:10.59327/IPCC/AR6-9789291691647
- Deribe, B., Tesema, Z., Lakew, M., Zegeye, A., Kefale, A., Shibesh, M., Yizengaw, L., Belayneh, N., 2021. Reproductive performance of indigenous sheep and survival of their Dorper crossbred lambs under extensive management in Raya Kobo area, Ethiopia. In 13th Annual Regional Conference on Completed Livestock Research Activities. p. 2021.
- Farrag, B., 2022. Effect of seasonal variations during dry and wet seasons on reproductive performance and biological and economic criteria of hair sheep under Halaieb rangeland conditions. *Archives Animal Breeding* 65, 319–327. doi:10.5194/aab-65-319-2022
- Gbangboche, A.B., Adamou-Ndiaye, M., Youssao, A.K.I., Farnir, F., Detilleux, J., Abiola, F.A., Leroy, P.L., 2006. Non-genetic factors affecting the reproduction performance, lamb

- growth and productivity indices of Djallonke sheep. *Small Ruminant Research* 64, 133–142. doi:10.1016/J.SMALLRUMRES.2005.04.006
- Getachew, T., Haile, A., Wurzinger, M., Rischkowsky, B., Gizaw, S., Abebe, A., Sölkner, J., 2016. Review of sheep crossbreeding based on exotic sires and among indigenous breeds in the tropics: An Ethiopian perspective. *African Journal of Agricultural Research* 11, 10626. doi:10.5897/ajar2013.10626
- Gonzalez-Ronquillo, M., Abecia, J.A., Gómez, R., Palacios, C., 2021. Effects of weather and other factors on milk production in the Churra dairy sheep breed. *Journal of Animal Behaviour and Biometeorology* 9, 21025. doi:10.31893/JABB.21025
- Haile, A., Getachew, T., Mirkena, T., Duguma, G., Gizaw, S., Wurzinger, M., Soelkner, J., Mwai, O., Dessie, T., Abebe, A., Abate, Z., Jembere, T., Reikik, M., Lobo, R.N.B., Mwacharo, J.M., Terfa, Z.G., Kassie, G.T., Mueller, J.P., Rischkowsky, B., 2020. Community-based sheep breeding programs generated substantial genetic gains and socioeconomic benefits. *Animal* 14, 1362–1370. doi:10.1017/S1751731120000269
- Haile, A., Hilali, M., Hassen, H., Lobo, R.N.B., Rischkowsky, B., 2019. Estimates of genetic parameters and genetic trends for growth, reproduction, milk production and milk composition traits of Awassi sheep. *Animal* 13, 240–247. doi:10.1017/S1751731118001374
- Joy, A., Dunshea, F.R., Leury, B.J., Clarke, I.J., Digiacomio, K., Chauhan, S.S., 2020. Resilience of small ruminants to climate change and increased environmental temperature: A review. *Animals* 10, 867–885. doi:10.3390/ani10050867
- Kosgey, I.S., Okeyo, A.M., 2007. Genetic improvement of small ruminants in low-input, smallholder production systems: Technical and infrastructural issues. *Small Ruminant Research* 70, 76–88. doi:10.1016/j.smallrumres.2007.01.007
- Kosgey, I.S., Rowlands, G.J., van Arendonk, J.A.M., Baker, R.L., 2008. Small ruminant production in smallholder and pastoral/extensive farming systems in Kenya. *Small Ruminant Research* 77, 11–24. doi:https://doi.org/10.1016/j.smallrumres.2008.02.005
- McLaren, A., Lambe, N.R., Conington, J., 2023. Genetic associations of ewe body condition score and lamb rearing performance in extensively managed meat sheep. *Livestock Science* 277, 105336. doi:10.1016/J.LIVSCI.2023.105336
- Mengistu, T.G., 2008. Characterization of Menz and Afar indigenous sheep breeds of smallholders and pastoralists for designing community-based breeding strategies in Ethiopia. MSc Thesis, Haramaya University, Ethiopia.

- Milne, C., 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. doi:10.1016/S0921-4488(99)00154-6
- Milne, Charlotte, 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. doi:https://doi.org/10.1016/S0921-4488(99)00154-6
- Mohammadi, H., Moradi Shahrababak, M., Moradi Shahrababak, H., 2012. Genetic analysis of ewe productivity traits in Makooei sheep. *Small Ruminant Research* 107, 105–110. doi:10.1016/J.SMALLRUMRES.2012.04.019
- Muigai, A.W.T., Okeyo, A.M., Kwallah, A.K., Mburu, D., Hanotte, O., 2009. Characterization of sheep populations of Kenya using microsatellite markers: Implications for conservation and management of indigenous sheep populations. *South African Journal of Animal Science* 39, 93–96.
- Muigai, A.W.T., Okeyo, A.M., Ojango, J.M.K., 2017. Goat Production in Eastern Africa: Practices, Breed Characteristics, and Opportunities for Their Sustainability. In *Sustainable Goat Production in Adverse Environments: Volume I: Welfare, Health and Breeding* (eds. Simões, J., Gutiérrez, C.). Springer International Publishing, Cham, pp. 31–57. doi:10.1007/978-3-319-71855-2_3
- Nabavi, R., Alijani, S., Taghizadeh, A., Rafat, S.A., Bohlouli, M., 2014. Genetic study of reproductive traits in Iranian native Ghezel sheep using Bayesian approach. *Small Ruminant Research* 120, 189–195. doi:10.1016/J.SMALLRUMRES.2014.05.008
- Ogutu, J.O., Owen-Smith, N., Piepho, H.P., Dublin, H.T., 2015. How rainfall variation influences reproductive patterns of African Savanna ungulates in an equatorial region where photoperiod variation is absent. *PLoS One* 10, 0133744. doi:10.1371/journal.pone.0133744
- Ojango, J.M.K., Okpeku, M., Osei-Amponsah, R., Kugonza, D.R., Mwai, O., Changunda, M.G.G., Olori, V.E., 2023. Dorper sheep in Africa: A review of their use and performance in different environments. *CABI Reviews* 18, 0042. doi:10.1079/cabireviews.2023.0042
- Oyieng, E., Mrode, R., Ojango, J.M.K., Ekine-Dzivenu, C.C., Audho, J., Okeyo, A.M., 2022. Genetic parameters and genetic trends for growth traits of the Red Maasai sheep and its crosses to Dorper sheep under extensive production system in Kenya. *Small Ruminant Research* 206, 106588. doi:10.1016/j.smallrumres.2021.106588
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Rosati, A., Mousa, E., Van Vleck, L.D., Young, L.D., 2002. Genetic parameters of reproductive traits in sheep. *Small Ruminant Research* 43, 65–74. doi:[https://doi.org/10.1016/S0921-4488\(01\)00256-5](https://doi.org/10.1016/S0921-4488(01)00256-5)
- Snyman, M.A., Olivier, J.J., Erasmus, G.J., van Wyk, J.B., 1997. Genetic parameter estimates for total weight of lamb weaned in Afrino and Merino sheep. *Livestock Production Science* 48, 111–116. doi:[https://doi.org/10.1016/S0301-6226\(96\)01418-2](https://doi.org/10.1016/S0301-6226(96)01418-2)
- Tera, A., Getachew, T., Melesse, A., Rekik, M., Rischkowsky, B., Mwacharo, J.M., Abate, Z., Haile, A., 2020. Estimates of genetic parameters and trends for reproduction traits in Bonga sheep, Ethiopia. *Tropical Animal Health and Production* 53, 42. doi:[10.1007/s11250-020-02445-w](https://doi.org/10.1007/s11250-020-02445-w)
- Tesema, Z., Deribe, B., Kefale, A., Lakew, M., Tilahun, M., Shibesh, M., Belayneh, N., Zegeye, A., Worku, G., Yizengaw, L., 2020. Survival analysis and reproductive performance of Dorper x Tumele sheep. *Heliyon* 6, 4. doi:<https://doi.org/10.1016/j.heliyon.2020.e03840>
- Toothaker, L., 1993. *Multiple Comparison Procedures*. SAGE Publications, Inc., Thousand Oaks, California. doi:[10.4135/9781412985178](https://doi.org/10.4135/9781412985178)
- Wanjala, George, Kichamu, N., Ciszter, L.T., Astuti, P.K., Kusza, S., 2023a. An On-Station Analysis of Factors Affecting Growth Traits of Pure Red Maasai and Dorper Sheep Breeds under an Extensive Production System. *Animals* 13, 300. doi:<https://doi.org/10.3390/ani13020300>
- Wanjala, G., Kichamu, N., Strausz, P., Astuti, P.K., Kusza, S., 2023. On-station comparative analysis of reproductive and survival performance between Red Maasai, Dorper, and Merino sheep breeds. *Animal* 17, 100715. doi:[10.1016/j.animal.2023.100715](https://doi.org/10.1016/j.animal.2023.100715)
- Wanjala, George, Kusuma Astuti, P., Bagi, Z., Kichamu, N., Strausz, P., Kusza, S., 2023b. A review on the potential effects of environmental and economic factors on sheep genetic diversity: Consequences of climate change. *Saudi Journal of Biological Sciences* 30, 103505. doi:[10.1016/j.sjbs.2022.103505](https://doi.org/10.1016/j.sjbs.2022.103505)
- Zhang, Yongxiang, Wang, G., Zhang, Yu, Zhao, S., Han, C., 2021. Climate Change is Likely to Alter Sheep and Goat Distributions in Mainland China. *Frontiers in Environmental Science* 9, 748734. doi:[10.3389/fenvs.2021.748734](https://doi.org/10.3389/fenvs.2021.748734)
- Zishiri, O.T., Cloete, S.W.P., Olivier, J.J., Dzama, K., 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. *Small Ruminant Research* 112, 39–48. doi:[10.1016/J.SMALLRUMRES.2013.01.004](https://doi.org/10.1016/J.SMALLRUMRES.2013.01.004)
- Zonabend König, E., Mirkena, T., Strandberg, E., Audho, J., Ojango, J., Malmfors, B., Okeyo, A.M., Philipsson, J., 2016. Participatory definition of breeding objectives for sheep breeds

under pastoral systems—the case of Red Maasai and Dorper sheep in Kenya. *Tropical Animal Health and Production* 48, 9–20. doi:10.1007/s11250-015-0911-7

CHAPTER 3: Lamb survival and ewe longevity in a crossbreeding program between indigenous and exotic sheep in semi-arid lands

E.Oyieng^{a b}, J.M.K Ojango^b, M.Gauly^c, R.Mrode^{b d}, A.M. Okeyo^b S.König^a

^a Institute of Animal Breeding and Genetics, Justus-Liebig-University Gießen, Ludwigstraße 21
b, 35390 Gießen, Germany

^b Livestock Genetics Nutrition and Feed Resources Program, International Livestock Research
Institute, P. O Box 30709-00100 Nairobi, Kenya

^c Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen –
Bolzano, Universitätsplatz 5, 39100 Bolzano, Italy

^d Animal and Veterinary Science, Scotland's Rural College, EH9 3JG Edinburgh, United
Kingdom

Published in

Smallruminant research, May 2025

<https://doi.org/10.1016/j.smallrumres.2025.107520>

Abstract

The survival of lambs and longevity of ewes within flocks are important for the sustainability of sheep populations especially in arid and semi-arid lands (ASAL). In this study we conducted pre- and post-weaning survival analysis of lambs and the longevity of ewes of indigenous pure Red Maasai (RRRR), pure Dorper (DDDD), and their crosses comprising F1 (DDRR) and 75%Dorper-25%Red Maasai (DDDR) using Cox and Weibull proportional hazard models. The objective was to determine the genetic and non-genetic factors affecting lamb survival to yearling as well as ewe longevity. Data comprised records on 6,313 lambs and 2,003 ewes. Overall pre-weaning mortality was lower (5%) compared to post-weaning mortality rate (17%). Lambs born during the long dry season had a higher risk of dying than those born during the wet seasons. For both lambs and ewes, the Dorper had the highest risk of dying or being culled. Among the crossbreds, the DDDR lambs and ewes had higher risks of dying or being culled relative to F1 lambs and ewes. The risk of ewes being culled reduced with increasing age at first lambing and parity. Heritability estimates for pre-weaning mortality were higher (0.10 - 0.14) than post-weaning mortality (0.01 - 0.05). The higher heritability for pre-weaning lamb survival indicates greater genetic variation, presenting an opportunity for selection for lamb survival. Interventions to improve the production environment in the ASAL areas would also improve the survival of lambs and longevity of ewes.

Keywords: Lamb survival, Ewe longevity, Dorper, Red Maasai, Risk ratios, Genetic parameters

3.1 Introduction

The survival of young animals and longevity of productive female animals in a flock are important for the success of any sheep production system. In arid and semi-arid lands (ASAL), sheep reared are exposed to climates characterized by high temperatures, droughts and limited forages. These harsh climatic conditions can increase animal mortality rates which not only threaten the sustainability of sheep farming but also present a significant economic loss to the farmer (Dwyer et al., 2015; Hossein-Zadeh et al., 2018; Riggio et al., 2008). Selection and breeding for lambs that are most resilient within the environment can achieve a desirable outcome in both flock performance and animal welfare (Rauw et al., 2021). Lamb survival is a compound trait influenced by both genetic factors of the ewe and lamb, and non-genetic factors such as management practices and environmental variables (Hossein-Zadeh et al., 2018; Mandal et al., 2007). The survival of female lambs to maturity determines their ability to become productive assets within a flock. At maturity, regular reproduction and longevity

of ewes within a flock is desirable for producing saleable animals with low costs of rearing of replacement animals. Therefore, increasing the number of lambs raised per ewe and the longevity of the ewes in a flock would result in improved overall productivity of the farm.

Indigenous sheep breeds that are resilient and productive within the arid and semi-arid environments play an important socio-economic role in the livelihoods of pastoralists (Nyariki and Amwata, 2019). However, information on the survival and productivity of such breeds under different arid climates is limited. In 2003, the International Livestock Research Institute (ILRI) began a selective breeding program of indigenous Red Maasai sheep and their crosses with Dorper sheep in Kenya. The Red Maasai sheep is a fat-tailed breed known for its genetic resistance to nematodes (e.g. *Haemonchus contortus*) (Baker et al., 2004; Mugambi et al., 2005) and is well adapted to semi-arid environments, while the Dorper is a composite breed imported from South Africa that is known for its good growth rates and carcass quality (Milne, 2000). The main goal of the breeding program is to improve the growth rates of the indigenous Red Maasai sheep, and crossbreed with the Dorper to improve the carcass quality of their offspring while maintaining the inherent genetic resistance of the Red Maasai to *Haemonchus contortus*. The changing climatic conditions and increasing demand of more productive and resilient animals by communities in arid areas of Eastern Africa present the challenge to expand the outlook in breeding programs to include critical traits related to survival and longevity of animals. By including the survival of lambs in the selection criteria for breeding animals, adaptability of flocks is promoted in a given environment (Mandal et al., 2007)

This paper investigates the genetic and non-genetic factors influencing the survival of indigenous and crossbred Red Maasai lambs pre- and post-weaning to yearling age, and the longevity of the ewes within a semi-arid environment to identify critical intervention points for their management to improve productivity and provide an evidence base for more optimal offtake and culling ages for sheep in the ASAL.

3.2 Materials and Methods

3.2.1 Study area and flock management

The dataset used in this study was obtained from the sheep flock at the ILRI Kapiti Research Station and Wildlife Conservancy (formerly known as Kapiti Plains Estate) in Machakos County, Kenya. The research station and conservancy is situated between 1,650 and 1,900 meters above sea level and at -1.6 latitude and 37.1 longitude. The area receives an average annual rainfall of around 552 mm, and the temperature ranges between 22 — 27 °C. It has four distinct seasons: the long-wet season (March to May), the short-dry season (January and

February), the long-dry season (June to September), and the short-wet season (October to December). The research station is mostly covered in grasses and shrubs and is home to both wild and domestic animals. Grazing pasture supply is often limited during prolonged dry seasons.

The sheep are managed in separate flocks depending on their age and sex and grazed on the naturally occurring pasture resources as outlined in Oyieng et al., 2022. Briefly, lambs are weighed at birth, at weaning (3 months), at 6, 9 and 12 months of age. From nine months of age, when female lambs weigh at least 24 kgs, they are exposed to rams for their first mating. As an initial objective was to grow the flock size, all female lambs in the flock were retained for mating. The best performing 10% of the young rams are selected based on their estimated breeding values (EBV) for growth to nine months and their dams' reproductive performance measured as the age at first lambing and intervals between lambing. Following physical examination of these animals for conformation attributes and health status, best rams are identified for breeding within the flock, taking special care to avoid inbreeding. Water is provided *ad libitum* for all the animals when in the pens during the night, and before setting out for grazing during the day. When animals are grazing in the open fields, water is provided twice in the day. Scheduled vaccination against anthrax, enterotoxaemia, and foot and mouth disease are provided annually, bi-annually, and every 5 months respectively. Anthelmintic treatment is given to animals before and after the rainy season based on age and body condition. Animals leave the flock due to several reasons including a) death from diseases confirmed by a veterinarian, predation, drought, accidents, general weakness and unknown causes, and b) culled due to deformities, extremely poor growth performance and old age for females more than 6 years old. Ewes may also be culled from the flock if they fail to produce offspring after exposure to rams in more than 3 matings. Surplus male animals and those ranked within the top 25% of their breed group and not earmarked for breeding on the ranch are sold as breeding rams for other livestock keepers. The remaining male animals are castrated and sold for meat.

3.2.2 Data structure

Data on 6,313 lambs and 2,003 ewes of either pure Red Maasai (RRRR), pure Dorper (DDDD) or their reciprocal crosses (75%Dorper-25%Red Maasai - DDDR, and 50%Dorper-50%Red Maasai - DRRR) were obtained from the ranch to study survival of lambs in two phases, from birth to weaning and post-weaning to yearling, and the length of productive life of female animals. The lambs were born between 2003 and 2022, while ewes were born between 2003 and 2020 and had lambed at least once. Lamb survival to weaning and post-weaning to

yearling was evaluated based on any culling date between its birth date and the date at which the animal reached 90 days (weaning) and 90 to 365 days, respectively. The length of productive life of the ewes was calculated as the difference between its culling date and the date of its first lambing. An upper limit for age of an ewe at culling was set to 6 years (2,190 days) of age based on the ranch policy of culling ewes for age at 6 years. The records on lambs, at 90 and 365 days, and ewes at 2,190 days were “censored”, respectively as described by Ducrocq (1997). Censored animals (animals that were alive by the end of the observation period i.e. 90, 365 and 2,190 days) were coded as 0 while uncensored animals (animals had died or been culled before the end of each observation period) were coded as 1 in the dataset. In addition to evaluating the differential survival rates, data from the lambs were used to estimate genetic parameters for lamb survival from birth to weaning, weaning to yearling and birth to yearling. The pedigree information used in the estimation of the genetic parameters had 11,964 animals spanning 12 generations, representing offspring of 206 sires and 2,591 dams.

3.2.3 Data analysis

The analysis was done using the Cox and Weibull hazard models of the Survival Kit version 6.12 software (Mészáros et al., 2013). The software uses hazard functions to account for all the information available from both censored and uncensored records and can consider time-dependent variables and non-normality of the data (Ducrocq, 1997; Ducrocq et al., 2000). This is important since survival data is usually heavily skewed.

3.2.3.1 Survival analyses

Pre- and post-weaning lamb survival

Analyses were initially implemented using a Cox proportional hazard model to investigate the influence of various factors on the risk of a lamb dying before weaning and post-weaning to yearling. The general model for the analysis of lamb survival at the different stages was:

$$\lambda(t) = \lambda_0(t) \exp(yob_i + sob_j + sex_k + tob_l + brd_m + ht_n + rc_o) \quad [1.1]$$

Where $\lambda(t)$ = the risk of death or probability of lamb being dying at time t , $\lambda_0(t)$ = is an arbitrary baseline hazard function representing the aging process over time t . yob_i is the fixed effect of i^{th} year of birth, sob_j is the fixed effect of the j^{th} season of birth, sex_k is the fixed effect of the k^{th} sex of the lamb, tob_l is the fixed effect of the l^{th} type of birth, brd_m is the fixed effect of the m^{th} breed group of the animal, ht_n is the fixed effect of the n^{th} level of heterosis in each

animal and rc_o is the fixed effect of the o^{th} level of recombination in each animal. The heterosis and recombination for each animal was calculated using equations [1.2] and [1.3] respectively. The proportions of one of the breeds in the population (i.e. either Red Maasai or Dorper) in the sire and dam of each animal was used to calculate the heterosis and recombination for each animal. The Red Maasai breed was chosen as the representative breed.

$$(S_{rm}(1 - D_{rm})) + D_{rm}((1 - S_{rm})) \quad [1.2]$$

$$(S_{rm}(1 - S_{rm})) + D_{rm}((1 - D_{rm})) \quad [1.3]$$

Where S_{rm} is the proportion of Red Maasai in the sire of the animal and D_{rm} is the proportion of Red Maasai in the dam of the animal. The proportions were either 0.00, 0.25, 0.50, 0.75 or 1.00.

The Likelihood ratio test was used to determine the significance of each fixed effect in the survival model and those that were not significant at $p=0.05$ were excluded from the final model. The parity and interactions between the fixed effects were not significant and were thus excluded from the final model.

In a second analyses, the different breeds of sheep in the flock were accounted for by defining each breed as a separate stratum with a different baseline. The model used for this analysis was:

$$\lambda_i(t) = \lambda_{0m}(t) \exp(yob_i + sob_j + sex_k + tob_l) \quad [1.4]$$

Where $\lambda_{0m}(t)$ is the baseline hazard function at time t stratified by breed m ; other effects are as defined in Model 1.1. The Weibull function was used to determine the risk ratios for different factor levels in the analyses. The analytical model was similar to the Cox model, however in the Weibull analysis, $\lambda_0(t) = \lambda_p(\lambda_0 t)^{p-1}$ which is the baseline hazard function with shape parameter p and scale parameter λ_0 of the Weibull distribution.

Ewe longevity

The general model for the analysis of ewe longevity to 2,190 days using both the Cox and Weibull functions was:

$$\lambda(t) = \lambda_0(t) \exp(Pr_i(t) + yol(t)_j + bwt_k + afl_i + sn_m + tob_n + brd_p) \quad [1.5]$$

Where, $\lambda(t)$ = the probability of an ewe being culled at time t , $\lambda_0(t)$ for the Cox model is the baseline hazard function representing the ageing process, while for the Weibull model the $\lambda_0(t) = \lambda_p(\lambda_o t)^{p-1}$ which is the baseline hazard function with shape parameter p and scale parameter λ_o of the Weibull distribution. $Pr_i(t)$ is the time-dependent effect of the i^{th} parity with parities numbered as 1 to 5 that changed with each lambing. The $yol_n(t)$ is the time-dependent effect of the j^{th} year of lambing. The time-dependent variables were fitted as described by (Mészáros et al., 2013). Fixed effects included in the model were bwt_k the k^{th} birth weight of the ewe classified into three groups as low birth weight (below 1 SD from the mean), medium birth weight (1 SD plus or minus from the mean) and high birth weight (1 SD above the mean); afl_i is the fixed effect of the i^{th} age at first lambing classified into four groups (<615 days, 615-795 days, 795-975 days and >975 days), sn_m is the fixed effect of the m^{th} season of birth of the ewe, tob_n is the fixed effect of the n^{th} type of birth, brd_p is the fixed effect of the p^{th} breed of the ewe. The suitability of the Weibull model was assessed by evaluation of the In-cumulative hazard plot $\ln(-\ln S(t))$ versus $\ln(t)$, where $S(t)$ and t are the Kaplan-Meier survivor function and number of days respectively. The plot showed a straight line which confirms that the data followed the Weibull distribution.

Kaplan-Meier survivor curves and risk ratios

Kaplan-Meier survivor functions for lambs for pre- and post-weaning, and ewes from first lambing to six years were plotted for the different breeds. The equation for estimating Kaplan-Meier survivor estimates is shown below (Kaplan and Meier, 1958)

$$\hat{S}(t) = \prod_{j:t_j \leq t} \frac{n_j - d_j}{n_j} \quad [1.6]$$

Where n_j is the number of lambs/ewes alive at time t_j and d_j is the number lambs/ewes dying or culled at time t_j .

The risk ratios within a contemporary group determined through the Weibull analyses was compared to the risk ratio of one level, the reference level, within the group which was set as risk ratio of 1.00. Risk ratios greater than one correspond to higher risk of death/culling while risk ratios less than one indicate a reduced risk of death/culling.

3.2.3.2 Estimation of genetic parameters and genetic trends for lamb survival

Animal models were run including pedigree information using the Weibull model to estimate genetic variance components, heritability, estimated breeding values (EBVs). Heritability was estimated using the equation below (Yazdi et al., 2002)

$$h^2 = \frac{\sigma_G^2}{\frac{1}{p} + \sigma_G^2}$$

Where h^2 is the coefficient of heritability for lamb survival, σ_G^2 is the genetic variance and p is the proportion of uncensored records. The EBVs were averaged within each breed group and year of birth to plot the genetic trend for risk of lambs exiting the flock before weaning age.

3.3 Results

3.3.1 Lamb survival

Survival patterns

Summary statistics of the lambs in the population and their survival from birth to weaning and weaning to yearling age by breed are presented in Table 1. In the overall population, 95% and 83% of lambs survived to weaning (90 days) and to yearling (365 days), respectively. The Red Maasai had the lowest mortality rates pre-weaning and post-weaning of 2% and 13%, respectively, while the Dorper had the highest post-weaning mortality rate of 24%.

Table 1 Summary statistics of lamb survival by breed

Period	Parameter	DDDD	DDDR	DDRR	RRRR	Overall
Birth to weaning	Total number of records	1406	1901	1634	1372	6313
	Censored records	1333	1805	1556	1344	6038
	Uncensored records	73	96	78	28	275
	Average failure time (days)	50	57	57	59	55
	Mortality rate	5%	5%	5%	2%	5%
Weaning to yearling	Total number of records	1333	1805	1556	1344	6038
	Censored records	1072	1513	1384	1191	5160
	Uncensored records	261	292	172	153	878
	Average failure time (days)	319	327	333	343	332
	Mortality rate	24%	19%	12%	13%	17%

Breed code: **DDDD** - pure dorper, **DDDR** - 75%Dorper-25%RedMaasai, **DDRR** - 50%Dorper-50% Red Maasai (F1), **RRRR** - pure Red Maasai

Factors affecting lamb survival from birth to weaning

Table 2 presents the risk ratios and mean age of failure for the significant ($P < 0.05$) fixed factors affecting survival of lambs from birth to weaning. The sex of the lamb did not significantly affect ($P > 0.05$) the survival of lambs between birth and weaning (90 days). Among the breeds, the pure dorper the highest risk of dying before weaning ($P < 0.05$). Lambs born during the wet seasons had a significantly ($P < 0.05$) lower risk of dying compared to lambs born during the dry seasons. The parity in which the lambs were born also affected their survival to weaning ($P < 0.05$). The risk of lambs dying decreased with increasing parity of the ewe. Heavier lambs and lambs born as single births had higher chances of surviving to weaning compared to lighter lambs and twins. Lambs with a heterosis and recombination of 0.2 had a significantly ($P < 0.05$) higher risk of dying before weaning.

Table 2 Factors affecting lamb survival from birth to weaning and their risk ratio, mean age at failure (days) and Weibull parameter estimate (ρ) \pm Standard Error

Effect and class	Risk ratio	Mean age at failure (days)	$\rho \pm SE$
Breed *			
DDDD	2.205	50	0.111 \pm 0.486*
DDDR	1.967	57	0.000 \pm 0.000 ^{ns}
DDRR	0.986	57	-0.153 \pm 0.468*
RRRR	1.000 ^a	59	-0.033 \pm 0.677*
Season of birth*			
Long wet	0.413	59	-0.884 \pm 0.209 ^{ns}
Short wet	0.574	58	-0.065 \pm 0.186*
Long dry	1.000 ^a	49	-0.555 \pm 0.234*
Short dry	0.937	58	0.000 \pm 0.000 ^{ns}
Type of birth*			
Single	1.000 ^a	57	0.000 \pm 0.000 ^{ns}
Twin	1.291	46	0.255 \pm 0.241*
Parity*			
1	1.000 ^a	50	0.000 \pm 0.000 ^{ns}
2	0.963	51	-0.038 \pm 0.185 ^{ns}
3	0.951	57	0.098 \pm 0.211*
4	0.405	59	0.340 \pm 0.213*
5	0.104	60	0.681 \pm 0.268*
6 and above	0.011	63	0.011 \pm 0.357*
Birth weight*			
1 – 3 kgs	1.000 ^a	49	0.000 \pm 0.000 ^{ns}
3 – 4kgs	0.400	55	-0.915 \pm 0.159 ^{ns}
> 4Kgs	0.174	62	-1.751 \pm 0.249*
Heterosis*			
0	1.000 ^a	61	0.2727 \pm 0.209 ^{ns}
0.25	27.524	50	3.345 \pm 0.000*
0.375	0.010	60	-2.875 \pm 0.822 ^{ns}
0.5	0.051	59	-1.246 \pm 0.430*
0.75	0.004	49	-5.701 \pm 0.456 ^{ns}
1	0.000	65	0.000 \pm 0.000 ^{ns}
Recombination*			
0	1.000 ^a	49	0.000 \pm 0.000 ^{ns}
0.1875	0.014	62	-1.547 \pm 0.146*
0.2	23.711	51	2.312 \pm 0.000*
0.375	0.010	63	-6.430 \pm 0.000*
0.5	0.007	57	-0.411 \pm 0.340 ^{ns}
Disposal reason*			
Died - Accident	0.862	65	-0.147 \pm 0.248 ^{ns}
Died - General weakness	2.972	42	1.089 \pm 0.209*
Died - Other diseases	1.000 ^a	45	0.000 \pm 0.000 ^{ns}
Died - Pneumonia	0.435	60	-0.832 \pm 0.319*
Died - Predation	0.569	59	1.273 \pm 0.287*
Died - Unknown cause	3.573	57	0.121 \pm 0.374*
Died - Drought	1.129	62	-2.589 \pm 0.237 ^{ns}
Culled	0.075	88	0.000 \pm 0.000 ^{ns}

Breed code: **DDDD** - pure dorper, **DDDR** - 75%Dorper-25%RedMaasai, **DDRR** - 50%Dorper-50% Red Maasai (F1), **RRRR** - pure Red Maasai ρ – Weibull parameter estimate, **SE** = Standard Error, * - significant at P<0.05, ^{ns}– Not significant, ^a– Reference level

Factors affecting lamb survival from weaning to yearling

All the fixed effects studied, except parity, significantly ($P < 0.05$) affected the survival of the lambs from weaning to yearling age (Table 3). The pure Dorper lambs the highest risk of dying among all breeds while between the crosses, the DDDR had a higher risk of dying compared to the F1. Lambs that were born during the long dry seasons had significantly ($P < 0.05$) higher likelihood of dying compared to those born during the other seasons. Single born and female lambs had a significantly ($P < 0.05$) lower risk of dying compared to lambs born as twins and male lambs. The birth weight of the lambs also significantly ($P < 0.05$) affected their survival, with lighter lambs (1 – 3kgs) having a higher risk of dying before yearling compared to lambs that were heavier (>3kgs) at birth. The risk of death declined as the heterosis and recombination in the animal increased past 0.375. Lambs had the highest risk of dying (12.99) from general weakness which can be due to poor body condition caused by poor nutrition. Other diseases such as enterotoxemia, black quarter, blue tongue and sheep pox had the third highest risk ratio of 6.006.

Table 3 Factors affecting lamb survival from weaning to yearling and their risk ratio, mean age at failure (days) and Weibull parameter estimate (ρ) \pm Standard Error

Effect and class	Risk ratio	Mean age at failure (days)	$\rho \pm SE$
Breed *			
DDDD	0.476	319	-0.953 \pm 0.734*
DDDR	1.000 ^a	327	0.000 \pm 0.000*
DDRR	0.581	333	-0.542 \pm 0.080*
RRRR	0.385	343	-0.742 \pm 0.101 ^{ns}
Season of birth*			
Long wet	1.000 ^a	335	0.000 \pm 0.000 ^{ns}
Short wet	1.139	332	0.129 \pm 0.116*
Long dry	2.166	320	0.773 \pm 0.131*
Short dry	1.051	329	0.049 \pm 0.132*
Type of birth*			
Single	1.000 ^a	332	0.000 \pm 0.000 ^{ns}
Twin	1.851	339	0.161 \pm 0.206*
Sex*			
Male	1.000 ^a	322	0.000 \pm 0.000 ^{ns}
Female	0.272	339	-1.301 \pm 0.075*
Birth weight*			
1 – 3 kgs	1.289	321	0.253 \pm 0.107*
3 – 4kgs	1.000 ^a	334	0.000 \pm 0.000 ^{ns}
> 4Kgs	0.873	333	-0.136 \pm 0.104*
Heterosis*			
0	1.000 ^a	329	0.000 \pm 0.000 ^{ns}
0.25	26.434	331	3.599 \pm 0.000*
0.375	0.007	345	-4.973 \pm 90.848 ^{ns}
0.5	0.037	332	-3.299 \pm 0.180*
0.75	0.001	353	-6.967 \pm 90.846 ^{ns}
1	0.000	325	-9.996 \pm 90.848 ^{ns}
Recombination*			
0	1.000 ^a	328	0.000 \pm 0.000 ^{ns}
0.1875	0.029	333	-3.511 \pm 0.156*
0.2	19.834	328	2.323 \pm 0.000*
0.375	0.005	345	-4.219 \pm 0.000*
0.5	0.001	344	-3.425 \pm 90.837 ^{ns}
Disposal reason*			
Died - Accident	5.848	263	1.679 \pm 0.132*
Died - General weakness	12.992	173	2.808 \pm 0.121*
Died - Other diseases	6.006	268	1.856 \pm 0.165*
Died - Pneumonia	2.073	321	0.567 \pm 0.129*
Died - Predation	5.616	276	1.523 \pm 0.145*
Died - Unknown cause	6.486	181	2.434 \pm 0.450*
Died - Drought	2.886	256	1.534 \pm 0.345*
Culled	1.000 ^a	344	0.000 \pm 0.000 ^{ns}
Breed code: DDDD - pure dorper, DDDR - 75%Dorper-25%RedMaasai, DDRR - 50%Dorper-50% Red Maasai (F1), RRRR - pure Red Maasai ρ – Weibull parameter estimate, SE = Standard Error, * - significant at $P < 0.05$, ^{ns} – Not significant, ^a – Reference level			

Differences in the relative survival pre-weaning and post-weaning to 365 days for the breeds in the population are illustrated as Kaplan-Meier survivor curves (Figure 1). Losses of lambs of all breed types typically began when they were one month old. Overall, the pre- and post-weaning survival rate for the Red Maasai was the best and that of the Dorper was the worst among the breeds studied.

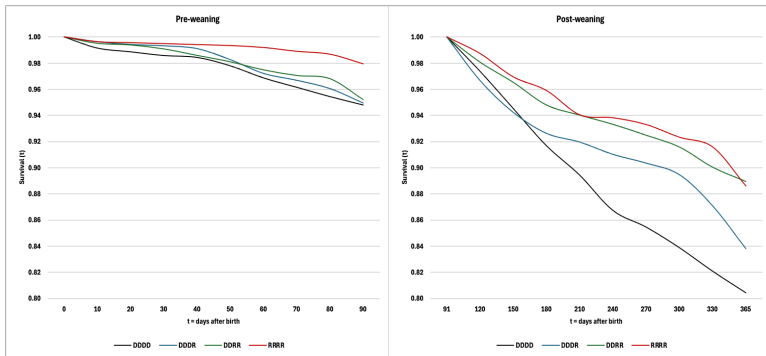


Figure 1 Pre-weaning and post-weaning Kaplan – Maier survivor curves for lambs of different breeds (DDDD- pure dorper, DDDR – 75%Dorper-25%Red Maasai, DRRR – 50%Dorper-50%Red Maasai, RRRR – pure Red Maasai)

3.3.2 Ewe longevity

Longevity patterns

Summary statistics on the longevity of ewes of the different breed types are presented in Table 4. The pure Red Maasai ewes had the lowest culling rate (43%) and were generally culled when they were older animals. This was reflected as their high average age at failure. The pure Dorper ewes had the highest culling rate (67%) and the lowest average age at failure. Among the crossbreds, the F1 ewes had a longer productive life within the flock compared to the DDDR ewes. Overall, 46% of the records on ewes were censored as these animals were alive and in good condition at 2190 days of age.

Table 4 Summary of statistics of ewe longevity from first lambing to culling at 2,190 days

	DDDD	DDDR	DRRR	RRRR	Overall
Total number of records	387	528	613	475	2003
Censored records	126	193	323	271	913
Uncensored records	261	335	290	204	1090
Average failure time (days)	1295	1466	1534	1587	1478
Culling rate	67%	63%	47%	43%	54%

Breed code: DDDD - pure dorper, DDDR - 75%Dorper-25%RedMaasai, DRRR - 50%Dorper-50% Red Maasai (F1), RRRR - pure Red Maasai

The Kaplan-Maier survival curves showed that up to 1325 days, the F1 ewes had better survival, however their survival rate subsequently declined (Figure 2). After 1,645 days, the pure Red Maasai ewes had a better survival rate than the other breeds up to the end of their

productive life at 2,190 days. Notably, the pure Dorper had the lowest survival rate from their first lambing to the end of their productive life.

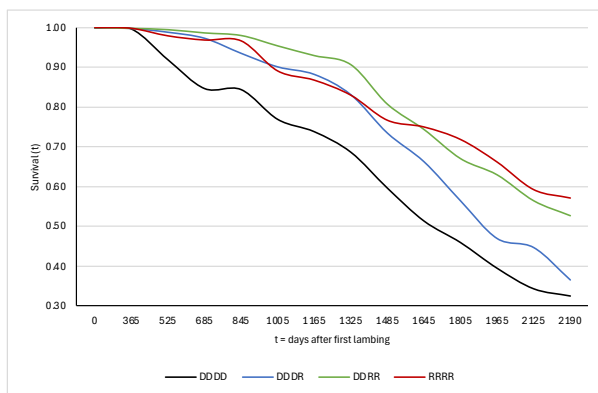


Figure 2 Kaplan – Maier survivor curves of ewes from first lambing to culling for the different breeds (DDDD- pure dorper, DDDR – 75%Dorper-25%Red Maasai, DDRR – 50%Dorper-50%Red Maasai, RRRR – pure Red Maasai)

Factors affecting ewe longevity

The factors that affected the ewe's longevity are presented in Table 5. The type of birth and season of birth of the ewe did not significantly ($P > 0.05$) affect the ewe's longevity within the flock. The breed significantly ($P < 0.05$) affected the ewes' longevity with the DDDR having a highest risk of being culled compared to the pure Red Maasai ewes'. Age at first lambing significantly ($P < 0.05$) affected the ewes' longevity with ewes having a higher age at first lambing (> 975 days) having the lowest risk of being culled while those that lambed early for the first time (< 615 days) having the highest risk of being culled. The parity of the ewe significantly ($P < 0.05$) affected the ewe's longevity with older ewes being less likely to be culled than younger ewes. Ewes that were heavier at birth (> 4 kgs) had a higher risk of being culled than ewes that were lighter at birth (1-3 kgs).

Table 5 Factors affecting ewe longevity and their risk ratio, mean culling age (days) and Weibull parameter estimate (ρ) \pm Standard Error

Effect and class	Risk ratio	Mean culling age (days)	$\rho \pm SE$
Breed *			
DDDD	1.232	1823	0.049 \pm 0.941 ^{ns}
DDDR	1.293	1932	0.105 \pm 0.085 ^{ns}
DDRR	1.182	2158	0.000 \pm 0.000 ^{ns}
RRRR	1.000 ^a	2190	-0.201 \pm 0.094*
Age at first lambing*			
<615 days	1.579	1796	0.456 \pm 0.100*
615 – 795 days	1.333	2058	0.287 \pm 0.101*
795 – 975 days	1.000 ^a	2110	0.000 \pm 0.000 ^{ns}
>975 days	0.726	2128	-0.3208 \pm 0.119*
Parity*			
1	1.000 ^a	1151	0.000 \pm 0.000 ^{ns}
2	1.390	1566	0.329 \pm 0.078*
3	0.728	1901	-0.317 \pm 0.100*
4	0.240	2056	-1.427 \pm 0.155*
5	0.009	2079	-4.748 \pm 1.005*
Birth weight*			
1 – 3 kgs	1.172	2086	0.155 \pm 0.077*
3 – 4kgs	1.000 ^a	2058	0.000 \pm 0.000 ^{ns}
> 4Kgs	1.229	1896	0.206 \pm 0.084*
Breed code: DDDD - pure dorper, DDDR - 75%Dorper-25%RedMaasai, DDRR - 50%Dorper-50% Red Maasai (F1), RRRR - pure Red Maasai ρ – Weibull parameter estimate, SE = Standard Error, * - significant at P<0.05, ^{ns} – Not significant, ^a – Reference level			

3.3.3 Genetic parameters and genetic trends for lamb survival

The genetic parameters for lamb survival from birth to weaning and weaning to yearling are presented in Table 6. The pre-weaning heritability estimates were higher than the post-weaning heritability estimates. The pre-weaning heritability estimates ranged from 0.10 \pm 0.05 in the DDDR breed combination to 0.14 \pm 0.05 in the pure Red Maasai breed. The maternal heritability could not be estimated with the current data.

Table 6 Genetic variance and heritability estimates \pm standard error for lamb survival from birth to yearling by breed

Trait	Parameter	Breed			
		DDDD	DDDR	DDRR	RRRR
Birth to weaning	Genetic variance (σ_g^2)	0.78 \pm 0.21	0.89 \pm 0.43	3.46 \pm 0.22	5.59 \pm 0.24
	Heritability (h^2)	0.12 \pm 0.03	0.10 \pm 0.05	0.11 \pm 0.03	0.14 \pm 0.05
Weaning to yearling	Genetic variance (σ_g^2)	0.22 \pm 0.45	0.17 \pm 0.75	0.02 \pm 0.42	1.99 \pm 0.47
	Heritability (h^2)	0.05 \pm 0.01	0.03 \pm 0.05	0.01 \pm 0.03	0.05 \pm 0.01
Breed code: DDDD - pure dorper, DDDR - 75%Dorper-25%RedMaasai, DDRR - 50%Dorper-50% Red Maasai (F1), RRRR - pure Red Maasai					

The genetic trends for pre-weaning survival for the different breeds are shown in Figure 3. The EBVs were high before 2008 then depicted a generally more stable trend from 2009 to

2022. The Red Maasai had the highest genetic gain for pre-weaning survival of -0.026. The genetic gain realized in the 75% Dorper-25% Red Maasai (DDDR), F1 (DDRR) and pure Dorper (DDDD) breeds were -0.018, -0.011 and -0.012 respectively.

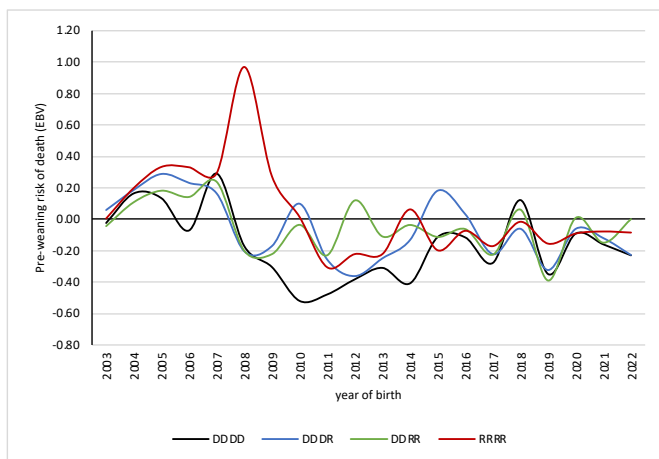


Figure 3 Genetic trends for pre-weaning lamb survival from 2003 to 2022 of different breeds (DDDD- pure dorper, DDDR – 75%Dorper-25%Red Maasai, DDRR – 50%Dorper-50%Red Maasai, RRRR – pure Red Maasai)

3.4 Discussion

3.4.1 Factors affecting survival of lambs to yearling

Environmental factors

The fixed factors significantly affecting pre-weaning mortality were similar to those affecting post-weaning mortality to yearling age, except for parity and sex. The pre-weaning mortality rates were consistent with those estimated by other researchers (Gowane et al., 2018; Vostrý and Milerski, 2013). Though the risk ratios for the fixed factors followed a similar pattern for pre- and post-weaning mortality, the level of risk differed within a given factor with pre-weaning risk ratios being generally lower than the post-weaning risk ratios. Pre-weaning mortality is highly dependent on mothering ability, while post-weaning mortality is more dependent on environmental factors. The Kaplan-Meier survivor curves also showed a sharp decline in survival post-weaning (Figure 1). The ability of an ewe to give birth to live lambs without complications, provide adequate colostrum and milk supply and a good mothering ability highly influence pre-weaning lamb survival (Brien et al., 2014). The sex of the lamb was not a significant factor affecting pre-weaning mortality, but it significantly affected post-

weaning mortality with males being three times more likely to leave the flock than females. Post-weaning, surplus young males not identified as potential breeding rams in the flock are culled and either sold to other farmers for breeding or to slaughterhouses for meat while female lambs are retained as replacement stock. Female lambs are important for the continuity and growth of sheep flocks. In other studies, the higher risk of death of male lambs compared to female lambs has been attributed to starvation mistothering exposure complex, respiratory and endoparasitic ailments, higher metabolic rates and farmers preference towards female lambs hence greater care in management (Bahri Binabaj et al., 2013; Besufkad et al., 2024; Mandal et al., 2007; Mukasa-Mugerwa et al., 2000; Tibbo, 2006). In this study population, any lambs that were observed to have a mistothering exposure complex were either bottle-fed or bonded with a foster mother until weaning. Therefore, deaths due to a breakdown of lamb-ewe bond were not reported in this population.

The season in which lambs were born had a significant effect on lamb survival pre- and post-weaning. Lambs that were born during the dry seasons had a higher risk of dying than those born during the wet seasons. Results reflecting differences in the survival of lambs depending on the seasons in which they are born have been reported for animals raised under farming systems of Ethiopia (Abdelqader et al., 2017; Besufkad et al., 2024). In this study area, the natural pastures used for grazing sheep vary in quality and quantity with the rainfall patterns. During the wet seasons, the quality and quantity of pasture is good and therefore the ewes have sufficient feed to support milk production which in turn helps the lamb survive better. To reduce the risk of death for lambs born during dry seasons the rearing practices ought to be improved through appropriate supplementation and animal health practices (Mukasa-Mugerwa et al., 2000; Sawalha et al., 2007).

In studies on indigenous sheep production under semi-intensive production systems of Ethiopia, lambs born as single, female and with average to high birth weights (2-4kgs) are reported to survive better than those born as twins, male and with very low birth weights (<2kgs) (Abdelqader et al., 2017; Besufkad et al., 2024; Hossein-Zadeh et al., 2018; Tesema et al., 2020). Twin lambs within this study population were found to have significantly lower birth weights than those born as single (Oyieng et al., 2022). Low birth weight of lambs reduced the risk of survival as also reported in other studies (Besufkad et al., 2024; Tesema et al., 2020). Additionally, twin lambs compete for mother care and milk which is vital for their survival. The parity in which the lambs were born in did not significantly affect the lamb survival post-weaning but significantly affected lamb survival pre-weaning. This observation was also reported in Lori-Bakhtiari sheep in Iran (Vatankhah and Talebi, 2009) and Menz and Awassi

sheep in Ethiopia (Getachew et al., 2015). The risk of lambs dying pre-weaning was higher for lambs born by ewes in their first parity than lambs born by older ewes i.e. 3rd parity and above, as were observed in similar studies (Bahri Binabaj et al., 2013; Besufkad et al., 2024; Sawalha et al., 2007). Ewes that have a lower age at first lambing (<365 days) tend to face challenges such as lower survival rates for their lambs due to inexperience (Keady and Hanrahan, 2022). Better management of first-time mothers can therefore contribute to better survival of lambs.

Genetic factors

The Kaplan-Meier curves showed that the survival trend of lambs from birth to yearling for the Red Maasai and F1 lambs was relatively smooth post-weaning (after 90 days) while the pure Dorper showed a steep decline. Though good mothering ability can affect the survival of lambs pre-weaning, the low heritability of this trait means that gains through selection are likely to be slow (Hinch and Brien, 2014). With the low heritability, better management practices especially at birth, ensuring a good body condition of the ewe through the pregnancy and at lambing can improve the survival rate of the lambs (Hatcher et al., 2010). The pre-yearling survival patterns shown in this study are an indication of the Red Maasai ewes having a better mothering ability than the other breeds, and the Red Maasai lambs being better adapted to the environment.

Between the crosses, the F1 lambs (DDRR) had better survival rates than the DDDR lambs. The crossbred lambs (DDDR and DDRR) performed better than pure bred Dorpers exhibiting better adaptability to the environment compared to pure Dorpers. The breed composition of the lambs had a significant effect on their risk of dying pre- and post-weaning. The lower mortality rate of Red Maasai sheep compared to the other breeds is an indication of the adaptability of the breed to the environment compared to other breeds studied. Higher mortality rates in the Red Maasai (20 - 28%) have been reported under experiments that were testing for resistance to *Haemonchus contortus* in sub-humid environments (Baker et al., 2004; Mugambi et al., 2005; Mwamachi et al., 1995). The mortality rates for the Dorper lambs reported here were in the same range as those reported by Tesema et al., 2020 but lower than those reported by Besufkad et al., 2024 under a semi-intensive management system. The study also observed that the higher the levels of heterosis and recombination within the animal, the less likelihood of the animal dying before yearling. The F1 cross (DDRR) had the highest heterosis and this corroborates with the lower mortality rates compared to the DDDR combination. Other studies measuring the effect of heterosis on different traits in sheep crosses have found that

the F1 always perform better than other cross combinations (Donald et al., 1963; Freking and Leymaster, 2004; Hielscher et al., 2006).

The pre-weaning heritability estimates were higher than the post-weaning heritability estimates which has been observed in several lamb survival studies (Besufkad et al., 2024; Brien et al., 2014). This implies that the survival of lambs pre-weaning is more dependent on genetic factors while post-weaning survival is more dependent on environmental factors rather than genetic factors. The heritability estimates for the Dorper breed in this study were lower than that obtained for the same breed in another study by Besufkad et al., 2024. However, the environment and management systems were different with the high heritability estimates being obtained in a highland environment under a semi-intensive management system while the low heritability estimate obtained in this study was in a semi-arid environment under an extensive management system. Therefore, direct selection for this trait in the Dorper breed under a semi-arid and extensive management system would achieve very little genetic progress but with very high selection intensity and the existence of high variability, selection can still be effective for traits with low heritability estimates (Boettcher, 2005). On the contrary, the heritability estimates for the pure Red Maasai was moderate enabling direct selection. A study by (Nel et al., 2021) achieved some desirable economic and welfare outcomes through direct selection of lamb survival in Merino sheep. The authors could not find similar studies for the Red Maasai sheep, and it's crosses for comparing genetic parameters for lamb survival. The low to moderate heritability estimates obtained for the crosses in this study can be attributed to the composite nature of lamb survival trait (Hosseinzadeh et al., 2018). Low to moderate heritability estimates for lamb survival have also been reported in other studies (Hatcher et al., 2010; Vatankhah and Talebi, 2009). The genetic trends shown in Figure 3 and gain show a gradual genetic improvement in pre-weaning lamb survival across all breeds. Though the Red Maasai lambs had the poorest pre-weaning survival genetic trend at the beginning of the breeding program, they had the highest genetic gain during the study period compared to the other breeds. This can be attributed to its better adaptability to the environment.

3.4.2 Longevity of ewes

The different ewe breeds in this study showed deferential survival rates from age at first lambing to culling at 2,190 days. Though the pure Red Maasai ewes had an overall lower culling rate, the F1 (DDRR) performed better during the first 1,645 days of their productive life compared to all the breeds. Crossbred ewes had a better longevity than purebred ewes as observed in a study by (Annett et al., 2011). Generally, the crossbred ewes (F1 and DDRR) had

better or similar longevity patterns during the first 3 to 4 years of their productive life compared to pure Red Maasai ewes. Overall, Red Maasai ewes showed better survival rates to the end of their productive life.

Ewe longevity was negatively correlated with the age at first lambing. Hoggets that were mated earlier, and therefore had a lower age at first lambing, had a higher risk of being culled from the flock compared to those that had a higher age at first lambing. A similar pattern in risk for culling was reported for Awassi and Nadji ewes reared in a semi-arid environment (Abdelqader et al., 2012). Therefore, early mating of hoggets under arid and semi-arid conditions could have a negative impact on the longevity of the ewes. Younger ewes tend to have poor mothering ability and early pregnancy has been noted to have negative impacts on an ewe's body condition and overall performance (Abdelqader et al., 2012). In this study population, hoggets are mated at around 9 months old which results into higher age at first lambing (> 400 days).

In this study, ewes in their first or second lambing undergo strict culling procedures compared to ewes that have more than two lambings hence the high risk ratio for younger ewes. Ewes with more parties have proven their reproductive potential and therefore stay longer in the flock until they are culled due to old age. This contributes to increasing the overall performance of the flock. A similar pattern in risk for culling by parity was reported for Awassi and Nadji ewes reared in a semi-arid environment (Abdelqader et al., 2012). Ewes that were very light (less than 1 standard deviation from the mean) or very heavy (more than 1 standard deviation from the mean) at birth were more likely to be culled than those that were within the average birth weight range. Various studies (Aktaş et al., 2015; Gaskins et al., 2005; Haslin et al., 2021) have shown that ewe's weight affects their reproductive performance with heavier than average ewes tending to have low fertility rates. Low fertility rates is one of the criteria used for culling ewes and consequently ewes with low fertility rates have reduced longevity within the flock. The birth weight of the ewe can therefore be used as an indirect indication of its longevity in a flock. An ewes' birth weight not more than one standard deviation below or above the average birth weight of the population is ideal for optimal reproductive performance and eventually better longevity.

3.5 Conclusion

Genetic and non-genetic factors influencing lamb survival pre- and post-weaning, and ewe longevity need to be understood and integrated in breeding programs to improve animal productivity in the arid and semi-arid lands. Genetic factors such as pre-weaning heritability estimates can be used for direct selection to improve lamb survival. Non-genetic factors such

as season of birth, birth weights, type of birth, sex of the lambs should be considered in the management practices to improve overall welfare and eventually the survival of the lambs to yearling. Management practices should prevent ewes from being mated at a very early age, select against ewes producing lambs with very low (<3kgs) or high (>4kgs) birth weights to improve the productive life of ewes. In a crossbreeding program between indigenous and exotic breeds, the breed proportion in the crosses should be considered since it affects the lamb survival pre- and post-weaning, and ewe longevity. For sustainability and to increase the overall performance of the flock, factors affecting lamb survival and ewe longevity should be considered in the daily management of the flock.

Ethics approval

Not applicable

Declaration of generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence assisted technologies in the writing process

Authors ORCIDs

E Oyieng: <https://orcid.org/0000-0002-5004-2060>

J M K Ojango: <https://orcid.org/0000-0003-0224-5370>

M Gauly: <https://orcid.org/0000-0003-4212-5437>

R Mrode: <https://orcid.org/0000-0003-1964-5653>

A M Okeyo : <https://orcid.org/0000-0003-2379-7801>

S König: <https://orcid.org/0000-0003-4226-3696>

Declaration of interest

None

Data availability statement

None of the data was deposited in an official repository. This can be made available upon request to the corresponding author

Acknowledgement

The authors would like to thank the Kapiti Research Station and Wildlife conservancy of International Livestock Research Institute (ILRI) for providing the data. Our deepest gratitude

goes to James Audho, Winfred Sila and Elias Mwarome Mwazonga who were responsible for managing the flock and ensuring timely and accurate data collection.

Author contributions

E Oyieng: Conceptualization, data curation, formal analysis, methodology, software, Writing - original draft, writing - reviewing and editing,

J M K Ojango: Conceptualization, methodology, software, Writing – reviewing and editing, supervision

M Gauly: Conceptualization, methodology, Writing – reviewing and editing, supervision

R Mrode: Conceptualization, methodology, Writing – reviewing and editing, supervision

A M Okeyo: Conceptualization, methodology, Writing – reviewing and editing, supervision

S König: Conceptualization, methodology, Writing – reviewing and editing, supervision

Financial Support

This study was supported through the Center for Tropical Livestock Genetics and Health (CTLGH) – Small ruminant genomics program (<https://www.ctlgh.org>). The authors also acknowledge funding by the Junior Scientists Tandems project (JST), which is part of the ATSAF Academy. JST, commissioned by the German Federal Ministry for Economic Cooperation and Development (BMZ), is being carried out by ATSAF (Council for Tropical and Subtropical Agricultural Research) e.V. on behalf of the Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH

References

- Abdelqader, A., Irshaid, R., Tabbaa, M.J., Abuajamieh, M., Titi, H., Al-Fataftah, A.-R., 2017. Factors influencing Awassi lambs survivorship under fields conditions. *Livest Sci* 199, 1–6. <https://doi.org/https://doi.org/10.1016/j.livsci.2017.03.007>
- Abdelqader, A., Yacoub, A. Al, Gauly, M., 2012. Factors influencing productive longevity of Awassi and Najdi ewes in intensive production systems at arid regions. *Small Ruminant Research* 104, 37–44. <https://doi.org/https://doi.org/10.1016/j.smallrumres.2011.11.007>
- Aktaş, A.H., Dursun, S., Dogan, S., Kiyima, Z., Demirci, U., Halici, I., 2015. Effects of ewe live weight and age on reproductive performance, lamb growth, and survival in Central

- Anatolian Merino sheep. *Arch Anim Breed* 58, 451–459. <https://doi.org/10.5194/aab-58-451-2015>
- Annett, R.W., Carson, A.F., Dawson, L.E.R., Irwin, D., Gordon, A.W., Kilpatrick, D.J., 2011. Comparison of the longevity and lifetime performance of Scottish Blackface ewes and their crosses within hill sheep flocks. *Animal* 5, 347–355. <https://doi.org/10.1017/S1751731110002107>
- Bahri Binabaj, F., Tahmoorespur, M., Aslaminejad, A.A., Vatankhah, M., 2013. The investigation of non-genetic factors affecting survival of Karakul lambs from birth to one year of age using linear and nonlinear models. *Small Ruminant Research* 113, 34–39. <https://doi.org/https://doi.org/10.1016/j.smallrumres.2013.01.011>
- Baker, R.L., Mugambi, J.M., J.O, A., Carles, A.B., Thorpe, W., 2004. Genotype by environment interactions for productivity and resistance to gastro-intestinal nematode parasites in Red Maasai and Dorper sheep. *Animal Science* 79, 343–353.
- Besufkad, S., Abebe, Aschalew, Getachew, T., Goshme, S., Bisrat, A., Abebe, Ayele, Zewdie, T., Alemayehu, L., Kebede, A., Gizaw, S., 2024. Survival analysis of genetic and non-genetic factors influencing lamb survival of different sheep breeds. *Small Ruminant Research* 232, 107206. <https://doi.org/https://doi.org/10.1016/j.smallrumres.2024.107206>
- Boettcher, P., 2005. Breeding for improvement of functional traits in dairy cattle, in: *Italian Journal of Animal Science*. Avenue Media, pp. 7–16. <https://doi.org/10.4081/ijas.2005.3s.7>
- Brien, F.D., Cloete, S.W.P., Fogarty, N.M., Greeff, J.C., Hebart, M.L., Hiendleder, S., Edwards, J.E.H., Kelly, J.M., Kind, K.L., Kleemann, D.O., Plush, K.L., Miller, D.R., 2014. A review of the genetic and epigenetic factors affecting lamb survival. *Anim Prod Sci*. <https://doi.org/10.1071/AN13140>
- Donald, H.P., Read, J.L., Russell, W.S., 1963. Heterosis in crossbred hill sheep. *Animal Science* 5, 289–299. <https://doi.org/DOL: 10.1017/S0003356100021826>
- Ducrocq, V., 1997. Survival analysis, a statistical tool for longevity data, in: *48th Annual Meeting of the European Association for Animal Production*. Vienna, Austria, 1997.
- Ducrocq, V., Besbes, B., Protais, M., 2000. Genetic improvement of laying hens viability using survival analysis. *Genetics Selection Evolution* 32, 23. <https://doi.org/10.1186/1297-9686-32-1-23>
- Dwyer, C.M., Conington, J., Corbiere, F., Holmoy, I.H., Muri, K., Nowak, R., Rooke, J., Vipond, J., Gautier, J.M., 2015. Invited review: Improving neonatal survival in small ruminants:

- Science into practice, in: *Animal*. Cambridge University Press, pp. 449–459.
<https://doi.org/10.1017/S1751731115001974>
- Freking, B.A., Leymaster, K.A., 2004. Evaluation of Dorset, Finnsheep, Romanov, Texel, and Montadale breeds of sheep: IV. Survival, growth, and carcass traits of F1 lambs^{1,2}. *J Anim Sci* 82, 3144–3153. <https://doi.org/10.2527/2004.82113144x>
- Gaskins, C.T., Snowden, G.D., Westman, M.K., Evans, M., 2005. Influence of body weight, age, and weight gain on fertility and prolificacy in four breeds of ewe lambs 1. *J. Anim. Sci.*
- Getachew, T., Gizaw, S., Wurzinger, M., Haile, A., Rischkowsky, B., Okeyo, A.M., Sölkner, J., Mészáros, G., 2015. Survival analysis of genetic and non-genetic factors influencing ewe longevity and lamb survival of Ethiopian sheep breeds. *Livest Sci* 176, 22–32. <https://doi.org/https://doi.org/10.1016/j.livsci.2015.03.021>
- Gowane, G.R., Swarnkar, C.P., Prince, L.L.L., Kumar, A., 2018. Genetic parameters for neonatal mortality in lambs at semi-arid region of Rajasthan India. *Livest Sci* 210, 85–92. <https://doi.org/10.1016/j.livsci.2018.02.003>
- Haslin, E., Corner-Thomas, R.A., Kenyon, P.R., Pettigrew, E.J., Hickson, R.E., Morris, S.T., Blair, H.T., 2021. Effect of breeding heavier romney ewe lambs at seven months of age on lamb production and efficiency over their first three breeding seasons. *Animals* 11, 3486. <https://doi.org/10.3390/ani11123486>
- Hatcher, S., Atkins, K.D., Safari, E., 2010. Lamb survival in Australian Merino Sheep: A genetic analysis. *J Anim Sci* 88, 3198–3205. <https://doi.org/10.2527/jas.2009-2461>
- Hielscher, A., Brandt, H., Erhardt, G., Gauly, M., 2006. Heterosis analysis of *Haemonchus contortus* resistance and production traits in Rhoen sheep, Merino Land sheep and crossbred lambs. *Vet Parasitol* 141, 279–284. <https://doi.org/https://doi.org/10.1016/j.vetpar.2006.05.027>
- Hinch, G.N., Brien, F., 2014. Lamb survival in Australian flocks: a review. *Anim Prod Sci* 54, 656–666.
- Hosseini-Zadeh, N.G., Noori, R., Shadparvar, A.A., 2018. Genetic analysis of longevity and lamb survival from birth to yearling in moghani sheep. *J Appl Anim Res* 46, 1363–1369. <https://doi.org/10.1080/09712119.2018.1511432>
- Kaplan, E.L., Meier, P., 1958. Nonparametric Estimation from Incomplete Observations. *J Am Stat Assoc* 53, 457–481. <https://doi.org/10.2307/2281868>
- Keady, T.W.J., Hanrahan, J.P., 2022. Effects of Age at First Joining and Ewe Genotype on the Performance of Two-Tooth Ewes and That of Their Progeny to Slaughter. *Animals* 12. <https://doi.org/10.3390/ani12050653>

- Mandal, A., Prasad, H., Kumar, A., Roy, R., Sharma, N., 2007. Factors associated with lamb mortalities in Muzaffarnagari sheep. *Small Ruminant Research* 71, 273–279. <https://doi.org/https://doi.org/10.1016/j.smallrumres.2006.07.010>
- Mészáros, G., Sölkner, J., Ducrocq, V., 2013. The Survival Kit: Software to analyze survival data including possibly correlated random effects. *Comput Methods Programs Biomed* 110, 503–510. <https://doi.org/https://doi.org/10.1016/j.cmpb.2013.01.010>
- Milne, C., 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. [https://doi.org/https://doi.org/10.1016/S0921-4488\(99\)00154-6](https://doi.org/https://doi.org/10.1016/S0921-4488(99)00154-6)
- Mugambi, J.M., Audho, J.O., Baker, R.L., 2005. Evaluation of the phenotypic performance of a Red Maasai and Dorper double backcross resource population: natural pasture challenge with gastro-intestinal nematode parasites. *Small Ruminant Research* 56, 239–251. <https://doi.org/https://doi.org/10.1016/j.smallrumres.2004.06.003>
- Mukasa-Mugerwa, E., Lahlou-Kassi, A., Anindo, D., Rege, J.E.O., Tembely, S., Tibbo, M., Baker, R.L., 2000. Between and within breed variation in lamb survival and the risk factors associated with major causes of mortality in indigenous Horro and Menz sheep in Ethiopia. *Small Ruminant Research* 37, 1–12. [https://doi.org/https://doi.org/10.1016/S0921-4488\(99\)00152-2](https://doi.org/https://doi.org/10.1016/S0921-4488(99)00152-2)
- Mwamachi, D.M., Audho, J.O., Thorpe, W., Baker, R.L., 1995. Evidence for multiple anthelmintic resistance in sheep and goats reared under the same management in coastal Kenya. *Vet Parasitol* 60, 303–313. [https://doi.org/https://doi.org/10.1016/0304-4017\(95\)00794-1](https://doi.org/https://doi.org/10.1016/0304-4017(95)00794-1)
- Nel, C.L., Swan, A.A., Dzama, K., Scholtz, A.J., Cloete, S.W.P., 2021. Genetic parameters and trends for lamb survival following long-term divergent selection for number of lambs weaned in the Elsenburg Merino flock, in: *Animal Production Science*. CSIRO, pp. 1965–1981. <https://doi.org/10.1071/AN21198>
- Nyariki, D.M., Amwata, D.A., 2019. The value of pastoralism in Kenya: Application of total economic value approach. *Pastoralism* 9. <https://doi.org/10.1186/s13570-019-0144-x>
- Oyieng, E., Mrode, R., Ojango, J.M.K., Ekine-Dzivenu, C.C., Audho, J., Okeyo, A.M., 2022. Genetic parameters and genetic trends for growth traits of the Red Maasai sheep and its crosses to Dorper sheep under extensive production system in Kenya. *Small Ruminant Research* 206, 106588. <https://doi.org/10.1016/j.smallrumres.2021.106588>
- Rauw, W.M., Dekkers, J.C.M., Gomez-Raya, L., 2021. Improving Animal Welfare Using Genetic and Genomic Tools. *CABI* 190–212. <https://doi.org/10.1079/9781789247886.0012>

- Riggio, V., Finocchiaro, R., Bishop, S.C., 2008. Genetic parameters for early lamb survival and growth in Scottish Blackface sheep1. *J Anim Sci* 86, 1758–1764. <https://doi.org/10.2527/jas.2007-0132>
- Sawalha, R.M., Conington, J., Brotherstone, S., Villanueva, B., 2007. Analyses of lamb survival of Scottish blackface sheep, in: *Animal*. pp. 151–157. <https://doi.org/10.1017/S1751731107340056>
- Tesema, Z., Deribe, B., Kefale, A., Lakew, M., Tilahun, M., Shibesh, M., Belayneh, N., Zegeye, A., Worku, G., Yizengaw, L., 2020. Survival analysis and reproductive performance of Dorper x Tumele sheep. *Heliyon* 6, 4. <https://doi.org/https://doi.org/10.1016/j.heliyon.2020.e03840>
- Tibbo, M., 2006. Productivity and Health of Indigenous Sheep Breeds and Crossbreds in the Central Ethiopian Highlands (PhD Thesis). Swedish University of Agricultural Sciences, Uppsala.
- Vatankhah, M., Talebi, M.A., 2009. Genetic and Non-genetic Factors Affecting Mortality in Lori-Bakhtiari Lambs. *Asian-Australas J Anim Sci* 22, 459–464. <https://doi.org/10.5713/ajas.2009.80318>
- Vostrý, L., Milerski, M., 2013. Genetic and non-genetic effects influencing lamb survivability in the Czech Republic. *Small Ruminant Research* 113, 47–54. <https://doi.org/10.1016/j.smallrumres.2013.02.008>
- Yazdi, M.H., Visscher, P.M., Ducrocq, V., Thompson, R., 2002. Heritability, Reliability of Genetic Evaluations and Response to Selection in Proportional Hazard Models. *J Dairy Sci* 85, 1563–1577. [https://doi.org/https://doi.org/10.3168/jds.S0022-0302\(02\)74226-4](https://doi.org/https://doi.org/10.3168/jds.S0022-0302(02)74226-4)

CHAPTER 4: The impact of heat stress on growth and resilience phenotypes of sheep raised in a semi-arid environment of sub-Saharan Africa

E. Oyieng^{ab}, J.M.K Ojango^b, M. Gauly^c, C.C. Ekine-Dzivenu^b, R. Mrode^{bd}, E.L.Clark^{e,f}, R. Oloo^b, S. König^a

^a Institute of Animal Breeding and Genetics, Justus-Liebig-University Gießen, Ludwigstraße 21 b, 35390 Gießen, Germany

^b Livestock Genetics Nutrition and Feed Resources Program, International Livestock Research Institute, P. O Box 30709-00100 Nairobi, Kenya

^c Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen – Bolzano, Universitätsplatz 5, 39100 Bolzano, Italy

^d Animal and Veterinary Science, Scotland's Rural College, EH9 3JG Edinburgh, United Kingdom

^e The Roslin Institute & Royal (University of Edinburgh, Easter Bush, Midlothian EH25 9RG, UK

^f Centre for Tropical Livestock Genetics and Health, Easter Bush, Midlothian, EH25 9RG, UK

Published in

Livestock Science, August 2025

<https://doi.org/10.1016/j.livsci.2025.105794>

Abstract

Sheep production in Arid and Semi-Arid lands face immense heat stress with the changing climate. This study assessed the effect of heat stress on growth and developed resilience phenotypes of sheep raised in a semi-arid environment. Heat stress was measured by Temperature-Humidity Index (THI). Live body weight records of 4,078 animals, belonging to pure Red Maasai (RRRR), pure Dorper (DDDD), and their crosses: 50%Dorper-50%RedMaasai (DDRR) and 75%Dorper-25%Red Maasai (DDDR) collected between 2003 and 2024 were analysed. Random regression models fitted with reaction norm functions were used to develop two resilience phenotypes: Response and Stability, at THI 70 and THI 85 representing varying heat stress. Animal mixed models were used to estimate genetic parameters. The THI breakpoints were 78.75, 78.71, 78.42 and 77.93 with a decline rate of 0.06 Kgs, 0.09 Kgs, 0.05 Kgs and 0.15 in live weight gain per unit change in THI for RRRR, DDDD, DDRR and DDDR respectively. The breed, sex, type of birth, dams' parity and season of birth significantly ($P<0.05$) affected the stability of growth at low and high heat stress. The heritability estimates of resilience traits ranged from 0.12 to 0.16. Genetic correlations of resilience phenotypes at THI 85 with pre-weaning live weight gain were antagonistic and significant ($P<0.05$). With the changing climate, resilience phenotypes should be included in selection programs for sheep in the Arid and Semi-Arid lands for robust growth.

Key words: *Climate change, Growth, Reaction norms, Resilience, Sheep*

4.1 Introduction

Arid and Semi-Arid Lands cover about 25% of the world's land mass and are home to approximately one billion people (Günter et al., 2009). They are a key feature of sub-Saharan Africa (SSA) covering approximately 43% of the land area which is estimated to host a quarter the world's cattle, sheep, and goats (FAO, 2021). In countries like Kenya, the Arid and Semi-Arid Lands cover nearly 80% of the country's land mass, are home to nearly 30% of its population and hosts approximately 70% of the national livestock herd (KNBS, 2019). Arid and Semi-Arid Lands are characterized by their aridity, consistently high temperatures and low rainfall throughout the year. Due to their tendency to experience drought, the Arid and Semi-Arid Lands are highly susceptible to climate-related disturbances hence the livestock production systems in these areas are more sensitive to the changes in climate patterns (Serrano et al., 2021, 2022; King et al., 2017).

Livestock production in Arid and Semi-Arid Lands is a key source of livelihood and an important source of nutrient requirements for households (Ojango et al., 2016). The main livestock kept in the Arid and Semi-Arid Lands are cattle and small ruminants i.e. sheep and goats. Of the small ruminants, sheep have greater socio-cultural importance compared to goats (Oyieng et al., 2021). Approximately 67% of the sheep population in the Arid and Semi-Arid Lands are indigenous sheep breeds (FAO, 2021) which are expected to survive, produce and reproduce, i.e. be 'resilient' or 'robust', with little assistance from human intervention despite the increasing ambient temperatures and changing humidity. Heat stress on sheep flocks in the Arid and Semi-Arid Lands is a key focus for environmental adaptation and will likely be of greater concern with the effects expected from climate change (Rust and Rust, 2013). The estimated increase in heat stress, due to high ambient temperature and humidity, on livestock is expected to negatively affect health, productive and reproductive performance and therefore the overall economical outcome of livestock (Rojas-Downing et al., 2017; Gauly et al., 2013).

Heat stress in livestock production arises when animals cannot dissipate heat effectively, impairing growth, reproduction, and yield. Heat stress can be measured using either thermal parameters such as temperature, humidity, wind speed and solar radiation or animal responses such as sweating rate, heart rate, respiration rate and rectal temperature (Ji et al., 2020). Thermal parameters such as temperature and humidity have been widely used as a Temperature-Humidity Index (THI) in the quantification of heat stress thresholds associated with the various aspects of animal production (Polsky and von Keyserlingk, 2017; Gantner et al., 2011). In cattle, high THI (>70) has been shown to cause drop in milk yield (Oloo et al., 2024), declining reproduction (Dash et al., 2016) and increasing disease risk (Gujar et al., 2023; Nardone et al., 2010). Heat stress has been found to lower body weight (Goo et al., 2019), decrease fertility, egg production and egg quality (Oluwagbenga et al., 2022; Mehaisen et al., 2019) and weaken the immunity (Hirakawa et al., 2020) in poultry.

With increasing climate change and the negative effects of heat stress on livestock, it is important to breed animals that are resilient. Resilience can be defined as "the capacity of the animal to be minimally affected by disturbances or to rapidly return to the state pertained before exposure to a disturbance" (Berghof et al., 2019). To identify resilient animals for a particular trait, relevant indicators for resilience must be defined. Many studies that focus on resilience are based on experimental set-ups to identify underlying physiological mechanisms, yet these mechanisms heavily rely on the type of disturbance, are frequently selected according to the study's focus and may describe a phenotype overly tied to the specific

disturbance under investigation (Colditz and Hine, 2016). Production traits that have repeated measures on an individual animal such as growth and reproduction traits provide an opportunity for more accurate estimation of resilience indicators and their variance components. Resilience can be expressed as the phenotypic response of animal performance to a changing environment using reaction norm functions (Berghof et al., 2019). Reaction norms have been used to quantify resilience and develop novel resilience phenotypes for milk production in cattle in SSA (Oloo et al., 2024), dairy sheep in the Mediterranean (Tsartsianidou et al., 2021) and meat sheep in sheep in Scotland (Sánchez-Molano et al., 2020). The slope of the reaction norm indicates the performance of the animal due to environmental changes (Berghof et al., 2019). Animals with a slope of zero are considered to be more resilient to the environment since their performance is not affected by the changes in weather while animals with a slope that greater than or less than zero reflect genotype by environment interaction (Oloo et al., 2024; Tsartsianidou et al., 2021). The slope of individual animal reaction norms can therefore be used to develop resilience phenotypes. These resilience phenotypes can further be analysed to produce breeding values and genetic parameters for selective breeding.

Studies on the effects of heat stress on growth in small ruminants in Arid and Semi-Arid Lands are rare as most studies focus on dairy goats or sheep in temperate environments. Information on the genetic components of heat tolerance for growth in sheep raised in Arid and Semi-Arid Lands is thus scarce. Using reaction norms, this study aimed to (i) assess the impact of heat stress on the growth of the Red Maasai, Dorper sheep, and their crosses, (ii) Develop novel resilience phenotypes for growth in response to the level of heat stress, and (iii) estimate genetic parameters for the novel resilience phenotypes.

4.2 Material and Methods

4.2.1 Study area and animal management

The study is part of a sheep selective breeding program by the International Livestock Research Institute (ILRI) that has been operational since 2003 at the Kapiti Research Station and Wildlife Conservancy in Machakos County, Kenya. The conservancy is located between 1,650 and 1,900 meters above sea level, at -1.6 latitude and 37.1 longitude. The area is characterized as semi-arid covered with grasses and shrubs and receives an average annual rainfall of approximately 552 mm with temperatures ranging from 22 to 27 °C. It experiences four distinct seasons: short-dry (January and February), long-wet (March to May), long-dry (June to September), and short-wet (October to December). For this analysis, the long and

short dry seasons have been grouped as dry seasons while the short and long wet seasons have been grouped as wet seasons.

The main breed groups in the sheep breeding program comprise pure Red Maasai (RRRR), pure Dorper (DDDD), the F1:50%Dorper-50%Red Maasai (DDRR) and the 75%Dorper-25%Red Maasai (DDDR). The Red Maasai sheep is a fat-tailed hair breed that is indigenous to East Africa. The breed demonstrates innate resistance to *Haemonchus contortus* (Mugambi et al., 2005; Baker et al., 2004) and can grow and reproduce regularly despite drastic changes in the climatic conditions of the rangelands (Oyieng et al., 2022, 2025). The Dorper is a composite breed developed in South Africa through crossbreeding the Blackhead Persian with the Dorset Horn. It is well defined as a hardy mutton sheep with a top-quality carcass at a relatively early age (Milne, 2000). It's performance traits have been reviewed by Ojango et al., (2023). The main objective of the breeding program is to selectively improve the growth and reproduction traits of the indigenous Red Maasai sheep while conserving them *in situ*. The crossbreeding component of the breeding program aims to combine the faster growth rate and mutton-producing ability of the Dorper breed and the resilience of the Red Maasai breed to gastrointestinal parasites.

In the breeding program, mating is done in April and October every year. The breeding rams are identified based on estimated breeding values for growth and fertility traits ensuring the best pure-bred lines are retained while at the same time producing crossbreds for both breeding and marketing. Water is provided *ad libitum* for all the animals when in the pens at night, and before setting out for grazing. When animals are grazing in the open fields, water is provided twice in the day. Scheduled vaccinations against anthrax, enterotoxaemia, and foot and mouth disease are provided annually, bi-annually, and every 5 months, respectively. Anthelmintic treatment is given to animals before and after the rainy season based on their age and body condition. More details on the management have been described by Oyieng et al., (2022).

4.2.2 Animal and weather data

12,234 live body weight records of 4,078 animals, belonging to the four breed groups, collected from 2003 to 2024 were available for analysis. Three live body weights are recorded on each animal at the following stages of growth: birth weight, recorded on each lamb within 24 hours of birth; weaning weight, recorded at three months of age and nine months weight. In this analysis, the weaning and nine months weight weights were corrected to 90 and 270 days respectively. For each animal, live weight gain between birth and weaning weight (LWG^1),

and between weaning and nine months weight (LWG²) was used to estimate the resilience phenotypes for growth.

Weather data including average daily temperature and relative humidity was obtained from the NASA POWER (National Aeronautics and Space Administration (NASA) Langley Research Center (LaRC) Prediction of Worldwide Energy Resource (POWER) Project funded through the NASA Earth Science/Applied Science Program based on the GPS coordinates of the farm (<https://power.larc.nasa.gov>)

4.2.3 Temperature-Humidity index (THI)

The Temperature-Humidity Index (THI) is commonly used as a measure of heat load experienced by animals. The THI was calculated using Equation [1] as proposed by the National Research Council (NRC, 1971) and recommended by Srivastava et al., (2021) for the measure of heat stress in small ruminants in semi-arid regions.

$$THI = T - (1.8 * T + 32) - [(0.55 - 0.0055 * RH) * (1.8 * T - 26.8)] \quad \text{Equation [1]}$$

Where T and RH represent the average daily temperature (°C) and relative humidity respectively. To account for possible cumulative effects of temperature and relative humidity, each live weight record for each animal was matched to the average THI in the period preceding the date the weight was recorded. Therefore, the THI associated with the live weight gain between birth and weaning (LGW¹) was the average THI between birth and corrected weaning time (90 days) and the THI associated with the live weight gain between weaning and nine months weight (LWG²) was the average THI between the corrected weaning time and corrected nine months (180 days).

A segmented regression of THI against live weight gain was plotted in R (R Core Team, 2021) to determine the THI threshold or breakpoint with respect to live weight gain in the studied breeds. The segmented regression splits the explanatory variable into two or more linear regressions and locates the point of change in the linear trend of THI which is considered as the breakpoint. The right of the THI breakpoint indicates the point at which animals start feeling heat stress (Pinto et al., 2020; Kumar et al., 2018). The existence of breakpoint was tested statistically at $P < 0.05$ by testing the difference between regression coefficients of linear regression lines.

4.2.4 Factors of variation on live weight gain

A fixed effect linear model, Equation [2], was fitted to determine the effect of the fixed factors on the live weight gain. The equation was fitted separately for LWG¹ and LWG².

$$Y_{ijklmno} = \mu + brd_i + sob_j + ysob_k + sex_l + pr_m + thi_n + e_{ijklmno} \quad \text{Equation [2]}$$

Where $Y_{ijklmno}$ is the vector for individual live weight gain measurement for nth animal, μ is the population mean, brd_i is the effect of the ith breed group (4 breed groups), sob_k is the effect of the kth season of birth (2 seasons), $ysob_j$ is the effect of the jth interaction between year of birth and season of birth year (44 classes), sex_l is the effect of the sex of the lamb (2 classes), pr_m is the parity in which the lamb was born (6 classes), thi_n is the level of THI (3 classes) and $e_{ijklmno}$ is the residual error. Least-square means (LSM) of the fixed effects were calculated and contrasted using Tukey HSD to determine significant differences (P<0.05) between the classes in each fixed effect.

4.2.5 Derivation of resilience phenotypes

To derive resilience phenotypes reflecting changes in growth in response to weather variability, a random regression model (Equation [3]) fitted with reaction norm functions were fitted without pedigree information

$$Y_{ij} = X + f(\beta, X_j) + f_i(a_i, X_j) + e_{ij} \quad \text{Equation [3]}$$

Where Y_{ij} corresponds to the performance record of animal i under THI _{j} , X corresponds to a set of fixed effects on growth, $f(\beta, X_j)$ represents the population reaction norm function using a Legendre polynomial of second degree and describing the relationship between the average animal performance and weather variable value j , a_i corresponds to the individual animal effect i , $f_i(a_i, X_j)$ represents the individual reaction norm function using a Legendre polynomial of second degree describing the relationship between individual animal i and THI _{j} (expressed as a deviation from the population reaction norm) and e_{ij} corresponds to the residual. The choice of Legendre polynomial of order 2 was based on a preliminary analysis that examined orders 1 to 3 to discover which one gave the best fit using Akaike information criterion and likelihood ratio test. The fixed effects fitted were breed, sex, parity of ewe at lambs' birth, birth type, the season the lamb was born and the interaction between the year of birth and season of birth which were found to be significant at p<0.05.

Equation [3] was fitted for the full dataset to determine the general shape of growth to changing heat loads for the entire population, and for each breed group by dividing the data into four subsets for each breed group. The population reaction norms were computed using the estimated random regression coefficients. After computation, the resilience phenotypes (*Slope* and *absolute slope*) were quantified and predicted for each animal at each THI levels ranging from 50 to 100. The slope of the animal reaction norm was determined as the relative steepness of change in individual animal growth performance due to changes in THI. It was the estimate of the first derivative at the threshold THI on the individual's response curve. Two animal resilience phenotypes were derived from the reaction norms: (i) the actual slope of the reaction norm which represents the response to changes in weather conditions thus indicating directionality of the change in weight gain per unit of THI change and (ii) the square-root transformed absolute value of the slope of the reaction norm which represents the stability of growth performance in varying heat load conditions. The two resilience phenotypes were estimated at no-heat stress and heat stress THI levels. The THI level for no-heat stress was calculated by subtracting 5 THI units from the lowest THI breakpoint in the population while the heat stress THI level was calculated by adding 5 THI units from the highest THI breakpoint in the population, rounded off to the nearest whole number.

4.2.6 Fixed effects factors of variation on resilience phenotypes

A fixed effect linear model, Equation [4], was fitted to determine the effect of the fixed factors on the resilience phenotypes.

$$Y_{ijklmn} = \mu + brd_i + tob_j + sob_k + ysob_l + sex_m + pr_n + e_{ijklmn} \quad \text{Equation [4]}$$

Where Y_{ijklmn} is the vector for individual resilience indicator measurement for n^{th} animal, μ is the population mean, brd_i is the effect of the i^{th} breed group (4 breed groups), tob_j is the effect of the j^{th} type of birth (2 classes), sob_k is the effect of the k^{th} season of birth (2 seasons), $ysob_l$ is the effect of l^{th} interaction of year and season of birth (44 classes), sex_m is the effect of the m^{th} sex of the lamb (2 classes), pr_n is the parity in which the lamb was born (6 classes) and e_{ijklmn} is the residual error. Least-square means (LSM) of the fixed effects were calculated and contrasted using Turkey HSD to determine significant differences ($P < 0.05$) between the classes in each fixed effect.

4.2.7 Genetic parameters of resilience indicators

Animal mixed models using pedigree information, Equation [5], were used to obtain variance components and genetic correlations estimates of the resilience and growth traits using ASReml-R 4.1 software (Butler et al., 2018).

$$y = X\beta + Za + e \quad \text{Equation [5]}$$

Where y represents the measurement of individual phenotype for the resilience and growth trait, β is the solutions of the fixed effects in the model; a is the solutions of random animal additive genetic effects and e is the vector of random residual effects. X and Z are the incidence matrices relating observations to fixed and random animal effects, respectively. The pedigree used to construct the numerator relationship matrix comprised 12,945 animals spanning 13 generations, including 233 sires and 3,327 dams. Univariate analyses were conducted separately for each trait to estimate the variance components and heritability estimates of the trait. Bivariate analyses were then performed to estimate phenotypic and genetic correlations between the traits with fixed effects similar to those in the univariate analyses. The likelihood ratio test was used to test the significance of the heritability estimates based on the comparison of the log-likelihoods of the model with and without the random animal genetic effect while the significance of genetic correlations was tested by comparing the modelled equation to a bivariate model with additive genetic covariance fixed at zero.

4.3 Results

4.3.1 Fixed factors affecting growth

Table 1 presents the summary statistics of the fixed factors and their effect on the growth of the sheep. The breed, sex, parity in which the lamb was born (dams' parity), the season of birth, type of birth, and year of birth significantly ($P < 0.05$) affected the live weight gain between birth and weaning (LWG^1). The parity of the ewe, season of birth of the lamb, and type of birth had no significant difference in post-weaning live weight gain (LWG^2). The pure Dorper breed, male lambs, lambs born by first-time ewes, lambs born during the dry seasons, and those born as single births had significantly ($P < 0.05$) higher LWG^1 compared to their counterparts. The DDDR breed combination had a significantly ($P < 0.05$) higher LWG^2 among all breeds. Based on the THI Threshold of the population of 77, the THI was grouped into 3 classes (THI < 76; No heat stress, THI 76-78; Normal and THI > 78; Heat stress) to evaluate the effect of level of heat stress on LWG^1 and LWG^2 separately. LWG^1 was significantly affected

($P < 0.05$) at all levels of THI while WLG^2 was not significantly ($P > 0.05$) affected by THI levels above 78.

Table 1 Least square means (LSM) and SE (in parentheses) of fixed factors affecting growth

	N (animals/records)	WLG ¹ (Kgs)	WLG ² (Kgs)
Population	4078	12.51 (0.30)	10.25 (0.22)
Breed			
DDDD	741	11.91 (0.15) ^a	10.37 (0.16) ^a
DDDR	1225	11.60 (0.14) ^a	11.36 (0.15) ^b
DDRR	1259	11.01 (0.14) ^c	10.66 (0.15) ^a
RRRR	853	9.56 (0.15) ^d	9.62 (0.16) ^c
Sex			
Male	1800	11.40 (0.13) ^a	11.47 (0.13) ^a
Female	2278	10.60 (0.12) ^b	9.50 (0.13) ^b
Dams' parity			
1	1366	10.80 (0.14) ^a	10.30 (0.15) ^a
2	1011	11.50 (0.14) ^b	10.40 (0.15) ^a
3	713	11.40 (0.15) ^{ab}	10.50 (0.16) ^a
4	474	11.10 (0.17) ^{ab}	10.60 (0.18) ^a
5	262	11.00 (0.21) ^{ab}	10.80 (0.23) ^a
6 and above	252	10.40 (0.22) ^{ac}	10.30 (0.23) ^a
Season of birth			
Wet season	2479	11.40 (0.13) ^a	10.50 (0.15) ^a
Dry Season	1599	10.70 (0.14) ^b	10.65 (0.14) ^a
Type of birth			
Single	3858	12.21 (0.08) ^a	10.30 (0.08) ^a
Twins	220	9.83 (0.21) ^b	10.70 (0.22) ^a
THI			
THI <76:No heat stress	1396	12.44 (0.12) ^a	11.04 (0.18) ^a
THI 76 – 78:Normal	884	13.31 (0.08) ^b	10.04 (0.06) ^b
THI >78:Heat stress	1798	10.55 (0.12) ^c	12.05 (0.31) ^b

DDDD= pure dorper, DDDR = 75%Dorper-25%Red Maasai, DDDR = 50%Dorper-50%Red Maasai, RRRR = pure Red Maasai. WLG¹ = Live weight gain between birth and weaning, WLG²= Live weight gain between weaning and 9 months. THI – Temperature-Humidity Index. ^{a,b,c}: Least square means within a column in a fixed effect that do not have a common superscript are significantly different ($P < 0.05$).

4.3.2 Threshold for heat stress on growth

Between the year 2003 and 2024, the average monthly THI in the study area ranged from 68.14 to 84.89. Generally, the months of February and March had the highest THI across the years while the months of April and May had the lowest average THI as illustrated in Figure 1. The fluctuation in THI across the months within a year illustrates weather variability in the study area within the study period.

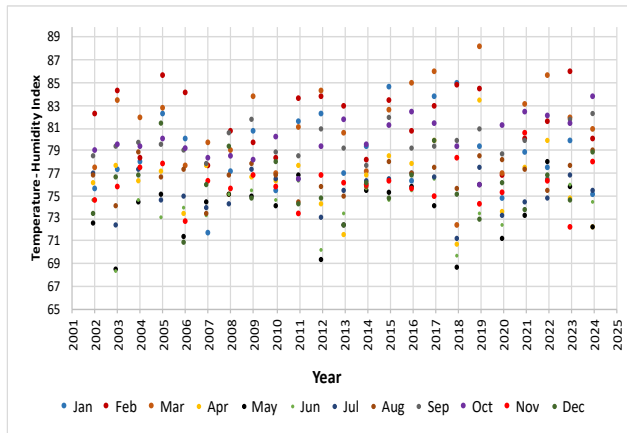


Figure 1 The average monthly THI for each year in the study area

The THI breakpoints for the population and breeds were significantly different from zero. The population THI breakpoint was 77.60. This represents the threshold for THI on growth with THI lower than the breakpoint indicating no heat stress and THI higher than the breakpoint indicating heat stress. The THI breakpoints were 78.75, 78.71, 78.42 and 77.93 with a decline rate of 0.06 Kgs, 0.09 Kgs, 0.05 Kgs and 0.15 in live weight gain per unit change in THI for RRRR, DDDD, DDDR and DDDR respectively. The pure Red Maasai had the highest THI breakpoint while the DDDR had the lowest live weight decline rate past its' THI breakpoint. Though the DDDR had the highest live weight gain, it had the lowest THI breakpoint and highest live weight decline rate as illustrated in Figure 2. Overall, there was a general decline in growth in both low and high THI past the threshold.

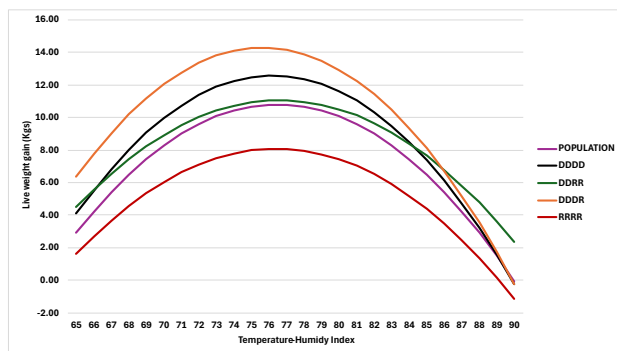


Figure 2 Reaction norms for changes in weight in response to average temperature-humidity index for the population and each breed (**DDDD**= pure dorper, **DDDR** = 75%Dorper-25%Red Maasai, **DDRR** = 50%Dorper-50%Red Maasai, **RRRR** = pure Red Maasai)

4.3.3 Resilience phenotypes

Using the THI breakpoint range for the breed groups (77.92 to 78.75), two resilience phenotypes were chosen to indicate changes in live weight gain at no heat stress (*Response A* at THI 70) and changes in live weight gain with heat stress (*Response B* at THI 85) at the population level. The values of the *Response* phenotype indicate the unit change in live weight gain for each unit change in THI. The corresponding measure of how stable the animal growth was under heat stress and no heat stress were *Stability A* for *Response A* and *Stability B* for *Response B*.

All fixed effects studied significantly ($P < 0.05$) affected the stability in live weight gain under heat stress and under no heat stress, however the dam's parity did not significantly ($P > 0.05$) affect the response in live weight gain in both environments (Table 2). The response of live weight gain under heat stress environment was negative while under no heat stress was positive. Though the response under heat stress was negative for all breeds, the pure Red Maasai had the lowest response (-0.014) among the breeds. Male lambs, lambs born as twins and those born during the wet season had a significantly ($P < 0.05$) higher loss in live weight gain under heat stress compared to their contemporaries. The pure Red Maasai, female lambs, lambs born during the dry season and those born from ewes in their early parities (1 and 2) and late parities (6 and above) did not have stable growth under heat stressed and no-heat stress environments.

Table 2 Least square means and SE (in parenthesis) of resilience phenotypes expressed as change in growth per unit increase in temperature-humidity index

	Response A	Response B	Stability A	Stability B
Breed				
DDDD	0.018 (0.024) ^a	-0.025 (0.025) ^a	0.261 (0.046) ^a	0.253 (0.038) ^a
DDDR	0.087 (0.022) ^b	-0.101 (0.023) ^b	0.068 (0.043) ^b	0.056 (0.031) ^b
DDRR	0.076 (0.022) ^a	-0.089 (0.023) ^a	0.097 (0.043) ^b	0.083 (0.031) ^c
RRRR	0.094 (0.024) ^b	-0.014 (0.025) ^b	-0.041 (0.047) ^c	0.186 (0.034) ^a
Sex				
Male	0.099 (0.020) ^a	-0.108 (0.022) ^a	0.064 (0.034) ^a	0.117 (0.039) ^a
Female	0.049 (0.019) ^b	-0.052 (0.021) ^b	-0.018 (0.033) ^b	0.048 (0.038) ^b
Type of birth				
Single	0.007 (0.011) ^a	-0.008 (0.012) ^a	0.016 (0.020) ^a	0.070 (0.034) ^a
Twins	0.156 (0.033) ^b	-0.168 (0.035) ^b	0.175 (0.067) ^b	-0.014 (0.033) ^b
Dam parity				
1	0.097(0.021)	-0.105(0.023)	-0.046(0.036) ^a	-0.042(0.036) ^a
2	0.069(0.022)	-0.074(0.024)	-0.036(0.037) ^a	-0.030(0.037) ^a
3	0.077(0.023)	-0.082(0.026)	0.099(0.040) ^b	0.106(0.040) ^b
4	0.521(0.027)	-0.056(0.029)	0.099(0.046) ^b	0.101(0.045) ^b
5	0.053(0.033)	-0.058(0.036)	0.047(0.057) ^a	0.047(0.056) ^a
6 and above	0.063(0.034)	-0.067(0.037)	-0.024(0.058) ^a	-0.018(0.058) ^a
Season of birth				
Wet season	0.129 (0.023) ^a	-0.139 (0.024) ^a	0.238(0.036) ^a	0.236 (0.036) ^a
Dry Season	0.019 (0.021) ^b	-0.021 (0.023) ^b	-0.192(0.039) ^b	-0.181 (0.039) ^b

Response A = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 70;
Response B = performance change per unit change in temperature-humidity index at THI 85;
Stability A = Absolute value of corresponding performance change (square root transformed) at THI 70;
Stability B = Absolute value of corresponding performance change (square root transformed) at THI 85;
DDDD= pure dorper, **DDDR** = 75%Dorper-25%Red Maasai, **DDRR** = 50%Dorper-50%Red Maasai, **RRRR** = pure Red Maasai

4.3.4 Genetic parameters for resilience phenotypes

The variance components and heritability estimates for the resilience phenotypes and live weight gain for the population are presented in Table 3. The heritability estimates were all significantly greater than zero ($P < 0.05$). The heritability estimates for the resilience phenotypes ranged from 0.12 to 0.16. Notably, the heritability estimates for *Stability* traits were higher than those for *Response* traits.

Table 3 Variance components and heritability estimates (SE in parenthesis) of resilience phenotypes and liver weight gain

Phenotype	V_a	V_e	V_p	h_2
Response A	0.024 (0.006)	0.190 (0.006)	0.215 (0.004)	0.115 (0.027)*
Response B	0.030 (0.007)	0.225 (0.007)	0.255 (0.005)	0.118 (0.028)*
Stability A	0.092 (0.017)	0.497 (0.017)	0.590 (0.028)	0.157 (0.028)*
Stability B	0.093 (0.017)	0.495 (0.017)	0.589 (0.013)	0.158 (0.013)*
LWG ¹	3.014 (0.341)	5.359 (0.250)	8.374 (0.218)	0.359 (0.035)*
LWG ²	2.104 (0.323)	7.236 (0.278)	9.341 (0.227)	0.225 (0.032)*

Response A = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 70;

Response B = performance change per unit change in temperature-humidity index at THI 85;

Stability A = Absolute value of corresponding performance change (square root transformed) at THI 70;

Stability B = Absolute value of corresponding performance change (square root transformed) at THI 85;

LWG¹ = Live weight gain between birth and weaning, **LWG²**= Live weight gain between weaning and 9 months.

V_a = Additive variance; V_e = Residual variance; V_p = Phenotypic variance; h_2 = heritability estimate.

* Parameters is significantly different from zero ($P < 0.05$)

Table 4 presents the genetic and phenotypic correlations between the traits studied. A significant ($P < 0.05$) antagonistic genetic correlation was evident between the resilience phenotypes at heat stress and pre-weaning live weight gain (LWG¹) while the correlations between the resilience phenotypes and post-weaning live weight gain (LWG²) were not significant ($P > 0.05$). This implies that heat stress significantly affects pre-weaning live weight gain compared to post-weaning live weight gain. There was very strong negative genetic and phenotypic correlation between *Response A* and *Response B*. Therefore, animals that perform better at no heat stress environments cannot have the same performance at heat stress environments. Additionally, there was a strong negative genetic correlation between *Response traits* and their opposite *Stability traits*. This further implies that animals that are able to have higher live weight gains at the extreme environments would not be able to maintain their growth performance in the opposite environment.

Table 4 Genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) of the traits

	Response A	Response B	Stability A	Stability B	LWG ¹	LWG ²
Response A		-0.987(0.001)*	0.977(0.060)*	-0.987(0.060)*	0.193 (0.062)	0.397 (0.059)
Response B	-0.990(0.001)*		-0.926(0.065)*	0.926(0.065)*	-0.212 (0.062)*	-0.418 (0.058)
Stability A	0.916(0.015)*	-0.989(0.016)*		-0.916(0.065)*	0.026 (0.075)	0.013 (0.080)
Stability B	-0.926(0.015)*	0.988(0.016)*	-0.989(0.016)*		-0.026 (0.075)*	-0.013 (0.080)
LWG ¹	0.018(0.017)	-0.216(0.018)*	0.001(0.018)	-0.001(0.018)*		0.536 (0.057)*
LWG ²	0.364(0.015)	-0.382(0.015)	0.022(0.018)	-0.022(0.018)	0.463 (0.014)*	

Response A = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 55;

Response B = performance change per unit change in temperature-humidity index at THI 75;

Stability A = Absolute value of corresponding performance change (square root transformed) at THI 55;

Stability B = Absolute value of corresponding performance change (square root transformed) at THI 75;

LWG¹ = Live weight gain between birth and weaning, **LWG²**= Live weight gain between weaning and 9 months.

*Parameter is significant at $P < 0.05$

4.4 Discussion

This study set out to investigate the influence of heat stress on growth and to estimate and promote the most resilience phenotypes in sheep reared under an Arid and Semi-Arid environment. The resilience phenotypes developed at different heat loads are a direct indication of how the growth of the animals is influenced by changes in weather. The development of these resilience phenotypes is important for the selection and breeding of animals with the changing weather conditions which is currently being exacerbated by climate change. To develop the resilience phenotypes, random regression models fitted with reaction norms were used. Reaction norms have been used to investigate the milk (Tsartsianidou et al., 2021) and growth (Sánchez-Molano et al., 2020) performance of sheep across different environments. In this study, reaction norms were fitted using a Legendre Polynomial of the second degree based on evaluation of linear and third degree Legendre Polynomial. In the study by (Sánchez-Molano et al., 2020) a linear reaction norm was fitted to evaluate the growth of sheep using air temperature as the environmental variable in a temperate

environment. In this study weather was measured using a Temperature Humidity Index. The type of weather parameters used, and the geographical area of study can have an impact on the type of reaction norm suitable for this type of analyses. The second degree of Legendre Polynomial has the advantage of estimating different slopes therefore developing multiple resilience phenotypes.

This study developed two resilience phenotypes, *Response* and *Stability*, at two different heat loads of heat stress and no heat stress. Both *Response* and *Stability* have a significance in breeding. While *Response* shows the direction and magnitude of live weight relative to the level of heat stress, *Stability* shows how stable the live weight gain is. Therefore, developing a multi-trait selection index, which has both *Response* and *Stability*, and other traits of economic importance would ensure an overall desirable genetic improvement.

Between birth and weaning, there are more factors affecting weight gain than post weaning. In this study, the breed of the animal, sex, season of birth, type of birth, the dam's parity and THI levels significantly affected the live weight gain between birth and weaning. These findings were similarly reported in other studies (Kelman et al., 2022; Goshme et al., 2021; Canaza-Cayo et al., 2015). However, only the breed, sex of the animal and THI levels below 78 significantly affected the post weaning growth. Pre-weaning live weight gain was significantly affected across all THI levels unlike post-weaning live weight gain which was not significantly affected with THI levels more than 78. This could be due to better adaptation of post-weaned animals to withstand higher levels of heat stress compared to pre-weaned animals. Therefore, considering that more fixed effects significantly affect pre-weaning live weight gain more care should be given to lambs from birth to weaning compared to post-weaning to ensure optimum growth. Improving the growth performance pre-weaning is necessary for any successful breeding program and provides a predictor for future animal performance (Sallam et al., 2019).

The integration of temperature and humidity into a Temperature-Humidity Index (THI) provided a more holistic measure of environmental stress, enabling a clearer assessment of its impact on the growth of sheep breeds in a semi-arid environment. With the changing climate, the conservation and selective breeding of climate resilient livestock breeds is one way animal breeders can use to combat the negative effects of climate change on livestock production. Indigenous sheep are one of the most climate resilient livestock breeds, and meat production is one of the important traits to farmers in Arid and Semi-Arid Lands (Ojango et al., 2023; Degen, 2007). Breeding sheep whose growth is more resilient to changes in climate is not only of importance to farmers but also aids in meeting the global demand for meat. To

identify sheep breeds that are more climate resilient for a particular trait of importance, it is critical to know the THI values above which the breed begins to experience stress. In this study, THI affected the growth of the different sheep breeds at different points ranging from 77.92 to 78.75. In Spanish Murciano-Granadina dairy goats, a THI above 77 potentially induced moderate heat stress whereas THI above 85 was considered as severe heat stress (Hamzaoui et al., 2013). A 6% reduction in milk yield was found in Alpine goats in Brazil when exposed to THI above 80 (Brasil et al., 2000).

The high THI threshold (78.75) for in live weight gain observed in the pure Red Maasai is an indication of better resilience for growth compared to other breeds in this study. However, the F1 (DDRR) had the lowest decline rate for live weight per unit increase in THI amongst all the breeds. This could be due to the high levels of heterosis associated with F1 generations. Heterosis (or 'hybrid vigour') is the superiority of first cross sheep over the mean of the two parental breeds. Heterosis has been shown to have a favourable impact on fitness and production traits in sheep (Quan et al., 2025), cattle (Bunning et al., 2019), chickens (Dzungwe et al., 2024) and pigs (Iversen et al., 2019). On the other hand, the DDDR breed had the lowest THI threshold and the highest growth decline rate. This could be attributed to recombination losses due to dilution of the local adapted genetics of the Red Maasai with exotic genetics from the less well adapted Dorper. This divergence in THI thresholds underscores the importance of within-breed selection and management, particularly in regions where climate change is expected to exacerbate heat stress conditions.

The development of novel resilience phenotypes, such as the slope of reaction norms across THI gradients, offers a promising avenue for breeding more adaptable sheep populations. These resilience phenotypes can be incorporated into breeding objectives to enhance the sustainability of sheep production systems. The reaction norms for the different breeds showed a general decline in growth below and above the THI threshold. Three resilience phenotypes were estimated for this population at THI 70 and THI 85. These resilience phenotypes were a) slope - which gives an indication of directional response of the change in weight with changing THI and b) absolute - which gives the stability of growth performance with changing THI. A slope of 0 indicates that the animal's growth are not influenced by changing in THI while a slope below 0 indicates that the animals growth is negatively influenced by changes in THI. In this study, slope 0 was found between THI 75 and 78. Hence, between these THI levels the growth of most of the sheep was not affected. In this population, the sheep had a negative response in growth at THI 85 and a positive response to growth at THI 70. This is a direct indication on the effect of heat stress on growth.

With regards to the season of birth, the stability of the animals' growth was negatively influenced at both THI 70 and 85 if the animal was born during the dry season. In this study area, the natural pastures used for grazing sheep vary in quality and quantity with the seasons. During the dry seasons, the quality and quantity of pasture is poor and therefore the ewes are likely not to get enough nutrition hence affecting the quality and quantity of milk they produce. This in turns affects the pre-weaning growth of lambs which eventually their growth performance for the rest of their lives. Additionally, during the dry seasons the ambient temperatures are high, and this results in reduced feed intake due to both direct and indirect effects of heat stress on the animal (Renaudeau et al., 2012). The reduced feed intake during hot weather is widely regarded as an adaptation to reduce metabolic heat production in animals (Lin et al., 2006; West, 2003). When feed intake of ewes is reduced, milk production will also be affected and so will the growth performance of lambs pre-weaning. This could be the reason for the unstable post-weaning growth performance of lambs born during the dry season regardless of the THI levels. To manage this situation, feeding modifications should be adopted to make sure the animals have feeds that satisfy their nutritional needs during heat stress. Studies in several species have shown that increasing the energy content of the diet via lipid addition can partially overcome the effect of heat stress (Attia et al., 2020; Renaudeau, 2010; Dean et al., 2006). Depending on the species and physiological stage of animals, the metabolic, physiological and immunological disturbances induced by heat strain must also be addressed through vitamins and mineral supplementation to aid in good animal performance (Liu et al., 2016; Ghazi Harsini et al., 2012).

The heritability estimates for the resilience phenotypes were moderate and significantly different from zero implying that there is a substantial genetic variation in the animal's capacity to cope with changes in environmental heat load therefore genetic selection for improved growth performance in heat-stressed environments is feasible. Generally, the heritability estimates for fitness related traits such as resilience are considerably low (Kruuk et al., 2000). Notably the heritability estimates for *Stability* were higher than for *Response*. The genetic correlation between *Response* and *Stability* traits, at the same THI level, were positive and very strong. This implies that animals with negative response in growth at a given THI will not have a stable growth while animals with a positive response to growth will have a stable growth. On the other hand, the strong and antagonistic genetic correlation between two the resilience phenotypes at THI 70 and THI 85 implies that the genetic control mechanism under heat-stress environments is also involved in no-heat-stress environments. Animals that respond better and are more stable in heat-stress environments will perform poorly in no-

heat-stress environments. In this study, only the genetic correlations between the resilience phenotypes at THI 70 and pre-weaning live weight gain were significantly different from zero. This means that the heat stress affects younger animals more than older animals. Younger animals are more vulnerable to weather changes thereby affecting their welfare and pre-weaning weights (Sánchez-Molano et al., 2020; Karakuş, 2014). Care should therefore be given to young lambs to avoid the negative effects of heat stress on the birth and weaning weights of the lambs.

4.5 Conclusion

The identification of breed-specific THI thresholds, coupled with the development of resilience phenotypes and estimation of genetic parameters, provides a strong foundation for breeding more adaptable and sustainable sheep populations. The genetic parameters estimated prove the existence of genetic control in sheep for growth and resilience. With the changing weather, this genetic control of growth and resilience should be further explored by including resilience phenotypes in a multi-trait selection index for improved growth performance, especially for birth and weaning weights under heat-stress environments. Breeding for resilience not only addresses the immediate challenges of heat stress but also contributes to the long-term sustainability of livestock systems. Moreover, the integration of genomic tools, such as genome-wide association studies and genomic selection, could accelerate the identification and selection of animals with desirable resilience traits. Intervention measures in feeding and shelter provision especially for lactating ewes and pre-weaned lambs should be incorporated into the management practices to reduce the effect of heat stress on the growth of young lambs. In a crossbreeding program between indigenous and exotic sheep breeds, the proportion of the breeds in the crossbreds should be considered as it affects their growth performance under heat stress.

Ethics approval

Not applicable

Declaration of generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence assisted technologies in the writing process

Authors ORCIDs

E Oyieng: <https://orcid.org/0000-0002-5004-2060>

J M K Ojango: <https://orcid.org/0000-0003-0224-5370>

M Gauly: <https://orcid.org/0000-0003-4212-5437>

C.C. Ekine-Dzivenu: <https://orcid.org/0000-0002-8526-435X>

R. Oloo: <https://orcid.org/0000-0002-6004-3729>

E. Clark: <https://orcid.org/0000-0002-9550-7407>

R Mrode: <https://orcid.org/0000-0003-1964-5653>

S König: <https://orcid.org/0000-0003-4226-3696>

Declaration of interest

None

Data availability statement

None of the data was deposited in an official repository. This can be made available upon request to the corresponding author

Acknowledgement

The authors would like to thank the Kapiti Research Station and Wildlife conservancy of International Livestock Research Institute (ILRI) for providing the data. Our deepest gratitude goes to James Audho, Winfred Sila and Elias Mwarome Mwazonga who were responsible for managing the flock and ensuring timely and accurate data collection.

Author contributions

E Oyieng: Conceptualization, data curation, formal analysis, methodology, software, Writing - original draft, writing - reviewing and editing,

J M K Ojango: Conceptualization, methodology, Writing – reviewing and editing, supervision

M Gauly: Conceptualization, methodology, Writing – reviewing and editing, supervision

C.C. Ekine-Dzivenu: Methodology, writing - reviewing and editing,

E. Clark: Methodology, writing - reviewing and editing,

R. Oloo: Methodology, writing - reviewing and editing,

R Mrode: Conceptualization, methodology, Writing – reviewing and editing, supervision

S König: Conceptualization, methodology, Writing – reviewing and editing, supervision

Financial Support

The project was supported by the Centre for Tropical Livestock Genetics and Health (CTLGH) Small Ruminant Genomics Programme (<https://www.ctlgh.org/research/small-ruminants-genomics/>) through Roslin Foundation Research Grant Reference: RF2302 – “Building a reference quality annotated genome assembly for Red Maasai sheep as a resource to understand complex traits such as susceptibility to GI helminth infection”. EC, EO and JO

also acknowledge support for the small ruminant programme activities from the Gates Foundation and UK aid from the UK Government's Department for International Development (Grant Agreement OPP1127286) under the auspices of the Centre for Tropical Livestock Genetics and Health (CTLGH), established jointly by the University of Edinburgh, Scotland's Rural College (SRUC), and the International Livestock Research Institute (ILRI).

References

- Attia, Y.A., Bovera, F., Wang, J., Al-Harhi, M.A., Kim, W.K., 2020. Multiple amino acid supplementations to low-protein diets: Effect on performance, carcass yield, meat quality and nitrogen excretion of finishing broilers under hot climate conditions. *Animals* 10, 1–11. doi:10.3390/ani10060973
- Baker, R.L., Mugambi, J.M., J.O, A., Carles, A.B., Thorpe, W., 2004. Genotype by environment interactions for productivity and resistance to gastro-intestinal nematode parasites in Red Maasai and Dorper sheep. *Animal Science* 79, 343–353.
- Berghof, T.V.L., Poppe, M., Mulder, H.A., 2019. Opportunities to improve resilience in animal breeding programs. *Frontiers in Genetics* 10. doi:10.3389/fgene.2018.00692
- Brasil, L.H. de A., Wechesler, F.S., Baccari Júnior, F., Gonçalves, H.C., Bonassi, I.A., 2000. Thermal stress effects on milk yield and chemical composition and thermoregulatory responses of lactating alpine goats. *Revista Brasileira de Zootecnia* 29, 1632–1641.
- Canaza-Cayo, A.W., Huanca, T., Gutiérrez, J.P., Beltrán, P.A., 2015. Modelling of growth curves and estimation of genetic parameters for growth curve parameters in Peruvian young llamas (*Lama glama*). *Small Ruminant Research* 130, 81–89. doi:https://doi.org/10.1016/j.smallrumres.2015.01.026
- Colditz, I.G., Hine, B.C., 2016. Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science*. doi:10.1071/AN15297
- Dash, S., Chakravarty, A.K., Singh, A., Upadhyay, A., Singh, M., Yousuf, S., 2016. Effect of heat stress on reproductive performances of dairy cattle and buffaloes: A review. *Veterinary World*. doi:10.14202/vetworld.2016.235-244
- Dean, D.W., Bidner, T.D., Southern, L.L., 2006. Glycine Supplementation to Low Protein, Amino Acid-Supplemented Diets Supports Optimal Performance of Broiler Chicks. *Poultry Science* 85, 288–296. doi:https://doi.org/10.1093/ps/85.2.288
- Degen, A.A., 2007. Sheep and goat milk in pastoral societies. *Small Ruminant Research* 68, 7–19. doi:10.1016/j.smallrumres.2006.09.020

- FAO, 2021. Food and Agriculture Organization of the United Nations. FAOSTAT Statistical Database.
- Gantner, V., Mijić, P., Kuterovac, K., Solić, D., Gantner, R., 2011. Temperature-humidity index values and their significance on the daily production of dairy cattle. *Mljekarstvo: časopis za naprjeđenje proizvodnje i prerade mlijeka* 61, 56–63.
- Gauly, M., Bollwein, H., Breves, G., Brügemann, K., Dänicke, S., Daş, G., Demeler, J., Hansen, H., Isselstein, J., König, S., Lohölter, M., Martinsohn, M., Meyer, U., Potthoff, M., Sanker, C., Schröder, B., Wrage, N., Meibaum, B., von Samson-Himmelstjerna, G., Stinshoff, H., Wrenzycki, C., 2013. Future consequences and challenges for dairy cow production systems arising from climate change in Central Europe – a review. *Animal* 7, 843–859. doi:<https://doi.org/10.1017/S1751731112002352>
- Ghazi Harsini, S., Habibiyan, M., Moeini, M.M., Abdolmohammadi, A.R., 2012. Effects of Dietary Selenium, Vitamin E, and Their Combination on Growth, Serum Metabolites, and Antioxidant Defense System in Skeletal Muscle of Broilers Under Heat Stress. *Biological Trace Element Research* 148, 322–330. doi:10.1007/s12011-012-9374-0
- Goo, D., Kim, J.H., Park, G.H., Reyes, J.B.D., Kil, D.Y., 2019. Effect of heat stress and stocking density on growth performance, breast meat quality, and intestinal barrier function in broiler chickens. *Animals* 9. doi:10.3390/ani9030107
- Goshme, S., Besufekad, S., Bisrat, A., Abebe, A., 2021. Reproductive and productive performance of Dorper sheep and their crossbreds with local highland sheep at Debre Birhan agricultural research center, Ethiopia. *Livestock Research for Rural Development* 33.
- Gujar, G., Tiwari, M., Yadav, N., Monika, Dr., 2023. Heat stress adaptation in cows – Physiological responses and underlying molecular mechanisms. *Journal of Thermal Biology* 118, 103740. doi:<https://doi.org/10.1016/j.jtherbio.2023.103740>
- Günter, H., Úrsula, B., Spring, O., 2009. UNCCD Report: Securitizing the ground, grounding security.
- Hamzaoui, S., Salama, A.A.K., Albanell, E., Such, X., Caja, G., 2013. Physiological responses and lactational performances of late-lactation dairy goats under heat stress conditions. *Journal of Dairy Science* 96, 6355–6365. doi:<https://doi.org/10.3168/jds.2013-6665>
- Hirakawa, R., Nurjanah, S., Furukawa, K., Murai, A., Kikusato, M., Nochi, T., Toyomizu, M., 2020. Heat Stress Causes Immune Abnormalities via Massive Damage to Effect Proliferation and Differentiation of Lymphocytes in Broiler Chickens. *Frontiers in Veterinary Science* 7.

- Ji, B., Banhazi, T., Perano, K., Ghahramani, A., Bowtell, L., Wang, C., Li, B., 2020. A review of measuring, assessing and mitigating heat stress in dairy cattle. *Biosystems Engineering* 199, 4–26. doi:<https://doi.org/10.1016/j.biosystemseng.2020.07.009>
- Karakuş, F., 2014. Weaning stress in Lambs. *Agriculture and Food* 2, 165–170.
- Kelman, K.R., Alston-Knox, C., Pethick, D.W., Gardner, G.E., 2022. Sire Breed, Litter Size, and Environment Influence Genetic Potential for Lamb Growth When Using Sire Breeding Values. *Animals* 12. doi:10.3390/ani12040501
- King, A.D., Karoly, D.J., Henley, B.J., 2017. Australian climate extremes at 1.5 °C and 2 °C of global warming. *Nature Climate Change* 7, 412–416. doi:10.1038/nclimate3296
- KNBS, 2019. Kenya Census Report.
- Kruuk, B., Loeske, E., Clutton-Brock, T.H., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F.E., 2000. Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences*.
- Kumar, D., Yadav, B., Choudhury, S., Kumari, P., Madan, A.K., Singh, S.P., Rout, P.K., Ramchandran, N., Yadav, S., 2018. Evaluation of adaptability to different seasons in goat breeds of semi-arid region in India through differential expression pattern of heat shock protein genes. *Biological Rhythm Research* 49, 466–478. doi:10.1080/09291016.2017.1377984
- Lin, H., Jiao, H.C., Buysse, J., Decuypere, E., 2006. Strategies for preventing heat stress in poultry. *World's Poultry Science Journal* 62, 71–86. doi:DOI: 10.1079/WPS200585
- Liu, F., Cottrell, J.J., Furness, J.B., Rivera, L.R., Kelly, F.W., Wijesiriwardana, U., Pustovit, R. V., Fothergill, L.J., Bravo, D.M., Celi, P., Leury, B.J., Gabler, N.K., Dunshea, F.R., 2016. Selenium and vitamin E together improve intestinal epithelial barrier function and alleviate oxidative stress in heat-stressed pigs. *Experimental Physiology* 101, 801–810. doi:10.1113/EP085746
- Mehaisen, G.M.K., Desoky, A.A., Sakr, O.G., Sallam, W., Abass, A.O., 2019. Propolis alleviates the negative effects of heat stress on egg production, egg quality, physiological and immunological aspects of laying Japanese quail. *PLOS ONE* 14, e0214839.
- Milne, C., 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. doi:[https://doi.org/10.1016/S0921-4488\(99\)00154-6](https://doi.org/10.1016/S0921-4488(99)00154-6)
- Mugambi, J.M., Audho, J.O., Baker, R.L., 2005. Evaluation of the phenotypic performance of a Red Maasai and Dorper double backcross resource population: natural pasture challenge with gastro-intestinal nematode parasites. *Small Ruminant Research* 56, 239–251. doi:<https://doi.org/10.1016/j.smallrumres.2004.06.003>

- Mulder, H.A., 2016. Genomic selection improves response to selection in resilience by exploiting genotype by environment interactions. *Frontiers in Genetics* 7. doi:10.3389/fgene.2016.00178
- Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livestock Science* 130, 57–69. doi:https://doi.org/10.1016/j.livsci.2010.02.011
- NRC, 1971. *Guide to Environmental Research on Animals*. National Academy of Sciences, Washington, DC.
- Ojango, J.M.K., Audho, J., Oyieng, E., Recha, J., Okeyo, A.M., Kinyangi, J., Muigai, A.W.T., 2016. System characteristics and management practices for small ruminant production in “Climate Smart Villages” of Kenya 1–10. doi:10.1017/S2078633615000417
- Ojango, J.M.K., Okpeku, M., Osei-Amponsah, R., Kugonza, D.R., Mwai, O., Changunda, M.G.G., Olori, V.E., 2023. Dorper sheep in Africa: A review of their use and performance in different environments. *CABI Reviews* 18, 0042. doi:10.1079/cabireviews.2023.0042
- Oloo, R.D., Ekine-Dzivenu, C.C., Mrode, R., Bennewitz, J., Ojango, J.M.K., Kipkosgei, G., Gebreyohanes, G., Okeyo, A.M., Chagunda, M.G.G., 2024. Genetic analysis of phenotypic indicators for heat tolerance in crossbred dairy cattle. *Animal* 18. doi:10.1016/j.animal.2024.101139
- Oluwagbenga, E.M., Tetel, V., Schober, J., Fraley, G.S., 2022. Chronic heat stress part 1: Decrease in egg quality, increase in cortisol levels in egg albumen, and reduction in fertility of breeder pekin ducks. *Frontiers in Physiology* 13.
- Oyieng, E., Mrode, R., Ojango, J.M.K., Ekine-Dzivenu, C.C., Audho, J., Okeyo, A.M., 2022. Genetic parameters and genetic trends for growth traits of the Red Maasai sheep and its crosses to Dorper sheep under extensive production system in Kenya. *Small Ruminant Research* 206, 106588. doi:10.1016/j.smallrumres.2021.106588
- Oyieng, E., Ojango, J., Audho, J., Gitau, J., Gachora, J., 2021. Improving small ruminant productivity in pastoral systems of Kenya. Nairobi, Kenya.
- Oyieng, E., Ojango, J.M.K., Gauly, M., Mrode, R., Dooso, R., Okeyo, A.M., Kalinda, C., König, S., 2025. Evaluating reproduction traits in a crossbreeding program between indigenous and exotic sheep in semi-arid lands. *Animal* 19. doi:10.1016/j.animal.2024.101391
- Pinto, S., Hoffmann, G., Ammon, C., Amon, T., 2020. Critical THI thresholds based on the physiological parameters of lactating dairy cows. *Journal of Thermal Biology* 88, 102523. doi:https://doi.org/10.1016/j.jtherbio.2020.102523

- Polsky, L., von Keyserlingk, M.A.G., 2017. Invited review: Effects of heat stress on dairy cattle welfare. *Journal of Dairy Science* 100, 8645–8657. doi:10.3168/jds.2017-12651
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renaudeau, D., 2010. Nutrition of the lactating sows in hot conditions.
- Renaudeau, D., Collin, A., Yahav, S., De Basilio, V., Gourdine, J.L., Collier, R.J., 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. In *Animal*. pp. 707–728. doi:10.1017/S1751731111002448
- Rojas-Downing, M.M., Nejadhashemi, A.P., Harrigan, T., Woznicki, S.A., 2017. Climate change and livestock: Impacts, adaptation, and mitigation. *Climate Risk Management* 16, 145–163. doi:https://doi.org/10.1016/j.crm.2017.02.001
- Rust, J.M., Rust, T., 2013. Climate change and livestock production: A review with emphasis on Africa. *South African Journal of Animal Science* 43, 256–267. doi:10.4314/sajas.v43i3.3
- Sallam, A.M., Ibrahim, A.H., Alsheikh, S.M., 2019. Estimation of genetic parameters and variance components of pre-weaning growth traits in Barki lambs. *Small Ruminant Research* 173, 94–100. doi:https://doi.org/10.1016/j.smallrumres.2018.11.027
- Sánchez-Molano, E., Kapsona, V. V., Oikonomou, S., McLaren, A., Lambe, N., Conington, J., Banos, G., 2020. Breeding strategies for animal resilience to weather variation in meat sheep. *BMC Genetics* 21. doi:10.1186/s12863-020-00924-5
- Schmid, M., Imort-Just, A., Emmerling, R., Fuerst, C., Hamann, H., Bennewitz, J., 2021. Genotype-by-environment interactions at the trait level and total merit index level for milk production and functional traits in Brown Swiss cattle. *Animal* 15, 100052. doi:https://doi.org/10.1016/j.animal.2020.100052
- Serrano, J.O., Mayea, A.L., Villares-Garachana, A., Correa-Herrera, N., González-Morales, A., Pérez-Bonachea, L., Hernández, L., Lorente, G., Hajari, E., Fonseca-Fuentes, N., Martínez-Melo, J., Lorenzo, J.C., 2022. Effect of short-term radiation stress on physiological and hematological parameters in Pelibuey sheep in Cuba. *Small Ruminant Research* 210, 106679. doi:https://doi.org/10.1016/j.smallrumres.2022.106679
- Serrano, J.O., Villares, A., Manuel-Malamba, F.D., Martínez-Melo, J., Mazorra, C., Borroto, Á., Hajari, E., Fonseca-Fuentes, N., Lorenzo, J.C., 2021. Euclidean distance: Integrated criteria to study sheep behaviour under heat stress. *Notulae Scientia Biologicae* 13. doi:10.15835/nsb13110859

- Shi, R., Brito, L.F., Liu, A., Luo, H., Chen, Z., Liu, L., Guo, G., Mulder, H., Ducro, B., van der Linden, A., Wang, Y., 2021. Genotype-by-environment interaction in Holstein heifer fertility traits using single-step genomic reaction norm models. *BMC Genomics* 22. doi:10.1186/s12864-021-07496-3
- Srivastava, A., Yadav, P., Mahajan, A., Anand, M., Yadav, S., Madan, A.K., Yadav, B., 2021. Appropriate THI model and its threshold for goats in semi-arid regions of India. *Journal of Thermal Biology* 96. doi:10.1016/j.jtherbio.2021.102845
- Tsartsianidou, V., Kapsona, V.V., Sánchez-Molano, E., Basdagianni, Z., Carabaño, M.J., Chatziplis, D., Arsenos, G., Triantafyllidis, A., Banos, G., 2021. Understanding the seasonality of performance resilience to climate volatility in Mediterranean dairy sheep. *Scientific Reports* 11. doi:10.1038/s41598-021-81461-8
- West, J.W., 2003. Effects of Heat-Stress on Production in Dairy Cattle. *Journal of Dairy Science* 86, 2131–2144. doi:[https://doi.org/10.3168/jds.S0022-0302\(03\)73803-X](https://doi.org/10.3168/jds.S0022-0302(03)73803-X)

CHAPTER 5: GENERAL DISCUSSION

5.1 Reproduction efficiency

The reproductive performance of sheep is one of the main factors on which the efficiency of meat production systems depends. Frequently used indicators of the reproductive performance of sheep include age at first lambing, lambing interval, conception rates, and lambs weaned per ewe per year. Fertility management improves farms overall efficiency of the ewe by increasing the number of lambs per ewe year. Fertility management is first and foremost done by selecting replacement ewe lambs that have a proven genetic potential in the indicator of interest.

Age at first lambing (AFL) significantly influences sheep productivity, affecting milk yield, lactation length, and reproductive efficiency. For instance, in Istrian sheep under semi-intensive management, early lambing (10-17 months) shortens lactation but maintains milk yield, suggesting benefits for reducing non-productive phases (Kasap et al., 2021). Lacaune dairy sheep under intensive systems show an optimal AFL range (391-450 days) for maximizing lifetime milk production and lactations, with deviations leading to lower yields (Hernandez et al., 2011). Different breeds exhibit varied AFL, influenced by genetics and environment. African breeds like Damara have an AFL of about 17 months, while studies suggest Wollo and Begait may have earlier lambing of 12-13 months for similar breeds (Lijalem M and Zereu H, 2024). Management practices, especially in sub-Saharan Africa's Arid (SSA) and Semi-Arid Lands (ASAL), also play a role, with traditional systems often favouring natural breeding cycles. Farmers should consider breed, management intensity, and ewe condition when deciding AFL. Early lambing can increase genetic gain and ewe production efficiency, but ensuring adequate nutrition and health is crucial to avoid negative impacts. Breed-specific strategies should be considered to balance productivity and ewe longevity.

Lambing interval, defined as the time between two consecutive lambings in a ewe, is a critical reproductive trait in sheep production, influencing fertility, lambing rates, and overall flock productivity. Studies show genetics, nutrition, and environmental conditions like heat stress impact lambing interval (Balehegn et al., 2021). For example, better nutrition can shorten intervals by improving ewe fertility, while heat stress may lengthen them, reducing reproductive efficiency. In sub-Saharan Africa, intervals often exceed 12 months due to seasonal breeding and nutritional constraints, with breeds like Damara showing adaptations to longer intervals (Tesema et al., 2020b). Studies show that sheep flock reared in harsh

environment like in ASALs areas are too late to start lambing and this lengthens their lambing intervals (Kao et al., 2022).

Heritability estimates for reproduction traits such as AFL and lambing interval are usually low, meaning that they are mostly affected by environmental factors. Strategies that farmers can use to optimize AFL and lambing interval to maximize sheep productivity include nutritional management, breeding practices and health care.

5.2 Pre- and post-weaning lamb survival

Lamb survival, pre and post weaning, directly impacts flock productivity and economic sustainability. Lamb survival is influenced by genetics, environmental and ewe-related factors. Genetic factors such as breed and sex of the lamb affect pre-weaning survival as shown by moderate heritability estimates and male lambs generally having lower survival rates. Environmental factors play a crucial role in pre-weaning lamb survival. Birth weight is a key predictor, with low-birth-weight lambs at higher risk of mortality. Litter size also affects survival, with lambs from multiple births (twins, triplets) often having lower rates due to smaller individual weights and increased competition for maternal resources. The nutritional status of the ewe during pregnancy and lactation significantly affects lamb survival. Ewes in good body condition at lambing produce healthier, heavier lambs with better survival prospects. For good lamb survival, the dam's ability to give birth to live lambs without complications and to provide adequate mothering, colostrum and milk supply is obviously crucial. Colostrum quality and quantity are critical for providing lambs with essential antibodies and nutrients, enhancing their immune system and survival chances (Brien et al., 2014). Infections and parasites are major causes of pre-weaning lamb mortality. Above all, ensuring that lambs receive colostrum within the first few hours after birth, providing adequate shelter, and monitoring for health issues can significantly improve survival rates.

Achieving ongoing genetic gains from selection relies on the existence of additive genetic variation, which is most readily exploited within breed, although between breed variation may also be tapped in breeding programs. Exploitation of non-additive genetic variation through crossbreeding is also a possibility. Exploiting hybrid vigour on an ongoing basis requires planned crossbreeding programs that do not suit all production systems. Further, the performance of crosses is ultimately influenced by the genetic merit of the contributing breeds, so a genetic improvement program involving within breed selection for lamb survival as part of a multi-trait breeding objective is likely to be a critical component of achieving longer-term genetic gain. Despite low heritability for lamb survival, modest rates of response

to selection may be achievable, since variation, selection intensity and generation interval are also factors determining genetic gain.

5.3 Ewe's length of productive life

Ewe longevity refers to how long a female sheep remains productive, typically measured by the number of years she can lamb and raise offspring. Ewe longevity is a critical economic factor in sheep farming, as it affects the number of lambings and the overall productivity of the flock. Factors that affect ewe longevity include genetics, early productivity with ewes with balanced early productivity tend to live longer, while extremes can lead to culling and management such as proper nutrition and disease control. Ewe longevity has long been regarded by sheep breeders as an economically important trait in a breeding ewe flock, due to the potential to reduce culling rates and female replacement costs. The ability to identify ewes that are able to outperform their contemporaries, in terms of how long they remain productive in the flock, will help towards improving flock efficiency and profitability. Fewer unproductive animals on farm will also reduce greenhouse gases emissions per kilogram of lamb produced, providing an additional environmental benefit.

Early productivity, particularly the number of lambs born in the first few years, plays a significant role in ewe longevity. The number of lambs born in years 2 and 3 has been found to result in maximum expected stay ability to various ages, 3.9 to 4.2 years in highly variable environments and 4.5 to 4.7 years in moderate environments (Douhard et al., 2016). High prolific ewes have low rearing ability, meaning they might not raise all their lambs, leading to premature culling, while low early productivity leads to early culling due to poor performance (Keady and Hanrahan, 2022). This trade-off highlights that both extremes can reduce longevity. Management practices are crucial for maximizing ewe longevity. Proper nutrition, disease control, and appropriate pasture management can extend productive life. For example, ensuring ewes have adequate body condition scores at lambing can improve their ability to rear lambs and stay in the flock longer. The specific production system and environmental conditions also affect ewe longevity. In extensive systems, ewes might face harsher conditions, potentially reducing longevity, while intensive systems with better management can extend it (Douhard et al., 2016).

5.4 Breeding for heat tolerance

Livestock production in tropical and subtropical regions is vital for global food security, providing meat, milk, and other products. However, these areas face numerous challenges,

with the climatic environment being a primary limiting factor. Heat stress, caused by high temperatures and humidity, is a significant concern, reducing animal productivity through impacts on growth, reproduction, and health. Global average surface temperature are predicted to increase by 1.8°C to 4.0°C by 2100 (Calvin et al., 2023), exacerbating these issues, especially as world population and food demand grow rapidly. Heat stress causes deleterious effects on welfare, immunology and physiology of the animal, shifting metabolic priorities away from production, growth, health, and reproduction hence impacting productivity (Oke et al., 2021).

Animals in outdoor environments face a complex climate where just knowing the air temperature isn't enough. Other factors like humidity, solar radiation, and wind speed also matter. The impact of heat stress can be assessed directly from physiological measurements (rectal, cloacal and skin temperatures, respiratory rate, panting and heat production) or indirectly from animal performance (growth rate, egg and milk production) that are related to the animal's ability or inability to efficiently cope with heat stress (Renaudeau et al., 2012). Heat stress makes animals eat less, which hurts their productivity and health, leading to less meat, milk, and eggs because they get less energy and nutrients. Additionally, when it's hot or cold, animals adjust their bodies to stay cool or generate heat to maintain normal body temperature, and this can reduce their performance. Animals living in Arid and Semi-Arid Lands (ASAL) face tough conditions like heat and drought and therefore need to be genetically adapted and resilient to the environment. One way of identifying resilient animals is through reaction norm analysis. Reaction norm analysis looks at how different genotypes perform under varying environments of heat stress as measured by the Temperature-Humidity Index (THI). In this type of analysis, the Estimated Breeding Value (EBV) has two parts: The slope of the reaction norm which indicates how animal performance responds to environmental shifts and the absolute value of the slope of the reaction norm measures the stability of performance under changing environments.

Growth is controlled genetically and environmentally. Environmentally, nutrients, hormones and enzymes, as well as heat stress are some of the factors that can influence growth. Exposure of sheep to elevated temperatures results in a decrease in growth (Marai et al., 2007; Abdel-Hafez, 2002). The decrease in growth is mainly because they don't get enough energy from food, especially metabolizable energy, needed for growth and maintenance. It is therefore important to include resilience phenotype in the breeding goal. Failing to include resilience in the breeding goal would result in losses in the growth potential of lambs amounting to 4–5% per 1 °C of air temperature change (Sánchez-Molano et al., 2020). When

breeding animals, it's essential to consider the predicted intensity and trend of climate change in a specific region, especially when incorporating resilience traits into breeding programs. If the slope is positive, it means the animal performs better as heat stress rises but struggles when temperatures drop. If the absolute slope is close to zero, the animal's performance remains consistent regardless of heat stress fluctuations. If the primary goal is to select animals that thrive better with increasing heat stress, selecting animals with positive slopes may be more effective but if the goal is select animals in an unpredictable weather, choosing animals with slopes near zero could be more beneficial.

5.5 Recommendations

Reducing the age at first lambing and lambing interval in the population will increase the reproduction efficiency of the flock. Through proper management in feeding and health, hoggets can be first mated at 6 - 7 months instead of 9 months as practiced in the farm. This will significantly reduce the age of first lambing. However, this study found out that ewes' length of productive life has an antagonistic relationship with age at first lambing. Therefore, ewes longevity should be selected based on individual animals estimated breeding values for longevity. Lambing interval had very low heritability and therefore selection for reduced lambing interval cannot achieve the desired outcome. However, with proper management of the ewes through proper feeding, health, shortening the period of exposing ewes to rams after they have weaned their lambs and culling unproductive ewes, the lambing interval can be reduced.

Lamb survival pre-weaning is important for the sustainability of the flock. Pre-weaning lamb survival is greatly influenced by ewes mothering ability. Pre-weaning survival had a moderate heritability and therefore selection of animals can be done using estimated breeding values which is also a reflection of ewes with good mothering ability. Post-weaning survival is greatly influenced by environmental factors and therefore it can be increased through good management practices.

With the changing climate, the effect of cold and heat stress on the growth of the sheep cannot be ignored. As shown in this study, the growth of the sheep is negatively affected by heat stress at different points for each breed. With the estimated breeding values and moderate heritability estimates, animals can be selected for cold or heat tolerance in this population depending on the direction of climate change.

Considering that the traits studied here are all of importance in this population, a selection index that in-cooperates growth, pre-weaning lambing lamb survival, ewes' longevity and heat

tolerance should be developed. Improved management of lambs depending on their sex, season of birth and birth weight should be adopted by the farm management to increase pre- and post-weaning survival rates. The Red Maasai sheep is valuable for its tolerance to drought, resistance to diseases, and for its high cultural value. The purebred sheep among commercial farms are, however, few compared to how it used to be. A breeding strategy for the Red Maasai needs to be established in order to conserve the breed to avoid further decline in numbers. Additionally, more concerted efforts need to be put in place to assemble genomes for the indigenous breeds in sub-Saharan Africa to accelerate their genomic selection, characterize and conserve their genetic diversity amid climate change and understand their genetic mechanisms to heat tolerance.

5.6 Future considerations

Sub-Saharan Africa (SSA) possesses a diverse array of indigenous sheep genetic resources, which over time adapted to thrive in challenging environmental conditions. These indigenous breeds are frequently considered to have limited genetic potential and are commonly replaced by exotic breeds via haphazard crossbreeding without clear breeding objectives. While enhancing sheep performance is possible through better management and nutrition, genetic improvement—though gradual—offers a more effective and enduring approach to boosting the overall productivity of the system. Community based breeding programs (CBBPs) carried out at farm level with the full involvement of farmers from the development of breeding objectives, selection, breeding, monitoring and evaluation have proven to be more efficient than national or regional breeding programs. CBBPs are therefore more sustainable in the long term because they are less dependent from external inputs, they are designed according to the needs of the farmers, and the technical and logistical management is at the level which farmers feel comfortable with. CBBPs have proven to be successful in the genetic improvement while conserving indigenous breeds *in situ*. *In situ* conservation is usually recommended for breeds which have a significant contribution to the current and future food production. This method of conservation, in comparison with *ex situ*, allows breeds to continue improving in the changing production environment while maintaining the socio-economic and cultural roles of the breed.

Heat stress cannot be totally eliminated by management practices aimed at alleviating heat load. In addition, these practices are for most part quite expensive and not economically or technically feasible for small-scale farmers and pastoralist. Consequently, breeding for heat tolerance, could be the most cost-effective approach for mitigating heat stress. Improving

animal adaptation to heat stress can be achieved either by selection in stressed conditions or by introgressing 'heat adaptation' genes from a local breed into a commercial breed. The high heat tolerance of tropical local breeds is generally correlated with their small size, their low-production level and some special morphological traits (properties of the skin or hair, sweating capacity, tissue insulation, special appendages) compared with mainstream breeds and commercial lines. When compared in similar experimental conditions, the productivity of indigenous tropical breeds is generally lower than that of exotic livestock breeds. However, in very harsh conditions (hot climate and/or poor nutritional resources or livestock management), the use of indigenous breeds would likely be most successful in improving production levels. The thermal tolerance of local breeds can be utilized by crossbreeding commercial breeds with an exotic breed in order to improve performance level by taking advantage of specific abilities.

5.7 Conclusions

The future of small ruminants production, and its contributing role in global food production, will become more apparent in coming decades due to predicted extremes of climate and a growing human population. Sheep are key components of smallholder production systems in Arid and Semi-Arid areas and need to be selectively bred and conserved. Improving ewe reproductivity, lamb survival and good growth rates in the midst of heat stress requires selective breeding strategies and context-specific management practices. Genotype by environment interaction in reproduction traits, lamb survival and ewe longevity, and heat tolerance was shown in this study. These differences should be taken into consideration when developing breeding objectives for within breed selection and crossbreeding programs between the Red Maasai and Dorper breeds. With the possibility of developing resilience phenotypes for growth and the existence of genetic variability between and within breeds, it is feasible to select for animals with good growth rates under heat stress. Ensuring better nutrition by improving pastures and providing feed supplements which ensure ewes and lambs get enough nutrients is crucial for better survival, and optimal reproductive and growth performance. Additionally, enhancing animal health care through better diagnostics and training farmers to control diseases can reduce pre-weaning lamb mortality. Environmental management through improved housing and cooling systems can also alleviate heat stress in the animals.

References

- Abdel-Hafez, M.A.M., 2002. Studies on reproductive performance in sheep. PhD Thesis, Zagazig University, Zagazig, Egypt.
- Baker, R.L., Mugambi, J.M., J.O. A., Carles, A.B., Thorpe, W., 2004. Genotype by environment interactions for productivity and resistance to gastro-intestinal nematode parasites in Red Maasai and Dorper sheep. *Animal Science* 79, 343–353.
- Balehgn, M., Kebreab, E., Tolera, A., Hunt, S., Erickson, P., Crane, T.A., Adesogan, A.T., 2021. Livestock sustainability research in Africa with a focus on the environment. *Animal Frontiers* 11, 47–56. doi:10.1093/af/vfab034
- Beauchemin, K.A., McAllister, T.A., McGinn, S.M., 2009. Dietary mitigation of enteric methane from cattle. *CABI Reviews* 1–18. doi:10.1079/PAVSNR20094035
- Bell, M.J., Wall, E., Simm, G., Russell, G., 2011. Effects of genetic line and feeding system on methane emissions from dairy systems. *Animal Feed Science and Technology* 166–167, 699–707. doi:https://doi.org/10.1016/j.anifeedsci.2011.04.049
- Brien, F.D., Cloete, S.W.P., Fogarty, N.M., Greeff, J.C., Hebart, M.L., Hiendleder, S., Edwards, J.E.H., Kelly, J.M., Kind, K.L., Kleemann, D.O., Plush, K.L., Miller, D.R., 2014. A review of the genetic and epigenetic factors affecting lamb survival. *Animal Production Science*. doi:10.1071/AN13140
- Butler, D.G., Cullis, B.R., Gilmour, A.R., Gogel, B.J., Thompson, R., 2018. ASReml-R Reference Manual Version 4.2. VSN International Ltd., Hemel Hempstead, HP2 4TP, UK.
- Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Jotzo, F., Krug, T., Lasco, R., Lee, Y.-Y., Masson-Delmotte, V., Meinshausen, M., Mintenbeck, K., Mokssit, A., Otto, F.E.L., Pathak, M., Pirani, A., Poloczanska, E., Pörtner, H.-O., Revi, A., Roberts, D.C., Roy, J., Ruane, A.C., Skea, J., Shukla, P.R., Slade, R., Slangen, A., Sokona, Y., Sörensön, A.A., Tignor, M., van Vuuren, D., Wei, Y.-M., Winkler, H., Zhai, P., Zommers, Z., Hourcade, J.-C., Johnson, F.X., Pachauri, S., Simpson, N.P., Singh, C., Thomas, A., Totin, E., Alegría, A., Armour, K., Bednar-Friedl, B., Blok, K., Cissé, G., Dentener, F., Eriksen, S., Fischer, E., Garner, G., Guivarch, C., Haasnoot, M., Hansen, G., Hauser, M., Hawkins, E., Hermans, T., Kopp, R., Leprince-Ringuet, N., Lewis, J., Ley, D., Ludden, C., Niamir, L., Nicholls, Z., Some, S., Szopa, S., Trewin, B., van der Wijst, K.-I., Winter, G., Witting, M., Birt, A., Ha, M., 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment

- Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. doi:10.59327/IPCC/AR6-9789291691647
- Cassandro, M., 2020. Animal breeding and climate change, mitigation and adaptation. *Journal of Animal Breeding and Genetics* 137, 121–122. doi:<https://doi.org/10.1111/jbg.12469>
- Cloete, S.W.P., Snyman, M.A., Herselman, M.J., 2000. Productive performance of Dorper sheep. *Small Ruminant Research* 36, 119–135. doi:[https://doi.org/10.1016/S0921-4488\(99\)00156-X](https://doi.org/10.1016/S0921-4488(99)00156-X)
- Cloete, S.W.P., Thutwa, K., Scholtz, A.J., Cloete, J.J.E., Dzama, K., Gilmour, A.R., van Wyk, J.B., 2021. Breed effects and heterosis for weight traits and tick count in a cross between an indigenous fat-tailed and a commercial sheep breed. *Tropical Animal Health and Production* 53, 165. doi:10.1007/s11250-021-02612-7
- Da Silva, A., Ahbara, A., Baazaoui, I., Jemaa, S. Ben, Cao, Y., Ciani, E., Dzomba, E.F., Evans, L., Gootwine, E., Hanotte, O., Harris, L., Li, M.-H., Mastrangelo, S., Missohou, A., Molotsi, A., Muchadeyi, F.C., Mwacharo, J.M., Tallet, G., Vernus, P., Hall, S.J.G., Lenstra, J.A., 2025. History and genetic diversity of African sheep: Contrasting phenotypic and genomic diversity. *Animal Genetics* 56, e13488. doi:<https://doi.org/10.1111/age.13488>
- De Vries, J., 2008. Goats for the poor: Some keys to successful promotion of goat production among the poor. *Small Ruminant Research* 77, 221–224. doi:10.1016/j.smallrumres.2008.03.006
- de Vries, M., Bokkers, E.A.M., Dijkstra, T., van Schaik, G., de Boer, I.J.M., 2011. Invited review: Associations between variables of routine herd data and dairy cattle welfare indicators. *Journal of Dairy Science* 94, 3213–3228. doi:<https://doi.org/10.3168/jds.2011-4169>
- de Waal, H.O., Combrinck, W.J., 2000. The development of the Dorper, its nutrition and a perspective of the grazing ruminant on veld. *Small Ruminant Research* 36, 103–117. doi:[https://doi.org/10.1016/S0921-4488\(99\)00155-8](https://doi.org/10.1016/S0921-4488(99)00155-8)
- Douhard, F., Jopson, N.B., Friggens, N.C., Amer, P.R., 2016. Effects of the level of early productivity on the lifespan of ewes in contrasting flock environments. *animal* 10, 2034–2042. doi:<https://doi.org/10.1017/S1751731116001002>
- Enahoro, D., Mason-D’Croz, D., Mul, M., Rich, K.M., Robinson, T.P., Thornton, P., Staal, S.S., 2019. Supporting sustainable expansion of livestock production in South Asia and Sub-Saharan Africa: Scenario analysis of investment options. *Global Food Security* 20, 114–121. doi:<https://doi.org/10.1016/j.gfs.2019.01.001>

- Falconer, D.S., 1996. Introduction to quantitative genetics, 4th Edition. ed. Longman.
- FAO, 2021. Food and Agriculture Organization of the United Nations. FAOSTAT Statistical Database.
- FAO, 2007. The state of the world's animal genetic resources for foos and agriculture. FAO, Rome.
- Fraser, D., Duncan, I.J.H., Edwards, S.A., Grandin, T., Gregory, N.G., Guyonnet, V., Hemsworth, P.H., Huertas, S.M., Huzzey, J.M., Mellor, D.J., Mench, J.A., Špinka, M., Whay, H.R., 2013. General Principles for the welfare of animals in production systems: The underlying science and its application. *The Veterinary Journal* 198, 19–27. doi:<https://doi.org/10.1016/j.tvjl.2013.06.028>
- Gerber, Steinfeld, H., Henderson, B., Mottet, A., Opio, C., Dijkman, J., Falcucci, A., Tempio, G., 2013. Tackling climate change through livestock: a global assessment of emissions and mitigation opportunities.
- Gibson, J.P., Pullin, R.S. V, 2005. Conservation of Livestock and Fish Genetic Resources: Joint Report of Two Studies Commissioned by the CGIAR Science Council. Rome, Italy.
- Goshme, S., Besufekad, S., Bisrat, A., Abebe, A., 2021. Reproductive and productive performance of Dorper sheep and their crossbreds with local highland sheep at Debre Birhan agricultural research center, Ethiopia. *Livestock Research for Rural Development* 33.
- Grossi, G., Goglio, P., Vitali, A., Williams, A.G., 2019. Livestock and climate change: impact of livestock on climate and mitigation strategies. *Animal Frontiers* 9, 69–76. doi:10.1093/af/vfy034
- Haile, A., Getachew, T., Mirkena, T., Duguma, G., Gizaw, S., Wurzinger, M., Soelkner, J., Mwai, O., Dessie, T., Abebe, A., Abate, Z., Jembere, T., Rekik, M., Lobo, R.N.B., Mwacharo, J.M., Terfa, Z.G., Kassie, G.T., Mueller, J.P., Rischkowsky, B., 2020. Community-based sheep breeding programs generated substantial genetic gains and socioeconomic benefits. *Animal* 14, 1362–1370. doi:10.1017/S1751731120000269
- Haile, A., Gizaw, S., Getachew, T., Mueller, J.P., Amer, P., Rekik, M., Rischkowsky, B., 2019. Community-based breeding programmes are a viable solution for Ethiopian small ruminant genetic improvement but require public and private investments. *Journal of Animal Breeding and Genetics* 136, 319–328. doi:<https://doi.org/10.1111/jbg.12401>
- Hernandez, F., Elvira, L., Gonzalez-Martin, J.-V., Gonzalez-Bulnes, A., Astiz, S., 2011. Influence of age at first lambing on reproductive and productive performance of Lacaune dairy

- sheep under an intensive management system. *Journal of Dairy Research* 78, 160–167. doi:DOI: 10.1017/S0022029911000033
- Hristov, A.N., Oh, J., Lee, C., Meinen, R., Montes, F., Ott, T., Firkins, J., Rotz, A., Dell, C., Adesogan, C., 2013. Mitigation of Greenhouse Gas Emissions in Livestock Production— A Review of Technical Options for Non-CO2 Emissions. Food and Agriculture Organization of the United Nations (FAO): Rome, Italy,.
- Kao, M.A., Van Wyk, J.B., Scholtz, A.J., Cloete, J.J.E., Matebesi, P.A., Cloete, S.W.P., 2022. Breed and crossbreeding effects on growth, fitness and reproduction of commercial sheep in South Africa. *Small Ruminant Research* 212, 106705. doi:https://doi.org/10.1016/j.smallrumres.2022.106705
- Kariuki, J., Galie, A., Birner, R., Oyieng, E., Chagunda, M.G.G., Jakinda, S., Milia, D., Ojango, J.M.K., 2022. Does the gender of farmers matter for improving small ruminant productivity? A Kenyan case study. *Small Ruminant Research* 206. doi:10.1016/j.smallrumres.2021.106574
- Kasap, A., Ramljak, J., Mioč, B., Držaić, V., Širić, I., Jurković, D., Špehar, M., 2021. The impact of age at first lambing on milk yield and lactation length in a population of istrian sheep under semi-intensive management. *Animals* 11. doi:10.3390/ani11061604
- Kayigema, V., Rugege, D., 2014. Women’s perceptions of the Girinka (one cow per poor family) programme, poverty alleviation and climate resilience in Rwanda.
- Keady, T.W.J., Hanrahan, J.P., 2022. Effects of Age at First Joining and Ewe Genotype on the Performance of Two-Tooth Ewes and That of Their Progeny to Slaughter. *Animals* 12. doi:10.3390/ani12050653
- Knapp, J.R., Laur, G.L., Vadas, P.A., Weiss, W.P., Tricarico, J.M., 2014. Invited review: Enteric methane in dairy cattle production: Quantifying the opportunities and impact of reducing emissions. *Journal of Dairy Science* 97, 3231–3261. doi:https://doi.org/10.3168/jds.2013-7234
- Kosgey, 2004. Breeding objectives and breeding strategies for small ruminants in the tropics. PhD Thesis, Wageningen University.
- Kosgey, I.S., Okeyo, A.M., 2007. Genetic improvement of small ruminants in low-input, smallholder production systems: Technical and infrastructural issues. *Small Ruminant Research* 70, 76–88. doi:10.1016/j.smallrumres.2007.01.007
- Kwallah, A.B.O., Okeyo, A.M., Mburu, D., Hanotte, O., 2008. Genetic Diversity and Relationships Of Sheep Breeds Of Kenya : Preliminary Results And Evidence of Dilution Of the Indigenous Red Maasai 7–10.

- Lebbie, S.H.B., Yapi-Gnoare, C. V, Rege, J.E.O., Baker, R.L., 1996. Current developments in the management of small ruminant genetic resources: Sub-Saharan Africa. In Of IGA/FAO Round Table On The Global Management of Small Ruminant Genetic Resources. International Goat Association, Beijing, China.
- Lijalem M, T., Zereu H, G., 2024. African sheep review: productivity and reproductive attributes indication. *Journal of Applied Animal Research* 52, 2385040. doi:10.1080/09712119.2024.2385040
- Liljestrand, J., 2012. Breeding practices of Red Maasai sheep in Maasai pastoralist communities. Master Thesis, Swedish University of Agricultural Sciences., Uppsala, Sweden.
- Llonch, P., Haskell, M.J., Dewhurst, R.J., Turner, S.P., 2017a. Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective. *Animal* 11, 274–284. doi:https://doi.org/10.1017/S1751731116001440
- Llonch, P., Haskell, M.J., Dewhurst, R.J., Turner, S.P., 2017b. Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective. *Animal* 11, 274–284. doi:https://doi.org/10.1017/S1751731116001440
- Lwelamira, J., Binamungu, H.K., Njau, F.B., 2010. Contribution of small scale dairy farming under zero-grazing in improving household welfare in Kayanga ward, Karagwe District, Tanzania. *Livestock Research for Rural Development* 22.
- Marai, I.F.M., El-Darawany, A.A., Fadiel, A., Abdel-Hafez, M.A.M., 2007. Physiological traits as affected by heat stress in sheep-A review. *Small Ruminant Research*. doi:10.1016/j.smallrumres.2006.10.003
- Mbuku, S.M., Okeyo, A.M., Kosgey, I.S., Kahi, A.K., 2015. Optimum crossbreeding systems for goats in low-input livestock production system in Kenya. *Small Ruminant Research* 123, 55–61. doi:10.1016/j.smallrumres.2014.10.001
- Milne, C., 2000. The history of the Dorper sheep. *Small Ruminant Research* 36, 99–102. doi:https://doi.org/10.1016/S0921-4488(99)00154-6
- Mohankumar Sajeev, E.P., Winiwarter, W., Amon, B., 2018. Greenhouse Gas and Ammonia Emissions from Different Stages of Liquid Manure Management Chains: Abatement Options and Emission Interactions. *Journal of Environmental Quality* 47, 30–41. doi:https://doi.org/10.2134/jeq2017.05.0199
- Mueller, J.P., Rischkowsky, B., Haile, A., Philipsson, J., Mwai, O., Besbes, B., Valle Zárate, A., Tibbo, M., Mirkena, T., Duguma, G., Sölkner, J., Wurzinger, M., 2015. Community-based

- livestock breeding programmes: essentials and examples. *Journal of Animal Breeding and Genetics* 132, 155–168. doi:<https://doi.org/10.1111/jbg.12136>
- Mugambi, J.M., Audho, J.O., Baker, R.L., 2005. Evaluation of the phenotypic performance of a Red Maasai and Dorper double backcross resource population: natural pasture challenge with gastro-intestinal nematode parasites. *Small Ruminant Research* 56, 239–251. doi:<https://doi.org/10.1016/j.smallrumres.2004.06.003>
- Muigai, A.W.T., Hanotte, O., 2013. The Origin of African Sheep: Archaeological and Genetic Perspectives. *African Archaeological Review* 30, 39–50. doi:10.1007/s10437-013-9129-0
- Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livestock Science* 130, 57–69. doi:<https://doi.org/10.1016/j.livsci.2010.02.011>
- NRC, 1971. *Guide to Environmental Research on Animals*. National Academy of Sciences, Washington, DC.
- Oke, O.E., Uyanga, V.A., Iyasere, O.S., Oke, F.O., Majekodunmi, B.C., Logunleko, M.O., Abiona, J.A., Nwosu, E.U., Abioja, M.O., Daramola, J.O., Onagbesan, O.M., 2021. Environmental stress and livestock productivity in hot-humid tropics: Alleviation and future perspectives. *Journal of Thermal Biology* 100, 103077. doi:<https://doi.org/10.1016/j.jtherbio.2021.103077>
- Oloo, R.D., Ekine-Dzivenu, C.C., Mrode, R., Bennewitz, J., Ojango, J.M.K., Kipkosgei, G., Gebreyohanes, G., Okeyo, A.M., Chagunda, M.G.G., 2024. Genetic analysis of phenotypic indicators for heat tolerance in crossbred dairy cattle. *Animal* 18. doi:10.1016/j.animal.2024.101139
- Otte, J., A. Costales, J. Dijkman, U. Pica-Ciamarra, T. Robinson, V. Ahuja, C. Ly, D. Roland-Holst, 2012. *Livestock sector development for poverty reduction : an economic and policy perspective : livestock's many virtues*. Food and Agricultural Organization of the United Nations, Rome.
- Oyieng, E., Mrode, R., Ojango, J.M.K., Ekine-Dzivenu, C.C., Audho, J., Okeyo, A.M., 2022. Genetic parameters and genetic trends for growth traits of the Red Maasai sheep and its crosses to Dorper sheep under extensive production system in Kenya. *Small Ruminant Research* 206, 106588. doi:10.1016/j.smallrumres.2021.106588
- Pender, J., Nkonya, E., Jagger, P., Sserunkuuma, D., Ssali, H., 2004. Strategies to increase agricultural productivity and reduce land degradation: evidence from Uganda. *Agricultural Economics* 31, 181–195. doi:<https://doi.org/10.1016/j.agecon.2004.09.006>

- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reid, R.S., Galvin, K.A., Kruska, R.S., 2008. Global Significance of Extensive Grazing Lands and Pastoral Societies: An Introduction. In Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems (eds. Galvin, K.A., Reid, R.S., Jr, R.H.B., Hobbs, N.T.). Springer Netherlands, Dordrecht, pp. 1–24. doi:10.1007/978-1-4020-4906-4_1
- Renaudeau, D., Collin, A., Yahav, S., De Basilio, V., Gourdiene, J.L., Collier, R.J., 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. In *Animal*. pp. 707–728. doi:10.1017/S1751731111002448
- Sánchez-Molano, E., Kapsona, V. V., Oikonomou, S., McLaren, A., Lambe, N., Conington, J., Banos, G., 2020. Breeding strategies for animal resilience to weather variation in meat sheep. *BMC Genetics* 21. doi:10.1186/s12863-020-00924-5
- Sejian, V., Hyder, I., Ezeji, T., Lakritz, J., Bhatta, R., Ravindra, J.P., Prasad, C.S., Lal, R., 2015. Global warming: role of livestock. *Climate change impact on livestock: Adaptation and mitigation* 141–169.
- Sölkner, J., Nakimbugwe, H.N., Zárate, A.V., 1998. Analysis of determinants for success and failure of village breeding programmes. In *In Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, 12–16 January 1998, Armidale, Australia*.
- Solomon, S., 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Cambridge university press.
- Tesema, Z., Deribe, B., Kefale, A., Lakew, M., Tilahun, M., Shibesh, M., Belayneh, N., Zegeye, A., Worku, G., Yizengaw, L., 2020a. Survival analysis and reproductive performance of Dorper x Tumele sheep. *Heliyon* 6, e03840. doi:https://doi.org/10.1016/j.heliyon.2020.e03840
- Tesema, Z., Taye, M., Kebede, D., 2020b. Current status of livestock crossbreeding in Ethiopia: Implications for research and extension. *Journal of Applied Animal Science* 13.
- Thornton, P.K., 2010. *Livestock production: Recent trends, future prospects*. Philosophical Transactions of the Royal Society B: Biological Sciences. doi:10.1098/rstb.2010.0134
- Toothaker, L., 1993. *Multiple Comparison Procedures*. SAGE Publications, Inc., Thousand Oaks, California. doi:10.4135/9781412985178
- Tsartsianidou, V., Kapsona, V.V., Sánchez-Molano, E., Basdagianni, Z., Carabaño, M.J., Chatziliplis, D., Arsenos, G., Triantafyllidis, A., Banos, G., 2021. Understanding the

- seasonality of performance resilience to climate volatility in Mediterranean dairy sheep. *Scientific Reports* 11. doi:10.1038/s41598-021-81461-8
- Walsh, S.W., Williams, E.J., Evans, A.C.O., 2011. A review of the causes of poor fertility in high milk producing dairy cows. *Animal Reproduction Science* 123, 127–138. doi:<https://doi.org/10.1016/j.anireprosci.2010.12.001>
- Wanjala, G., Kichamu, N., Cizshter, L.T., Astuti, P.K., Kusza, S., 2023. An On-Station Analysis of Factors Affecting Growth Traits of Pure Red Maasai and Dorper Sheep Breeds under an Extensive Production System. *Animals* 13, 300. doi:<https://doi.org/10.3390/ani13020300>
- Wurzinger, M., Sölkner, J., Iñiguez, L., 2011. Important aspects and limitations in considering community-based breeding programs for low-input smallholder livestock systems. *Small Ruminant Research* 98, 170–175. doi:<https://doi.org/10.1016/j.smallrumres.2011.03.035>
- Zishiri, O.T., Cloete, S.W.P., Olivier, J.J., Dzama, K., 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. *Small Ruminant Research* 112, 39–48. doi:10.1016/J.SMALLRUMRES.2013.01.004
- Zonabend, E., Mirkena, T., Strandberg, E., Audho, J., Ojango, J., Malmfors, B., Okeyo, A.M., Philipsson, J., 2014. Breeding objectives for Red Maasai and Dorper sheep in Kenya – a participatory approach. In *10th World Congress on Genetics Applied to Livestock Production*. pp. 1–3.
- Zonabend König, E., Strandberg, E., Ojango, J.M.K., Mirkena, T., Okeyo, A.M., Philipsson, J., 2017. Purebreeding of Red Maasai and crossbreeding with Dorper sheep in different environments in Kenya. *Journal of Animal Breeding and Genetics* 134, 531–544. doi:<https://doi.org/10.1111/jbg.12260>

LIST OF PUBLICATIONS

This thesis is based on the work contained in the following papers:

1. **E. Oyieng, J.M.K. Ojango, M. Gauly, R. Mrode, R. Dooso, A.M. Okeyo, C. Kalinda, S. König.** 2025. **Evaluating reproduction traits in a crossbreeding program between indigenous and exotic sheep in semi-arid lands.** *Animal*.
<https://doi.org/10.1016/j.animal.2024.101391>
2. **E. Oyieng, J.M.K. Ojango, M. Gauly, R. Mrode, A.M. Okeyo, S. König.** 2025. **Lamb survival and ewe longevity in a crossbreeding program between indigenous and exotic sheep in semi-arid lands.** *Small Ruminant Research*.
<https://doi.org/10.1016/j.smallrumres.2025.107520>
3. **E. Oyieng, J.M.K. Ojango, M. Gauly, C.C. Ekine-Dzivenu, R. Mrode, E. Clark, R. Oloo, S. König.** 2025. **The impact of heat stress on growth and resilience phenotypes of sheep in a semi-arid land of sub-Saharan Africa.** *Livestock Science*.
<https://doi.org/10.1016/j.livsci.2025.105794>

ACKNOWLEDGEMENTS

First and foremost, I thank **God** for the gift of life, health, sound mind and sufficient grace to help me through my PhD.

My warm and deepest gratitude goes to my supervisors, **Prof. Dr. Sven König, Prof. Dr. Dr. Matthias Gauly, Prof. Dr. Raphael Mrode** and **Dr. Julie Ojango**. Your timely and invaluable feedback on my manuscripts, unwavering support and unquestionable commitment to make sure I excel are recognized and highly appreciated. Specifically, I want to thank **Dr. Julie Ojango** and **Prof. Dr. Dr. Matthias Gauly** for the immense support they gave me during the difficult times of my PhD journey when there seemed to be no light at the end of the tunnel. It's because of you that I got to have hope and continue with my PhD. God bless you.

Special thanks to my colleague and close friend **Dr. Richard Dooso Oloo** who was instrumental when I was stuck with softwares and scripts for analysis. Thank you for the time you sacrificed and knowledge you shared to make sure the analyses and scripts ran properly.

I am grateful to my colleague **Winfred Sila** who made sure that I got the data I needed timely and complete to enable me to do the analysis I needed to do.

I would like to thank **Kapiti Research Station and Wildlife Conservancy** for giving me access to the data to be able to carry out my analyses. I hope the findings of my PhD will be of great value to further inform the breeding and management of the sheep flock. More specifically, I would like to acknowledge the dedication and tireless efforts of **James Audho** and **Elias Mwarome Mwazonga** who religiously made sure that the data from the sheep flock is accurately and timely recorded, from the start of the breeding program in 2003, and they were always available to clarify any data related issues.

Thanks to my colleagues at the International Livestock Research Institute (ILRI) namely: **Eric Anyona, Geoffrey Muiruri, David Barasa, Gideon Kipkosgei, Jabes Yusuf, Linda Njeri** and **Gertrude Nangheke**. Thank you for your camaraderie, laughter, encouragement, moral support and stimulating discussions that made this journey enjoyable and enriching.

I am deeply grateful to the Center for Tropical Livestock Genetics and Health (CTLGH) – Small ruminant genomics program through **Roslin Foundation** (Research Grant Reference RF2302) and International Livestock Research Institute (ILRI) for offering the financial support that made this PhD possible.

Last but not least, I would like to thank my **family** for being a pillar of strength and my **friends** for the moral support and friendship throughout this journey.

FORMAL DECLARATION

Erklärung gemäß der Promotionsordnung des Fachbereichs 09 vom 07. Juli 2004 § 17 (2)

“Ich erkläre Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe. Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-LiebigUniversität Gießen zur Sicherung guter wissenschaftlicher Praxis“ niedergelegt sind, eingehalten.“

“I declare that the dissertation here submitted is entirely my own work, written without any illegitimate help by any third party and solely with materials as indicated in the dissertation. I have indicated in the text where I have used texts from already published sources, either word for word or in substance, and where I have made statements based on oral information given to me. At all times during the investigations carried out by me and described in the dissertation, I have followed the principles of good scientific practice as defined in the “Statutes of the Justus Liebig University Gießen for the Safeguarding of Good Scientific Practice”.

Gießen, den

Edwin Pancras Oyieng'

