Novel applications of genetic evaluation in livestock: gas fluxes and metabolic heat production in grazing beef cattle, and cashmere fiber in goats of two origins

by

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B.S., Kansas State University, 2020
M.S., Kansas State University, 2022

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Animal Sciences and Industry
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2025

Abstract

Two distinct genetic evaluations were performed, each offering novel contributions within their respective species. The first was a genetic evaluation of gas fluxes and metabolic heat production in grazing Angus beef cattle, which are emerging, but understudied traits. The second was a genetic evaluation of cashmere fiber characteristics in goats from two origins: the United States and New Zealand. While cashmere fiber traits have been studied more extensively, a genetic evaluation for U.S. cashmere goats had never been published before.

Cashmere producers, particularly in the United States where no genetic selection tools currently exist, would greatly benefit from the development of a national cashmere fiber genetic evaluation system. In this study, three genetic evaluations for cashmere fiber traits were performed depending on the goat's origin: U.S., New Zealand, and combined from both origins. International collaboration and data sharing were leveraged to increase sample size and strengthen the accuracy of the evaluations, given that there was gene flow between the two populations. Producers voluntarily submitted fiber samples to either the Texas A&M Bill Sims Wool and Mohair Research Laboratory (San Angelo, Texas) or SGS Wool Testing Services (Kilbirnie, New Zealand). A total of 3,336 fiber records from 2,572 goats were available between the U.S. and New Zealand. Fiber traits studied in all three analyses included mean fiber diameter (MFD), standard deviation of diameter (SDD), coefficient of variation of diameter (CVD), curvature (CURV), standard deviation of curvature (SDCURV), spinning fineness (SpinF), and percentage of fibers with diameter $\leq$ 19 μm (Perc19). Additional fiber traits analyzed in the U.S.-only analysis were staple length, greasy fleece weight, and coarse edge micron. Additional fiber traits analyzed in the N.Z.-only analysis were down staple length, yield, fleece weight, down weight, coarse edge, and percentage of medullated fibers. All animals were genotyped

using the Goat GGP 70K BeadChip (Neogen Corp.) and pedigree records were provided by participating producers. Variance components for each trait were estimated using single step genomic BLUP (ssGBLUP) with the BLUPF90 suite of programs. Fixed effects tested for model inclusion were age at fiber collection, sex, and contemporary group. In general, heritability estimates for shared traits were similar and moderate to high across all three analyses. In the combined analysis, the heritability of MFD, SDD, CVD, CURV, SDCURV, SpinF, and Perc19 was 0.46 ± 0.04, 0.26 ± 0.04, 0.26 ± 0.04, 0.33 ± 0.04, 0.24 ± 0.04, 0.40 ± 0.04, and 0.29 ± 0.04. Repeatability of cashmere fiber traits were moderate to high. Mean fiber diameter had unfavorable genetic correlations with CVD and SCURV. Genome-wide association studies identified several significant single nucleotide polymorphisms (SNPs) for cashmere traits. Many candidate genes located within ± 50 kb of these SNPs have been previously associated with fiber related biological processes or skin and hair biology in other species, including humans and mice. These findings demonstrate that cashmere fiber traits are heritable, and that genetic improvement through selection is feasible. Together, these findings provide a foundational resource for future development of a selection tool for cashmere goat breeding.

Ruminant animals produce methane (CH_4) as a by-product of enteric fermentation, a digestive process unique to ruminants. In beef cattle, CH_4 production represents both an energetic inefficiency and environmental concern. Methane mitigation efforts in grazing beef cows have the potential to have greater impact within the beef industry than mitigation within any other sector. Methane, carbon dioxide (CO_2), and oxygen (O_2) fluxes were collected from 330 grazing Angus beef females using a GreenFeed system (C-Lock Inc.). These gas fluxes were used to calculate metabolic heat production (MHP). All available fluxes were either averaged for the single record analysis or each visit to the GreenFeed system was treated as an individual

record in the repeat-record analysis. A pedigree for phenotyped animals, as well as genotypes for animals with gas flux data and their relatives were provided by the American Angus Association (Saint Joseph, Missouri). Variance components were estimated using the BLUPF90 software suite and the single step genomic BLUP methodology in both the single record and repeated records analyses. Fixed effects tested for model inclusion included contemporary group (GreenFeed trial group), age at GreenFeed trial start, body condition score, and mature weight estimated progeny difference (EPD). In the single record analysis, the heritabilities of average CH_4, average CO_2, average O_2, and average MHP were 0.23 ± 0.16, 0.32 ± 0.15, 0.20 ± 0.15, and 0.24 ± 0.15, respectively. In the repeated records analysis, the heritabilities of CH_4, CO_2, O_2, and MHP were 0.09 ± 0.03, 0.14 ± 0.04, 0.12 ± 0.04, and 0.13 ± 0.04, respectively. The repeatability of gas flux traits and MHP was low, ranging from 0.14 ± 0.01 to 0.21 ± 0.02. Estimated progeny differences (EPD) were generated for gas flux traits and MHP. Correlations between these gas flux EPDs and EPDs for other production traits and economic index values were calculated. Notably, gas flux and MHP EPDs had significant correlations with EPDs related to weight and feed intake, as well as economic index values. Significant single nucleotide polymorphisms for average gas flux traits were near QTLs previously associated with body weight, dry matter intake, residual feed intake, and average daily gain. This study provides preliminary genetic parameter estimates for gas fluxes and metabolic heat production in grazing beef cattle.

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Major Professor
Dr. Megan Rolf

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Acknowledgements

I would like to thank my major professor, Dr. Rolf, who introduced me to the Animal Breeding and Genetics discipline around 6 years ago by hiring me as an undergraduate student worker for the laboratory group. Since then, she has given me countless opportunities to become a better researcher, writer, and presenter. My committee, Drs. Bormann, Weaber, and Hefley, have provided me with additional support, resources, and knowledge to be successful.

I will be forever grateful for my time as a graduate student at Kansas State. I have worked alongside many amazing graduate students in Weber 119, who I know will be lifelong friends and colleagues. The Department of Animal Science has great professors and staff, many of which have directly contributed to my experience as a graduate student.

This would not have been possible without the funding and support from many people for the research projects described below.

My family is a great support system and has always encouraged me to do my best. No matter the circumstance, my family will show up to support you- the number of trips my parents have made up and down I-70 between Topeka and MHK for me and my sisters is countless. I would not be where I am today without my husband, Chase. He spent countless hours providing technical and mechanical consulting for the GreenFeed, that I am so thankful for. He can always make me laugh no matter how difficult things are and believes in me more than anyone else. I am excited for the next chapter of my life, but I will always be grateful for my time as a graduate student at KSU as it truly shaped me into the person I am today.

Chapter 1 - A review of cashmere fiber phenotypes: Production, heritabilities, and genetic correlations

Introduction

Cashmere is one of the finest, warmest, and most expensive animal fibers. Cashmere is the down fiber or undercoat that is produced by the secondary hair follicles of some goats, whereas the primary hair follicles produce a coarser fiber called guard hair. Many different breeds can grow this fiber. Cashmere goats originated throughout Asia in the Tibetan highlands, the Himalayas, and Mongolia. The down fiber produced by these goats protected them from harsh winter temperatures. The cashmere name originated from Kashmir, a region in India and Pakistan. Historically, cashmere referred to any type of goat fiber that met the mean fiber diameter (MFD) international standard set by textile processors. Therefore, cashmere was a textile marketing definition rather than a biological one (FTC, 1939). In 2019, the United States Department of Agriculture recognized the North American Cashmere goat (NACG) as a breed. According to the NACG breed standards, a goat's cashmere fleece must have a MFD of 19 µm or less.

Cashmere goats produce a coat which has three components: guard hair, down fiber, and natural contaminants. Guard hair is the outer layer of the coat that provides the skin protection against the environment. The inner layer of the coat called down fiber is very fine and provides a layer of insulation, also protecting the skin. Total fleece weight (FW) equals down weight (DW) plus guard hair weight plus natural or other contaminants. Down is typically 15 to 50% of total FW (Pattie et al., 1990; Bigham et al., 1993). The down fiber is soft and used to produce cashmere products, whereas guard hair is coarse and separated out (Burns et al., 1962). Guard

hair is either treated as waste or used for other low-value products like brushes or interlinings (Patil et al., 2013).

Background

Cashmere is primarily produced in China and Mongolia, which together contribute approximately 85 to 90% of the world's cashmere supply. Other major cashmere producers include Iran, Afghanistan, Pakistan, and India (Kerven et al., 2009). There has been interest in producing cashmere in other locations such as Australia, New Zealand, the United States and Europe. However, current populations of cashmere goats in these locations are relatively low. Central Asian countries are also emerging as important producers of cashmere as the goat population increases in this area.

The United States Federal Trade Commission's (FTC) Wool Products Labeling Act of 1939 set four required guidelines that must be met for goat fiber to be labeled as cashmere: (a) the product is the fine undercoat fibers of the *Capra hircus laniger*; (b) the average diameter does not exceed 19 μm; (c) no more than 3% of fibers exceed 30 μm; and (d) the average fiber diameter coefficient of variation does not exceed 24% (FTC, 1939).

Building upon the requirements of the Wool Products Labeling Act of 1939, the Cashmere Goat Association (CGA) set breed standards for the NACG. These standards were set by the CGA for breed development, herd improvement, and breeding decisions. Cashmere goats are considered a dual-purpose breed, providing both fiber and meat products. Therefore, the CGA has standards for both fiber and conformation. Fiber standards include MFD, uniformity, style, length, differentiation, total DW, and cover. The standard for MFD is a maximum of 19 μm. Mean fiber diameter calculated using a distribution histogram from a laboratory instrument is the recommended practice. Fiber diameter should be uniform. Uniformity is expressed as

coefficient of variation (CV) and should be 24% CV or less. Style is the crimp or curvature of individual fibers and is expressed in degrees of circular arc per mm. Individual fibers should have a 3-dimensional, irregular crimp and the mean style measurements must be greater than 45 deg/mm. Fiber length in its relaxed state must be greater than 1.25 inches (32 mm). The differentiation standard from the CGA requires that guard hairs are course enough to easily differentiate from down fibers which is usually evaluated by eye. Down weight is the total amount of down collected from a single fleece and must be no less than 2 ounces (57 g). This weight is taken after the fiber is cleaned and processed. The last fiber standard set by the CGA is for cover and states that all four harvest sites (neck, shoulder, side, and hip) should produce cashmere fiber. Conformation standards set by the CGA include specific metrics for the head, teeth, forequarters, barrel/back, hindquarters, feet, and reproductive system. Goats that meet these standards are eligible to be registered as a NACG. It is vital to understand these metrics because typically only registered goats would be included in genetic evaluation of fiber characteristics, pending the development of such program in the US. In addition to the fiber characteristics important to meet the FTC's guidelines or breed standards, characteristics that are particularly important for textile processing may also need to be considered in selection programs. Cashmere fiber properties important for textiles include fiber curvature, crimp frequency, and resistance to compression (McGregor, 2014; McGregor and Butler, 2009).

During the cashmere growing season, maintaining proper goat live weight (LW) is important for cashmere production (McGregor, 1992). McGregor (1992) found that for each 1 kg increase in LW, cashmere growth increased by 4.7 g, but fiber diameter also increased by 0.08 μm. McGregor (1992) acknowledged that these regression coefficients may not apply in all situations but emphasized that the important principle is that changing LW alters cashmere

growth. Several other management practices influence cashmere production such as nutrient supplementation, stocking rate, animal heath procedures, and forage type (McGregor, 1998). All these management practices can affect LW during cashmere growing season and therefore influence cashmere production and cashmere fiber quality traits.

Cashmere is harvested in the spring which is near the time goats naturally molt. In the Northern Hemisphere, goats will molt anytime from March to May. Typically, goats must be at least 1 year old for cashmere to be harvested. Typically, fiber characteristics change throughout a cashmere goat's lifetime, with fiber diameter increasing and becoming coarser (Redden et al., 2010; Toigonbaev et al., 2023). Therefore, one fiber sample may not be representative of a goats' lifetime fiber characteristics because these qualities change as goats LW fluctuates.

There are two ways that cashmere can be collected: hand combing or shearing. Traditionally, cashmere was hand combed with a metal comb having closely spaced, fine teeth. Combing takes advantage of a goat's natural seasonal shedding and results in collecting longer fibers. In the spring, producers will notice small amounts of cashmere on fences, branches, etc., indicating that cashmere is ready to be collected. Most producers will gather this cashmere as well because individual animal production is low. Early production reports for Chinese goats included combed weight comprising some guard hair, scurf, grease, dust, and soil (McGregor et al., 2011). In western countries, shearing is a common method of collecting cashmere although some producers still comb individual goats. Producers shear fleeces because hand combing is a tedious and time-consuming process. A goat does not release its cashmere all at once, therefore several combing sessions are required to harvest all the fibers. One disadvantage of shearing is that the entire fleece, including both down hair and all guard hair, is shorn and subsequently the guard hairs must be removed in a process called dehairing.

After fiber is collected either by hand-combing or shearing, there are several steps to process the cashmere into a useable product. First, the fleeces are sorted by color. Cashmere goat coats can be a wide range of colors including white, grey, brown, black, or a combination of these colors (Pattie et al., 1990). Cashmere that is all white (down and guard hair) is preferred and receives a premium from processors over mixed or colored cashmere. After fleeces are sorted by color, the fleece is scoured. This process provides the initial wash and dry of the fiber to remove environmental debris (McGregor, 2012). Then the fiber undergoes a process called dehairing which separates the guard hair from the fine down fibers. This is done with specialized machinery or by hand for small quantities and results in extremely soft and clean cashmere (McGregor and Butler, 2008b). Once the fiber is clean, it can be used in a variety of ways. The desired end product of the cashmere determines the final steps in processing, such as yarn or fabric manufacturing.

As technology capable of testing fiber quality advanced, fleece sampling methods were studied to avoid sending an entire fleece to a testing facility. Couchman and McGregor (1983) found that samples combined from 3 sites (neck, mid-side, and hindquarter) fairly represented an entire fleece and could be used to estimate MFD and yield. Mid-side samples were subsequently found to be the best single predictor of MFD in Australian feral goats. Due to this research, Hopkins et al. (1984) recommended two options for fleece testing: send the entire fleece to Australian Wool Testing Authority for subsampling or send a mid-side sample. Mid-side samples can be taken in various sizes but are typically a small area (approximately 15cm x 10cm) taken over the last rib. While mid-side sampling made testing fleeces easier, caution should be applied when using mid-side samples to evaluate yield (Couchman, 1986; Couchman and Holt, 1990; McGregor, 1994). McGregor (1994) estimated a correlation of 0.78 between

entire fleece and mid-side sample estimates of cashmere yield. The author reported that mid-side samples overestimated cashmere yield by 29.7%. However, high correlations between entire fleece and mid-side sample estimates of cashmere weight and diameter (0.92 and 0.89, respectively) were reported (McGregor, 1994). This means that although mid-side samples should not be used to determine actual cashmere yield for fleece valuation, animal rankings for weight and diameter based on mid-side samples would be comparable to rankings on entire fleece measurements.

There are several different technologies that can be used to analyze fiber. Sample collection for fiber analysis is similar to that described above for Australia in that a 2-inch by 2-inch (50 x 50 mm) mid-side sheared sample is used. The Optical Fibre Diameter Analyser (OFDA) 100 was introduced in the early 1990's to measure fiber characteristics such as MFD and CV (Baxter et al., 1992). The OFDA 100 requires that samples are washed and dried in preparation for testing. The OFDA 2000, which succeeds the OFDA 100, was the first instrument capable of measuring greasy fibers (Baxter, 2001). The OFDA 2000 analyses fiber using one of two modes: snippet or staple. The OFDA 2000 snippet mode is similar to the OFDA 100 in the preparation and processing of samples. The OFDA 2000 staple mode calculates a grease adjustment factor prior to testing; therefore, samples require less laboratory preparation and are not washed. Another instrument called the Laserscan^{TM} can be used to measure fiber characteristics. These instruments are primarily used for wool testing but can also be used to test cashmere.

An individual cashmere goat produces very little clean cashmere each year. Of 11 different Australian farms representing 1,244 goats, average clean cashmere production ranged from 21 to 389 grams across the farms (McGregor and Butler, 2008a). Average greasy combed

cashmere production ranged from 299 to 499 grams, depending upon group, across 80 cashmere goats in China (Duan et al., 2022). Due to low production, cashmere producers also rely on other income sources such selling pelts, breeding stock, and meat from cull animals. The small amount of clean cashmere produced by individual goats is another reason cashmere producers would benefit from genetic selection tools that could help increase productivity.

Genetic Parameters

Genetic Selection Tools

Genetic selection tools, such as a national genetic evaluation or genomics, are lacking in most countries for cashmere producers, which has hindered the amount of improvement cashmere producers can make. For example, a benchmarking project from McGregor (2006) revealed that several selected flocks in Australia with animals born in 2001 had similar productivity per head to the unselected feral base flock studied in the early 1980's (Restall and Pattie, 1989). There was little improvement to average clean cashmere production and MFD throughout this time period in the flocks reported by McGregor (2006), in part due to the lack of selection tools for producers. However, McGregor (2006) noted that 2001 experienced a severe drought which likely hindered production in that year. Another reason increases in productivity were slow in Australia was that elite animals were not transferred across herds from 1995 to 2005 due to an outbreak of Johne's disease in sheep (James, 2009). Johne's disease can be spread to goats that are near infected sheep so transfer of cashmere goat genetics across Australia was minimal during this time (James, 2009). However, the heritabilities of MFD and DW are high (0.47 ± 0.15 and 0.61 ± 0.18, respectively; Pattie and Restall, 1989), so response to selection should have been relatively quick and some improvements would have been expected. During

this time, cashmere producers lacked sophisticated selection tools such as a national genetic evaluation and standardized performance recording.

In 2003, the Australian Cashmere Growers Association (ACGA) developed a database called ACGA Achievement to encourage cashmere producers to consistently record MFD and DW for 2-year-old goats (James, 2009). Additionally, since 2006 the ACGA has conducted an across-herd genetic evaluation called ACGA Merrrit (James, 2009). Through the ACGA, estimated breeding values (EBV) are available for three traits: MFD, DW, and the McGregor Index. The McGregor Index was developed to identify goats with high clean cashmere production in relation to both MFD and staple length (SL; McGregor and Butler, 2015). Since ACGA Merrrit became available for cashmere producers, trends in EBVs for DW and MFD have shown rapid improvement (James, 2012). Despite the unfavorable genetic correlation between DW and MFD (Pattie and Restall, 1989), the rate of improvement was 6 and 22-fold faster for MFD and DW, respectively, under the ACGA Merrrit program compared to before the programs existed (James, 2012). Though not specifically for cashmere, Australia has an extensive national genetic evaluation for Merino sheep called MERINOSELECT. This genetic evaluation generates EBV for several economically important traits for reproduction, maternal ability, growth, carcass, health, and wool attributes. Large, long-term studies of the genetics of Australian Merino wool have been conducted (Safari et al., 2007) and there is potential to utilize these frameworks for establishing genetic evaluation for cashmere goats.

Currently, Australia is the only country with a national genetic evaluation for cashmere goats. However, there are other countries such as Kyrgyzstan, China, and Iran working to select and breed for cashmere improvement. Since 2008, an organization in Kyrgyzstan has been developing a flock of cashmere goats (Toigonbaev et al., 2023). This program is intended to

conserve the genetics of native goats while also providing additional income to participating farmers. For goats enrolled in this program, cashmere weight increased significantly from 2016 to 2021 (2.6 g/year; Toigonbaev et al., 2023). Additionally, the flock was selected to only consist of white colored goats whose fiber receives a higher price. In 2010, a different cashmere breeding program was implemented in Iran (Mueller et al., 2015). This program involved policies for sire selection, systematic culling, and phenotype recording, but faced difficulties in sustaining the formal program for more than a few years (Mueller et al., 2015).

In the United States, the only breeding tool most cashmere goat producers have is phenotypic selection. This is a disadvantage for cashmere producers in the United States because phenotypic selection has several drawbacks. Phenotypic selection is a less accurate type of selection compared to EBV obtained through a national genetic evaluation, such as ACGA Merrrit. Additionally, goat kids must be raised until cashmere can be harvested, usually around 1 year, before the fleece can be tested for quality. Only then can the producer make informed selection decisions, and these may also be biased because fiber quality will change throughout the animal's lifetime. Raising all progeny to 1-year-old requires a significant time and monetary investment.

Heritability Estimates of Fiber Characteristics

Although cashmere goats do not have a national genetic evaluation in most countries, variance component estimates for important cashmere production traits (Table 1.1) have been generated in the research studies summarized below. Published literature from cashmere goats in the United States is sparse with more studies having been conducted in other countries such as China, Australia, and New Zealand (Table 1.2). Due to the sparsity of literature published on this subject, studies were not excluded based on sample size, publication date, or publication country.

Literature search terms included genetics, variance components, heritability, genetic correlation, cashmere goat, and fiber production traits listed in Table 1.1.

Mean fiber diameter

Mean fiber diameter is arguably the most important trait for cashmere producers because according to textile definitions fiber must be 19 μm or less to be considered cashmere. One of the first large-scale genetic evaluations for cashmere goats was performed by Pattie and Restall (1989) in Australia. Mean fiber diameter was measured on subsamples taken from an entire shorn fleece with the diameters of 1,000 fibers measured with a Fibre Fineness Distribution Analyser (FDA). Pattie and Restall (1989) found the heritability of MFD was 0.47 ± 0.15 and the repeatability from records across various ages was 0.60 ± 0.02 in a population of feral goats. A few years later, another Australian study reported a slightly lower, but similar, heritability for MFD of 0.39 ± 0.16 from 10-month-old unselected feral goats (Rose et al., 1992).

Gifford et al. (1990) reported that 10-month-old kids that were the progeny of feral breeding females in South Australia had a MFD heritability of 0.70 ± 0.19. In another Australian study, Couchman and Wilkinson (1987) reported the heritability of MFD from yearling goats that had a degree of Angora infusion was 0.68 ± 0.23. During the 1980s, New Zealand imported selected cashmere goats from Australia. Therefore, heritabilities estimated during this time period are expected to be similar between Australia and New Zealand. The heritability of MFD was 0.79 ± 0.23 for New Zealand goats using a univariate mixed model analysis (Baker et al., 1991). In a multivariate mixed model analysis including three other fiber traits, the MFD heritability increased slightly to 0.82 ± 0.23 (Baker et al., 1991).

Bigham et al. (1993) estimated the heritability of MFD as well as other fiber traits on 300 does and their progeny using 5 years of data in New Zealand. The measurement method for

MFD in this study was similar to that done in Australia by Pattie and Restall (1989) in that 1,000 fibers taken from a subsample of a shorn fleece were analyzed on a FDA. The heritability of MFD for kids was 0.19 ± 0.07 and for yearlings was 0.99 ± 0.19 (Bigham et al., 1993). Bigham et al. (1993) mentioned that kid heritabilities included only 2 years of data whereas yearlings used 5 years, which could be the reason that kid heritabilities were lower for MFD and most other traits analyzed. The authors did not speculate why the yearling MFD heritability was extremely high but did mention high estimates from other Australian studies suggesting that there is great potential for genetic improvement of MFD (Bigham et al., 1993).

The United Kingdom (UK) does not have an indigenous cashmere-bearing goat breed; therefore, semen and embryos were imported from Iceland, Siberia, Tasmania, and New Zealand from 1986 to 1988 for a crossbreeding program with native Scottish goats (Bishop and Russel, 1994). Genetic parameters were estimated from progeny during the first seven years of this crossbreeding program and the heritability for MFD was 0.63 ± 0.07 (Bishop and Russel, 1996). Using a subset of the same animals, Bishop and Allain (2000) reported a similar heritability for MFD of 0.64 in a larger analysis of the Scottish crossbred cashmere goats. Both studies of Scottish cashmere goats utilized a similar MFD measurement technique of projection microscopy on midside fleece samples that were manually dehaired. The genetics imported for these studies were from animals born approximately 40 years ago, highlighting the need for more current research in this area.

Bai et al. (2006) reported a heritability for MFD of 0.28 for Inner Mongolian White cashmere goats, which is much lower than the heritabilities reported in New Zealand and Australia. The authors speculated that this difference in heritability could be due to differences in genetic structure and environment among breeds in different countries. Additionally, Bai et al.

(2006) collected a shorn sample on the side of the shoulder prior to comb harvesting and MFD was measured on 200 fibers by projection microscopy. The difference in collection and measurement of MFD across studies could be another reason for differences in heritability estimates. Similar to Bai et al. (2006), Zhou et al. (2002) measured MFD on a shoulder sample under a microscope and reported a heritability for MFD of 0.32. The MFD heritability from yearling goats was 0.41 ± 0.08 as reported by Pallotti et al. (2018). Studies published most recently reported MFD heritability estimates of 0.36 ± 0.03 and 0.22 ± 0.02 for Inner Mongolia cashmere goats (Rong et al., 2024 and Yan et al., 2024, respectively). Jinquan et al. (2001) reported one of the lowest heritabilities for MFD of 0.14. Zhou et al. (2002) discussed that prior studies from New Zealand and Australia used animals that were a composite of cashmere-bearing and feral goats that had been under only a few generations of selection. Cashmere goats indigenous to China typically have a higher producing potential compared to the composite populations of New Zealand and Australia (Zhou et al., 2002), which could be reasons for the discrepancy in MFD heritability between studies from different countries.

Since 2008, a non-government organization has been developing a breeding flock of cashmere goats indigenous to Kyrgyzstan to preserve the genetics of high-quality Kyrgyz cashmere (Toigonbaev et al., 2023). Genetic parameters for fiber characteristics were estimated from a subset of this flock and the MFD heritability was reported as 0.58 ± 0.16 (Toigonbaev et al., 2023). This heritability estimate is higher than estimates reported by Zhou et al. (2002), Bai et al. (2006), Jinquan et al. (2001), and Pallotti et al. (2018) in the neighboring Asian countries of Mongolia and China. This could be because goats from the Kyrgyzstan flocks were relatively unselected compared to Chinese flocks. However, considering the standard errors, the heritability

estimate from Toigonbaev et al. (2023) is not different than the estimates reported in New Zealand and Australia in the late 1980's and early 1990's from feral type goats.

It has been shown that cashmere quality changes throughout a goat's lifetime, namely MFD becomes coarser as the animal ages (Redden et al., 2010; Toigonbaev et al., 2023). Wang et al. (2015) estimated genetic parameters for fiber characteristics from Inner Mongolia White cashmere goats across age groups from 1 to 5 years old. The heritability of MFD from 1 to 5 years old were 0.40 ± 0.06, 0.39 ± 0.07, 0.29 ± 0.07, 0.38 ± 0.08, and 0.29 ± 0.09, respectively (Wang et al., 2015). The genetic correlations of EBV between any two age groups were high and positive (0.90 to 0.99; Wang et al., 2015). The authors concluded that there is opportunity to improve MFD using selection based on phenotypic records and EBV at earlier ages (Wang et al., 2015).

In summary, MFD has been shown to be a heritable trait and the range of heritability in literature is 0.14 to 0.99 (Jinquan et al., 2001 and Bigham et al., 1993, respectively). This is a very large range and encompasses two extreme estimates. However, most other literature estimates for MFD indicated moderate to high heritability (Table 1.2). This suggests that genetic selection for MFD is possible and that response to selection would likely be relatively high. However, the impact of selection to reduce fiber diameter on other factors such as DW, fiber processing, and producer income is unclear. Additional research is needed to weigh the costs and benefits of achieving a MFD below the required threshold.

Standard deviation of diameter and coefficient of variation of fiber diameter

Standard deviation of diameter (SDD) is the standard deviation of fiber diameter expressed in μm and describes variability in diameter. Bishop and Russel (1996) estimated a heritability of 0.43 ± 0.08 for SDD of 5-month-old kids. A similar heritability of 0.38 ± 0.14 was

found for 10-month-old Australian cashmere goats (Gifford et al., 1990). The lowest heritability for SDD of 0.28 was estimated for 5-month-old kids by Bishop and Allain (2000). Another measure of uniformity is coefficient of variation of fiber diameter (CVD). The heritability of CVD was estimated to be 0.52 ± 0.06 for yearling cashmere goats (Pallotti et al., 2018). Although heritability estimates for SDD and CVD are relatively limited in literature, literature suggests that measures of fiber diameter uniformity are moderate to highly heritable (Table 1.2).

Down fiber length

Typically, down fiber length (DFL) refers to the length of cashmere down fibers in a relaxed state (Cashmere Goat Association, 2023). However, another definition of DFL is the stretched or unbent length of fiber (Bai et al., 2006). There is not a standardized method for DFL measurement. McGregor (2007) reported a large range in individual cashmere fiber length within raw cashmere staples from China, Iran and Australia. A simple method to measure DFL is by parting the fleece and placing a ruler on the skin to measure an individual unstretched down fiber on the neck, mid-side, and hip with the average of the three measurements reported. Fiber length can also be measured in a laboratory using a microscope or graphical technique. Longer DFL is superior due to improvements in processing efficiency and ability to be used for worsted spinning (McGregor and Butler, 2008b). Goats fed to gain weight during the cashmere growing period have longer DFL but also increased MFD (McGregor, 2003). A New Zealand study reported both kid and yearling heritabilities for DFL of 0.57 ± 0.15 and 0.87 ± 0.29, respectively (Bigham et al., 1993). Fiber length was the only trait reported by Bigham et al. (1993) with a higher heritability reported for yearlings compared to kids. Bigham et al. (1993) did not speculate why the yearling heritability was higher but did acknowledge the associated high standard error. Pattie and Restall (1989) reported a heritability for DFL of 0.70 ± 0.19 for

Australian feral goats. The repeatability of DFL was 0.63 ± 0.02 suggesting DFL at first shearing is a reasonable predictor of DFL in the future (Pattie and Restall, 1989). Both Bigham et al. (1993) and Pattie and Restall (1989) measured DFL prior to shearing at 3 sites on the animal which could be one reason heritability estimates are similar between these two studies.

Other heritability estimates for DFL have been published that are lower or more moderate. Fiber length heritabilities of 0.50 ± 0.24 and 0.56 were published from studies conducted in Kyrgyzstan and China, respectively (Toigonbaev et al., 2023; Jinquan et al., 2001). Toigonbaev et al. (2023) measured DFL with a graphic technique on hand dehaired combed samples. Dehairing is a process that causes some fibers to break, which could have impacted the fiber length phenotype in this study. In a large study of crossbred Scottish cashmere goats, Bishop and Allain (2000) reported a heritability for DFL of 0.57 for 5-month kids. Another study of Scottish cashmere goats in the UK reported a heritability for DFL of 0.49 ± 0.15 (Bishop and Russel, 1996). For the first two years of this trial, DFL was directly measured on the animal during sampling. During the remaining years of the trial, SL was measured on laboratory samples, but was treated as fiber length for genetic analysis. Varying fiber length measurement techniques could have impacted the heritability in this study and highlights the necessity of a standardized fiber length measurement method.

Conversely, low heritability estimates for DFL have been reported in Mongolian and Chinese studies. Zhou et al. (2002) reported a heritability for DFL of 0.23 for Inner Mongolia cashmere goats in China. Another study of Inner Mongolia goats reported a very similar heritability estimate of 0.21 (Bai et al., 2006). Wang et al. (2015) reported heritabilities of 0.19 ± 0.04, 0.34 ± 0.08, 0.21 ± 0.07, 0.23 ± 0.07, and 0.18 ± 0.08 for Inner Mongolia cashmere goats 1 to 5 years old, respectively. These heritability estimates are lower than those reported in

Australia and New Zealand as well estimates from other Asian countries. All three of these studies (Zhou et al., 2002; Bai et al., 2006; Wang et al., 2015) measured DFL on samples shaved from the shoulder site. Bai et al. (2006) and Wang et al. (2015) used projection microscopy to measure DFL on washed and dehaired shoulder samples.

Fiber length is an important production trait for cashmere, particularly as it relates to fiber processing. A wide range of heritability estimates for DFL have been published from 0.18 ± 0.08 to 0.87 ± 0.29 (Bigham et al., 1993; Wang et al., 2015, respectively). Although the majority of published estimates suggest the heritability of DFL is moderately high (around 0.50), there are discrepancies, likely due to animal age at sampling, country of origin, and measurement method.

Staple length

Staple length is the length of fibers in an entire cluster of fibers or the staple. Staple length is important for the same reason as DFL in that longer SL is related to better fiber processing. Staple entanglement, or adhesions between fibers growing at different speeds, can result in altered crimp and apparently shorter length (McGregor and Butler, 2014). Fewer heritability estimates are available in the literature for SL as compared to DFL, which contrasts with studies of wool from sheep which normally report SL. Cashmere studies usually only report one trait for length (either DFL or SL) which is typically DFL. However, Bai et al. (2006) reported a genetic correlation of 0.34 between DFL and SL. This is a relatively low genetic correlation suggesting that animals may rank differently for these two traits. Jinquan et al. (2001) reported the heritability of SL for Inner Mongolia cashmere goats was 0.32. In another study of Inner Mongolia cashmere goats, a similar heritability estimate for SL of 0.29 was reported (Bai et al., 2006). Staple length has a moderate heritability in Inner Mongolia cashmere goats but

would need to be evaluated in other populations to ensure no large discrepancies exist between populations.

Clean down weight

Clean DW is the total amount of cashmere, after dehairing and cleaning, from the fleece of a single goat (Cashmere Goat Association, 2023). This trait is especially important for cashmere producers because they receive payment from processors or consumers based upon the total clean DW. Rose et al. (1992) estimated a heritability for clean DW of 0.61 ± 0.21 from 10-month-old goats in Australia. Interestingly, Pattie and Restall (1989) also reported the heritability of clean DW as 0.61 ± 0.18 for Australian feral goats. Gifford et al. (1990) reported a heritability for DW of 0.36 ± 0.13 for 10-month-old goats in Australia. Bigham et al. (1993) estimated heritabilities for clean DW in New Zealand from both yearlings and kids as 0.62 ± 0.15 and 0.20 ± 0.07, respectively. Baker et al. (1991) reported the univariate heritability of clean DW as 0.45 ± 0.17. However, when clean DW was run in a multivariate analysis with other fiber traits, the heritability increased to 0.57 ± 0.19.

Down weight of a patch sample measured from the midside had an estimated heritability of 0.61 in crossbred Scottish 5-month-old kids (Bishop and Allain, 2000). In another study using Scottish 5-month-old kids, a lower heritability of 0.39 ± 0.05 was reported for DW in a midside patch sample (Bishop and Russel, 1996). However, Bishop and Russel (1996) observed that DW was significantly positively skewed, and a log transformation normalized the data. When Bishop and Russel (1996) analyzed the logarithm value of DW, the heritability was 0.60 ± 0.06, which is much closer to other published estimates.

The lowest heritability estimate reported for clean DW was 0.12 ± 0.03 (Pallotti et al., 2018). However, Pallotti et al. (2018) measured DW from a midside fleece sample prior to

combing, whereas Australian and New Zealand studies measured DW of an entire or subsampled shorn fleece. Most estimates suggest that clean DW is a highly heritable trait which is advantageous because producers can use genetic selection to improve this trait. However, more current research is needed because the most recent estimate from 2018 (Pallotti et al.) suggests that clean DW is lowly heritable.

Greasy down weight

Greasy DW is the total weight of the down prior to cleaning and processing; therefore, the weight includes the weight of grease and other natural contaminants. Although several Australian studies reported high heritabilities for clean DW, the heritability of greasy DW in one Australian study was only moderate. Couchman and Wilkinson (1987) found the heritability of greasy DW in yearling goats was 0.38 ± 0.17.

Low heritability estimates were reported by several studies of goats in China and Kyrgyzstan. Inner Mongolian cashmere goats in China have greasy DW heritabilities reported in two studies with large sample sizes: 0.28 (Zhou et al., 2002) and 0.30 (Bai et al., 2006). The highest heritability estimate for greasy DW from China was 0.69 for the Chinese Liaoning goat (Ning et al., 1995). The lowest greasy DW heritability estimate reported was 0.12 ± 0.12 for cashmere goats in Kyrgyzstan (Toigonbaev et al., 2023). In these studies from Asian countries, DW is reported as the total weight of combed cashmere including undefined quantities of grease, guard hair, and other natural contaminants. Additionally, Chinese cashmere goat populations have been under selection for decades to improve cashmere production. In contrast, goat populations studied in Australia, New Zealand, and the UK were unselected feral goats or composites of feral and imported cashmere-type goats.

Greasy fleece weight

Traditionally, cashmere was harvested using a metal comb which allows producers to collect the down fibers with low but undefined quantities of guard hairs. This cashmere harvesting practice is still used by cashmere producers in some Asian countries. However, most producers in Australia, New Zealand, and the United States have opted to shear the entire fleece because of the convenience. Therefore, the trait FW has been evaluated in countries that shear; but no literature is available from Asian countries that still hand comb or use small mid-side samples. There is a relationship between FW, clean DW, guard hair weight, and down yield (DY) when measuring fiber characteristics. Greasy FW multiplied by clean DY (%) equals clean DW. Also, greasy FW minus clean DW and the weight of grease and natural contaminants (McGregor, 2003) equals guard hair weight.

Rose et al. (1992) reported the heritability of greasy FW for 10-month-old goats in Southwest Queensland to be 0.67 ± 0.22, which is the highest heritability reported in literature for FW. Gifford et al. (1990) also studied 10-month-old goats and reported the heritability of greasy FW to be 0.42 ± 0.16. Bigham et al. (1992) found the same heritability (0.42 ± 0.13) as Gifford et al. (1990) for yearling goats. Bigham et al. (1992) reported the heritability of greasy FW for kid goats as 0.14 ± 0.06. This estimate for kids is much lower than other estimates and is the lowest estimate in published literature.

Pattie and Restall (1989) studied feral goats in Australia and reported a heritability for greasy FW of 0.29 ± 0.11. The repeatability of greasy FW was 0.68 ± 0.02 meaning that FW from the first shear would be a reasonable predictor of FW from future shears (Pattie and Restall, 1989). Other moderate heritabilities have been published. Baker et al. (1991) found the heritability for greasy FW was 0.31 ± 0.14. Couchman and Wilkinson (1987) reported the heritability for yearling goats in Australia was 0.45 ± 0.18. Literature suggests that greasy FW of

cashmere goats is moderate to highly heritable (Table 1.2) and selection for heavier FW is possible.

Down yield

Down yield is calculated as the weight of clean down fiber divided by the total weight of the raw fleece, as a percentage (Cashmere Goat Association, 2023). A fleece with a low yield percentage would have more guard hair and non-hair material like dust and grease compared to a high yielding fleece that would provide more down relative to waste. Cashmere producers' main income source is down fiber, therefore, increasing DY would make cashmere producers more efficient and profitable. Few studies have reported heritability estimates for DY unlike numerous estimates for other traits like MFD, DW, and DFL. Pattie and Restall (1989) reported the highest heritability of 0.90 ± 0.23 for DY, which the authors acknowledged was extremely high. Baker et al. (1991) found the heritability of DY in a univariate analysis was 0.52 ± 0.19 but when included in a multivariate analysis, the heritability was 0.64 ± 0.21. The heritability of DY of 10-month-old goats was 0.57 ± 0.20 (Rose et al., 1992). The same heritability (0.57 ± 0.15) for DY was also published by Bigham et al. (1993) for yearling goats although the authors reported a much lower heritability estimate of 0.19 ± 0.07 for kids.

Other studies have reported similar low heritability estimates for the DY. Gifford et al. (1990) found a heritability of 0.23 ± 0.11 for 10-month-old goats. The only study that reported a heritability for DY from cashmere goats in an Asian country was Jinquan et al. (2001), which reported a heritability of 0.26 for Inner Mongolia cashmere goats. One study that measured greasy yield reported a heritability of 0.30 ± 0.15 (Couchman and Wilkinson, 1987). This heritability is near the lower end of the range in literature for DY. Overall, the heritability of DY is highly variable in the literature (Table 1.2).

Skin follicle density

Cashmere is produced by the secondary hair follicles while guard hair grows from the primary hair follicles. Pattie and Restall (1989) took skin biopsies from the midside of feral goats to measure follicle densities. Primary follicle density and secondary follicle density had heritability estimates of 0.16 ± 0.11 and 0.17 ± 0.11, respectively (Pattie and Restall, 1989). In the same study, the ratio of secondary to primary follicle density had a heritability of 0.29 ± 0.15. Due to the difficulty of collecting skin biopsies and the low heritability estimates, the authors concluded that skin parameter traits are not justified in a selection program.

Live weight

Although not a fiber characteristic trait, LW has been shown to influence cashmere production and fiber characteristics (McGregor, 1992; McGregor and Butler, 2008a). Carcass characteristics and sale value at the end of the goat's cashmere productive life are also influenced by LW (McGregor, 1990). In the evaluation of fiber characteristics, several studies also estimated heritabilities for LW. The highest heritability estimate for LW reported in literature was 0.71 ± 0.08 for Scottish crossbred cashmere goats in the UK. This estimate is high for LW when compared to other species such as cattle that have a mature LW heritability around 0.50 as reviewed by Koots et al. (1994) and sheep of around 0.30 (Nasholm and Danell, 1996; Lewis et al., 2002).

Other heritabilities reported for LW of cashmere goats are moderate and compare to mature weight heritability estimates for sheep. Pattie and Restall (1989) reported a heritability of 0.29 ± 0.10 for feral goats in Australia. A similar LW heritability of 0.26 ± 0.11 was found for 10-month-old cashmere goats in Australia (Gifford et al., 1990). Rose et al. (1992) reported a

LW heritability of 0.33 ± 0.15. Bishop and Allain (2000) found a LW heritability of 0.25 for Scottish cashmere goats.

However, heritability estimates for LW from Inner Mongolia cashmere goats in China are much lower. Jinquan et al. (2001) reported a heritability of 0.16 for LW. A heritability of 0.10 from Inner Mongolia cashmere goats was reported by Zhou et al. (2002). The lowest published heritability for LW was 0.07 (Bai et al., 2006).

Despite a few extreme estimates, the heritability of LW is likely moderate (Table 1.2). Live weight would respond to genetic selection which could influence cashmere fiber characteristics and value of cull animals (McGregor, 1992; McGregor and Butler, 2008a). The genetics of LW could be influenced by population structure or environmental factors that differ between countries, as seen by the lower heritability estimates from cashmere goats in China.

Genetic Correlations between Fiber Characteristics

Generally, the three most important traits for maximizing income from cashmere goats are clean DW, MFD, and yearling LW (Pattie et al., 1990; Ponzoni and Gifford, 1990a). Therefore, research has been focused on evaluating the genetic relationships between these three traits and other fiber characteristics (Table 1.3).

Genetic correlations between live weight and fiber characteristics

Live weight and most fiber characteristics have a negative genetic correlation, except for FW. Live weight and greasy FW had a genetic correlation of 0.17 ± 0.18 and 0.17 ± 0.27 in two Australian studies (Pattie and Restall, 1989; Gifford et al., 1990). A larger positive correlation of 0.27 ± 0.33 between LW and greasy FW was reported by Bigham et al. (1992) for cashmere goats in New Zealand. These correlations do have high standard errors and were collected on goats that had been under management for only a short period of time (approx. 10 years);

therefore, additional research would be useful. However, it is logical that FW and LW have an allometric relationship (McGregor et al., 2012). As LW increases, FW would also increase simply due to the increase in size and available surface area to grow fiber.

Other fiber characteristics have a negative genetic correlation with LW. Live weight and DY had a genetic correlation of -0.24 ± 0.17 in feral goats in Australia (Pattie and Restall, 1989). In New Zealand, Bigham et al. (1992) reported a similar correlation between LW and DY of -0.22 ± 0.32. A more negative correlation of -0.39 ± 0.26 was reported by Gifford et al. (1990) for 10-month-old cashmere goats in Australia. A negative genetic correlation between LW and DY means that selection to increase LW would be accompanied with a decreased proportion of down in the greasy fleece. In a nutrition management study, cashmere goats fed to have lower LW had higher down yields, but less total down fiber compared to goats fed to have higher LW (McGregor, 1998). Therefore, it may be more favorable for producers to place selection focus on a different trait, such as clean DW, rather than DY.

The genetic correlation between clean DW and LW reported in Australian studies was -0.18 ± 0.17 and -0.13 ± 0.27 (Pattie and Restall, 1989; Gifford et al., 1990). For Scottish cashmere cross goats, the genetic correlation between LW and DW in a midside patch sample was -0.29 and -0.25 ± 0.10 (Bishop and Allain, 2000; Bishop and Russel, 1996). For cashmere goats in New Zealand, Bigham et al. (1992) reported a correlation of -0.34 ± 0.34 between clean DW and LW. The lowest correlation was reported by Bai et al. (2006) of -0.06 between LW and greasy DW of combed cashmere. Due to large standard errors associated with the correlation estimates, the genetic correlation between LW and DW does not appear to be different from zero. Additional research in very large populations with standardized phenotype collection may be required to more fully elucidate the genetic correlation between LW and DW.

The correlation between LW and DFL is unclear in literature. In Australia and New Zealand, the correlation between LW and DFL was -0.31 ± 0.17 and -0.32 ± 0.31, respectively (Pattie and Restall, 1989; Bigham et al., 1992). The estimate from Bigham et al. (1992) does have a large standard error associated with the estimate. Correlations from the UK and China differ compared to correlations reported in Australia and New Zealand. Bishop and Allain (2000) and Bishop and Russel (1996) reported a genetic correlation between DFL and LW in the UK of 0.02 and 0.02 ± 0.12, respectively. The estimate from Bishop and Russel (1996) was also associated with a large standard error providing no evidence the genetic correlation differs from zero. A similar correlation of 0.04 was published in China (Bai et al., 2006). Unfortunately, collection of length measurements is not standardized and would likely benefit from availability of a standardized performance recording guideline, such as those available for performance traits in other species (BIF Guidelines, 2024; ICAR Guidelines, 2024). Additionally, differing age of population samples (yearling, adults, or both) could have an influence on variance component estimates and make direct comparisons across studies difficult (McGregor, 2009). Due to the range of correlations published as well as high standard errors, the genetic correlation between LW and DFL is unclear but may be slightly negative.

Live weight and down diameter had a negative correlation of -0.16 ± 0.23 in Australian cashmere goats (Gifford et al., 1990). Bigham et al. (1992) found a genetic correlation of -0.25 ± 0.33 for cashmere goats in New Zealand. A very small negative correlation of -0.06 ± 0.18 was reported for Australian feral goats (Pattie and Restall,1989). However, these genetic correlations had large standard errors that overlapped zero which suggests that there is no genetic correlation between LW and down diameter. Three studies reported a genetic correlation of 0.03 between down diameter and LW (Bishop and Russel, 1996; Bishop and Allain, 2000; Bai et al., 2006).

Additional research is needed to elucidate the genetic correlation between down diameter and LW. However, current literature suggests that these traits are not correlated. This means that producers can select to decrease down diameter without sacrificing goat LW. This is favorable for cashmere producers as a lower MFD is more valuable.

Published genetic correlations between LW and down fiber characteristics are associated with large standard errors making it difficult to discern the true genetic relationships between these traits (Table 1.3). Additional research with larger study populations is needed to establish more precise correlation estimates for contemporary cashmere goat populations.

Genetic correlations between MFD and fiber characteristics

According to textile definitions**,** fiber must be less than 19 µm in diameter to be considered cashmere (FTC, 1939). As MFD decreases, the value of the fiber increases; therefore, fiber with a MFD even lower than 19 µm is sought after. Internationally, Chinese cashmere averages around 15 µm in diameter (Toigonbaev et al., 2023). There is opportunity for genetic improvement of MFD, especially for North American cashmere goats. However, the genetic relationships between MFD and other fiber characteristics need to be evaluated to avoid any unfavorable responses to selection in other correlated traits.

Mean fiber diameter and DY had a correlation of 0.57 ± 0.04 in a large group of feral goats in Australia (Pattie and Restall, 1989). This correlation estimate has one of the lowest standard errors compared to fiber characteristic correlations from other authors and between other traits. Other published correlations between MFD and DY are somewhat similar. Bigham et al. (1992) published the highest correlation of 0.70 ± 0.11. A group of yearling cashmere goats in Australia had a similar correlation of 0.63 ± 0.33 between MFD and DY (Couchman and Wilkinson, 1987). Baker et al. (1991) published the lowest genetic correlation of 0.30 ± 0.27

between MFD and DY. Although this study had a large number of animals in the analysis, the standard error for this correlation and others in this study are high. Differences in the magnitude of this correlation in the literature could be due to differences in fleece collection and processing methodology between studies. More current genetic correlation estimates between MFD and DY are needed in the literature, but historic estimates suggest that MFD and DY have a moderate to high positive correlation. This is unfavorable because genetic selection to decrease MFD will be accompanied by a decrease in DY, or proportion of down in a greasy fleece. Similarly, as producers select to increase DY, MFD would increase as well. The positive correlation between DY and MFD could be due to a bias in methodology where down that is coarser is reported to have a higher DY, even if there are not more down fibers. However, DY has little commercial value because producers are paid based upon total clean DW, rather than DY. It is likely more economically important to understand the genetic relationship between MFD and clean DW.

The genetic correlation MFD has with clean DW is similar in direction and magnitude to the correlation MFD has with DY. Pattie and Restall (1989) and Bishop and Russel (1996) reported similar correlations of 0.62 ± 0.03 and 0.65 ± 0.08, respectively. The same correlation of 0.81 was reported by Bishop and Allain (2000) and Bigham et al. (1992). Baker et al. (1991) found a correlation of 0.38 ± 0.28, but estimates from this study have large standard errors. A correlation between MFD and greasy DW of 0.77 ± 0.22 was reported for yearling goats in Australia (Couchman and Wilkinson, 1987). These estimates suggest that MFD and DW have a highly positive genetic correlation meaning that with selection to decrease MFD, cashmere goats will also produce less DW.

While most literature suggests a highly positive genetic correlation between MFD and DW, a few published estimates suggest there is no genetic correlation. Gifford et al. (1990)

reported a correlation of 0.04 ± 0.23 between MFD and clean DW. Similarly, Bai et al. (2006) found the correlation between MFD and greasy DW of combed cashmere for Inner Mongolia cashmere goats was 0.03. These two genetic correlation estimates are likely not different from zero. Bai et al. (2006) acknowledged that genetic correlations between all fiber traits found in their study were lower than previously published literature, with the genetic correlation between MFD and greasy DW being the most different. Bai et al. (2006) was one of the first to report this correlation for Chinese cashmere goats and suggested that differences in genetic structure, environment, and statistical modeling could be reasons for lower genetic correlations in their study. Additionally, the Chinese goats studied by Bai et al. (2006) were highly selected cashmere flocks whereas, Australian and New Zealand studies used unselected goats descending from feral flocks, making direct comparisons between studies difficult.

More recent literature reports a negative correlation between MFD and DW. Pallotti et al. (2018) reported a genetic correlation of -0.27 ± 0.20 between MFD and clean DW for Chinese Alashan Left Banner White cashmere goats. Similarly, cashmere goats indigenous to Kyrgyzstan had a genetic correlation of -0.22 ± 0.54 between MFD and greasy DW of combed cashmere (Toigonbaev et al., 2023). Both these estimates have large standard errors and are from cashmere goats in Asian countries. More recent data from Australia, New Zealand, and North America is needed to determine if the correlation between MFD and DW has changed over time or is dependent on cashmere breed and country of origin.

Literature suggests that MFD and DFL have an unfavorable correlation. Two studies of Scottish crossbred cashmere goats found the same genetic correlation (0.60) between MFD and DFL (Bishop and Russel, 1996; Bishop and Allain, 2000). A genetic correlation of 0.52 ± 0.04 was found for Australian feral goats (Pattie and Restall, 1989). In New Zealand, Bigham et al.

(1992) reported a genetic correlation of 0.75 ± 0.10 for yearling cashmere goats. More recently, Toigonbaev et al. (2023) found a genetic correlation of 0.48 ± 0.25 between MFD and DFL in cashmere goats indigenous to Kyrgyzstan. There is only one correlation estimate for MFD and DFL in literature that isn't moderate to highly positive, which was -0.01 (Bai et al., 2006). The genetic correlation between MFD and DFL appears to be moderate to highly positive. This means that selection to decrease MFD would also result in shorter DFL. In selection programs aimed to decrease MFD, selection for increased DFL may be needed to ensure that down fiber stays an appropriate length (greater than 3.175 cm). Incorporation of MFD and DFL into a selection index that accounts for this antagonistic genetic correlation would be one way to ensure that selection for one of these traits does not lead to the other trait entering an unacceptable range for breed or market standards.

Genetic correlations between down weight and fiber characteristics

Down yield and therefore clean DW are expensive traits to measure so an alternative way of measuring DW would be beneficial to producers and make phenotype collection easier. Evaluating genetic correlations between DW and fiber characteristics is one way that researchers have identified possible indicator traits for DW (Table 1.3).

Down length has been evaluated as a possible indicator trait for DW. Clean DW and DFL had a genetic correlation of 0.92 ± 0.06 in New Zealand (Bigham et al., 1992). This is the highest genetic correlation reported between DFL and DW. Similar correlations of 0.88 ± 0.02 and 0.89 were reported by Pattie and Restall (1989) and Bishop and Allain (2000), respectively. These correlation estimates could be so similar because they used similar measurement methodology. Bigham et al. (1992) and Pattie and Restall (1989) used the average length from three measurement sites on the body and Bishop and Allain (2000) measured once on the animals

midside. A smaller correlation of 0.57 between DW in a midside patch sample and DFL was reported for Scottish crossbred cashmere goats (Bishop and Russel, 1996). In China, Bai et al. (2006) reported an even smaller genetic correlation between greasy DW of combed cashmere and stretched unbent fiber length of 0.25. The most recent estimate in literature from Toigonbaev et al. (2023) found the genetic correlation between greasy DW and DFL was 0.16 ± 0.57 in a population of goats indigenous to Kyrgyzstan. Although this estimate is much smaller than previously published estimates, it is associated with a very large standard error. Based on the majority of estimates in the literature, DW and DFL are likely moderately to highly correlated.

The second trait that has been suggested as a possible indicator for DW is FW. Clean DW and FW had a moderate correlation of 0.39 ± 0.04 in Australian feral goats (Pattie and Restall, 1989). Another moderate correlation of 0.47 ± 0.30 was reported by Baker et al. (1991) for cashmere goats in New Zealand. Higher correlations between clean DW and FW have been reported in the literature. Gifford et al. (1990) found a correlation of 0.83 ± 0.08 for 10-month-old cashmere goats in Australia. A correlation of 0.71 ± 0.11 was reported for cashmere goats in New Zealand (Bigham et al., 1992). Greasy FW is multiplied by DY to calculate clean DW; therefore, there is a positive correlation between FW and DW due to the part-whole relationship (Bigham et al., 1992). Additionally, FW encompasses both DW and guard hair weight. Therefore, selection to increase FW aimed at increasing DW would also likely increase guard hair weight (Bigham et al., 1992). Thus, FW should not be used as an indicator trait for DW, unless an increase in hair weight can be tolerated (Baker et al., 1991; Bigham et al., 1992). In most cases, producers may permit increased hair weight if it is accompanied by increased DW. In those situations, utilizing FW as a practical method of improving DW is a viable option due to the high genetic correlation between the two traits.

Multi-trait Selection

Selection indices are a form of multi-trait selection that allows multiple traits to be selected for simultaneously while accounting for their relative values and the relationships between traits in the index. A selection index is a viable selection tool for cashmere breeders due to the genetically antagonistic relationships that exist between fiber traits, particularly involving MFD. A few selection indices have been proposed throughout time. Pattie and Restall (1987) proposed a two-stage selection index with the goal of screening a large number of animals on traits inexpensive to measure in the first stage. Then only the top proportion of animals that passed the first stage of the index were screened with the second stage of the index that involved traits which required laboratory analysis. Application of this selection index was evaluated relative to a single index that included all of these traits in the breeding objective and the two-stage index could be used without severely reducing the total economic gain. This result was partially due to the reduction in laboratory costs for fleece samples that no longer needed to be tested but the two-stage index resulted in goats with heavier, coarser fleeces (Ponzoni and Gifford, 1990b).

McGregor and Butler (2014) proposed indices that could be used to compare cashmere fleeces across farms, after little genetic progress in fiber traits for Australian cashmere goats was observed during the previous 25 years. One year later, indices based on biological value rather than market prices were published (McGregor and Butler, 2015). Producers could use these indices within herd to identify biologically efficient goats which have high clean cashmere weight in relation to MFD and SL (McGregor and Butler, 2015). More recently, economic selection indices were evaluated for Mongolian cashmere goats (Tseveenjav et al., 2020). The authors concluded that selection using a net merit economic index would result in desirable

change for both fiber characteristics and LW, and further development of these indexes would be useful in breeding programs.

Conclusion

Cashmere fiber has several important characteristics including MFD, clean DW, FW, DFL, and DY. Previously published literature suggests that these fiber characteristics are moderate to highly heritable. Published genetic correlations between LW and other fiber characteristics are not different from zero suggesting that selection for LW may not have a correlated response in other fiber traits. However, these genetic correlations were associated with large standard errors making it difficult to decern the genetic relationships. Additional research in larger populations with standardized phenotype collection should be done before these traits are incorporated into genetic evaluation programs. Mean fiber diameter has an unfavorable genetic correlation with all other fiber characteristics. Incorporation of these fiber traits into a properly weighted index would be a useful selection tool and benefit producers because it would allow producers to make selection decisions without concern for the antagonistic relationships between the fiber traits. Lastly, DW has a high genetic correlation with FW and DFL. Therefore, either FW or DFL could be useful indicator traits for selection of DW because these traits are easier and less expensive to measure. In general, heritabilities and genetic correlation estimates were associated with a high standard error or are decades old, suggesting that more recently published estimates are needed before generating a selection index.

Table 1.1. Definition of cashmere production traits.

Trait	Definition
Mean fiber diameter, µm	Average fiber diameter of tested sample
Down fiber length, inch or cm	Length of a single cashmere down fiber in a relaxed state
Staple length, inch or cm	Length of cashmere staple
Clean down weight, g	Total weight of cashmere down after cleaning and processing; =Greasy fleece weight * clean down yield (%)
Greasy down weight, g	Total weight of cashmere before cleaning and processing, including grease and other natural contaminants
Guard hair weight, g	Total weight of guard hair (coarser fiber produced by primary follicles)
Greasy fleece weight, g	Total weight of entire fleece
Clean down yield, %	$= \frac{Clean\ down\ weight}{Greasy\ fleece\ weight} * 100$
Live weight, lb or kg	Goat bodyweight at time of measurement

Table 1.2. Heritability estimates for cashmere production traits.

Trait	Heritability ± SE	Source	n	Animal age	Mean live weight at assessment (kg)	Country
Mean fiber diameter	0.99 ± 0.19	Bigham et al., 1993	806	Yearling	16.3	New Zealand
	0.19 ± 0.07	Bigham et al., 1993	270	Kid	11.8	New Zealand
	0.63 ± 0.07	Bishop and Russel, 1996	1,298	5-month kid	16.1	Scotland
	0.47 ± 0.15	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.70 ± 0.19	Gifford et al., 1990	1,320	10-month-old	15.5-18.6[2]	Australia
	0.68 ± 0.23	Couchman and Wilkinson, 1987	375	Yearling feral herd	Not reported	Australia
	0.82 ± 0.23	Baker et al., 1991	624	Yearling	18.2	New Zealand
	0.32	Zhou et al., 2002	4,949	Various ages	28.3	China
	0.28	Bai et al., 2006	3,608	Various ages	28.5	China
	0.14	Jinquan et al., 2001	598	Various ages	26.5-30.7[3]	China
	0.41 ± 0.08	Pallotti et al., 2018	1,375	Yearling	Not reported	China
	0.39 ± 0.16	Rose et al., 1992	487	10-month-old	21.4-23.4[2]	Australia
	0.58 ± 0.16	Toigonbaev et al., 2023	332	Yearling	23.2	Kyrgyzstan
	0.40 ± 0.06	Wang et al., 2015	3,206	Yearling	Not reported	China
	0.29 ± 0.09	Wang et al., 2015	821	5-year-old	Not reported	China
	0.64	Bishop and Allain, 2000	2,831	5-month kid	16.8	Scotland
	0.36 ± 0.03	Rong et al., 2024	3,842	Rams and ewes, age 1-3 years old	Not reported	China
	0.22 ± 0.02	Yan et al., 2024	2,256	Rams and ewes, age 18 years old	Not reported	China
Down fiber length	0.57 ± 0.15	Bigham et al., 1993	815	Yearling	16.3	New Zealand
	0.87 ± 0.29	Bigham et al., 1993	271	Kid	11.8	New Zealand

	0.70 ± 0.19	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.23	Zhou et al., 2002	4,949	Various ages	28.3	China
	0.21	Bai et al., 2006	3,607	Various ages	28.5	China
	0.19 ± 0.04	Wang et al., 2015	3,257	Yearling	Not reported	China
	0.18 ± 0.08	Wang et al., 2015	810	5-year-old	Not reported	China
	0.50 ± 0.24	Toigonbaev et al., 2023	200	Yearling	32.2	Kyrgyzstan
	0.56	Jinquan et al., 2001	4,786	Various ages	26.5-30.7[3]	China
	0.57	Bishop and Allain, 2000	2,097	5-month kid	16.8	Scotland
	0.49 ± 0.15	Bishop and Russel, 1996	521	5-month kid	16.1	Scotland
Staple length	0.29	Bai et al., 2006	5,274	Various ages	28.5	China
	0.32	Jinquan et al., 2001	4,786	Various ages	26.5-30.7[3]	China
Clean down weight	0.62 ± 0.15	Bigham et al., 1993	808	Yearling	16.3	New Zealand
	0.20 ± 0.07	Bigham et al., 1993	266	Kid	11.8	New Zealand
	0.39 ± 0.05	Bishop and Russel, 1996	1,321	5-month kid	16.1	Scotland
	0.61 ± 0.18	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.36 ± 0.13	Gifford et al., 1990	1,320	10-month-old	15.5-18.6[2]	Australia
	0.57 ± 0.19	Baker et al., 1991	623	Yearling	18.2	New Zealand
	0.12 ± 0.03	Pallotti et al., 2018	1,375	Yearling	Not reported	China
	0.61 ± 0.21	Rose et al., 1992	487	10-month-old	21.4-23.4[2]	Australia
	0.61	Bishop and Allain, 2000	2,841	5-month kid	16.8	Scotland
Greasy down weight	0.38 ± 0.17	Couchman and Wilkinson, 1987	375	Yearling feral herd	Not reported	Australia
	0.28	Zhou et al., 2002	11,406	Various ages	28.3	China
	0.30	Bai et al., 2006	5,289	Various ages	28.5	China

	0.12 ± 0.12	Toigonbaev et al., 2023	240	Yearling	32.2	Kyrgyzstan
Guard hair weight	0.35 ± 0.12	Bigham et al., 1993	808	Yearling	16.3	New Zealand
	0.04 ± 0.04	Bigham et al., 1993	266	Kid	11.8	New Zealand
Greasy fleece weight	0.42 ± 0.13	Bigham et al., 1993	814	Yearling	16.3	New Zealand
	0.14 ± 0.06	Bigham et al., 1993	266	Kid	11.8	New Zealand
	0.29 ± 0.11	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.45 ± 0.18	Couchman and Wilkinson, 1987	375	Yearling feral herd	Not reported	Australia
	0.31 ± 0.14	Baker et al., 1991	654	Yearling	18.2	New Zealand
	0.42 ± 0.16	Gifford et al., 1990	1,320	10-month-old	15.5-18.6[2]	Australia
	0.67 ± 0.22	Rose et al., 1992	487	10-month-old	21.4-23.4[2]	Australia
Down yield	0.57 ± 0.15	Bigham et al., 1993	812	Yearling	16.3	New Zealand
	0.19 ± 0.07	Bigham et al., 1993	270	Kid	11.8	New Zealand
	0.90 ± 0.23	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.23 ± 0.11	Gifford et al., 1990	1,320	10-month-old	15.5-18.6[2]	Australia
	0.64 ± 0.21	Baker et al., 1991	623	Yearling	18.2	New Zealand
	0.26	Jinquan et al., 2001	4,998	Various ages	26.5-30.7[3]	China
	0.57 ± 0.20	Rose et al., 1992	487	10-month-old	21.4-23.4[2]	Australia
Greasy down yield	0.30 ± 0.15	Couchman and Wilkinson, 1987	375	Yearling feral herd	Not reported	Australia
Primary follicle density	0.16 ± 0.11	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
Secondary follicle density	0.17 ± 0.11	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia

Secondary/ Primary follicle density ratio	0.29 ± 0.15	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
Live weight	0.71 ± 0.08	Bishop and Russel, 1996	1,245	5-month kid	16.1	Scotland
	0.29 ± 0.10	Pattie and Restall, 1989	1,169	Feral Australian goats, various ages and sex	13.7-37.9[1]	Australia
	0.26 ± 0.11	Gifford et al., 1990	1,320	10-month-old	15.5-18.6[2]	Australia
	0.10	Zhou et al., 2002	10,760	Various ages	28.3	China
	0.07	Bai et al., 2006	5,048	Various ages	28.5	China
	0.16	Jinquan et al., 2001	4,769	Various ages	26.5-30.7[3]	China
	0.33 ± 0.15	Rose et al., 1992	487	10-month-old	21.4-23.4[2]	Australia
	0.25	Bishop and Allain, 2000	2,856	5-month kid	16.8	Scotland

[1]depending on age and sex
[2]depending on sex
[3]depending on phase (differing years)

Table 1.3. Summary of published genetic correlations between cashmere fiber characteristics (standard error)*.

		Study									
Trait 1	**Trait 2**	Pattie and Restall (1989)[1]	Gifford et al. (1990)[2]	Bishop and Allain (2000)[3]	Bai et al. (2006)[1]	Bishop and Russel (1996)[3]	Bigham et al. (1992)[4]	Couchman and Wilkinson (1987)[4]	Baker et al. (1991)[4]	Pallotti et al. (2018)[4]	Toigonbaev et al. (2023)[4]
Live weight	Fleece weight	0.17 (0.18)	0.17 (0.27)				0.27 (0.33)		0.10		
	Down yield	-0.24 (0.17)	-0.39 (0.26)				-0.22 (0.32)		-0.20		
	Down weight	-0.18 (0.17)	-0.13 (0.27)	-0.29	-0.06	-0.25 (0.10)	-0.34 (0.34)		-0.17		
	Mean fiber diameter	-0.06 (0.18)	-0.16 (0.23)	0.03	0.03	0.03 (0.12)	-0.25 (0.33)		-0.14		
	Down length	-0.31 (0.17)		0.02	0.04	0.02 (0.12)	-0.32 (0.31)				
Mean fiber diameter	Fleece weight	0.39 (0.05)	0.12 (0.23)				0.69 (0.13)	0.48 (0.11)	0.13 (0.30)		
	Down yield	0.57 (0.04)					0.70 (0.11)	0.63 (0.33)	0.30 (0.27)		
	Down weight	0.62 (0.03)	0.04 (0.23)	0.81	0.03	0.65 (0.08)	0.81 (0.08)	0.77 (0.22)	0.38 (0.28)	-0.27 (0.20)	-0.22 (0.54)
	Down length	0.52 (0.04)		0.60	-0.01	0.60 (0.14)	0.75 (0.10)				0.48 (0.25)
Down weight	Fleece weight	0.39 (0.04)	0.83 (0.08)				0.71 (0.11)		0.47 (0.30)		
	Down length	0.88 (0.02)		0.89	0.25	0.57	0.92 (0.06)				0.16 (0.57)
	Down yield	0.84 (0.02)	0.85 (0.08)				0.94 (0.03)	0.80 (0.30)	0.86 (0.08)		

*If a table cell is blank, no correlation was reported in that study for that specific correlation.
[1]Various ages
[2]10-month-old
[3]5-month-old kid
[4]Yearling

Chapter 2 - Genetic parameter estimation and genome-wide association study of fiber characteristics for cashmere goats in the United States

Introduction

Cashmere, one of the finest and softest animal fibers (McGregor, 2014), is the down produced from the secondary hair follicles of some goats. Cashmere-type goats originated throughout the Himalayan region, and China and Mongolia currently produce approximately 85% of the world's cashmere (Van Der Westhuysen, 2005). However, cashmere production also occurs in other countries including Australia, New Zealand, the United Kingdom, and the United States. The cashmere industry in the United States is relatively new, but it is an important commodity to small stakeholders. Production occurs across the entire U.S., predominantly from relatively small operations, rather than large-scale commercial enterprises. Many breeds of goats can grow down fiber. However, only fiber that meet certain standards can be marketed as cashmere; primarily, fiber must not exceed a mean fiber diameter (MFD) of 19 μm in the United States (FTC, 1939).

Fiber characteristics such as MFD, measures of diameter variation such as standard deviation (SDD) and coefficient of variation (CVD), curvature (CURV), length and weight are important in cashmere production. The genetic parameters associated with these economically relevant fiber phenotypes and others have been studied in populations across the world including China, New Zealand, the United Kingdom, Australia, and Kyrgyzstan. Estimated heritabilities of these fiber traits vary widely across studies, both within and between countries (as reviewed by Dressler et al., 2024). For example, the estimated heritability of MFD in Australian studies ranges from 0.39 ± 0.16 to 0.70 ± 0.19 (Couchman and Wilkinson, 1987; Pattie and Restall,

1989; Gifford et al., 1990; Rose et al., 1992). In contrast, the heritability of MFD reported in studies from China range from 0.14 to 0.41 ± 0.08 (Jinquan et al., 2001; Zhou et al., 2002; Bai et al., 2006; Wang et al., 2015; Pallotti et al., 2018). Heritability estimates may differ for a variety of reasons, such as differences in selection history, population structure, breed, statistical modeling, or trait measurement technique.

Although cashmere fiber traits have been evaluated in other countries, no genetic analyses have been published in the United States. Further, the United States lacks a national genetic evaluation program for cashmere traits, which remains a key challenge for U.S. cashmere producers. The only selection tools U.S. cashmere producers currently have are phenotypic selection and/or selection with pedigree information (Rupp et al., 2016). This has hindered the breeding progress possible for producers (Shumbusho et al., 2013; Shumbusho et al., 2016). Thus, U.S. cashmere producers would greatly benefit the development of a national genetic evaluation program for cashmere fiber traits. Establishing such a program requires foundational research on genetic parameters in U.S. cashmere populations.

The objective of this study was to estimate the heritability of economically relevant cashmere fiber traits, estimate the phenotypic and genetic correlations between fiber traits, and perform a genome-wide association study (GWAS) to identify regions of the genome associated with fiber traits for cashmere goats in the United States.

Materials and Methods

Study population and design

Animal procedures on Langston University goats were performed as a part of Langston University Institutional Animal Care and Use project number OKLUMERKEL2020, experiment number RM-22-03 in accordance with Federation of Animal Science Societies guidelines (FASS,

2010). Data from other U.S. cashmere goats were collected by producers with normal animal management processes, therefore Animal Care and Use Committee approval was not required.

Thirty-two cashmere producers located across the continental United States voluntarily contributed data to this study. Cashmere flocks that participated in this study were located in 17 different states (Table 2.1; Figure 2.1). In exchange for participation in this study, participants received the genotype and fiber testing results for animals in their flock at no cost. A total of 1,248 records from 1,040 cashmere goats were available. All sexes were used in the study: wether (n= 191, 242 records), doe (n= 720, 845 records), and buck (n=128, 160 records). The age at cashmere collection ranged from 0.17 years (~2 months) to 18.7 years, but the average was 2.72 years and median was 1.83 years.

Fiber test

Collaborating producers collected fiber samples between December 2021 and May 2024 during cashmere harvest. Fiber samples were collected by clipping a 2 inch by 2 inch fiber sample from the mid-side (McGregor, 1994) of each goat. Mid-side samples are the best single predictor of overall fleece characteristics (Couchman and McGregor, 1983). A mid-side sample is clipped above the last rib with standard hair clippers. A size 30 clipping blade or similar was used to retain the full length of the clip. Producers individually packaged and labeled cashmere samples for submission to the testing laboratory. During sample collection, some producers measured staple length (SL; mm) and total fleece weight (FW; g). Staple length was measured on the clipped, unstretched fiber sample using a ruler. Fleece weight was measured using a scale for the entire greasy fleece after harvest, with nearly all fleeces collected by shearing and a small number (n=22) by hand combing.

Fiber samples were sent to the Texas A&M Bill Sims Wool and Mohair Research Laboratory in San Angelo, Texas. Analysis of the cashmere fiber was done with an Optical Fibre Diameter Analyser 100 (OFDA 100; Baxter et al., 1992). The OFDA 100 was introduced in the early 1990's to analyze fiber characteristics of wool, but the instrument can also be used to evaluate cashmere fiber. Samples were processed upon arrival at the laboratory in preparation for testing with the OFDA 100 including 'guillotining' samples into short ~2mm snippets, washing and drying samples to remove grease, dirt, and other impurities, and arranging snippets on a slide for analysis.

The fiber characteristics analyzed by the OFDA 100 were MFD, SDD, CVD, coarse edge micron (CEM), CURV, standard deviation of curvature (SDCurv), and spinning fineness (SpinF). A frequency histogram was also generated by the OFDA 100 for each sample. The frequency histogram specifies the total number of fibers present in the sample at each 1 µm diameter interval from 4 µm to 27 µm (12/5/2023 to 01/25/2024; 68 records) or 4 µm to 30 µm (all other records). Using the diameter frequency histogram data, the trait Percentage ≤ 19µm (Perc_19) was calculated. Cashmere fiber trait definitions are in Table 2.2.

Genotype information

Collaborating cashmere producers provided DNA samples for genotyping via a hair sample. Producers were encouraged to collect the hair samples at the same time as the mid-side fiber sample was clipped. Hair samples for genotyping were collected by the producer from each goat by plucking ~20 guard hairs from the tail or spinal ridge, ensuring that the follicle was still attached at the base. Hair samples were sent to Neogen Corporation (Lincoln, NE) for DNA extraction and genotyping. DNA samples were genotyped on the Goat GGP 70K BeadChip (Version 1; Neogen Corp.). A total of 1,462 genotypes were available on 1,036 U.S. animals and

426 related New Zealand animals, but phenotypes and pedigree from New Zealand animals were not utilized in this analysis. Genotypes from animals with a call rate less than 0.90 were removed, leaving 1,372 genotyped animals for analysis. Genotypes were further filtered for quality control by removing 4,393 single nucleotide polymorphisms (SNPs) with minor allele frequency less than 0.05 and 9,449 SNPs with a SNP call rate less than 0.90. The number of SNPs remaining for analysis was 54,363.

Pedigree information

Available pedigree information was provided by collaborating cashmere producers. The depth of the provided pedigree was variable, but included all available pedigree information. The number of generations in the pedigree ranged from 1 to 5 and the final pedigree included 1,910 animals from 26 farms. Pedigree connectedness among farms was primarily through shared male germplasm, with 24 sires used on more than one farm.

Statistical analysis

Summary statistics including minimum, mean, maximum, and standard deviation were calculated in R Studio (RStudio Team, 2023). Phenotypic correlations between fiber characteristics were calculated in SAS v9.4 using the PROC CORR function.

Established scientific literature indicates factors such as age at sampling, birth type, rearing type, liveweight at sampling and sex influence cashmere fiber production (James, 2009; Wang et al., 2019). All available factors were extracted from the data and used in model selection for each fiber trait. Forward stepwise selection was used to select the model with the best fit. Model fit was assessed with Akaike information criterion (AIC) where the model was considered final when the addition of another variable did not reduce AIC by at least 3.
The base model for each trait was as follows:

$$y_i = b_0 + e_i$$

where y_i is the fiber trait being evaluated, b_0 is the intercept, and e_i is the residual. The following fixed effects were tested with forward selection: sex (doe, buck, wether), age at cashmere collection (yrs), liveweight (kg) and contemporary group (farm x fiber testing year). Liveweight was only reported by a portion of participating cashmere producers resulting in only 631 out of 1,243 records with a liveweight observation. Therefore, model selection was conducted in two ways: one considering liveweight as a possible fixed effect, and the other excluding liveweight. This was done to assess the importance of including liveweight as a fixed effect, while also considering the limitations of using a much smaller dataset. To directly compare the inclusion of liveweight versus age at collection, two univariate genetic evaluations of MFD were run on a subset of the data which had records available for all possible fixed effects (n=536). Both models included the other significant fixed effects for MFD including sex and contemporary group; one model also included liveweight (not age at collection), and the other also included age at collection (not liveweight). Final models for MFD, CVD, and SDCurv included the fixed effects of contemporary group, age at collection, and sex. Contemporary group and age at collection were the fixed effects included in the final model for SDD, CEM, SpinF, and Perc_19. Final models for CURV and SL included contemporary group and sex. Sex was the only significant fixed effect included in the model for FW.

Genetic parameter estimation

For all traits, variance components were estimated using average information restricted maximum likelihood in the BLUPF90 suite programs (Misztal et al., 2014). Single-step genomic BLUP was used where the numerator relationship matrix, $\mathbf{A}^{-1}$ is replaced by $\mathbf{H}^{-1}$ (Aguilar et al., 2010) as follows:

$$\boldsymbol{H^{-1}} = \boldsymbol{A^{-1}} + \begin{bmatrix} 0 & 0 \\ 0 & \boldsymbol{G^{-1}} - \boldsymbol{A_{22}^{-1}} \end{bmatrix}$$

where **H** is the relationship coefficients matrix between animals, **A** is the additive relationship matrix, $\mathbf{A}_{22}$ is the numerator relationship matrix for genotyped animals, and **G** is the genomic relationship matrix (VanRaden, 2008) as **G= ZZ'**, where:

$$\mathbf{Z} = \frac{\mathbf{M} - \mathbf{P}}{\left[2\Sigma \mathrm{p_j}(1 - \mathrm{p_j})\right]^{\mathbf{1/2}}}$$

where **Z** is the centered genotype matrix, **M** is the matrix of marker genotypes for each individual (coded as 0, 1, 2 copies of the second allele), and **P** is the matrix of $2\mathrm{p_j}$ (frequency of second allele, p, at locus *j*).

First, a univariate single record analysis was performed with only the first record available from each animal included in the analysis. The general univariate animal models were:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + e$$

where y is a vector of dependent variables, b is a vector of fixed effects selected from forward selection (Table 2.3), u is a vector of direct additive genetic effects, e is a vector of random residuals and **X** and **Z** are incidence matrices for b and u, respectively.

Next, bivariate animal models were run with each pairwise combination of fiber traits to obtain genetic correlations. Then, a repeated records analysis was run for each trait which included every fiber record available using the following animal model:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + \boldsymbol{W}p + e$$

where elements are the same as the previous animal model with the addition of **W**, the incidence matrix relating p to y, and p which is a vector of permanent environmental effects.

Genome-wide association study

For each trait, the SNP effects were obtained from the single record univariate analysis. The postGSf90 program within the BLUPF90 program suite (Misztal et al., 2014) was used to estimate SNP effects, prediction error variance, and *P*-values. A single-step GWAS was done to predict SNP effects as follows (Wang et al., 2012):

$$a = \boldsymbol{Z}u$$

where a is a vector of breeding values for genotyped animals, Z is a matrix relating genotypes of each locus, and u is a vector of SNP effects. The variances are as follows:

$$\text{var}(a) = \text{var}\,(\boldsymbol{Z}u) = \boldsymbol{G}\sigma_a^2 = \boldsymbol{ZIZ}'\lambda$$

where I is an identity matrix, λ is the variance ratio for SNP effects and breeding values, and a, u, **G**, and **Z** were defined previously (Masuda, 2025).

The prediction of SNP effects is as follows:

$$\hat{u} = \boldsymbol{IZ}'(\boldsymbol{ZIZ}')^{-1}\hat{a}$$

where $\hat{u}$ is a vector of SNP effects, $\hat{a}$ is a vector of breeding values, and **I** and **Z** were defined previously (Masuda, 2025).

False discovery rate was calculated for each SNP using the q-value package in R (Storey et al., 2023) and no SNPs were significant at a threshold of < 0.05. A suggestive significance threshold of -$\log_{10}$ *P*-value ≥ 4 was set for identifying SNPs of interest. Manhattan plots of the SNP effects were created using the qqman package in R (Turner, 2018).

Quantitative trait loci (QTL) regions of ± 50 kb were formed around significant SNP positions to account for linkage disequilibrium in the caprine genome (Brito et al., 2015). The GALLO package in R (Fonseca et al., 2020) and the National Center for Biotechnology Information Capra hircus GFF annotation file for the USDA ARS 1.2 genome assembly (Bickart

et al., 2017; accession GCF_001704415.2) was used to identify genes within each QTL region. The UniProt Consortium (2023) was used to identify molecular and biological gene functions. The QTL regions were compared with previously reported trait associations in the Goat QTLdb (Hu et al., 2022). Because there are far fewer genomic studies in goats compared to other livestock species, gene candidates were searched in the Sheep QTLdb to identify previous associations with traits in sheep.

Results and Discussion

Model selection

The results of both model selection approaches are described in Appendix Table A.1. When considered, liveweight was a significant fixed effect in model selection for MFD, CVD, SDCurv, SpinF, FW and Perc_19, while age at collection was not, with the exception of SDCurv where both liveweight and age at collection were significant. However, when liveweight was not considered, age at collection was a significant fixed effect and replaced liveweight or both liveweight and sex for all traits except FW. To directly compare the inclusion of liveweight against age at collection, the variance components and heritability estimates were compared between the two univariate genetic evaluations of MFD ran on the subset of data which had records for all possible fixed effects: the two models included either liveweight or age at collection in addition to other significant fixed effects. The inclusion of liveweight resulted in higher heritability (0.44 ± 0.09 vs. 0.39 ± 0.09) and greater partitioning of variance to genetic instead of residual compared to the model that included age at collection. However, a final model for MFD that included age at collection instead of liveweight allowed for a much larger dataset. Using the full dataset available, the model including age at collection, contemporary group, and sex had the highest heritability estimate and smallest standard error (0.49 ± 0.07), and the

greatest genetic variance across the models considered. Due to the substantial reduction in sample size from including liveweight as a fixed effect in the current dataset, final models did not include liveweight. These results suggest that liveweight is likely an important effect for modeling cashmere traits and in the future, particularly for the purposes of a national genetic evaluation, more cashmere producers should consider weighing their goats at cashmere harvest.

Summary statistics

Summary statistics for fiber trait phenotypes are presented in Table 2.4. The average MFD was 15.34 µm for this population of goats. MFD is a determinant of fiber quality, and is one of the most economically relevant traits for cashmere production because textile standards often specify a threshold for MFD. The average MFD in this population is below the maximum threshold for fiber to be considered cashmere, which is 19 µm. The average MFD in this study is very similar to the average reported by Pattie and Restall (1989), which was 15.4 µm. The population of goats studied by Pattie and Restall (1989) was an Australian feral, unselected population of goats. Cashmere goats in the U.S. primarily originate from Australia and New Zealand, and were first imported in the late 1980's (OSU, 2025). In contrast, a mean MFD of 13.59 µm was reported by Bai et al. (2006) for a population of Inner Mongolia White Cashmere goats, which is lower than the average from this study. The Inner Mongolia Cashmere goat is one of the major cashmere goat breeds in China and is known for its extremely fine fiber. Therefore, it is logical that studies in China would have smaller MFD than studies in Australia and the U.S.

The average SDD was 3.17 µm. This trait explains diameter variability, which is important because it affects spinning quality and yarn uniformity (Lupton, 1995). The average SDD in this study is very similar to the average of 3.35 µm reported by Bishop and Russel (1996). Goats in that study were Scottish feral goats mated to imported germplasm from Iceland,

Tasmania, New Zealand, and Siberia. In another study using a subset of the same animals as Bishop and Russel (1996), a lower average SDD of 2.9 µm was reported (Bishop and Allain, 2000). Gifford et al. (1990) reported average SDD across different sexes, birth types, and ages, with values ranging from 3.6 to 3.9 µm, which is slightly larger than the average in the current study.

Diameter coefficient of variation had an average of 20.67%. Both SDD and CVD are measures of variability in fiber diameter. SDD indicates the spread around the mean in absolute terms (µm), whereas CVD indicates the variability relative to the mean, which provides a more standardized measure of variability. In general, CVD is not widely utilized in scientific literature. However, a similar CVD of 22.5% was reported by McGregor and Butler (2010) for Australian goats. Averages for CVD based on sex and cohort ranged from 27.09 to 41.39 % in a study of Left Banner Alashan White Cashmere goats (Pallotti et al., 2018), which is more variable than current study possibly due to harsher and more variable environments in Inner Mongolia.

Fiber curvature had an average of 67.76 º/mm. Fibers with greater curvature are associated with more efficient fiber processing however, lower curvature is associated with softer fiber (McGregor, 2004; McGregor and Butler, 2008a). Because of this, breeding objectives for CURV may differ between producers depending on their desired end product for the cashmere fiber. Traditional cashmere-producing regions (e.g., Iran, Afghanistan, Mongolia, and China) typically have greater fiber CURV compared to regions where production has been more recently established, such as Australia, New Zealand, and the U.S. (McGregor and Butler, 2009). The average CURV of Australian goats was 48 º/mm as reported by McGregor and Butler, (2010). This is lower than the average in the current study, so these goats would be expected to have softer fibers that may be slightly more difficult to process.

The average SDCurv was 40.81 º/mm. Fiber curvature standard deviation is not a frequently measured fiber trait and has only become available since the adoption of the OFDA100 and newer fiber testing equipment (McGregor and Butler, 2010). A study of Australian goats reported a slightly lower average SDCurv of 33 º/mm indicating that animals in this population had fibers with less variation in curvature compared to the current study's population (McGregor and Butler, 2010).

Staple length had an average of 60.34 mm, which is substantially shorter than lengths reported in other studies. Average staple length of sheared cashmere goats across 11 farms in Australia was 87 mm (McGregor and Butler, 2008b). Combed Inner Mongolia cashmere goats had an average staple length of 168.6 mm across 11,854 records (Bai et al., 2006). The method used to harvest cashmere can influence staple length, with combing generally producing longer staples compared to shearing which could be one reason average SL is shorter in this study compared to others.

The average greasy FW was 237.8 g, however only 260 records had a FW recorded. A slightly lower average FW of 216 g was reported for New Zealand yearling cashmere goats (Bigham et al., 1993). Female and male progeny of feral Australian goats had average FW of 287 g and 338 g, respectively (Restall and Pattie, 1989). More recently, average greasy FW of Australian cashmere goats across 11 farms was reported as 394 g, which suggests that improvement in FW has been made in Australian populations (McGregor and Butler, 2008b). The average FW of these U.S. goats is most similar to the primarily unselected feral Australian goats from the 1980's, indicating substantial potential for genetic improvement in U.S. populations.

Course edge micron, SpinF, and Perc_19 had averages of 6.16 µm, 14.90 µm, and 87.51% respectively. These traits have not been widely studied and currently lack information in the literature to make comparisons.

Heritability and repeatability of cashmere fiber traits

Single record heritability estimates from the univariate analysis are on the diagonal of Table 2.5 and from each bivariate analysis in Table 2.6. For all traits, the heritability estimate from the single record univariate analysis was very similar to the average heritability of single record bivariate analyses. Heritability and repeatability estimates from the repeated records analysis are in Table 2.7. In general, heritability estimates were similar between the single record and repeated records analyses for each trait, except for FW. The heritability estimates for FW differed considerably between the univariate single record and repeated records analyses, which may be due to the very small number of FW records available in the single record analysis.

The univariate single record and repeated records heritabilities for MFD were 0.49 ± 0.07 and 0.54 ± 0.06, respectively. The repeatability was 0.76 ± 0.03. The heritability of MFD is generally moderate to highly heritable in literature, despite many factors that could influence estimates. Pattie and Restall, (1989) reported a heritability and repeatability for MFD of 0.47 ± 0.15 and 0.60 ± 0.02, respectively. This heritability estimate is similar to the current study, while the repeatability is slightly lower. There were differences in population and fiber analysis machinery between this study and the current study, which could contribute to the slight differences. In China, Pallotti et al. (2017) reported a similar MFD heritability of 0.41 ± 0.08. Lower heritabilities were reported in other Chinese studies of 0.36 ± 0.03, 0.32 and 0.28 (Rong et al., 2024, Zhou et al., 2002, and Bai et al., 2006). Differences in animal age at collection and cashmere collection method could be reasons for differences in estimates.

Measures of fiber diameter uniformity (SDD and CVD) had moderate univariate heritabilities in both the single record and repeated records analyses (Table 2.5 and 2.7). Repeatability of SDD and CVD was high (Table 2.7). The heritability of SDD for 5-month-old kids in two studies were 0.43 ± 0.08 and 0.28 (Bishop and Russel, 1996; Bishop and Allain, 2000). 10-month-old Australian cashmere goats had a heritability of 0.38 ± 0.14 for SDD (Gifford et al., 1990). These estimates are similar to those reported in the current study for SDD, especially considering the standard errors associated with the estimates. Compared to SDD, there is less literature available about CVD. Pallotti et al., (2018) reported a higher heritability for CVD (0.52 ± 0.06) compared to the current study.

Coarse edge micron had similar moderate heritability estimates in both the single and repeated records analyses and high repeatability (Table 2.5 and 2.7). Several different descriptors of the coarse edge of the fiber diameter distribution have been described (Whiteley and Thompson, 1985). In the current study, CEM is defined as the number of micron above the MFD at which the coarsest 5% of fibers begin. For example, the average MFD in the dataset is 15.34 μm and the average CEM is 6.16 μm, meaning that on average the coarsest 5% of fibers begin at 21.5 μm. Lower CEM values indicate a more consistent, finer fiber, and higher values indicate a broader distribution of fiber diameter with more coarse fibers. Others have defined coarse edge as the percentage of fibers with diameters above a threshold, usually 30 or 35 μm. There are no heritability estimates in the literature for cashmere using the same CEM definition to compare results.

Heritability and repeatability of CURV were high (Table 2.5 and 2.7). Style refers to the subjective assessment of fiber crimp characteristics, with curvature being a key contributing factor (McGregor, 2007). The fiber style category of Faure Island cashmere goats at 10 and 17

months of age had heritabilities of 0.27 ± 0.11 and 0.38 ± 0.12, respectively (McGregor, 1997). This is lower than the current study, but differences could be expected because these are not the exact same traits. Heritability estimates in literature for cashmere fiber CURV are limited; however, our estimates are similar to CURV heritabilities measured in other species. A study of alpacas with extremely fine fiber (average MFD= 16.67 μm) in the U.S. reported a heritability for fiber CURV of 0.50 (Wuliji, 2017). In Merino sheep, similar heritability (0.39 ± 0.04) and repeatability (0.64 ± 0.02) estimates for CURV were reported by Mortimer et al. (2017) and Hatcher and Atkins (2000), respectively.

In both the single and repeated records analysis, the univariate heritability of SDCurv was moderate (Tables 2.5 and 2.7). The repeatability of SDCurv was 0.51 ± 0.07, which is high, but not as high as the other fiber characteristics in this study (Table 2.7). Interestingly, SDCurv was less heritable than CURV. The range in fixed effect solutions for contemporary group (farm x year) was substantial (26.35 to 61.40) with a standard deviation of 7.85, indicating considerable variation in SDCurv across contemporary groups. This supports the findings of McGregor and Butler (2010), who reported that SDCurv varied largely by farm, and accounted for 41% of the phenotypic variation in SDCurv. As with CURV, literature on genetic parameters associated with SDCurv is scarce, so comparisons of heritability and repeatability estimates is not possible.

The single record and repeated records univariate heritabilities of SpinF were 0.45 ± 0.07 and 0.48 ± 0.07, respectively. The repeatability of SpinF was 0.76 ± 0.03. In their foundational paper on SpinF, Butler and Dolling (1992) proposed an approach to approximate the heritability of SpinF using the phenotypic and genetic parameters of MFD and CVD, rather than SpinF itself. Derived heritabilities were 0.43, 0.56, and 0.70, varying with the application of the methodology to different sets of previously published estimates (Butler and Dolling, 1992). Two

of these estimates are greater than the heritability in the current study, which could be because they were derived from other parameters instead of directly estimated.

The univariate heritability of SL in both the single record and repeated records analysis was moderately high (Table 2.5 and 2.7). In contrast to most other traits where repeatability was much higher than the heritability, the repeatability for SL was similar to the heritability (Table 2.7). Inner Mongolia cashmere goats had heritability estimates for SL of 0.32 and 0.29 (Jinquan et al., 2001 and Bai et al., 2006, respectively). However, SL measurement methods used in these two studies are unclear, which may contribute to differences in estimates compared to the current study. Additionally, Inner Mongolia cashmere goats have experienced different selection and management than the US goats in this study. Down fiber length is more commonly reported in cashmere studies and is generally moderate to highly heritable, though there is a wide range of published estimates (as reviewed by Dressler et al., 2024). These estimates are not directly comparable to the current study because down fiber length refers to the length of only the fine undercoat fibers, typically after dehairing. In contrast, staple length is the length of an entire lock or cluster of fibers and reflects a more general fleece trait measured prior to processing.

The univariate heritability of FW was high at 0.52 ± 0.19 for the single record analysis. However, the heritability and repeatability of FW was much lower at 0.22 ± 0.11 and 0.22 ± 0.11, respectively in the repeated records analysis. The FW reported in this study is a greasy FW, which was weighed immediately after harvest without any dehairing or cleaning of containments. Since greasy FW includes variable amounts of environmental material such as dirt and vegetable matter, this may cause greater phenotypic variance and as a result, lower heritability and repeatability estimates, as observed in the repeated records analysis. Bigham et al. (1993) reported a greasy FW heritability of 0.42 ± 0.13 for yearling goats in New Zealand.

Heritability of greasy FW was reported as 0.42 ± 0.16 and 0.67 ± 0.22 in two studies of 10-month-old Australian goats (Gifford et al., 1990 and Rose et al., 1992, respectively). These three previously published FW heritability estimates were from single record analyses and align better with the estimate from the single record analysis in the current study. The repeatability of greasy FW in Australian feral goats was 0.68 ± 0.02 (Pattie and Restall, 1989), which is much higher than the current study. Heritability estimates differed largely between the univariate single-record and repeated records analysis in this study. Only one farm provided FW data, with 177 records used in the single-record analysis and 260 records in the repeated records analysis. The additional data provided from the repeated records provided more data for parameter estimation, and may have better captured the environmental noise associated with greasy FW. The standard errors associated with FW estimates are larger than other traits where more data was available, as expected. Due to these factors, the FW estimates in this study should be viewed with caution and need to be validated in a subsequent study with a larger sample size and data from a more diverse array of producers.

Heritability and repeatability of Perc_19 was high (Table 2.5 and 2.7). The most notable standard for cashmere is a threshold for MFD of ≤ 19 μm, which is how the textile industry defines and markets cashmere. This novel phenotype characterizes the proportion of down fibers (≤ 30 μm) within an individual fiber sample that meet this criterion. Selection for Perc_19 may be valuable because increasing the percentage of fine down fibers would help lower the MFD and reduce the number of fibers on the coarse edge. Because Perc_19 is a novel trait, there are no heritability, or repeatability estimates available in literature for comparison.

Genetic and phenotypic correlations between cashmere fiber traits

Correlations between mean fiber diameter and other fiber characteristics

Phenotypic correlations between fiber traits reported in this study are shown in the upper diagonal portion of Table 2.5 and genetic correlations in the lower diagonal of Table 2.5 from single record bivariate analyses. Genetic covariances between fiber characteristics are presented in Appendix Table A.2. Selection for decreased MFD, or at least maintaining MFD, is a common breeding objective. However, the correlations MFD has with other fiber characteristics are important considerations so that selection focused on MFD does not lead to unacceptable quality of other fiber characteristics. Mean fiber diameter had moderate to strong phenotypic and genetic correlations with most other fiber traits. The phenotypic and genetic correlations between MFD and SDD were 0.60 and 0.52 ± 0.14, respectively. This strong positive correlation is favorable because it suggests that selection to decrease MFD would result in decreased SDD, or less variability. Similar phenotypic and genetic correlations between MFD and SDD of 0.50 and 0.68 ± 0.09 were reported for cashmere goats in the U.K. (Bishop and Russel, 1996). A slightly lower phenotypic correlation of 0.41 and higher genetic correlation of 0.79 ± 0.09 was reported by Bigham et al. (1993).

Interestingly, the phenotypic and genetic correlations between MFD and CVD are negative, at -0.13 and -0.32 ± 0.16, respectively. Given the standard error, the genetic correlation may be lower; however, selection for decreased MFD could result in increased CVD. This difference could be because SDD is a direct measure of fiber diameter uniformity, whereas CVD expresses variability relative to MFD. If MFD decreases but SDD does not decrease proportionally, CVD increases. Thus, the negative correlation suggests that finer fleeces tend to have greater variability when fiber diameter is expressed as a proportion of their mean. This result is not in agreement with a study of Alashan Left Banner White cashmere goats which reported positive phenotypic and genetic correlations between MFD and CVD of 0.29 ± 0.07 and

0.39 ± 0.10 (Pallotti et al., 2018). This is more consistent with the correlation between MFD and SDD in the current study, where variability decreases with smaller diameter.

The phenotypic and genetic correlations between MFD and CEM were positive and favorable, at 0.52 and 0.48 ± 0.13, respectively. These correlations indicate that a higher MFD tends to be associated with a greater CEM, or the spread between MFD and the coarsest 5% of fibers, indicating more down fibers on the coarse end of the distribution. Alternatively, selection for finer MFD would have an advantageous effect on CEM, resulting in improved fiber quality and handle, or the subjective feel of softness.

Both the phenotypic and genetic correlations between MFD and CURV were strongly negative, at -0.70 and -0.74 ± 0.06, respectively. This suggests that fiber with finer MFD will have greater curvature, which is likely a favorable correlation. Greater curvature is associated with more efficient processing (McGregor and Butler, 2008a). Additionally, North American cashmere goat breed standards require fiber to have curvature greater than 45 º/mm. In a study of Australian cashmere goats, increased MFD was strongly associated with a decline in fiber curvature and MFD accounted for 39% of the variation in fiber curvature (McGregor and Butler, 2009). Mean fiber diameter and SDCurv had negative phenotypic and genetic correlations, -0.49 and -0.59 ± 0.10, respectively. These correlations suggest that selection for decreased MFD would also lead to increased CURV and SDCurv.

The phenotypic and genetic correlations between MFD and SpinF were very strong (0.93 and 0.98 ± 0.01, respectively). SpinF is calculated with an equation that includes MFD and CVD (Butler and Dolling, 1992), therefore, a strong correlation would be expected due to a part-whole relationship. In the foundational paper that introduced the spinning fineness equation, genetic correlations between SpinF and MFD ranged from 0.93 to 0.98, depending on test dataset (Butler

and Dolling, 1992). Originally, these authors proposed SpinF as a characteristic of spinning performance to be used as an alternative to MFD. Given the strong genetic correlation between MFD and SpinF, only one of these traits needs to be considered in selection decisions. However, SpinF had weak genetic and phenotypic correlations with CVD at -0.15 ± 0.18 and 0.08, respectively. Coefficient of variation of diameter has a minor contribution in the SpinF equation where its influence is only though an adjustment factor, which could be why the relationship is weak.

The only phenotypic correlation involving MFD that was not significantly different from zero was with SL (0.06). The genetic correlation between MFD and SL was 0.34 ± 0.13. A much smaller genetic correlation of 0.09 ± 0.01 between MFD and SL was reported for Inner Mongolian White cashmere goats (Bai et al., 2006). Down fiber length is a more commonly reported trait in cashmere production compared to staple length but are not the same trait and cannot be compared. Additionally, there is not a standardized definition or measurement method for length traits, which makes direct comparisons difficult.

MFD had a positive phenotypic correlation with FW (0.38), and very similar genetic correlation of 0.40 ± 0.22. Although FW sample size was small and standard errors were large, the moderate, positive genetic correlation suggests that selection for lower MFD would also lead to lighter FW, which is unfavorable. A very similar genetic correlations of 0.48 ± 0.11 was reported for feral Australian goats (Couchman and Wilkinson, 1987). A higher genetic correlation of 0.69 ± 0.13 was reported for New Zealand goats (Bigham et al., 1993). Two studies reported low genetic correlations between MFD and FW of 0.12 ± 0.23 and 0.13 ± 0.30, although these estimates were also associated with high standard errors (Gifford et al., 1990 and Baker et al., 1991, respectively). A future study with a large FW sample size is needed to better

understand the relationship between MFD and FW. Since cashmere producers are paid based on clean down weight, it would potentially be more useful to evaluate that trait in the future as well.

The correlations between MFD and Perc_19 were very strongly negative, with a genetic correlation of -0.95 ± 0.02 and phenotypic correlation of -0.94. This means as MFD becomes finer, the percentage of fibers with diameter ≤ 19 μm increases, which is a logical relationship. Given this extremely strong genetic correlation, Perc_19 does not appear to characterize additional information beyond what is already explained by MFD. Including both MFD and Perc_19 in selection decisions is likely unnecessary. Because Perc_19 is a novel cashmere trait, there are no correlations published in literature for comparison.

Correlations between curvature and other fiber characteristics

The phenotypic correlation between CURV and SpinF was -0.66 and genetic correlation was -0.71 ± 0.07. This suggests that increased CURV is associated with a lower SpinF, which indicates finer, higher-quality fiber for spinning. This aligns with results from McGregor and Butler, (2008a) which reported that greater fiber CURV is associated with more efficient processing, particularly dehairing. This is similar to the relationship between CURV and MFD, where increased CURV was associated with finer MFD, which is logical because SpinF is calculated largely based on MFD.

CURV had a negative phenotypic correlation of -0.41 with SDD and similar genetic correlation of -0.42 ± 0.16. This correlation suggests that selection for decreased SDD, or more uniform fiber diameter, would be associated with an increase in CURV. This may be favorable if the breeding objective is to increase CURV, although this will depend on the individual producer and their textile processor's requirements. McGregor and Butler (2009) reported the same directionality for the relationship between CURV and SDD, where increased SDD was

associated with a small decline in CURV. Phenotypically, as SDD increased from 2.5 to 5.5 µm, CURV decreased slightly from 48 to 46 º/mm (McGregor and Butler, 2009). The relationship between CURV and the other measure of diameter variation, CVD, was opposite in direction. The genetic and phenotypic correlations between CURV and CVD was 0.21 ± 0.17 and 0.12, respectively. Although the standard error is relatively high, this suggests that selection for decreased CVD would be associated with a decrease in CURV. Overall, the relationship between CURV and fiber diameter variation appears to depend on how variation is defined and its application to selection decisions will depend on individual producers' breeding goals.

CURV and SDCurv had high phenotypic and genetic correlations of 0.70 and 0.78 ± 0.07, respectively. The positive correlation between CURV and SDCurv means that increased CURV tends to be associated with increased variability in CURV. CURV had negative phenotypic and genetic correlations with SL of -0.16 and -57 ± 0.11, respectively. The phenotypic and genetic correlations between CURV and FW were also negative at -0.20 and -0.48 ± 0.25, respectively. These correlations suggest that fiber with greater curvature has a shorter staple length and lighter fleece weighs. This is similar to the relationship between cashmere length and curvature observed by McGregor (2003), where a 10 mm increase in length was associated with a decrease in curvature by 3 to 13.1 º/mm, depending on cashmere origin, although this referred to down length rather than SL.

The remaining phenotypic and genetic correlations involving CURV are listed in Table 2.5. Based on the genetic correlations, producers selecting for increased CURV can expect a favorable correlated response in the diameter related traits of CEM and Perc_19. In contrast, the genetic correlations between CURV and both SL and FW were unfavorable, suggesting that selection for increased CURV would be associated with reduced fiber length and weight.

Literature comparisons for these genetic correlations are not currently available. Incorporation of CURV into selection decisions should be done with careful consideration of the desired fiber end-product and its relationships with other fiber traits.

Correlations between other fiber characteristics

The genetic and phenotypic correlations between SL and other fiber traits were both favorable and unfavorable (Table 2.5). The genetic and phenotypic correlations between SL and FW were 0.66 ± 0.25 and 0.55, respectively. This suggests that selection for longer SL would lead to greater FW, which is a logical and favorable relationship. There was also a favorable genetic correlation between SL and SDCURV (-0.67 ± 0.12). In contrast, SL had unfavorable genetic correlations with SDD, CEM, SpinF and Perc19 (Table 2.5). These genetic correlations involving SL are not available in literature for comparison.

Although clean down weight is the economically relevant trait in cashmere production, greasy FW is often evaluated as an indicator of clean down weight. Therefore, the relationship greasy FW has with other fiber characteristics is important to consider. In this study, sample size of FW was much smaller compared to other fiber traits, resulting in estimates with relatively large standard errors that should be evaluated with caution. Nonetheless, correlations significantly different from zero involving FW were both favorable and unfavorable (Table 2.5). The genetic and phenotypic correlations between FW and SpinF were 0.37 ± 0.24 and 0.32, respectively. This suggests that selection for increased FW would lead to fiber with poor spinning performance. Favorable genetic correlations were estimated between FW and both SDCURV and Perc19. Comparable estimates in literature are not currently available. Therefore, additional research with a larger FW sample size from many different farms would be necessary to further elucidate the relationship FW has with other fiber traits.

Genome-wide association study

Table 2.8 reports significant SNPs for cashmere fiber characteristics and Manhattan plots are shown in Figures 2.2 through 2.4. All genes within ±50 kilobases of the significant SNP are presented in Appendix Table A.3. Results for FW GWAS are not presented due to convergence issues from small sample size.

Three SNPs were significant for MFD including snp12723-scaffold1489-359636, NC_030830.1_831663, and snp1433-scaffold104-453661 (Table 2.8). The SNP NC_030830.1_831663 was near two genes: FOXC1 (Forkhead box C1) and GMDS (GDP-mannose 4,6-dehydratase; Appendix Table A.3). The gene FOXC1 has biological processes that could be related to MFD, making it a possible candidate gene. FOXC1 is involved with the biological process of 'collagen fibril organization', which is a process that determines the size and arrangement of collagen fibrils (The UniProt Consortium, 2023). Collagen fibrils are the structural units that make up collagen fibers and are a key component of the extracellular matrix which provides structural support for skin and hair follicles. Proper organization of collagen fibrils is important for follicle development and therefore could influence the diameter of hair grown from secondary hair follicles (cashmere down). In addition, FOXC1 is involved with the biological process of 'cellular response to epidermal growth factor stimulus' (The UniProt Consortium, 2023). This process refers to any change in cell behavior in response to epidermal growth factor (EGF) signaling. Epidermal growth factor has a role in hair follicle morphogenesis and the growth phase of the follicle cycle. Altered EGF signaling could affect the activity and size of cells involved with fiber production such as matrix keratinocytes, potentially impacting MFD. The gene FOXC1, is involved with many other functions and processes, but another notable process potentially related to MFD is 'positive regulation of keratinocyte differentiation'

(The UniProt Consortium, 2023). This refers to any biological process that increases the rate, frequency, or extent of keratinocyte differentiation. Keratinocytes are epithelial cells that originate in the basal layer of skin or hair follicles. As they move upward, these cells differentiate and produce different types of keratins at each stage, which is essential for fiber formation. Given the importance of the biological processes of FOXC1 for fiber growth, it is a candidate gene for MFD. While not specifically FOXC1, other members of the Forkhead box gene family including FOXN1, FOXE1, and FOXI3 have a regulatory effect on the growth and development of hair follicles and the hair growth cycle and were differentially expressed in a study of Inner Mongolia cashmere goats (Han et al., 2017).

Nine significant SNPs were identified for SDD (Table 2.8), and a total of 25 genes were within the QTL regions of these nine SNPs (Appendix Table A.3). The SNP 14:81337066 was near nine genes including SCX (Scleraxis basic helix-loop-helix transcription factor). This gene has the biological process of 'cellular response to transforming growth factor-beta (TGF-β)' (The UniProt Consortium, 2023). Transforming growth factor-beta is a growth factor involved in various cellular processes including extracellular matrix formation. Signaling for TGF-β plays a role in the differentiation of fibroblasts and keratinocytes in the skin and hair follicle. This is important for hair growth and influences collagen production. Other biological processes related to collagen associated with SCX were 'collagen fibril organization' and 'positive regulation of collagen biosynthetic process' (The UniProt Consortium, 2023). Due to SCX's involvement in biological processes that influence the formation and structure of fibers, it is a candidate gene for SDD. Another gene near the significant SNP 14:81337066 is DGAT1 (Diacylglycerol O-acyltransferase 1). The DGAT1 gene encodes an enzyme that catalyzes the final and rate-limited step of triglyceride synthesis, playing a central role in lipid metabolism. Due to its role in lipid

metabolism, DGAT1 could impact skin and sebaceous gland function, potentially affecting the skin lipid barrier and follicular environment. While not directly related to fiber characteristics, the DGAT1 gene was previously associated with 11 different traits in sheep, including: body weight, hot carcass weight, longissimus muscle area, shoulder weight, and subcutaneous fat thickness (Armstrong et al., 2018); leg yield, loin yield, and shoulder yield (Dai et al., 2022); and milk fat percentage, milk protein percentage, and milk yield (Scata et al., 2009).

For CVD, eight SNPs were significant (Table 2.8). There were 24 genes within the QTL regions (Appendix Table A.3). Of the 24 genes, 7 were uncharacterized and 6 were variants of the histone gene family. The SNP 12:54926371 was near the gene FLT1 (fms related receptor tyrosine kinase 1), which encodes a receptor tyrosine kinase involved in receptor binding of several growth factors including EGF and fibroblast growth factor (FGF). Both these ligands are highly involved in skin and follicle development. The role of EGF in follicle morphogenesis and cycling was discussed previously for FOXC1, a candidate gene for MFD, as it is also involved with cellular response to EGF stimulus. Fibroblast growth factors are involved in a wide range of biological processes but play a critical role in hair follicle development and cycling. For example, FGFs regulate hair follicle induction during embryonic development. They also signal the transition from the anagen (growth) to the catagen (regression) phase of the hair cycle, promote proliferation of dermal papilla cells, and interact with keratinocytes. In cashmere goats, different members of the FGF gene family have been associated with secondary hair follicle development (He et al., 2016; Diao et al., 2023; Gao et al., 2023). These connections support FLT1 as a candidate gene for fiber diameter variation, or CVD.

Twelve SNPs were significant for CEM (Table 2.8). The SNP 10:37886722 was significant for both CEM and SDD. The QTL region of this SNP contained six genes including

SORD (sorbitol dehydrogenase), DUOX2 (dual oxidase 2), DUOXA2 (dual oxidase maturation factor 2), DUOXA1 (dual oxidase maturation factor 1), DUOX1 (dual oxidase 1), and SHF (SH2 domain-containing protein). These genes are broadly involved in oxidative stress regulation, epithelial cell function, and various signaling pathways. Specifically, SORD encodes an enzyme involved in sorbitol metabolism and redox balance. The DUOX gene family produces hydrogen peroxide in epithelial tissues and plays a role in mucosal immunity. SHF is an adaptor protein involved with intracellular signaling, including growth factor pathways. Although their direct connection to fiber development is unclear, their functions in oxidative stress response and epithelial signaling could impact follicle environment and in turn, fiber characteristics like CEM. Three genes near significant SNPs for CEM, IL22RA2 (interleukin-22 receptor subunit alpha-2), IFNGR1 (interferon gamma receptor 1), and CGN (collectin-46), are involved in immune and inflammatory pathways. The gene IL22RA2 encodes a receptor that modulates interleukin-22 (IL-22) signaling, which is important for epithelial cell repair, proliferation, and immune response in the skin. In humans, it has been reported that IL-22 induces keratinocyte proliferation and inhibits keratinocyte differentiation in connection to Psoriasis, a skin disease characterized by hyperproliferation of keratinocytes and infiltration of inflammatory cells (Zhuang et al., 2020). The influence that IL-22 has on keratinocyte behavior makes IL22RA2 a gene candidate for CEM. Another gene, CGN, is involved in the innate immune system and binds to carbohydrate patterns on pathogens to initiate immune response. Additionally, CGN is associated with the cellular component ‘collagen trimer’ (The UniProt Consortium, 2023), which is the basic structural unit of collagen giving it its strength and stability. Thus, CGN is another candidate gene for CEM due to its potential roles in immune response or extracellular matrix interactions that could influence the follicular environment.

Curvature had four significant SNPs above the -$\log_{10}$ *P*-value threshold of 4 (Table 2.8). Four genes were within the QTL regions of significant SNPs for CURV including TGS1 (trimethylguanosine synthase 1), TMEM68 (transmembrane protein 68), KMO (kynurenine 3-monooxygenase), and FH (fumarate hydratase). The gene TMEM68 was near snp37050-scaffold449-1431692 and is involved in lipid metabolism, specifically the biosynthesis of triglycerides. Alterations in lipid metabolism could influence the lipid composition of cell membranes in hair follicles, affecting hair follicle function. The gene KMO was near snp6477-scaffold123-797664. It is involved in the kynurenine pathway and is associated with immune response and oxidative stress, which could potentially impact hair follicle health and activity. While these genes do not have direct implications for fiber curvature, TMEM68 and KMO are plausible gene candidates due to their roles in lipid metabolism and immune response, respectively.

Standard deviation of curvature had 12 significant SNPs (Table 2.8). The most notable gene within the QTL regions of these significant SNPs was EFNB2 (ephrin-B2). This gene is important for various developmental processes and expressed in the skin during hair follicle development. One of EFNB2's biological processes is 'negative regulation of keratinocyte proliferation' (The UniProt Consortium, 2023). Since keratinocytes are the predominant cell type in the epidermis and outer root sheath of hair follicles, this biological process is particularly relevant in the context of a fiber trait such as SDCurv. In mice, the influence EFNB2 has on hair follicle biology has been studied. Negative regulation of cell proliferation in the epidermis and hair follicle was observed in vivo in mice where disruption of ephrin receptor interactions was associated with increased cell proliferation (Genander et al., 2010). Additionally, it has been reported that EFNB2 is transiently expressed in hair buds during embryogenesis and in dermal

mesenchymal cells during the perinatal period (Egawa et al., 2009), suggesting a role in hair follicle morphogenesis. The influence EFNB2 has on keratinocyte cell behavior makes it a reasonable candidate gene for SDCurv. The gene NEFH (neurofilament heavy polypeptide) was near snp9919-scaffold1354-42468. This gene encodes heavy neurofilament chains, which help maintain neuron structure. Although NEFH is primarily expressed in nervous tissue and not the skin or hair follicles, it was previously associated with fleece yield in Chinese fine-wool sheep (Zhao et al., 2021), suggesting a potential indirect or regulatory role on fiber production that warrants further research.

Six SNPs were significant for SpinF (Table 2.8). Of those six SNPs, only three had genes within their QTL region (Appendix Table A.3). Two genes were uncharacterized and the gene CNTNAP5 (contactin-associated protein-like 5) was near snp12723-scaffold1489-359636. This gene is a member of the neurexin family and is involved in nervous system development and function through cell adhesion and intercellular communication. More research would be needed to elucidate whether CNTNAP5 could be functionally linked to SpinF and a plausible candidate gene.

Staple length had 11 SNPs above the $-\log_{10}$ *P*-value threshold of 4 (Table 2.8). Thirteen genes were identified within the QTL regions of these SNPs (Appendix Table A.3). The EPHA4 (EPH receptor A4) gene encodes a receptor in the Eph family of receptor tyrosine kinases. It is directly connected to EFNB2, previously discussed with SDCurv, as both genes are members of the ephrin signaling pathway. Gene Ontology molecular functions for EPHA4 include ‘EGF receptor activity’, ‘FGF receptor activity’, and ‘protein tyrosine kinase collagen receptor activity’ (The UniProt Consortium, 2023), which are all relevant to skin and hair follicle development. Specifically, FGF signaling influences hair follicle morphogenesis and anagen

phase initiation, which could impact SL. Additionally, EPNA4 has an influence on collagen and extracellular matrix interactions, which could affect tissue structure and thus SL. The identification of both EPHA4 and EFNB2, genes within the same signaling pathway, near significant SNPs in this analysis suggest that ephrin signaling is connected to cashmere fiber production.

Nine SNPs were significant for Perc_19 (Table 2.8) and 11 genes were in the QTL regions of these SNPs (Appendix Table A.3). One SNP, NC_030830.1_831663, was common between Perc_19 and MFD. This SNP was near the gene FOXC1, which has obvious connections to fiber production as discussed previously. It is logical that Perc_19 and MFD would share significant SNPs as these two traits are highly genetically correlated. Another SNP, snp57298-scaffold912-1705662, was near the gene RORA (retinoic acid-related orphan receptor A). This gene encodes a nuclear receptor involved in a range of biological processes, including circadian rhythm, metabolism, and immune response. It has been reported that RORA regulates autophagy of hair follicle stem cells (HFSCs) and that increased autophagy of HFSCs promotes the start of the anagen phase of the hair cycle (Zhao et al., 2025). Additionally, RORA has been connected to melatonin signaling and seasonal hair molting, where daylight changes influence melatonin levels thus affecting RORA activity and the hair growth cycle (Zhang et al., 2025). Given its roles in the timing of hair growth cycle and HFSC regulation, RORA is a strong candidate gene for Perc_19. Lastly, the gene FGF12 (fibroblast growth factor 12) was in the QTL region for snp36326-scaffold435-307186. This gene encodes a member of the FGF family, which has known roles in cell growth, tissue repair, and development. Fibroblast growth factor 12 is primarily expressed in the outer root sheath cells of hair follicles and has high expression during the anagen phase of the hair cycle (Woo et al., 2022). In mice, knockdown of FGF12

delayed telogen to anagen phase transition, further supporting that FGF12 is associated with hair growth promotion (Woo et al., 2022). Further, Wang et al. (2021) identified FGF12 as a candidate gene for fiber length in a GWAS on Inner Mongolia cashmere goats. These findings suggest FGF12 is a reasonable candidate gene for cashmere fiber traits like Perc_19.

Conclusions

Literature on the genetic control of cashmere production is limited, especially in the U.S. Producers in the U.S. lack a genetic selection tool to inform their breeding decisions. Development and implementation of a national genetic evaluation would aid producers in improving their cashmere flocks leading to increased production, profitability, and efficiency. In general, fiber characteristics are moderate to highly heritable. Most fiber characteristics have high repeatability, suggesting that the first fiber record tested on an animal is a good indicator of subsequent records and animals likely only need their fiber tested once in their lifetime, not every year. Phenotypic and genetic correlations varied depending upon the pair of traits. Genetic correlations between MFD and other traits were favorable for SDD, CEM, CURV, SpinF, and Perc_19. However, genetic antagonisms between MFD and CVD, SDCURV, SL, and FW need to be considered when placing heavy selection emphasis on reduced MFD. Therefore, a selection index that properly weights each trait may be beneficial for cashmere producers. The genome-wide association study identified many significant SNPs that were in proximity to genes previously implicated in fiber production or related biological processes. Notable candidate genes include FOXC1, SCX, FLT1, EFNB2, EPHA4, RORA, and FGF12. These results could serve as a foundation for the creation of genetic selection tools for cashmere production in the U.S.

Table 2.1. Cashmere producer information.

Farm Number	Location	Number of records	Number of animals
01	OK	182	182
02	OK	541	391
03	CA	58	30
04	OR	14	13
05	NY	9	9
06	WA	20	20
07	MI	13	13
08	KS	80	73
09	VT	7	7
10	AR	3	3
11	CO	46	32
12	VT	16	16
13	IN	15	15
14	NJ	8	8
15	IN	18	18
16	OR	37	33
17	WI	49	49
18	OK	4	4
19	KY	2	2
20	NY	6	6
21	CA	26	22
22	CO	5	5
23	CO	14	14
24	GA	8	8
25	MD	4	4
26	WI	6	6
27	WI	31	31
28	MT	10	10
29	OR	4	4
30	OK	4	4
31	CA	1	1
32	WA	7	7
Total		1,248	1,040

Table 2.2. Definitions and abbreviations of cashmere fiber characteristics.

Trait	Abbreviation	Definition
Mean Fiber Diameter, µm	MFD	Average fiber diameter of fibers in the tested sample ≤ 30µm
Standard deviation of diameter, µm	SDD	Standard deviation of fiber diameter calculated by: $\sqrt{\frac{\Sigma(MFD_i - \overline{MFD})^2}{n}}$
Coefficient of variation of diameter, %	CVD	Coefficient of fiber diameter calculated by: $\left(\frac{SD\ Mean}{MFD}\right) * 100$
Course edge micron, µm	CEM	The number of micron above the average diameter where the coarsest 5% of fibers lie
Curvature, º/mm	CURV	The average fiber curvature
Standard deviation of curvature, º/mm	SDCurv	Standard deviation of fiber curvature calculated by: $\sqrt{\frac{\Sigma(CURV_i - \overline{CURV})^2}{n}}$
Spinning fineness, µm	SpinF	A measure of the performance of the fiber when spun into yarn calculated from CVD and MFD. Original theory proposed by Martindale (1945) and formula used proposed by Butler and Dolling (1992).
Staple length, mm	SL	Length of clipped fiber sample
Fleece weight, g	FW	Total fleece weight after harvest
Percentage ≤ 19, %	Perc_19	Percentage of fibers with diameters between 4 and 30 µm that are less than or equal to 19 µm

Table 2.3. Fixed effects determined to improve model fit[1] by forward selection as denoted by an "X" and were included in the final model for each trait.

	Fixed effect		
Trait	**Contemporary group (farm x testing year)**	**Sex (doe, buck, wether)**	**Age at cashmere collection (years)**
Mean fiber diameter, µm	X	X	X
Standard deviation of diameter, µm	X		X
Coefficient of variation of diameter, %	X	X	X
Coarse edge micron, µm	X		X
Curvature, °/mm	X	X	
Standard deviation of curvature, °/mm	X	X	X
Spinning fineness, µm	X		X
Staple length, mm	X	X	
Fleece weight, g		X	
Percentage less than 19 µm, %	X		X

[1]Addition of this fixed effect to the model reduced Akaike Information Criterion by 3 or more.

Table 2.4. Summary statistics of animal information and fiber traits for all records.

Trait	n	Mean	Minimum	Maximum	Standard deviation
Age at Collection, yrs	1,080	2.72	0.17	18.74	2.87
Mean fiber diameter, µm	1,079	15.34	11.30	22.52	1.76
Standard deviation of diameter, µm	1,080	3.17	2.03	6.92	0.52
Coefficient of variation of diameter, %	1,079	20.67	15.20	41.80	2.86
Coarse edge micron, µm	1,080	6.16	3.07	14.6	1.22
Curvature, °/mm	1,242	67.76	21.30	123.80	11.87
Standard deviation of curvature, °/mm	1,079	40.81	17.00	75.20	8.43
Spinning fineness, µm	1,080	14.90	11.01	21.76	1.70
Staple length, mm	987	60.34	4.30	120.0	21.57
Fleece weight, g	260	237.8	20.0	644.0	94.11
Percentage less than 19 µm, %	1,080	87.51	27.7	99.7	11.52

Table 2.5. Estimates from the single record analysis of cashmere fiber traits: univariate heritability estimates (diagonal), phenotypic correlations (upper diagonal), and genetic correlations ± standard error (lower diagonal) from each bivariate analysis.

	MFD	SDD	CVD	CEM	CURV	SDCurv	SpinF	SL	FW	Perc_19
MFD, µm	**0.49 ± 0.07**	0.60**	-0.13**	0.52**	-0.70**	-0.49**	0.93**	0.06	0.38**	-0.94**
SDD, µm	0.52 ± 0.14	**0.27 ± 0.07**	0.70**	0.91**	-0.41**	-0.18**	0.73**	-0.07*	-0.01	-0.70**
CVD, %	-0.32 ± 0.16	0.63 ± 0.15	**0.29 ± 0.07**	0.66**	0.12**	0.22**	0.08*	-0.15**	-0.34**	-0.04
CEM, µm	0.48 ± 0.13	0.95 ± 0.03	0.47 ± 0.15	**0.36 ± 0.07**	-0.33**	-0.12**	0.65**	-0.02	0.07	-0.60**
CURV, °/mm	-0.74 ± 0.06	-0.42 ± 0.16	0.21 ± 0.17	-0.38 ± 0.14	**0.48 ± 0.06**	0.70**	-0.66**	-0.16**	-0.20*	0.64**
SDCurv, °/mm	-0.59 ± 0.10	-0.22 ± 0.19	0.27 ± 0.18	-0.14 ± 0.17	0.78 ± 0.07	**0.38 ± 0.07**	-0.42**	-0.19**	-0.18*	0.42**
SpinF, µm	0.98 ± 0.01	0.68 ± 0.10	-0.15 ± 0.18	0.63 ± 0.10	-0.71 ± 0.07	-0.55 ± 0.12	**0.45 ± 0.07**	0.03	0.32**	-0.92**
SL, mm	0.34 ± 0.13	0.30 ± 0.18	0.08 ± 0.18	0.30 ± 0.16	-0.57 ± 0.11	-0.67 ± 0.12	0.35 ± 0.14	**0.48 ± 0.07**	0.55**	-0.04
FW, g	0.40 ± 0.22	0.05 ± 0.58	-0.39 ± 0.61	0.08 ± 0.46	-0.48 ± 0.25	-0.56 ± 0.27	0.37 ± 0.24	0.66 ± 0.25	**0.52 ± 0.19**	-0.29**
Perc_19, %	-0.95 ± 0.02	-0.58 ± 0.11	0.25 ± 0.17	-0.52 ± 0.11	0.71 ± 0.08	0.55 ± 0.12	-0.96 ± 0.01	-0.31 ± 0.13	-0.62 ± 0.21	**0.50 ± 0.07**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CVD- coefficient of variation of fiber diameter; CEM- coarse edge micron; CURV- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; SL- staple length; FW-fleece weight; Perc_19- percentage of fibers with diameter less than or equal 19 µm.

*Phenotypic correlations significantly different from zero at $P < 0.05$.

**Phenotypic correlations significantly different from zero at $P < 0.0001$.

Table 2.6. Heritability estimates (with SE below) of traits listed in the first column from single record bivariate analysis with all other traits. Average heritability from all bivariate analyses for a trait is bolded on the diagonal.

Trait:	Heritabilities from bivariate analyses with all other traits									
	MFD	**SDD**	**CVD**	**CEM**	**CURV**	**SDCurv**	**SpinF**	**SL**	**FW**	**Perc_19**
MFD, µm	**0.497** **0.06-0.07**	0.50 0.07	0.50 0.06	0.49 0.07	0.50 0.06	0.50 0.06	0.49 0.07	0.49 0.06	0.50 0.06	0.50 0.06
SDD, µm	0.27 0.07	**0.274** **0.07**	0.27 0.07	0.29 0.07	0.27 0.07	0.28 0.07	0.27 0.07	0.28 0.07	0.27 0.07	0.27 0.07
CVD, %	0.29 0.07	0.29 0.07	**0.289** **0.07**	0.29 0.07	0.29 0.07	0.29 0.07	0.29 0.07	0.29 0.07	0.29 0.07	0.30 0.07
CEM, µm	0.36 0.07	0.37 0.07	0.38 0.07	**0.367** **0.07**	0.37 0.07	0.37 0.07	0.36 0.07	0.37 0.07	0.37 0.07	0.36 0.07
CURV, º/mm	0.45 0.07	0.45 0.07	0.45 0.07	0.45 0.07	**0.458** **0.06-0.07**	0.46 0.07	0.45 0.07	0.47 0.06	0.48 0.06	0.45 0.07
SDCurv, º/mm	0.38 0.07	0.38 0.07	0.38 0.07	0.38 0.07	0.39 0.07	**0.381** **0.07**	0.38 0.07	0.37 0.07	0.38 0.07	0.38 0.07
SpinF, µm	0.44 0.07	0.45 0.07	0.45 0.07	0.45 0.07	0.45 0.07	0.45 0.07	**0.451** **0.07**	0.45 0.07	0.45 0.07	0.47 0.07
SL, mm	0.45 0.07	0.45 0.07	0.45 0.07	0.45 0.07	0.49 0.07	0.47 0.07	0.45 0.07	**0.457** **0.07**	0.46 0.07	0.45 0.07
FW, g	0.55 0.16	0.29 0.18	0.38 0.18	0.39 0.19	0.62 0.17	0.59 0.17	0.58 0.17	0.49 0.15	**0.506** **0.15-0.19**	0.65 0.16
Perc_19, %	0.50 0.07	0.51 0.07	0.51 0.07	0.50 0.07	0.50 0.07	0.50 0.07	0.50 0.07	0.49 0.07	0.50 0.07	**0.501** **0.07**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CVD- coefficient of variation of MFD; CEM- coarse edge micron; CURV- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; SL- staple length; FW-fleece weight; Perc_19- percentage of fibers with diameter less than or equal 19 µm.

Table 2.7. Heritability, repeatability, and variance components for repeated records of cashmere fiber traits.

Trait	Genetic variance	Residual variance	Permanent environmental variance	Heritability ± standard error	Repeatability ± standard error
Mean fiber diameter, µm	1.0777	0.47348	0.44715	0.54 ± 0.06	0.76 ± 0.03
Standard deviation of diameter, µm	0.05677	0.05251	0.09205	0.28 ± 0.07	0.74 ± 0.04
Coefficient of variation of diameter, %	2.3138	1.7794	3.0379	0.32 ± 0.06	0.75 ± 0.04
Coarse edge micron, µm	0.4658	0.2436	0.5591	0.37 ± 0.07	0.81 ± 0.03
Curvature °/mm	59.531	38.201	14.377	0.53 ± 0.06	0.66 ± 0.04
Standard deviation of curvature, °/mm	13.035	17.162	4.9845	0.37 ± 0.07	0.51 ± 0.07
Spinning fineness, µm	0.8919	0.4436	0.5125	0.48 ± 0.07	0.76 ± 0.03
Staple length, mm	124.07	141.54	15.676	0.44 ± 0.06	0.49 ± 0.07
Fleece weight, g	1834.70	6374.0	0.0023	0.22 ± 0.11	0.22 ± 0.11
Percentage less than 19 µm, %	49.703	27.129	16.35	0.53 ± 0.06	0.71 ± 0.04

Table 2.8. Genomic regions significantly[1] associated with cashmere fiber traits identified through univariate single record genome-wide association study.

Trait	SNP name	Chromosome: Position	-$\log_{10}$ *P*-value
Mean Fiber Diameter, µm	snp12723-scaffold1489-359636	2:59355109	4.308
	NC_030830.1_831663	23:831663	4.182
	snp1433-scaffold104-453661	10:25164538	4.167
Standard deviation of diameter, µm	14:81337066	14:81337066	6.386
	snp15933-scaffold1674-201551	28:9579785	4.864
	snp46308-scaffold639-126113	7:70168742	4.645
	10:37886722	10:37886722	4.594
	snp13153-scaffold1501-2062871	14:63367161	4.173
	snp15526-scaffold1641-174478	14:45652554	4.126
	snp38104-scaffold475-621550	10:38517075	4.097
	snp38108-scaffold475-788703	10:38683034	4.031
	NC_030811.1_90987564	4:90987564	4.002
Coefficient of variation of diameter, %	snp54122-scaffold825-1014475	29:25497494	4.840
	snp9068-scaffold133-715	10:19535805	4.530
	12:54926371	12:54926371	4.529
	snp17668-scaffold183-1269493	3:112157042	4.494
	snp13583-scaffold1525-1372817	24:60678782	4.492
	snp15933-scaffold1674-201551	28:9579785	4.471
	NC_030830.1_18993272	23:18993272	4.266
	snp52988-scaffold796-515837	29:29276909	4.011
Coarse edge micron, µm	snp15933-scaffold1674-201551	28:9579785	6.021
	10:37886722	10:37886722	5.613
	snp46521-scaffold644-229314	12:80654586	5.095
	snp43455-scaffold579-4131867	9:62199424	4.550
	snp1151-scaffold1030-421845	12:77016411	4.526
	snp10912-scaffold1390-330847	28:10278379	4.477
	4:2755170	4:2755170	4.466
	NC_030810.1_118553838	3:118553838	4.456
	12:79404524	12:79404524	4.426
	snp52526-scaffold782-3618961	20:2739578	4.319
	snp14293-scaffold157-2174674	5:17950877	4.227
	snp29462-scaffold319-383364	10:77019517	4.012
Curvature, °/mm	snp51228-scaffold75-3195161	14:54743414	4.158
	4:105934903	4:105934903	4.071
	snp37050-scaffold449-1431692	14:59014501	4.043
	snp6477-scaffold123-797664	16:33795985	4.030
Standard deviation of curvature, °/mm	snp31365-scaffold347-1783379	12:4003713	5.413
	NC_030813.1_11981581	6:11981581	4.545
	snp12495-scaffold1479-395260	17:62391045	4.484
	snp27887-scaffold299-3305456	16:76709383	4.380
	8:33818616	8:33818616	4.349
	snp9919-scaffold1354-42468	17:2617367	4.304
	snp15342-scaffold163-2570163	22:38596654	4.300
	snp48248-scaffold683-100458	29:12983250	4.255

	NC_030835.1_35266324	28:35266324	4.197
	snp22469-scaffold2223-95469	13:22938705	4.115
	snp19615-scaffold1980-634136	5:46781804	4.105
	snp11445-scaffold1417-386228	23:32736234	4.014
Spinning fineness, µm	NC_030808.1_29075396	1:29075396	4.873
	snp12723-scaffold1489-359636	2:59355109	4.475
	snp10357-scaffold1370-1004058	14:41058959	4.377
	snp1433-scaffold104-453661	10:25164538	4.313
	snp55570-scaffold861-1053172	26:25703901	4.241
	14:49533115	14:49533115	4.193
Staple length, mm	NC_030831.1_40583446	24:40583446	5.103
	11:104347406	11:104347406	4.724
	snp54557-scaffold833-1303845	24:40263321	4.708
	18:2875561	18:2875561	4.481
	NC_030831.1_43366786	24:43366786	4.348
	snp4218-scaffold1130-1285272	21:38165973	4.321
	snp54553-scaffold833-1114417	24:40073220	4.299
	2:26320799	2:26320799	4.297
	snp57722-scaffold93-471433	7:36257418	4.253
	6:68919933	6:68919933	4.247
	NC_030835.1_11100855	28:11100855	4.042
Percentage ≤ 19, %	snp1433-scaffold104-453661	10:25164538	4.611
	snp12723-scaffold1489-359636	2:59355109	4.439
	19:9949651	19:9949651	4.355
	snp36430-scaffold438-690423	25:20239001	4.176
	NC_030815.1_24816118	8:24816118	4.107
	NC_030830.1_831663	23:831663	4.103
	snp55570-scaffold861-1053172	26:25703901	4.101
	snp57298-scaffold912-1705662	10:54284488	4.090
	snp36326-scaffold435-3071866	1:74472653	4.048

[1]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.

Figure 2.1. Map of 32 producer locations across the United States.

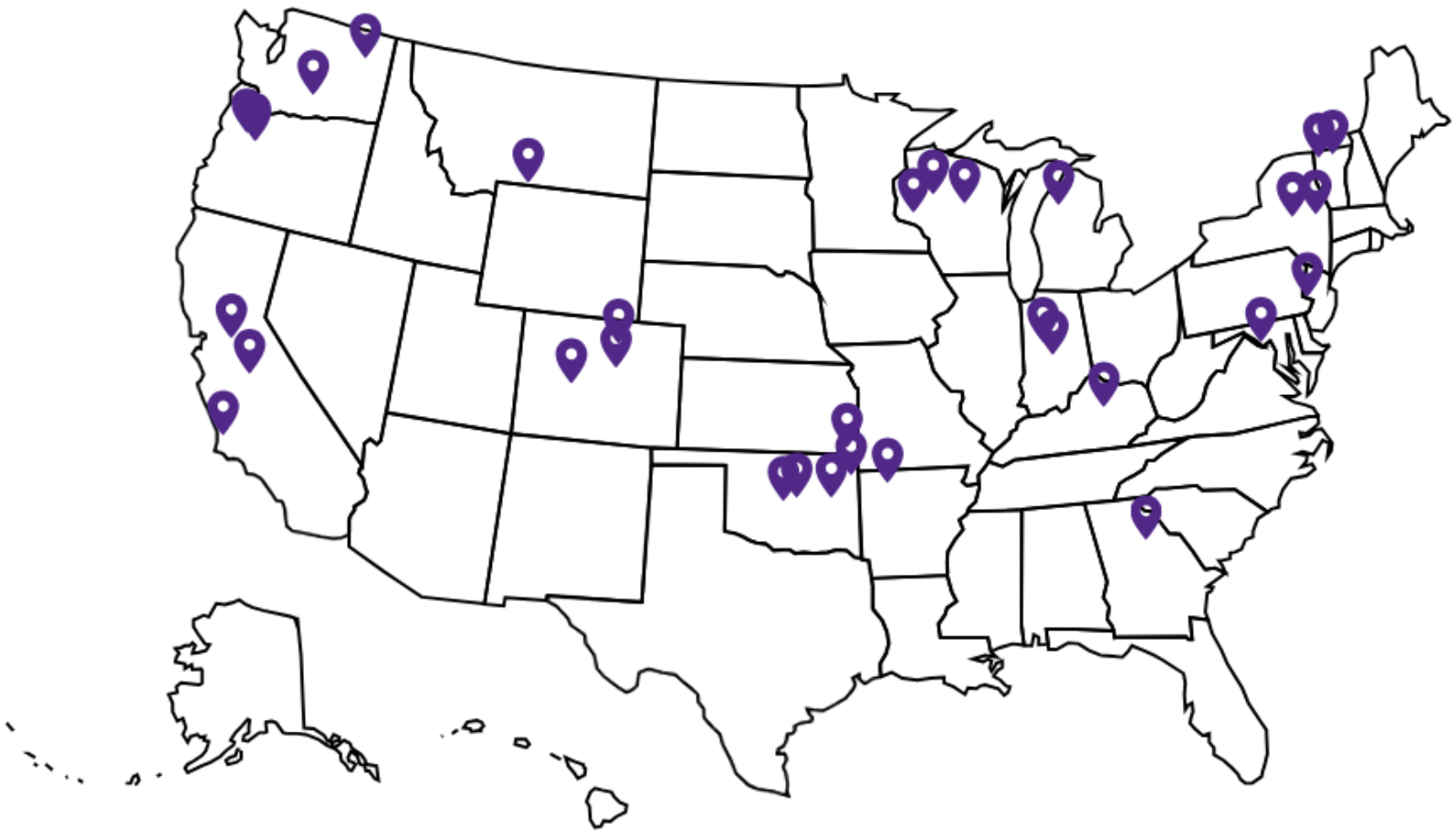


Figure 2.2. Manhattan plots for univariate, single-record genome-wide association study of mean fiber diameter and diameter variation traits with a significance threshold of 4. Panel A- mean fiber diameter; Panel B- standard deviation of diameter; Panel C- coefficient of variation of diameter

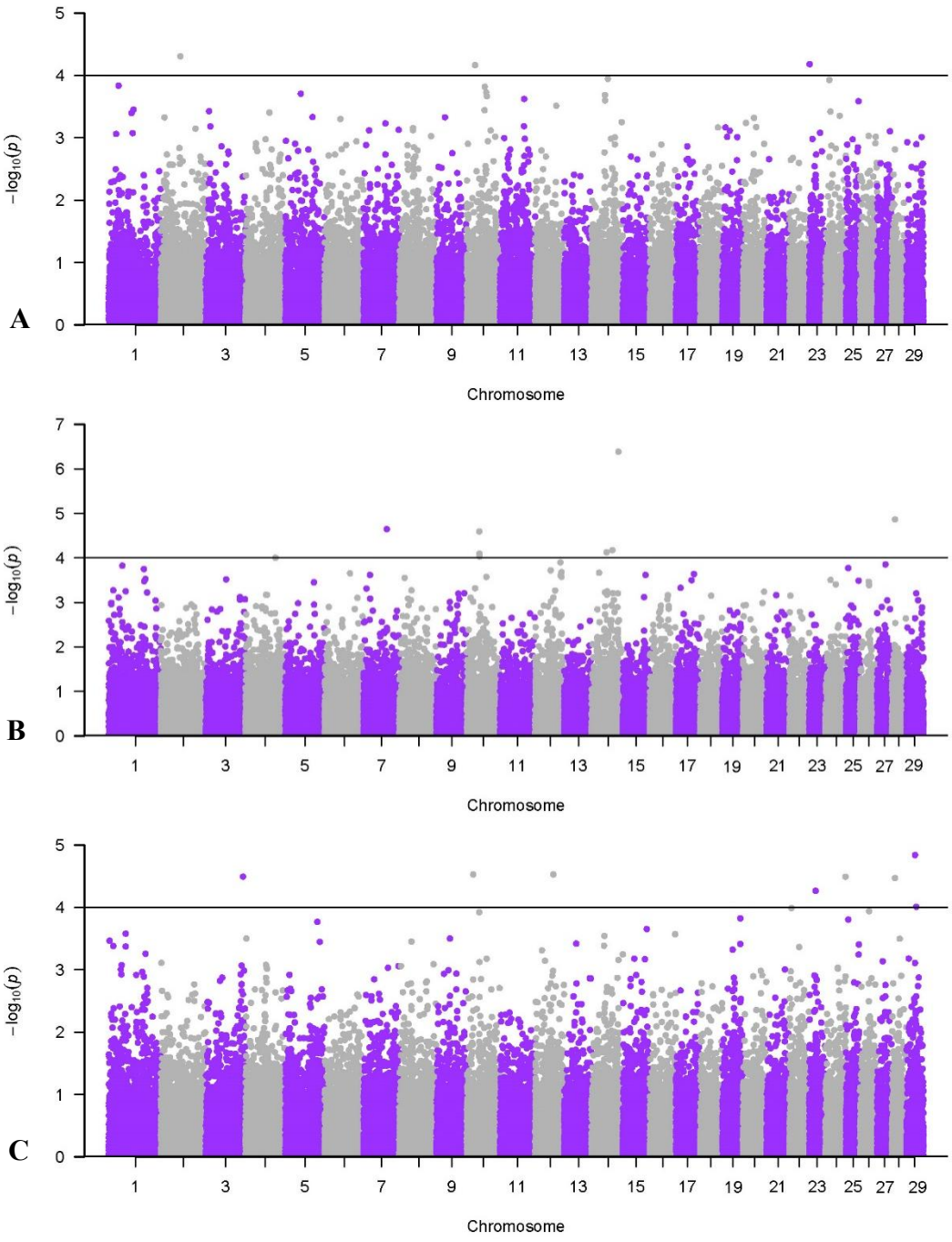


Figure 2.3. Manhattan plots for univariate, single-record genome-wide association study of traits to describe the fiber diameter distribution with a significance threshold of 4. Panel A- coarse edge micron; Panel B- spinning fineness; Panel C- percentage of fibers ≤ 19 µm.

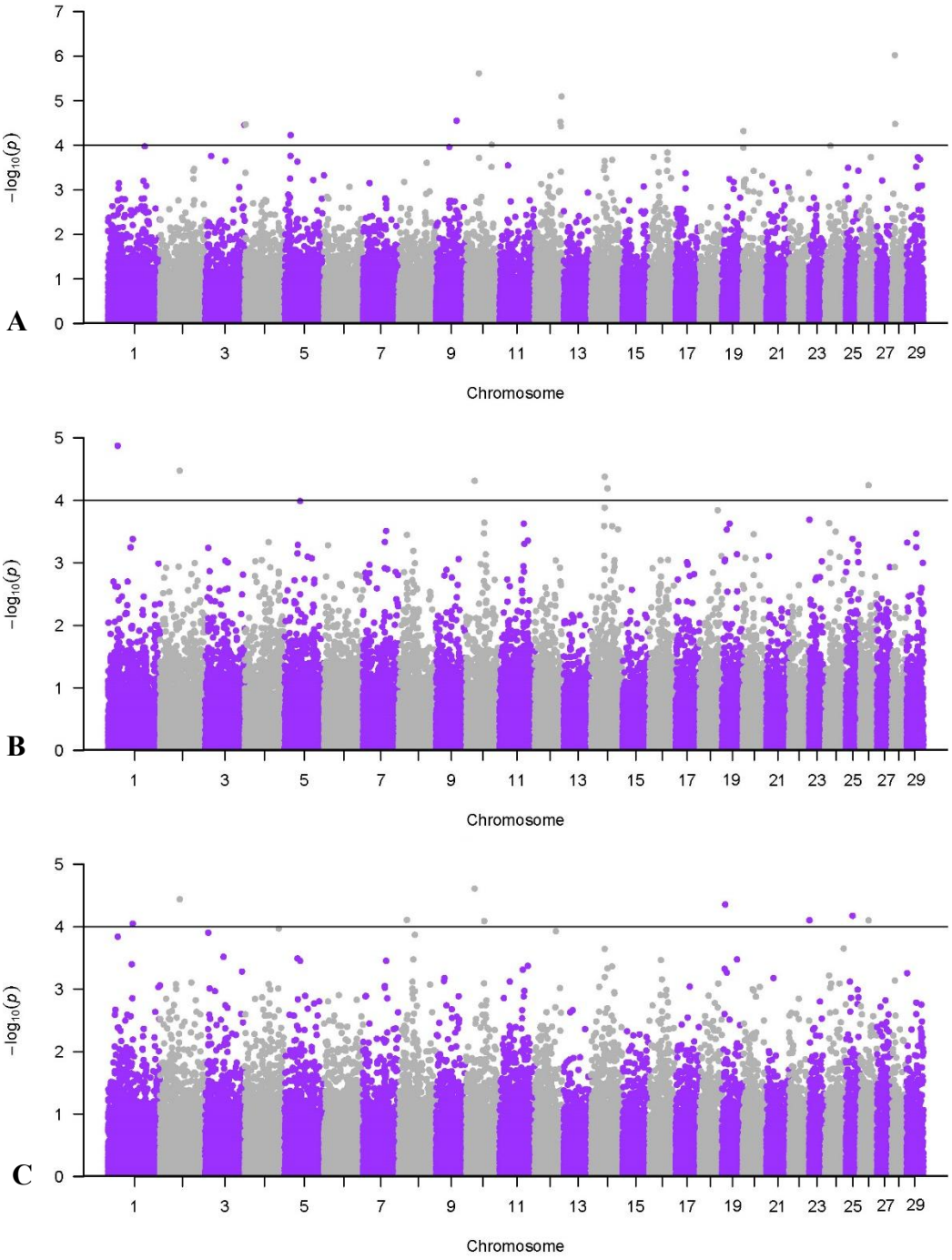
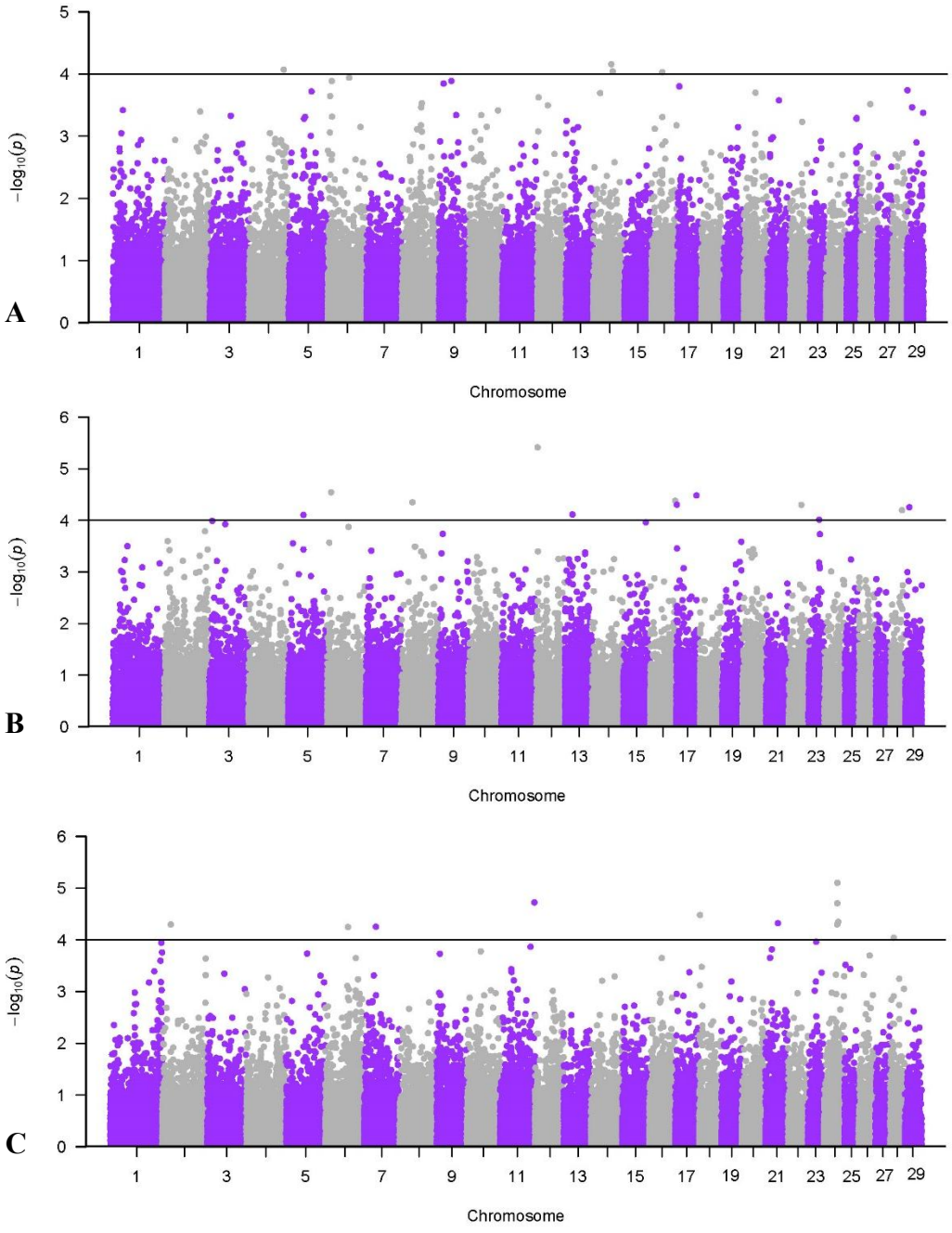


Figure 2.4. Manhattan plots for univariate, single-record genome-wide association study of curvature and length traits with a significance threshold of 4. Panel A- curvature; Panel B- standard deviation of curvature; Panel C- staple length.



Chapter 3 - Genetic parameter estimation and genome-wide association study of cashmere fiber traits in goats from two origins: New Zealand and an international New Zealand-United States population

Introduction

Cashmere is a widely regarded animal fiber due to its soft handle. Although cashmere products are typically priced higher than other animal fibers and are considered a luxury product, global cashmere demand has increased in recent years. In 2024, the global cashmere market was valued at $3.48 billion and is projected to reach $4.86 billion by 2032, due to experiencing a compound annual growth rate of 4.29% (Fortune Business Insights, 2024). While China and Mongolia remain the primary producers of cashmere, there has been growing interest in several other countries including Australia, New Zealand, and the United States. Lack of structured breeding programs and genetic evaluation tools has limited progress in improving cashmere production, particularly in the United States. There is gene flow between these populations, so increased collaboration and data sharing between non-traditional cashmere producing countries with relatively small populations, such as the U.S. and New Zealand, could be a beneficial strategy to increase sample size and statistical power for genetic analyses.

Cashmere goats originated in the Himalayan region, which is a mountainous region with high altitudes and cold temperatures. Goats adapted to these extreme conditions by developing a fine insulating undercoat produced by secondary hair follicles, called down or cashmere (Wu et al., 2023). Cashmere goats were brought to Australia and New Zealand in the late 1700's to early 1800's but were mostly abandoned to form feral flocks (Restall and Pattie, 1989). In the late 1900's, efforts were made to re-domesticate these feral goats for cashmere production. Since then, cashmere production in Australia and New Zealand has become more established, with

structured breeding programs and coordinated efforts for cashmere improvement amongst breeders. In contrast, the U.S. cashmere population was developed through a combination of imports from Australia and New Zealand and selection for fiber production within local populations, particularly Spanish meat goats (Cashmere Goat Association, 2025). Compared to other countries, the U.S. cashmere industry remains underdeveloped, with fewer resources and less infrastructure for cashmere producers.

Given the shared ancestry and challenges that non-traditional cashmere-producing countries face, such as relatively recent industry development, limited genetic resources, and smaller population size, collaboration could be a strategy to advance genetic improvement. This analysis aims to contribute to the foundation for a potential international genetic evaluation or platform for cashmere producers, which should be mutually beneficial for all contributors. The objectives of this study were to estimate variance components and genetic correlations, and to perform a genome-wide association study (GWAS) for cashmere fiber traits in two analyses: one consisting of New Zealand goats alone and a second combining U.S. and New Zealand goats.

Materials and Methods

Study population and design

Animal procedures on Langston University goats were performed as a part of Langston University Institutional Animal Care and Use project number OKLUMERKEL2020, experiment number RM-22-03 in accordance with Federation of Animal Science Societies guidelines (FASS, 2010). Data from other U.S. cashmere goats and the New Zealand goats were collected by producers with normal animal management processes, therefore Animal Care and Use Committee approval was not required.

The U.S. dataset consisted of records from goats located across the continental United States on 32 farms in 17 states. In the U.S. dataset, a total of 1,243 records from 1,035 unique animals were available. The New Zealand dataset consisted of records from goats located on one farm in New Zealand. There were a total of 2,093 records from 1,537 unique animals in the New Zealand dataset. Participation by cashmere producers in this study was voluntary. Producers in both the U.S. and New Zealand received genotype results at no cost, and U.S. producers also received fiber testing results at no cost as a part of the study. In total for the combined U.S. and New Zealand dataset, there were 3,336 records from 2,572 unique animals. Both males (n=546, 630 records) and females (n=1,890, 2,562 records) were used in this study. Table 3.1 shows the distribution of age at cashmere collection across records in the U.S. and New Zealand combined dataset. Most of the fiber records in the combined dataset were from animals in age levels 1 and 2 years. The 1-year age level encompassed all goats 1-year-old and younger; therefore, kid fleeces were in this age grouping, with the youngest goat being 0.17 years (~2 months-old).

Fiber testing

Cashmere collection from U.S. goats was described in Dressler (2025). Briefly, a 2 inch by 2 inch sample from the mid-side was clipped from each goat using standard hair clippers. Samples for each animal were individually packaged and labeled to be sent to the fiber testing laboratory. The Texas A&M Bill Sims Wool and Mohair Research Laboratory in San Angelo, Texas prepared and tested the submitted cashmere fiber samples using an Optical Fibre Diameter Analyser 100 (OFDA100).

In New Zealand, cashmere was harvested in August 2022 and August 2023. Goats were shorn with a standard shearing handpiece with a 17-tooth comb and standard cutter. After the entire fleece was shorn, a sample was taken by pulling approximately 10 random pinches from

the fleece. The sample was labeled with animal identification and sent to SGS Wool Testing Services in Kilbirnie, New Zealand. New Zealand fiber samples were also evaluated using an OFDA100.

The threshold for guard hair is different between U.S. and New Zealand fiber testing. Cashmere traits in the New Zealand dataset are measured on all fibers in the sample under 35 µm, whereas traits in the U.S. dataset are measured on all fibers in the sample under 30 µm. Other than the threshold for guard hair, seven traits were measured and defined the same way between the U.S. and New Zealand datasets. The seven traits were mean fiber diameter (MFD; µm), standard deviation of diameter (SDD; µm), coefficient of variation of diameter (CVD; %), curvature (Curv; º/mm), standard deviation of curvature (SDCurv; º/mm), spinning fineness (SpinF; µm), and percentage ≤ 19 µm (Perc19, %), which are defined in Table 3.2. Additional fiber traits were only available and analyzed in the New Zealand dataset including down staple length (DSL; mm), yield (YD; %), fleece weight (FW; g), down weight (DW; g), coarse edge (CE, %), and percentage of medullated fibers (PercMed; %), which are also defined in Table 3.2.

Genotype information

Hair samples for both U.S. and New Zealand goats were collected by collaborating cashmere producers for DNA for genotyping. Producers plucked ~20 guard hairs, with follicles still attached, from the tail or spinal ridge. Hair samples were sent to Neogen Corporation (Lincoln, NE) for genotyping on the Goat GGP 70K BeadChip (Version 1; Neogen Corp.). For the analysis of only New Zealand animals, there were 426 animals with genotypes. After removing genotypes with animal call rate less than 0.90, 391 remained for the analysis. Quality control filtering of genotypes included removing 6,793 single nucleotide polymorphisms (SNPs)

with SNP call rate less than 0.90 and 11,256 SNPs with minor allele frequency less than 0.05, leaving 53,226 SNPs for analysis.

For the U.S and New Zealand combined analysis, there were 1,462 animals (1,036 U.S. animals and 426 New Zealand animals) with genotypes available. Ninety animals' genotypes were removed for call rate less than 0.90, which left 1,372 animal genotypes available for analysis. Genotypes underwent quality control for removal of SNPs with SNP call rate less than 0.90 (4,393) and minor allele frequency less than 0.05 (9,449). There were 54,363 SNPs remaining after quality control.

Pedigree information

Collaborating cashmere producers provided within-herd pedigree records for the animals. Provided pedigrees varied in depth and completeness, ranging from 1 to 5 generations. The final pedigree for the analysis of only New Zealand animals included 1,967 animals. The final pedigree for the U.S. and New Zealand combined analysis included 3,874 animals. Twenty-four sires were used on more than one U.S. farm. Pedigree connectedness between the U.S. and New Zealand goats was through shared male germplasm. Germplasm from three New Zealand sires was used extensively in one U.S. cashmere farm and was highly influential on this farm. Those genetics were disseminated to other U.S. producers through the sale of live animals. The three New Zealand sires appear within the pedigree of 366 U.S. animals, or approximately 32% of U.S. animals.

Statistical analysis

Summary statistics were calculated in R Studio (R Studio Team, 2023) to obtain minimum, mean, maximum, and standard deviation for each fiber trait. The PROC CORR function in SAS 9.4 was used to calculate phenotypic correlations between fiber traits.

Model selection was done by forward stepwise selection. The model with the best fit was chosen based on Akaike information criterion (AIC) where the addition of another effect reduced AIC by less than 3.

The base model for each trait was as follows:

$$y_i = b_0 + e_i$$

where y_i is the fiber trait being evaluated, b_0 is the intercept, and e_i is the residual. In the New Zealand only analysis, the fixed effects that were tested for model inclusion were sex (male, female), age at cashmere collection (level; 1 to 8 years), and contemporary group (fiber testing year). In the U.S. and New Zealand combined analysis, the fixed effects that were tested for model inclusion were sex (male, female), age at cashmere collection (level; 1-19 years), and contemporary group (farm x fiber testing year). Significant fixed effects used in final models for each trait in both analyses are shown in Table 3.3.

Genetic parameter estimation

Average information restricted maximum likelihood in the BLUPF90 suite programs (Misztal et al., 2014) was used to estimate variance components for all traits and analyses. Single-step genomic best linear unbiased prediction (BLUP) was used because both pedigree and genomic information was available. In single-step genomic BLUP, the numerator relationship matrix, $\mathbf{A^{-1}}$, is replaced by $\mathbf{H^{-1}}$ in the mixed model equation (Aguilar et al., 2010) as follows:

$$\boldsymbol{H}^{-1} = \boldsymbol{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \boldsymbol{G}^{-1} - \boldsymbol{A}_{22}^{-1} \end{bmatrix}$$

where $\boldsymbol{A}^{-1}$ is the inverse of the pedigree relationship matrix, $\boldsymbol{A}_{22}^{-1}$ is the subset of the numerator relationship matrix for genotyped animals, and $\boldsymbol{G}^{-1}$ is the inverse of the genomic relationship matrix, G, which is constructed as in (VanRaden, 2008) as $\mathbf{G= ZZ'}$, where:

$$\mathbf{Z} = \frac{\mathbf{M} - \mathbf{P}}{\left[2\Sigma p_j(1 - p_j)\right]^{\mathbf{1/2}}}$$

where **Z** is the centered genotype matrix, **M** is the matrix of marker genotypes for each individual (as 0, 1, 2 copies of the second allele), and **P** is the matrix of $2p_j$ (frequency of second allele, p, at locus *j*).

Two analyses were performed: one only using the New Zealand dataset, and one using both the U.S. and New Zealand datasets combined. The following procedures were used for both analyses, with the only difference being the dataset analyzed. First, univariate analyses for each trait were performed using only the first record available from each animal according to the general univariate animal model:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + e$$

where y is a vector of dependent variables, b is a vector of fixed effects (Table 3.3), **X** is an incidence matrix relating b to y, u is a vector of direct additive genetic effects, **Z** is an incidence matrix relating u to y, and e is a vector of random residuals.

Next, also using only the first record from each animal, genetic correlations were estimated with bivariate animal models including each pairwise combination of fiber traits within each of the two analyses. For the N.Z. only analysis, bivariate models were run between each combination of the 13 traits available in the N.Z. dataset. For the Combined analysis, bivariate models were run between each of 7 traits available in both the U.S. and New Zealand datasets. Lastly, repeatability of each trait was estimated through a repeated records analysis that included every fiber record available for each animal within the two separate analyses. The repeatability animal model is as follows:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + \boldsymbol{W}p + e$$

where **W** is the incidence matrix relating p to y, p is a vector of permanent environmental effects, and other elements were defined previously in the animal model.

Genome-wide association study

Genome-wide association study procedures were the same in both the New Zealand only analysis and the U.S./New Zealand combined analysis. Single nucleotide polymorphism effects were obtained from the single record univariate analyses for each trait. The BLUPF90 program suite (Misztal et al., 2014), specifically the postGSf90 program, was used to estimate SNP effects and *P*-values. Prediction of SNP effects was done in a single-step GWAS (Wang et al., 2012) as follows:

$$a = \mathbf{Z}u$$

where a is a vector of breeding values for genotyped animals, Z is a matrix relating genotypes of each locus, and u is a vector of SNP effects. The prediction of SNP effects ($\hat{u}$) is as follows:

$$\hat{u} = IZ'(ZIZ')^{-1}\hat{a}$$

where $\hat{a}$ is a vector of estimated breeding values, **I** is an identity matrix, and **Z** was defined previously (Masuda, 2025).

Using the q-value package in R (Storey et al., 2023), false discovery rate was calculated for each SNP. No SNPs were significant at a threshold of < 0.05. In order to facilitate initial discovery, a suggestive significance threshold was set at -$\log_{10}$ *P*-value ≥ 4 for the New Zealand analysis and -$\log_{10}$ *P*-value ≥ 4.5 for the combined analysis. The qqman package in R (Turner, 2018) was used to generate Manhattan plots for each trait in each analysis.

To account for linkage disequilibrium, a quantitative trait loci (QTL) region of 50kb upstream and downstream of each significant SNP was investigated (Brito et al., 2015). Gene candidates were identified within each QTL region using the GALLO package in R (Fonseca et

al., 2020) and the National Center for Biotechnology Information Capra hircus GFF annotation file for the USDA ARS 1.2 genome assembly (Bickart et al., 2017; accession GCF_001704415.2). Molecular functions and biological processes of each gene candidate were identified using The UniProt Consortium (2023). Previously reported trait associations in the QTL regions were searched in the Goat QTLdb (Hu et al., 2022).

Results and Discussion

Summary statistics

Descriptive statistics for all traits in both analyses are reported in Table 3.4. For traits that were included in both analyses, the combined analysis was associated with a larger range between minimum and maximum values as well as a larger standard deviation in comparison to the New Zealand only analysis. This is logical as the combined dataset encompasses animals across different farms from both U.S. and New Zealand data sources and a larger sample size.

The average MFD for the New Zealand and the combined analyses was 15.68 µm and 15.65 µm, respectively. The addition of U.S. data to the New Zealand data to form the combined analysis dataset slightly decreased the average MFD. This is somewhat unexpected as U.S. cashmere is generally considered to be coarser compared to other countries, including New Zealand. However, for the New Zealand dataset, MFD was calculated using fibers with diameter from 0 to 35 µm, whereas in the U.S. dataset used in the combined analysis, only fibers ranging from 0 to 30 µm were included which may have removed some of the coarser cashmere fibers from the US samples. There are very few studies published from the United States or New Zealand specifically. Baker et al. (1991) reported an average MFD of 15.8 µm for 624 cashmere goats in New Zealand. In Australia, which has similar cashmere production and population history to New Zealand, the average MFD was 16.4 µm across 1,244 goats on 11 farms

(McGregor and Butler, 2008b). These estimates are slightly greater than the average MFD in the current study, indicating some improvement in MFD over time. Regardless, the average MFD in both analyses remained well below the international threshold of 19 µm for classification as cashmere fiber (CCMI, 2025).

The average SDD was 3.46 µm for the New Zealand analysis and 3.37 µm for the combined analysis. The average SDD for the U.S. animal subset of the combined analysis was 3.17 µm, indicating slightly less variation in diameter compared to the two analyses in this study (Dressler, 2025). Bishop and Russel (1996) studied the progeny of Scottish feral goats that were mated to germplasm imported from other countries, including New Zealand, and reported a very similar average SDD of 3.35 µm. A range in average SDD from 3.6 to 3.9 µm, depending on sex, birth type, and age, was reported for Australian cashmere goats (Gifford et al., 1990). The average SDD for the two analyses in this study falls reasonably in the range of previously published means.

Similar to SDD, CVD is a measure of the variation in diameter and the average was slightly smaller in the combined analysis (21.66%) compared to New Zealand (22.22%). In a subset of the combined analysis dataset including only U.S. animals, the average CVD was 20.67% (Dressler, 2025). For Australian goats, a similar CVD of 22.5% was reported (McGregor and Butler, 2008b). A large range in CVD from 27.09% to 41.39%, depending on sex and cohort, was reported for Left Banner Alashan White Cashmere goats (Pallotti et al., 2017). Although literature comparisons are somewhat limited, average CVD in the current studies analyses is slightly lower, indicating less variation in diameter.

The average Curv for the New Zealand and combined analyses was 62.69 º/mm and 64.78 º/mm, respectively. In general, fiber with lower curvature is softer (McGregor and Butler,

2008a), which is a key characteristic of cashmere. However, it has been reported that greater Curv is one characteristic associated with more efficient processing (McGregor, 2004). Thus, if Curv becomes too small according to textile processors, producers breeding objectives may need to change to account for this. Although literature from the U.S. or New Zealand for comparison is sparse, Australian cashmere goats had an average Curv of 48 º/mm (McGregor and Butler, 2010), which is much smaller than the current study indicating fiber from that population may have softer handle. An average Curv that is more similar to the current study of 53.8 º/mm to 55.2 º/mm (depending on cohort) was reported for cashmere goats in Scotland (Redden et al., 2010).

Average SDCurv for the New Zealand analysis was 47.82 º/mm and for the combined analysis was 45.32 º/mm. Although the combined analysis had a greater average Curv, the average SDCurv was lower, indicating less variation in Curv. In two related studies of Australian goats, average SDCurv was 33 º/mm and 34 º/mm (McGregor and Butler, 2010 and McGregor and Butler, 2008b, respectively). Redden et al. (2010) also reported SDCURV averages that were lower than the current study of 39.1 º/mm and 39.8 º/mm, depending upon cohort. Therefore, Curv was more variable in the current study compared to other published studies.

The average SpinF was very similar between the NZ and combined analyses at 15.55 µm and 15.33 µm, respectively. In a subset of the combined dataset that only included U.S. animals, the average SpinF was 14.90 µm (Dressler, 2025). The equation for SpinF was first proposed by Butler and Dolling, (1992) based on theory proposed in Martindale (1945). The equation uses both MFD and CVD to give a measure for a fiber's future spinning performance and yarn strength. Lower SpinF values indicate better spinning performance. No studies have reported average SpinF for comparison to the current study.

The last trait included in both analyses was Perc19. This trait measures the percentage of fibers with diameter ≤ 19 μm of those fibers with diameter 0 to 30 μm in diameter (0 to 35 μm for the New Zealand dataset). The Perc19 for the New Zealand and combined analyses was 86.35% and 86.75%, respectively. Despite the difference in the upper guard hair threshold between New Zealand and U.S. datasets, averages for Perc19 were similar. No other information is available in literature for comparison because Perc19 is a novel trait.

Down staple length in the New Zealand analysis had an average of 75 mm across the 374 records available. In a study of New Zealand cashmere goats, down length measured at the midside for yearlings had an average of 57 mm (Bigham et al., 1993), which is shorter than the current study. An average down length of 51.4 mm was reported for feral Australian goats (Restall and Pattie, 1989); however, this was an average of lengths measured at three sites on the animal: neck, midside, and hip. In contrast, both the current study and Bigham et al. (1993) reported down length measured only at the midside. A longer cashmere staple length of 91 mm was reported by McGregor and Butler (2008a) for Australian goats. Length is a commonly reported trait for cashmere production, however, lack of standardized and unclear measurement methodology makes literature comparisons difficult.

The New Zealand analysis had an average yield of 44.43%. In this analysis, yield was calculated by the testing laboratory using the OFDA100, following the method described in Peterson and Gheradrdi (1996). Yield represents the percentage of cashmere down in the total shorn fleece weight. Using the same methodology, cashmere yield has been reported in a few other studies. McGregor (2004) reported an average cashmere yield of 33.3% in commercial bales of Australian cashmere. In three related studies, McGregor and Butler (2008a, 2008b, 2010) reported average yields of 39.9%, 37%, and 37.7%, respectively for Australian cashmere.

These values are lower than the yield observed in the current study, suggesting that goats in the current study produce a greater proportion of down fiber.

Average greasy FW in the New Zealand analysis was 400.3 g. Studies from the early 1990's in Australia and New Zealand reported lower greasy FWs compared to more recent studies and the current study. The average greasy FW of New Zealand goats was 258 g (Baker et al., 1991). Similarly, Gifford et al. (1990) reported average greasy FWs for Australian goats ranging from 223.1 g to 254.4 g, depending on birth type, sex, and age of dam. In another Australian study, greasy FW ranged from 282.8 g to 427.8 g, depending on sex, year, and birth type (Rose et al., 1992). While this is a broad range, the upper end is comparable to the average observed in the current study. More recent Australian studies report averages that are closer to the current study, with average greasy FWs of 394 g and 397 g reported in two related studies (McGregor and Butler 2008b, 2010). This shows that in general, improvements have been made to increase greasy fleece weight over time in Australia and New Zealand.

Down weight, calculated by multiplying greasy FW by yield, in the New Zealand analysis had an average of 207.5 g. Two Australian studies used the same calculation and reported average DWs of 134 g and 137g (McGregor and Butler 2008b, 2010), which are lower than the current study. For New Zealand goats, Baker et al. (1991) reported an average DW of 93 g. Gifford et al. (1990) reported average DWs for Australian goats ranging from 90.6 g to 118.3 g, depending on birth type, sex, and age of dam. Similarly, average DW of Australian goats ranged from 112.5 g to 165.2 g, depending on sex, year, and birth type (Rose et al., 1992). In contrast, studies from traditional cashmere-producing countries such as China and Mongolia report much larger average DWs. For Chinese Alashan Left Banner White cashmere goats, clean combed DW ranged from 404.47 g to 514.49 g (Pallotti et al., 2017). Zhou et al. (2002) and Bai

et al. (2006) reported average raw cashmere weights for Inner Mongolian White cashmere goats of 527.7 g and 529.7 g, respectively. However, the averages from Bai et al. (2006) are for raw combed DW, rather than clean DW as described for other studies, which means these DWs include unknown amounts of guard hair and other contaminants.

The New Zealand analysis had an average CE of 0.605%. There are many ways to examine the coarse edge of the fiber diameter distribution; CE as defined in the current study as the percentage of fibers with diameter >30 μm out of all fibers with diameter ≤ 35 μm. In practice, that is the percentage of fibers with diameters between 30 μm and 35 μm or in other words the coarse edge of the diameter distribution. McGregor and Naebe (2015) reported a lower CE of 0.2% in a study on fiber handle properties of superfine wool blended with cashmere. Literature on CE in cashmere is limited, making additional comparisons difficult.

The average PercMed in the New Zealand analysis was 0.596%, meaning that less than 1% of fibers in the tested sample were medullated. Medullated fibers are those that have a large medulla, or hollow space at the center of the fiber. These fibers have a different appearance when dyed and contribute to the prickle sensation in garments; therefore, they must be removed during fiber processing (McGregor, 2018). Even a small number of medullated fibers can negatively impact the value and potential end-use of cashmere (McGregor and Butler, 2004). Therefore, it is important to reduce or maintain medullation under an acceptable threshold. Naebe and McGregor (2013) reported an average PercMed of 0.1% for superfine wool/cashmere blends. Generally, cashmere has a lower incidence of medullation compared to fiber from other species. In alpacas, the percentage of medullated fibers was 18.3% (Pinares et al., 2018) and ranged from 32.74% to 37.31% depending on breed type (Cruz et al., 2019). In contrast, in angora rabbit fiber, medullated fibers are considered desirable, contributing to the fiber's fluffy appearance

(McGregor, 2018). Rafat et al. (2007) reported an average PercMed of 1.7% for French Angora rabbit fiber. These comparisons highlight the relatively low incidence of medullated fibers in cashmere compared to other fiber-producing species.

Heritability and repeatability of cashmere fiber traits

For the New Zealand analysis, univariate heritability estimates from single record models are on the diagonal of Table 3.5 and from each bivariate single record model in Table 3.6. For the combined analysis, univariate heritability estimates from single record models are on the diagonal of Table 3.7 and from each bivariate single record model in Table 3.8. Results from the repeated records models for both the New Zealand and the combined analysis, including heritability and repeatability estimates, are presented in Table 3.9.

Mean fiber diameter was evaluated in both the New Zealand and combined analyses with single record heritability estimates of 0.49 ± 0.06 and 0.46 ± 0.06, respectively. Heritability estimates from repeated records models were also similar between the two analyses and were similar to those from the single-record models (Table 3.9). Repeatability of MFD in both analyses was similar and high (Table 3.9). Similar heritability and repeatability estimates of 0.47 ± 0.15 and 0.60 ± 0.02 were reported for feral Australian goats (Pattie and Restall, 1989). Although no estimates have been published for populations in the United States, several from populations in New Zealand exist. A heritability estimate of 0.99 ± 0.19 for yearling goats and 0.19 ± 0.07 for kid goats was reported by Bigham et al. (1993), which encompasses a very large range with extreme estimates. Another heritability estimate published in New Zealand was high (0.82 ± 0.23) for 624 yearling cashmere goats (Baker et al., 1991). Estimates from other New Zealand studies specifically, are very high with large standard errors. But, in general, the

heritability of MFD is moderate to high in literature (as reviewed by Dressler et al., 2024), which is consistent with estimates from the current study.

Single record univariate heritability of SDD was 0.18 ± 0.05 in the New Zealand analysis and 0.26 ± 0.04 in the combined analysis. Within each analysis, heritability estimates from the single record and repeated records models were very similar (Tables 3.8 and 3.9). Between analyses, the combined analysis had slightly higher estimates overall, with the highest estimate for SDD observed in the repeated records model at 0.28 ± 0.04. The same heritability estimate (0.28) was published for 5-month-old Scottish goats (Bishop and Allain, 2000). Other heritability estimates published for SDD have been slightly higher at 0.38 ± 0.14 and 0.43 ± 0.08, as reported by Gifford et al. (1990) and Bishop and Russel (1996), respectively. Repeatability of SDD was high in both the New Zealand and combined analyses with estimates of 0.42 ± 0.03 and 0.50 ± 0.03, respectively. These relatively high repeatability estimates for SDD suggest that a single SDD measurement would be a good indicator of diameter variation in subsequent years.

The single record univariate heritability for CVD was very similar in the New Zealand (0.25 ± 0.05) and combined analyses (0.26 ± 0.04). Heritability estimates from the repeated records models were comparable to those from the single record models, and consistent across analyses (Table 3.9). Although literature on CVD is limited, a heritability estimate of 0.52 ± 0.06 was reported for Chinese Alashan Left Banner White cashmere goats (Pallotti et al., 2018). This higher estimate may reflect differences in breed type or historical population structure. Similar to SDD, another measure of diameter variation, the repeatability of CVD was high. These findings suggest that measures of diameter variation, SDD and CVD, are moderately heritable and highly repeatable.

The heritability of Curv in the single record analyses ranged from 0.33 ± 0.04 to 0.46 ± 0.06 (Tables 3.5 and 3.7). The range in heritability estimates of Curv in the repeated records analyses was 0.34 ± 0.04 to 0.46 ± 0.05, so the inclusion of repeated records did not substantially change heritability estimates. Estimates were very similar between single and repeated records models within each analysis, but the combined analysis had slightly lower heritabilities compared to New Zealand. In contrast, repeatability was higher in the combined analysis (0.67 ± 0.02) compared to the New Zealand analysis (0.51 ± 0.03). While there is limited literature on genetic parameters of Curv, some studies have assessed Curv phenotypically. McGregor (2013) identified Curv as the single largest determinant of resistance to compression, an objective measure of fiber softness. This indicates that Curv is a relevant trait for cashmere production and supports its inclusion in genetic analyses. Additionally, McGregor (2003) reported that Curv in Australian and Chinese Liaoning cashmere goats was impacted by nutrition, with goats undergoing weight loss producing cashmere with significantly greater fiber Curv. While there were also significant differences in Curv based on sex and age, this highlights that bodyweight or weight changes from nutrition may also be important effects for cashmere producers to measure for inclusion in future genetic evaluations. In all, Curv has practical relevance to fiber quality and is a heritable and repeatable trait that could be included in genetic selection programs.

Heritability estimates for SDCurv were moderate and very similar between single record and repeated records models, as well as between analyses (Tables 3.5, 3.7, and 3.9). The repeatability of SDCurv in the New Zealand analysis (0.35 ± 0.04) was lower than the combined analysis (0.55 ± 0.03), a pattern also observed for Curv. This could partly reflect the larger sample size and greater number of repeated records in the combined analysis. When the subset of U.S. animals included in the combined analysis were analyzed separately, the repeatability

estimate (0.51 ± 0.07) was similar to that estimated from the combined analysis (Dressler, 2025). The limited availability of genetic parameter estimates for SDCurv, much like Curv, makes comparisons to other studies challenging.

Spinning fineness was moderately to highly heritable across all models in both analyses, with estimates ranging from 0.40 ± 0.04 to 0.42 ± 0.06 (Tables 3.5, 3.7, and 3.9). Repeatability of SpinF was also similar between the New Zealand analysis (0.54 ± 0.03) and the combined analysis (0.61 ± 0.02). Spinning fineness is calculated with an equation that includes MFD and CVD (Butler and Dolling, 1992). In their original publication on the theory of SpinF, the authors approximated heritability of SpinF using genetic parameters for MFD and CVD and reported derived heritabilities of 0.43, 0.56, and 0.70, depending on the test dataset. In the current study, heritability and repeatability estimates of MFD were similar to those of SpinF, which is logical given MFD is a large component of the SpinF equation. These results suggest that SpinF is a heritable and repeatable trait. However, given its dependance on MFD and CVD, the inclusion of SpinF in breeding programs should be weighed against selecting on its component traits directly.

In the New Zealand analyses, the heritability of Perc19 ranged from 0.06 ± 0.03 to 0.13 ± 0.05. In the combined analysis, heritability estimates were slightly higher, with values ranging from 0.19 ± 0.03 to 0.29 ± 0.04. Differences in estimates between single and repeated records models and across analyses were relatively small when considering standard errors. Repeatability estimates were close to or the same as their corresponding heritability estimates in both analyses (Table 3.9), indicating minimal permanent environmental variance. Given the relatively low heritability and repeatability estimates for Perc19 compared to MFD, it may be more effective for selection to remain directly on MFD for improving fiber fineness. However, if the breeding objective includes a more targeted control of the fiber diameter distribution to distinguish

between fine and coarse fibers, Perc19 could be considered for inclusion instead of other traits that characterize fiber coarseness like coarse edge or comfort factor.

Yield phenotypes were only available in the New Zealand dataset; therefore, yield was not evaluated in the combined analysis. The single record heritability of yield was 0.35 ± 0.05. In the repeated records analysis, the heritability and repeatability of yield was 0.31 ± 0.03, indicating very little permanent environmental variance. Rong et al. (2024) reported a heritability of 0.23 ± 0.03 for cashmere yield in Inner Mongolia cashmere goats. However, these authors reported cashmere yield (g) as the weight of cashmere after the cashmere is cleaned measured with a scale, which is also commonly known as cashmere or down weight whereas the current study reports yield (%) as the percentage of down fibers in the entire shorn fleece according to Peterson and Gheradrdi (1996). Therefore, these estimates are likely related but not directly comparable, which emphasizes the necessity of standardized phenotype measurement and naming for cashmere fiber characteristics. Two New Zealand studies reported heritability estimates for cashmere yield of 0.57 ± 0.15 and 0.64 ± 0.21 (Bigham et al., 1993 and Baker et al., 1991, respectively). Yield was defined similarly to the current study but measured with laboratory equipment more standard for that time period. The heritability estimates from Bigham et al. (1993) and Baker et al. (1991) are higher than those in the current study, although they are associated with relatively large standard errors.

The single record heritability of DW was 0.45 ± 0.11 in the New Zealand analysis. Repeated records were not available for DW in the New Zealand data, therefore a repeated records analysis was not performed. In the current study, DW (g) was back-calculated using greasy FW (g) and down yield (%). Defining DW in a similar way, two New Zealand studies reported heritabilities of 0.62 ± 0.15 and 0.45 ± 0.17 (Bigham et al., 1993 and Baker et al., 1991,

respectively). In feral Australian goats, Pattie and Restall (1989) reported a comparable heritability of 0.61 ± 0.18. These estimates are similar, particularly considering the relatively large standard errors. As one of the most economically relevant cashmere traits, DW is highly heritable with strong potential for improvement through genetic selection.

As non-traditional cashmere regions began shearing entire fleeces rather than hand-combing them, FW emerged as a relevant production trait. The single record heritability of FW was 0.59 ± 0.12. This trait was not analyzed in the combined analysis or with a repeated records model in the New Zealand analysis because phenotypes were not available. For Australian goats, heritability estimates for FW of 0.29 ± 0.11, 0.67 ± 0.22, and 0.42 ± 0.16 have been reported (Pattie and Restall, 1989; Rose et al., 1992; Gifford et al., 1990). In New Zealand, heritability estimates of 0.14 ± 0.06, 0.42 ± 0.13, and 0.31 ± 0.14 have been reported (Bigham et al., 1993 and Baker et al. 1991). A wide range in heritability estimates have been published and the estimate from our current study falls toward the higher end of that range.

The single record heritability for DSL was 0.35 ± 0.13 in the New Zealand analysis. The closest estimate in published literature is 0.29 in Inner Mongolian White cashmere goats, although this was from combed cashmere (Bai et al., 2006). One of the highest estimates for down length is 0.70 ± 0.19 for feral Australian goats, which was measured as the average from lengths taken at the neck, midside, and hip (Pattie and Restall, 1989). The current study measured DSL as the length at the midside only, which could partly explain the difference in estimates. Bigham et al. (1993) measured down length at the midside for New Zealand goats and reported a heritability of 0.55 ± 0.15. Although this study has similar measurement technique and country of origin to the current study, the estimate was still higher. There is a wide range in

published heritability estimates for DSL which could be due to differences in harvest method and measurement technique, highlighting the need for standardized phenotype collection.

In the New Zealand analysis, PercMed had a single record heritability of 0.26 ± 0.06. The heritability and repeatability in the repeated records analysis were the same (0.19 ± 0.05), indicating that permanent environmental effects contributed minimally, if at all, to variation in Perc19 across repeated records. While literature is limited on genetic parameters of PercMed in cashmere, a few studies have examined PercMed in alpacas. Although it does not have the same fine qualities as cashmere, alpaca fiber is still widely used in the textile industry. The heritability of PercMed for Huacaya type alpacas was 0.23 ± 0.01 and was 0.66 ± 0.02 for Suri type alpacas (Cruz et al., 2019). Despite being a different species, the heritability reported for Huacaya type alpacas was very similar to the current study. Pinares et al. (2018) categorized fibers by degree of medullation according to size of the medulla into 5 categories. The heritability estimates for each category of medullation ranged from 0.11 ± 0.05 to 0.36 ± 0.13. The current study's heritability estimate for PercMed falls directly within that range. High incidence of medullated fibers in cashmere negatively impacts the value of fiber, therefore it is important to maintain low incidence of medullation. The heritability of PercMed appears to be moderate indicating genetic selection is possible if needed to reduce incidence of medullated fibers.

The heritability of CE in the New Zealand analysis was the same from both the single record (0.14 ± 0.05) and repeated records (0.14 ± 0.04) models. The repeatability of CE was slightly higher (0.19 ± 0.04), although still low. This indicates a single measurement of CE is not a strong predictor of future measurements and there is value in testing CE each year. Although CE may be useful for categorizing the coarse end of the diameter distribution, there is limited literature on this trait in cashmere goats for comparison.

It is common practice for cashmere producers to test the fiber from their goats each year. In the absence of a genetic selection tool, these fiber test results are one of the only objective metrics available to make selection decisions. In terms of developing a genetic evaluation for cashmere, repeated records should be utilized if the producer already conducted the fiber test or collects this data for other purposes. However, most fiber traits have moderate to high repeatability, suggesting that additional records for the same animal contribute relatively little new information to the genetic evaluation. Producers could weigh the cost of a fiber test against the potential increase in estimated breeding value (EBV) accuracy. Table 3.10 summarizes EBV accuracies for cashmere fiber traits in both the single record and repeated records analyses from the combined U.S. and New Zealand dataset. Average EBV accuracy in the repeated records analysis was only slightly higher than that from the single record analysis for all traits (Table 3.10). Traits with lower heritability generally had larger increases in average EBV accuracy from including repeated records. For example, MFD (heritability of 0.47) only had a 1% increase in average EBV accuracy with repeated records, while SDD (heritability of 0.28) had a 5% increase, the highest increase in average accuracy observed. Given the high repeatability and modest gains in EBV accuracy, annual fiber testing of every animal may not be necessary in a future genetic evaluation program, particularly if fiber testing costs are a concern.

Genetic and phenotypic correlations between cashmere fiber traits

Tables 3.5 and 3.7 present phenotypic correlations (upper diagonal) and genetic correlations (lower diagonal) between fiber traits for the New Zealand and combined analyses, respectively. Phenotypic and genetic correlations were consistent in direction within each of the two separate analyses. Furthermore, phenotypic and genetic correlations from the New Zealand and combined analyses were consistent in direction, with slight differences magnitudes.

The phenotypic and genetic correlations between MFD and SDD were moderate, positive, and favorable, indicating that selection to decrease MFD would also reduce variation in diameter. Stronger phenotypic (0.41) and genetic (0.79 ± 0.09) correlations were reported for New Zealand goats (Bigham et al., 1993). A lower genetic correlation of 0.68 ± 0.09, albeit still higher than the current study, was reported for goats in the UK (Bishop and Russel, 1996). The closest genetic correlation to the current study was 0.52 ± 0.14 for the U.S. subset of goats used in the combined analysis (Dressler, 2025). This suggests that the genetic correlation between MFD and SDD is positive, and likely moderate to highly correlated.

Coefficient of variation of diameter is another measure of diameter variability. The phenotypic and genetic correlations between MFD and CVD were negative in both analyses (Table 3.5 and 3.7). This is unfavorable as it suggests finer fleeces have greater variation in diameter when it's expressed relative to MFD. A negative genetic correlation (-0.32 ± 0.16) between MFD and CVD was also observed in a separate evaluation of the portion of goats from the combined analysis that were from the U.S. only (Dressler, 2025). This relationship is logical because CVD is a ratio trait with MFD in the denominator. At the same SDD, coarser fleeces will have a lower CVD, and finer fleeces will have a higher CVD. Ratio traits like CVD pose challenges for genetic selection due to difficulties in interpretating the selection response (McCaw et al., 2025). The observed genetic change could result from changes in the numerator, denominator, or both components. In contrast to the current study, Pallotti et al. (2018) reported positive phenotypic (0.29 ± 0.07) and genetic (0.39 ± 0.10) correlations between MFD and CVD for Chinese Alashan Left Banner White cashmere goats. However, these authors acknowledged that their correlations generally differed from other published literature.

The same phenotypic correlation of -0.68 between MFD and Curv was observed in both the New Zealand and combined analyses. The genetic correlation between MFD and Curv was strongly negative and very similar between the New Zealand and combined analyses (Tables 3.5 and 3.7). A similar phenotypic correlation of -0.65 between MFD and Curv was reported by Ansari-Renani et al. (2012) for Raeini cashmere goats in Iran. The negative genetic correlation between MFD and Curv indicates that selection to reduce MFD would simultaneously increase Curv. However, the role of fiber curvature in the commercial classification and trading of cashmere has yet to be clearly established. Whether this genetic correlation is considered favorable may depend on individual cashmere producers' breeding objectives. Fiber with lower curvature has lower resistance to compression, which is associated with softer handle (McGregor, 2004), whereas greater curvature is associated with better processing efficiency and increased fiber bulk, which improves loft and insulation (McGregor and Butler, 2008a). Given these trade-offs, selection strategies that balance improvements in MFD with the maintenance of moderate curvature may be the best approach in the absence of a marketing structure that differentiates value based on fiber curvature.

Similar to correlations estimated between MFD and Curv, correlations between MFD and SDCurv were also strongly negative with phenotypic correlations ranging from -0.35 to -0.59 and genetic correlations ranging from -0.60 ± 0.08 to -71 ± 0.08. These results indicate that selection for finer fiber diameter would increase SDCurv, or the variation in curvature. This is an unfavorable correlation because greater variability in Curv results in a less uniform fiber, which is undesirable, regardless of a producers' goals for Curv.

The phenotypic and genetic correlations between MFD and SpinF were very high in both the New Zealand and combined analyses. This is expected since MFD is a major component of

the SpinF calculation. Butler and Dolling (1992) proposed the equation to calculate SpinF, as well as formulas to approximate its heritability and genetic correlations using genetic parameters of its component traits: MFD and CVD. These authors reported derived genetic correlations between MFD and SpinF ranging from 0.93 to 0.98, depending on published genetic parameters used. Given the high genetic correlation, these traits are likely to have great overlap in their underlying genetic control. As a result, including both traits in a breeding objective would be redundant and focusing on MFD would be sufficient.

In the New Zealand analysis, MFD and Perc19 had genetic and phenotypic correlations of -0.85 ± 0.23 and -0.44, respectively. The combined analysis had a similar genetic correlation while the phenotypic correlation was higher (-0.71). Because finer MFD is associated with a higher percentage of fibers with diameter ≤ 19 μm, this high correlation is logical. As Perc19 is a potential novel trait for cashmere production, no published correlation estimates are currently available for comparison.

The genetic correlation between MFD and yield in the New Zealand analysis was not significantly different from zero (0.08 ± 0.11). Although yield, as defined in the current study, has been evaluated in some studies, literature reporting genetic parameters for this trait remains scarce. Several studies from the late 1980's to early 1990's in New Zealand and Australia evaluated percentage yield of down measured with laboratory equipment more standard for that time period. These earlier studies reported a wide range in correlations between MFD and yield. Gifford et al. (1990) found a phenotypic correlation of 0.25 and a genetic correlation of 0. These authors did not indicate if the model truly converged at 0 for this correlation. If it did, that would agree with the results of the current study, suggesting there is no genetic correlation between MFD and yield. Baker et al. (1991) and Rose et al. (1992) published genetic correlations of 0.30

± 0.27 and 0.17 ± 0.31, respectively. Considering the large standard errors, these estimates also support that the genetic correlation between MFD and yield is not significant to very weak. In contrast, strong positive genetic correlations of 0.70 ± 0.11 and 0.57 ± 0.04 between MFD and yield were reported by Bigham et al. (1992) and Pattie and Restall (1989), respectively. Interestingly, the phenotypic correlation reported by Bigham et al. (1992) was only 0.10, which is consistent with estimates in the current study (Table 3.5). More research is needed to further elucidate the genetic relationship between MFD and yield given the large range in published estimates and the lack of contemporary literature using a consistent definition of yield.

In the New Zealand analysis, the phenotypic correlation between MFD and DW was 0.38 and the genetic correlation was 0.13 ± 0.15. It should be noted that a much smaller sample size was available for both DW and FW compared to other traits, likely contributing to a higher standard error. Early 1990's studies in Australia reported similarly low or nonsignificant genetic correlations between MFD and DW of 0.04 ± 0.23 (Gifford et al., 1990) and 0.33 ± 0.28 (Rose et al. 1992). A genetic correlation of 0.38 ± 0.28 was reported for New Zealand goats (Baker et al. 1991), albeit with a large standard error. The phenotypic correlation reported by those authors (0.42) was very similar to the present study. A study of Inner Mongolian white cashmere goats in China had a genetic correlation between MFD and DW of 0.03 ± 0.04 (Bai et al., 1006), which despite being combed cashmere from a different breed, was consistent with the current estimate. In contrast, Pattie and Restall (1989) and Bigham et al. (1992) reported strong genetic correlations of 0.62 ± 0.03 and 0.81 ± 0.08, respectively. Pallotti et al. (2018) reported phenotypic (0.20± 0.05) and genetic (-0.27 ± 0.20) correlations that differed in direction. Overall, the phenotypic correlation between MFD and DW appears to be moderate and positive.

However, the genetic correlation remains uncertain given large standard errors and inconsistency across literature.

Similar to MFD and DW, the phenotypic correlation between MFD and FW was moderate and positive, while the genetic correlation was not significantly different from zero (Table 3.5). Other studies have also reported genetic correlations with standard errors that overlap zero, including 0.13 ± 0.30 (Baker et al., 1991) and 0.12 ± 0.23 (Gifford et al., 1990). Pattie and Restall (1989) reported a low correlation (0.14 ± 0.05) between MFD and FW. However, as with MFD and DW, correlation estimates between MFD and FW in literature vary widely. Strong genetic correlations of 0.69 ± 0.13 (Bigham et al., 199) and 0.47 ± 0.25 (Rose et al., 1992) have also been reported. No correlation estimates are available from traditional cashmere-producing countries, where cashmere is harvested by combing rather than shearing the entire fleece. While the phenotypic correlation between MFD and FW appears to be moderate, the underlying genetic relationship may be weaker or obscured by large standard errors due to limited sample size.

In the New Zealand analysis, MFD and DSL had moderate phenotypic and genetic correlations. Although the genetic correlation was associated with a relatively large standard error, it indicates that selection to reduce MFD would also lead to fiber with shorter down length. This is an unfavorable correlation because both fine diameter and long length are desirable characteristics. Phenotypic correlations of 0.28 (Bigham et al. 1992) and 0.35 (Pattie and Restall, 1989) have been reported, which agree with the present study. Previously reported genetic correlations of 0.52 ± 0.04 (Pattie and Restall, 1989) and 0.75 ± 0.10 (Bigham et al. 1992) are stronger than the estimate in this study. Some of this discrepancy may be attributed to differences in measurement methodology. These two studies measured down length as the average from

three sites (neck, midside, and rump), whereas DSL in the current study was measured only at the midside.

Mean fiber diameter and PercMed had a phenotypic correlation of -0.39 and a genetic correlation of -0.46 ± 0.14 in the New Zealand analysis. This is an unfavorable relationship because this suggests that selection for finer diameter would also lead to a greater percentage of medullated fibers. This is interesting because medullation is generally associated with coarse fibers (McGregor, 2018). The genetic relationship between MFD and PercMed has not previously been evaluated in cashmere goats. However, Cruz et al. (2018) reported positive genetic correlations between MFD and PercMed in alpacas ranging from 0.21 ± 0.04 to 0.37 ± 0.03, depending on breed type. These findings contrast with the estimates from this study and may reflect species differences, as alpaca fiber generally has a higher incidence of medullation compared to cashmere. Given that medullation can substantially reduce the value of cashmere fiber and that selection for lower MFD is a common breeding goal, this genetic relationship warrants validation and careful consideration in breeding programs.

In the New Zealand analysis, MFD and CE had a phenotypic correlation of -0.14 and a genetic correlation not significantly different from zero (Table 3.5). Although weak, this phenotypic correlation suggests that fiber with finer MFD also tends to have a greater CE, or percentage of fibers at the coarse end of the diameter distribution (30-35 μm). However, this relationship was not observed in the genetic correlation between MFD and CE. Further investigation across additional populations is needed to evaluate the relationship between MFD and CE.

Prior literature has primarily focused on correlations involving MFD due to its economic relevance. While Tables 3.5 and 3.7 present additional phenotypic and genetic correlations

among other fiber characteristics, these relationships have not been previously evaluated in literature, limiting opportunities for comparison.

Genome-wide association study

For the New Zealand analysis, significant SNPs for cashmere traits are in Table 3.11 and Manhattan plots are shown in Figure 3.1. For the combined analysis, significant SNPs for cashmere traits are in Table 3.12 and Manhattan plots are shown in Figure 3.2. All genes ± 50 kb of the significant SNPs are presented in Appendix Tables B.1 and B.2 for the New Zealand and combined analyses, respectively.

Mean fiber diameter

In the combined analysis of MFD, four SNPs were significant (Table 3.12). All four of those SNPs were also significant for either another trait in the combined analysis or traits in the New Zealand analysis. In the combined analysis, NC_030817.1_60685789 was significant for both MFD and Curv. Also, NC_030817.1_53553840 was significant for MFD, CURV, Perc19, and SpinF in the combined analysis. In the New Zealand analysis, MFD and SpinF shared 3 SNPs: snp6974-scaffold1257-459805, snp32293-scaffold366-3596533, and NC_030823.1_14537267. Between the New Zealand and combined analyses, 8:85169943 was significant in both analyses for MFD and snp26238-scaffold275-766124 was significant in the combined analysis for MFD and Curv in the New Zealand analysis.

The gene RORA (RAR related orphan receptor A) was near the SNP, NC_030817.1_53553840. This gene was also identified near a significant SNP for Perc19 utilizing a subset of these animals from the U.S. only (Dressler, 2025). RORA encodes a nuclear receptor and is involved in a wide range of biological processes. In rats, RORA activation significantly promoted autophagy of hair follicle stem cells (HFSC; Zhao et al., 2025).

Autophagy is a cellular process where cells degrade and recycle damaged or unnecessary cellular components, and it has been suggested to support hair follicle development during in the anagen (growth) phase of the hair cycle (Chai et al., 2019). Additionally, gene silencing of RORA in human keratinocytes inhibited differentiation (Dai et al., 2013). Keratinocytes differentiate as they migrate through the epidermal layers and eventually form the outermost skin layer. They also contribute to the formation of the hair shaft by producing keratin, a structural protein. Another function of RORA relevant to cashmere production is its role in melatonin signaling. During the seasonal transition from summer to winter, melatonin levels rise in response to shorter day lengths. Elevated melatonin has been shown to inhibit RORA, in turn promoting HFSC viability (Zhang et al., 2025). This regulatory pathway may be important for the transition from a summer to winter coat in animals. RORA is a strong gene candidate for MFD given its roles in hair follicle dynamics, keratinocyte differentiation, and seasonal hair cycling.

Standard deviation of diameter

For SDD, only two SNPs were above the $-\log_{10}$ *P*-value threshold of 4 in the New Zealand analysis (Table 3.11). The gene ADAMTS3 (ADAM metallopeptidase with thrombospondin type 1 motif 3) was in proximity to snp59884-scaffold996-137936. This gene was recently reported to be associated with hair follicle morphogenesis in Inner Mongolia cashmere goats. Ma et al. (2025) discovered that the long non-coding RNA MSTRG.14227.1 acts as a competing endogenous RNA by sponging chi-miR-433, thus increasing the expression of ADAMTS3. Upregulation of ADAMTS3 through this regulatory axis inhibits the proliferation and migration of dermal fibroblasts, which are essential for secondary hair follicle morphogenesis. Since secondary hair follicles produce the fine undercoat fibers (cashmere), ADAMTS3 is a promising gene candidate for SDD due to its influence on fiber development.

Six SNPs were significant in the combined analysis and one of those SNP (snp13153-scaffold1501-2062871) was also significant for Perc19 and SpinF. The SNP 11:104566389 was located near two members in the lipocalin family: LCN6 (Lipocalin 6) and LCN10 (Lipocalin 10). The lipocalin family comprises a group of genes that encode small secreting proteins involved in the transport of hydrophobic molecules and are typically expressed in epithelial tissues such as skin. While LNC6 and LCN10 specifically have not been directly linked to fiber production, another member of the lipocalin family, LCN2 (Lipocalin 2) has been. Xu et al. (2016) found that overexpression of the transcription factor Tcf7l1 lead to increased expression of LCN2, which disrupted normal keratocyte differentiation. This suggests that LCN2 is involved in regulating keratinocyte differentiation, an important process in skin biology and hair follicle function. Additionally, elevated expression of LCN2 by keratinocytes and granulocytes has been observed in the skin lesions of patients with a chronic inflammatory skin disease in humans (Wolk et al., 2017). This indicates that LCN2 may have broader involvement in skin homeostasis and response to stress/inflammation. The results of the current study suggest that the lipocalin family, including LCN6 and LCN10, warrants further investigation for its potential role in fiber production.

Coefficient of variation of diameter

In the New Zealand analysis, four significant SNPs were identified for CVD. The SNP snp32217-scaffold366-80065 was also identified for CURV, SDCURV, and PercMed. The gene TP53I3 (Tumor protein p53 inducible protein 3) was identified near the significant SNP snp20700-scaffold204-820288. This gene is transcriptionally activated by p53 (tumor suppressor protein) in response to cellular stressors. While no studies have directly linked TP53I3 to fiber production, the broader p53 signaling pathway plays a key role in hair follicle regression during

the catagen phase by promoting apoptosis in follicular keratinocytes (Botchkarev et al., 2001). Further research is warranted to investigate the specific role of TP53I3 in skin and hair follicle physiology, but it remains a potential gene candidate due to its involvement in the regulation of hair follicle dynamics through p53.

The combined analysis of CVD identified two significant SNPs. One of those SNP, NC_030830.1_19792976, was significant in both the New Zealand and combined analyses. The other SNP, snp22273-scaffold220-99341, was near two members of the secretory phospholipase A2 family: PLA2G2F (Phospholipase A2 IIF) and PLA2G2C (Phospholipase A2 IIC). The UniProt Consortium (2023) reports that PLA2G2C has a biological function of 'positive regulation of fibroblast proliferation'. Dermal fibroblasts are essential for the dermal papilla in hair follicles, influencing their development and growth. PLA2G2F is primarily expressed in the epidermis (Shao et al., 2021) and has been studied in the context of skin conditions. Yamamoto et al. (2015) reported that PLA2G2F-knockout mice had fragile stratum corneum (outer layer of the epidermis) and keratinocytes with impaired differentiation and activation. In contrast, mice overexpressing PLA2G2F developed psoriasis-like epidermal hyperplasia (Yamamoto et al., 2015). Similarly, Shao et al. (2021) found that gene silencing of PLA2G2F in mice led reduced epidermal thickness and immune response. These studies indicate that PLA2G2F is a regulator of epidermal barrier integrity and inflammation. Given its expression in the skin and its role in epidermal homeostasis, PLA2G2F may influence hair follicle function and fiber characteristics like CVD.

Curvature

Significant SNPs for Curv from the New Zealand analysis are listed in Table 3.11. In the combined analysis, seven significant SNPs were shared between Curv and SDCurv (Table 3.12),

suggesting common underlying biological mechanisms may influence both fiber curvature and its variation. One gene of interest, STAT5B (Signal transducer and activator of transcription), was near the significant SNP 19:42000809 in the combined analysis. STAT5B is expressed in dermal papilla (DP) cells, which are key regulators of hair follicle growth and cycling (Legrand et al., 2016). Activation of STAT5A/B in the DP begins in the late catagen phase and peaks in early anagen, suggesting that STAT5 signaling plays a role in initiating the anagen (growth) phase of the hair cycle (Legrand et al., 2016). Further, these authors reported that mice with a conditional knockout of STAT5A/B in DP cells had delayed entry into the anagen phase. Given STAT5B's role in initiating the anagen phase of the hair growth cycle which could influence fiber characteristics like Curv, it is a potential gene candidate.

Another gene, CD36 (Platelet glycoprotein 4) was located near snp58437-scaffold950-588104 in the combined analysis. This gene is expressed in dermal sheath (DS) cells, which surround the hair follicle and contribute to its structural support. Yoshida et al. (2019) found that CD36-expressing DS cells were associated with the formation of capillary networks within the human hair follicle during the anagen phase. These capillary networks regressed during the catagen and telogen phases, indicating CD36 may play a role in modulating blood supply in accordance with the hair cycle (Yoshida et al., 2019). Therefore, CD36 may influence fiber traits like Curv through regulation of blood supply and nutrient delivery to the hair follicle during the hair growth cycle.

Standard deviation of curvature

Tables 3.11 and 3.12 list the significant SNPs for SDCurv in the New Zealand analysis and the combined analysis, respectively. As mentioned, there were shared significant SNPs between Curv and SDCurv in both analyses. In the combined analysis, the gene STAT5B, was

near significant SNPs for both SDCurv and Curv. Interestingly, the gene EFNB2 (Ephrin B2) was near significant SNPs in both the combined analysis and the separate analysis of the U.S. subset from the combined analysis (Dressler, 2025). EFNB2 has been reported to have an influence on keratinocyte cell behavior, hair follicle morphogenesis, and cell proliferation in the epidermis (Genander et al., 2010; Egawa et al., 2009). EFNB2 is a reasonable gene candidate for SDCurv because it was near significant SNP identified in both the combined and U.S. only analyses, and it has functions related to hair follicle development.

In the combined analysis, another gene of interest is BMP7 (Bone morphogenetic protein 7) which was in proximity to the significant SNP 13:58243749. This gene is a member of the TGF-β superfamily, which regulates a wide range of developmental processes. Relative to skin and hair biology, bone morphogenetic proteins regulate melanin production, hair follicle growth, and epidermal homeostasis (Botchkarev, 2003). In Hu sheep skin, BMP7 expression was elevated during the anagen phase (Li et al., 2022). These authors also found that overexpression of BMP7 in vitro promoted proliferation of DP cells, while knockdown inhibited their growth. In Inner Mongolia Albas cashmere goat kids, BMP7 was implicated in the regulation of secondary hair follicle development during the first six months of a goat's life (Diao et al., 2023). Since secondary hair follicles produce cashmere, BMP7 is a strong candidate gene for fiber traits, including SDCurv.

Spinning fineness

Five SNPs were significant for SpinF in both the New Zealand (Table 3.11) and combined analyses (Table 3.12), with one SNP (8:85169943) shared between analyses. Notably, the SNP NC_030817.1_53553840 was significant for both MFD and SpinF in the combined analysis, which is sensible given these two traits are highly related. The gene RORA, located

near this SNP, is also a strong gene candidate for SpinF and likely the most promising among identified genes. While other genes within the QTL region of significant SNPs for SpinF have not been directly connected to skin or hair biology, RACK1 (receptor for activated C kinase 1) emerges as another potential candidate based on its biological functions. RACK1 coordinates interactions among signaling molecules (McCahill et al., 2002) and therefore is involved in cellular homeostasis controlling processes like proliferation and migration (Buoso et al., 2017). Since these processes are required for proper hair follicle development and function, RACK1 could indirectly impact cashmere fiber characteristics like SpinF.

Percentage ≤ 19µm

Significant SNPs for Perc19 in the New Zealand and combined analyses are shown in Tables 3.11 and 3.12, respectively. In the combined analysis, the significant SNP NC_030814.1_106635437 was near the gene, ADAMTS2 (ADAM metallopeptidase with thrombospondin type 1 motif 2). According to The UniProt Consortium (2023), ADAMTS2 has biological processes of 'collagen fibril organization' and 'skin development'. Its primary function is to process several types of procollagen proteins, which are the precursors of collagens (Colige et al., 2005). This processing step is necessary for proper assembly of collagen fibrils, making ADAMTS2 important for collagen maturation and extracellular matrix organization. In humans, mutations in ADAMTS2 cause Ehlers-Danlos syndrome, characterized by fragile, sagging skin resulting from to improper collagen fibril formation (NCBI, 2025). Given that collagen organization is essential for healthy skin and hair follicle structure, ADAMTS2 is a potential gene candidate for Perc19.

Down staple length

Eight SNPs were above the -$\log_{10}$ *P*-value threshold of 4 in the New Zealand analysis for DSL (Table 3.11). Three genes within the QTL regions of the significant SNP for DSL have been previously associated with skin or hair biology: PRRX2 (Paired related homeobox 2), PTGES (Prostaglandin E synthase), and SPTAN1 (Spectrin alpha chain, non-erythrocytic 1). PRRX2 is involved in mesenchymal cell differentiation during embryonic development. Stelnicki et al. (1998) found that PRRX2 is differentially expressed in human fetal skin compared to adult skin, particularly in proliferating fibroblasts and developing dermis. These authors also reported increased expression during wound healing in fetal skin, suggesting PRRX2 has a role in dermal regeneration. Similarly, PTGES is highly expressed in the embryonic epidermis (Sennett et al., 2015). PTGES encodes an enzyme involved in the biosynthesis of prostaglandin E_2, which is important for skin homeostasis and inflammatory signaling. Yamamoto et al. (2011) reported that prostaglandin E_2 signaling, mediated in part by PTGES, influenced hair follicle regeneration in mice. Lastly, SPTAN1 has been reported to be crucial for the morphology and function of cochlear hair cells in mice (Yao et al., 2021). These three genes (PRRX2, PTGES, and SPTAN1) all have functions pertinent to skin and hair biology, making them excellent gene candidates for a fiber trait like DSL.

Yield

The SNPs that were significant for Yield in the New Zealand analysis are listed in Table 3.11. The gene KCTD1 (Potassium channel tetramerization domain containing 1) is in proximity to the significant SNP snp35163-scaffold421-141252. KCTD1 encodes a transcriptional repressor that is involved in the development of the ectoderm (Ding et al., 2008). The ectoderm is an embryonic germ layer that develops into body tissues including the skin, hair, nails, and teeth. Mutations to KCTD1 and its homolog, KCTD15, are the known cause of aplasia cutis

congenita, a birth defect of the scalp skin in humans (Marneros, 2024). In mice, conditional inactivation of KCTD1/KCTD15 in keratinocytes resulted in abnormal skin structures, including hair, sebaceous glands, and sweat glands (Raymundo et al., 2023). Because KCTD1 has been strongly implicated in skin and hair development, it is a promising candidate gene for the cashmere fiber trait Yield.

Down weight

Down weight had six significant SNPs (Table 3.11), with four genes within the respective QTL regions (Appendix Table B.1). While none of the identified genes have been directly implicated in skin or hair biology, NYAP2 (Neuronal tyrosine-phosphorylated phosphoinositide-3-kinase adaptor 2) may have an indirect connection through its involvement in intracellular signaling. NYAP2 has been primarily studied in neurons and acts as an adaptor protein that interacts in PI3K/AKT signaling (Yokoyama et al., 2011). The PI3K/AKT pathway itself has been previously associated with multiple aspects of hair follicle biology, including HFSC activation (Wang et al., 2022), hair follicle regeneration (Chen et al., 2020), and DP cell function (Yamane et al., 2022). Although NYAP2 has not been directly studied in the context of skin or hair biology, its regulatory role in the PI3K/AKT signaling cascade may suggest a link to hair follicle function and, in turn, impact cashmere down weight.

Fleece weight

For FW, only 4 SNPs were above the $-\log_{10}$ *P*-value threshold of 4 in the New Zealand analysis (Table 3.11). Only one gene, PTPRM (protein tyrosine phosphatase, receptor type m), was within the respective QTL regions of those SNPs. PTPRM encodes a receptor-type protein tyrosine phosphatase involved in regulating cell-cell adhesion, proliferation, and migration (Sallee et al., 2006; Soulsby and Bennett, 2009). In humans, PTPRM has been connected to

psoriasis, a complex immune-mediated skin disease. In a 3D psoriatic skin model, downregulation of PTPRM increased keratinocyte proliferation via excessive ERK1/2 signaling (Rioux et al., 2022). Given its regulatory roles in skin cell dynamics, PTPRM is a candidate that warrants further investigation for a potential influence on fleece weight.

Coarse edge

The significant SNPs for CE identified in the New Zealand analysis are shown in Table 3.11. One SNP, snp22272-scaffold220-61665, was near three genes: PLA2G2F, PLA2G2C, and UBXN10 (UBX domain-containing protein 10). These same genes were also identified within the QTL region of a significant SNP for CVD in the combined analysis. PLA2G2F and PLA2G2C were discussed as gene candidates for CVD due to their roles in epidermal homeostasis, and for the same reasons, are also possible gene candidates for CE. The remaining genes identified near significant SNP for CE lack direct evidence or known biological functions linking them to skin or hair biology. Therefore, PLA2G2F and PLA2G2C remain as the most promising gene candidates for CE identified in this study.

Percentage of medullated fibers

Thirteen SNPs were significant for PercMed in the New Zealand analysis (Table 3.11), with twelve genes located within their respective QTL regions (Appendix Table B.1). The gene CSMD1 (CUB and sushi multiple domains 1) was near the significant SNP snp30720-scaffold34-1029239. CSMD1 encodes a large transmembrane protein involved in modulating immune system response and is highly expressed in both the central nervous system and epithelial tissues (Kraus et al., 2006). CSMD1 has also been implicated as a tumor suppressor gene with involvement in inhibiting cell proliferation, migration, and invasion of various human cancers (reviewed by Akyuz and Bell, 2022). Its strong expression in epithelial tissues suggests a

potential role in skin biology, and consequently, could influence the amount of medullated fibers in cashmere.

Conclusions

Genetic parameter estimates for cashmere fiber characteristics are scarce in literature, especially from the U.S. and from recent research in other non-traditional cashmere producing countries, like New Zealand. International collaboration and data sharing may be an effective strategy to increase sample size and pool resources for the development of a genomic selection tool. This study presents results from analyses of New Zealand animals alone, as well as from a combined dataset including both New Zealand and U.S. animals. For traits evaluated in both analyses, heritability and repeatability estimates were similar between the two analyses. Most fiber traits had moderate to high heritability and high repeatability. Mean fiber diameter had favorable genetic correlations with SDD, CURV, SpinF, and Perc19. There were genetic antagonisms between MFD and other fiber traits including CVD, SDCURV, DSL, and PercMed. Mean fiber diameter did not have significant genetic correlations with yield, DW, greasy FW, and CE. This suggests that cashmere producers can select for lower MFD without making sacrifices to cashmere yield or weight, but these results need to be validated in other populations. The GWAS identified significant SNPs for each trait, many of which were located near genes previously connected to hair and skin biology in species like humans and mice. These gene candidates merit further investigation for their potential role in cashmere fiber production.

Table 3.1. Distribution of age at cashmere collection across records in the U.S./ New Zealand combined dataset.

Age at cashmere collection (year)	Number of animal records (repeated records)	Number of animal records (1st record)
1	1,229	1,228
2	778	491
3	451	240
4	280	193
5	196	146
6	102	71
7	46	40
8	18	18
9	14	14
10	10	9
11	9	7
12	5	4
13	4	3
14	2	1
15	0	0
16	1	1
17	1	1
18	0	0
19	9	9
Not available	181	96
Total	**3,336**	**2,572**

Table 3.2. Definition, abbreviation, and dataset availability of cashmere fiber traits.

Trait	Abbrev.	Definition	Available in:
Mean fiber diameter, µm	MFD	Average fiber diameter of fibers in the tested sample	U.S. and N.Z.
Standard deviation of diameter, µm	SDD	Standard deviation of fiber diameter calculated by: $\sqrt{\frac{\Sigma(MFD_i - \overline{MFD})^2}{n}}$	U.S. and N.Z.
Coefficient of variation of diameter, %	CVD	Coefficient of fiber diameter calculated by: $\left(\frac{SD\ Mean}{MFD}\right) * 100$	U.S. and N.Z.
Curvature, °/mm	Curv	The average fiber curvature	U.S. and N.Z.
Standard deviation of curvature, °/mm	SDCurv	Standard deviation of fiber curvature calculated by: $\sqrt{\frac{\Sigma(CURV_i - \overline{CURV})^2}{n}}$	U.S. and N.Z.
Spinning fineness, µm	SpinF	A measure of the performance of the fiber when spun into yarn calculated from CVD and MFD. Original theory proposed by Martindale (1945) and formula used proposed by Butler and Dolling (1992).	U.S. and N.Z.
Percentage ≤ 19 µm, %	Perc19	Percentage of fibers with diameters less than or equal to 19 µm out of all fibers in the tested sample	U.S. and N.Z.
Down staple length, mm	DSL	Unstretched down staple length measured at the midside with a ruler	N.Z. only
Yield, %	YD	Percentage of cashmere down in total fleece weight (Peterson and Gheradrdi, 1996)	N.Z. only
Fleece weight, g	FW	Total greasy weight of fleece after harvest	N.Z. only
Down weight, g	DW	=Fleece weight * Yield	N.Z. only
Coarse edge, %	CE	Percentage of fibers with diameter greater than 30 µm out all fibers with diameter ≤ 35 µm	N.Z. only
Percentage of medullated fibers, %	PercMed	Percentage of fibers that are medullated of those less than 35 µm in diameter	N.Z. only

*Animals with fiber tested in the United States had traits measured for fibers with diameter up to 30 µm, while animals with fiber tested in New Zealand had traits measured for fibers with diameter up to 35 µm.

Table 3.3. Significant fixed effects from forward selection that were included in final models for each fiber trait in both analyses: New Zealand only and U.S./New Zealand combined. "X" designates that fixed effect was significant and included in the final model for that trait in that analysis.

		Fixed effect		
Trait	**Analysis**	**Contemporary group***	**Age at collection**	**Sex**
Mean fiber diameter, µm	New Zealand	X	X	
	Combined	X	X	X
Standard deviation of diameter, µm	New Zealand	X	X	X
	Combined	X		X
Coefficient of variation of diameter, %	New Zealand	X	X	X
	Combined	X	X	X
Curvature, °/mm	New Zealand	X	X	X
	Combined	X	X	X
Standard deviation of curvature, °/mm	New Zealand		X	X
	Combined	X	X	X
Spinning fineness, µm	New Zealand	X	X	
	Combined	X	X	
Percentage ≤ 19 µm, %	New Zealand	X	X	
	Combined	X	X	
Down staple length, mm	New Zealand		X	
Yield, %	New Zealand	X	X	
Fleece weight, g**	New Zealand		X	X
Down weight, g**	New Zealand		X	
Coarse edge, %	New Zealand	X	X	
Percentage of medullated fibers, %	New Zealand		X	

*Contemporary group for the New Zealand analysis was testing year. Contemporary group for the combined analysis was farm x testing year.

**Down weight and fleece weight records were only available in one contemporary group (testing year) in the New Zealand analysis.

Table 3.4. Summary statistics of fiber traits for all records for fiber traits in both the New Zealand analysis and the analysis with U.S. and New Zealand records (Combined).

Trait	Analysis	n	Mean	Minimum	Maximum	Standard deviation
Mean fiber diameter, µm	New Zealand	2,075	15.68	12.76	20.34	1.26
	Combined	3,020	15.65	11.30	22.52	1.47
Standard deviation of diameter, µm	New Zealand	1,941	3.46	2.40	5.64	0.40
	Combined	3,192	3.37	2.03	6.92	0.48
Coefficient of variation of diameter, %	New Zealand	1,941	22.22	14.54	35.49	2.96
	Combined	3,020	21.66	14.54	41.8	3.02
Curvature, º/mm	New Zealand	1,941	62.69	47.95	81.83	5.29
	Combined	3,020	64.78	21.3	123.80	8.59
Standard deviation of curvature, º/mm	New Zealand	1,941	47.82	39.83	58.05	2.77
	Combined	3,020	45.32	17.00	75.2	6.45
Spinning fineness, µm	New Zealand	2,075	15.55	12.65	19.49	1.09
	Combined	3,155	15.33	11.01	21.76	1.37
Percentage ≤ 19 µm, %	New Zealand	2,071	86.35	19.43	98.34	8.52
	Combined	3,151	86.75	19.43	99.69	9.67
Down staple length, mm	New Zealand	374	75.00	30.00	110.00	13.29
Yield, %	New Zealand	2,075	44.43	3.90	96.86	15.91
Fleece weight, g	New Zealand	567	400.30	44.00	870.00	134.37
Down weight, g	New Zealand	582	207.50	2.00	704.00	107.26
Coarse edge, %	New Zealand	2,075	0.605	0.00	3.63	0.397
Percentage of medullated fibers, %	New Zealand	2,075	0.596	0.00	4.83	0.513

Table 3.5. Estimates from the single record analysis including univariate heritability estimates (diagonal), phenotypic correlations (upper diagonal), and bivariate genetic correlations ± standard error (lower diagonal) for cashmere fiber traits in the New Zealand analysis.

	MFD	SDD	CvD	Curv	SDCurv	SpinF	Perc19	Yield	DW	FW	DSL	PercMed	CE
MFD, µm	**0.49 ± 0.06**	0.12**	-0.49**	-0.68**	-0.59**	0.94**	-0.44**	0.09**	0.38**	0.43**	0.35**	-0.39**	-0.14**
SDD, µm	0.29 ± 0.16	**0.18 ± 0.05**	0.80**	0.05*	0.26**	0.44**	-0.12**	0.09**	-0.21**	-0.30**	0.03	0.49**	0.73**
CvD, %	-0.61 ± 0.11	0.57 ± 0.14	**0.25 ± 0.05**	0.45**	0.58**	-0.17**	0.16**	0.02	-0.39**	-0.49**	-0.20**	0.68**	0.72**
Curv, °/mm	-0.72 ± 0.06	-0.28 ± 0.17	0.38 ± 0.13	**0.46 ± 0.06**	0.82**	-0.60**	0.31**	-0.29	-0.52**	-0.46**	-0.34**	0.40**	0.24**
SDCurv, °/mm	-0.71 ± 0.08	0.02 ± 0.22	0.60 ± 0.13	0.89 ± 0.04	**0.26 ± 0.06**	-0.44**	0.28**	-0.18**	-0.47**	-0.52**	-0.31**	0.42**	0.33*
SpinF, µm	0.97 ± 0.01	0.48 ± 0.13	-0.42 ± 0.14	-0.72 ± 0.07	-0.65± 0.10	**0.42 ± 0.06**	-0.44**	0.11**	0.27**	0.29**	0.31**	-0.19**	0.13**
Perc19, %	-0.85 ± 0.23	-0.72 ± 0.21	-0.03 ± 0.22	0.58 ± 0.16	0.38 ± 0.22	-0.98 ± 0.12	**0.13 ± 0.05**	-0.04*	-0.24**	-0.27**	-0.02	0.18**	0.04
Yield, %	0.08 ± 0.11	0.26 ± 0.16	0.23 ± 0.16	-0.34 ± 0.10	-0.30 ± 0.13	0.12 ± 0.12	-0.01 ± 0.19	**0.35 ± 0.05**	0.76**	0.31**	0.27**	-0.001	-0.04
DW, g	0.13 ± 0.15	0.22 ± 0.24	0.21 ± 0.23	-0.29 ± 0.14	-0.35 ± 0.18	0.16 ± 0.16	-0.11 ± 0.58	0.88 ± 0.06	**0.45 ± 0.11**	0.82**	0.55	-0.38**	-0.36**
FW, g	-0.03 ± 0.14	-0.22 ± 0.21	-0.14 ± 0.18	-0.19 ± 0.14	-0.44 ± 0.17	-0.09 ± 0.15	0.02 ± 0.27	0.81 ± 0.15	0.99 ± 0.03	**0.59 ± 0.12**	0.41	-0.45**	-0.40**

DSL, mm	0.26 ± 0.19	-0.15 ± 0.43	-0.17 ± 0.31	-0.38 ± 0.23	-0.44 ± 0.29	0.19 ± 0.22	0.76 ± 0.87	0.33 ± 0.29	0.82 ± 0.37	0.84 ± 0.39	**0.35 ± 0.13**	-0.17*	-0.14*
PercMed, %	-0.46 ± 0.14	0.29 ± 0.21	0.63 ± 0.12	0.34 ± 0.14	0.36 ± 0.17	-0.35 ± 0.16	0.06 ± 0.25	0.43 ± 0.23	-0.15 ± 0.26	0.11 ± 0.26	-0.24 ± 0.37	**0.26 ± 0.06**	0.68**
CE, %	-0.05 ± 0.21	0.51 ± 0.25	0.42 ± 0.21	-0.02 ± 0.20	0.22 ± 0.23	0.07 ± 0.20	-0.16 ± 0.30	0.27 ± 0.22	0.11 ± 0.36	-0.36 ± 0.27	-0.23 ± 0.51	0.66 ± 0.15	**0.14 ± 0.05**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CvD- coefficient of variation of fiber diameter; Curv- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; Perc19- percentage of fibers with diameter less than or equal 19 µm; DW- down weight; FW- fleece weight; DSL- down staple length; PercMed- percentage of medullated fibers; and CE- coarse edge.

*Correlations significantly different from zero at $P < 0.05$.

**Correlations significantly different from zero at $P < 0.0001$.

Table 3.6. Heritability estimates (with SE below) of traits listed in the first column from single record bivariate analysis with all other traits for the New Zealand only dataset. Average heritability from all bivariate analyses for a trait is bolded on the diagonal.

Trait:	Heritabilities from bivariate analyses with all other traits												
	MFD	**SDD**	**CvD**	**Curv**	**SDCurv**	**SpinF**	**Perc19**	**Yield**	**DW**	**FW**	**DSL**	**PercMed**	**CE**
MFD, µm	**0.483** **0.06**	0.49 0.06	0.49 0.06	0.49 0.06	0.49 0.06	0.48 0.06	0.49 0.06	0.48 0.06	0.50 0.06	0.51 0.06	0.41 0.06	0.48 0.06	0.48 0.06
SDD, µm	0.18 0.05	**0.183** **0.05**	0.18 0.05	0.18 0.05	0.18 0.05	0.18 0.05	0.19 0.05	0.18 0.05	0.19 0.05	0.18 0.05	0.19 0.05	0.18 0.05	0.18 0.05
CvD, %	0.24 0.05	0.24 0.05	**0.248** **0.05-0.06**	0.25 0.05	0.25 0.05	0.24 0.05	0.25 0.05	0.24 0.05	0.26 0.06	0.27 0.06	0.24 0.05	0.25 0.05	0.25 0.05
Curv, °/mm	0.45 0.06	0.46 0.06	0.46 0.06	**0.453** **0.06**	0.46 0.06	0.45 0.06	0.46 0.06	0.46 0.06	0.45 0.06	0.44 0.06	0.42 0.06	0.46 0.06	0.46 0.06
SDCurv, °/mm	0.26 0.06	0.26 0.06	0.26 0.06	0.27 0.06	**0.258** **0.06**	0.26 0.05	0.26 0.06	0.26 0.06	0.25 0.06	0.25 0.06	0.25 0.06	0.26 0.06	0.26 0.06
SpinF, µm	0.42 0.06	0.43 0.06	0.43 0.06	0.44 0.06	0.43 0.06	**0.421** **0.06**	0.42 0.06	0.42 0.06	0.43 0.06	0.45 0.06	0.36 0.06	0.41 0.06	0.41 0.06
Perc19, %	0.14 0.04	0.17 0.05	0.16 0.05	0.17 0.05	0.16 0.05	0.14 0.04	**0.138** **0.04-0.05**	0.13 0.05	0.11 0.04	0.13 0.05	0.06 0.04	0.14 0.05	0.14 0.05
Yield, %	0.35 0.05	0.35 0.05	0.34 0.05	0.35 0.05	0.35 0.05	0.35 0.05	0.35 0.05	**0.34** **0.05**	0.31 0.05	0.32 0.05	0.34 0.05	0.33 0.05	0.34 0.05
DW, g	0.46 0.11	0.43 0.11	0.42 0.11	0.50 0.11	0.50 0.10	0.47 0.11	0.44 0.11	0.46 0.08	**0.455** **0.08-0.11**	0.50 0.11	0.45 0.11	0.43 0.10	0.40 0.10
FW, g	0.61 0.12	0.56 0.12	0.57 0.12	0.60 0.12	0.60 0.12	0.61 0.12	0.57 0.12	0.46 0.11	0.56 0.12	**0.569** **0.11-0.12**	0.57 0.12	0.58 0.11	0.54 0.12
DSL, mm	0.41 0.13	0.33 0.13	0.33 0.13	0.39 0.13	0.38 0.13	0.41 0.13	0.35 0.13	0.33 0.12	0.36 0.12	0.32 0.12	**0.384** **0.12-0.13**	0.35 0.12	0.32 0.12
PercMed. %	0.24 0.06	0.24 0.06	0.24 0.06	0.24 0.06	0.24 0.06	0.24 0.06	0.26 0.06	0.22 0.06	0.21 0.06	0.19 0.05	0.17 0.05	**0.231** **0.05-0.06**	0.28 0.06
CE, %	0.14 0.05	0.15 0.05	0.15 0.05	0.15 0.05	0.14 0.05	0.14 0.05	0.14 0.05	0.14 0.05	0.14 0.05	0.14 0.05	0.17 0.05	0.15 0.05	**0.146** **0.05**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CvD- coefficient of variation of fiber diameter; Curv- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; Perc19- percentage of fibers with diameter less than or equal 19 µm; DW- down weight; FW- fleece weight; DSL- down staple length; PercMed- percentage of medullated fibers; and CE- coarse edge.

Table 3.7. Estimates from the single record analysis including univariate heritability estimates (diagonal), phenotypic correlations (upper diagonal), and bivariate genetic correlations ± standard error (lower diagonal) for cashmere fiber traits for the Combined analysis.

	MFD	SDD	CvD	Curv	SDCurv	SpinF	Perc19
MFD, µm	**0.46 ± 0.04**	0.38**	-0.28**	-0.68**	-0.35**	0.93**	-0.71**
SDD, µm	0.39 ± 0.10	**0.26 ± 0.04**	0.77**	-0.30**	0.15**	0.62**	-0.40**
CvD, %	-0.41 ± 0.10	0.69 ± 0.07	**0.26 ± 0.04**	0.15**	0.40**	0.004	0.06*
Curv, º/mm	-0.70 ± 0.05	-0.33 ± 0.12	0.19 ± 0.12	**0.33 ± 0.04**	0.44**	-0.65**	0.50**
SDCurv, º/mm	-0.60 ± 0.08	-0.08 ± 0.14	0.37 ± 0.12	0.81 ± 0.05	**0.24 ± 0.04**	-0.24**	0.29**
SpinF, µm	0.98 ± 0.01	0.59 ± 0.08	-0.20 ± 0.12	-0.68 ± 0.06	-0.54 ± 0.09	**0.40 ± 0.04**	-0.71**
Perc19, %	-0.73 ± 0.06	-0.66 ± 0.10	-0.27 ± 0.13	0.61 ± 0.09	0.45 ± 0.11	-0.85 ± 0.05	**0.29 ± 0.04**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CvD- coefficient of variation of fiber diameter; Curv- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; and Perc19- percentage of fibers with diameter less than or equal 19 µm.

*Correlations significantly different from zero at $P < 0.05$.

**Correlations significantly different from zero at $P < 0.0001$.

Table 3.8. Heritability estimates (with SE below) of traits listed in the first column from single record bivariate analysis with all other traits for the Combined dataset. Average heritability from all bivariate analyses for a trait is bolded on the diagonal.

Trait:	Heritabilities from bivariate analyses with all other traits						
	MFD	**SDD**	**CvD**	**Curv**	**SDCurv**	**SpinF**	**Perc19**
MFD, µm	**0.444** **0.04**	0.44 0.04	0.44 0.04	0.45 0.04	0.44 0.04	0.44 0.04	0.44 0.04
SDD, µm	0.23 0.04	**0.23** **0.04**	0.23 0.04	0.23 0.04	0.23 0.04	0.23 0.04	0.23 0.04
CvD, %	0.25 0.04	0.26 0.04	**0.253** **0.04**	0.25 0.04	0.25 0.04	0.25 0.04	0.26 0.04
Curv, °/mm	0.33 0.04	0.32 0.04	0.32 0.04	**0.327** **0.04**	0.33 0.04	0.33 0.04	0.33 0.04
SDCurv, °/mm	0.25 0.04	0.24 0.04	0.24 0.04	0.25 0.04	**0.247** **0.04**	0.25 0.04	0.25 0.04
SpinF, µm	0.40 0.04	0.39 0.04	0.40 0.04	0.40 0.05	0.40 0.05	**0.397** **0.04-0.05**	0.39 0.04
Perc19, %	0.29 0.05	0.30 0.05	0.31 0.05	0.29 0.05	0.30 0.05	0.26 0.04	**0.292** **0.04-0.05**

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CvD- coefficient of variation of fiber diameter; Curv- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; and Perc19- percentage of fibers with diameter less than or equal 19 µm.

Table 3.9. Heritability and repeatability for univariate repeated records of cashmere fiber traits in the New Zealand analysis[1] and the Combined analysis.

Trait	Analysis	Heritability ± SE	Repeatability ± SE	Genetic variance	Permanent environmental variance	Residual variance
Mean fiber diameter, µm	New Zealand	0.47 ± 0.05	0.57 ± 0.03	0.55905	0.12713	0.51361
	Combined	0.47 ± 0.04	0.62 ± 0.02	0.64073	0.20329	0.52083
Standard deviation of diameter, µm	New Zealand	0.16 ± 0.04	0.42 ± 0.03	0.024586	0.039649	0.087338
	Combined	0.28 ± 0.04	0.50 ± 0.03	0.049104	0.038617	0.084966
Coefficient of variation of diameter, %	New Zealand	0.23 ± 0.05	0.45 ± 0.03	1.5169	1.4937	3.7011
	Combined	0.28 ± 0.04	0.50 ± 0.03	1.8891	1.4963	3.3986
Curvature, °/mm	New Zealand	0.46 ± 0.05	0.51 ± 0.03	10.923	1.113	11.67
	Combined	0.34 ± 0.04	0.67 ± 0.02	16.846	16.036	16.084
Standard deviation of curvature, °/mm	New Zealand	0.26 ± 0.05	0.35 ± 0.04	1.6131	0.58849	4.0343
	Combined	0.26 ± 0.04	0.55 ± 0.03	4.0097	4.6710	6.9471
Spinning fineness, µm	New Zealand	0.41 ± 0.05	0.54 ± 0.03	0.41221	0.13997	0.46354
	Combined	0.42 ± 0.04	0.61 ± 0.02	0.50968	0.23571	0.47316
Percentage ≤ 19 µm, %	New Zealand	0.06 ± 0.03	0.07 ± 0.04	4.0945	0.68858	59.940
	Combined	0.19 ± 0.03	0.19 ± 0.03	13.146	0.00007	55.827
Yield, %	New Zealand	0.31 ± 0.03	0.31 ± 0.03	61.245	0.00065	133.58
Percentage of medullated fibers, %	New Zealand	0.19 ± 0.04	0.19 ± 0.05	0.03805	0.00006	0.16099
Coarse edge, %	New Zealand	0.14 ± 0.04	0.19 ± 0.04	0.019081	0.007403	0.1128

*No repeat records for down staple length, down weight, or fleece weight were available in the New Zealand analysis, therefore they are not included in this table.

Table 3.10. Summary of the accuracy of estimated breeding values from both the single record and repeated records univariate analyses from the combined U.S. and New Zealand dataset.

Trait	Analysis	Mean	Minimum	Maximum	Standard deviation
Mean fiber diameter, µm	Single record	0.59	0.001	0.95	0.25
	Repeated records	0.60	0.002	0.96	0.26
Standard deviation of diameter, µm	Single record	0.50	0.003	0.93	0.22
	Repeated records	0.55	0.01	0.94	0.21
Coefficient of variation of diameter, %	Single record	0.52	0.007	0.93	0.20
	Repeated records	0.54	0.007	0.93	0.21
Curvature, °/mm	Single record	0.55	0.01	0.94	0.21
	Repeated records	0.55	0.01	0.94	0.24
Standard deviation of curvature, °/mm	Single record	0.49	0.003	0.92	0.22
	Repeated records	0.53	0.01	0.93	0.20
Spinning fineness, µm	Single record	0.59	0.01	0.95	0.21
	Repeated records	0.60	0.001	0.95	0.23
Percentage ≤ 19 µm, %	Single record	0.53	0.002	0.93	0.20
	Repeated records	0.50	0.01	0.93	0.20

Table 3.11. Genomic regions significantly[1] associated with cashmere fiber traits identified through univariate single record genome-wide association study in the New Zealand population.

Trait	SNP name	Chromosome: Position	-log$_{10}$ *P*-value
Mean fiber diameter, µm	snp6974-scaffold1257-459805	1:103720380	5.048
	27:25610526	27:25610526	4.670
	snp32293-scaffold366-3596533	8:83675077	4.629
	8:85169943	8:85169943	4.612
	NC_030823.1_14537267	16:14537267	4.185
Standard deviation of diameter, µm	NC_030812.1_60507364	5:60507364	4.426
	snp59884-scaffold996-137936	6:88058923	4.281
Coefficient of variation of diameter, %	snp28883-scaffold310-7623498	5:70500098	4.840
	NC_030830.1_19792976	23:19792976	4.652
	snp20700-scaffold204-820288	11:74681564	4.111
	snp32217-scaffold366-80065	8:87218533	4.080
Curvature, °/mm	snp26238-scaffold275-766124	27:25580723	4.648
	snp32217-scaffold366-80065	8:87218533	4.156
	25:35852095	25:35852095	4.139
	NC_030812.1_38122758	5:38122758	4.133
Standard deviation of curvature, °/mm	snp29237-scaffold315-227227	3:109476096	4.301
	snp32217-scaffold366-80065	8:87218533	4.285
Spinning fineness, µm	8:85169943	8:85169943	4.731
	snp32293-scaffold366-3596533	8:83675077	4.460
	snp48133-scaffold681-723097	8:14380776	4.352
	snp6974-scaffold1257-459805	1:103720380	4.214
	NC_030823.1_14537267	16:14537267	4.101
Percentage ≤ 19 µm, %	snp36267-scaffold435-498787	1:77070767	5.090
	snp40517-scaffold519-881449	1:78451066	4.364
	1:54345204	1:54345204	4.052
	snp24902-scaffold2547-223010	21:33956209	4.024
Yield, %	24:28750106	24:28750106	4.858
	snp35163-scaffold421-141252	24:30755155	4.527
	snp13404-scaffold1518-229207	14:50539552	4.198
	NC_030811.1_110865749	4:110865749	4.126
	14:50659317	14:50659317	4.113
	NC_030831.1_28044740	24:28044740	4.039
Down weight, g	snp7530-scaffold127-6406156	2:21942232	4.880
	snp27847-scaffold299-1505220	16:74913766	4.769
	snp11323-scaffold1409-700104	1:101294434	4.252
	11:76819675	11:76819675	4.193
	8:43450514	8:43450514	4.127
	NC_030815.1_89647438	8:89647438	4.019

Fleece weight, g	snp43076-scaffold572-1402901	10:6805840	4.517
	snp7394-scaffold127-695561	2:27684644	4.371
	snp54570-scaffold833-1805827	24:40761692	4.045
	snp14478-scaffold1579-179971	24:34354058	4.015
Down staple length, mm	snp9258-scaffold1337-33653	14:3929608	4.841
	snp46806-scaffold653-1537540	11:99577135	4.729
	NC_030818.1_98628971	11:98628971	4.379
	11:99272927	11:99272927	4.219
	12:46091411	12:46091411	4.194
	1:88793844	1:88793844	4.091
	2:86070436	2:86070436	4.050
	snp45044-scaffold614-2931393	2:87080026	4.028
Percentage of medullated fibers, %	snp35677-scaffold43-2995292	18:23106361	5.598
	snp32217-scaffold366-80065	8:87218533	5.405
	snp23832-scaffold240-1941123	21:14032519	4.679
	snp30720-scaffold34-1029239	27:41823387	4.591
	NC_030822.1_1802835	15:1802835	4.455
	snp48998-scaffold7-1419288	13:31594543	4.445
	snp4191-scaffold1130-92139	21:36964203	4.416
	snp6402-scaffold1229-174051	19:23587864	4.266
	snp20821-scaffold204-6152369	11:80018885	4.150
	NC_030822.1_1656016	15:1656016	4.134
	snp43345-scaffold578-349979	17:48198379	4.130
	snp13313-scaffold1513-738732	22:49398985	4.079
	snp55505-scaffold86-569077	24:28198848	4.077
Coarse edge, %	snp22272-scaffold220-61665	2:3501685	4.557
	snp47120-scaffold659-2908957	3:94823167	4.215
	20:32827242	20:32827242	4.131

[1]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.

Table 3.12. Genomic regions significantly[1] associated with cashmere fiber traits identified through univariate single record genome-wide association study in the U.S. and New Zealand combined population.

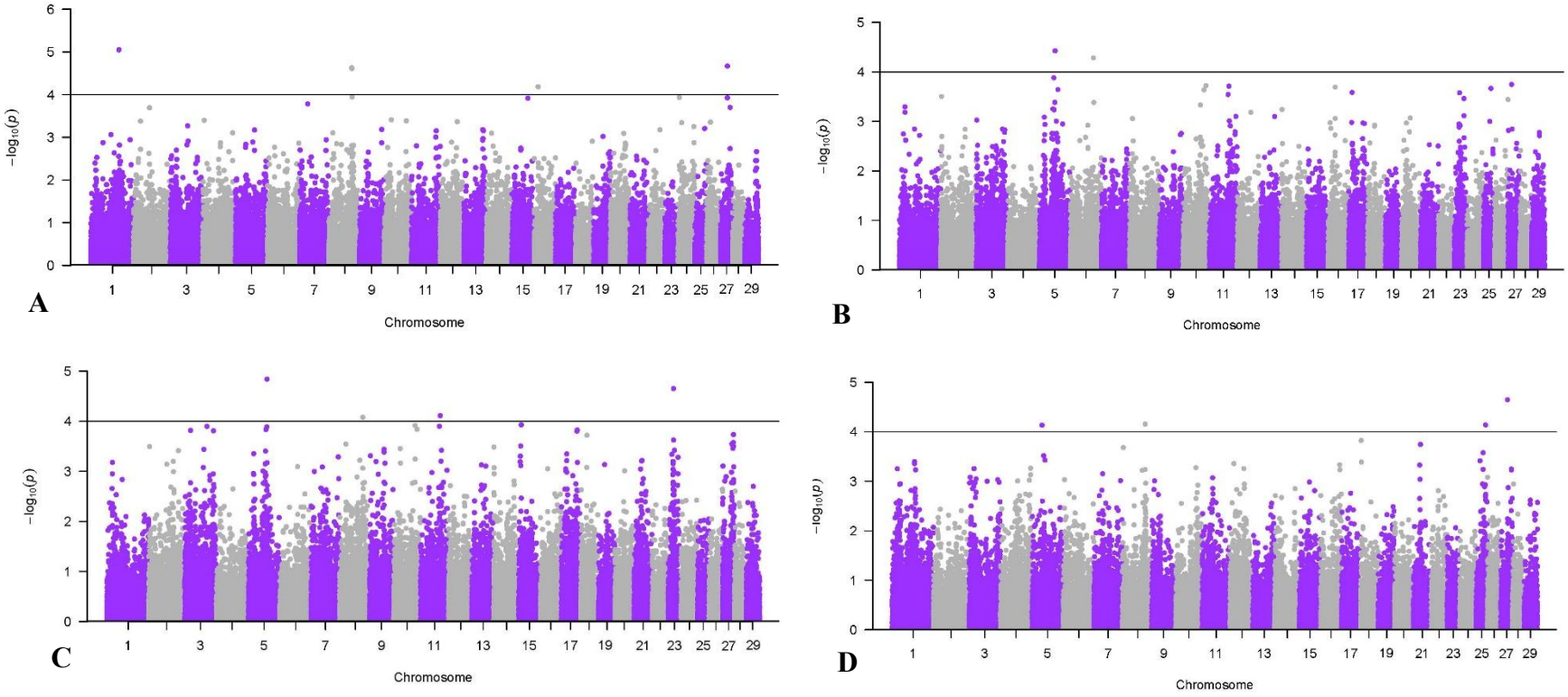
Trait	SNP name	Chromosome: Position	-log$_{10}$ *P*-value
Mean fiber diameter, µm	NC_030817.1_60685789	10:60685789	4.846
	snp26238-scaffold275-766124	27:25580723	4.740
	NC_030817.1_53553840	10:53553840	4.569
	8:85169943	8:85169943	4.507
[2]Standard deviation of diameter, µm	snp44192-scaffold600-619536	8:15945639	4.999
	snp13153-scaffold1501-2062871	14:63367161	4.629
	IMAU11	1:115382807	4.508
	snp8244-scaffold13-3372417	24:15664369	4.236
	11:104566389	11:104566389	4.100
	1:110854497	1:110854497	4.068
Coefficient of variation of diameter, %	NC_030830.1_19792976	23:19792976	5.465
	snp22273-scaffold220-99341	2:3463848	4.720
Curvature, °/mm	NC_030813.1_11981581	6:11981581	7.942
	NC_030811.1_115149546	4:115149546	7.394
	snp37050-scaffold449-1431692	14:59014501	7.26
	snp48822-scaffold694-1694486	20:34804768	6.359
	19:42000809	19:42000809	6.319
	NC_030817.1_60685789	10:60685789	6.279
	IMAU944	29:16471416	6.102
	snp52330-scaffold778-361557	1:29641780	5.645
	NC_030834.1_42548547	27:42548547	5.586
	snp46071-scaffold632-588199	18:58960722	5.496
	snp15996-scaffold1683-141593	27:44588263	5.483
	6:7122325	6:7122325	5.479
	snp9563-scaffold1343-2780570	25:31025967	5.476
	snp31365-scaffold347-1783379	12:4003713	5.445
	snp58437-scaffold950-588104	4:79836857	5.353
	snp11344-scaffold141-980707	16:42623026	5.334
	NC_030811.1_102313711	4:102313711	5.283
	snp45485-scaffold620-2131839	9:56674616	5.191
	snp34580-scaffold409-292384	8:57990759	5.147
	snp44002-scaffold595-4547283	3:26550959	5.010
	2:9580060	2:9580060	5.007
	4:105934903	4:105934903	4.963
	snp13987-scaffold1551-311753	16:9326730	4.899
	NC_030817.1_53553840	10:53553840	4.880
	6:6627869	6:6627869	4.842
	snp19615-scaffold1980-634136	5:46781804	4.774
	12:79404524	12:79404524	4.765

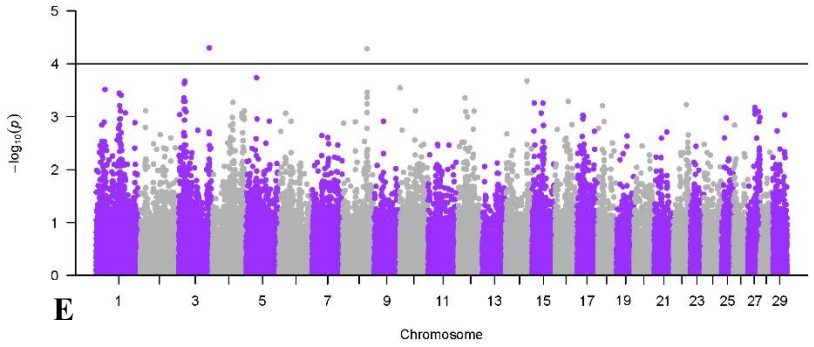
	snp31186-scaffold345-2282027	4:64685331	4.744
	IMAU59	2:107519970	4.648
	IMAU602	10:26348848	4.643
	snp47224-scaffold662-375708	10:39089429	4.564
	snp45295-scaffold618-2649648	11:19660202	4.561
	snp47817-scaffold673-1125686	23:34696336	4.559
	snp50044-scaffold716-3083078	7:30418858	4.551
	snp17691-scaffold1834-77678	13:1880526	4.521
	NC_030828.1_32308828	21:32308828	4.516
Standard deviation of curvature, °/mm	NC_030813.1_11981581	6:11981581	8.729
	snp31365-scaffold347-1783379	12:4003713	8.062
	19:42002634	19:42002634	6.487
	snp15342-scaffold163-2570163	22:38596654	6.262
	snp22469-scaffold2223-95469	13:22938705	6.120
	6:6627869	6:6627869	6.090
	snp9563-scaffold1343-2780570	25:31025967	5.987
	13:58243749	13:58243749	5.691
	snp12495-scaffold1479-395260	17:62391045	5.664
	IMAU602	10:26348848	5.625
	snp48248-scaffold683-100458	29:12983250	5.555
	27:31381125	27:31381125	5.530
	snp19615-scaffold1980-634136	5:46781804	5.497
	NC_030835.1_35266324	28:35266324	5.470
	snp2516-scaffold1071-376636	2:15152105	5.421
	NC_030809.1_123147967	2:123147967	5.362
	NC_030811.1_115149546	4:115149546	5.337
	snp46209-scaffold637-2844494	20:43554947	5.250
	snp43739-scaffold588-408914	9:13543114	5.161
	snp11911-scaffold144-3129826	3:48878375	5.121
	snp44662-scaffold607-235676	20:37226270	5.049
	snp47817-scaffold673-1125686	23:34696336	5.017
	NC_030811.1_63838279	4:63838279	4.996
	snp9675-scaffold1347-109324	12:83309319	4.921
	snp27887-scaffold299-3305456	16:76709383	4.899
	snp28299-scaffold301-2995719	2:106431151	4.867
	snp39297-scaffold50-1480921	11:87964494	4.863
	8:60160322	8:60160322	4.809
	6:7122325	6:7122325	4.777
	snp45371-scaffold62-1473796	20:28805878	4.763
	snp6589-scaffold1235-105689	2:131617753	4.757
	snp40532-scaffold519-1512011	1:79082101	4.756
	snp12218-scaffold1455-178454	8:87723644	4.703
	snp9919-scaffold1354-42468	17:2617367	4.696
	snp21062-scaffold2061-439597	9:9012510	4.639
	snp46634-scaffold648-504478	21:2624353	4.625
	13:23113494	13:23113494	4.610

	snp49944-scaffold714-1877773	23:39202383	4.607
	24:56358828	24:56358828	4.601
	snp19409-scaffold196-1103346	7:106343223	4.595
	snp38140-scaffold477-280593	2:125035805	4.580
	12:79404524	12:79404524	4.576
	snp16707-scaffold1750-770875	11:6767967	4.550
Spinning fineness, µm	snp46308-scaffold639-126113	7:70168742	5.285
	NC_030817.1_53553840	10:53553840	4.998
	8:85169943	8:85169943	4.845
	snp13153-scaffold1501-2062871	14:63367161	4.587
Percentage ≤ 19 µm, %	snp57298-scaffold912-1705662	10:54284488	5.636
	snp36430-scaffold438-690423	25:20239001	5.365
	snp13153-scaffold1501-2062871	14:63367161	5.307
	snp1628-scaffold1046-1340143	19:14879682	4.826
	8:46210811	8:46210811	4.772
	NC_030814.1_106635437	7:106635437	4.623
	NC_030817.1_53553840	10:53553840	4.594

[1]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.5.
[2]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.

Figure 3.1. Manhattan plots for each univariate, single-record genome-wide association study of cashmere fiber characteristics from the New Zealand analysis. Panel A- Mean fiber diameter (µm), Panel B- Standard deviation of diameter (µm), Panel C- Coefficient of variation of diameter (%), Panel D- Curvature (°/mm), Panel E- Standard deviation of curvature (°/mm), Panel F- Spinning fineness (µm), Panel G- Percentage less than 19 µm (%), Panel H- Yield (%), Panel I- Down weight (g), Panel J- Fleece weight (g), Panel K- Down staple length (mm), Panel L- Percentage of medullated fibers (%), and Panel M- Coarse edge (%).

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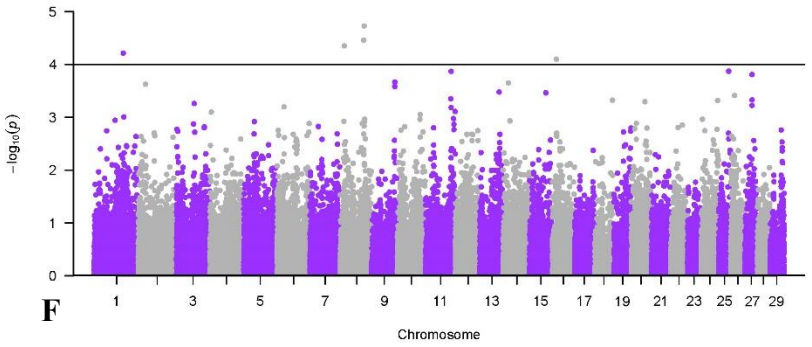
E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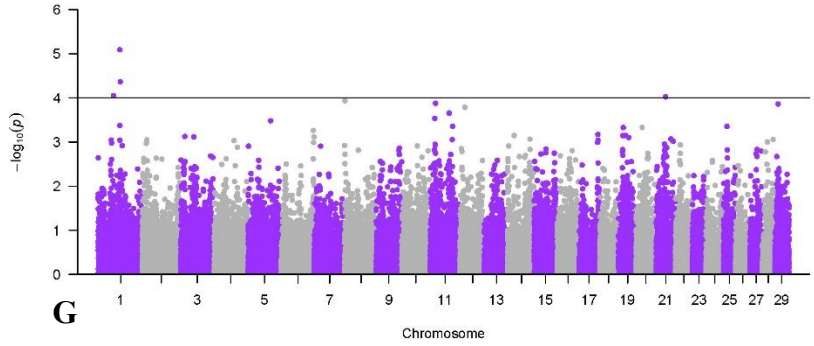
F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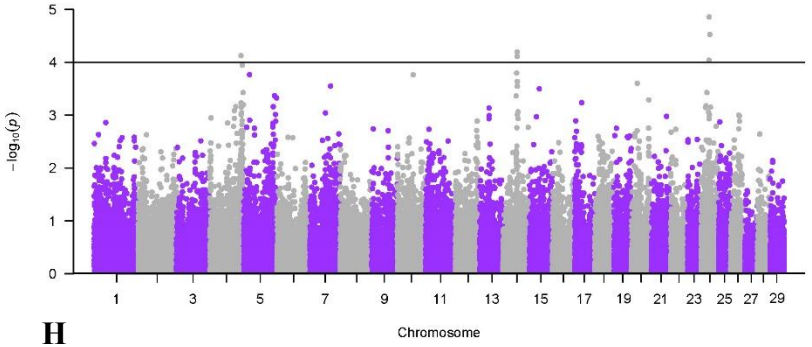
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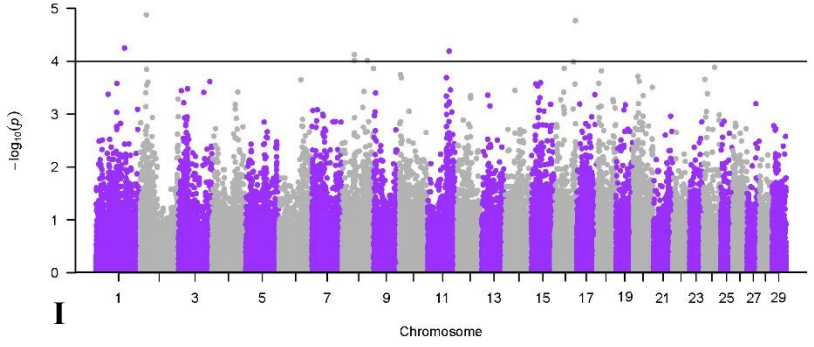
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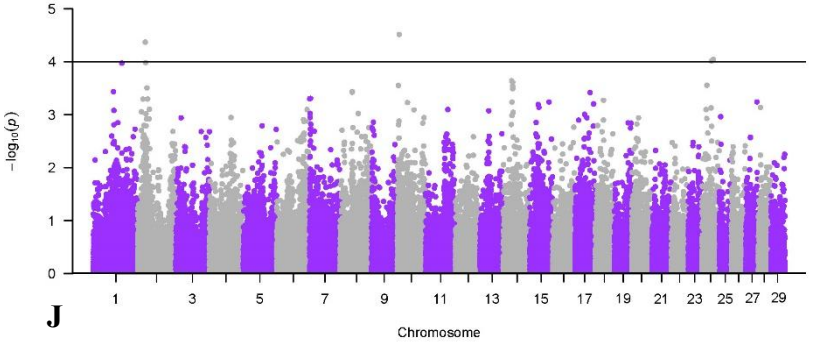
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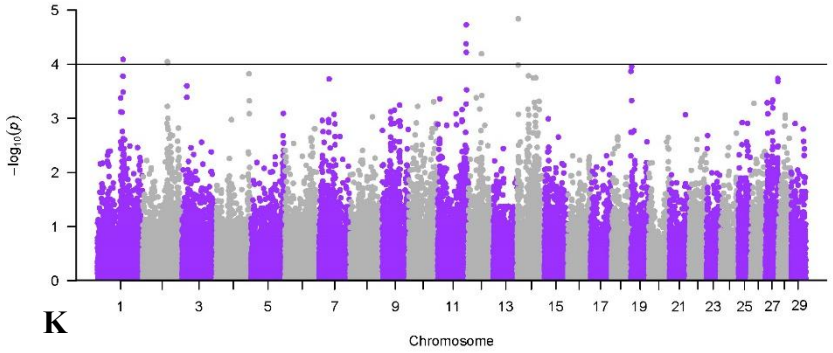
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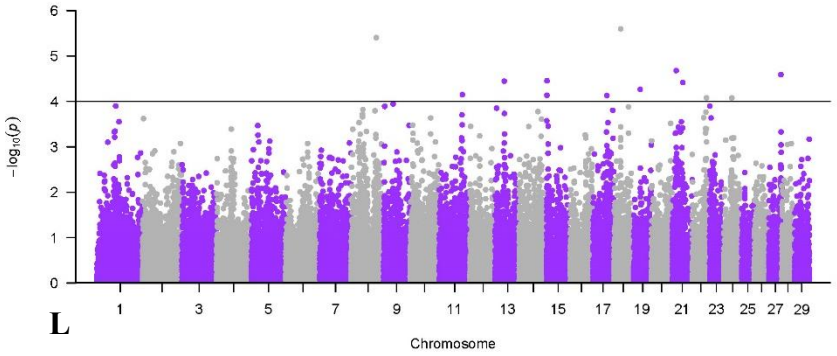
Chromosome

K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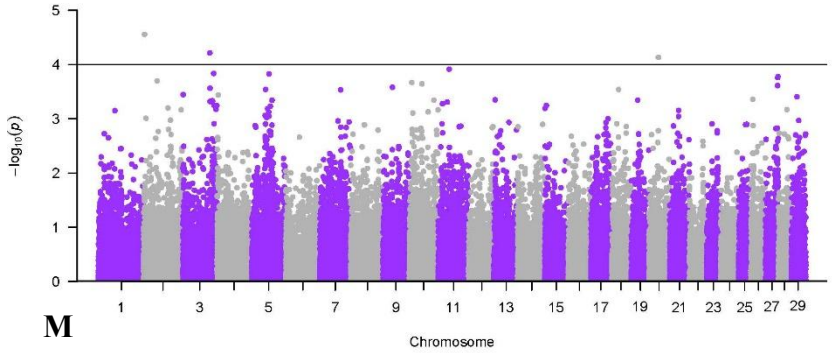
Chromosome

L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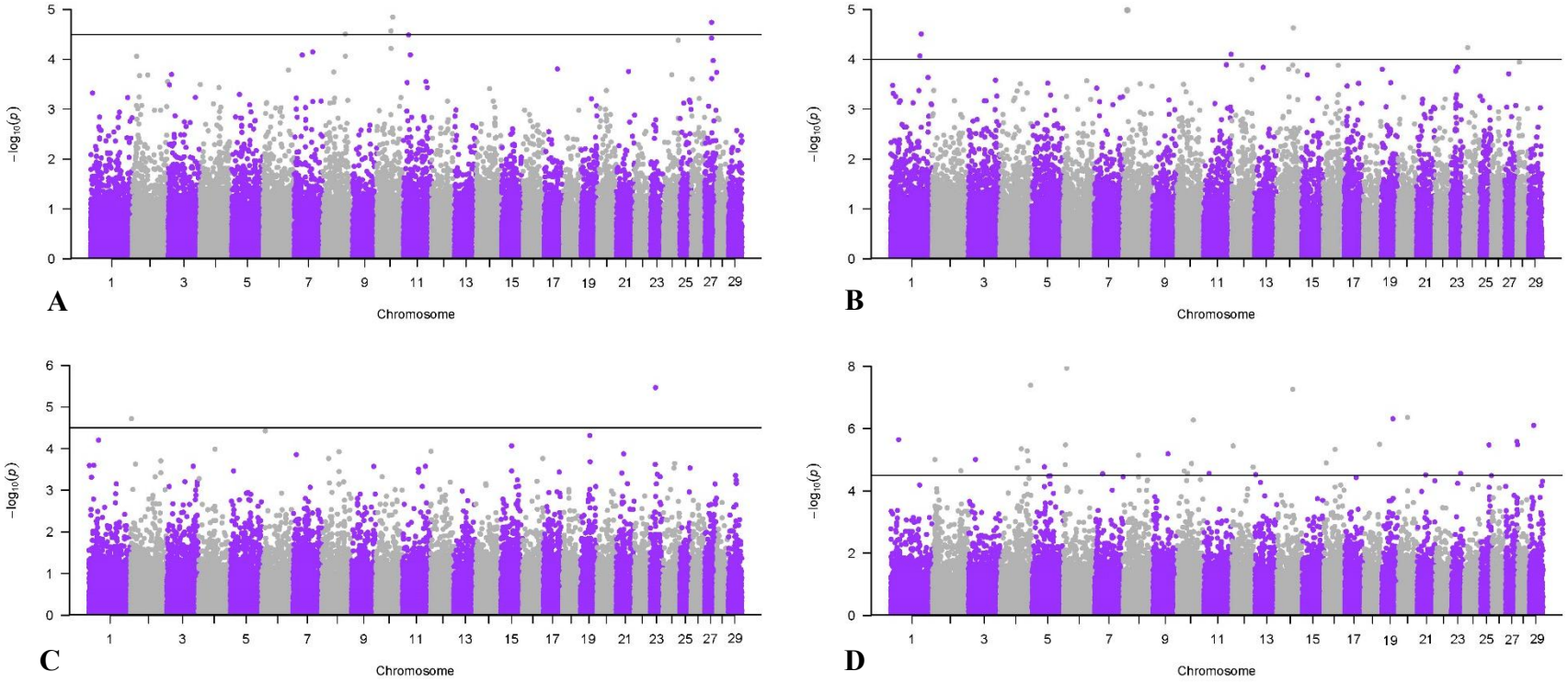
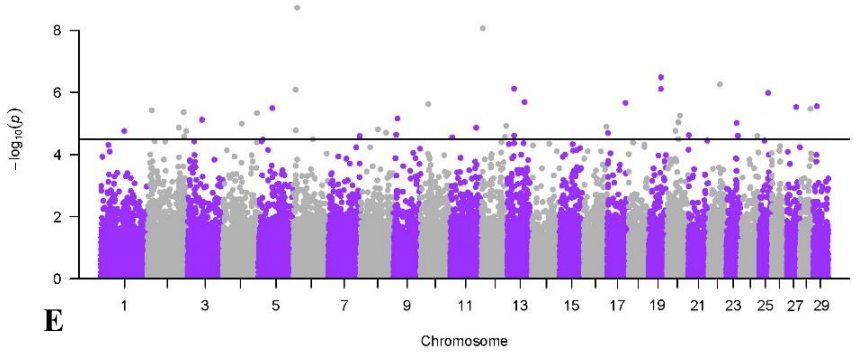
Chromosome

M

Figure 3.2. Manhattan plots for each univariate, single-record genome-wide association study of cashmere fiber characteristics from the combined analysis. Panel A- Mean fiber diameter (µm), Panel B- Standard deviation of diameter (µm), Panel C- Coefficient of variation of diameter (%), Panel D- Curvature (°/mm), Panel E- Standard deviation of curvature (°/mm), Panel F- Spinning fineness (µm), Panel G- Percentage less than 19 µm (%).

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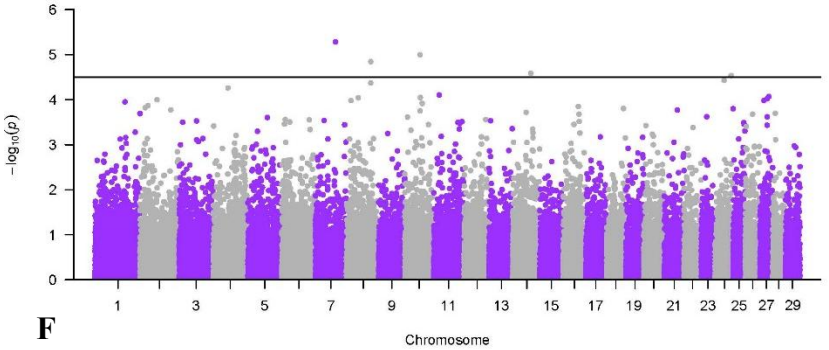
Chromosome

E


6
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4
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2
1
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$-\log_{10}(p)$
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29
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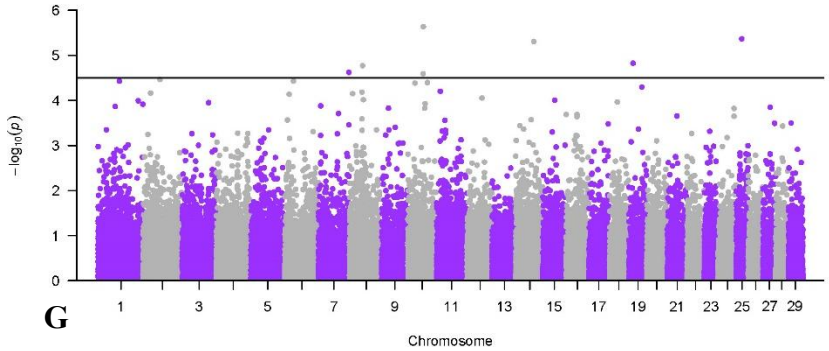
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Chapter 4 - Heritability and variance components of gas fluxes and metabolic heat production in grazing Angus beef cattle collected with a GreenFeed system

Introduction

Enteric fermentation is a normal digestive process that allows ruminant animals to upcycle forage into nutrient-dense products for human consumption, but also produces methane (CH_4) as a byproduct. In the beef industry, gas emissions have an impact on all three pillars of sustainability: environmental, social, and economic. Environmentally, CH_4 is the second most abundant greenhouse gas (GHG) in the United States, accounting for 11.1% of gas emissions (U.S. EPA, 2024). Enteric fermentation accounts for 25% of CH_4 emissions in the United States (U.S. EPA, 2024). Socially, CH_4 production has an impact on consumers' perception of beef production. Economically, CH_4 is an energetic inefficiency that represents a loss of 2% to 12% of gross feed intake (Johnson & Johnson, 1995) for beef producers. Therefore, there has been significant investment in identifying potential enteric CH_4 mitigation strategies. Most research on enteric fermentation has focused on animals in confined settings. However, within the beef supply chain, the cow-calf sector accounts for an estimated 68% to 80% of total GHG emissions, which is the largest contributor (Beauchemin et al., 2010; Stackhouse-Lawson et al., 2012). Approximately 84% of enteric CH_4 within the beef production system comes from the cow-calf sector, primarily from mature cows (Beauchemin et al., 2010). This is largely because animals spend the majority of their lives in this phase of production and primarily consume a forage-based diet, which produces more CH_4 than concentrate-based diets (Blaxter and Clapperton, 1965). Thus, targeting enteric CH_4 reduction in mature, grazing beef cows offers the greatest opportunity for impactful mitigation in the beef industry.

Far fewer mitigation strategies are available in grazing production systems without feed supplementation, compared to confined settings (Beauchemin et al., 2022). One of the few anti-methanogenic strategies available in extensive production systems is genetic selection for low CH_4 producing animals. One advantage of genetic selection is that changes to CH_4 production would be permanent and cumulative. Individual animal variation in CH_4 production for beef and dairy cattle has been shown among contemporaries and heritability estimates are low to moderate (as reviewed by Dressler et al., 2024). However, prior published literature is limited for beef cattle, particularly mature, grazing beef cows. The objectives of this study were to estimate the variance components, heritability, and repeatability of CH_4, carbon dioxide (CO_2), oxygen, (O_2), and metabolic heat production (MHP); examine the relationships among these gas flux traits and other production traits; and perform a genome-wide association study.

Materials and Methods

Ethics statement

All animal procedures were approved by the Institutional Animal Care and Use Committee at Kansas State University (protocol 4463 and 4929) in accordance with Federation of Animal Science Societies (FASS, 2020) guidelines.

Study population and design

Gas fluxes were collected on 330 grazing Angus beef cattle across 10 trial groups from May 24, 2021 to December 28, 2024. These animals were from four different cooperator operations in the Flint Hills of Kansas. Group and animal information is shown in Table 4.1 and the distribution of animal age at the start of GreenFeed trials in provided Appendix Table 4.1. An open-circuit gas quantification system (OCGQS) called the GreenFeed system (C-Lock, Inc., Rapid City, South Dakota, USA) was used to collect daily CH_4, CO_2, and O_2 gas fluxes. The

OCGQS used for this study is described further in Dressler et al. (2023). Briefly, a GreenFeed Pasture System with two units side-by-side on a single trailer was used, which allowed for testing of larger contemporary groups. The two units had separate alleyways allowing only one animal access to each feed dish and intake manifold at a time. High-density polyethylene boards were mounted on both sides of the alleyways to avoid airflow between the units and interference from the wind. The system was powered by both solar panels and a gas generator. At the beginning, end, and monthly during each trial group, CO_2 recovery tests were performed.

Trials were conducted on-site at the cooperator producers' operations by placing the OCGQS with the trial group in the pasture, near either a mineral feeder or water source. Pastures varied in size from approximately 45 to 2,200 acres. Each trial began with an acclimation period, which was a period of time that animals could use the OCGQS with the alleyways stored in an upright position. This allowed animals to train to use the system with easier access to the units. The length of the acclimation period varied by group, depending on each group's speed of adoption (Table 4.1). After acclimation, the alleyways were lowered to the ground and the phenotype collection began.

During the trial, animals grazed the pasture and were offered mineral supplement. Animal visitation to the OCGQS was completely voluntary. Animals were incentivized to visit the OCGQS by the pelleted feed released upon the scan of the animals' radio frequency electronic ID (RFID) tag. The pelleted feed was less than 7 mm in diameter in order to flow through the OCGQS. One trial used PowerPellets® (Pellet Technology USA, LLC), a dried distillers grains-based pellet and all other trials used alfalfa pellets. During each visit, the OCGQS was programmed to drop feed every 30 s up to eight times, with each drop releasing approximately 25 to 35 g of feed. Therefore, the amount of pelleted feed animals receive is a relatively small

proportion of their diet and only serves as an incentive for animals to visit and maintain proper head position in the intake manifold long enough to capture an eructation event. Animals could visit each GreenFeed unit up to 5 times per day, with a minimum of one hour between each visit. The distribution of the number of GreenFeed visits per animal is shown in Figure S1. The average number of animal visits to the GreenFeed during trial was 59, and ranged from 1 to 261 visits. Animals visited the GreenFeed an average of 0.54 times per day across the whole trial period, which is about every other day. The distribution of average daily GreenFeed visits is shown in Figure S2.

Phenotypic data

Raw gas collection data was validated by C-Lock Inc. according to their protocols including checks for head proximity, CO_2 response, standard gas calibrations, CO_2 recovery tests, airflow and wind. C-Lock, Inc. considers visits that are a minimum of 2 minutes in duration a valid visit, therefore that was the visit duration minimum used for the current study. First, the OCGQS calculates gas emission rates, which are then used to calculate gas fluxes (g/d) according to equations described in Huhtanen et al. (2015) for CH_4, CO_2, and O_2. Each gas flux value from every animal visit to the OCGQS was considered a record in the repeated records analysis. On rare occasions, an individual gas sensor (CH_4, 4 visits; O_2, 97 visits) would malfunction for a visit. In such cases, the gas measurement from the malfunctioning sensor was considered missing, while valid readings from the other functioning gas sensors were retained for analysis. As a result, the number of observations varies by gas in the repeated records analysis. Gas flux values from the entire trial were averaged for each animal to obtain an average CH_4 (Avg_CH_4), average CO_2 (Avg_CO_2), and average O_2 (Avg_O_2) for the single record analysis. A total of 60 animals were measured with the OCGQS in two different trial groups. For these

animals, only the gas flux values from the trial group in which that animal had the most visits were used in the calculation of average gas flux, so that fixed effects could be clearly assigned to that average gas phenotype.

Using the gas fluxes from the OCGQS, MHP was calculated with the Brouwer, (1965) equation as follows:

$$MHP\ \left(\frac{kcal}{day}\right) = (3.866 * O_2) + (1.2 *\ CO_2) - (0.518 *\ CH_4) - (1.431 * N),$$

where O_2, CO_2, and CH_4 are each animals' values from the OCGQS in liters. Nitrogen (N) was not available in the current study and was omitted from the calculation of MHP. Metabolic heat production estimates calculated by omitting N are not significantly different from MHP estimates that include N, and therefore omission of N is an appropriate MHP calculation approach (Proctor et al., 2024). Metabolic heat production was calculated for each animal's visit to the OCGQS in the repeated records analysis. Then MHP was averaged per animal across all their visits to obtain an average MHP (Avg_MHP) for the single record analysis.

Genetic data

A pedigree for animals that had gas flux phenotypes, and their relatives (6,404 animals) was provided by the American Angus Association (AAA; Saint Joesph, MO, USA). In addition, AAA provided genomic information on 54,609 SNPs for animals that had phenotypes and their relatives in the pedigree. Genomic information was available for 323 animals that had gas flux phenotypes and 4,940 animals total. Quality control of genotypes was performed to remove animals with call rate less than 0.90, leaving 4,917 animals with effective genotypes for analysis. Single nucleotide polymorphisms (SNPs) with call rate less than 0.90 were removed (3,156) and minor allele frequency less than 0.05 (13,568), leaving 39,616 effective SNPs.

For animals with gas flux phenotypes, AAA provided the following estimated progeny differences (EPDs) and economic index values from their genetic evaluation (as of March 25, 2025): calving ease direct (CED), birth weight (BW), weaning weight (WW), yearling weight (YW), residual average daily gain (RADG), dry matter intake (DMI), yearling height (YH), scrotal circumference (SC), docility (Doc), claw set (Claw), foot angle (Angle), pulmonary arterial pressure (PAP), hair shed (HS), heifer pregnancy (HP), calving ease maternal (CEM), maternal milk (Milk), mature weight (MW), mature height (MH), cow energy value ($EN), carcass weight (CW), marbling (Marb), ribeye area (RE), fat thickness (Fat), maternal weaned calf value ($M), weaned calf value ($W), feedlot value ($F), grid value ($G), beef value ($B), and combined value ($C). In addition, for animals with gas flux phenotypes, AAA provided adjusted weaning weights of their calves. These weights were used to calculate the average calf adjusted weaning weight (calfWW) per dam.

Statistical analysis

Model selection

Forward stepwise regression was used for model selection, and model fit was assessed with Akaike information criterion (AIC). The model with the best fit was determined when the addition of another effect did not reduce the AIC by more than 3. The base model for each phenotype was:

$$y_i = b_0 + e_i$$

where y_i is each gas flux or MHP trait, b_0 is the intercept, and e_i is the residual. Four fixed effects were tested with forward selection to be added to the above base model: contemporary group (GreenFeed trial group), age at trial start (continuous covariate in decimal years), body condition score (BCS; 1 to 9 scale), and mature weight (MW) EPD. Final models for CH_4, CO_2,

O_2, and MHP included contemporary group, age at trial start, and BCS. Final models for Avg_CH_4, Avg_CO_2, Avg_O_2 and Avg_MHP included contemporary group, and age at trial start. Mature weight EPD was also a significant effect based on AIC for both the repeated records and the averages. However, due to concerns about overfitting and limited sample size, variance component estimation was done twice for each trait: once including and once excluding MW EPD.

Genetic parameter estimation

First, a univariate analysis was performed for each of the average gas flux traits: Avg_CH_4, Avg_CO_2, Avg_O_2, and Avg_MHP. The univariate animal model used was as follows:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + e$$

where y is a vector of observations, b is a vector of fixed effects including contemporary group, age at trial start, and where applicable, MW EPD, **X** is an incidence matrix relating observations to fixed effects, u is a vector of additive direct genetic effects, **Z** is an incidence matrix relating observations to additive direct genetic effects, and e is a vector of residuals.

Following the univariate analysis of average gas flux traits, a repeated records analysis was performed for each gas flux trait which included records from every OCGQS visit as a separate record. The following repeatability model was used:

$$y = \boldsymbol{X}b + \boldsymbol{Z}u + \boldsymbol{W}p + e$$

where y, **X**, **Z**, u, and e were as defined previously, b is a vector of fixed effects including contemporary group, age at trial start, BCS, and where applicable, MW EPD, p is a vector of permanent environmental effects, and **W** is an incidence matrix relating observations to permanent environmental effects.

The BLUPF90 suite of programs (Misztal et al., 2014) was used to estimate variance components using average information restricted maximum likelihood. The single-step genomic best linear unbiased prediction (ssGBLUP) method was used where the pedigree relationship matrix (**A**) is blended with the genomic relationship matrix (**G**; VanRaden, 2008) to form the unified relationship matrix (**H**), according to Aguilar et al. (2010).

Correlations

Pearson and Spearman phenotypic correlations were calculated between average gas flux and metabolic heat production phenotypes. In addition, Pearson and Spearman correlations were calculated among the estimated progeny difference (EPD) solutions from the analysis of average gas flux traits (models without MW EPD).

For animals tested twice in separate GreenFeed groups (n=60), the average daily CH_4, CO_2, O_2, and MHP were calculated within each group. Then Spearman correlations were calculated between these average values from the two groups to assess the re-ranking of animals when tested more than once.

Due to sample size limitations, multi-trait analyses between gas flux traits or with other production traits were not performed. In order to characterize the relationship between gas fluxes and other production traits, Spearman and Pearson correlations were calculated between the EPD solutions from the analysis of average gas flux traits (models without MW EPD) and the EPDs, indexes, and calfWW provided by AAA. Only the values from animals that had gas flux phenotypes were included in the calculation of these correlations.

Genome-wide association study

A single-step genome-wide association study (ssGWAS) was performed to generate SNP effects and p-values. The ssGWAS was conducted using the postGSf90 program in the

BLUPF90 suite of programs (Misztal et al., 2014) for Avg_CH_4, Avg_CO_2, Avg_O_2, and Avg_MHP. The following methodology was used to derive SNP effects (Wang et al., 2012):

$$a = \boldsymbol{Z}u$$

where a is a vector of breeding values for genotyped animals, **Z** is a matrix relating genotypes of each locus, and u is a vector of SNP effects. The SNP effects were estimated as follows:

$$\hat{u} = IZ'(ZIZ')^{-1}\hat{a}$$

where $\hat{u}$ is a vector of SNP effects, **I** is an identity matrix, **Z** is a matrix relating genotypes of each locus, and $\hat{a}$ is a vector of estimated breeding values for genotyped individuals.

A suggestive significance threshold was set at -$\log_{10}$ *P*-value ≥ 4 for SNPs. Manhattan plots were generated using -$\log_{10}$ *P*-values and the qqman package in R (Turner, 2018).

Quantitative trait loci (QTL) regions were defined 250 kilobases upstream and downstream of the significant SNPs to account for linkage disequilibrium. Putative candidate genes which overlap the QTL regions of significant SNPs were identified using the GALLO package in R (Fonseca et al., 2020) and the National Center for Biotechnology Information bovine annotation file for the USDA ARS-UCD 1.2 genome assembly (Rosen et al., 2020; accession GCF_002263795.1). The Cattle QTLdb (Hu et al., 2022) was used to identify previously reported trait associations in the QTL regions. The UniProt Consortium (2023) was used to identify biological processes of putative candidate genes.

Results and Discussion

Summary statistics

Summary statistics are presented in Table 4.2. The range in minimum and maximum values, as well as the standard deviation, was smaller for the average gas flux traits compared to the repeated records observations, as expected. The mean Avg_CH_4 was 252.66 g/d. Donoghue

et al. (2016) reported an average CH_4 production of 132.2 g/d for young Angus bulls and heifers. Using primarily the same animals, an average CH_4 production of 132.6 g/d was reported in two other studies (Manzanilla-Pech et al., 2016; Hayes et al., 2016). While both the current study and these studies used Angus cattle, the latter primarily used young animals, whereas the current study used animals of all ages. Methane production increases with age and body size (Grandl et al., 2016), likely explaining the higher average CH_4 production observed in the current study. Crossbred beef heifers measured with a GreenFeed had an average CH_4 production of 204.7 g/d as reported in Manafiazar et al. (2016). Mature grazing Simbrah cows measured with the sulfur hexafluoride tracer technique had a range in daily CH_4 emissions of 165 to 294 g/d (DeRamus et al., 2003), which is similar to the average in the current study. A literature review by Broucek (2014) reported that mature beef cows typically emit between 240 to 396 g/d, and the animals in the current study fall in that range.

The mean Avg_CO_2 was 7,494 g/d. For beef heifers, lower average CO_2 emissions of 6,408 g/d (Manafiazar et al., 2016) and 5,760 g/d (Arthur et al., 2018) have been reported. These differences may be attributed to age, size of the animals, and the diet/nutritional environment. Animals in the current study grazed pastures, which requires greater energy expenditure (Brosh et al., 2010) and may have contributed to the greater CO_2 production observed compared to the dry-lot housed animals in Manafiazar et al. (2016) and Arthur et al. (2018). Beef steers on a finishing diet had an average CO_2 production of 10,250 g/d (Proctor et al., 2024). A few studies report CO_2 production in dairy cattle. The average CO_2 production from nine Holstein steers was 8,860 g/d (Berdos et al., 2023). Grazing dairy cattle measured with a GreenFeed produced between 9,360 and 11,500 g/d of CO_2, depending on stocking rate (Waghorn et al., 2016). Lactating dairy cattle measured with a GreenFeed had an average CO_2 production of 11,619 g/d

(Huhtanen et al., 2015). The higher CO_2 production observed in dairy cattle, particularly in lactating animals, could be due to the greater nutritional and energy requirements associated with milk production (NASEM, 2021), compared to the beef cattle in the current study.

Whereas CH_4 and CO_2 are expired from the animal, O_2 is consumed during respiration. The mean Avg_O_2 was 5,354 g/d in the current study. Eight beef steers fed a high-concentrate diet had an average O_2 consumption of 2,906.4 L/d (4,153.2 g/d) measured with a respiration headbox (Nienaber et al., 1993). Young beef bulls measured with a GreenFeed had O_2 consumption ranging from 5,963.2 to 6,443.4 g/d (Guarnido-Lopez et al., 2022), which is slightly greater than the average in the current study. Judy et al. (2018) reported that 12 lactating Jersey cows ranged from 6,176 to 6,431.4 g/d in O_2 consumption. A meta-analysis of 987 dairy cows of various physiological stages and breeds had an average O_2 consumption of 7,922.4 g/d (Aubry and Yan, 2015). Differences O_2 consumption may reflect differences in physiological demands between beef and dairy cattle, or greater feed intake as higher oxygen consumption is expected as intake increases (Blaxter, 1962).

The mean Avg_MHP in the current study was 18,881 kcal/d. Metabolic heat production for 27 feedlot beef steers ranged from 129.32 to 163.97 kcal/kg $BW^{0.75}$, or 13,675.59 to 17,218.49 kcal/d (Nkrumah et al., 2006). This range is slightly lower than the average in the current study, which is likely due to differences in animal type (feedlot steers vs. grazing females), diet (forage vs. concentrate) and production system (grazing vs. confinement). Using data from an OCGQS, Proctor et al. (2024) compared equations to calculate MHP and reported that beef steers on finishing diets had MHP ranging from 24.54 to 24.65 Mcal/d (24,540 to 24,650 kcal/d), depending on the equation. Similarly, Herd et al. (2020) reported average MHP of 104 MJ/d (24,856.59 kcal/d) for steers fed a concentrate diet. These averages for steers are

higher than the current study. However, Herd et al. (2020) reported that heifers on a forage diet had an average MHP of 67 MJ/d (16,013.38kcal/d), which is more comparable to the current study, likely due to the similar forage-based diets. This average could be slightly lower because heifers generate less metabolic heat than cows (West, 2003).

Heritability and repeatability of gas flux traits

Heritability and variance components for the average gas flux traits are presented in Table 4.3. Heritability, repeatability, and variance components from the repeated records analysis are presented in Table 4.4. In general, the addition of MW EPD as an effect in models lead to lower heritability estimates compared to estimates for the same trait that didn't include MW EPD. Heritability estimates from the single record analyses of average gas fluxes were higher than those from the repeated records analyses of single spot measures. Similarly, Ryan et al. (2025) estimated the heritability of CH_4 production measured with a GreenFeed for both single spot measurements and from full test averages and reported a higher heritability for the full test average. Interestingly, when comparing variance components between the single and repeated records analyses for the same trait, the genetic variances were comparable, but the residual variance was substantially greater for the repeated records. In this study, the repeated records analysis considered each visit an animal made to the OCGQS as a separate record. Measurement variation from the OCGQS equipment (Manafiazar et al., 2016) may have contributed to the increased residual variance observed in the repeated records analysis, and in turn, lower heritability estimates. van Breukelen et al. (2023) performed a genetic evaluation of CH_4 emissions collected with a sniffer in an automatic milking system in dairy cattle. These authors analyzed both weekly average and individual visit records for CH_4 emissions and

observed that averaging visits substantially reduced residual variance, consistent with the pattern observed in the current study.

Methane

The heritability of Avg_CH_4 was 0.23 ± 0.16 and the heritability of CH_4 in the repeated records analysis was 0.09 ± 0.03. Genetic parameters for gas production traits in ruminant animals are limited in literature, presumably due to the difficulty of collecting a sufficient number of phenotypes for genetic evaluation (Dressler et al., 2024). Two approaches have been taken in literature: estimation on predicted gas emissions, or estimation on direct measured traits, as in the current study. A research group in Australia measured CH_4 production from a large group of young beef bulls and heifers using respiration chambers. Using primarily the same 1,020 to 1,043 animals, heritability estimates of 0.27 ± 0.07, 0.28 ± 0.06, and 0.30 ± 0.06 were reported (Donoghue et al. 2016; Hayes et al. 2016; and Manzanilla-Pech et al. 2016). These estimates are similar to the Avg_CH_4 heritability the current study. A meta-analysis of heritability estimates for CH_4 production in cattle reported a heritability of 0.25 ± 0.02 (Brito et al., 2018). When only estimates on direct measured CH_4 production were included, the heritability was 0.21 ± 0.01 (Brito et al., 2018), which is very similar to current study's heritability estimate for Avg_CH_4.

In general, literature estimates for heritability of predicted CH_4 production are higher than for direct measured CH_4 production. Uemoto et al. (2020) predicted CH_4 production based on body weight, DMI, and diet information on 4,578 Japanese Black steers. Heritability of predicted CH_4 production was 0.59 ± 0.05 (Uemoto et al., 2020). Similar heritability estimates were reported by Lakamp et al. (2023) for predicted CH_4 production ranging from 0.59 ± 0.13 to 0.62 ± 0.13, depending on the prediction equation. These heritability estimates are much higher

than the current study and are likely due to a difference between direct measured and predicted CH_4 production. Predicted CH_4 production is derived from component traits such as body weight and DMI, which tend to have higher heritability, possibly contributing to the higher heritability of predicted traits compared to direct measurement. The heritability estimate for predicted CH_4 production that is closest to the current study was 0.32 ± 0.01 reported for 955 Nellore animals (Sobrinho et al., 2015).

Although still sparse, slightly more literature is available on the genetic parameters of CH_4 production for dairy cattle, compared to beef cattle. Kamalanathan et al. (2023) measured CH_4 production from 330 Holstein cattle with a GreenFeed and reported a heritability estimate of 0.16 ± 0.10. This study is very comparable to the current study due to similarities in sample size and measurement technique, which may be reasons for similar heritability estimates. Other heritability estimates for direct measured CH_4 production in dairy cattle are similar to the current study. Lassen and Lovendahl (2016) measured CH_4 production using a portable Fourier transform infrared air-sampler on 3,121 Holstein cows. The heritability of CH_4 production was 0.21 ± 0.06, which is similar to the Avg_CH_4 estimate despite differences in cattle type and measurement technique. Using a sniffer in an automatic milking system, CH_4 emissions (ppm) were collected from 1,746 Holstein cows and had a heritability of 0.13 ± 0.01 (van Breukelen et al., 2023). Similarly, Sypniewski et al. (2021) used a gas analyzer in an automated milking system to collect CH_4 emissions and reported a range in heritability from 0.13 to 0.26, depending on days in milk. Although from dairy cattle, these heritability estimates for CH_4 production are consistent with the estimates in the current study.

Methane production has been predicted in dairy cattle as well. Pickering et al. (2015) and de Haas et al. (2011) utilized similar prediction equations based on feed intake and reported

heritability estimates for predicted CH_4 production of 0.13 ± 0.06 and 0.35 ± 0.12, respectively. In dairy cattle, mid-infrared spectrometry (MIR) of milk samples have been used to predict CH_4 production. The heritability of predicted daily CH_4 production from milk MIR was 0.25 ± 0.01 (Kandel et al. 2017). These estimates are similar to the current study considering the associated standard errors, but differences could be due to measurement or prediction technique, and population.

Sheep are another ruminant livestock animal that emits CH_4 from enteric fermentation. Pinares-Patino et al. (2013) measured CH_4 production from 1,225 sheep in respiration chambers and reported a heritability estimate of 0.29 ± 0.05. This is higher than the current study's estimate for Avg_CH_4, although standard errors overlap. A meta-analysis of heritability estimates of CH_4 production in sheep reported an overall heritability of 0.21 ± 0.02 (Hossein-Zadeh, 2022), which is similar to the Avg_CH_4 estimate in the current study.

The repeatability of CH_4 production was 0.14 ± 0.01 in the current study. Few studies have examined repeatability using genetic models where each visit is treated as a separate record. van Breukelen et al. (2023) fit a repeatability model for a daily CH_4 production collected with both sniffers and a GreenFeed and reported the same repeatability (0.34 ± 0.01) for both methods. These authors used dairy cows under controlled conditions, with more consistent visit times (e.g. during milking for sniffers), which may have contributed to the higher repeatability. In another study using a sniffer system, the repeatability of a single observation was 0.12 ± 0.002 for growing beef x dairy calves (Johansen et al., 2025), which is very similar to the current estimate. When all sniffer visits for an animal were averaged daily and fit as the trait, the repeatability increased only slightly to 0.16 ± 0.003 (Johansen et al., 2025). Log-transformed CH_4 (ppm) collected with an infrared sensor on an automated milk station had a repeatability of

0.27 ± 0.008 (van Engelen et al., 2018). Although this estimate is higher than the current study, it is for a different CH_4 trait, measurement technique, and population. A notably higher repeatability of 0.54 ± 0.03 was reported by Kamalanathan et al. (2023) for CH_4 production collected with a GreenFeed system on Holstein cows. Cows were housed in tie-stalls, and the GreenFeed was rotated to ensure every animal was measured twice daily over 12 days on a fixed schedule. The controlled measurement frequency and timing of visits likely contributed to the higher repeatability compared to the voluntary GreenFeed visits in the current study.

Carbon dioxide

The heritability of Avg_CO_2 was 0.32 ± 0.15. In the repeated records analysis, the heritability of CO_2 was 0.14 ± 0.04 and the repeatability was 0.20 ± 0.02. Donoghue et al. (2020) reported a higher heritability estimate for CO_2 production of 0.53 ± 0.17 measured in growing beef bulls and heifers using respiration chambers in Australia. Differences in measurement technique and study population may explain the higher estimate compared to the current study, although both estimates have relatively large standard errors. A study that used a GreenFeed system like the present study (Ryan et al., 2024), reported estimates similar to those from the repeated records analysis. Ryan et al. (2024) reported a heritability of 0.17 ± 0.04 for individual visit CO_2 production and a repeatability of 0.31. This heritability is comparable to the current study's repeated records estimate, considering the standard errors. The higher repeatability may reflect their use of feedlot animals, which had more frequent visits over a shorter trial period, compared to grazing animals.

In dairy cattle, the heritability of CO_2 breath concentration (ppm) has been estimated using sniffers in automated milking systems. Difford et al. (2020) reported heritabilities of 0.23 ± 0.12 and 0.13 ± 0.13, depending on testing population. Similarly, van Breukelen et al. (2022)

reported a heritability of 0.16 ± 0.02 for CO_2 concentration. Although these studies used a different CO_2 trait and measurement technique, the estimates are comparable to those in the current study. In a study on dairy cattle that utilized a GreenFeed, the heritability of daily or weekly average CO_2 production (g/d) was 0.24 ± 0.03 and 0.34 ± 0.05 (van Breukelen et al., 2023), which is comparable to the heritability of Avg_CO_2 in the current study.

In sheep, Wahinya et al. (2022) used a portable accumulation chamber to measure CO_2 production from grazing animals and reported a heritability of 0.26 ± 0.05, which is similar to the current study's estimate for grazing beef cattle. A meta-analysis of nine studies in sheep reported a heritability of 0.22 ± 0.03 for CO_2 production (Hossein-Zadeh, 2022). Across ruminant species and various measurement techniques, CO_2 production appears to have moderate heritability.

Oxygen

The heritability of Avg_O_2 was 0.20 ± 0.15. In the repeated records analysis, the heritability of O_2 was 0.12 ± 0.04 and the repeatability was 0.20 ± 0.02. In this study, O_2 consumption was measured using an additional, optional sensor for the GreenFeed system. Measurement of O_2 consumption is less common than CH_4 or CO_2 collected with the GreenFeed system or respiration chambers. Currently, there are no published heritability estimates for O_2 consumption in beef or dairy cattle. However, a few estimates are available in other species. Wahinya et al. (2022) measured O_2 consumption from 1,382 grazing sheep using a portable accumulation chamber. These authors reported a heritability of 0.32 ± 0.05 and repeatability of 0.38 ± 0.02. These estimates are higher than those reported in the current study, possibly due to species differences or measurement technique, although the standard errors do overlap. A meta-analysis of six sheep studies reported a heritability of 0.24 ± 0.04 for O_2 consumption, which is

similar to the current estimate (Hossein-Zadeh, 2022). While mice have different digestive anatomy, they can be used as models for livestock research. Ogawa et al. (2022) reported a heritability of 0.22 ± 0.04 for O_2 consumption in 4,670 mice, which is comparable to the estimate in the current study despite many differences between the studies. Oxygen consumption and its genetic parameters in cattle is a novel research area. Our results suggest that O_2 consumption in beef cattle is lowly heritable, although additional research is needed in other, and larger populations.

Metabolic heat production

The heritability of Avg_MHP was 0.24 ± 0.15 and a lower heritability of 0.13 ± 0.04 was estimated in the repeated records analysis. The repeatability of MHP was 0.21 ± 0.02. There are currently no other heritability estimates for MHP of beef cattle in published literature. However, two studies have estimated genetic parameters for metabolizable energy for maintenance (MEm), a related trait. Metabolic heat production refers to the thermal byproduct of metabolism, whereas MEm is the feed energy intake required to maintain body weight. Metabolic heat production is one component of MEm, as energy lost as heat contributes to overall maintenance requirements. Freetly et al. (2023) reported a heritability of 0.31 ± 0.11 for MEm in a population of 887 pregnant, 5-year-old beef cows. The heritability of MEm was 0.52 ± 0.22 in a twin study of 20-month-old beef cattle (Hotovy et al., 1991). Together, these results suggest that components of metabolism are heritable, and that genetic selection for metabolic efficiency is possible.

Phenotypic correlations

Correlations among gas flux phenotypes and among gas flux EPDs

The Spearman and Pearson phenotypic correlations between average gas flux and MHP traits are presented in Table 4.5, ranging from 0.63 to 0.99. Average O_2 consumption and MHP

were highly correlated (0.99), which is logical given that O_2 is the largest contributor in the equation used to calculate MHP (Brouwer, 1965). Average CH_4 production had Pearson phenotypic correlations of 0.81 and 0.76 with CO_2 and O_2, respectively. High phenotypic and genetic correlations between CH_4 and CO_2 have also been reported in literature. Donoghue et al. (2020) measured gas emissions using respiration chambers for young Angus beef bulls and heifers and reported genetic and phenotypic correlations between CO_2 and CH_4 production of 0.75 ± 0.10 and 0.83 ± 0.02, respectively. This phenotypic correlation is similar to that observed in the current study. In a study that used a GreenFeed to measure CH_4 and CO_2 production, the phenotypic correlation between the two gases was 0.61 (Ryan et al., 2022). Another GreenFeed study reported phenotypic correlations between CH_4 and CO_2 production of 0.83 and 0.86, depending on testing population (Renand et al., 2019), which is very similar to the current study.

The Spearman and Pearson phenotypic correlations between Avg_CO_2 and Avg_O_2 were 0.95 and 0.96, respectively. A strong phenotypic correlation is biologically expected because both gases are associated with respiration. Animals inhale O_2 and exhale CO_2 in nearly stoichiometric proportions and largely reflect the same underlying metabolic process. As a result, measurement of both O_2 and CO_2 may not be necessary, unless the objective is to calculate MHP, respiratory quotient, or other metrics that require values for both gases.

The Spearman and Pearson correlations between average gas flux and MHP EPDs are presented in Table 4.6. A summary of these EPDs and their accuracy is in Table 4.7. The correlations between average gas flux and MHP EPDs ranged from 0.71 to 0.99 and followed a similar pattern to that observed for gas flux phenotypes (Table 4.5).

Correlations between average gas flux phenotypes tested in different groups

Spearman correlations between average gas flux phenotypes are reported in Table 4.8 for those animals that were tested in two different GreenFeed groups. Thirty animals tested in group 5 were also tested again in group 6, with both groups measured over a span of about five months. Animals in group 5 were bred heifers that calved and began lactating during group 6. The Spearman correlations between average gas flux phenotypes across groups 5 and 6 ranged from 0.47 to 0.54, depending on the gas (Table 4.8). During this time, forage quality and availability likely changed (Table 4.1), impacting animal diet. Furthermore, animals underwent several changes in physiological status. Yet, correlations between average gas flux phenotypes from different testing groups were moderate.

Thirty different animals were tested in group 4 and again in group 7, approximately one year apart (Table 4.1). The Spearman correlations for average gas flux phenotypes between groups 4 and 7 ranged from 0.44 to 0.46, depending on the gas (Table 4.8). Although animals were in the same physiological status during both testing periods, the longer time interval could have allowed for changes in animal weight or body condition. Differences in annual rainfall may have affected forage quality and grazing diets. While the impact of diet on CH_4 production is relatively well-known, the individual influence of other factors such as physiological status and timing of measurement needs to be examined further. This has implications for when phenotypes should be collected if CH_4 production is to be incorporated into a national genetic evaluation program.

Correlations between gas flux EPDs and weight EPDs

Pearson and Spearman correlations between gas flux/MHP trait EPDs and AAA-provided EPDs/indexes are shown in Table 4.9. There were no significant correlations between BW EPD and any of the gas trait EPDs. In contrast, Donoghue et al. (2016) reported phenotypic and

genetic correlations of 0.26 ± 0.04 and 0.36 ± 0.18, respectively, between BW and CH_4 production. Using a subset of the same animals, a phenotypic correlation of 0.19 ± 0.05 between BW and CH_4 production was reported (Herd et al., 2014). These studies reported correlations between observed BW and CH_4 production, whereas the current study used EPDs with varying accuracies, which may be why correlations are different.

For WW EPD, the correlations with gas trait EPDs ranged from 0.26 to 0.34 (Table 4.9), depending on the gas trait and type of correlation (Pearson or Spearman). Herd et al. (2014) measured CH_4 production with respiration chambers and reported a phenotypic correlation between CH4 production and WW of 0.50 ± 0.04. Using an expanded dataset, Donoghue et al. (2016) reported phenotypic and genetic correlations of 0.53 ± 0.03 and 0.84 ± 0.09, respectively, between CH_4 production and WW. These correlations are higher than the current study and could reflect differences in populations, CH_4 measurement technique, and trait type used for correlations.

The correlations between YW EPD and gas trait EPDs ranged from 0.31 to 0.40 (Table 4.9). Higher phenotypic (0.61 ± 0.03) and genetic correlations (0.86 ± 0.06) between YW and CH_4 production were reported by Donoghue et al. (2016). Herd et al. (2014) reported a slightly lower phenotypic correlation of 0.57 ± 0.03, although still higher than the current study. The current study's lower correlations, compared to the phenotypic correlations from Herd et al. (2014) and Donoghue et al. (2016), may be because the EPDs used reflect only additive genetic effects. In contrast, observed phenotypes also include non-additive genetic effects and environmental variation.

The range in correlations between MW EPD and gas flux EPDs was 0.37 to 0.47 (Table 4.9). Both Herd et al. (2014) and Donoghue et al. (2016) reported correlations between CH_4

production and a trait called final weight, which was defined as the weight close to maturity. The phenotypic correlation between final weight and CH_4 production was 0.49 ± 0.05 (Herd et al., 2014). In a follow-up study, Donoghue et al. (2016) reported phenotypic and genetic correlations between final weight and CH_4 production of 0.56 ± 0.03 and 0.79 ± 0.08, respectively. In general, animals with greater body weight have higher maintenance energy requirements, leading to greater feed intake and subsequently more CH_4 (Negussie et al., 2017). Moreover, as body weight increases, rumen capacity generally increases, which lowers passage rate and increases CH_4 production (Demment and Van Soest, 1985; Moraes et al., 2014).

The correlations between MH EPD and gas flux EPDs ranged from 0.31 to 0.37 (Table 4.9), indicating a moderate relationship between frame size and gas production. Mature height and MW have a strong genetic correlation (r=0.69; American Angus Association, 2025). As such, the relationship between MH and CH_4 production is likely driven by similar biological mechanisms underlying the relationship between MW and CH_4 production. These include increased maintenance energy requirements, greater feed intake, and larger rumen capacity in larger-framed animals, which all contribute to greater CH_4 production.

For CW EPD, the correlations with gas flux EPDs ranged from 0.25 to 0.32 (Table 4.9). Ryan et al. (2022) measured CH_4 production of feedlot animals with a GreenFeed and reported a phenotypic correlation between CW and CH_4 production to be 0.24, which is similar to current study. In a subsequent study, the genetic correlation between CW and CH_4 production was 0.49 ± 0.06. Interestingly, the genetic correlation between CW and CO_2 production was higher (0.82 ± 0.04; Ryan et al., 2025). This relationship is likely driven by increased feed intake in animals with heavier carcasses, resulting in greater CO_2 production (Ryan et al., 2025).

Correlations between gas flux EPDs and feed intake/efficiency EPDs

The range in correlations between DMI EPD and gas flux EPDs was 0.33 to 0.37 (Table 4.9). Ryan et al. (2022) reported a similar phenotypic correlation of 0.31 between CH_4 production measured with a GreenFeed and DMI. Using an expanded dataset, Ryan et al. (2025) reported high genetic correlations between DMI and both average CH_4 (0.76 ± 0.06) and CO_2 production (0.87 ± 0.03), which are higher than the correlations in the current study. These differences may be partially attributed to differences in type of correlation (EPD compared to actual phenotypes). Similarly, Manzanilla-Pech et al. (2016) reported strong phenotypic and genetic correlations between CH_4 production and DMI of 0.70 ± 0.02 and 0.83 ± 0.05, respectively. In Nellore cattle, CH_4 production measured using the sulfur hexafluoride (SF_6) tracer technique had a phenotypic correlation of 0.77 with DMI (Sakamoto et al., 2021). Renand et al. (2019) measured CH_4 production with a GreenFeed system from heifers on a roughage diet. The phenotypic correlation between CH_4 production and DMI was 0.36 to 0.48, depending on the testing group (Renand et al., 2019), which is very similar to the correlation in the current study. In contrast, van Breukelen et al. (2025) reported much lower phenotypic (0.06 ± 0.10) and genetic (0.02 ± 0.03) correlations between DMI and CH_4 concentration in dairy cattle, where CH_4 concentration was measured using sniffers in automated milking systems. Differences in type of cattle, measurement methodology, and CH_4 trait may have contributed to the differing results. In general, the correlations between DMI and gas flux traits appear to be positive, suggesting that lower DMI would be associated with lower CH_4 production. While higher DMI often supports greater productivity, this relationship is not consistent across all animals, reflecting differences in efficiency (Koch et al., 1963). Thus, the interconnected relationships between intake, productivity, and CH_4 production should be considered.

For RADG EPD, correlations with gas flux EPDs ranged from 0.30 to 0.37 (Table 4.9). While the relationship between gas production and RADG has not been directly studied, it has been with average daily gain (ADG). Renand et al. (2019) reported phenotypic correlations between CH_4 production and ADG ranging from 0.26 to 0.44, depending on the testing population. These correlations are similar to those in the current study, likely due to comparable CH_4 measurement equipment (GreenFeed), study population (female beef cattle), and diet (roughage-based). A higher phenotypic correlation of 0.70 between ADG and CH_4 production was reported for Nellore cattle measured with the SF_6 tracer technique (Sakamoto et al., 2021). These findings suggest that CH_4 production has a positive correlation with RADG and ADG. Therefore, selection solely for reduced CH_4 production could reduce daily gain, assuming all other factors remained constant.

Correlations between gas flux EPDs and Angus index values

The correlations between $EN and gas flux EPDs ranged from -0.35 to -0.45 (Table 4.9). Cow energy value is expressed in dollar savings per cow per year, with larger values indicating greater savings on feed energy expenses (American Angus Association, 2025). The negative correlations between $EN and gas flux EPDs suggests that lower gas production is associated with greater $EN, or dollars saved on feed energy expenses. This relationship is biologically plausible, as enteric CH_4 production is an energetic inefficiency for ruminants, accounting for a 2% to 12% loss of gross energy intake (Johnson & Johnson, 1995). Since $EN reflects differences in cow energy requirements, it is logical that animals with lower CH_4 EPD would have greater $EN, or dollars saved on feed energy expenses.

The range in correlations between $M and gas flux EPDs was -0.12 to -0.17 (Table 4.9). Maternal weaned calf value predicts profitability differences from conception to weaning,

expressed in dollars per head. This negative correlation suggests that animals with lower gas production EPDs tend to have greater $M values. The $M economic index incorporates several maternal traits such as weaning weight, milk, and heifer pregnancy (American Angus Association, 2025). In this study, the Pearson correlation between Avg_CH_4 EPD and calfWW was -0.13. While no other gas flux correlations with calfWW were significant, this correlation with Avg_CH_4 EPD suggests that dams that produce less CH_4 tend to have calves with greater adjusted WW, on average. Because CH_4 production is an energy sink (Johnson and Johnson, 1995), animals that have lower CH_4 production would theoretically have more energy to allocate to other physiological functions such as pregnancy and lactation, thereby better supporting a calf until weaning.

While gas flux EPDs were favorably correlated with $EN and $M, their correlations with $F and $B were unfavorable. Correlations between $F and gas flux EPDs ranged from 0.22 to 0.29, while those between $B and gas flux EPDs ranged from 0.19 to 0.26 (Table 4.9). These two economic indexes are terminal-focused and include postweaning gain, dry matter intake, and carcass weight, with $B also incorporating carcass characteristics (American Angus Association, 2025). These positive correlations suggest that animals with lower gas flux EPDs tend to have lower predicted profitability in the feedlot. Positive correlations with the terminal indexes appear to be primarily attributable to DMI EPD and CW EPD, which had similar positive correlations with Avg_CH_4 EPD, whereas the carcass characteristics did not have significant correlations. Previous research has shown that both CH_4 and CO_2 production have positive genetic correlations with DMI (Ryan et al., 2025). In the current study, gas flux EPDs had unfavorable correlations with RADG EPD. Due to the influence reduced CH_4 production could have on

reduced intake and gain, exclusive selection to reduce CH_4 would have a negative impact on performance and profitability in the feedlot.

For $C, the correlations with gas flux EPDs ranged from 0.12 to 0.17 among those that were significantly different from zero (Table 4.9). Combined value is an economic index that incorporates traits from both $M and $B and is intended for producers that retain replacement heifers while marketing cull progeny to the feedlot (American Angus Association, 2025). This positive correlation suggests that lower gas flux EPDs would be associated with lower predicted profitability in a combined maternal-terminal system. Although gas flux EPDs were favorably correlated with the $M component, their unfavorable correlations with the $B component likely offset those benefits. As a result, correlations with $C were low and only significantly different from zero for some gases and types of correlations. This suggests that while reducing CH_4 production may improve energetic efficiency beneficial for a maternal system, sacrifices to intake and gain in terminal settings may ultimately hinder overall economics in a combined system. Incorporation of CH_4 production into a selection index with an appropriate weighting would allow producers to select for reduced emissions without sacrificing productivity or profitability. To include CH_4 production in an economic index, its economic value would need to be more clearly defined in the U.S. market so that an appropriate economic weighting could be assigned.

Genome-wide association study

Due to the proprietary nature of the genomic data used in this study, SNP names and exact base pair positions are not reported. Instead, each SNP was assigned an anonymized identification (ID) number and each SNP will be referred to as ‘chromosome number:SNP ID’. Chromosome, SNP ID and $-\log_{10}$ *p*-values are reported in Table 4.10. All previously reported

QTL that are within ± 250kb of significant SNPs are reported in Table 4.11. Genes that were within the QTL regions of significant SNPs are listed in Appendix Tables 4.2 through 4.5. Putative candidate genes discussed for gas flux traits are outlined in Table 4.12. Manhattan plots are shown in Figure 4.1.

Methane

Fifteen significant SNPs were identified for Avg_CH_4 across eleven different chromosomes (Table 4.10). Several beef production traits have previously been mapped to QTL regions that are near these significant SNPs (Table 4.11). No traits specifically related to CH_4 production were identified, which is expected given the limited literature in this area. However, many of the QTL regions have been previously associated with traits known to influence or correlate with CH_4 production. Notably, QTL regions near five significant SNPs were previously associated with body weight: 15:F (Keogh et al., 2021), 16:H (Snelling et al., 2010), 20:M (Snelling et al., 2010), 20:N (Saatchi et al., 2014; Smith et al., 2020; Akanno et al., 2018), and 29:O (Peters et al., 2012; Snelling et al., 2010). Furthermore, QTL regions near 9:E and 20:M were linked to body weight gain (Snelling et al., 2010). These overlaps likely reflect the underlying biological relationship between CH_4 production and animal size, where larger animals generally consume more feed and produce more CH_4. This is consistent with correlations in the current study and existing literature reporting a positive genetic correlation between body weight and CH_4 production (Donoghue et al., 2016). Also, residual feed intake was previously associated with the QTL regions near 9:E (Duarte et al., 2019), 18:K (Sherman et al., 2010), and 20:N (Saatchi et al., 2014). Furthermore, DMI has been linked to QTL regions near 15:G and 20:N (Tetens et al., 2014; Zhang et al., 2020). A GWAS of CH_4 production in Angus and Holstein cattle also found large overlaps with body weight and DMI (Manzanilla-

Pech et al., 2016). These findings suggest that the genetic architecture influencing CH_4 production may partially overlap with that of growth and intake traits, which has implications for selection strategies aimed at reducing emissions without compromising performance.

All genes identified within the QTL regions of significant SNPs for Avg_CH4 are listed in Appendix Table 4.2. The 4:C QTL region for Avg_CH_4 was near OGDH (oxoglutarate dehydrogenase), which encodes a key enzyme in the mitochondrial citric acid cycle. This gene catalyzes a rate limiting step in the conversion of α-ketoglutarate to succinyl-CoA and CO_2 (The UniProt Consortium, 2023). As a central component of cellular energy metabolism, OGDH influences ATP production and redox balance, processes that can affect metabolic byproducts. Although OGDH has not been directly linked to CH_4 production, its upstream role in energy metabolism may contribute to variation in CH_4 production through effects on substrate availability for rumen microbial fermentation.

Another gene in the QTL region of 4:C was NPC1L1 (Niemann-Pick C1-Like 1). This gene encodes a transmembrane transporter critical for intestinal and hepatic absorption of cholesterol (The UniProt Consortium, 2023). Because of its central role in lipid uptake, NPC1L1 may be relevant to CH_4 production pathways influenced by diet. The use of dietary lipids as a CH_4 mitigation strategy has been widely studied. Lipids from dietary fats can reduce CH_4 production because they are not fermented by rumen microbes, thereby limiting hydrogen availability for methanogenesis (Popova et al., 2019). Beauchemin et al. (2007) reported that lipid supplementation reduced CH_4 production by 14% to 33%, depending on the lipid source. Genes related to lipid metabolism have also been identified in other GWAS of CH_4 production. Notably, Pszczola et al. (2018) identified CYP51A1, also located on chromosome 4, as a candidate gene involved in lipid metabolic processes, specifically synthesis of cholesterol and

other lipids. By regulating lipid absorption, NPC1L1 may influence the availability of dietary lipids in the gastrointestinal tract, with downstream impacts on microbial fermentation and methanogenesis.

Carbon dioxide

The fewest number of SNPs were identified for Avg_CO_2, compared to the other gas flux traits. Significant SNPs were identified on chromosome 1, 7, and 18 (Table 4.10). Similar to Avg_CH_4, QTL regions near two of the three significant SNPs overlapped with previously reported QTLs for body weight (1:P, Snelling et al., 2010; 18:R, Porto-Neto et al., 2015). The QTL region near 7:Q was previously associated with stature, or height (Bouwman et al., 2018). Larger animals typically produce more CO_2 due to higher basal and metabolic demands (Kleiber, 1961). Carbon dioxide is a by-product of cellular respiration, and animals with greater body mass have higher overall metabolic activity due to more tissue undergoing respiration. In addition, larger animals generally consume more feed to meet energy requirements, which increases oxidative metabolism and CO_2 production. Arthur et al. (2018) reported a phenotypic correlation of 0.78 between CO_2 production and DMI. Body size also influences lung volume and cardiac output, which affect gas exchange rates and overall CO_2 exhalation capacity (West et al., 1997). The phenotypic correlation between CO_2 production and body weight was 0.82 for Angus heifers and steers (Arthur et al., 2018). Together, these findings suggest that genetic variants influencing CO_2 production may overlap with those related to body size.

Appendix Table 4.3 lists all genes in the QTL regions of significant SNPs identified for Avg_CO_2. The gene ATP1B3 (ATPase Na^+/K^+ transporting subunit β-3) was in the QTL region of 1:P. This gene encodes the β3 subunit of the Na^+/K^+ ATPase, an essential membrane-bound enzyme responsible for maintaining cellular ion gradients (The UniProt Consortium, 2023). The

Na^+/K^+ ATPase pump is a major consumer of ATP in animal cells, accounting for a substantial portion of basal energy expenditure (Rolfe and Brown, 1997). Since CO_2 is a byproduct of cellular respiration, genes that influence ATP demand or utilization, like ATP1B3, may also influence CO_2 production.

The gene ZBTB38 (Zinc finger and BTB domain containing 38) was also located within the QTL region of 1:P. This gene encodes a transcription factor involved in key biological processes including DNA replication and cell growth (The UniProt Consortium, 2023). In Chinese cattle breeds, Li et al. (2013) reported associations between ZBTB38 and several body measurement traits including body length, withers height, and rump length. The SNP at 1:P, located near ZBTB38, also overlaps with previously reported QTLs for body weight (Snelling et al., 2010). These findings suggest that genomic regions related to body size may also be relevant to CO_2 production.

Oxygen

Eleven significant SNPs were identified for Avg_O_2 across nine different chromosomes (Table 4.10). The SNP 1:P was significant for both Avg_CO_2 and Avg_O_2 and is located near QTLs previously associated with body weight (Snelling et al., 2010). Like CO_2 production, O_2 consumption scales allometrically with body mass, since larger animals have higher basal metabolic rates and therefore greater O_2 consumption (Kleiber, 1961). In addition, QTLs previously linked to DMI were near 2:U (Zhang et al., 2020; Lu et al., 2013) and 3:V (Seabury et al., 2017). In beef cows, Holder et al. (2022) reported phenotypic correlations between O_2 consumption and DMI of 0.56 and 0.64, depending on diet. The recurrence of SNPs near body weight and intake-related QTLs across all three gas flux traits (Avg_CH_4, Avg_CO_2, Avg_O_2) suggests overlapping genetic influences for gas exchange and energetics in beef cattle.

All genes identified within the QTL regions of significant SNPs for Avg_O_2 are outlined in Appendix Table 4.4. The genes near 1:P (ATP1B3 and ZBTB38) that were discussed as candidate genes for Avg_CO_2, remain relevant candidates for Avg_O_2 as well. The QTL region for 3:V was near TNNI3K (TNNI3 interacting kinase), which encodes a cardiac-specific kinase involved in regulating cardiac muscle contraction and heart rate (The UniProt Consortium, 2023). In mouse cardiomyocytes, overexpression of TNNI3K significantly reduced basal oxygen consumption and increased reactive oxygen species production (Vagnozzi et al., 2013). Given its direct role in cellular oxygen utilization, TNNI3K is a compelling candidate gene for further investigation in relation to O_2 consumption in cattle.

Metabolic heat production

Eight significant SNPs were identified for Avg_MHP, and six of those were also identified for Avg_O_2. This overlap is logical because O_2 consumption was the main component used to calculate MHP in this study. Furthermore, the phenotypic correlation between the two traits was very high (0.99). Metabolic heat production reflects the energy lost as heat during cellular respiration and is therefore closely linked to O_2 consumption. As with Avg_O_2, significant SNPs for Avg_MHP were located near QTLs previously associated with body weight (Snelling et al., 2010) and DMI (Seabury et al., 2017). Animals with greater body mass or intake generate more metabolic heat (Kumar et al., 2016). Furthermore, multiple candidate genes identified for Avg_O_2, including ATP1B3, ZBTB38, and TNNI3K, also were near QTL regions for Avg_MHP, making them relevant targets for future study in relation to MHP as well. Interestingly, the QTL region of SNP 20:Z overlapped with QTLs previously associated with heat tolerance (Howard et al., 2014). While the relationship between heat tolerance and MHP is complex, animals with higher endogenous heat production may have greater difficulty in

thermoregulation under heat stress conditions. These results suggest shared genetic influences for Avg_MHP, body size, intake, and other gas exchange traits (Avg_O_2), reflecting shared underlying biological mechanisms for energy metabolism in beef cattle.

Conclusions

Genetic selection for reduced CH_4 production is one of the only mitigation strategies available for cattle in extensive grazing settings. However, genetic parameter estimates for directly measured gas production traits are limited in literature. The heritability of Avg_CH_4, Avg_CO_2, Avg_O_2, and Avg_MHP was 0.23 ± 0.16, 0.32 ± 0.15, 0.20 ± 0.15, and 0.24 ± 0.15, respectively. The heritability of CH_4, CO_2, O_2, and MHP using repeated records analysis was 0.09 ± 0.03, 0.14 ± 0.04, 0.12 ± 0.04, and 0.13 ± 0.04, respectively. Heritability estimates for average gas fluxes were higher than those for single-spot measures in the repeated records analyses. The repeatability of gas flux traits and MHP ranged from 0.14 ± 0.01 to 0.21 ± 0.02. The Pearson and Spearman correlations between average gas flux EPDs and Angus EPDs and economic index values showed significant correlations with EPDs related to weight and feed intake, as well as economic index values. Significant single nucleotide polymorphisms for average gas flux traits frequently overlapped known QTLs for body weight, and dry matter intake. These findings represent some of the first estimates of genetic parameters for gas fluxes and metabolic heat production for grazing beef cattle in the United States.

Table 4.1. GreenFeed testing group information.

Group Number	n*	Farm Number	Number of acclimation days	Acclimation Dates	Number of trial days**	Trial dates**	Type of animal	BCS Collection Date
1	10	1	36	5/24/21 to 6/29/21	72	6/29/21 to 9/9/21	2-4 year old cows	5/15/2021
2	5	1	11	11/8/21 to 11/19/21	46	11/19/21 to 1/4/22	2-4 year old cows	5/15/2021
3	12	2	59	6/6/22 to 8/4/22	69	8/4/22 to 10/12/22	Cows, all ages	5/20/2022
4	41	3	26	11/27/22 to 12/13/22; 4/4/23 to 4/14/23	41	12/13/22 to 1/5/23; 4/14/23 to 5/2/23	Calving cows	12/2/2022
5	93	3	16	5/7/23 to 5/23/23	102	5/23/23 to 9/2/23	Growing heifers	5/12/2023
6	37	3	0***	NA	40	9/2/23 to 10/12/23	Calving animals	9/15/2023
7	36	3	10	10/20/23 to 10/30/23	64	10/30/23 to 1/2/24	3-4 year old cows	12/29/2023
8	48	3	34	2/10/24 to 3/15/24	50	3/15/24 to 5/4/24	Bred heifers	5/9/2024
9	59	3	19	5/31/24 to 6/19/24	71	6/19/24 to 8/29/24	Bred heifers	6/6/2024
10	49	4	21	8/29/24 to 9/19/24	100	9/19/24 to 12/28/24	Cows, all ages	6/17/2025

*Number of animals tested per group. 60 animals were measured more than once across multiple groups.
**Excluding acclimation.
***A large portion of cows had already used the system in group 5.
BCS, body condition score

Table 4.2. Summary statistics for body condition score, age at GreenFeed trial start, and gas flux and metabolic heat production traits from 330 grazing Angus females.

Trait	n	Minimum	Mean	Maximum	Standard deviation
Body condition score, 1-9 scale	319	4.0	5.78	8.0	0.712
Age at GreenFeed trial start, yrs	329	1.04	1.98	10.83	1.24
Mature weight, EPD	328	-3.0	62.1	150.0	26.81
Average CH_4, g/d	330	91.15	252.66	439.04	43.16
Average CO_2, g/d	330	4,015	7,494	12,470	1,082.70
Average O_2, g/d	330	2,777	5,354	9,097	804.98
Average metabolic heat production, kcal/d	330	9,903	18,881	31,930	2,798.5
CH_4, g/d	19,553	15.93	262.23	611.49	78.33
CO_2, g/d	19,557	2,687	7,673	14,996	1,725.83
O_2, g/d	19,460	1,722	5,494	11,921	1,284.70
Metabolic heat production, kcal/d	19,456	6,464	19,365	40,168	4,438.28

Table 4.3. Heritability and variance component estimates from univariate analysis of daily average methane (CH_4), carbon dioxide (CO_2), oxygen (O_2) and metabolic heat production (MHP) from grazing beef cattle. Models included contemporary group and age, and either included or excluded mature weight (MW) EPD.

	Excluding MW EPD				Including MW EPD			
Trait	n	Heritability ± standard error	Genetic variance	Residual variance	n	Heritability ± standard error	Genetic variance	Residual variance
Average CH_4, g/d	329	0.23 ± 0.16	270.52	867.76	328	No convergence		
Average CO_2, g/d	329	0.32 ± 0.15	199,300	415,160	328	0.17 ± 0.13	87,948	426,800
Average O_2, g/d	329	0.20 ± 0.15	68,126	257,110	328	0.04 ± 0.10	11,256	258,970
Average MHP, kcal/d	329	0.24 ± 0.15	975,070	2,960,800	328	0.08 ± 0.11	257,200	3,005,100

Table 4.4. Heritability (h^2; SE below), repeatability (r; SE below), and variance component estimates of methane (CH_4), carbon dioxide (CO_2), oxygen (O_2), and metabolic heat production (MHP) from the repeated records analysis. Models included contemporary group, body condition score, and age at the trial start, and either included or excluded mature weight (MW) EPD.

	Excluding MW EPD						Including MW EPD					
Trait	n[1];n[2]	h^2	r	σ_a^2	σ_e^2	σ_{pe}^2	n[1];n[2]	h^2	r	σ_a^2	σ_e^2	σ_{pe}^2
CH_4, g/d	19,111; 318	0.09 0.03	0.14 0.01	451.87	4,390.9	242.05	19,073; 317	0.04 0.02	0.11 0.01	191.47	4,394.9	333.74
CO_2, g/d	19,115; 318	0.14 0.04	0.20 0.02	315,290	1,772,800	118,960	19,077; 317	0.11 0.03	0.17 0.02	226,950	1,774,700	129,790
O_2, g/d	19,019; 318	0.12 0.04	0.20 0.02	145,510	948,190	93,841	18,981; 317	0.08 0.03	0.17 0.02	92,645	949,080	99,714
MHP, kcal/d	19,015; 318	0.13 0.04	0.21 0.02	1,858,600	11,241,000	1,049,900	18977; 317	0.09 0.03	0.17 0.02	1,226,600	11,252,000	1,120,600

[1]Number of records; [2]number of animals

σ_a^2, additive genetic variance;σ_e^2, residual variance; σ_{pe}^2, permanent environmental variance.

Table 4.5. Pearson (upper diagonal) and Spearman (lower diagonal) phenotypic correlations* between average daily gas production and metabolic heat production traits.

	Average CH_4	Average CO_2	Average O_2	Average metabolic heat production
Average CH_4, g/d		0.81	0.76	0.77
Average CO_2, g/d	0.71		0.96	0.98
Average O_2, g/d	0.63	0.95		0.99
Average metabolic heat production, kcal/d	0.65	0.97	0.99	

*Correlations significantly different from zero at p-value < 0.01.

Table 4.6. Pearson (upper diagonal) and Spearman (lower diagonal) correlations* between average daily gas production and metabolic heat production (MHP) estimated progeny differences (EPD).

	Average CH_4 EPD	**Average CO_2 EPD**	**Average O_2 EPD**	**Average MHP EPD**
Average CH_4 EPD		0.97	0.97	0.97
Average CO_2 EPD	0.76		0.98	0.99
Average O_2 EPD	0.71	0.93		0.99
Average MHP EPD	0.73	0.95	0.99	

*Correlations significantly different from zero at p-value < 0.01.

Table 4.7. Summary of average daily gas production and metabolic heat production estimated progeny differences (EPDs) and EPD accuracy.

EPD	Minimum	Mean	Maximum	Average EPD accuracy
Average CH_4	-10.4	0.02	13.35	0.23
Average CO_2	-389.45	3.865	360.9	0.26
Average O_2	-138.25	0.03	154.65	0.22
Average metabolic heat production	-620.45	1.995	658.75	0.24

Table 4.8. Spearman correlations of daily gas production and metabolic heat production averages between two GreenFeed testing groups for animals that were tested twice (n=60).

Trait	Groups 5 and 6 (n=30)	Groups 4 and 7 (n=30)
Average CH_4, g/d	0.474	0.463
Average CO_2, g/d	0.529	0.436
Average O_2, g/d	0.528	0.447
Average MHP, kcal/d	0.536	0.443

Table 4.9. Pearson (Pear) and Spearman (Spear) correlations between gas trait estimated progeny differences (EPDs) and AAA-provided EPDs, indexes, and average calf adjusted weaning weight (calfWW).

EPD, index, or trait	Avg_CH_4 EPD, Pear	Avg_CH_4 EPD, Spear	Avg_CO_2 EPD, Pear	Avg_CO_2 EPD, Spear	Avg_O_2 EPD, Pear	Avg_O_2 EPD, Spear	Avg_MHP EPD, Pear	Avg_MHP EPD, Spear
CED	-0.04	0.01	-0.006	0.01	-0.03	-0.02	-0.02	-0.01
BW	0.02	-0.02	0.02	0.01	0.03	0.03	0.04	0.03
WW	0.34**	0.33**	0.31**	0.26**	0.33**	0.29**	0.33**	0.28**
YW	0.40**	0.39**	0.36**	0.31**	0.40**	0.36**	0.39**	0.35**
RADG	0.37**	0.36**	0.31**	0.30**	0.37**	0.35**	0.35**	0.34**
DMI	0.33**	0.35**	0.36**	0.34**	0.37**	0.37**	0.37**	0.36**
YH	0.27**	0.25**	0.30**	0.25**	0.29**	0.24**	0.30**	0.25**
SC	0.15**	0.16**	0.05	0.04	0.03	0.04	0.06	0.04
Doc	0.13*	0.16**	0.18**	0.19**	0.11	0.10	0.13*	0.13*
Claw	0.02	0.01	-0.003	-0.03	0.04	0.004	0.03	-0.005
Angle	0.09	0.09	0.11	0.09	0.10	0.08	0.10	0.09
PAP	-0.08	-0.11*	-0.09	-0.12*	-0.02	-0.04	-0.04	-0.05
HS	-0.06	-0.06	-0.18**	-0.14*	-0.15**	-0.13*	-0.16**	-0.14*
HP	0.08	0.10	0.07	0.06	0.06	0.05	0.06	0.05
CEM	0.05	0.06	0.10	0.08	0.12*	0.10	0.11*	0.09
Milk	-0.08	-0.09	-0.11	-0.12*	-0.12*	-0.12*	-0.12*	-0.13*
MW	0.47**	0.44**	0.42**	0.37**	0.44**	0.39**	0.44**	0.39**
MH	0.36**	0.34**	0.36**	0.31**	0.36**	0.31**	0.37**	0.32**
$EN	-0.45**	-0.42**	-0.40**	-0.35**	-0.41**	-0.37**	-0.41**	-0.37**
CW	0.32**	0.31**	0.29**	0.25**	0.31**	0.27**	0.30**	0.27**
Marb	0.05	0.05	0.14*	0.09	0.11*	0.06	0.12*	0.07
RE	0.03	0.03	-0.03	-0.01	-0.02	-0.01	-0.02	-0.01
Fat	0.08	0.11	0.05	0.05	0.06	0.07	0.06	0.06
$M	-0.17**	-0.11	-0.12*	-0.10	-0.15**	-0.14*	-0.15**	-0.13*
$W	0.11*	0.12	0.09	0.04	0.09	0.05	0.09	0.05
$F	0.29**	0.27**	0.24**	0.22**	0.27**	0.25**	0.26**	0.24**
$G	0.04	0.04	0.12*	0.08	0.09	0.05	0.10	0.06
$B	0.24**	0.21**	0.26**	0.19**	0.26**	0.19**	0.26**	0.19**

$C	0.13*	0.12*	0.17**	0.11	0.16**	0.09	0.16**	0.09
CalfWW	-0.13*	-0.10	-0.12	-0.07	-0.11	-0.07	-0.11	-0.07

*Significant at *p*-value < 0.05; **Significant at *p*-value < 0.01.

CED, calving ease direct; BW, birth weight; WW, weaning weight; YW, yearling weight; RADG, residual average daily gain; DMI, dry matter intake; YH, yearling height; SC, scrotal circumference; Doc, docility; Claw, claw set; Angle, foot angle; PAP, pulmonary arterial pressure; HS, hair shed; HP, heifer pregnancy; CEM, calving ease maternal; Milk, maternal milk; MW, mature weight; MH, mature height; $EN, cow energy value; CW, carcass weight; Marb, marbling; RE, ribeye area; Fat, fat thickness; $M, maternal weaned calf value; $W, weaned calf value; $F, feedlot value; $G, grid value; $B, beef value; and $C, combined value.

Table 4.10. Summary of significant genomic regions for average gas flux and metabolic heat production traits including chromosome, anonymous SNP ID, and -log$_{10}$ p-values.

Trait	Chromosome	SNP ID[1]	-log$_{10}$ p-value
Average methane production, g/d	3	A	4.07
	4	B	4.29
	4	C	4.03
	7	D	4.19
	9	E	4.07
	15	F	4.78
	15	G	4.20
	16	H	4.47
	17	I	4.40
	17	J	4.26
	18	K	4.04
	19	L	4.59
	20	M	4.14
	20	N	4.05
	29	O	4.60
Average carbon dioxide production, g/d	1	P	4.32
	7	Q	4.20
	18	R	4.07
Average oxygen production, g/d	1	P	4.43
	1	S	4.38
	2	T	4.47
	2	U	4.19
	3	V	4.30
	5	W	4.06
	7	X	4.75
	10	Y	4.34
	20	Z	4.39
	21	AA	4.46
	25	BB	4.58
Average metabolic heat production, kcal/d	1	P	4.28
	1	S	4.17
	2	T	4.31
	3	V	4.12
	4	B	4.51
	7	CC	4.87
	20	Z	4.02
	25	BB	4.22

[1]SNPs that are the same, but were identified for more than one trait are assigned the same SNP ID.

Table 4.11. Previously reported quantitative trait loci (QTL) associated with beef production (non-milk related traits) which overlap significant single nucleotide polymorphism (SNP) identified for average gas fluxes and metabolic heat production.

Trait	Chr:SNP ID	QTL trait	Source
Average methane production, g/d	3:A	Age at puberty	Zhou et al., 2019
		Conception rate	Kiser et al., 2019
		Lean meat yield	Doran et al., 2014
	4:B	Average daily gain	Lu et al., 2013
	4:C	Maturity rate	Crispim et al., 2015
		Shear force	Leal-Gutierrez et al., 2020
		Connective tissue amount	
		Tenderness score	
	7:D	Tick resistance	Mapholi et al., 2016
		Marbling score	Leal-Gutierrez et al., 2020
	9:E	Residual feed intake	Duarte et al., 2019
		Connective tissue amount	Leal-Gutierrez et al., 2020
		Body weight gain	Snelling et al., 2010
	15:F	Average daily gain	Peters et al., 2012; Seabury et al., 2017
		Body weight	Keogh et al., 2021
		Tenderness score	Leal-Gutierrez et al., 2020
		Longissimus muscle area	Medeiros de Oliveira Silva et al., 2017
	15:G	Carcass hind leg circumference	Bordbar et al., 2022
		Dry matter intake	Tetens et al., 2014
	16:H	Body weight	Snelling et al., 2010
		Connective tissue amount	Leal-Gutierrez et al., 2020
		Tenderness score	
		Marbling score	
		Kidney, pelvic, and heart fat percentage	Mateescu et al., 2017
	17:I	Connective tissue amount	Leal-Gutierrez et al., 2020
		Meat color	Allais et al., 2014
	17:J	Finishing precocity	Silva et al., 2019
		Muscularity	
		Average daily gain	Peters et al., 2012
	18:K	Age at puberty	Hawken et al., 2012
		Feed conversion ratio	Sherman et al., 2010

		Residual feed intake	
		Tenderness score	Leal-Gutierrez et al., 2020
	19:L	Carcass weight	Doran et al., 2014
	20:M	Average daily gain	Saatchi et al., 2014
		Body weight	Snelling et al., 2010
		Body weight gain	
		Kidney, pelvic, and heart fat percentage	Mateescu et al., 2017
		Conception rate	Kiser et al., 2019
		Inseminations per conception	Haque et al., 2024
	20:N	Body weight	Saatchi et al., 2014; Smith et al., 2020; Akanno et al., 2018
		Carcass weight	Saatchi et al., 2014; Wang et al., 2020
		Subcutaneous fat thickness	Saatchi et al., 2014
		Calving ease	
		Yield grade	
		Residual feed intake	
		Average daily gain	Zhang et al., 2020; Peters et al., 2012
		Dry matter intake	Zhang et al., 2020
		Metabolic body weight	Zhang et al., 2020; Seabury et al., 2017
		Stature	Bouwman et al., 2018
	29:O	Body weight	Peters et al., 2012; Snelling et al., 2010
		Subcutaneous fat thickness	Peters et al., 2012
		Shear force	Leal-Gutierrez et al., 2020
Average carbon dioxide production, g/d	1:P	Conception rate	Kiser et al., 2019
		Inseminations per conception	Hoglund et al., 2015
		Interval from first to last insemination	
		Non-return rate	
		Heel horn erosion	Croue et al., 2019
		White line disease	
		Average daily gain	Peters et al., 2012
		Body weight	Snelling et al., 2010

		Bovine respiratory disease susceptibility	Neupane et al., 2018
		Marbling score	Leal-Gutierrez et al., 2020
	7:Q	Length of productive life	Nayeri et al., 2017
		Subcutaneous fat thickness	Saatchi et al., 2014
		Marbling score	Leal-Gutierrez et al., 2020
		Stature	Bouwman et al., 2018
		Muscle zinc content	Mateescu et al., 2013
	18:R	Residual gain	Brunes et al., 2021
		Body weight	Porto-Neto et al., 2015
Average oxygen consumption, g/d	1:P	Conception rate	Kiser et al., 2019
		Inseminations per conception	Hoglund et al., 2015
		Interval from first to last insemination	
		Non-return rate	
		Heel horn erosion	Croue et al., 2019
		White line disease	
		Average daily gain	Peters et al., 2012
		Body weight	Snelling et al., 2010
		Bovine respiratory disease susceptibility	Neupane et al., 2018
		Marbling score	Leal-Gutierrez et al., 2020
	1:S	Connective tissue amount	Leal-Gutierrez et al., 2020
		Lean meat yield	Doran et al. 2014
	2:T	Body weight gain	Snelling et al., 2010
	2:U	Meat color	Marin-Garzon et al., 2020
		Marbling score	Leal-Gutierrez et al., 2020
		Tenderness score	
		Connective tissue amount	
		Dry matter intake	Zhang et al., 2020; Lu et al., 2013
		Metabolic body weight	Lu et al., 2013
	3:V	Dry matter intake	Seabury et al., 2017
		Carcass weight	Doran et al., 2014

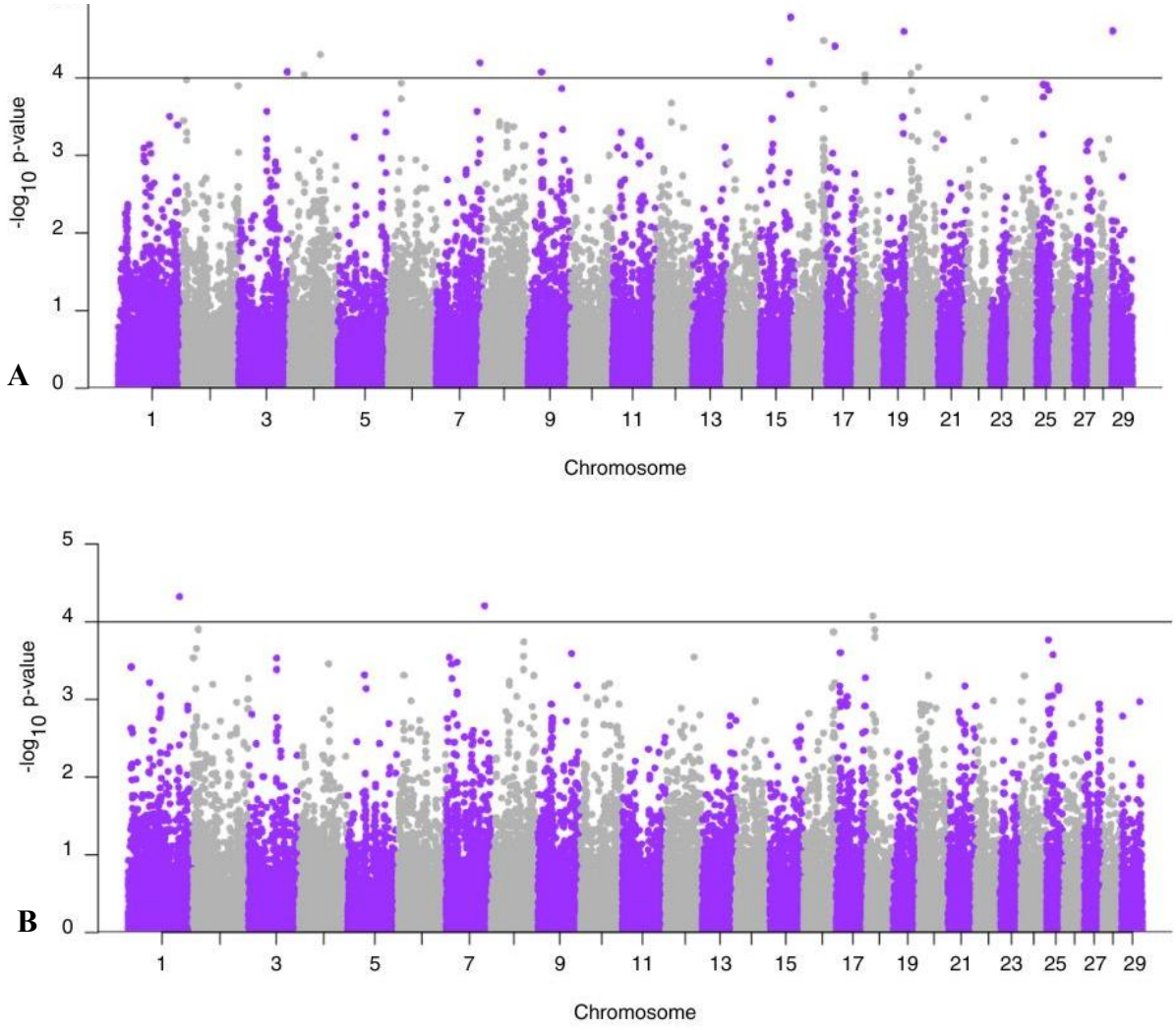
		Shear force	Leal-Gutierrez et al., 2020
	5:W	Intramuscular fat	Peters et al., 2012
		Subcutaneous fat thickness	
	7:X	Blood cortisol level	Chen et al., 2020
	10:Y	Body weight gain	Snelling et al., 2010
		Carcass depth	Bordbar et al., 2022
		Connective tissue amount	Leal-Gutierrez et al., 2020
	20:Z	Shear force	McClure et al., 2012
		Heat tolerance	Howard et al., 2014
		Body weight	Akanno et al., 2018; Snelling et al., 2010
		Average daily gain	Saatchi et al., 2014
		Body weight gain	Snelling et al., 2010
	21:AA	Bovine coronavirus susceptibility	Kiser et al., 2021
	25:BB	Body weight	Snelling et al., 2010
		Tenderness score	Leal-Gutierrez et al., 2020
Average metabolic heat production, kcal/d	1:P	Conception rate	Kiser et al., 2019
		Inseminations per conception	Hoglund et al., 2015
		Interval from first to last insemination	
		Non-return rate	
		Heel horn erosion	Croue et al., 2019
		White line disease	
		Average daily gain	Peters et al., 2012
		Body weight	Snelling et al., 2010
		Bovine respiratory disease susceptibility	Neupane et al., 2018
		Marbling score	Leal-Gutierrez et al., 2020
	1:S	Connective tissue amount	Leal-Gutierrez et al., 2020
		Lean meat yield	Doran et al. 2014
	2:T	Body weight gain	Snelling et al., 2010
	3:V	Dry matter intake	Seabury et al., 2017
		Carcass weight	Doran et al., 2014
		Shear force	Leal-Gutierrez et al., 2020
	4:B	Average daily gain	Lu et al., 2013
	7:CC	Blood cortisol level	Chen et al., 2020

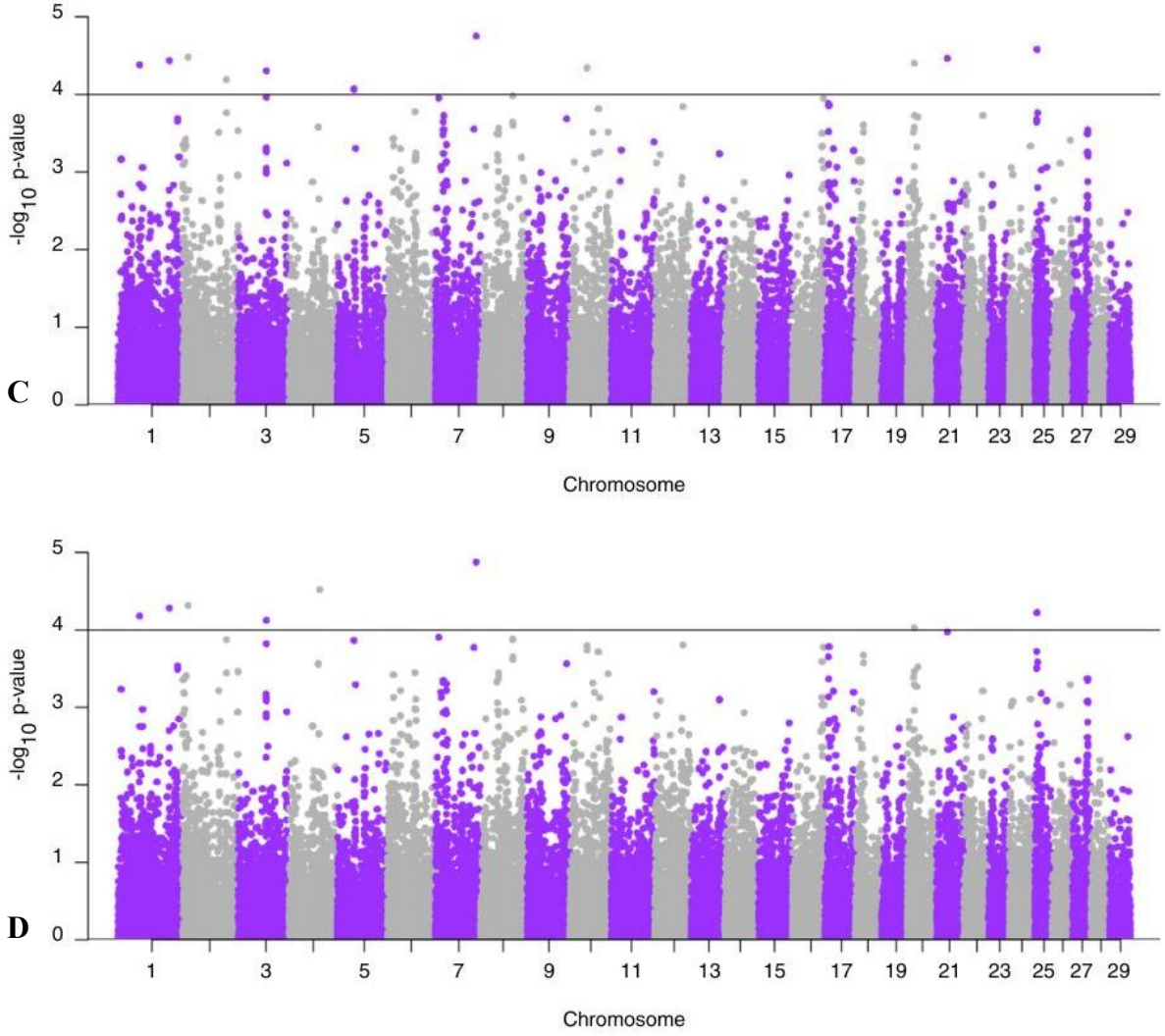
	20:Z	Shear force	McClure et al., 2012
		Heat tolerance	Howard et al., 2014
		Body weight	Akanno et al., 2018; Snelling et al., 2010
		Average daily gain	Saatchi et al., 2014
		Body weight gain	Snelling et al., 2010
	25:BB	Body weight	Snelling et al., 2010
		Tenderness score	Leal-Gutierrez et al., 2020

Table 4.12. Putative candidate genes within close proximity of significant single nucleotide polymorphisms (SNPs) associated with gas flux traits.

Trait	Chr:SNP ID	Gene name	Biological function
Avg_CH_4	4:C	OGDH	Energy metabolism (citric acid cycle)
		NPC1L1	Lipid metabolism (cholesterol absorption)
Avg_CO_2	1:P	ATP1B3	Cellular ion gradients
		ZBTB38	Transcription factor
Avg_O_2	1:P	ATP1B3	Cellular ion gradients
		ZBTB38	Transcription factor
	3:V	TNNI3K	Cardiac muscle regulation
Avg_MHP	1:P	ATP1B3	Cellular ion gradients
		ZBTB38	Transcription factor
	3:V	TNNI3K	Cardiac muscle regulation

Figure 4.1. Manhattan plots for average gas fluxes and metabolic heat production with a significance threshold of -log$_{10}$ *P*-value ≥ 4. Panel A- average methane production; Panel B- average carbon dioxide production; Panel C- average oxygen consumption; and Panel D- average metabolic heat production.




C
D
-log10 p-value
Chromosome
0
1
2
3
4
5
1
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Chapter 1

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Chapter 4

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Appendix A - Additional Chapter 2 Tables

Appendix Table A.1. Selection of model fixed effects to be added to the base model by two approaches: considering liveweight for inclusion and excluding liveweight from model selection where "-" indicates effect was not significant and 'n/a' indicates liveweight was not considered for inclusion.

		Approach 1: Considering liveweight			Approach 2: Without considering liveweight		
Trait	**Effect**	**Order added**	**AIC**	**AIC difference***	**Order added**	**AIC**	**AIC difference***
Mean fiber diameter, µm	Base model		466.51			1,134.33	
	Contemporary group	1	228.63	237.88	1	669.60	464.73
	Liveweight	2	149.82	78.81	n/a		
	Sex	3	111.70	38.12	3	523.62	7.85
	Age	-	110.60	1.1	2	531.47	138.13
Standard deviation of diameter, µm	Base model		-719.72			-1,195.29	
	Contemporary group	1	-902.89	183.17	1	-1,534.74	339.45
	Liveweight	-	-901.82	-1.07	n/a		
	Sex	-	-900.35	-2.54	-	-1,547.20	-0.4
	Age	-	-902.05	-0.84	2	-1,547.60	12.86
Coefficient of variation of diameter, %	Base model		1,196.66			2,049.50	
	Contemporary group	1	1,099.55	97.11	1	1,879.04	170.46
	Liveweight	2	1,073.32	26.23	n/a		
	Sex	3	1,050.74	22.58	3	1,845.35	12.97
	Age	-	1,052.60	-1.86	2	1,858.32	20.72
Coarse edge micron, µm	Base model		228.83			433.21	
	Contemporary group	1	107.41	121.42	1	189.75	243.46
	Liveweight	-	106.06	1.35	n/a		
	Sex	-	107.39	0.02	-	175.16	1.34
	Age	-	108.23	-0.82	2	176.50	13.25
Curvature, º/mm	Base model		2,598.61			4,719.39	
	Contemporary group	1	2,420.50	178.11	1	4,395.15	324.24

	Liveweight	-	2,390.20	0.48	n/a		
	Sex	2	2,390.68	29.82	2	4,363.70	31.45
	Age	-	2,392.40	-1.72	-	4,364.80	-1.10
Standard deviation of curvature, °/mm	Base model		2,335.00			4,127.01	
	Contemporary group	1	1,818.76	516.24	1	3,362.77	764.24
	Liveweight	4	1,795.01	12.19	n/a		
	Sex	2	1,810.28	8.48	2	3,352.00	10.77
	Age	3	1,807.20	3.08	3	3,348.02	3.98
Spinning fineness, µm	Base model		442.72			1,073.13	
	Contemporary group	1	187.63	255.09	1	591.10	482.03
	Liveweight	2	129.23	58.4	n/a		
	Sex	3	111.50	17.73	-	472.31	1.79
	Age	-	111.00	0.5	2	474.1	117.00
Staple length, mm	Base model		2,910.86			4,823.88	
	Contemporary group	1	2,685.73	225.13	1	4,322.54	501.34
	Liveweight	-	2,685.5	0.23	n/a		
	Sex	-	2,689.2	-3.47	2	4,318.56	3.98
	Age	-	2,687.7	-1.97	-	4,319.10	-0.54
Fleece weight, g	Base model		1,491.03			1,491.03	
	Contemporary group	-	1,418.32	0.46	-	1461.90	1.43
	Liveweight	1	1,429.80	61.23	n/a		
	Sex	3	1,418.78	3.68	1	1,463.33	27.7
	Age	2	1,422.46	7.34	-	1,465.30	-1.97
Percentage less than 19 µm, %	Base model		-2,575.15			-4,062.67	
	Contemporary group	1	-2,815.36	240.21	1	-4,468.12	405.45
	Liveweight	2	-2,894.84	79.48	n/a		
	Sex	3	-2,908.46	13.62	-	-4,583.93	0.23
	Age	-	-2,910.6	2.14	2	-4,583.70	115.58

*Difference in AIC from previously selected model to next model tested in stepwise model selection.

Appendix Table A.2. Genetic covariances between fiber characteristics from bivariate analyses.

	MFD	SDD	CVD	CEM	CURV	SDCurv	SpinF	SL	FW	Perc_19
MFD, µm		0.1176	-0.4424	0.3143	-4.904	-2.105	0.8309	3.4928	22.585	-6.1779
SDD, µm			0.2184	0.1598	-0.6712	-0.1860	0.1424	0.7544	0.0863	-0.9345
CVD, %				0.4974	2.0614	1.5017	-0.1754	1.2069	-24.95	2.3779
CEM, µm					-1.769	-0.3452	0.3814	2.1777	1.7813	-2.3703
CURV, °/mm						20.174	-4.4062	-47.310	-190.36	32.69
SDCurv, °/mm							-1.7922	-26.156	-109.13	13.738
SpinF, µm								3.3794	19.376	-5.9148
SL, mm									371.62	-21.859
FW, g										-255.52
Perc_19, %										

MFD- mean fiber diameter; SDD- standard deviation of fiber diameter; CVD- coefficient of variation of fiber diameter; CEM- coarse edge micron; CURV- curvature; SDCurv- curvature standard deviation; SpinF- spinning fineness; SL- staple length; FW-fleece weight; Perc_19- percentage of fibers with diameter less than or equal 19 µm.

Appendix Table A.3. Gene candidates in the linkage disequilibrium range (± 50 kb)[1] associated with each significant[2] single nucleotide polymorphism (SNP) for each fiber trait.

Trait	SNP name	Chromosome: Position	Gene abbreviation	Full gene name
Mean fiber diameter	NC_030830.1_831663	23:831663	FOXC1	Forkhead box C1
			GMDS	GDP-mannose 4,6-dehydratase
	snp12723-scaffold1489-359636	2:59355109	CNTNAP5	Contactin-associated protein-like 5
	snp1433-scaffold104-453661	10:25164538	LOC108636956	Uncharacterized
Standard deviation of diameter	snp15526-scaffold1641-174478	14:45652554	SBSPON	Somatomedin B and thrombospondin type 1 domain containing
			TERF1	Telomeric repeat-binding factor
	14:81337066	14:81337066	MROH1	Maestro heat like repeat family member 1
			BOP1	Ribosome biogenesis protein
			SCX	Basic helix-loop-helix transcription factor scleraxis
			HSF1	Heat shock transcription factor 1
			DGAT1	Diacylglycerol O-acyltransferase
			SCRT1	Scratch family transcriptional repressor 1
			TMEM249	Transmembrane protein 249
			FBXL6	F-box/LRR-repeat protein 6 isoform X1
			SLC52A2	Riboflavin transporter
			ADCK5	AarF domain-containing protein kinase 5 isoform X2
			CPSF1	Cleavage and polyadenylation specificity factor subunit 1 isoform X2
	snp46308-scaffold639-126113	7:70168742	LOC102183958	IRG-type G domain-containing protein
			LOC102171703	Ig-like domain-containing protein

			TRIM52	Small ribosomal subunit protein RACK1
			RACK1	Small ribosomal subunit protein RACK1
			TRIM41	E3 ubiquitin-protein ligase TRIM41 isoform X1
	10:37886722	10:37886722	SORD	Sorbitol dehydrogenase
			DUOX2	Dual oxidase 2
			DUOXA2	Dual oxidase maturation factor 2
			DUOXA1	Dual oxidase maturation factor 1
			DUOX1	Dual oxidase 1
			SHF	SH2 domain-containing protein
	NC_030811.1_90987564	4:90987564	SP8	Transcription factor Sp8
Coefficient of variation of diameter	snp9068-scaffold133-715	10:19535805	RGS6	Regulator of G protein signaling 6
	12:54926371	12:54926371	PAN3	PAN2-PAN3 deadenylation complex subunit
			FLT1	fms related receptor tyrosine kinase 1
	snp17668-scaffold183-1269493	3:112157042	TRNAL-CAG	Uncharacterized
			TRNAG-UCC	Uncharacterized
			TRNAD-GUC	Uncharacterized
			TRNAN-GUU	Uncharacterized
			LOC102185698	Low affinity immunoglobulin gamma Fc region receptor III-A
			LOC108635605	Endogenous retrovirus group K member 6 Gag polyprotein-like
	snp54122-scaffold825-1014475	29:25497494	TMEM86A	lysoplasmalogenase
			SPTY2D1	Protein SPT2 homolog
			LOC106503731	Uncharacterized

			UEVLD	Ubiquitin-conjugating enzyme E2 variant 3 isoform X3
	snp13583-scaffold1525-1372817	24:60678782	PIGN	GPI ethanolamine phosphate transferase 1
	NC_030830.1_18993272	23:18993272	LOC108633414	Histone H2B
			LOC102178586	Histone H2A
			LOC102178319	Histone H3
			LOC102180307	Histone H4
			LOC102178901	Histone H3.1-like
			LOC106501755	H1.5 linker histone, cluster member
			TRNAM-CAU	Uncharacterized
			TRNAG-GCC	Uncharacterized
			LOC102181115	Olfactory receptor
	snp52988-scaffold796-515837	29:29276909	KIRREL3	Kirre like nephrin family adhesion molecule 3
Course edge micron	snp10912-scaffold1390-330847	28:10278379	CGN	Collectin-46
	snp52526-scaffold782-3618961	20:2739578	KCNIP1	Potassium voltage-gated channel interacting protein 1
			GABRP	Gamma-aminobutyric acid receptor subunit pi
	4:2755170	4:2755170	LOC106502073	uncharacterized
			INSIG1	Insulin-induced gene protein
	10:37886722	10:37886722	SORD	Sorbitol dehydrogenase
			DUOX2	Dual oxidase 2
			DUOXA2	Dual oxidase maturation factor 2
			DUOXA1	Dual oxidase maturation factor 1
			DUOX1	Dual oxidase 1
			SHF	SH2 domain-containing protein
	snp29462-scaffold319-383364	10:77019517	LOC102169186	Olfactory receptor

			HNRNPC	Heterogeneous nuclear ribonucleoproteins C1/C2 isoform X2
			RPGRIP1	RPGR interacting protein 1
	12:79404524	12:79404524	LOC108637264	Germinal center-associated signaling and motility-like protein
	snp43455-scaffold579-4131867	9:62199424	LOC108636733	uncharacterized
			IL22RA2	Interleukin-22 receptor subunit alpha-2
			IFNGR1	Interferon gamma receptor 1
Curvature	snp37050-scaffold449-1431692	14:59014501	TGS1	Trimethylguanosine synthase 1
			TMEM68	Transmembrane protein 68
	snp6477-scaffold123-797664	16:33795985	KMO	Kynurenine 3-monooxygenase
			FH	Fumarate hydratase, mitochondrial
Standard deviation of curvature	snp9919-scaffold1354-42468	17:2617367	NEFH	Neurofilament heavy polypeptide
			LOC106503044	Uncharacterized
			AP1B1	AP complex subunit beta
			RASL10A	RAS like family 10 member A
	snp31365-scaffold347-1783379	12:4003713	ARGLU1	Arginine and glutamate rich 1
			EFNB2	Ephrin-B2
	NC_030813.1_11981581	6:11981581	LOC108636202	Uncharacterized
			ARSJ	Arylsulfatase J
	snp22469-scaffold2223-95469	13:22938705	SPAG6	Sperm-associated antigen 6
	11:73305234	11:73305234	ASXL2	Polycomb group protein ASXL2 isoform X1
	snp11445-scaffold1417-386228	23:32736234	TRERF1	Transcriptional-regulating factor 1 isoform X2
Spinning fineness	snp12723-scaffold1489-359636	2:59355109	CNTNAP5	Contactin-associated protein-like 5
	14:49533115	14:49533115	C14H8orf34	Uncharacterized
	snp1433-scaffold104-453661	10:25164538	LOC108636956	Uncharacterized

Staple length	snp54557-scaffold833-1303845	24:40263321	ARHGAP28	Rho GTPase activating protein 28
			LAMA1	Laminin subunit alpha-1 isoform X1
	NC_030831.1_40583446	24:40583446	SPIRE1	Protein spire homolog 1 isoform X2
			CEP76	Centrosomal protein of 76 kDa
			PSMG2	Proteasome assembly chaperone 2
	11:104347406	11:104347406	LOC108637096	Uncharacterized
	18:2875561	18:2875561	SF3B3	Splicing factor 3B subunit 3
			COG4	Conserved oligomeric Golgi complex subunit 4
			FUK	L-fucose kinase isoform X1
	2:26320799	2:26320799	EPHA4	EPH receptor A4
	6:68919933	6:68919933	USP46	Ubiquitin carboxyl-terminal hydrolase 46
			LOC108636224	Uncharacterized
			LOC102170130	Uncharacterized
Percentage ≤ 19µm	NC_030815.1_24816118	8:24816118	ACER2	Alkaline ceramidase
			RPS6	40S ribosomal protein S6
			DENND4C	DENN domain containing 4C
	NC_030830.1_831663	23:831663	FOXC1	Forkhead box C1
			GMDS	GDP-mannose 4,6-dehydratase
	snp1433-scaffold104-453661	10:25164538	LOC108636956	Uncharacterized
	snp57298-scaffold912-1705662	10:54284488	RORA	Retinoic acid-related orphan receptor A
	snp12723-scaffold1489-359636	2:59355109	CNTNAP5	Contactin-associated protein-like 5
	19:9949651	19:9949651	YPEL2	Protein yippee-like 2 isoform X2
	snp36326-scaffold435-3071866	1:74472653	FGF12	Fibroblast growth factor 12
			LOC106502093	Uncharacterized

[1]If no genes were within the linkage disequilibrium range, then the SNP was not listed in the table.
[2]SNPs significant at -$\log_{10}$ *P*-value of 4.

Appendix B - Additional Chapter 3 Tables

Appendix Table B.1. Gene candidates in the linkage disequilibrium range (± 50 kb)[1] associated with each significant[2] single nucleotide polymorphism (SNP) for each fiber trait in the New Zealand analysis.

Trait	SNP name	Chromosome: Position	Gene abbreviation	Gene name
Mean fiber diameter, µm	27:25610526	27:25610526	CNOT7	poly(A)-specific ribonuclease
			VPS37A	VPS37A subunit of ESCRT-I
			MTMR7	Myotubularin related protein 7
			TRNAE-UUC	uncharacterized
	snp32293-scaffold366-3596533	8:83675077	IARS	isoleucyl-tRNA synthetase 1
			NOL8	Nucleolar protein 8
			CENPP	centromere protein P
	8:85169943	8:85169943	PTPDC1	Protein tyrosine phosphatase domain containing 1
			LOC106502423	Tripartite motif-containing protein 54
			MIRLET7F	microRNA let-7f
			MIRLET7D	microRNA let-7d
Standard deviation of diameter, µm	snp59884-scaffold996-137936	6:88058923	ADAMTS3	ADAM metallopeptidase with thrombospondin type 1 motif 3
Coefficient of variation of diameter, %	snp28883-scaffold310-7623498	5:70500098	LARGE1	LARGE xylosyl- and glucuronyltransferase 1
	NC_030830.1_19792976	23:19792976	TRNAA-AGC	tRNA- Alanine
			TRNAA-CGC	tRNA- Alanine
			TRNAK-UUU	tRNA- Lysine
			TRNAF-GAA	tRNA- Phenylalanine
			TRNAL-AAG	tRNA- Leucine
			TRNAT-AGU	tRNA- Threonine
			TRNAA-UGC	tRNA- Alanine
			TRNAR-CCG	tRNA- Arginine
	snp20700-scaffold204-820288	11:74681564	FAM228A	Protein FAM228A
			FAM228B	Protein FAM228B
			PFN4	Profilin

			TP53I3	Tumor protein p53 inducible protein 3
			SF3B6	Splicing factor 3b subunit 6
Curvature, °/mm	snp26238-scaffold275-766124	27:25580723	ZDHHC2	Palmitoyltransferase
			CNOT7	poly(A)-specific ribonuclease
			VPS37A	VPS37A subunit of ESCRT-I
			MTMR7	Myotubularin-related protein 7
	25:35852095	25:35852095	CUX1	Protein CASP
	NC_030812.1_38122758	5:38122758	GXYLT1	Glucoside xylosyltransferase 1
Standard deviation of curvature, °/mm	snp29237-scaffold315-227227	3:109476096	LOC102168875	Pentraxin family member
			LOC102168592	G-protein coupled receptors family 1 profile domain-containing protein
			FCER1A	Fc epsilon receptor Ia
			LOC102191662	uncharacterized
			TRNAC-ACA	tRNA Cysteine
Spinning fineness, µm	snp32293-scaffold366-3596533	8:83675077	IARS	isoleucyl-tRNA synthetase 1
			NOL8	Nucleolar protein 8
			CENPP	Uncharacterized
	8:85169943	8:85169943	PTPDC1	Protein tyrosine phosphatase domain containing 1
			LOC106502423	Tripartite motif-containing protein 54
			MIRLET7F	microRNA let-7f
			MIRLET7D	microRNA let-7d
Percentage ≤ 19 µm, %	snp36267-scaffold435-498787	1:77070767	P3H2	procollagen-proline 3-dioxygenase
	snp40517-scaffold519-881449	1:78451066	LPP	LIM domain containing preferred translocation partner in lipoma
	snp24902-scaffold2547-223010	21:33956209	STRA6	Receptor for retinol uptake STRA6
			ISLR	Immunoglobulin superfamily containing leucine rich repeat
			ISLR2	Immunoglobulin superfamily containing leucine rich repeat 2
Down staple length, mm	snp9258-scaffold1337-33653	14:3929608	RALYL	RRM domain-containing protein
	NC_030818.1_98628971	11:98628971	ODF2	Outer dense fiber protein 2
			GLE1	mRNA export factor GLE1
			SPTAN1	Spectrin alpha chain, non-erythrocytic 1

	snp46806-scaffold653-1537540	11:99577135	PRRX2	Paired related homeobox 2
			PTGES	Prostaglandin E synthase
	12:46091411	12:46091411	PCDH9	Protocadherin 9
Yield, %	snp35163-scaffold421-141252	24:30755155	KCTD1	Potassium channel tetramerization domain containing 1
	snp13404-scaffold1518-229207	14:50539552	CPA6	Peptidase M14 carboxypeptidase A domain-containing protein
	14:50659317	14:50659317	ARFGEF1	ADP ribosylation factor guanine nucleotide exchange factor 1
	NC_030811.1_110865749	4:110865749	GATAD1	GATA zinc finger domain-containing protein 1
			LOC102178878	uncharacterized
			ANKIB1	RBR-type E3 ubiquitin transferase
Fleece weight, g	snp54570-scaffold833-1805827	24:40761692	PTPRM	protein tyrosine phosphatase, receptor type m
Down weight, g	snp7530-scaffold127-6406156	2:21942232	NYAP2	Neuronal tyrosine-phosphorylated phosphoinositide-3-kinase adaptor 2
	snp27847-scaffold299-1505220	16:74913766	CRB1	Crumbs cell polarity complex component 1
	8:43450514	8:43450514	DMRT3	Doublesex and mab-3 related transcription factor 3
			DMRT1	Doublesex and mab-3 related transcription factor 1
Coarse edge, %	snp22272-scaffold220-61665	2:3501685	PLA2G2F	Phospholipase A2
			PLA2G2C	Phospholipase A2
			UBXN10	UBX domain-containing protein 10
	snp47120-scaffold659-2908957	3:94823167	MAN1A2	alpha-1,2-Mannosidase
	20:32827242	20:32827242	OXCT1	Succinyl-CoA:3-ketoacid-coenzyme A transferase
Percentage of medullated fibers, %	snp35677-scaffold43-2995292	18:23106361	CHD9	DNA helicase
	snp30720-scaffold34-1029239	27:41823387	CSMD1	CUB and Sushi multiple domains 1
	NC_030822.1_1656016	15:1656016	LOC102188787	Uncharacterized
	NC_030822.1_1802835	15:1802835	LOC106501738	Uncharacterized
			LOC106502924	Uncharacterized

			LOC102187419	Uncharacterized
			TRNAE-UUC	tRNA Glutamic acid
	snp48998-scaffold7-1419288	13:31594543	TMEM236	Transmembrane protein 236
			MRC1	Mannose receptor C-type 1
	snp6402-scaffold1229-174051	19:23587864	RAP1GAP2	RAP1 GTPase activating protein 2
	snp13313-scaffold1513-738732	22:49398985	LOC102191471	Uncharacterized
			DCAF1	DDB1 and CUL4 associated factor 1

[1]If no genes were within the linkage disequilibrium range, then the SNP was not listed in the table.
[2]SNPs significant at -$\log_{10}$ *P*-value of 4.

Appendix Table B.2. Gene candidates in the linkage disequilibrium range (± 50 kb)[1] associated with each significant[2] single nucleotide polymorphism (SNP) for each fiber trait in the combined analysis.

Trait	SNP name	Chromosome: Position	Gene abbreviation	Gene name
Mean fiber diameter, µm	NC_030817.1_53553840	10:53553840	RORA	RAR related orphan receptor A
	snp26238-scaffold275-766124	27:25580723	ZDHHC2	Palmitoyltransferase
			CNOT7	poly(A)-specific ribonuclease
			VPS37A	VPS37A subunit of ESCRT-I
			MTMR7	Myotubularin related protein 7
	8:85169943	8:85169943	PTPDC1	Protein tyrosine phosphatase domain containing 1
			LOC106502423	Tripartite motif-containing protein 54
			MIRLET7F	microRNA let-7f
			MIRLET7D	microRNA let-7d
[3]Standard deviation of diameter, µm	1:110854497	1:110854497	KCNAB1	Voltage-gated potassium channel subunit beta-1
	11:104566389	11:104566389	LOC108637179	uncharacterized
			LOC108637180	uncharacterized
			RABL6	RAB, member RAS oncogene family like 6
			CCDC183	Coiled-coil domain containing 183
			TMEM141	Transmembrane protein 141
			LOC108637125	Lipocalin
			LOC102173384	Lipocalin/cytosolic fatty-acid binding domain-containing protein
			LCN6	Lipocalin 6
			LCN10	Lipocalin 10
Coefficient of variation of diameter, µm	NC_030830.1_19792976	23:19792976	TRNAA-AGC	tRNA- Alanine
			TRNAA-CGC	tRNA- Alanine
			TRNAK-UUU	tRNA- Lysine
			TRNAF-GAA	tRNA- Phenylalanine
			TRNAL-AAG	tRNA- Leucine
			TRNAT-AGU	tRNA- Threonine
			TRNAA-UGC	tRNA- Alanine
			TRNAR-CCG	tRNA- Arginine
	snp22273-scaffold220-99341	2:3463848	LOC108633234	secretory phospholipase A2-like
			PLA2G2F	Phospholipase A2 IIF
			PLA2G2C	Phospholipase A2 IIC

			UBXN10	UBX domain protein 10
Curvature, °/mm	6:6627869	6:6627869	SYNPO2	Synaptopodin 2
	6:7122325	6:7122325	METTL14	N(6)-adenosine-methyltransferase non-catalytic subunit METTL14
	NC_030813.1_11981581	6:11981581	LOC108636202	uncharacterized
			ARSJ	Arylsulfatase family member J
	snp31186-scaffold345-2282027	4:64685331	TMEM168	Transmembrane protein 168
			BMT2	S-adenosylmethionine sensor upstream of mTORC1
	snp58437-scaffold950-588104	4:79836857	CD36	Platelet glycoprotein 4
	NC_030811.1_115149546	4:115149546	DDC	Aromatic-L-amino-acid decarboxylase
			GRB10	Growth factor receptor bound protein 10
	snp37050-scaffold449-1431692	14:59014501	TGS1	Trimethylguanosine synthase
			TMEM68	Transmembrane protein 68
	19:42000809	19:42000809	GHDC	GH3 domain containing
			STAT5B	Signal transducer and activator of transcription
			LOC102185866	uncharacterized
	NC_030817.1_53553840	10:53553840	RORA	RAR related orphan receptor A
	IMAU944	29:16471416	TENM4	Teneurin transmembrane protein 4
	snp46071-scaffold632-588199	18:58960722	LOC102175434	uncharacterized
	snp31365-scaffold347-1783379	12:4003713	ARGLU1	Arginine and glutamate rich 1
			EFNB2	Ephrin B2
	12:79404524	12:79404524	LOC108637264	uncharacterized
	snp11344-scaffold141-980707	16:42623026	SPSB1	SplA/ryanodine receptor domain and SOCS box containing 1
			LOC108637774	uncharacterized
	snp44002-scaffold595-4547283	3:26550959	TXNDC12	Thioredoxin domain-containing protein 12
			KTI12	KTI12 chromatin associated homolog
			BTF3L4	basic transcription factor 3 like 4
			LOC102188103	uncharacterized
	2:9580060	2:9580060	ARID1A	AT-rich interaction domain 1A
			PIGV	phosphatidylinositol glycan anchor biosynthesis class V

			LOC108637297	uncharacterized
			ZDHHC18	Palmitoyltransferase 18
	snp19615-scaffold1980-634136	5:46781804	GRIP1	Glutamate receptor interacting protein 1
			HELB	DNA helicase B
	snp45295-scaffold618-2649648	11:19660202	PRKD3	Serine/threonine-protein kinase
			QPCT	Glutaminyl-peptide cyclotransferase
	snp50044-scaffold716-3083078	7:30418858	LOC108633191	uncharacterized
	snp17691-scaffold1834-77678	13:1880526	PLCB4	Phospholipase C beta 4
	NC_030828.1_32308828	21:32308828	LINGO1	Leucine rich repeat and Ig domain containing 1
Standard deviation of curvature, °/mm	6:6627869	6:6627869	SYNPO2	Synaptopodin 2
	6:7122325	6:7122325	METTL14	N(6)-adenosine-methyltransferase non-catalytic subunit METTL14
	NC_030813.1_11981581	6:11981581	LOC108636202	uncharacterized
			ARSJ	Arylsulfatase family member J
	snp31365-scaffold347-1783379	12:4003713	ARGLU1	Arginine and glutamate rich 1
			EFNB2	Ephrin B2
	12:79404524	12:79404524	LOC108637264	uncharacterized
	19:42002634	19:42002634	STAT5B	Signal transducer and activator of transcription
			LOC102185866	uncharacterized
	snp15342-scaffold163-2570163	22:38596654	CADPS	Calcium dependent secretion activator
	snp22469-scaffold2223-95469	13:22938705	SPAG6	Sperm associated antigen 6
	13:23113494	13:23113494	PIP4K2A	Phosphatidylinositol 5-phosphate 4-kinase type-2 alpha
			TRNAS-GGA	uncharacterized
	13:58243749	13:58243749	BMP7	Bone morphogenetic protein 7
	snp9919-scaffold1354-42468	17:2617367	NEFH	neurofilament heavy chain
			LOC106503044	uncharacterized
			AP1B1	AP complex subunit beta
			RASL10A	RAS like family 10 member A
	27:31381125	27:31381125	TRNAG-CCC	uncharacterized
			LOC102186657	Claudin

			WWC2	WW and C2 domain containing 2
	snp19615-scaffold1980-634136	5:46781804	GRIP1	Glutamate receptor interacting protein 1
			HELB	DNA helicase B
	NC_030835.1_35266324	28:35266324	RYR2	Ryanodine receptor 2
	snp2516-scaffold1071-376636	2:15152105	LOC108638640	uncharacterized
			AZIN2	Antizyme inhibitor 2
			LOC106503418	uncharacterized
			TRIM62	Tripartite motif containing 62
	snp28299-scaffold301-2995719	2:106431151	SCN7A	Sodium voltage-gated channel alpha subunit 7
	snp6589-scaffold1235-105689	2:131617753	MYO7B	Myosin VIIB
			LIMS2	LIM and senescent cell antigen-like-containing domain protein
			GPR17	G protein-coupled receptor 17
	NC_030811.1_63838279	4:63838279	DOCK4	Dedicator of cytokinesis 4
	NC_030811.1_115149546	4:115149546	DDC	Aromatic-L-amino-acid decarboxylase
			GRB10	Growth factor receptor bound protein 10
	snp45371-scaffold62-1473796	20:28805878	EMB	Embigin
	snp44662-scaffold607-235676	20:37226270	NIPBL	Nipped-B protein
	snp49944-scaffold714-1877773	23:39202383	TULP1	Tubby-like protein
	snp16707-scaffold1750-770875	11:6767967	IL1R1	Interleukin 1 receptor type 1
	snp39297-scaffold50-1480921	11:87964494	MBOAT2	Membrane bound O-acyltransferase domain containing 2
	8:60160322	8:60160322	GLIPR2	SCP domain-containing protein
			CCIN	Calicin
			CLTA	Clathrin light chain
			GNE	Glucosamine (UDP-N-acetyl)-2-epimerase/N-acetylmannosamine kinase
	snp12218-scaffold1455-178454	8:87723644	LOC106502454	uncharacterized
		1:79082101	LOC108636846	uncharacterized

	snp40532-scaffold519-1512011		LOC102169221	uncharacterized
	24:56358828	24:56358828	WDR7	WD repeat domain 7
	snp19409-scaffold196-1103346	7:106343223	LOC102176218	uncharacterized
			GRM6	Glutamate metabotropic receptor 6
Spinning fineness, µm	snp46308-scaffold639-126113	7:70168742	LOC102183958	IRG-type G domain-containing protein
			LOC102171703	Ig-like domain-containing protein
			TRIM52	tripartite motif containing 52
			RACK1	receptor for activated C kinase 1
			TRIM41	Tripartite motif containing 41
	NC_030817.1_53553840	10:53553840	RORA	RAR related orphan receptor A
	8:85169943	8:85169943	PTPDC1	Protein tyrosine phosphatase domain containing 1
			LOC106502423	Tripartite motif-containing protein 54
			MIRLET7F	microRNA let-7f
			MIRLET7D	microRNA let-7d
Percentage ≤ 19 µm, %	NC_030817.1_53553840	10:53553840	RORA	RAR related orphan receptor A
	8:46210811	8:46210811	MAMDC2	MAM domain containing 2
			LOC102187766	uncharacterized
			SMC5	Structural maintenance of chromosomes protein 5
	NC_030814.1_106635437	7:106635437	ADAMTS2	ADAM metallopeptidase with thrombospondin type 1 motif 2

[1]If no genes were within the linkage disequilibrium range, then the SNP was not listed in the table.
[2]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.5.
[3]SNPs (single nucleotide polymorphism) significant at -$\log_{10}$ *P*-value of 4.

Appendix C - Additional Chapter 4 Tables and Figures

Appendix Table C.1. Distribution of animal age at GreenFeed trial start.

Age at GreenFeed trial start (years)	n
1 to 2	233
2 to 3	70
3 to 4	13
4 to 5	4
5 to 6	3
6 to 7	1
7 to 8	1
8 to 9	2
10+	2
Not available	1

Appendix Table C.2. Genes within close proximity to significant single nucleotide polymorphisms associated with average methane production.

Chromosome	Gene name	Gene description
3	KIF1A	Kinesin family member 1A
	AGXT	Alanine-glyoxylate aminotransferase
	C3H2orf54	Chromosome 3 open reading frame 54
	CROCC2	Ciliary rootlet coiled-coil, rootletin family member 2
	LOC107132365	uncharacterized
	SNED1	Sushi, nidogen and EGF-like domains 1
	MTERF4	Mitochondrial transcription termination factor 4
	LOC112446053	uncharacterized
	PASK	PAS domain containing serine/threonine kinase
	PPP1R7	Protein phosphatase 1 regulatory subunit 7
	ANO7	Anoctamin 7
	HDLBP	High density lipoprotein binding protein
	SEPT2	Septin 2
	FARP2	FERM, ARH/RhoGEF and pleckstrin domain protein 2
4	PCLO	Piccolo presynaptic cytomatrix protein
	LOC112446518	Uncharacterized
4	TBRG4	Transforming growth factor β regulator 4
	LOC112446496	Uncharacterized
	LOC112446495	Uncharacterized
	NACAD	NAC alpha domain containing
	CCM2	Cerebral cavernous malformations 2 (malcavernin)
	LOC100140586	Uncharacterized
	LOC112446500	Uncharacterized
	LOC101904529	Uncharacterized
	MYO1G	Myosin IG
	LOC112446527	Uncharacterized
	PURB	Purine rich element binding protein B
	MIR4657	MicroRNA 4657
	H2AFV	H2A histone family member V
	PPIA	Peptidylprolyl isomerase A (cyclophilin A)
	ZMIZ2	Zinc finger MIZ-type containing 2
	LOC112446406	Uncharacterized
	OGDH	Oxoglutarate dehydrogenase
	TMED4	Transmembrane p24 trafficking protein 4
	DDX56	DEAD-box helicase 56
	NPC1L1	Niemann-Pick C1-Like 1
	NUDCD3	NudC domain containing 3
	LOC104972146	Uncharacterized
7	LOC104969022	Uncharacterized
	LOC112447534	Uncharacterized
	LOC100140403	Uncharacterized
	FER	Fer tyrosine kinase

9	CEP85L	Centrosomal protein 85 like
	TRNAV-CAC	Transfer RNA valine
	LOC112448172	Uncharacterized
	SLC35F1	Solute carrier family 35 member F1
15	NXPE2	Neurexophilin and PC-esterase domain family member 2
	LOC101908225	Uncharacterized
15	HARBI1	Harbinger transposase derived 1
	ATG13	Autophagy related 13
	ARHGAP1	Rho GTPase activating protein 1
	ZNF408	Zinc finger protein 408
	F2	Coagulation factor II (thrombin)
	CKAP5	Cytoskeleton associated protein 5
	LOC112441674	Uncharacterized
	MIR2319A	microRNA 2310A
	MIR2319B	microRNA 2319B
	LRP4	LDL receptor related protein 4
	C15H11orf49	Chromosome 15 open reading frame 49
	LOC112441656	Uncharacterized
	ARFGAP2	ADP ribosylation factor GTPase activating protein 2
	PACSIN3	Protein kinase C and casein kinase substrate in neurons 3
16	HSD11B1	Hydroxysteroid 11-beta dehydrogenase 1
	G0S2	G0/G1 switch 2
	LOC112441869	Uncharacterized
	LAMB3	Laminin subunit β3
	CAMK1G	Calcium/calmodulin-dependent protein kinase IG
	LOC104974529	Uncharacterized
	MIR205	MicroRNA 205
	LOC104974530	Uncharacterized
	LOC112441794	Uncharacterized
17	LOC112442114	Uncharacterized
18	TOX3	TOX high mobility group box family member 3
	TRNAC-ACA	Transfer RNA valine
19	CHMP6	Charged multivesicular body protein 6
	RPTOR	Regulatory associated protein of mTOR complex 1
	ENDOV	Endonuclease V
	NPTX1	Neuronal pentraxin 1
	LOC509283	Uncharacterized
20	ATP6V0E1	ATPase H+ transporting V0 subunit e1
	CREBRF	CREB3 regulatory factor
	LOC112442980	Uncharacterized
	BNIP1	BCL2 interacting protein 1
	LOC112443038	Uncharacterized
	NKX2-5	NK2 homeobox 5
	LOC104975192	Uncharacterized
	STC2	Stanniocalcin 2
	LOC107131404	Uncharacterized

20	PLPP1	Phospholipid phosphatase 1
	MTREX	MTR4 exosome RNA helicase
	DHX29	DEAH-box helicase 29
	CCNO	Cyclin O
	MCIDAS	Multiciliate differentiation and DNA sysnthesis-associated cell cycle protein
	LOC104975246	Uncharacterized
	LOC112442998	Uncharacterized
	CDC20B	Cell division cycle 208
	MIR449C	MicroRNA 449c
	MIR449B	MicroRNA 449b
	MIR449A	MicroRNA 449c
	GPX8	Glutathione peroxidase 8
	GZMA	Granzyme A
	GZMK	Granzyme K
	ESM1	Endothelial cell-specific molecule 1
29	FAT3	FAT atypical cadherin 3
	LOC112444854	Uncharacterized
	LOC112444945	Uncharacterized

Appendix Table C.3. Genes within close proximity to significant single nucleotide polymorphisms associated with average carbon dioxide production.

Chromosome	Gene name	Gene description
1	ATP1B3	ATPase Na^+/K^+ transporting subunit beta 3
	GRK7	G protein-coupled receptor kinase 7
	RNF7	Ring finger protein 7
	LOC104968752	Uncharacterized
	LOC112448294	Uncharacterized
	RASA2	RAS p21 protein activator 2
	ZBTB38	Zinc finger and BTB domain containing 38
7	TTC37	Tetratricopeptide repeat domain 37
	ARSK	Arylsulfatase K
	GPR150	G protein-coupled receptor 150
	RFESD	Ribosomal frameshift stimulation element domain containing
	SPATA9	Spermatogenesis associated 9
	RHOBTB3	RHO related BTB domain containing 3
	GLRX	Glutaredoxin
	LOC112447572	Uncharacterized
	ELL2	Elongation factor for RNA polymerase II 2
18	PHKB	Phosphorylase kinase regulatory subunit beta
	ABCC12	ATP binding cassette subfamily C member 12

Appendix Table C.4. Genes within close proximity to significant single nucleotide polymorphisms associated with average oxygen production.

Chromosome	Gene name	Gene description
1	MORC1	MORC family CW-type zinc finger 1
	C1H3orf85	Chromosome 1 open reading frame 85
	DPPA2	Developmental pluripotency associated 2
	DPPA4	Developmental pluripotency associated 2
1	ATP1B3	ATPase N+/K+ transporting subunit beta 3
	GRK7	G protein-coupled receptor kinase 7
	RNF7	Ring finger protein 7
	LOC104968752	Uncharacterized
	LOC112448294	Uncharacterized
	RASA2	RAS p21 protein activator 2
	ZBTB38	Zinc finger and BTB domain containing 38
2	LOC112443657	Uncharacterized
2	DES	Desmin
	SPEG	SPEG complex locus
	LOC513894	Uncharacterized
	GMPPA	GDP-mannose pyrophosphorylase A
	ASIC4	Acid sensing ion channel subunit 4
	CHPF	Chondroitin polymerizing factor
	TMEM198	Transmembrane protein 198
	OBSL1	Obscurin-like 1
	INHA	Inhibin subunit alpha
	STK11IP	Serine/threonine kinase 11 interacting protein
	SLC4A3	Solute carrier family 4 member 3
	LOC112442385	Uncharacterized
	LOC112443121	Uncharacterized
3	CRYZ	Crystallin zeta
	ERICH3	Glutamate rich 3
	TNNI3K	TNNI3 interacting kinase
5	LRRK2	Leucine rich repeat kinase 2
	SLC2A13	Solute carrier family 2 member 13
7	TRNAE-UUC	Transfer RNA glutamic acid
	SLCO4C1	Solute carrier organic anion transporter family member 4C1
	LOC104969005	Uncharacterized
	SLCO6A1	Solute carrier organic anion transporter family member 6A1
10	LOC107132849	Uncharacterized
	TRIM9	Tripartite motif containing 6
	TMX1	Thioredoxin related transmembrane protein 1
	FRMD6	FERM domain containing 6
20	TRNAR-GCG	Transfer RNA arginine
	LOC104975232	Uncharacterized

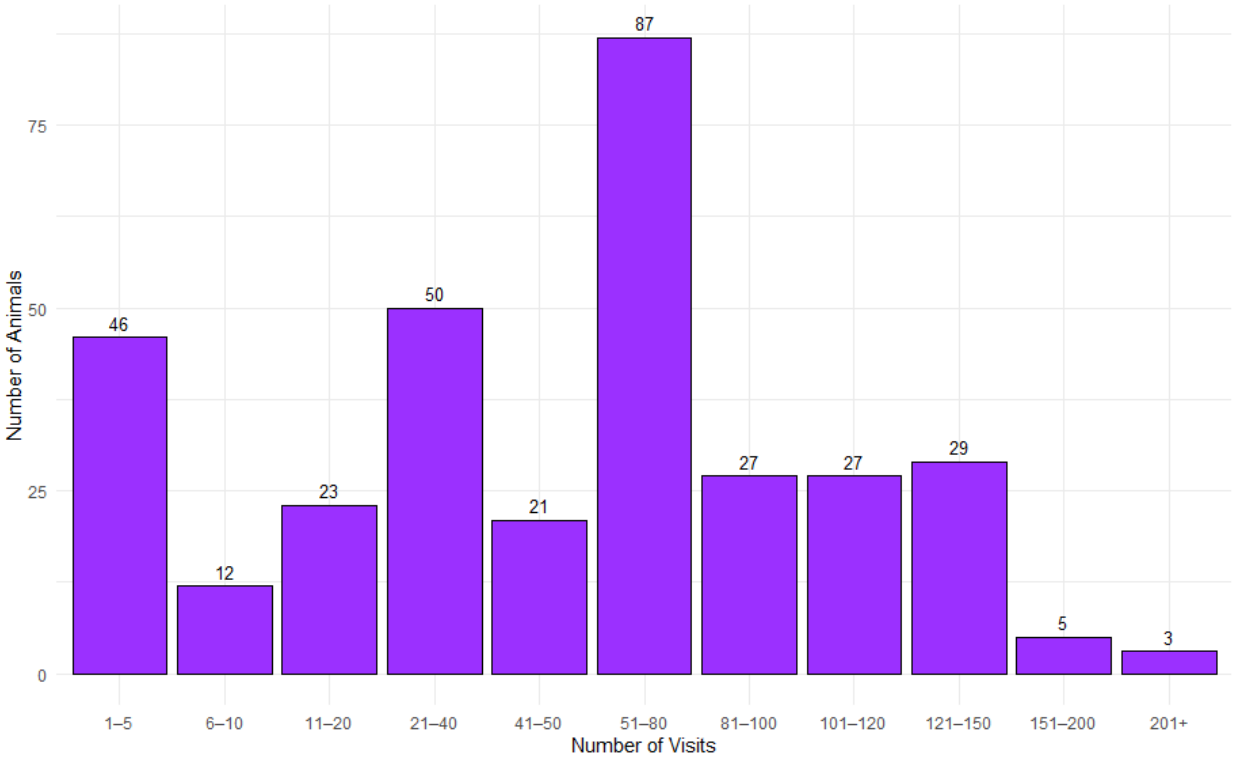
	TRNAG-CCC	Transfer RNA glycine
	LOC781741	Uncharacterized
21	LOC104975373	Uncharacterized
	OTUD7A	OTU deubiquitinase 7A
25	RBFOX1	RNA binding fox-1 homolog 1
	LOC112444378	Uncharacterized

Appendix Table C.5. Genes within close proximity to significant single nucleotide polymorphisms associated with average metabolic heat production.

Chromosome	Gene name	Gene description
1	MORC1	MORC family CW-type finger 1
	C1H3orf85	Chromosome 1 open reading frame 85
	DPPA2	Developmental pluripotency associated 2
	DPPA4	Developmental pluripotency associated 4
1	ATP1B3	ATPase Na+/K+ transporting subunit beta 3
	GRK7	G protein-coupled receptor kinase 7
	RNF7	Ring finger protein 7
	LOC104968752	Uncharacterized
	LOC112448294	Uncharacterized
	RASA2	RAS p21 protein activator 2
	ZBTB38	Zinc finger and BTB domain containing 38
2	LOC112443657	Uncharacterized
3	CRYZ	Crystallin zeta
	ERICH3	Glutamate rich 3
	TNNI3K	TNNI3 interacting kinase
4	TBRG4	Transforming growth factor β regulator 4
	LOC112446496	Uncharacterized
	LOC112446495	Uncharacterized
	NACAD	NAC alpha domain containing
	CCM2	Cerebral cavernous malformations 2
	LOC100140586	Uncharacterized
	LOC112446500	Uncharacterized
	LOC101904529	Uncharacterized
	MYO1G	Myosin IG
	LOC112446527	Uncharacterized
	PURB	Purine rich element binding protein B
	MIR4657	microRNA 4657
	H2AFV	H2H histone family member V
	PPIA	Peptidylprolyl isomerase A
	ZMIZ2	Zinc finger MIZ-type containing 2
	LOC112446406	Uncharacterized
	OGDH	Oxoglutarate dehydrogenase
	TMED4	Transmembrane p24 trafficking protein 4
	DDX56	DEAD-box helicase 56
	NPC1L1	Niemann-Pick C1-Like 1
	NUDCD3	NudC domain containing 3
	LOC104972146	Uncharacterized
7	TRNAE-UUC	tRNA glutamic acid
	SLCO4C1	Solute carrier organic anion transporter family member 4C1
	LOC104969005	Uncharacterized

	SLCO6A1	Solute carrier organic anion transporter family member 6A1
20	TRNAR-GCG	tRNA arginine
	LOC104975232	Uncharacterized
	TRNAG-CCC	tRNA glycine
	LOC781741	Uncharacterized
25	RBFOX1	RNA binding fox-1 homolog 1
	LOC112444378	Uncharacterized

Appendix Figure 4.1. Distribution of the number of visits to the GreenFeed per animal during the trial.



Appendix Figure 4.2. Distribution of the average daily GreenFeed visits per animal.