

THESIS

MODERATE GLOBAL NUTRIENT RESTRICTION DURING LATE GESTATION DID NOT  
IMPACT WETHER LAMB DEVELOPMENT, GROWTH, AND PERFORMANCE FROM  
WEANING TO HARVEST; EVALUATION OF ASSESSMENT STRATEGY ON STUDENT  
RETENTION OF KNOWLEDGE IN SEQUENTIAL ANIMAL SCIENCE COURSES

Submitted by

Alison Kuderka

Department of Animal Sciences

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2025

Master's Committee:

Advisor: Caitlin N. Cadaret

Co- Advisor: Shawn L. Archibeque

Jennifer Bennett

Copyright by Alison Marie Kuderka 2025

All Rights Reserved

## ABSTRACT

### MODERATE GLOBAL NUTRIENT RESTRICTION DURING LATE GESTATION DID NOT IMPACT WETHER LAMB DEVELOPMENT, GROWTH, AND PERFORMANCE FROM WEANING TO HARVEST; EVALUATION OF ASSESSMENT STRATEGY ON STUDENT RETENTION OF KNOWLEDGE IN SEQUENTIAL ANIMAL SCIENCE COURSES

During gestation, pregnant ewes are often managed extensively on rangeland that is not sufficient to meet the nutritional needs of the dam and the fetus, causing nutrient restriction. The performance of these offspring in the pre-weaning period has been well studied; however, there is a lack of studies investigating the effects of maternal nutrient restriction on feedlot and carcass performance of wether lambs after weaning. Thus, the objective of the first study was to investigate the post-weaning performance of lambs from ewes restricted from 110 days of gestation (dGA) to parturition at 65% of NRC requirements. Lambs from restricted dams did not differ in bodyweight or growth rate at any point from lambs born from fully nourished dams. Likewise, lambs from restricted dams did not show evidence of altered nutrient utilization during the balance trial, nor did they have any carcass differences from their control counterparts at harvest. This data demonstrates that nutrient restriction at a moderate level when following full nourishment through early and mid-gestation can be overcome without deficit when also born into a nutrient rich environment.

While formative assessment is acknowledged as a meaningful teaching strategy to improve student learning and experience, there is a lack of evidence and implementation of it in undergraduate education. Thus, the objective of the second study was to evaluate student

information retention coming from a prerequisite course divergent in assessment strategy and/or environment. The prerequisite course, ANEQ 328: Foundations of Animal Genetics, was delivered in person or online and implemented either exam or quiz-based assessments. At the end of each semester, all students received the same post-test. Furthermore, in the quiz-based courses, students were surveyed at the end of the semester to gather perceptions of learning. In the subsequent course, ANEQ 330: Principles of Animal Breeding, the same post-test from ANEQ 328 was given as a pre-test. Student final grade was greater ( $P < 0.05$ ) in the quiz-based classroom and in the online classroom. Students in the exam-based classroom performed better ( $P < 0.05$ ) on the post-test in the prerequisite course. There were no differences in pre-test score or retention across the courses. Student perceptions indicated a preference for formative assessment over summative assessment, yet regardless of classroom type, students felt they could keep up with the material and were well prepared for the subsequent course. These data indicate that both assessment strategies are effective when considering impacts on long-term retention; however, survey data showed that formative assessments are better received than summative assessments, as they help to ease testing anxiety, better pace student learning, and provide consistent feedback. Therefore, instructors may choose to use formative assessments to improve student perceptions of learning without impacting knowledge retention.

## ACKNOWLEDGEMENTS

I would like to first thank my advisor, Dr. Caitlin Cadaret, for making my graduate school experience as rich as it was. Thank you for being the best mentor and role model especially in hard moments with lots of sheep and little sleep. I could not be more grateful for your support, kindness, guidance, sass, and humor to not only finish my masters but to see me through vet school. Thank you for teaching me the value of “working with” not “for”. Thank you for helping me grow into a good scientist and build a foundation to become a good veterinarian.

Next, I would like to thank my co-advisor, Dr. Shawn Archibeque, for the opportunity to find my love for nutrition and teaching in your classroom as a student and TA, as well as for your guidance with my research. Thank you to Jenny Bennett for taking the time out of your schedule last minute to help share your expertise and passion.

I would also like to thank Sally Gallop for giving her heart and soul to caring and loving our ewes and 2022 lamb crop. Thank you for the level of care you helped hold as standard for our lambs. Thank you to the student volunteers who spent many mornings and afternoons in the summer feeding, cleaning, weighing, and wrangling the boys with me. I could not have finished my project without your help.

I want to express my gratitude to my co-grad students, Allison Vautier and Rachael Stucke. To Allison- thank you for being my other half of Al(l)ison<sup>2</sup>, for showing me the ropes of sheep without judgement despite me knowing nothing about them, and for being an amazing friend in the trenches of lambing and research. To Rachael- thank you for sharing in the hard moments, for making those moments better, and for all the laughs that made our research fun.

I would also like to thank Dr. Terry Engle for being a constant figure of support throughout all of my time in the animal sciences department and now. Thank you to Dr. Tim Holt for his deep care for our animals and for being a veterinarian to look up to.

And finally, I want to express my gratitude to my family and friends who have supported me from start to end. To Alex- thank you for always supporting my dreams. Thank you for the time spent driving out to help hold a lamb because I just needed a hand, for understanding when I was late getting home or didn't make it all together, for keeping me sane through every hard day. To my family, for always celebrating the adventures I've taken, for cheering me on from the other side of the country through grad school and now, for coming to me when I couldn't leave my sheep, for answering the phone calls to keep me awake on the drive home after being at the barn all night. And to my friends- thank you for your love, understanding, patience, and support through it all. I wouldn't have made it without you.

## DEDICATION

To the animals- past, present, and future- who will always be my greatest teachers.

## TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS .....	iv
DEDICATION.....	vi
CHAPTER 1- LITERATURE REVIEW .....	1
1.1 The United States Sheep Industry.....	1
1.3 Maternal nutrient requirements through gestation.....	4
1.4 Fetal Programming and the thrifty phenotype .....	8
1.5 Fetal Development.....	9
1.6 Lamb development.....	11
1.7 Post-weaning growth .....	12
1.7.3 Carcass characteristics .....	15
1.8 Conclusion .....	15
Figures.....	17
Literature Cited .....	20
CHAPTER 2- MODERATE GLOBAL NUTRIENT RESTRICTION DURING LATE GESTATION DID NOT IMPACT WETHER LAMB DEVELOPMENT, GROWTH, AND PERFORMANCE FROM WEANING TO HARVEST.....	36
2.1 Introduction.....	36
2.2 Materials & Methods .....	37
2.2.1 Animals and Experimental design. ....	37
2.2.6 Harvest Characteristics .....	39
2.3 Results.....	40
2.3.1 Feedlot Performance .....	40
2.3.2 Digestibility.....	40
2.3.3 Harvest. ....	40
2.4 Discussion.....	40
2.4.1 Limitations .....	44
2.5 Conclusions.....	44
Figures and tables .....	46
Literature Cited .....	50
CHAPTER 3- EVALUATION OF ASSESSMENT STRATEGY ON STUDENT RETENTION OF KNOWLEDGE IN SEQUENTIAL ANIMAL SCIENCE COURSES .....	56

3.1 Extended Introduction.....	56
3.1.1 Formation of Memory.....	56
3.1.2 Memory Consolidation .....	58
3.1.3 Assessments of Learning, For Learning, and As Learning.....	59
3.1.4 Cramming and Spacing.....	60
3.1.5 Environmental Influence.....	61
3.2 Methods.....	63
3.2.1 Informed consent of participants .....	63
3.2.2 Prerequisite course structure.....	64
3.2.3 Subsequent course structure.....	64
3.2.4. Assessment structure.....	65
3.2.5 Retention of knowledge.....	65
Perceptions of learning.....	66
3.2.6 Statistical analysis .....	66
3.3 Results.....	66
3.3.1 Short-term performance and retention .....	66
3.3.2 Long-term retention .....	67
3.3.3 Perceptions of learning .....	67
3.4 Discussion.....	68
3.5 Implications.....	72
Figures.....	73
Literature Cited .....	79

## CHAPTER 1- LITERATURE REVIEW

### *1.1 The United States Sheep Industry*

The United States (U.S.) sheep industry produces meat, milk, and wool contributing \$5.1 billion dollars in total sales between the production, processing and manufacturing sectors, as well as 22,600 jobs in 2021 (Marsh, 2023). Once a robust industry, the market for lamb has declined over time. The total number of lambs and breeding stock have continued to decline, decreasing 3.2% and 4.1%, respectively since 2016, aligning with their steady decline since the early 2000's (USDA NASS, 2024). Once comprised of 56 million head, the industry has contracted to around 5 million head of sheep from 1942 to now (Thorne et al., 2021). The contraction of the industry has been attributed to many factors such as changes in legislation around grazing lands, predation of range sheep, the shift to synthetic fiber usage, and the importation of lower cost lamb from other countries (NRC, 2007; USDA APHIS, 2014; Thorne et al., 2021). Within the industry, common top challenges include grazing and forage management, feeder lamb availability, and labor costs across all sectors (ASI, 2015). With increasing pressures on the sheep industry, making decisions that are financially conscious and that prioritize animal efficiency can ultimately help to support the U.S. market.

#### *1.1.1 The sheep production cycle*

The sheep production cycle, detailed in Figure 1, begins in the Fall as shortening days prolong melatonin production from the pineal gland and upregulates the hypothalamic-pituitary-gonadal axis (HPG; Matthews et al, 1993; Reiter et al., 2010). Signaling through the HPG increases the pulsatile release of gonadotropin releasing hormone (GnRH) increasing follicle stimulating hormone (FSH) and luteinizing hormone (LH) secretion. Together, these hormones stimulate the

ovaries in the female and testes in the male to increase the production of sex steroids, estrogen, and testosterone respectively, promoting reproductive behavior and activity (Sherwood et al., 2012). In the U.S. breeding is primarily accomplished through live cover with one or multiple rams, yet; a small population of operations may opt for laparoscopic artificial insemination (AI). Additionally, the use of a marking harness on the ram is often used in smaller operations where it is easier to observe and take note of the marked ewes to estimate a breeding date (Ganaie et al., 2009). Once bred, pregnancy detection varies by producer preference. Ultrasound around 50-90 dGA remains the predominant method (Jones et al., 2016), while blood testing as early as 30 dGA is becoming more popular. The use of ultrasound and blood tests are common, though they incur added expenses for the operation due to labor and laboratory costs.

After breeding, ewes in the western United States are often extensively managed through early and mid-gestation. Extensive systems are a low-input method using large amounts of land, that is typically unsuitable for crop farming, for grazing (Murphy et al., 2022). These ewes are largely dependent on their environment and subject to the variation of nutrient availability, weather patterns, predation, and more for the early and mid-gestational period (Goddard et al., 2006). The late gestation period is managed variably based on the operation. It is estimated that as many as 69% of lambs are born on pasture or range without human assistance (USDA APHIS, 2014). Some producers utilize intensive lambing practices, bringing lambs into a shed or barn for lambing before returning pairs to pasture (Shiels et al., 2021). Producers may also choose an intermediate approach by moving ewes to closer pens or onto better pasture in late gestation to be able to watch ewes more closely and to provide additional nutritional support (Holmøy et al., 2012). In all management strategies, within the last weeks of pregnancy, ewes should be administered vaccines and parasite prevention to protect both dams and lambs against disease (Fthenakis et al., 2012). In

preparation for lambing, some producers may choose to crutch ewes, shearing strictly around the udders and hind end for cleanliness during parturition and ease of nursing for new lambs (McGarry and Butler, 1952).

After lambing, lambs are often ear tagged, tail docked, castrated, and vaccinated in the first eight weeks of life, ideally within the first two, as younger lambs recover from this stress easier (Bell, 2010). Dams are shorn in the late spring months of May and June once the weather is warm enough, and fleeces can contribute to wool production as revenue for the flock (Goddard et al., 2006; Field and Taylor, 2015). The weaning age of lambs varies across management styles and production goals; lambs raised for meat and wool are commonly weaned between 30 days and 120 days, but lambs from dairy breeds are weaned within the first few days of life. Range ewes and lambs are sometimes allowed to wean themselves which typically occurs when the lamb is about 6 months of age (Freitas-de-Melo et al., 2022; Campbell et al., 2017). Once weaned, lambs may be sold to feedlots, packers, other producers, or retained as replacement rams and ewes (ASI, 2015).

### *1.2 Forage quality in Extensive Range Systems*

In the U.S., a considerable proportion of extensively managed sheep reside in the Southwest, Mountain, and Pacific regions with 30% of the nation's stock in Texas, California, and Colorado (Hahn 2025; USDA NASS 2024). Rangeland is characterized by limited irrigation and nutrients, and low productivity with high variation based on location and season (Havstad et al., 2009; Holechek et al., 2020) The flocks that spend significant portions of the year on rangeland are subject to the changing quality and varied availability of resources (George et al., 2001). During the winter months, plants on the range are largely dormant until the warmer temperatures and increased moisture of the spring months allow for significant growth (George et al., 2020). In this

rapid spring growth before flowering, forage has the highest quality with most nutrients available. When vegetation blooms, nutrients are directed to the flower, decreasing the nutritional value of the stems and leaves (Collins et al., 2017). After going to seed, the plant is considered mature, and the quality continues to decline into the winter months when the plant will become dormant once again (Coleman et al., 2004). In the dormant stage, the range is not nutritious enough to meet the requirements of grazing livestock and appropriate management should be taken to ensure the flock receives adequate supplementation during these months (George and Rice, 2020; USDA NRCS 2003).

### *1.3 Maternal nutrient requirements through gestation*

During gestation, maternal nutrients are used to meet the mother's own nutritional demands while also supporting the needs of the fetus and the placenta. At the time of breeding in the Fall, mature ewes should be maintained at a BCS of 2.5 to 3.5 out of 5, and ewe lambs should be 80% of their mature body weight for optimal breeding rates (Jolly and Cottle, 2010; NRC, 2007). The available forage in the fall months is typically inadequate and should be supplemented for a brief time before breeding according to the needs of the ewes in a practice called 'flushing' (Shad et al., 2011). For the first 15 of 21 weeks of pregnancy, the ewe's nutrient requirements are only slightly higher than her maintenance and increase slowly to support the development of maternal tissues and the fetus (NRC, 2007). In late gestation, the nutritional requirements increase significantly as the fetus or fetuses enter the phase of substantial growth, and the dam develops mammary tissue in preparation for lactation postpartum (Caton et al., 2019). A dam's nutritional needs may be compounded by her own body condition, maturity, number of fetuses, and stress, both maternal and fetal (Wu et al., 2006; Reynolds et al., 2010; Caton et al., 2019). Along with the use of National

Research Council (NRC) guidelines, regular monitoring of ewes to ensure ideal body condition is valuable in the prevention of over- or under conditioning.

According to the NRC, the diet for an early gestation 70 kg mature ewe with twin lambs should contain 1.69 kg of daily dry matter intake (DMI) with 0.89 kg/d total digestible nutrients (TDN) and 3.22 Mcal/d of metabolizable energy (ME). As this ewe progresses through her pregnancy to late gestation, her dietary requirements increase to 1.83 kg/d DMI with 1.21 kg/d TDN and 4.37 Mcal/d ME (NRC 2007). For yearling range ewes, their nutritional requirements increase to reflect the need to feed the still growing dam in addition to the fetus. The early gestational diet of a 70 kg yearling range ewe with twins should be 2.25 kg DMI with 1.49 kg/d TDN and 5.37 Mcal/d ME. As this ewe progresses into late gestation, her needs shift to 2.12 kg DMI with 1.69 kg/d TDN and 6.09 Mcal/d ME (NRC, 2007). Regardless of dam age or number of fetuses, as the ewe progresses through gestation the increased size of the uterus decreases ruminal capacity demanding the need for increasingly nutrient dense feed to fully support the pregnancy (Jolly and Cottle, 2010). Additional care should also be taken in adequately providing essential vitamins and minerals to prevent deficiencies for both the dam and her fetus (Masters 2018; Aliarabi 2019).

### *1.3.1 Industry standard supplementation*

As previously discussed, ewes are commonly maintained on rangeland throughout most, if not all, of gestation in the intermountain West. Throughout the year, there is a cycle to the availability and quality of forage for range livestock to live off (Squires, 2010). The forage quality available in the late fall and winter months that aligns with breeding and gestation is usually suboptimal to the needs of the dam and fetuses warranting the need for supplementation (George and Rice, 2020). In addition to availability, sheep grazing selectivity can change nutrient intake as

they show tendencies towards familiar plants and areas, potentially limiting nutrient intake in this way (Wild et al., 2023; Parnell et al., 2022). Whether due to the pasture itself or the preferences of the flock on it, grazing livestock are at risk of deficient levels of nutrition and are often supplemented to overcome potential nutritional deficits.

Commonly, supplementation to grazing sheep is provided before breeding (flushing) and in the last 4 to 6 weeks of gestation (Jolly and Cottle, 2010). The intent of flushing is to increase body condition to improve conception rates (NRC, 2007; Gunn et al., 1979). Concentrates are offered at 0.5 to 1 lb per head per day for 2 to 3 weeks before and the first 2 to 3 weeks into the season with the goal of maintaining a BCS around 3 out of 5 (ASI, 2015; Sormunen-Cristian and Jauhiainen, 2002). Increasing feed in the last 4 to 6 weeks of pregnancy is with the intent of providing the dam with significant enough nutrition to support the rapid growth of the fetus while also supporting the dam's own maternal tissue maintenance. Concentrates are fed at a rate of .5 lb to 2 lbs depending on the expected number of progeny (ASI, 2015).

### *1.3.2 Undernutrition of the dam.*

The failure to reach adequate nutrition can occur at any stage of gestation and be detrimental to the health of the dam and fetus, with the detriments being reflective of major milestones occurring at the time of insult. Undernutrition around breeding can negatively impact ovulation, conception rates, and increase the rate of early embryonic death, contributing to poor fertility (Shad et al., 2011; Hull et al., 2023; Chaturvedi et al., 2006). The lambs born from dams with poor nutrition at conception have been found to be smaller by crown rump and metacarpal lengths (Kleeman et al., 2015). When poor nutrition occurs in the early gestation period, dams have reduced body weights, altered metabolite concentrations, and longer gestations (Sosa et al., 2009; Cleal et al., 2007). Additionally, lambs born to these dams were similar in size to fully

nourished lambs at birth, but had altered glucose metabolism with increased fat deposition and decreased skeletal muscle mass (Ford, et al., 2007). Restriction isolated to early and mid-gestation decreased maternal body conditions, increased number of smaller placentomes, and reduced fetal: placental components, but did not impact fetal weights (Clarke et al., 1998; Heasman et al., 1998; Scheaffer et al., 2004). As pregnancy progresses, restriction in mid-gestation has shown increased placental weight without impact on fetal weight (McCrabb et al., 1991). Late gestation nutrient restriction resulted in decreased birth weights of restricted lambs and decreased weight, insulin concentrations, and NEFA concentrations of the dam (Gao et al., 2007). Additionally, maternal cortisol levels increased, though fetal cortisol was similar to that of the fully nourished group (Edwards and McMillen, 2001). Lambs born to late gestational nutrient restricted ewes were lighter and smaller with lighter placentas and altered muscle development (Mellor and Murray, 1982; Costello et al., 2008). These studies demonstrate the necessity for attention to maternal nutrition at all parts of gestation, to ensure the success of offspring.

### *1.3.3 Overnutrition of the dam.*

The overnutrition of dams is shown to also be related to difficulties concerning conception, pregnancy, and fetal outcomes. Ewes of high body condition scores do not benefit from flushing in the breeding season (Rankins and Pugh, 2011), and in fact, early overnutrition reduces placental weights and nutrient delivery to the fetus by late gestation (Redmer et al., 2009). However, when overnutrition begins in early gestation, lambs born to these ewes have demonstrated similar body weights, organ sizes, and muscle area when compared to adequately nourished lambs (Pillai et al., 2017). Alterations in placental angiogenesis occur during mid-gestational overnutrition, ultimately causing reduced birth weights due to placental insufficiency (Redmer et al., 2005; Wallace et al., 2004). Similarly, when overfeeding ewes in late gestation, fetal growth is impaired resulting in

low birthweights (Matsuzaki et al., 2006; Wallace et al., 2002). Over conditioned (BCS > 4.0) and under conditioned (BCS < 2.0) ewes are at risk of developing pregnancy toxemia, characterized by excessive mobilization of fat stores and high levels of ketones (Kelay and Assefa, 2018). Lastly, indicators of healthy gestation, including colostrum quality and gestation length, are reduced while spontaneous abortions and neonatal mortality increase in dams with high feed intake (Wallace, 2007).

#### *1.4 Fetal Programming and the thrifty phenotype*

A heavy emphasis should be placed on the proper nutritional management of dams to allow for the fetus, placenta, and maternal tissues to develop and grow correctly at every stage to result in a successful pregnancy (Fthenakis et al., 2012). When needs are not adequately met, fetal programming can occur and change the physiological performance of that lamb in the long-term (Kenyon and Blair, 2014; Greenwood and Bell, 2019; Reynolds et al., 2019). Inadequate nutrition of the dam causes competition for the allocation of those nutrients between the fetus, placenta, and the dam herself. In the face of insufficient nutrition, the blood flow to the placenta can be compromised, causing placental stunting and further decreasing the available nutrients to the fetus (Reynolds et al., 2006; 2010). To adapt, nutrients in the fetus are shunted to support vital organs such as the heart and brain, while other tissues develop at a deficit causing issues once born (Hales and Barker, 2001; Zhu et al., 2006; Sartori et al., 2020). Aberrant metabolism, muscle and adipose development, and organ growth are present in these offspring (Reed et al., 2014; Raja et al., 2016; Hoffman et al., 2016; Vautier and Cadaret, 2022; Barcellos et al., 2024).

In concert with fetal programming during gestation, the thrifty phenotype hypothesis attempts to explain the connection between poor neonatal growth and metabolic complications into adulthood (Hales and Barker, 2001). This theory ascertains that offspring of nutrient

challenged dams develop a metabolism that is efficient at storing nutrients and well suited for living in the same nutrient-challenged state the individual experienced in-utero. Yet, when born into a nutrient-rich environment, they experience shortfalls due to adaptive tissue development and function. Adaptive tissue development present in the lamb as metabolic dysfunction (Rezende et al., 2014; Veiga-Lopez et al., 2013), increased adipose deposition (Ford et al., 2007; Du et al., 2010), and decreased muscle development (Zhu et al., 2006; Lemley et al., 2012). Often, these offspring are born into those nutrient rich environments, and the available nutrition exceeds their metabolic capacity resulting in increased risk for altered body composition, asymmetrical growth, and metabolic dysfunction persisting throughout their life (Baig et al., 2011; Khanal et al., 2016; Rhodes et al., 2009).

### *1.5 Fetal Development*

Early gestation is marked by embryogenesis, maternal recognition of pregnancy, implantation, and placentation. Following the formation of the zygote, cleavage divisions occur to form the blastocyst which is defined by two distinct populations of cells; the inner cell mass which will become the fetus and the trophoblasts which will become the fetal portion of the placenta called the chorion (Senger, 2012). Once it has entered the uterus, the early embryo signals its presence to maternal tissues by releasing interferon tau to promote the maintenance of the corpus luteum and progesterone synthesis (Spencer and Bazer, 2004). The layers of the embryo are further differentiated into the ectoderm, mesoderm, and endoderm in a process referred to as gastrulation (Hue et al., 2007). Each germinal layer has its own distinct set of organs that arise. The ectoderm will form the outermost organs such as skin, eyes, ears, brain, and mammary glands (Pispa and Thesleff, 2003). The mesoderm forms bones, muscle, cartilage, and connective tissue to build the musculoskeletal system as well as the cardiovascular and reproductive systems (Ferretti and

Hadjantonakis, 2019). The endoderm form parts of the digestive and respiratory systems as well as specialized organs such as the thyroid and parathyroid glands (Zorn and Wells, 2009).

Midgestational development is characterized by organogenesis, the process of developing the germinal layers into functional organs. Oxygenation and nutrition of the fetus increases as placental vasculature develops and reaches peak size, supporting the growth of the heart, brain and liver (Solomonson et al., 2022; Thion et al., 2018). Primary and secondary muscle fibers are sensitive to nutritional conditions during their development, altering their number, proportion and metabolism when faced with insufficient nutrients (Bee, 2004; Yates et al., 2012). A small amount of adipose tissue development will begin as well, but most will develop in late gestation (Symonds et al., 2012). Despite mid-gestation being overlooked as an important timepoint to supplement during production, a substantial amount of development takes place in this period that is critical to the success of the neonate.

Until late gestation, the fetus remains relatively small, with the first two thirds of pregnancy prioritizing appropriate development of all tissue types. Approximately 70% of fetal growth occurs in late gestation, marked by brown adipose tissue development and hypertrophy of organs in preparation for parturition (Symonds et al., 2012; Robinson et al., 1977). Final muscle development occurs with the increase of fiber size, formation of satellite cells, and intramuscular adipocytes (Du et al., 2010). Myogenesis only takes place in utero and negative impacts to muscle development cannot be compensated for in postnatal life. At the end of gestation, the fetal portion of the placenta stimulates the beginning of parturition by releasing corticotropic releasing hormone (CRH) into circulation, signals to produce ACTH from the anterior pituitary and upregulate cortisol production from the fetal adrenal glands (Senger, 2012; Sherwood et al., 2012). Increased

cortisol promotes conversion of progesterone into estradiol and stimulates the release of PGF<sub>2a</sub> to begin labor (Poore et al., 1998).

### *1.6 Lamb development*

The neonatal period is a delicate time for lambs and their success, or lack thereof, can dictate the performance of that offspring for the rest of their life. About half of lamb mortality in the pre-weaning period happens in the first 24 hours of life (Dwyer, 2008). In this first day, lambs need to bond with and nurse from their dams, while also drying off and thermoregulating appropriately (Nowak et al., 2000). Early interactions between lamb and dam should help build a strong bond to drive the dam's desire to support her young (Nowak and Poindron, 2006). The dam should lick and clean off her offspring to dry them and stimulate them (Alexander, 1988). Subsequently, once the lamb is up, the dam should be willing to let them nurse, providing colostrum to the neonate. Prior to consuming colostrum, lambs utilize shivering thermogenesis along with their brown adipose tissue stores for non-shivering thermogenesis, but these stores are limited, making it crucial to be able to nurse (Plush et al., 2016). Colostrum is the first milk produced from the dam which is valuable both to the lamb's hydration, nutrition, and immunity. Colostrum contains active immunoglobulins which provide immunological protection for the lamb for its first several weeks of life along with hormones, growth factors, enzymes, and neuroendocrine peptides (Agenbag et al., 2021; Nowak and Poindron, 2005). After the first 24 hours, colostrum production converts to milk production and will support the lamb's dietary needs for the next several weeks.

As a newborn, a lamb's digestive tract functions as a monogastric with an underdeveloped rumen and predominant abomasum. When they suckle, the physical motion engages ridges of tissue that act as a tube from the esophagus through the first three chambers of the stomach to

deliver milk directly to the glandular abomasum (Goda et al., 2017; Lalatta-Costerbosa et al., 2011). The esophageal or gastric groove keeps large volumes of milk from fermenting in the rumen which can cause health issues in young neonates (Kaba et al., 2018). From 3 to 8 weeks of age, lambs will start to eat solid feedstuffs in its environment, picking at forages and concentrates, which will begin to develop the microbiome of the rumen by bacterial colonization (Li et al., 2022; Abou-Ward, 2008). Rumen microbes are essential in the ability to digest complex plant materials into volatile fatty acids (VFAs), a primary energy source for ruminants (Henderson et al., 2015).

### *1.7 Post-weaning growth*

The industry has a varied approach and timeline to weaning depending on management style and purpose of the lambs. Weaning is a notably stressful event for lambs, marking the permanent physical separation of dam and lamb, and the conversion of the lamb off milk to a fully solid diet (Damián et al., 2013). Weaning is often done by an abrupt physical separation of the dams and lambs, the stress from which is a significant cause of decreased growth in the newly weaned lambs (Frietas-de-Melo et al., 2022). Lambs are more susceptible to disease during the weaning period due to high cortisol and lower levels of IGF-1 (McCoard et al., 2020; Mears and Brown, 1997). Increased observation in the days following weaning is useful in detecting illness and quick care can help minimize the detriment of disease during this time.

After rebounding from the stress of weaning, lambs' growth rates begin to taper off as physical maturity is reached (Field and Taylor, 2015). Ewe lambs will start to reach puberty once they reach 50 to 80% of their mature body weight while ram lambs reach puberty sooner, around 35 to 65% of their mature weight (Nieto et al., 2013; Dyrmondsson, 1973). At this point, lambs may be retained in the flock or sold as replacement breeding stock and can be used in the breeding cycle once they reach puberty (Nieto et al., 2013).

### *1.7.1 Feedlot efficiency*

After weaning, the feedlot is an option for ewe and wether lambs to finish growing before slaughter, with the intent of adding weight and fat to produce higher quality meat (Duddy et al., 2016). The lambs enter an intensive management system which is characterized by using dry lots and feeding concentrate diets intended to raise sheep in smaller spaces (Kochewad et al., 2017). Once acclimated to the feedlot, lambs are transitioned from their roughage-based diets, typically fed during the preweaning period, to a grain-based diet that meets all nutritional needs and supports high rates of growth needed to finish lambs (Campbell, 2017). Ideally, lambs spend about 40-60 days at the feedlot, gaining 0.5 to 0.8 lb per head per day (Field and Taylor, 2015), to reach a market weight of about 55 to 70 kgs (Bradford et al., 2003; Field and Taylor, 2015). Lambs are offered a diet composed of grain, roughage, vitamins, and minerals that meets all their nutrient requirements for growth (Duddy et al., 2016). A finishing ration for 110 lb lambs with the goal of gaining 0.45 lb per head per day should be formulated to feed 3.5 lb DMI with 2.7 lb TDN, 4.4 Mcal ME, and 0.35 lb crude protein (CP) on a dry matter basis (Field and Taylor, 2015; NRC 2007). In forming a complete diet for sheep in the feedlot, care should be taken in balancing calcium and phosphorus ratios for the risk of urinary calculi, copper, and molybdenum to mitigate copper toxicity and thiamin for the concern of polioencephalomalacia (NRC, 2007). Monitoring growth and feeding is important to ensure adequate nutrition; the amount of feed should increase as lambs grow to properly support their maintenance needs. Outside of performance studies focused on improving weaning (Campbell et al., 2017; Karakus 2014; Freitas-de-Melos et al., 2022; Wang et al., 2019) and how lambs perform on specific feedstuffs or supplementations (Saleem et al., 2016; Ramos et al., 2020; Izuddin et al., 2019), there is little research that observes the performance of gestationally nutrient restricted wether lamb in the feedlot setting and at

slaughter. Shipping to slaughter is another notably stressful event for lambs and can have a significant impact on the quality of the carcass produced. Adequate space on the trailer, non-slip clean footing, moderate temperatures and short transportation times should be achieved whenever possible (Ivanov, 2022). Good husbandry and low-stress handling should be prioritized to minimize muscle acidification and bruising (Hopkins, 2014; Gallo et al., 2018; Cockram and Velarde, 2022).

### *1.7.2 Wether lamb metabolism*

The uniqueness of the ruminant's gastrointestinal tract is the key to their ability to graze and successfully utilize poor-quality rangelands to produce quality meat and wool. The rumen and its microbiome function to ferment and upcycle the value of ingested nutrients to be valuable to the sheep. The rumen microbes consist largely of bacteria and protozoa that function best in a slightly acidic, anaerobic environment with ratios of the microbiota shifting depending on the diet (Cottle, 2010). The microbes are responsible for the conversion of structural plant carbohydrates into the desired end product: acetate, propionate, and butyrate. In addition to the VFAs, byproducts of fermentation such as carbon dioxide, methane, and heat are also produced (Waters et al., 2025). VFAs are the major energy source for ruminants, rather than glucose as seen in non-ruminants, with each being used at various stages of metabolism. Propionate can enter the Krebs's cycle or be used in gluconeogenesis for glucose production (Bademkiran et al., 2008) while acetate and butyrate are used as precursors to lipid synthesis (Wallace and Metallo, 2020). In addition to VFA production, microbes also provide microbial crude protein (MCP) as a source of protein to the animal when bacteria die (Walker et al., 1975).

Outside of the acknowledged differences, digestion and metabolism in ruminants looks relatively similar to that in a non-ruminant. After nutrient digestion in the rumen, abomasum, and

small intestine, nutrients are absorbed from the gut at the small intestine mostly. In the maturing wether in the feedlot, nutrients are allocated between maintenance and growth needs while also promoting gain. Maintenance needs include supporting basal metabolism and day to day energy requirements (McDonald et al., 2011; Yang et al., 2020). Though growth slows in the post weaning period, feedlot lambs also need to be supported in growth and weight gain in the form of increased fat deposition and muscle formation to reach market weight.

### *1.7.3 Carcass characteristics*

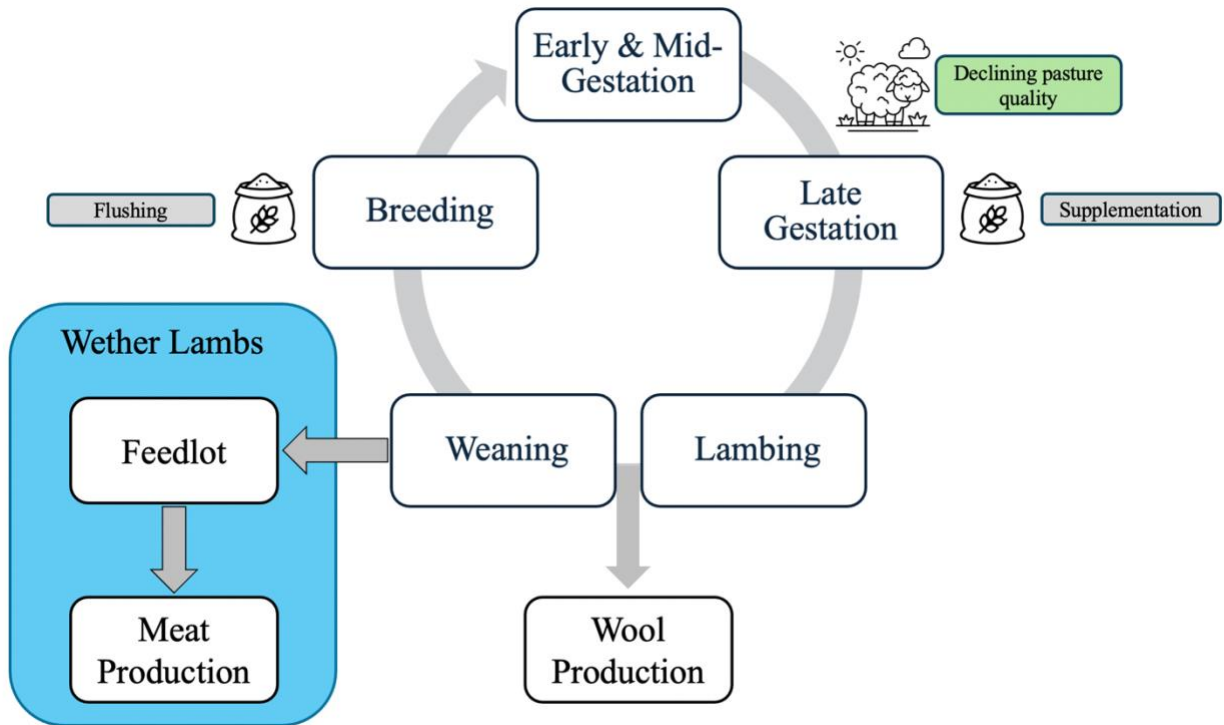
At slaughter, the quality of the carcass is determined by fat thickness, yield grade, and carcass weight (Prache et al., 2022; Corazzin et al., 2019). Carcass composition is the ratio of muscle, fat, and bone of an animal at harvest. The quality and quantity of the carcass is dependent on factors such as breed, age, sex, and production management (Irshad et al., 2013) Nutrition is significant to developing a quality carcass as it dictates the ability to grow and gain. Carcasses are graded for quality and yield based on standards set by the USDA. Quality grades consist of prime, choice, good, and utility grades which are determined by maturity, conformation of the carcass, and flank streaking (marbling). Yield grades are based on a scale of 1-5 and are determined by the backfat thickness over the ribeye muscle (USDA, 1992; Ramirez-Retamal and Morales, 2014). From these grades, value is assigned to the carcass, and they are further processed into retail cuts for consumption. Carcasses of nutrient restricted offspring have resulted in lower carcass yields, reduced loin muscle area and increased fat mass at the time of slaughter (Piaggio et al., 2018; Lemley et al., 2012; Larson et al., 2009).

### *1.8 Conclusion*

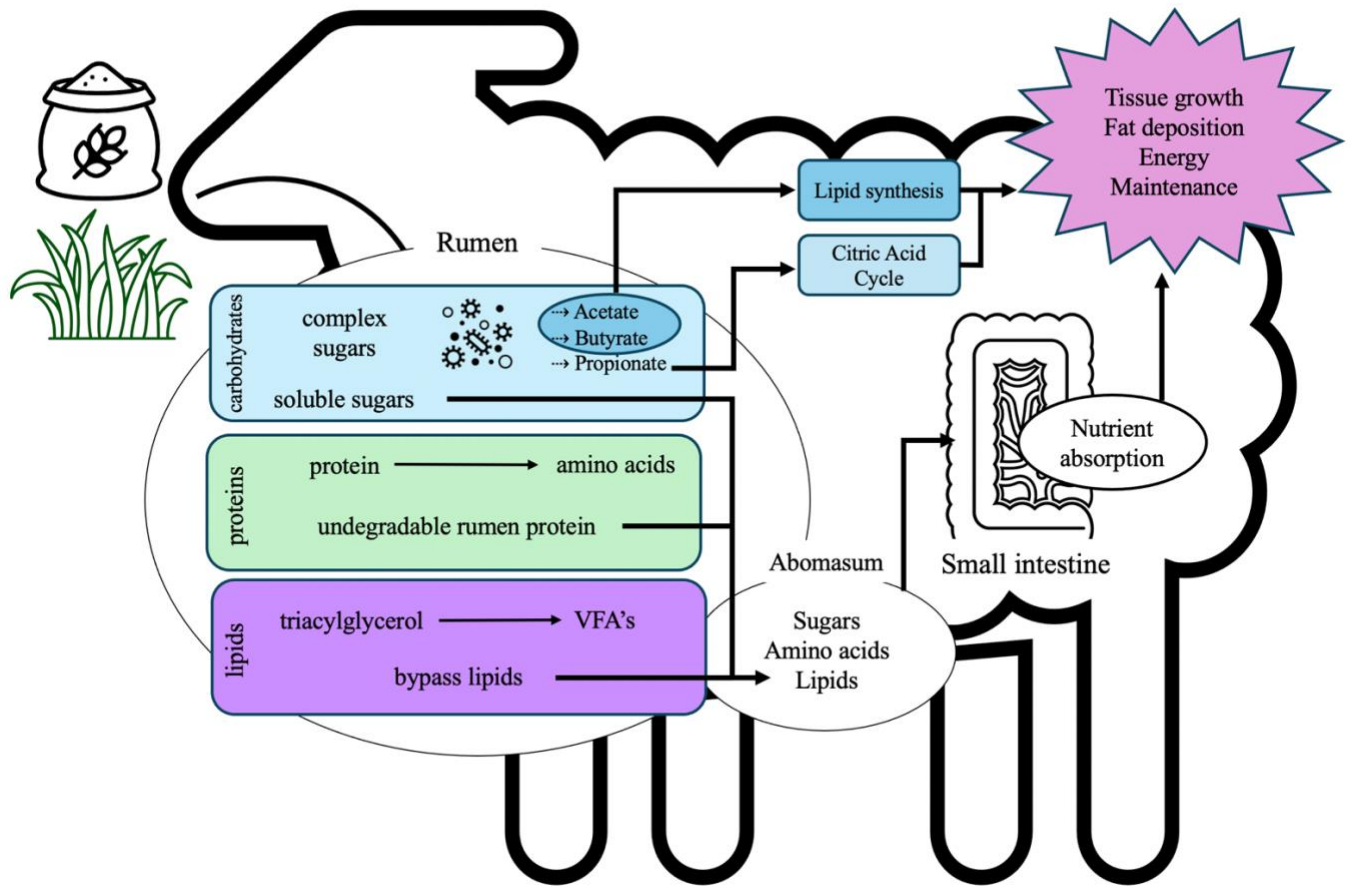
Maternal nutrition is a key factor in the physiological success of offspring, as it has significant impacts on the growth and development of lambs well before they are born and may

have long lasting impacts into adulthood. As increasing studies investigate the range of effects fetal programming can have, an understanding of the duration and significance of these effects needs to be pursued to better understand the care needed to prevent negative repercussions of poor maternal nutrition. While many studies focus on severe restriction levels, studies reflecting locally relevant information are lacking, leaving producers with data that is not applicable to many of their operations. Outcomes of maternal nutritional challenge can affect the subsequent generation and negatively impact the profitability of the crop. Offspring from nutrient restricted dams may have altered adipose and muscle tissue metabolism, rates of gain, and carcass quality resulting in slower growing lambs with inferior quality carcasses, however, outcomes depend on timing, duration, and severity of insult. Little is known about the impact of nutrient restriction during late gestation on the postweaning consequences and carcass performance of the offspring. It is important that the impact of traditional feeding strategies be understood to be able to inform producers of the long-term outcomes of their management strategies and identify how prenatal care impacts the success of offspring for the betterment of the industry.

Figures



**Figure 1.** The sheep production cycle with interest in wether lamb production



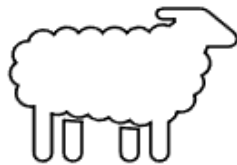
**Figure 2.** Overview of wether lamb metabolism and nutrient utilization

## Impacts of Severe Maternal Undernutrition



### Fetal Response:

- ↓ Adipogenesis
- ↓ Myogenesis
- Δ Organ Development



### Lamb response:

- ↓ birthweight
- ↓ metabolism
- ↓ skeletal muscle



### Carcass response:

- ↓ carcass yield
- ↓ loin eye area
- ↑ fat thickness

**Figure 3.** The outcomes of severe maternal undernutrition in the fetus, offspring, and carcass.

### *Literature Cited*

- Abou-Ward, G. 2008. Effect of pre-weaning diet on lamb's rumen development. *American-Eurasian Journal of Agricultural and Environmental Science* 3:561–567.
- Agenbag, B., A. M. Swinbourne, K. Petrovski, and W. H. van Wettere. 2021. Lambs need colostrum: A review. *Livestock Science*. 251:104624.
- Alexander, G. 1988. What makes a good mother: components and comparative aspects of maternal behaviour in ungulates. *Australian Society of Animal Production*. 17:25-41
- Aliarabi, H., A. Fadayifar, R. Alimohamady, and A. H. Dezfoulian. 2019. The effect of maternal supplementation of zinc, selenium, and cobalt as slow-release ruminal bolus in late pregnancy on some blood metabolites and performance of ewes and their lambs. *Biological trace element research* 187:403–410.
- APHIS, U. 2014. Lambing Management Practices on U.S. Sheep Operations.
- Association, A. S. I., and S. I. D. Program. 1992. Sheep production handbook. American Sheep Industry Association.
- Bademkiran, S., B. Yokus, H. Icen, U. Cakir, and D. Kurt. 2008. Assessment of Serum Mineral and Certain Biochemical Variables in Self-Sucking Dairy Cows. *Journal of Animal and Veterinary Advances*. 7
- Baig, U., P. Belsare, M. Watve, and M. Jog. 2011. Can thrifty gene (s) or predictive fetal programming for thriftiness lead to obesity? *Journal of obesity*. 2011(1):861049.
- Barcellos, J. O. J., D. Zago, H. X. Fagundes, G. R. Pereira, and E. D. Sartori. 2024. Foetal programming in sheep: Reproductive and productive implications. *Animal Reproduction Science* 265:107494.
- Bee, G. 2004. Effect of early gestation feeding, birth weight, and gender of progeny on muscle fiber characteristics of pigs at slaughter. *Journal of Animal Science* 82(3):826–836.

- Bell, K. 2010. Sheep management. *International sheep and wool handbook*:407–411.
- Bradford, D., J. McConkey, R. B. Levalley, L. Allen, R. Allen, B. Farmer, and J. Sperry. 2003. Rocky Mountain woolies: Raising sheep in the new West. *Rangelands* 25(1):16-22
- Campbell, B., A. Pullin, M. Pairis-Garcia, J. McCutcheon, G. Lowe, M. Campler, and F. Fluharty. 2017. The effects of alternative weaning strategies on lamb health and performance. *Small Ruminant Research* 156:57–65.
- Caton, J. S., M. S. Crouse, L. P. Reynolds, T. L. Neville, C. R. Dahlen, A. K. Ward, and K. C. Swanson. 2019. Maternal nutrition and programming of offspring energy requirements. *Translational Animal Science* 3(3):976–990.
- Chaturvedi, O., R. Bhatta, D. Verma, and N. Singh. 2006. Effect of flushing on nutrient utilization and reproductive performance of ewes grazing on community rangeland. *Asian-Australasian Journal of Animal Sciences* 19(4):521–525.
- Clarke, L., L. Heasman, D. T. Juniper, and M. E. Symonds. 1998. Maternal nutrition in early-mid gestation and placental size in sheep. *British Journal of Nutrition* 79(4):359–364.
- Cleal, J. K., K. R. Poore, J. P. Newman, D. E. Noakes, M. A. Hanson, and L. R. Green. 2007. The effect of maternal undernutrition in early gestation on gestation length and fetal and postnatal growth in sheep. *Pediatric Research* 62(4):422–427.
- Cockram, M., and A. Velarde. 2022. Sheep, Preslaughter handling and slaughter of meat animals. Wageningen Academic. p. 267–310.
- Coleman, S. W., J. E. Moore, and J. R. Wilson. 2004. Quality and utilization. Warm-season (C4) grasses 45:267–308.
- Collins, M., Y. C. Newman, C. Nelson, R. Barnes, and K. Moore. 2017. Forage quality. *Forages* 1:269–286.

- Corazzin, M., S. Del Bianco, S. Bovolenta, and E. Piasentier. 2019. Carcass characteristics and meat quality of sheep and goat. More than beef, pork and chicken—the production, processing, and quality traits of other sources of meat for human diet:119–165.
- Costello, P. M., A. Rowleron, N. A. Astaman, F. E. W. Anthony, A. A. Sayer, C. Cooper, M. A. Hanson, and L. R. Green. 2008. Peri-implantation and late gestation maternal undernutrition differentially affect fetal sheep skeletal muscle development. *The Journal of physiology* 586(9):2371–2379.
- Cottle, D. J. 2010. *International sheep and wool handbook*. Nottingham University Press.
- Damián, J., M. Hötzel, G. Banchemo, and R. Ungerfeld. 2013. Behavioural response of grazing lambs to changes associated with feeding and separation from their mothers at weaning. *Research in veterinary science* 95(3):913–918.
- Du, M., J. Tong, J. Zhao, K. R. Underwood, M. Zhu, S. P. Ford, and P. W. Nathanielsz. 2010. Fetal programming of skeletal muscle development in ruminant animals<sup>1</sup>. *Journal of Animal Science* 88(suppl\_13):E51–E60.
- Duddy, G., C. Shands, A. Bell, R. Hegarty, and G. Casburn. 2016. *Feedlotting lambs*. NSW Department of Primary Industries: Orange
- Dwyer, C. 2008. The welfare of the neonatal lamb. *Small Ruminant Research* 76(1-2):31–41.
- Dyrmundsson, O. 1973. Puberty and early reproductive performance in sheep. II. Ram lambs. *Commonwealth Bureau of Animal Breeding and Genetics* 41(9):419-430
- Edwards, L. J., and I. McMillen. 2001. Maternal undernutrition increases arterial blood pressure in the sheep fetus during late gestation. *The Journal of physiology* 533(2):561–570.
- Ferretti, E., and A.K. Hadjantonakis. 2019. Mesoderm specification and diversification: from single cells to emergent tissues. *Current opinion in cell biology* 61:110–116.

- Field, T. G., and R. E. Taylor. 2015. *Scientific Farm Animal Production: An Introduction to Animal Science*. 11<sup>th</sup> edition. Pearson Prentice Hall, Boston.
- Ford, S. P., B. W. Hess, M. M. Schwope, M. J. Nijland, J. S. Gilbert, K. A. Vonnahme, W. J. Means, H. Han, and P. W. Nathanielsz. 2007. Maternal undernutrition during early to mid-gestation in the ewe results in altered growth, adiposity, and glucose tolerance in male offspring<sup>1</sup>. *Journal of Animal Science* 85(5):1285–1294.
- Freitas-de-Melo, A., A. Orihuela, M. J. Hötzel, and R. Ungerfeld. 2022. What do we know and need to know about weaning in sheep? An overview of weaning practices, stress and welfare. *Frontiers in Animal Science* 3:823188.
- Fthenakis, G., G. Arsenos, C. Brozos, I. Fragkou, N. Giadinis, I. Giannenas, V. Mavrogianni, E. Papadopoulou, and I. Valasi. 2012. Health management of ewes during pregnancy. *Animal reproduction science* 130(3-4):198–212.
- Gallo, C., J. Tarumán, and C. Larrondo. 2018. Main factors affecting animal welfare and meat quality in lambs for slaughter in Chile. *Animals* 8(10):165.
- Ganaie, B. A., M. Z. Khan, R. Islam, D. M. Makhdoomi, S. Qureshi, and G. M. Wani. 2009. Evaluation of different techniques for pregnancy diagnosis in sheep. *Small Ruminant Research* 85(2):135–141.
- Gao, F., Y. Liu, and X. Hou. 2009. Effect of maternal undernutrition during late pregnancy on growth and development of ovine fetal visceral organs. *Asian-Australasian Journal of Animal Sciences* 22(12):1633–1639.
- George, M., J. Harper, J. Davy, T. Becchetti, and G. Maier. 2020. Ecology and management of annual rangelands series: Livestock production. University of California, Division of Agriculture and Natural Resources. 7:1-23.

- George, M., G. Nader, and J. Dunbar. 2001. Balancing beef cow nutrient requirements and seasonal forage quality on annual rangeland. University of California, Division of Agriculture and Natural Resources. 8021.
- George, M., and K. Rice. 2020. Ecology and Management of Annual Rangelands Series: Range Plant Growth and Development. University of California, Division of Agriculture and Natural Resources. 5:1-18.
- Goda, N., W. El-Raheem, H. Salem, and D. Alsadek. 2017. Postnatal development on gastric groove of small ruminants. *Journal of Animal and Veterinary Advances* 16(8-12):101–107.
- Goddard, P., T. Waterhouse, C. Dwyer, and A. Stott. 2006. The perception of the welfare of sheep in extensive systems. *Small Ruminant Research* 62(3):215–225.
- Greenwood, P. L., and A. W. Bell. 2019. Developmental programming and growth of livestock tissues for meat production. *Veterinary Clinics: Food Animal Practice* 35(2):303–319.
- Gunn, R., J. Doney, and W. Smith. 1979. Fertility in Cheviot ewes. 3. The effect of level of nutrition before and after mating on ovulation rate and early embryo mortality in South Country Cheviot ewes in moderate condition at mating. *Animal Science* 29(1):25–31.
- Hahn, W. 2025. Sheep, Lamb, Mutton- Sector at a Glance.
- Hales, C. N., and D. J. P. Barker. 2001. The thrifty phenotype hypothesis: Type 2 diabetes. *British Medical Bulletin* 60(1):5–20.
- Havstad, K., D. Peters, B. Allen-Diaz, J. Bartolome, B. Bestelmeyer, D. Briske, J. Brown, M. Brunson, J. Herrick, and L. Huntsinger. 2009. The western United States rangelands: a major resource. *Grassland quietness and strength for a new American agriculture.* p. 75–93.

- Heasman, L., L. Clarke, K. Firth, T. Stephenson, and M. E. Symonds. 1998. Influence of restricted maternal nutrition in early to mid gestation on placental and fetal development at term in sheep. *Pediatric Research* 44(4):546–551.
- Henderson, G., F. Cox, S. Ganesh, A. Jonker, W. Young, and P. H. Janssen. 2015. Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. *Scientific reports* 5(1):14567.
- Hoffman, M., K. Peck, M. Forella, A. Fox, K. Govoni, and S. Zinn. 2016. The effects of poor maternal nutrition during gestation on postnatal growth and development of lambs. *Journal of animal science* 94(2):789–799.
- Holechek, J. L., H. M. Geli, A. F. Cibils, and M. N. Sawalhah. 2020. Climate change, rangelands, and sustainability of ranching in the Western United States. *Sustainability* 12(12):4942.
- Holmøy, I. H., C. Kielland, S. M. Stubsjøen, L. Hektoen, and S. Waage. 2012. Housing conditions and management practices associated with neonatal lamb mortality in sheep flocks in Norway. *Preventive Veterinary Medicine* 107(3-4):231–241.
- Hopkins, D. 2014. Beef processing and carcass and meat quality. *Beef Cattle Production and Trade* p. 14–46.
- Hue, I., S. Degrelle, E. Champion, and J. Renard. 2007. Gene expression in elongating and gastrulating embryos from ruminants. *Society of Reproduction and Fertility Supplement* 64:365.
- Hull, J., C. Neillans, and E. Canavan-Hicks. 2023. Fertility management of sheep and optimising flock returns. *In Practice* 45(7):410–419.
- Irshad, A., G. Kandeepan, S. Kumar, K. Ashish, M. Vishnuraj, and V. Shukla. 2013. Factors influencing carcass composition of livestock: A review. *J. Anim. Prod. Adv* 3(1):1.

- Ivanov, N. T. 2020. Sheep welfare during transport and slaughter in Bulgaria-Impact of welfare on slaughter carcass and meat quality: a review. *Turkish Journal of Veterinary & Animal Sciences* 44(2):174–181.
- Izuddin, W. I., T. C. Loh, A. A. Samsudin, H. L. Foo, A. M. Humam, and N. Shazali. 2019. Effects of postbiotic supplementation on growth performance, ruminal fermentation and microbial profile, blood metabolite and GHR, IGF-1 and MCT-1 gene expression in post-weaning lambs. *BMC veterinary research* 15:1–10.
- Jolly, S., and D. Cottle. 2010. Feeding. *International Sheep and Wool Handbook* (ed. DJ Cottle) Nottingham University Press, Nottingham
- Jones, A. K., R. E. Gately, K. K. McFadden, S. A. Zinn, K. E. Govoni, and S. A. Reed. 2016. Transabdominal ultrasound for detection of pregnancy, fetal and placental landmarks, and fetal age before Day 45 of gestation in the sheep. *Theriogenology* 85(5):939–945.
- Kaba, T., B. Abera, and T. Kassa. 2018. Esophageal groove dysfunction: a cause of ruminal bloat in newborn calves. *BMC veterinary research* 14:1–5.
- Karakus, F. 2014. Weaning stress in lambs. *Journal of International Scientific Publications: Agriculture & Food* 2:165–170.
- Kelay, A., and A. Assefa. 2018. Causes, Control and Prevention Methods of Pregnancy Toxemia in Ewe: A Review. *Journal of Life Science and Biomedicine* 8(4):69–76.
- Kenyon, P., and H. Blair. 2014. Foetal programming in sheep—effects on production. *Small Ruminant Research* 118(1-3):16–30.
- Khanal, P., L. Johnsen, A. M. D. Axel, P. W. Hansen, A. H. Kongsted, N. B. Lyckegaard, and M. O. Nielsen. 2016. Long-term impacts of foetal malnutrition followed by early postnatal obesity on fat distribution pattern and metabolic adaptability in adult sheep. *PloS One*. 11(6):e0156700.

- Kleemann, D. O., J. M. Kelly, S. R. Rudiger, I. C. McMillen, J. L. Morrison, S. Zhang, S. M. MacLaughlin, D. H. Smith, R. J. Grimson, K. S. Jaensch, F. D. Brien, K. J. Plush, S. Hiendleder, and S. K. Walker. 2015. Effect of periconceptual nutrition on the growth, behaviour and survival of the neonatal lamb. *Animal Reproduction Science* 160:12–22.
- Kochewad, S., L. Meena, S. Kumar, V. Kumar, and L. Meena. 2017. Sheep Rearing Systems and their Productive Performances—A Review. *Trends in Biosciences* 10(9):1716–1719.
- Lalatta-Costerbosa, G., P. Clavenzani, G. Petrosino, and M. Mazzoni. 2011. An immunohistochemical study of the distribution of nitric oxide synthase-immunoreactive neurons and fibers in the reticular groove of suckling lambs. *Journal of Anatomy* 218(4):439–448.
- Larson, D., J. Martin, D. C. Adams, and R. N. Funston. 2009. Winter grazing system and supplementation during late gestation influence performance of beef cows and steer progeny. *Journal of Animal Science* 87(3):1147–1155.
- Lemley, C. O., A. M. Meyer, L. E. Camacho, T. L. Neville, D. J. Newman, J. S. Caton, and K. A. Vonnahme. 2012. Melatonin supplementation alters uteroplacental hemodynamics and fetal development in an ovine model of intrauterine growth restriction. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 302(4):R454–R467.
- Li, C., Q. Zhang, G. Wang, X. Niu, W. Wang, F. Li, F. Li, and Z. Zhang. 2022. The functional development of the rumen is influenced by weaning and associated with ruminal microbiota in lambs. *Animal biotechnology* 33(4):612–628.
- Marsh, D. 2023. U.S. Sheep Industry Economic Contribution Analysis.
- Masters, D. G. 2018. Practical implications of mineral and vitamin imbalance in grazing sheep. *Animal Production Science* 58(8):1438–1450.

- Matsuzaki, M., J. S. Milne, R. P. Aitken, and J. M. Wallace. 2006. Overnourishing pregnant adolescent ewes preserves perirenal fat deposition in their growth-restricted fetuses. *Reproduction, Fertility and Development* 18(3):357–364.
- Matthews, C. D., M. V. Guerin, and J. R. Deed. 1993. Melatonin and photoperiodic time measurement: seasonal breeding in the sheep. *Journal of pineal research* 14(3):105–116.
- McCoard, S. A., O. Cristobal-Carballo, F. W. Knol, A. Heiser, M. A. Khan, N. Hennes, P. Johnstone, S. Lewis, and D. R. Stevens. 2020. Impact of early weaning on small intestine, metabolic, immune and endocrine system development, growth and body composition in artificially reared lambs. *Journal of Animal Science* 98(1):356.
- McCrabb, G., A. Egan, and B. Hosking. 1991. Maternal undernutrition during mid-pregnancy in sheep. Placental size and its relationship to calcium transfer during late pregnancy. *British Journal of Nutrition* 65(2):157–168.
- McDonald, P., R. Edwards, J. Greenhalgh, C. Morgan, L. Sinclair, and R. Wilkinson. 2011. *Animal Nutrition*. 7<sup>th</sup> ed. Pearson Education Limited, Edinburgh, Sc
- McGarry, W., and M. Butler. 1952. Sheep crutching technique. *Journal of the Department of Agriculture, Western Australia, Series 3* 1(2):11–30.
- Mears, G., and F. Brown. 1997. Cortisol and  $\beta$ -endorphin responses to physical and psychological stressors in lambs. *Canadian Journal of Animal Science* 77(4):689–694.
- Mellor, D., and L. Murray. 1982. Effects of long term undernutrition of the ewe on the growth rates of individual fetuses during late pregnancy. *Research in veterinary science* 32(2):177–180.
- Murphy, T. W., B. A. Freking, and G. L. Bennett. 2022. Comparison of three maternal composite sheep breeds managed under pasture lambing and purebred or terminal mating systems: ewe body weight, reproductive efficiency, and longevity. *Journal of Animal Science* 101

- NASS, U. 2024. Sheep and Goats.
- Nieto, C. R., M. Ferguson, C. Macleay, J. Briegel, G. Martin, and A. Thompson. 2013. Selection for superior growth advances the onset of puberty and increases reproductive performance in ewe lambs. *animal* 7(6):990–997.
- Nowak, R., and P. Poindron. 2006. From birth to colostrum: early steps leading to lamb survival. *Reproduction Nutrition Development* 46(4):431–446.
- Nowak, R., R. H. Porter, F. Lévy, P. Orgeur, and B. Schaal. 2000. Role of mother-young interactions in the survival of offspring in domestic mammals. *Reviews of reproduction* 5(3):153–163.
- NRC. 2007. Nutrient requirements of small ruminants: sheep, goats, cervids, and new world camelids. Natl. Acad. Press, Washington, DC
- NRCS, U. 2003. Livestock nutrition, husbandry and behavior. National range and pasture handbook. Washington DC: USDA Natural Resources Conservation Service
- Parnell, D., I. Kardailsky, J. Parnell, W. B. Badgery, and L. Ingram. 2022. Understanding sheep behaviour: Investigating the relationship between pasture and animal grazing patterns. *Grassland Research* 1(3):143–156.
- Piaggio, L., G. Quintans, R. San Julián, G. Ferreira, J. Ithurralde, S. Fierro, A. S. C. Pereira, F. Baldi, and G. Banchemo. 2018. Growth, meat and feed efficiency traits of lambs born to ewes submitted to energy restriction during mid-gestation. *Animal* 12(2):256–264.
- Pillai, S. M., A. K. Jones, M. L. Hoffman, K. K. McFadden, S. A. Reed, S. A. Zinn, and K. E. Govoni. 2017. Fetal and organ development at gestational days 45, 90, 135 and at birth of lambs exposed to under- or over-nutrition during gestation<sup>1,2,3</sup>. *Translational Animal Science* 1(1):16–25.
- Pispa, J., and I. Thesleff. 2003. Mechanisms of ectodermal organogenesis. *Developmental biology* 262(2):195–205.

- Plush, K., F. Brien, M. Hebart, and P. Hynd. 2016. Thermogenesis and physiological maturity in neonatal lambs: a unifying concept in lamb survival. *Animal Production Science* 56(4):736–745.
- Prache, S., N. Schreurs, and L. Guillier. 2022. Review: Factors affecting sheep carcass and meat quality attributes. *Animal* 16:100330.
- Raja, J., M. Hoffman, K. Govoni, S. Zinn, and S. Reed. 2016. Restricted maternal nutrition alters myogenic regulatory factor expression in satellite cells of ovine offspring. *Animal* 10(7):1200–1203.
- Ramírez-Retamal, J., and R. Morales. 2014. Influence of breed and feeding on the main quality characteristics of sheep carcass and meat: A review. *Chilean journal of agricultural research* 74(2):225–233.
- Ramos, Z., I. De Barbieri, E. Van Lier, and F. Montossi. 2020. Carcass and meat quality traits of grazing lambs are affected by supplementation during early post-weaning. *Small Ruminant Research* 184:106047.
- Rankins, D., and D. Pugh. 2011. Feeding and nutrition. *Sheep and Goat Medicine*, 2nd ed.; Pugh, DG, Baird, AN, Eds:18–49.
- Redmer, D. A., R. P. Aitken, J. S. Milne, L. P. Reynolds, and J. M. Wallace. 2005. Influence of maternal nutrition on messenger RNA expression of placental angiogenic factors and their receptors at midgestation in adolescent sheep. *Biology of Reproduction* 72(4):1004–1009.
- Redmer, D. A., J. S. Luther, J. S. Milne, R. P. Aitken, M. L. Johnson, P. P. Borowicz, M. A. Borowicz, L. P. Reynolds, and J. M. Wallace. 2009. Fetoplacental growth and vascular development in overnourished adolescent sheep at day 50, 90 and 130 of gestation. *Reproduction* 137(4):749.

- Reed, S. A., J. S. Raja, M. L. Hoffman, S. A. Zinn, and K. E. Govoni. 2014. Poor maternal nutrition inhibits muscle development in ovine offspring. *Journal of animal science and biotechnology* 5:1–11.
- Reiter, R. J., D.-X. Tan, and L. Fuentes-Broto. 2010. Melatonin: a multitasking molecule. *Progress in brain research* 181:127–151.
- Reynolds, L. P., P. P. Borowicz, J. S. Caton, M. S. Crouse, C. R. Dahlen, and A. K. Ward. 2019. Developmental programming of fetal growth and development. *Veterinary Clinics of North America: Food Animal Practice* 35(2):229–247.
- Reynolds, L. P., P. P. Borowicz, J. S. Caton, K. A. Vonnahme, J. S. Luther, C. J. Hammer, K. R. Maddock Carlin, A. T. Grazul-Bilska, and D. A. Redmer. 2010. Developmental programming: The concept, large animal models, and the key role of uteroplacental vascular development<sup>1,2</sup>. *Journal of Animal Science* 88(suppl\_13):E61–E72.
- Reynolds, L. P., J. S. Caton, D. A. Redmer, A. T. Grazul-Bilska, K. A. Vonnahme, P. P. Borowicz, J. S. Luther, J. M. Wallace, G. Wu, and T. E. Spencer. 2006. Evidence for altered placental blood flow and vascularity in compromised pregnancies. *The Journal of physiology* 572(1):51–58.
- Rezende, L. F., R. L. Camargo, R. C. Branco, A. P. Cappelli, A. C. Boschero, and E. M. Carneiro. 2014. Reduced insulin clearance and lower insulin-degrading enzyme expression in the liver might contribute to the thrifty phenotype of protein-restricted mice. *British journal of nutrition* 112(6):900–907.
- Rhodes, P., J. Craigon, C. Gray, S. M. Rhind, P. T. Loughna, and D. S. Gardner. 2009. Adult-onset obesity reveals prenatal programming of glucose-insulin sensitivity in male sheep nutrient restricted during late gestation. *PLoS One* 4(10):e7393.

- Robinson, J., I. McDonald, C. Fraser, and R. Crofts. 1977. Studies on reproduction in prolific ewes: I. Growth of the products of conception. *The Journal of Agricultural Science* 88(3):539–552.
- Saleem, A., A. Zanouny, and A. Singer. 2016. Growth performance, nutrients digestibility, and blood metabolites of lambs fed diets supplemented with probiotics during pre-and post-weaning period. *Asian-Australasian journal of animal sciences* 30(4):523.
- Sartori, E. D., A. G. Sessim, D. D. Brutti, J. F. Lopes, C. M. McManus, and J. O. Barcellos. 2020. Fetal programming in sheep: effects on pre-and postnatal development in lambs. *Journal of Animal Science* 98(9):294.
- Scheaffer, A. N., J. S. Caton, D. A. Redmer, and L. P. Reynolds. 2004. The effect of dietary restriction, pregnancy, and fetal type in different ewe types on fetal weight, maternal body weight, and visceral organ mass in ewes<sup>1</sup>. *Journal of Animal Science* 82(6):1826–1838.
- Senger, P., and P. TO. 2012. *Pathways to pregnancy and parturition* 3rd edition. Redmond, OR
- Shad, F., N. Tufanil, A. Ganie, and H. Ahmed. 2011. Flushing in ewes for higher fecundity and fertility. *Livestock international* 15(2):10–11.
- Sherwood, L., H. Klandorf, and P. Yancey. 2012. *Animal Physiology: From Genes to Organisms*. Second ed. Belmont, CA
- Shiels, D., J. Loughrey, C. M. Dwyer, K. Hanrahan, J. F. Mee, and T. W. Keady. 2021. A survey of farm management practices relating to the risk factors, prevalence, and causes of lamb mortality in Ireland. *Animals* 12(1):30.
- Solomonson, A., B. Faubert, W. Gu, A. Rao, M. A. Cowdin, I. Menendez-Montes, S. Kelekar, T. J. Rogers, C. Pan, and G. Guevara. 2022. Compartmentalized metabolism supports midgestation mammalian development. *Nature* 604(7905):349–353.

- Sormunen-Cristian, R., and L. Jauhiainen. 2002. Effect of nutritional flushing on the productivity of Finnish Landrace ewes. *Small Ruminant Research* 43(1):75–83.
- Sosa, C., J. Abecia, M. Carriquiry, F. Forcada, G. Martin, I. Palacín, and A. Meikle. 2009. Early pregnancy alters the metabolic responses to restricted nutrition in sheep. *Domestic Animal Endocrinology* 36(1):13–23.
- Spencer, T. E., and F. W. Bazer. 2004. Conceptus signals for establishment and maintenance of pregnancy. *Reproductive Biology and Endocrinology* 2:1–15.
- Squires, V. R. 2010. Nutrition of small ruminants on rangelands. *Range and Animal Sciences and Resources Management* 2:25.
- Symonds, M., M. Pope, D. Sharkey, and H. Budge. 2012. Adipose tissue and fetal programming. *Diabetologia* 55:1597–1606.
- Thion, M. S., F. Ginhoux, and S. Garel. 2018. Microglia and early brain development: An intimate journey. *Science* 362(6411):185–189.
- Thorne, J., B. Murdoch, B. Freking, R. Redden, T. W. Murphy, J. Taylor, and H. D. Blackburn. 2021. Evolution of the sheep industry and genetic research in the United States: opportunities for convergence in the twenty-first century. *Animal genetics* 52(4):395–408.
- USDA. 1992. United States Standards for Grades of Lamb, Yearling Mutton, and Mutton Carcasses.
- Vautier, A. N., and C. N. Cadaret. 2022. Long-term consequences of adaptive fetal programming in ruminant livestock. *Frontiers in Animal Science* 3:778440.
- Veiga-Lopez, A., J. Moeller, D. Patel, W. Ye, A. Pease, J. Kinns, and V. Padmanabhan. 2013. Developmental programming: impact of prenatal testosterone excess on insulin sensitivity, adiposity, and free fatty acid profile in postpubertal female sheep. *Endocrinology* 154(5):1731–1742.

- Walker, D., A. Egan, C. Nader, M. Ulyatt, and G. Storer. 1975. Rumen microbial protein synthesis and proportions of microbial and non-microbial nitrogen flowing to the intestines of sheep. *Australian Journal of Agricultural Research* 26(4):699–708.
- Wallace, J. M., D. A. Bourke, R. P. Aitken, N. Leitch, and W. W. Hay Jr. 2002. Blood flows and nutrient uptakes in growth-restricted pregnancies induced by overnourishing adolescent sheep. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 282(4):R1027–R1036.
- Wallace, J. M., J. S. Milne, and R. P. Aitken. 2004. Maternal growth hormone treatment from day 35 to 80 of gestation alters nutrient partitioning in favor of uteroplacental growth in the overnourished adolescent sheep. *Biology of Reproduction* 70(5):1277–1285.
- Wallace, J. M., J. S. Milne, R. P. Aitken, and W. W. Hay Jr. 2007. Sensitivity to metabolic signals in late-gestation growth-restricted fetuses from rapidly growing adolescent sheep. *American Journal of Physiology-Endocrinology and Metabolism* 293(5):E1233–E1241.
- Wallace, M., and C. M. Metallo. 2020. Tracing insights into de novo lipogenesis in liver and adipose tissues. In: *Seminars in Cell & Developmental Biology*. p 65–71.
- Wang, S., T. Ma, G. Zhao, N. Zhang, Y. Tu, F. Li, K. Cui, Y. Bi, H. Ding, and Q. Diao. 2019. Effect of age and weaning on growth performance, rumen fermentation, and serum parameters in lambs fed starter with limited ewe–lamb interaction. *Animals* 9(10):825.
- Waters, S. M., E. Roskam, P. E. Smith, D. A. Kenny, M. Popova, M. Eugène, and D. P. Morgavi. 2025. International Symposium on Ruminant Physiology: The role of rumen microbiome in the development of methane mitigation strategies for ruminant livestock. International Symposium on Ruminant Physiology, August 2024. *Journal of Dairy Science* 108(7):7591–7606.

- Wild, M., M. Gauly, T. Zanon, J. Isselstein, and M. Komainda. 2023. Tracking free-ranging sheep to evaluate interrelations between selective grazing, movement patterns and the botanical composition of alpine summer pastures in northern Italy. *Pastoralism* 13(1):25.
- Wu, G., F. Bazer, J. Wallace, and T. Spencer. 2006. Board-invited review: intrauterine growth retardation: implications for the animal sciences. *Journal of animal science* 84(9):2316–2337.
- Yang, C., C. Wang, Y. Zhao, T. Chen, A. Aubry, A. Gordon, and T. Yan. 2020. Updating maintenance energy requirement for the current sheep flocks and the associated effect of nutritional and animal factors. *Animal* 14(2):295–302.
- Yates, D. T., A. R. Macko, M. Nearing, X. Chen, R. P. Rhoads, and S. W. Limesand. 2012. Developmental Programming in Response to Intrauterine Growth Restriction Impairs Myoblast Function and Skeletal Muscle Metabolism. *Journal of Pregnancy* 2012(1):631038.
- Zhu, M. J., S. P. Ford, W. J. Means, B. W. Hess, P. W. Nathaniels, and M. Du. 2006. Maternal nutrient restriction affects properties of skeletal muscle in offspring. *The Journal of physiology* 575(1):241–250.
- Zorn, A. M., and J. M. Wells. 2009. Vertebrate endoderm development and organ formation. *Annual Review of Cell and Developmental* 25(1):221–251.

## CHAPTER 2- MODERATE GLOBAL NUTRIENT RESTRICTION DURING LATE GESTATION DID NOT IMPACT WETHER LAMB DEVELOPMENT, GROWTH, AND PERFORMANCE FROM WEANING TO HARVEST

### *2.1 Introduction*

In the sheep industry, extensive management systems often maintain their ewes on rangeland throughout their gestation (Soder et al., 1995; Thomas et al., 2007; ASI, 2015; Karthik et al., 2021). Late winter pastures typically cannot support ewes to parturition due to reduced energy, crude protein, and digestibility and thus ewes are often supplemented during the last 4 to 6 weeks of gestation to support the 70% of fetal growth that occurs (Jensen et al., 2002; Reynolds et al., 2018, Caton et al., 2019). When gestational nutrient requirements are not met, adaptive fetal programming may occur due to redirecting nutrients to critical organs at the expense of others deemed non-critical as a means of survival (Wu et al., 2006; Caton and Hess, 2010; Reynolds et al., 2010, 2017, 2019; Reynolds and Caton, 2012; Caton et al., 2019). The redirection of nutrients away from less crucial organs may lead to their adaptive development and reduced functionality, ultimately altering the metabolism and productivity of affected offspring (Gao et al., 2009; Hyatt et al., 2011; Redifer et al., 2024). Previous studies have shown that with moderate reductions in metabolizable energy (ME) around 100 days of gestational age (dGA), lambs have reduced birthweights, rate of gain in the preweaning period, and lack vigor (Van Emon et al., 2014; Tygesen et al., 2008; Sartori et al., 2020). The performance of globally restricted lambs later in life past the weaning period is not well characterized. At harvest, maternal undernutrition is associated with reduced carcass weights, increased lean muscle mass and decreased fat depth (Zhu et al., 2004; Du et al., 2010; Maresca et al., 2019; Ramirez et al., 2020; Knight, et al., 2020) though one study

found no carcass differences at harvest (Tygesen et al., 2008). Previous research has centered on the effects of late gestation global nutrient restriction on pre-weaning performance, but long-term performance during the post-weaning period has yet to be explored in depth. We hypothesize that maternal restriction in late gestation will impact offspring beyond the perinatal period, altering nutrient utilization and thus reducing growth and carcass performance. Therefore, the objective of this study was to determine the effects of moderate global nutrient restriction during late gestation on long-term performance of wether lambs from birth through harvest.

## *2.2 Materials & Methods*

### *2.2.1 Animals and Experimental design.*

This study was approved by the Institutional Animal Care and Use Committee at Colorado State University (CSU). Animal studies were performed at the CSU Agricultural Research, Development, and Education Center in Fort Collins, Colorado.

### *2.2.2 Gestational Management*

Twenty-two timed-bred yearling Merino x Rambouillet ewes were bred to a single sire, confirmed pregnant, and assigned a dietary treatment via simple randomization. All ewes were individually fed a pelleted diet to meet 100% of the National Research Council's (NRC) requirements until the 110<sup>th</sup> day of gestation (dGA). From 110 dGA until parturition, ewes were either maintained on the fully nourished diet or globally restricted by intake to 65% of their NRC requirements (Figure 1). Throughout the treatment period, daily feed intake was recorded and offered feed amounts were adjusted according to 110% of previous intake. Individual housing included automatic waterers and ad libitum access to mineral blocks (Redmond Agriculture, Redmond, UT). For the entire treatment period, maternal body weights (BW) were collected

weekly, and blood samples and body condition scores (BCS) were collected bi-monthly (once every two weeks).

### *2.2.3 Preweaning lamb management*

Ewes lambed in individual jugs on their own unless assistance was needed due to dystocia. At birth, number of lambs per ewe (progeny), birth weight, morphometrics (crown-rump length: CRL; crown circumference: CC; abdominal circumference: AC; cannon bone length: CBL), and plasma were collected. Lambs were born to either fully nourished dams (CONT; n= 14 from 10 ewes: 6 singletons, 8 twins; 6 males and 8 females) or nutrient restricted dams (NR; n= 14 from 11 ewes: 8 singletons, 6 twins; 7 males and 7 females). Lambs were ear tagged, tail docked, and castrated before being released from the jug with their dam into group housing. Weight and blood samples were taken daily for the first seven days of life. Lamb BW continued to be taken daily until 30 d and taken weekly through weaning. Morphometrics and blood samples were taken weekly through weaning.

### *2.2.4 Feedlot trial.*

At weaning, wether lambs (CONT= 4, NR= 5) were moved to individual pens and daily feed intake was collected for 90 days until harvest. Wethers were fed a pelleted diet based on body weight that met 100% of NRC requirements (NRC, 2007). Feed was offered once per day, and theorts were weighed and discarded the following day before new feed was offered. Wethers had ad libitum access to water and mineral blocks. Lambs were let out daily into a large dry lot to exercise and socialize with one another. Weekly weights, bimonthly BCS, and blood samples were collected for the duration of the trial. Weekly weights were used to determine average daily gain within treatment groups.

### *2.2.5 Balance trial.*

On day 115 of life wethers were placed into metabolism crates with individual feed bunks, automatic waterers, and rubber mat footing and allowed two days to acclimate prior to sample collection. While in metabolism crates, wethers continued to receive their regular diet, ab libitum water, and enrichment toys. Total feed intake, fecal, and urine output were measured as previously described (Archibeque et al. 2006) for five days. Feed was weighed and offered once daily at the time of collection. Orts were collected from the previous day; feces were collected using a canvas diaper attached to a harness, and urine was collected by funnel system into a urine jug. Feces and urine were collected daily, weighed, and a 10% subsample was pooled for each animal and frozen for further analysis to determine energy intake and loss. Feed and fecal samples were ground through a 2 mm Wiley mill (Thomas Scientific, Swedesboro, NJ) and submitted to The Dairy Authority LLC (Greeley, CO) for composition analysis. Nutrient digestibility was calculated by determining nutrient intake and subtracting elimination in feces and urine.

#### *2.2.6 Harvest Characteristics.*

At the feedlot trial's completion at 90 days, lambs were transported to the Colorado State University Global Food Innovation Center abattoir where they were humanely slaughtered. Carcass measurements (hot carcass weight, fat thickness, loin eye area), yield grade, organ weights, and tissue morphometrics (heart, lung, liver, kidney) were collected. Tissue samples collected and frozen for further analysis.

#### *2.2.7 Statistical analysis.*

All data was analyzed using the MIXED procedure of SAS 9.4 (SAS Institute, Cary, NC). Recurrent data was analyzed as repeated measures considering the effects of treatment, time, and the interaction. Single timepoint data was analyzed by ANOVA considering the effect of treatment. Progeny was not included as an effect due to insufficient power. Significance was determined as

$P \leq 0.05$  and tendencies were determined as  $P \leq 0.10$ . All data is expressed as means  $\pm$  standard error.

### *2.3 Results*

#### *2.3.1 Feedlot Performance.*

No differences were found between CONT and NR lambs in feedlot performance measurements (Table 1). ADG, dry matter intake (DMI), daily feed intake, and feed efficiency did not differ between CONT and NR lambs.

#### *2.3.2 Digestibility.*

No differences were found in digestibility of nutrients between CONT and NR lambs. Dry matter, ADF, NDF, CP, calcium, and phosphorus digestibility did not differ between groups.

#### *2.3.3 Harvest.*

Carcass performance and quality did not differ between CONT and NR lambs (Table 2). Hot carcass weight, loin eye area, fat thickness, yield grade, flank streaking, and individual organ weights were all similar between groups.

### *2.4 Discussion*

In this study, we show that moderate global nutrient restriction in late gestation is not impactful to the post-weaning performance of wether lambs when the dam is adequately fed in the prior gestational periods. Additionally, nutrient utilization in restricted lambs was unaffected, indicating that metabolic processes were unaffected by late gestational restriction. Though the insult occurred at a key stage in fetal growth, carcass quality and characteristics of restricted lambs were not altered by the insult, indicating that when initial development of muscle and adipose tissue occurs in a fully nourished environment, poor nutrition in late gestation can be overcome. Together these findings demonstrate that traditional supplementation is not as necessary if the

needs of early and mid-gestation have been fully met and offer the opportunity to shift the focus of supplementation to support tissue development with late gestation adequately being supported by rangeland alone, especially in late spring born lambs.

An acute moderate global nutrient restriction in late gestation does not impact the long-term productivity of weaned lambs if ewes enter late gestation in a positive condition. Despite the nutrient restriction, these offspring grew and gained at the same rate as control lambs. It is known that outcomes of gestational environment are dependent upon timing, duration, and severity of the insult (Vautier and Cadaret, 2022). The timing of the nutritional insult occurred during the phase of gestation where fetal development is largely complete, and growth is the predominant event significant to the fetus. Likewise, as the restriction was moderate in nature and only lasted four weeks, it was likely not significant enough to cause fetal programming. In late gestation, mild restriction of metabolizable energy after being on pasture for early and mid-gestation does not affect birthweight, suggesting the dam may be able to allocate enough nutrients to her fetus to make nutrient restriction imperceivable in offspring (McGovern et al., 2015). When specific nutrients such as energy and crude protein are moderately to severely restricted in late gestation, offspring are born lighter and gain weight faster in the preweaning period, weaning at the same average weight as their counterparts (Tygesen et al., 2008; Lopez Valiente et al., 2022). This is likely due to compensatory gain when the animal enters a nutrient rich environment, as late gestation restriction impacts tissue hypertrophy rather than hyperplasia and can often be overcome. If restriction occurs in the window of gestation in which tissue development is occurring and is severe enough, deficits are often not able to be overcome, as tissue formation and function has been altered and persists lifelong (Funston et al., 2010; Long et al., 2009; Lopez Valiente et al., 2022; Maresca et al., 2019). Undernutrition of the dam carrying twins in early pregnancy has been

associated with an increased rate of gain in offspring during the preweaning period (Cleal et al. 2007). Early to midgestational restriction of ~50% reduced placental mass, size, and placentome number, making delivery of nutrients very difficult and resulting in offspring that were lighter at birth (Clarke et al., 1998; Deandrea et al., 2001; McMillen and Robinson, 2005; Symonds et al., 2007; Aysondu and Ozyurek 2020; Toschi and Baratta 2021). Timing and severity of nutritional insults are key to the observed outcomes of poor nutrition but given the parameters of this study, lasting effects were not observed.

Nutrient restricted lambs did not demonstrate altered nutrient absorption or utilization in the face of the applied insult. In a similar study in cattle, mid-to-late gestational nutrient restriction following the grazing of pasture through early and mid-gestation, produced nutrient restricted calves that were lighter at birth and at weaning but had similar metabolic profiles to control calves (Redifer et al., 2024). This suggests that metabolically active organs were able to develop without issue from the restriction but could not compensate weight gain likely due to the negative impact to muscle development. Metabolically active tissues, like skeletal muscle, brain and liver, develop significantly during mid-gestation, meaning the restriction was applied after metabolism had largely been established. Restriction that overlaps with organ development of metabolic tissues in the susceptible timeframe changes carbohydrate, lipid, and amino acid metabolism (Hyatt et al., 2011; Smith et al., 2024). In chronic cases of undernutrition, restricted lambs have altered insulin metabolism with greater levels of serum insulin compared to normal lambs, suggesting dysregulated glucose: insulin dynamics due to extended durations of poor nutrition (Rhodes et al., 2009; George et al., 2012; Hoffman et al., 2016). Metabolism can be significantly impacted by nutrient restriction if it coincides with the development of metabolically significant organs,

however, this study did not overlap notable organ development with substantial enough restriction and this may explain the lack of observable differences between groups.

Carcass quality and characteristics are similar when dams are adequately nourished before the insult. In ruminants, adipose and final muscle tissues are developed in late gestation and risk poor formation depending on the degree of suboptimal nutrition, potentially decreasing carcass quality and marbling at the time of harvest (Zhu et al., 2004; Du et al., 2010; Maresca et al., 2019; Ramirez et al., 2020). In the event of mild nutrient restriction in late gestation, no effects are seen on carcass quality and performance (Mulliniks et al., 2015) indicating that restriction could be overcome to not permanently effect muscle metabolism in this study. When dams grazed low quality native grasslands during mid-gestation, calves had reduced weaning weights, carcass weights, and tougher meat than those whose dams grazed on high quality pasture (Underwood et al., 2010). These offspring likely developed abnormal muscle tissue and intramuscular fat, contributing to poor meat quality. Another study from the midgestational timepoint did not observe differences in hot carcass weight, dressing scores, or intramuscular fat but did find tendencies of restricted lambs to have better back fat at the 12<sup>th</sup> rib and greater USDA yield grade as result (Mohrhauser et al., 2015). These offspring developed normal muscle tissue but had higher adipose deposition like that which is seen in the thrifty phenotype (Ford et al., 2007; Du et al., 2010). With longer duration insults, lambs from restricted dams experience asymmetric growth with lighter visceral organs and heavier brains than fully nourished animals, but data on these animals in the post weaning period is lacking (Gao et al., 2009). Though carcass difference do occur with nutrient restriction, further investigation is needed to better understand the connection between timing of insult and their ultimate impact on carcass quality at harvest.

#### *2.4.1 Limitations*

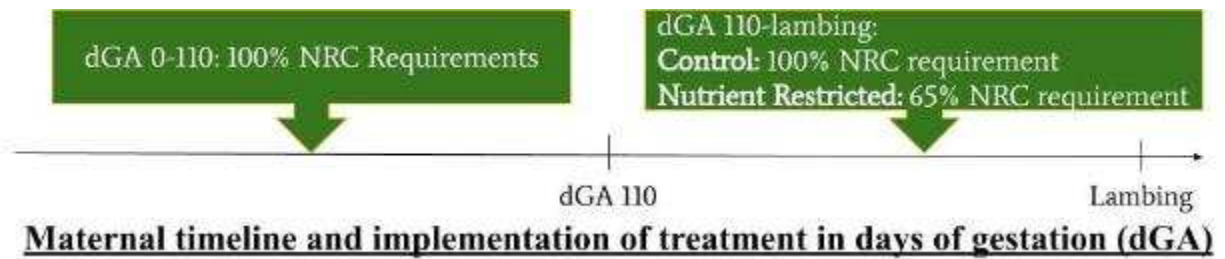
Limitations within this study exist and should be acknowledged. One key limitation is that the intended dietary treatment was not implemented as planned due to logistical challenges during the feeding period. As a result, animals did not receive the desired timing or duration of nutrient restriction which hinders interpretation of this study. Additionally, the overall sample size of this study is small which limits the statistical power to detect differences between treatments. These constraints reduce the generalizability of the findings and highlight the need for further research to validate and expand upon the current study.

#### *2.5 Conclusions*

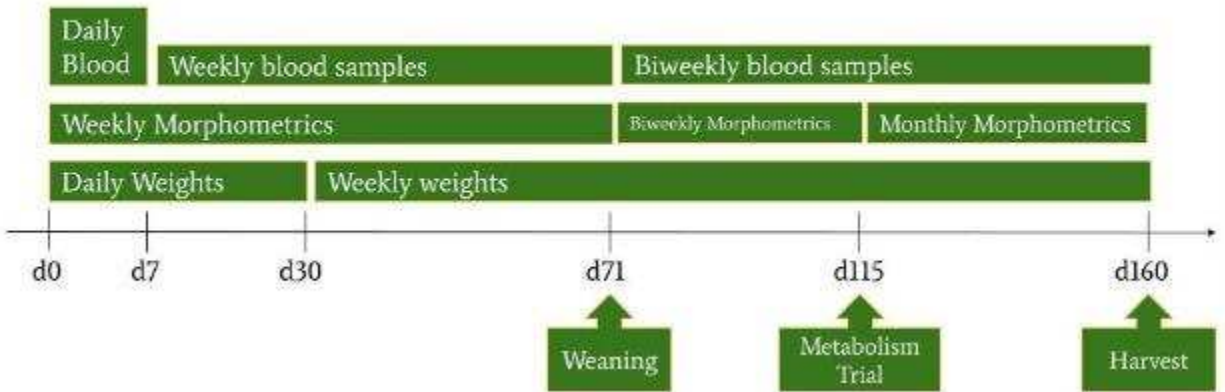
Our findings demonstrate that moderate global nutrient restriction in late gestation yields lambs that perform equally to their control counterparts in all aspects during the post-weaning period and at harvest when the dam has received adequate nutrition prior to the insult. Nutrient restricted lambs had similar rates of gain and nutrient utilization throughout their time in the feedlot and produced similar quality carcasses at harvest. This information can be offered to producers as evidence that late gestation nutritional deficits can be overcome if the dam has not been challenged earlier in pregnancy and her offspring will be equally productive members of the flock. Should producers find that their ewes have been maintained on a reduced plane of nutrition through the late term of their gestation, they should prioritize increased labor for monitoring and intervention around the time of lambing to give these offsprings better chances of survival. It is not recommended that these findings be used as a production strategy to decrease costs but rather serve as perspective to the tradeoffs that occur in sheep management as it pertains to maternal nutrition and neonatal care as factors of offspring success. Additionally, the economic tradeoff between

labor, intensive management systems, and maternal supplementation should be evaluated to help producers quantify the additional costs that incur when rearing nutrient restricted lambs.

*Figures and tables*



*Figure 1.* Maternal timeline of nutrient restriction. Ewes were maintained on 100% of NRC requirements until dGA 110 when they were allocated to one of two groups. Control (CONT) ewes were maintained on 100% of NRC requirements until lambing. Nutrient restricted (NR) were restricted to 65% global intake until lambing.



*Figure 2.* Wether lamb timeline of data collection and major events in the trial.

Table 1. Daily growth, feed, and nutrient use by wether lambs born from dams fed adequate nutrients during late gestation (CONT) or wether lambs born from dams that were nutrient restricted during late-gestation (NR).

	Experimental Group		<i>P</i> -value
	<b>CONT</b>	<b>NR</b>	
N	4	5	
Dry Matter Intake, kg/d	1.73 ± 0.22	1.71 ± 0.22	0.95
Average Daily Gain, kg/d	0.25 ± 0.03	0.27 ± 0.03	0.30
Daily Feed Intake, kg/d	1.95 ± 0.25	1.92 ± 0.25	0.95
Feed Efficiency	6.85 ± 1.49	6.27 ± 1.27	0.67
DM Digestibility, %	46.52 ± 2.27	45.75 ± 2.50	0.84
ADF Digestibility, %	38.57 ± 3.44	37.07 ± 3.08	0.75
NDF Digestibility, %	45.08 ± 3.96	44.16 ± 3.54	0.87
CP Digestibility, %	31.43 ± 5.31	24.03 ± 4.75	0.33
Calcium Digestibility, %	-38.38 ± 8.17	-21.22 ± 7.31	0.16
Phosphorus Digestibility, %	11.22 ± 12.83	12.47 ± 11.47	0.94

<sup>1</sup>dry matter (DM); acid detergent fiber (ADF); neutral detergent fiber (NDF); crude protein (CP).

Table 2. Evaluation of carcass characteristics and organ weights at harvest from wether lambs of dams that had adequate nutrients during late gestation (CONT) or wether lambs born from dams that were nutrient restricted during late-gestation (NR).

	Experimental Group		SEM	P-value
	CONT	NR		
N	4	5		
Hot Carcass Weight, kg	61.00	64.50	4.31	0.59
Loin Eye Area, cm <sup>2</sup>	2.33	2.33	0.20	1.00
Fat Thickness	0.28	0.16	0.05	0.19
Yield Grade	3.15	2.03	0.54	0.19
Quality Grade	Choice+ (2.00)	Choice+ (2.00)	0.50	1.00
Flank Streaking	Small-Modest (2.75)	Small-Modest (2.25)	0.63	0.60
Liver Weight, g	1044.30	1111.55	172.83	0.60
Lung Weight, g	588.03	598.93	64.74	0.82
Heart Weight, g	264.13	276.05	24.38	0.52
Kidney Weight, g	68.73	71.50	7.20	0.61

<sup>1</sup>Quality grade was ranked numerically for analysis as 1 (Choice-), 2 (Choice+), 3 (Prime-)

<sup>2</sup>Flank streaking was ranked numerically for analysis as 1 (slight); 2 (small); 3 (modest); 4 (moderate)

### *Literature Cited*

- Archibeque, S., D. Miller, H. Freetly, and C. Ferrell. 2006. Feeding high-moisture corn instead of dry-rolled corn reduces odorous compound production in manure of finishing beef cattle without decreasing performance. *Journal of animal science* 84(7):1767–1777.
- American Sheep Industry Association (ASI). 2015. *Sheep Production Handbook*. 8:604,1008.
- Aysondu, M. H., and S. Ozyurek. 2020. Influences of maternal undernutrition on placental development and birth weight in sheep. *Large Animal Review* 26(3):127–130.
- Caton, J., and B. Hess. 2010. Maternal plane of nutrition: Impacts on fetal outcomes and postnatal offspring responses. In: *Proc. 4th Grazing Livestock Nutrition Conference*. BW Hess, T. DelCurto, JGP Bowman and RC Waterman (eds.) West. Sect. Am. Soc. Anim. Sci., Champaign, Ill. p 104–122.
- Caton, J. S., M. S. Crouse, L. P. Reynolds, T. L. Neville, C. R. Dahlen, A. K. Ward, and K. C. Swanson. 2019. Maternal nutrition and programming of offspring energy requirements<sup>1</sup>. *Translational Animal Science* 3(3):976–990
- Clarke, L., L. Heasman, D. T. Juniper, and M. E. Symonds. 1998. Maternal nutrition in early-mid gestation and placental size in sheep. *British Journal of Nutrition* 79(4):359–364.
- Cleal, J. K., K. R. Poore, J. P. Newman, D. E. Noakes, M. A. Hanson, and L. R. Green. 2007. The effect of maternal undernutrition in early gestation on gestation length and fetal and postnatal growth in sheep. *Pediatric Research* 62(4):422–427.
- Dandrea, J., V. Wilson, G. Gopalakrishnan, L. Heasman, H. Budge, T. Stephenson, and M. Symonds. 2001. Maternal nutritional manipulation of placental growth and glucose transporter 1 (GLUT-1) abundance in sheep. *Reproduction-Cambridge* 122(5):793–800.

- Du, M., J. Tong, J. Zhao, K. Underwood, M. Zhu, S. Ford, and P. Nathanielsz. 2010. Fetal programming of skeletal muscle development in ruminant animals. *Journal of animal science* 88(suppl\_13):E51–E60.
- Funston, R. N., D. M. Larson, and K. Vonnahme. 2010. Effects of maternal nutrition on conceptus growth and offspring performance: implications for beef cattle production. *Journal of animal science* 88(suppl\_13):E205–E215.
- Gao, F., Y. C. Liu, and X. Z. Hou. 2009. Effect of Maternal Undernutrition during Late Pregnancy on Growth and Development of Ovine Fetal Visceral Organs. *Asian-Australas J Anim Sci* 22(12):1633–1639.
- George, L. A., L. Zhang, N. Tuersunjiang, Y. Ma, N. M. Long, A. B. Uthlaut, D. T. Smith, P. W. Nathanielsz, and S. P. Ford. 2012. Early maternal undernutrition programs increased feed intake, altered glucose metabolism and insulin secretion, and liver function in aged female offspring. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 302(7):R795–R804.
- Hyatt, M., D. Gardner, S. Sebert, V. Wilson, N. Davidson, Y. Nigmatullina, L. Chan, H. Budge, and M. Symonds. 2011. Suboptimal maternal nutrition, during early fetal liver development, promotes lipid accumulation in the liver of obese offspring. *Reproduction-Cambridge* 141(1):119.
- Jensen, K. B., D. A. Johnson, K. H. Asay, and K. C. Olson. 2002. Seasonal-accumulated growth and forage quality of range grasses for fall and winter grazing. *Canadian Journal of Plant Science* 82(2):329–336.
- Karthik, D., J. Suresh, Y. R. Reddy, G. Sharma, J. Ramana, G. Gangaraju, Y. Pradeep Kumar Reddy, D. Yasaswini, M. Adegbeye, and P. R. K. Reddy. 2021. Farming systems in sheep rearing: Impact

- on growth and reproductive performance, nutrient digestibility, disease incidence and heat stress indices. *Plos one* 16(1):e0244922.
- Knight, M., K. Butler, L. Slocombe, N. Linden, M. Raeside, V. Burnett, A. Ball, M. McDonagh, and R. Behrendt. 2020. Reducing the level of nutrition of twin-bearing ewes during mid to late pregnancy produces leaner prime lambs at slaughter. *Animal* 14(4):864–872.
- Long, N., K. Vonnahme, B. Hess, P. Nathanielsz, and S. Ford. 2009. Effects of early gestational undernutrition on fetal growth, organ development, and placentomal composition in the bovine. *Journal of animal science* 87(6):1950–1959.
- López Valiente, S., A. M. Rodriguez, N. M. Long, I. M. Lacau-Mengido, and S. Maresca. 2022. The degree of maternal nutrient restriction during late gestation influences the growth and endocrine profiles of offspring from beef cows. *Animal Production Science* 62(2):163–172.
- Maresca, S., S. L. Valiente, A. M. Rodriguez, L. M. Testa, N. M. Long, G. I. Quintans, and E. Pavan. 2019. The influence of protein restriction during mid-to late gestation on beef offspring growth, carcass characteristic and meat quality. *Meat science* 153:103–108.
- McGovern, F. M., F. P. Champion, T. Sweeney, S. Fair, S. Lott, and T. M. Boland. 2015. Altering ewe nutrition in late gestation: II. The impact on fetal development and offspring performance<sup>1</sup>. *Journal of Animal Science* 93(10):4873–4882.
- McMillen, I. C., and J. S. Robinson. 2005. Developmental origins of the metabolic syndrome: prediction, plasticity, and programming. *Physiological reviews* 85(2):571–633.
- Mohrhauser, D., A. Taylor, K. Underwood, R. Pritchard, A. Wertz-Lutz, and A. Blair. 2015. The influence of maternal energy status during midgestation on beef offspring carcass characteristics and meat quality. *Journal of animal science* 93(2):786–793.

- Mulliniks, J., J. Sawyer, F. Harrelson, C. Mathis, S. Cox, C. Löest, and M. Petersen. 2015. Effect of late gestation bodyweight change and condition score on progeny feedlot performance. *Animal Production Science* 56(12):1998–2003.
- NRC. 2007. Nutrient requirements of small ruminants: sheep, goats, cervids, and new world camelids. Natl. Acad. Press, Washington, DC
- Ramírez, M., L. M. Testa, S. L. Valiente, M. E. Latorre, N. M. Long, A. M. Rodriguez, E. Pavan, and S. Maresca. 2020. Maternal energy status during late gestation: Effects on growth performance, carcass characteristics and meat quality of steers progeny. *Meat Science* 164:108095.
- Redifer, C. A., L. G. Wichman, S. L. Davies-Jenkins, A. R. Rathert-Williams, H. C. Freetly, and A. M. Meyer. 2024. Late gestational nutrient restriction in primiparous beef females: Performance and metabolic status of lactating dams and pre-weaning calves. *Journal of Animal Science* 102
- Reynolds, L., P. Borowicz, J. Caton, K. Vonnahme, J. Luther, C. Hammer, K. Maddock Carlin, A. Grazul-Bilska, and D. Redmer. 2010. Developmental programming: the concept, large animal models, and the key role of uteroplacental vascular development. *Journal of animal science* 88(suppl\_13):E61–E72.
- Reynolds, L. P., P. P. Borowicz, J. S. Caton, M. S. Crouse, C. R. Dahlen, and A. K. Ward. 2019. Developmental programming of fetal growth and development. *Veterinary Clinics of North America: Food Animal Practice* 35(2):229–247.
- Reynolds, L. P., and J. S. Caton. 2012. Role of the pre-and post-natal environment in developmental programming of health and productivity. *Molecular and cellular endocrinology* 354(1-2):54–59.
- Reynolds, L. P., A. T. Grazul-Bilska, and P. P. Borowicz. 2018. Placental Angiogenesis. In: M. K. Skinner, editor, *Encyclopedia of Reproduction (Second Edition)*. Academic Press, Oxford. p. 521–529.

- Reynolds, L. P., A. K. Ward, and J. S. Caton. 2017. Epigenetics and developmental programming in ruminants: Long-term impacts on growth and development, *Biology of domestic animals*. CRC Press. p. 85–121.
- Sartori, E. D., A. G. Sessim, D. D. Brutti, J. F. Lopes, C. M. McManus, and J. O. Barcellos. 2020. Fetal programming in sheep: effects on pre-and postnatal development in lambs. *Journal of Animal Science* 98(9):294.
- Smith, B. I., M. A. Vásquez-Hidalgo, X. Li, K. A. Vonnahme, A. T. Grazul-Bilska, K. C. Swanson, T. E. Moore, S. A. Reed, and K. E. Govoni. 2024. The Effects of Maternal Nutrient Restriction during Mid to Late Gestation with Realimentation on Fetal Metabolic Profiles in the Liver, Skeletal Muscle, and Blood in Sheep. *Metabolites* 14(9):465.
- Toschi, P., and M. Baratta. 2021. Ruminant placental adaptation in early maternal undernutrition: An overview. *Frontiers in Veterinary Science* 8:755034.
- Tygesen, M., A.-H. Tauson, D. Blache, S. Husted, and M. Nielsen. 2008. Late foetal life nutrient restriction and sire genotype affect postnatal performance of lambs. *Animal* 2(4):574–581.
- Underwood, K., J. Tong, P. Price, A. Roberts, E. Grings, B. Hess, W. Means, and M. Du. 2010. Nutrition during mid to late gestation affects growth, adipose tissue deposition, and tenderness in cross-bred beef steers. *Meat science* 86(3):588–593.
- Van Emon, M., C. Schauer, L. Lekatz, S. Eckerman, K. Maddock-Carlin, and K. Vonnahme. 2014. Supplementing metabolizable protein to ewes during late gestation: I. Effects on ewe performance and offspring performance from birth to weaning. *Journal of Animal Science* 92(1):339–348.
- Vautier, A. N., and C. N. Cadaret. 2022. Long-term consequences of adaptive fetal programming in ruminant livestock. *Frontiers in Animal Science* 3:778440.

- Wu, G., F. Bazer, J. Wallace, and T. Spencer. 2006. Board-invited review: intrauterine growth retardation: implications for the animal sciences. *Journal of animal science* 84(9):2316–2337.
- Zhu, M.J., S. P. Ford, P. W. Nathanielsz, and M. Du. 2004. Effect of maternal nutrient restriction in sheep on the development of fetal skeletal muscle. *Biology of reproduction* 71(6):1968–1973.

## CHAPTER 3- EVALUATION OF ASSESSMENT STRATEGY ON STUDENT RETENTION OF KNOWLEDGE IN SEQUENTIAL ANIMAL SCIENCE COURSES

### *3.1 Extended Introduction*

In deciding how to best assess student knowledge in the classroom, professors may also be affecting their students' knowledge retention and performance in the future. In undergraduate education, there are often sequential classes that rely on the information learned in the prerequisite course as a foundation to build on in later classes. By using different types of assessments, professors can encourage students to interact with material more frequently, helping to promote long-term memory formation and supporting their success in subsequent courses.

#### *3.1.1 Formation of Memory.*

In order to understand how to best support retention of knowledge, it is important to understand how memory is formed. Memory is defined as the way information is processed, stored, and remembered in the brain for use at a later period in time (Eysenck, 1988). The multistore memory (MSM) model, or modal model of memory developed by Atkinson and Shiffrin, proposes how memory is formed and how it is controlled by using different stages of interaction with information. The formation of memory is dependent on the sequential progression of information through the environment, into the working memory, and practiced until becoming part of the long-term memory (LTM; Atkinson and Shiffrin, 1968; Alsaeed, 2017).

Once a stimulus has had enough attention paid to it, it will be held in the short-term memory. Short-term memory, or working memory, handles the external stimulus from the sensory memory and internal, stimulated by internal thought processes that one is actively aware of. In young adults, short-term memory has a small capacity of about three to five items and a short

duration of about 15-30 seconds (Gilchrist et al., 2008). Keeping information in this store requires maintenance retrieval which goes beyond paying attention to it but also actively pulling it back to the forefront of one's attention by practicing it (Camos et al., 2009; Bartsch et al., 2018). Maintenance retrieval can look like flash cards or repeating a name over and over, so it is not forgotten. Working memory is particularly valuable as it is used to comprehend, solve problems, plan, and learn (Cowan, 2010). Not only is working memory a space where memorization occurs but also where connections between information happen, leading to LTM formation if the connections are strong enough.

When information from working memory is rehearsed repeatedly, longer periods of time can pass between retrievals, as this information becomes encoded into the long-term memory. Long-term memory is the last storage in the MSM model and describes memory stored for long durations that is subject to constant reconstruction due to the information being brought into sensory and working memory (Lindell, 2014). LTM allows for unlimited amounts of information to go long periods of time without attention but with proper maintenance, to still be recalled accurately (Tulving, 1973).

There are different forms of LTM which describe how they came to be stored. Explicit knowledge is information about various aspects in one's life that are intentionally noted and can be recalled consciously (Felten, et al., 2016). Types of explicit memory include semantic memories which are distinct facts unrelated to personal life events, and episodic memory which describe the recollection of precise experiences in one's life events (Almaraz-Espinoza and Grinder, 2022). Semantic memories include general facts about the world we live in, definitions, or academic knowledge. Information that is actively committed to memory by repeated studying is stored as semantic memory. The other form of LTM is implicit memory which is independent of conscious

learning or cognition and consists of procedural and emotional memory (Dharani, 2015; Dew and Cabeza, 2011). Procedural memory helps us navigate the world as it holds information about how we do things. This motor memory is formed by repeated trial and error and learning the correct order for success in the task (Breed and Moore, 2016) but lacks conscious thought about the steps to complete the task once learned. The type of LTM that a memory is stored in effects the maintenance needed to successfully and accurately maintain these memories so that they can be accessed in the future (Nishiyama, 2014). Understanding the differences in memory can help form targeted strategies to strengthen the LTM, building a more durable memory for longer periods of time.

### *3.1.2 Memory Consolidation.*

The transition of information from short-term memory to long-term memory, called memory consolidation, is dependent on encoding, storage, and retrieval (McDermott and Roediger, 2018). Consolidation stabilizes newly learned information so that it can enter more durable memories and be accessed over longer periods of time. It also allows for memory to be updated and modified as new learning occurs (Girardeau and Zugaro, 2011). Rate of memory consolidation can be affected by one's previous knowledge on the subject, allowing connections to new information and long-term memory to form faster (Tse et al., 2007). Encoding is the filing and storage of information in a specific format that is important to the development of long-term memory (Mujawar et al., 2021). To build long-term memories, memories must be recalled back into the working memory and new information be incorporated. Once the new information is successfully "updated", the memory can be reconsolidated by the same encoding processes that allowed for the initial LTM to form (Lee et al., 2017). When the new information supports the old

memories, the retrieval of the LTM into the working memory and its reconsolidation tends to positively strengthen the knowledge.

Rehearsal of information allows for reactivation of memory around information, permitting attention, to bring this detail back to the short-term memory before it is forgotten, effectively extending the duration of this information retention (Cowan, 2008; Roediger and Butler, 2011). Information retention, or the accurate maintenance of long-term memories, depends on the maintenance of this knowledge through retrieval practice and elaboration. To prevent the decay of long-term memory, recalling or retrieving information from long-term memory into the working memory helps to maintain a memory's integrity and accuracy over time (Ruchkin et al., 2003)

### *3.1.3 Assessments of Learning, For Learning, and As Learning.*

Conventional assessment methods include tests and assignments that utilize true/ false, multiple-choice, short answer, and essay responses typically presented as summative assessment (Fook and Sidhu, 2014). Summative assessment refers to higher stake assessment administered at the end of an instruction period used to measure student performance. Summative assessments tend to test over a high volume of content and have a higher impact on the students' grade. Performance on a summative assessment is often important for students to progress in their program and represents performance with a single snapshot in time (Daka et al., 2021). In a systematic review of summative assessments conducted by the Assessment and Learning Research Synthesis Group in 2002, the group identified that large exams are often used to set the standard and indicate performance surrounding that standard of performance. At the same time, exams may motivate students for performance over learning, causing them to chase grades over true comprehension of the material being tested (Harlen et al., 2002).

Formative assessments are intended to provide students with a gauge of their understanding without heavy impacts to their grades (Kibble, 2017, Black and William, 2009; Rolfe and McPherson 1995). They are used to underscore important topics to enhance student learning, usually during the unit and often present as smaller, lower stakes assessments (Bell and Cowie, 2001). For formative assessments to be useful, they need to provide information about the student's performance that can be used as feedback to continue to grow towards their goals, such as mastery of a topic. Any assessment can be a formative one, but it is important that these provide a learning experience via feedback to the student in order to be valuable in their education (Trumbull and Lash, 2013). Students generally perceive formative assessment as lower risk than summative assessment. For those who have anxiety in the classroom, the use of formative assessment can help with equity in the testing space, allowing them to perform without being inhibited by their anxiety (Buck and Trauth-Nare, 2009; Lim, 2019).

#### *3.1.4 Cramming and Spacing.*

Students may utilize a multitude of study strategies for their upcoming assessments but very often cramming is heavily relied upon to get by on tests. Cramming refers to mass practice, reviewing all the material at once, the day or days prior to an exam. Educators regularly warn their students against this habit and in-turn suggest spaced learning, spreading the study of information into many smaller sessions (Kornell, 2009; Cepeda et al., 2008). Many researchers have found that students who use spaced practice, in a variety of forms, perform better on assessments than students who cram (Hartwig and Malain, 2022; Leppänen, et al., 2016). In the role of an educator, assessments can be organized in a way that helps promote one type of study habit over another. The utilization of smaller more frequent assessments promotes study habits to shift towards spaced

practice, whereas larger, more infrequent assessments generally promote cramming due to the reliance on students to self-pace their study habits (Carpenter and Agarwal, 2020).

### *3.1.5 Environmental Influence.*

The environment in which information is presented and assessed within may also impact a student's performance and their ability to recall that information later, impacting their retention and success in future classes (Godden and Baddeley, 1975). While the goals of assessments in-person and online are the same, the variable conditions surrounding the assessment change with this environmental shift. In person, students take the same assessment, at the same time, in the same location, while online students can take their assessment at different times in different locations (Rovai, 2000). While being assessed in-person provides students with the same environment, online assessment may allow for equity in the educational space, allowing more students to be successful (Hysaj et al., 2023). Some studies have reported no difference in student performance from in-person classrooms to the online space (El Said, 2021), while others found the online space had a negative impact on student performance (Elnour et al., 2023; De Paola et al., 2023) and others, positive effects (Perez et al., 2023; Grønlien et al., 2021). Like many decisions in education, shifting to the online environment is not without its downsides as unproctored online assessments often have higher scores than other assessment environments due to dishonest academic behaviors of students (Montenegro-Rueda et al., 2021). However, studies have also investigated such concerns and found that students performed the same online compared to in-person environments, which may support students who are less anxious in locations and times of their choosing without harming the success of other students (Hollister and Berenson, 2009). Additionally, online spaces have the ability to be powerful learning environments when students are able to apply metacognitive skills, positive time management, and critical thinking to their

classes (Broadbent and Poon, 2015). Lastly, within the online environment, synchronous and asynchronous methods give students differing experiences, with the synchronous classroom perceived to be more supportive for their learning and competency (Fabriz et al., 2021). Despite the varied opinions on its use and accuracy, the online environment in comparison to the in-person environment is a setting that should be explored to understand its value in the education space.

The ability to perform well on an assessment is often due to scaffolding learning and processing of that information into memory. It allows for facts, past events, and skills to be recalled on and used today, tomorrow, and years to come when stored correctly (Sandrini and Cohen, 2014). For information to move through these stores, retrieval practice and encoding must take place. Retrieval practices are interactions with memories, pulling the information from the long-term memory into the short-term memory, or by interacting with information in the environment and connecting it to an existing memory. Retrieval practice with recently learned information can help encode knowledge into the long-term memory. At any point in the memory formation process, failures can occur leading to forgetting or decaying of information. Decay happens for a variety of reasons such as interference, when two memories conflict in fact, or retrieval failure, when the cues in the environment are unable to encourage the correct information to be retrieved (Ricker et al., 2016; Hardt et al., 2013; Godden and Baddeley, 1975). To prevent the decay of long-term memory, recalling information from long-term memory into the short-term helps to maintain a memory's integrity and accuracy over time (Ruchkin et. al., 2003). These retrieval practices can be encouraged by professors through learning tools and assessments. Homework, online low-stakes quizzes, and educational games can be used to increase student engagement with course material to promote increased retrieval practices (Roediger and Karpicke, 2006; Cadaret and Yates, 2018; Förster et al., 2018; Yu et al., 2021). Information retention is a multistep process that

relies on practice, repetition, and retrieval to form accurate and accessible memories. Educators can assist in this process by using various tools at key points in time to promote their students' interaction with class material and strengthen learning.

In education, there is a keen interest in understanding how to take information taught in the classroom and promote its preservation in long-term memory for its successful use in the future. Divergence in assessment strategy targets the interest of retrieval practice of the material, aiding in the maintenance of more durable and accurate long-term memory (Ruchkin et al., 2003). For example, changing the spacing and difficulty of assessments is intended to shift student interaction with material so that they come to their assessments working from long-term memory rather than short-term memory, accomplished by spaced studying compared to cramming, respectively (Cadaret and Yates, 2018; Carpenter and Agarwal, 2020; Cousins et al., 2018). However, there is still a lack of knowledge regarding how formative and summative assessment impacts the durability and retention of information after a course is complete. We hypothesize that a formative assessment-based classroom will encourage a higher number of retrieval practices than a summative assessment-based classroom to promote stronger long-term retention of information. Additionally, we hypothesize that the opportunity to take assessments online compared to in-person will allow for more relaxed environmental pressures allowing for better performance and retention. Thus, the objective of this study was to evaluate student performance and knowledge retention in an upper division genetics course after coming from a prerequisite course divergent in assessment strategy and environment.

### *3.2 Methods*

#### *3.2.1 Informed consent of participants.*

All procedures in this study were approved by the Colorado State University's Institutional Review Board. Study procedures took place as part of the courses, regardless of participation in the study. Students were informed of their option to participate via a survey on the Canvas learning platform, which provided information on the study, and instructed students to indicate their willingness to be involved. Data was only included from consenting individuals who passed the prerequisite course with a C or better and enrolled in the subsequent course during the study period. Students received points for completion of the post-test and survey, regardless of their participation in the study.

### *3.2.2 Prerequisite course structure.*

Foundations in Animal Genetics (ANEQ 328) is a 16-week course with two 1.25 hour lectures each week, that meets the degree requirements of an introductory genetics course for all equine and animal science majors in the Department of Animal Sciences. The course is designed to introduce key concepts related to genetics and animal breeding, including principles of molecular genetics, inheritance, familial relations, and heritability. During the study period, students completed the course in one of two environments (online or in-person) and one of two assessment types (summative or formative). ANEQ 328 was used as the prerequisite course in this study for three semesters: Fall of 2020 as a *formative online* course (FO=57); Fall of 2021 as a *formative in-person* course (FI=22); Spring of 2022 as a *summative in-person* course (SI=26).

### *3.2.3 Subsequent course structure.*

Students who successfully completed ANEQ 328 were followed into ANEQ 330: Animal Breeding. Animal Breeding is a progression of ANEQ 328 and serves as one of two options students have to meet upper division genetics requirements. It is a natural progression from ANEQ

328, focused on applying foundational principles to genomics, genetic prediction, and selection for genetic improvement.

#### *3.2.4. Assessment structure.*

Within ANEQ 328, students were assessed by either summative or formative assessments. In the summative-based classroom, 4-unit exams were administered evenly spaced throughout the semester. In the formative assessment classroom, 16 weekly quizzes were administered. The questions were identical on both the exam and quizzes and consisted of multiple choice and free response formats. These assessment strategies were also applied in one of two environments. For the in-person classroom, students receiving summative exams were allotted an entire lecture period (1.25 hours) to complete the exam. The quizzes were administered at the beginning of class time the first day of lecture every week, and students had approximately 15 minutes to complete the quizzes. For the online environment, the exams and quizzes were administered on the same timeline and utilized time limits to discourage academic dishonesty. Students were allotted 1.25 hours to complete the exams and 15 minutes for quizzes, the same amount of time provided for the in-person environment.

#### *3.2.5 Retention of knowledge.*

At the end of the semester, students were administered a post-test via the Canvas learning platform, consisting of 50 multiple choice questions, covering all the content they were introduced to during the ANEQ 328 course, to determine short-term retention of knowledge. Students were encouraged not to study, given one hour to complete the exam, and would receive full credit for completion.

In the subsequent course, ANEQ 330, a pre-test identical to the post-test in ANEQ 328, was administered in the same way at the beginning of the semester, to determine long-term

retention of knowledge (Figure 1). Students were also asked to identify in which semester they completed ANEQ 328, to determine time between courses and which assessment strategy and environment they completed the prerequisite course in.

*Perceptions of learning.* At the end of the ANEQ 328 semester, students were asked to complete an anonymous survey via the Canvas learning platform to collect student perceptions of the course format, assessment strategy employed, and general satisfaction with their learning. Students were presented with a variety of questions to rank on a Likert scale, with 1 being strongly disagree, 3 being neutral and 5 being strongly agree.

### *3.2.6 Statistical analysis*

Scores were analyzed using the MIXED procedure of SAS 9.4 (SAS Institute, Cary, NC) for the main effects of assessment strategy, environment, time between courses, and the interactions where relevant. Student performance scores on pre/post-tests and final scores were determined as the percentage of total points earned. Post-test scores were subtracted from pre-test scores and utilized as an indicator of retention of knowledge between courses. All data are presented as mean score  $\pm$  SE.

Summary statistics were performed on survey data and reported as a percentage of the total number of responses. Likert scale responses were combined for agreeance and disagreeance simplicity in that responses of 1 and 2 indicate disagreement, 3 is neutral, and 4 and 5 indicate agreement with the statement provided.

## *3.3 Results*

### *3.3.1 Short-term performance and retention*

Students who completed the prerequisite course (ANEQ 328) with a formative (quiz) assessment strategy had higher ( $P < 0.05$ ) final grades compared to students who completed the

course with a summative (exam) assessment strategy (Figure 2). Additionally, students who completed the course online, regardless of assessment type, received higher ( $P < 0.05$ ) final scores compared to those that completed the course in-person. Scores on the post-test were higher ( $P < 0.05$ ) for students in an exam-based classroom compared to those in a quiz-based classroom (Figure 3). Post-test scores did not differ between online and in-person environments.

### *3.3.2 Long-term retention*

Score on the pre-test did not differ between students who completed the prerequisite course in a quiz-based or exam-based course (Figure 4). Pre-test scores were also not influenced by environment or time elapsed between courses. Similarly, retention did not differ based on assessment type, environment, or time elapsed between courses (Figure 5).

### *3.3.3 Perceptions of learning*

Regardless of assessment format or environment that students completed ANEQ 328 in, perceptions indicated preferences for low-stakes quiz-based assessments as opposed to high stakes exams, with ~94% of students from the formative assessment classroom and ~95% of students from the summative assessment classroom agreeing over three semesters (Figure 6). Students also felt that weekly quizzes accurately demonstrated their knowledge on the assessed topics and that they could keep up with the course material in their respective formats. Students had varied opinions about the delivery of the class based on environment, with online students preferring asynchronous learning more so than the in-person student (~74% versus ~48%, respectively). However, when considered based on assessment type, preferences were similar. Despite these mixed perceptions of the online learning space, all classes generally felt confident in their preparation moving into the subsequent genetics course.

### *3.4 Discussion*

In this study, we found no differences between the use of formative assessment or summative assessment on long-term information retention for students, which offers instructors different opportunities for assessing students without negatively affecting long-term learning. Post-test performance was higher among students evaluated by summative assessment though final grades were higher in the formative assessment classroom. Pre-test performance in the subsequent semester was the same between both assessment strategies. These results were seen regardless of the environment, indicating that matching assessment styles in the short-term is valuable to student performance but over time, students can adapt to different formats. Additionally, student perceptions favored formative assessments over summative assessments, despite students from both formats highlighting their confidence in the course material and expected success in subsequent classes. Together these findings reflect an opportunity to change the style of assessments in the college curriculum to better support students' satisfaction in the learning environment without diminishing learning outcomes.

Implementing formative assessments in place of summative assessments did not impact a student's long-term information retention into the subsequent course, yet students from the formative assessment classroom had lower performance on the post-test at the end of the semester despite higher final grades. The same information was tested in both assessment types using identical questions, but the difference in testing format and space between interaction with the material may have made the post-test more difficult for the students who took formative assessments throughout the semester. For the formative assessment group, the post-test was presented in a different format than their previous assessments, which may have contributed to both increased stress and increased difficulty in this retrieval (Schwabe and Wolf, 2009), while

students who had been assessed by summative assessment throughout the semester may have felt more familiar with the assessment conditions. Additionally, the smaller volume of information assessed by weekly quizzes may have caused students to shorten the time between first exposure to information and assessment, improving performance on quizzes and improving final grades. However, shortening this period without repeated recall throughout the semester decreases information retention (Kang, 2016). To improve this portion of the formative assessment experience, subsequent quizzes could be cumulative to encourage increased interaction with previously tested material. Students studying for unit exams had increased time between first exposure of information and assessment. An increased time interval between those two key events has been shown to increase long-term retention (Cadaret and Yates, 2018; Dobson et al., 2017). However, when students from the formative assessment classroom were asked to recall information in the subsequent class, the difficult retrieval of information for the post-test may have strengthened the connection of information by functioning as a recall event. The post-test may have also encouraged learning by Bjork's retrieval effort theory and desirable difficulty framework. "Desirable difficulties" are applied when the retrieval of information is appropriately difficult for the learner, which is accomplished by asking for retrieval of information they have learned but have possibly forgotten over time. Given the effort it takes to retrieve the information, a recall that is more difficult than others is thought to strengthen the encoding, improving the duration of the memory moving forward (Bjork and Bjork, 2011; 2020). Together, these theories propose that a more difficult retrieval practice will promote better long-term retention over easy retrieval (Pyc and Rawson, 2009; Bjork and Bjork, 2011).

The environment that a student learns in and is assessed in did not impact their knowledge later in their educational career. Students were equally successful in the online space as in-person,

regardless of the format of assessment, which is interesting given the notion that online learning is thought to be less effective due to difficulty understanding the material and technical difficulties (Erlangga, 2022). While these challenges may be true, they exist in the place of other difficulties that happen in face-to-face learning. The in-person learning space can present distractions from other students, difficulty physically attending class, and technical difficulties (McCoy, 2020; Flanigan and Babchuk 2020; Tesch et al., 2011). Likewise, the online space may offer different opportunities to students than in-person spaces, promoting the success of different types of students. The online learning space offers slightly more choice to students about when they take their assessments, increased flexibility in learning schedule and equity to students who find the in-person learning space to be challenging (Castro and Tumibay, 2021; Dhawan, 2020). In contrast, the online space may put some students at a disadvantage due to their access to technology. Though possession of technology is not indicative of student success as a single factor, not being able to reliably access course content limits student success and is a significant source of stress for online students (Facer and Selywn, 2021; Zhang et al., 2022). With student performance and information retention being similar between environment, an opportunity exists to implement online assessments with in-person instruction to maximize the use of in-person class time, while also encouraging increased retrieval practices.

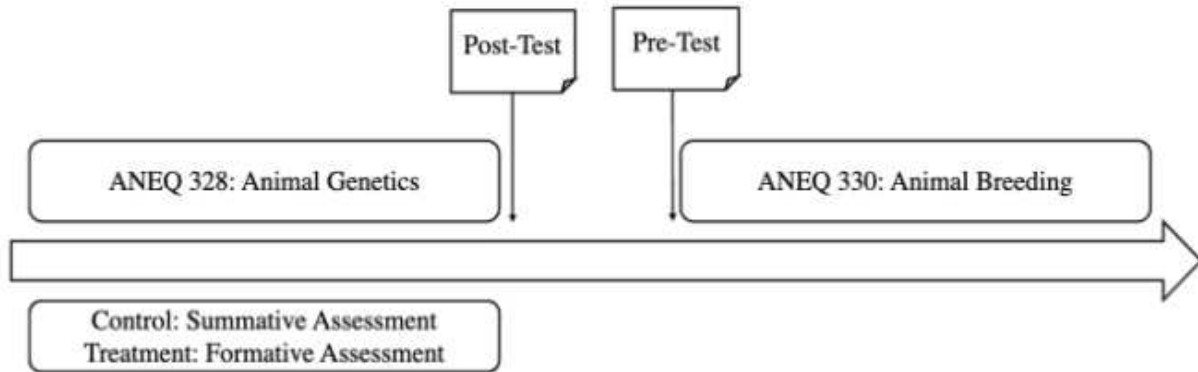
Lastly, we show that students are more satisfied and confident in a formative assessment based classroom. Though it was to be expected that students would appreciate lower stake assessment, students also cited being able to comfortably keep up with the course material and preparedness for the next course. In combination with similar long-term performance of both groups, it should be considered how student perceptions of learning affect academic performance. Prior experiences and negative and positive connotations about learning and understanding of

usefulness, are predictors of a student's academic success in the classroom (Entwistle et al., 2002; Ferreira and Santoso, 2008). The use of the favorable low-stakes assessment may not only decrease negative perceptions of the learning space but also encourage positive connotation in the classroom. Students who are more satisfied in the classroom perform better (Oja, 2011; Karemera et al., 2003; Sockalingham, 2013). Additionally, students who feel they can keep up with the course load experience lower testing anxiety than those who feel they cannot (Sansgiry and Sail, 2006). For students who have a difficult time regulating their studies and time management, the formative assessment classroom may offer equity and support to those students by encouraging them not to fall behind. Combined with similar student performance, the perception of formative assessments may lend itself as more than just a tool for student learning, but also promote later student success by supporting new confidence in the classroom. It should be acknowledged that transitioning to a classroom based in a formative assessment model can initially be challenging. The educational value of a formative assessment classroom comes from how the professor integrates the timeline of delivery between learning material, assessment, and feedback (Schildcamp et al., 2020). Tools available for professors with information about building this classroom are generic and limited, making it difficult to achieve success (Bennett, 2011; Van der Kleij et al., 2018). Beyond the workload of making an effective formative assessment classroom, the model encourages professors to learn and adapt from misunderstanding as much as it does the students (Veugen et al., 2021). Despite its effectiveness when done correctly, the barrier to entry for professors is high in establishing and maintaining a formative assessment-based classroom when compared to the use of summative assessments.

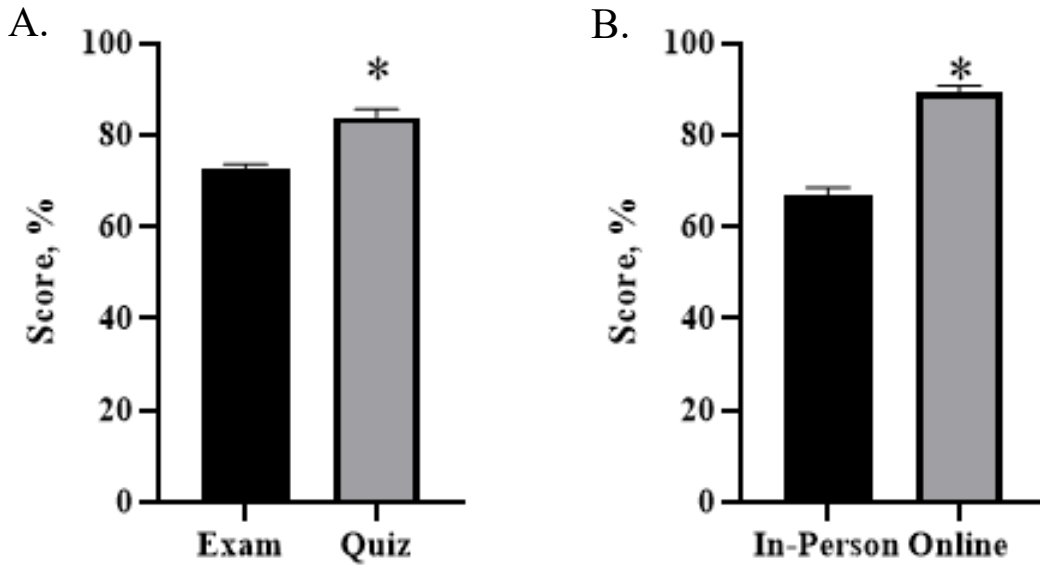
### *3.5 Implications*

Our findings demonstrate that formative and summative assessments yield similar levels of performance in subsequent classrooms. Despite the appearance of less rigor in a classroom based in formative assessment, the student's information retention is similar to that of students tested in a summative assessment classroom. Student surveys indicate that students prefer a formative assessment classroom to the alternative and feel more satisfied with the workload and their own ability to keep up in class when quizzes are used. With this information and the student perceptions of them, formative assessment can improve the quality of the student experience without compromising retention of knowledge. Instructors could reduce dissatisfaction around the course and improve student confidence in their understanding by replacing large exams with smaller quizzes containing the same information spread out over time, while continuing to produce the same level of successful students ready to take on the next course. This shift in assessments may work to improve equity in the classroom for those who struggle with test anxiety while supporting the class with more regular feedback about their performance.

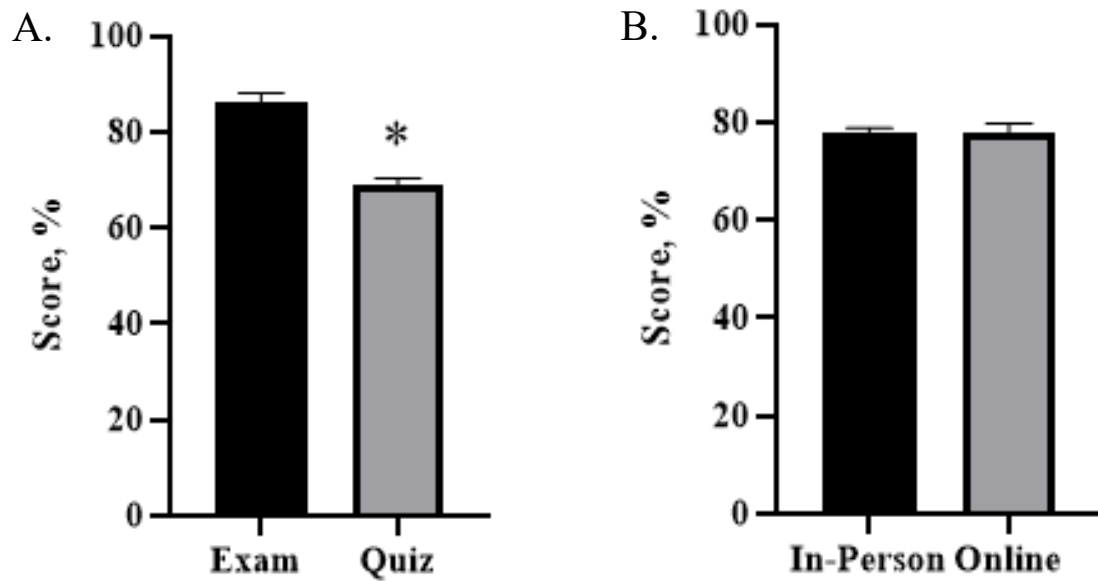
*Figures*



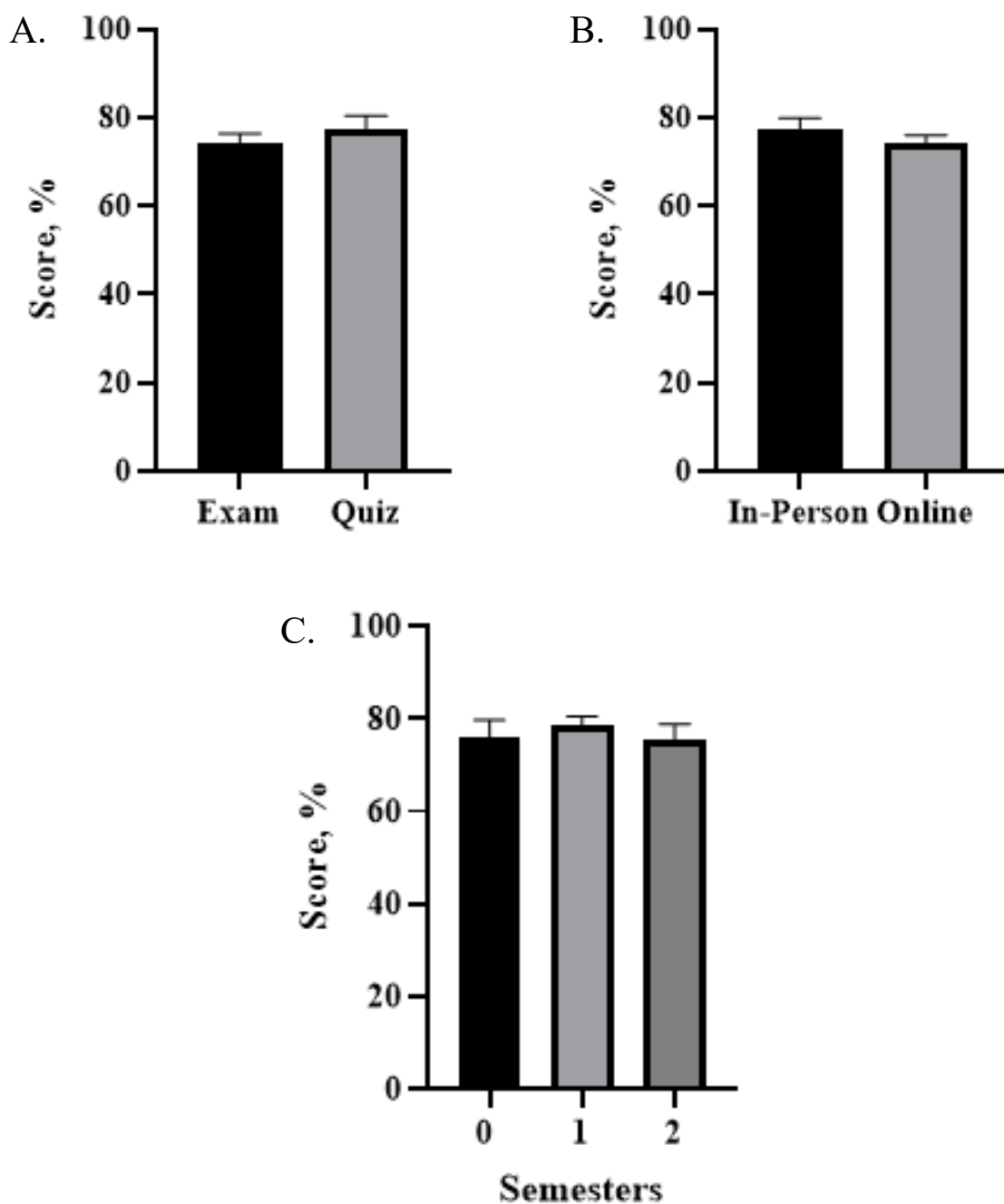
**Figure 1.** Schematic timeline of sequential courses and administration of post- and pre-test assessments in each classroom.



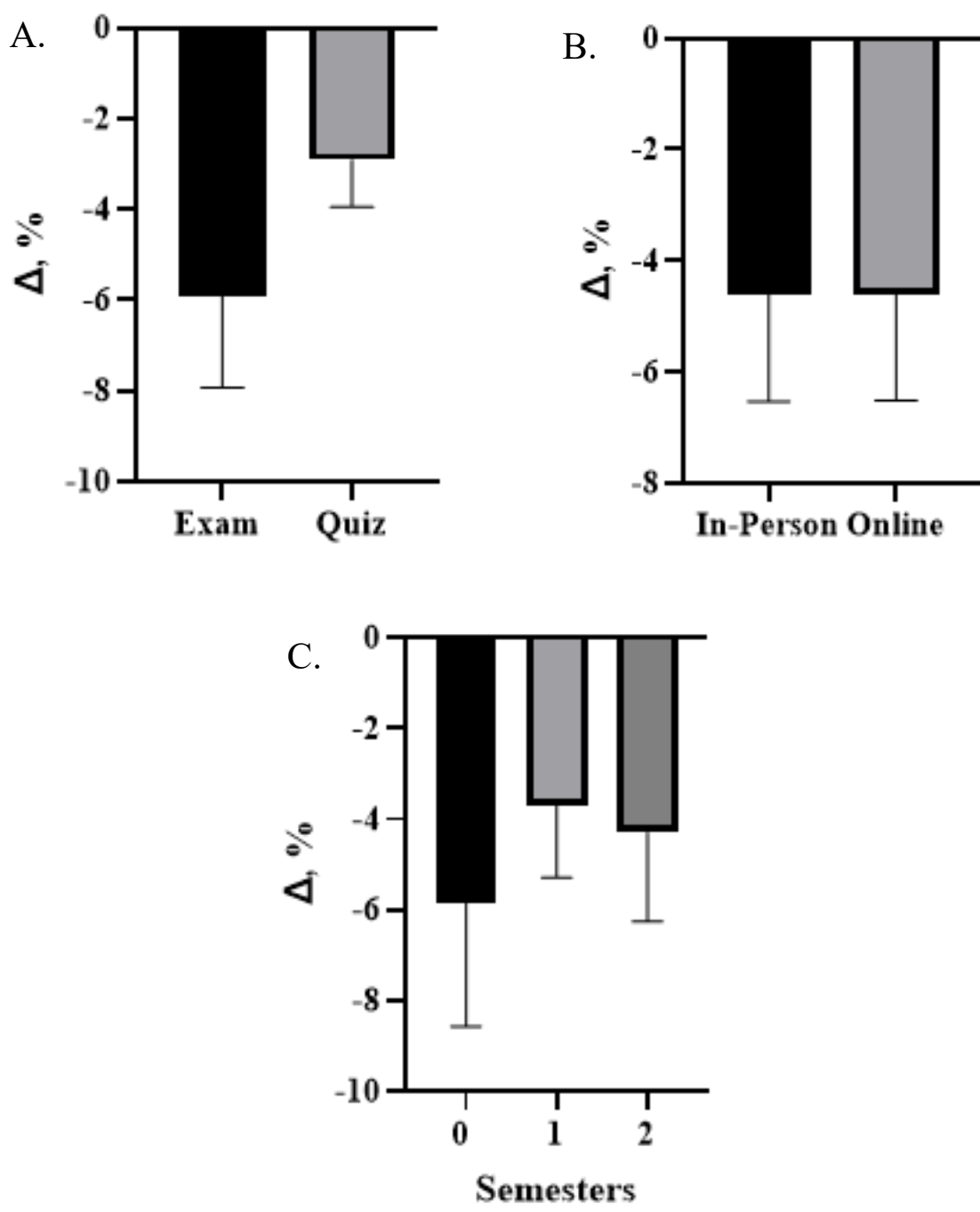
**Figure 2.** Final grade in the prerequisite course for students based on assessment strategy (A) and environment in which course was completed (B). No interactions between assessment strategy and environment were observed. \* means differ  $P < 0.05$



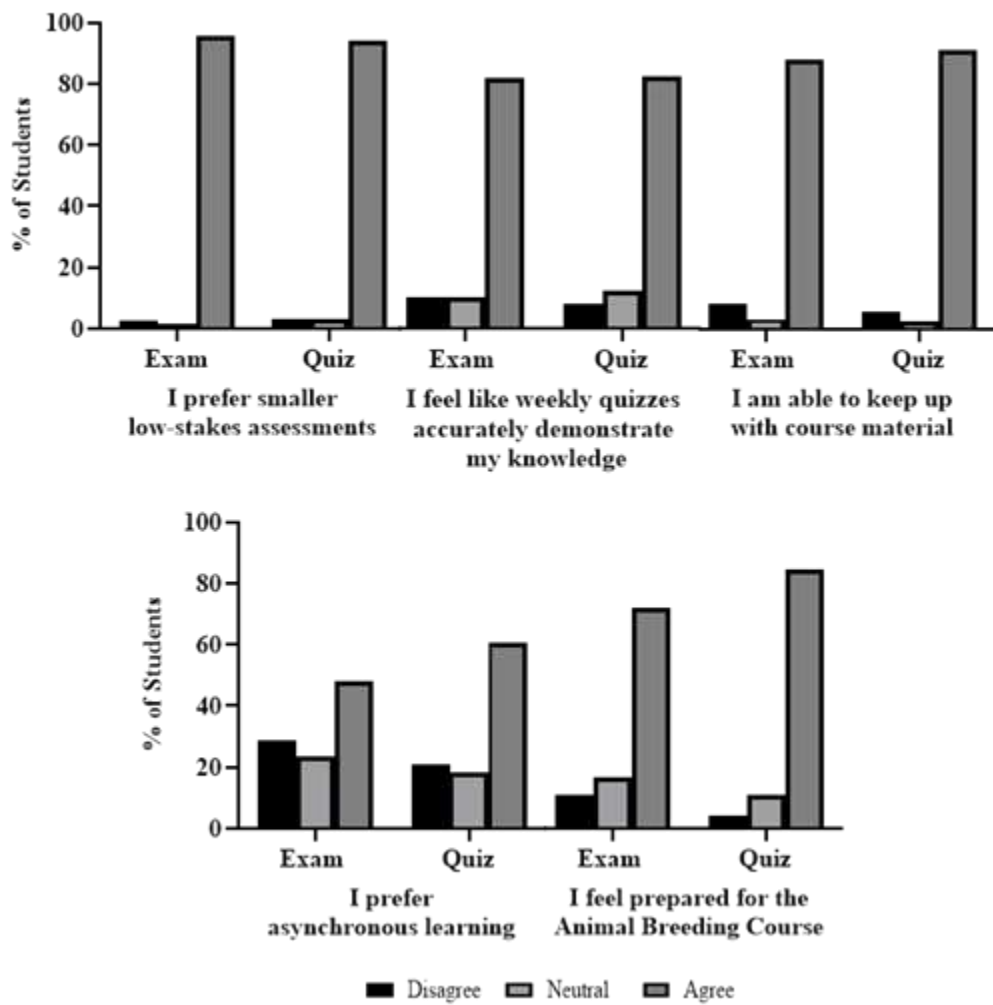
**Figure 3.** Post-test score in the prerequisite course for students based on assessment strategy (A) and environment in which course was completed (B). No interactions between assessment strategy and environment were observed. \* means differ  $P < 0.05$



**Figure 4.** Pre-test score in the subsequent course for students based on assessment strategy (A) environment in which course was completed (B), and time elapsed between courses (C). No interactions were observed.



**Figure 5.** Retention was determined as the change between scores on the post-test in the prerequisite course and scores on the pre-test in the subsequent course. Retention was evaluated for the effects of assessment strategy (A) environment in which course was completed (B), and time elapsed between courses (C). No interactions were observed.



**Figure 6.** Perceptions of course format and success between students given summative (exam) or formative (quiz) assessments.

*Literature Cited*

- Almaraz-Espinoza, A., and M. H. Grider. 2023. Physiology, Long Term Memory, StatPearls. StatPearls Publishing Copyright © 2023, StatPearls Publishing LLC., Treasure Island (FL).
- Alsaeed, N. H. 2017. Wish you were here: A psychological analysis using Atkinson-Shiffrin memory mode. *Journal of Literature and Art Studies* 6(5):521–527.
- Atkinson, R. C., and R. M. Shiffrin. 1968. Human memory: A proposed system and its control processes, *Psychology of learning and motivation* No. 2. Elsevier. p. 89–195.
- Bartsch, L. M., H. Singmann, and K. Oberauer. 2018. The effects of refreshing and elaboration on working memory performance, and their contributions to long-term memory formation. *Memory & Cognition* 46(5):796–808.
- Bell, B., and B. Cowie. 2001. The characteristics of formative assessment in science education. *Science Education* 85(5):536–553.
- Bennett, R. E. 2011. Formative assessment: A critical review. *Assessment in education: principles, policy & practice* 18(1):5–25.
- Bjork, E. L., and R. A. Bjork. 2011. Making things hard on yourself, but in a good way: Creating desirable difficulties to enhance learning. *Psychology and the real world: Essays illustrating fundamental contributions to society* 2(59-68)
- Bjork, R. A., and E. L. Bjork. 2020. Desirable difficulties in theory and practice. *Journal of Applied research in Memory and Cognition* 9(4):475.
- Black, P., and D. Wiliam. 2009. Developing the theory of formative assessment. *Educational Assessment, Evaluation and Accountability (formerly: Journal of personnel evaluation in education)* 21:5–31.
- Breed, M., and J. Moore. 2016. *Animal Behavior*. Second Edition ed. Elsevier Inc.

- Broadbent, J., and W. L. Poon. 2015. Self-regulated learning strategies & academic achievement in online higher education learning environments: A systematic review. *The Internet and Higher Education* 27:1–13.
- Buck, G. A., and A. E. Trauth-Nare. 2009. Preparing teachers to make the formative assessment process integral to science teaching and learning. *Journal of Science Teacher Education* 20(5):475–494.
- Cadaret, C. N., and D. T. Yates. 2018. Retrieval practice in the form of online homework improved information retention more when spaced 5 days rather than 1 day after class in two physiology courses. *Advances in physiology education* 42(2):305–310.
- Camos, V., P. Lagner, and P. Barrouillet. 2009. Two maintenance mechanisms of verbal information in working memory. *Journal of Memory and Language* 61(3):457–469.
- Carpenter, S. K., and P. K. Agarwal. 2020. How to use spaced retrieval practice to boost learning.
- Castro, M. D. B., and G. M. Tumibay. 2021. A literature review: efficacy of online learning courses for higher education institution using meta-analysis. *Education and Information Technologies* 26(2):1367–1385.
- Cepeda, N. J., E. Vul, D. Rohrer, J. T. Wixted, and H. Pashler. 2008. Spacing effects in learning: A temporal ridgeline of optimal retention. *Psychological science* 19(11):1095–1102.
- Cousins, J. N., K. F. Wong, B. L. Raghunath, C. Look, and M. W. L. Chee. 2018. The long-term memory benefits of a daytime nap compared with cramming. *Sleep* 42(1)
- Cowan, N. 2008. Chapter 20 What are the differences between long-term, short-term, and working memory? In: W. S. Sossin, J.-C. Lacaille, V. F. Castellucci and S. Belleville, editors, *Progress in Brain Research* No. 169. Elsevier. p. 323–338.
- Cowan, N. 2010. The Magical Mystery Four: How Is Working Memory Capacity Limited, and Why? *Current Directions in Psychological Science* 19(1):51–57.

- Daka, H., M. L. Mulenga-Hagane, M. Mukalula-Kalumbi, and S. Lisulo. 2021. Making summative assessment effective.
- De Paola, M., F. Gioia, and V. Scoppa. 2023. Online teaching, procrastination and student achievement. *Economics of Education Review* 94:102378.
- Dew, I. T. Z., and R. Cabeza. 2011. The porous boundaries between explicit and implicit memory: behavioral and neural evidence. *Annals of the New York Academy of Sciences* 1224(1):174–190.
- Dharani, K. 2015. Chapter 3 - Memory. In: K. Dharani, editor, *The Biology of Thought*. Academic Press, San Diego. p. 53–74.
- Dhawan, S. 2020. Online learning: A panacea in the time of COVID-19 crisis. *Journal of educational technology systems* 49(1):5–22.
- Dobson, J. L., J. Perez, and T. Linderholm. 2017. Distributed retrieval practice promotes superior recall of anatomy information. *Anatomical Sciences Education* 10(4):339–347.
- El Said, G. R. 2021. How Did the COVID-19 Pandemic Affect Higher Education Learning Experience? An Empirical Investigation of Learners' Academic Performance at a University in a Developing Country. *Advances in Human-Computer Interaction* 2021(1):6649524.
- Elnour, A. A., A. Abou Hajal, R. Goaddar, N. Elsharkawy, S. Mousa, N. Dabbagh, M. Mohamad Al Qahtani, S. Al Balooshi, N. Othman Al Damook, and A. Sadeq. 2023. Exploring the pharmacy students' perspectives on off-campus online learning experiences amid COVID-19 crises: A cross-sectional survey. *Saudi Pharmaceutical Journal* 31(7):1339–1350.
- Entwistle, N., V. McCune, and J. Hounsell. 2002. Approaches to studying and perceptions of university teaching-learning environments: Concepts, measures and preliminary findings. *Occasional report* 1:1–19.

- Erlangga, D. T. 2022. Student problems in online learning: Solutions to keep education going on.
- Eysenck, M. W. 1988. Models of Memory: Information Processing. In: Benzodiazepine Receptor Ligands, Memory and Information Processing, Berlin, Heidelberg. p 3–11.
- Fabriz, S., J. Mendzheritskaya, and S. Stehle. 2021. Impact of synchronous and asynchronous settings of online teaching and learning in higher education on students' learning experience during COVID-19. *Frontiers in psychology* 12:733554.
- Facer, K., and N. Selwyn. 2021. Digital technology and the futures of education: Towards 'Non-Stupid' optimism. Futures of Education initiative, UNESCO
- Felten, D. L., M. K. O'Banion, and M. S. Maida. 2016. 16 - Autonomic-Hypothalamic-Limbic Systems. In: D. L. Felten, M. K. O'Banion and M. S. Maida, editors, *Netter's Atlas of Neuroscience (Third Edition)*. Elsevier, Philadelphia. p. 421–461.
- Ferreira, A., and A. Santoso. 2008. Do students' perceptions matter? A study of the effect of students' perceptions on academic performance. *Accounting & Finance* 48(2):209–231.
- Flanigan, A. E., and W. A. Babchuk. 2022. Digital distraction in the classroom: exploring instructor perceptions and reactions. *Teaching in Higher Education* 27(3):352–370.
- Fook, C. Y., and G. K. Sidhu. 2014. Assessment Practices in Higher Education in United States. *Procedia - Social and Behavioral Sciences* 123:299–306.
- Förster, M., C. Weiser, and A. Maur. 2018. How feedback provided by voluntary electronic quizzes affects learning outcomes of university students in large classes. *Computers & Education* 121:100–114.
- Gilchrist, A. L., N. Cowan, and M. Naveh-Benjamin. 2008. Working memory capacity for spoken sentences decreases with adult ageing: Recall of fewer but not smaller chunks in older adults. *Memory* 16(7):773–787.

- Girardeau, G., and M. Zugaro. 2011. Hippocampal ripples and memory consolidation. *Current Opinion in Neurobiology* 21(3):452–459.
- Godden, D. R., and A. D. Baddeley. 1975. Context-dependent memory in two natural environments: On land and underwater. *British Journal of psychology* 66(3):325–331.
- Grønlien, H. K., T. E. Christoffersen, Ø. Ringstad, M. Andreassen, and R. G. Lugo. 2021. A blended learning teaching strategy strengthens the nursing students' performance and self-reported learning outcome achievement in an anatomy, physiology and biochemistry course—A quasi-experimental study. *Nurse education in practice* 52:103046.
- Hardt, O., K. Nader, and L. Nadel. 2013. Decay happens: the role of active forgetting in memory. *Trends in Cognitive Sciences* 17(3):111–120.
- Harlen, W., R. D. Crick, P. Broadfoot, R. Daugherty, J. Gardner, M. James, and G. Stobart. 2002. A systematic review of the impact of summative assessment and tests on students' motivation for learning. *Motivation for Learning*. EPPI-Centre, University of London.
- Hartwig, M. K., and E. D. Malain. 2022. Do students space their course study? Those who do earn higher grades. *Learning and Instruction* 77:101538.
- Hollister, K. K., and M. L. Berenson. 2009. Proctored versus unproctored online exams: Studying the impact of exam environment on student performance. *Decision Sciences Journal of Innovative Education* 7(1):271–294.
- Hysaj, A., G. Farouqa, S. A. Khan, and L. Hiasat. 2023. Reducing stress through formative assessments: a case of the digital platform. In: *International Conference on Human-Computer Interaction*. p 486–500.

- Kang, S. H. 2016. Spaced repetition promotes efficient and effective learning: Policy implications for instruction. *Policy Insights from the Behavioral and Brain Sciences* 3(1):12–19.
- Karemera, D., L. J. Reuben, and M. R. Sillah. 2003. The effects of academic environment and background characteristics on student satisfaction and performance: The case of South Carolina State University's School of Business. *College Student Journal* 37(2):298–309.
- Kibble, J. D. 2017. Best practices in summative assessment. *Advances in Physiology Education* 41(1):110–119.
- Kornell, N. 2009. Optimising learning using flashcards: Spacing is more effective than cramming. *Applied Cognitive Psychology: The Official Journal of the Society for Applied Research in Memory and Cognition* 23(9):1297–1317.
- Lee, J. L., K. Nader, and D. Schiller. 2017. An update on memory reconsolidation updating. *Trends in cognitive sciences* 21(7):531–545.
- Leppänen, L., J. Leinonen, and A. Hellas. 2016. Pauses and spacing in learning to program. In: *Proceedings of the 16th Koli Calling International Conference on Computing Education Research*. p 41–50.
- Lim, Y. S. 2019. Students' perception of formative assessment as an instructional tool in medical education. *Medical Science Educator* 29(1):255–263.
- Lindell, M. K. 2014. Judgment and decision-making, Laboratory experiments in the social sciences. Elsevier. p. 403–431.
- McCoy, B. R. 2020. Gen Z and digital distractions in the classroom: Student classroom use of digital devices for non-class related purposes. *Journal of Media Education* 11(2):5-23

- McDermott, K. B., and H. L. Roediger. 2018. Memory (encoding, storage, retrieval). *General Psychology* FA2018. Noba Project: Milwaukie, OR:117–153.
- Montenegro-Rueda, M., A. Luque-de la Rosa, J. L. Sarasola Sánchez-Serrano, and J. Fernández-Cerero. 2021. Assessment in higher education during the COVID-19 pandemic: A systematic review. *Sustainability* 13(19):10509.
- Mujawar, S., J. Patil, B. Chaudhari, and D. Saldanha. 2021. Memory: Neurobiological mechanisms and assessment. *Industrial psychiatry journal* 30(Suppl 1):S311–S314.
- Nishiyama, R. 2014. Active maintenance of semantic representations. *Psychonomic bulletin & review* 21:1583–1589.
- Oja, M. 2011. Student satisfaction and student performance. *Journal of Applied Research in the Community College* 19(1):47–53.
- Pérez, M. A., P. Tiemann, and G. P. Urrejola-Contreras. 2023. The impact of the learning environment sudden shifts on students' performance in the context of the COVID-19 pandemic. *Educación Médica* 24(3):100801.
- Pyc, M. A., and K. A. Rawson. 2009. Testing the retrieval effort hypothesis: Does greater difficulty correctly recalling information lead to higher levels of memory? *Journal of Memory and Language* 60(4):437–447.
- Ricker, T. J., E. Vergauwe, and N. Cowan. 2016. Decay theory of immediate memory: From Brown (1958) to today (2014). *Quarterly Journal of Experimental Psychology* 69(10):1969–1995.
- Roediger, H. L., and A. C. Butler. 2011. The critical role of retrieval practice in long-term retention. *Trends in cognitive sciences* 15(1):20–27.
- Roediger III, H. L., and J. D. Karpicke. 2006. Test-enhanced learning: Taking memory tests improves long-term retention. *Psychological science* 17(3):249–255.

- Rolfe, I., and J. McPherson. 1995. Formative assessment: how am I doing? *The Lancet* 345(8953):837–839.
- Rovai, A. P. 2000. Online and traditional assessments: what is the difference? *The Internet and Higher Education* 3(3):141–151.
- Ruchkin, D. S., J. Grafman, K. Cameron, and R. S. Berndt. 2003. Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences* 26(6):709–728.
- Sandrini, M., and L. G. Cohen. 2014. Chapter 9 - Effects of Brain Stimulation on Declarative and Procedural Memories. In: R. Cohen Kadosh, editor, *The Stimulated Brain*. Academic Press, San Diego. p. 237–263.
- Sansgiry, S. S., and K. Sail. 2006. Effect of students' perceptions of course load on test anxiety. *American journal of pharmaceutical education* 70(2):26.
- Schildkamp, K., F. M. van der Kleij, M. C. Heitink, W. B. Kippers, and B. P. Veldkamp. 2020. Formative assessment: A systematic review of critical teacher prerequisites for classroom practice. *International journal of educational research* 103:101602.
- Schwabe, L., and O. T. Wolf. 2009. The context counts: congruent learning and testing environments prevent memory retrieval impairment following stress. *Cognitive, Affective, & Behavioral Neuroscience* 9(3):229–236.
- Sockalingam, N. 2013. The Relation between Student Satisfaction and Student Performance in Blended Learning Curricula. *International Journal of Learning: Annual Review* 18(12)
- Tesch, F., D. Coelho, and R. Drozdenko. 2011. We have met the enemy and he is us: Relative potencies of classroom distractions. *Business Education Innovation Journal* 3(2)
- Trumbull, E., and A. Lash. 2013. Understanding formative assessment. *Insights form Learn theory Meas theory San Fr WestEd*:1–20.

- Tse, D., R. F. Langston, M. Takeyama, I. Bethus, P. A. Spooner, E. R. Wood, M. P. Witter, and R. G. Morris. 2007. Schemas and memory consolidation. *Science* 316(5821):76–82.
- Tulving, E., and D. M. Thomson. 1973. Encoding specificity and retrieval processes in episodic memory. *Psychological review* 80(5):352.
- Van der Kleij, F. M., J. J. Cumming, and A. Looney. 2018. Policy expectations and support for teacher formative assessment in Australian education reform. *Assessment in Education: Principles, Policy & Practice* 25(6):620–637.
- Veugen, M., J. Gulikers, and P. Den Brok. 2021. We agree on what we see: Teacher and student perceptions of formative assessment practice. *Studies in Educational Evaluation* 70:101027.
- Yu, Z., M. Gao, and L. Wang. 2021. The Effect of Educational Games on Learning Outcomes, Student Motivation, Engagement and Satisfaction. *Journal of Educational Computing Research* 59(3):522–546.
- Zhang, L., R. A. Carter Jr, X. Qian, S. Yang, J. Rujimora, and S. Wen. 2022. Academia's responses to crisis: A bibliometric analysis of literature on online learning in higher education during COVID-19. *British Journal of Educational Technology* 53(3):620–646.