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Ewe udder and teat traits as potential selection criteria for improvement of Merino lamb survival and growth

E.G. Smith [a,b,*], B.C. Hine [a], G.A. Acton [a], A.M. Bell [a], E.K. Doyle [b], J.L. Smith [a]

[a] CSIRO Agriculture and Food, F.D. McMaster Laboratory, Armidale, NSW 2350, Australia
[b] School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

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ABSTRACT

Neonatal lamb mortality is a major economic and welfare issue for Australian sheep producers. The contribution of udder and teat traits of the dam to the survival and subsequent growth of the lamb is relatively unknown. This study aimed to estimate phenotypic and genetic parameters associated with objectively measured and visually scored udder and teat traits in Australian Merino sheep, and to evaluate the impacts of udder and teat traits of the dam on survival and growth of their lambs to weaning. Ewes from the New England Merino Lifetime Productivity flock (n = 1341 ewes) were assessed for udder and teat traits, and phenotypic and genetic parameters for individual traits and relationships among them were estimated using linear mixed models. Odds ratios were calculated to investigate the influence of udder soundness on lamb mortality. Further, the influence of udder traits on variation in lamb weaning weight was explored. Measured udder and teat size traits were estimated to have moderate to high heritabilities (0.32 (0.09) to 0.56 (0.10)), while the heritabilities of visually scored traits were lower (0.09 (0.05) to 0.17 (0.07)). Measured traits were highly correlated genetically with their equivalent visually scored traits. The odds ratio of mortality for lambs born to ewes with unsound versus sound udders was 1.54 (95 %CI 1.1–2.2, $P < 0.05$). The odds ratio of lamb mortality from starvation compared to all other causes of death for lambs born to ewes with unsound versus sound udders was 4.62 (95 %CI 2.4–8.9, $P < 0.001$). Dam udder and teat traits collectively contributed 8 % of the variation in lamb weaning weight observed. Results suggest that targeting optimal ewe udder and teat characteristics in sheep breeding programs has the potential to significantly improve lamb survival and growth in extensive production systems.

1. Introduction

Reproductive wastage in the form of neonatal mortality is a major financial and welfare concern for sheep enterprises worldwide. In Australia, lamb mortality is the single most important health or disease issue for sheep enterprises in terms of lost productivity, and cost of treatment and prevention (Shephard et al. 2022). Neonatal lamb losses in Australian production systems are primarily attributed to dystocia/birth injury or the starvation/mismothering/exposure (SME) complex, with each accounting for approximately 40 % of neonatal deaths (Holst et al., 2002; Hinch and Brien, 2014; Refshauge et al., 2016; Jacobson et al., 2020). The SME complex is a multifactorial issue characterised by several interacting factors, of which defective udder and teat function are implicated (Jordan and Mayer, 1989). Colostrum, and subsequently milk, are integral to the survival of neonatal lambs through the provision of nutritional requirements for growth, transfer of passive immunity and aiding thermoregulatory processes (Nowak and Poindron, 2006). Mortality rates in lambs born to ewes with defective udder function were double that observed in lambs born to ewes with sound udder conformation (Moule, 1954; Hayman et al., 1955; Griffiths et al., 2019b). Milk from the dam also remains an important source of energy and protein in older lambs as they transition to pasture-based diets, especially under Australian pastoral conditions (Doney et al., 1984).

There is currently little to no selection emphasis applied to udder conformation in Merino breeding flocks in Australia, aside from independent culling of obvious faults (mastitis, bottle/balloon teats, or blind teats). Historically, udder traits have been measured using various methods, broadly categorised as typology, linear scoring, and objective measurements including technologies such as ultrasound and image analysis (reviewed Pourlis, 2020). These methods have predominantly been applied in selection for improved milk yield, udder health and suitability for machine milking in dairy sheep breeds (Fernandez et al.,

* Correspondence to: CSIRO Agriculture and Food, F.D. McMaster Laboratory, Armidale, NSW, Australia.
E-mail address: esmith76@myune.edu.au (E.G. Smith).

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1997; Casu et al., 2006), and more recently for improving survival and growth in meat sheep (Griffiths et al., 2019a, b). Overall, udder and teat traits are reported to have moderate heritabilities and show generally favourable genetic correlations (Pourlis, 2020). Traits describing udder size are also positively phenotypically and genetically correlated with milk yield (Fernandez et al., 1997; Legarra and Ugarte, 2005). This has important implications for lamb production given the well-established link between milk yield and lamb growth (Snowder and Glimp, 1991; Morgan et al., 2007; Afolayan et al., 2009). Maximising milk yield however is not the sole objective when selecting for udder traits, with udder health and ewe longevity important considerations (Pourlis, 2020). Long term selection for improved milk yield alone, without considering conformation, can inadvertently select for excessive udder depth which is associated with increased risk of mastitis and physical injury to the udder (Casu et al., 2010; Huntley et al., 2012). Therefore, a balanced selection approach is required, simultaneously targeting lamb survival and growth with ewe udder health and longevity.

The objectives of the present study were to a) provide preliminary genetic parameter estimates for objectively measured (likely more precise) and visually scored (faster and easier in large scale extensive production systems) udder and teat traits in Australian Merino sheep, to evaluate whether visual scores may be appropriate selection criteria for udder conformation traits, and (b) to investigate the relationships between udder and teat traits of the dam with survival and growth to weaning of their lambs. The hypothesis was that lambs born to ewes with unsound udders or udders with unfavourable characteristics would have lower neonatal survival and lower growth to weaning than lambs born to ewes with sound udders with desirable characteristics.

2. Materials and methods

2.1. Animals and management

All experimental procedures conducted on animals were approved by the CSIRO Armidale Animal Ethics Committee (Animal Research Authority no. 19/29). The study was conducted using animals from the New England Merino Lifetime Productivity (MLP) flock (Ramsay et al., 2019) during the 2020 calendar year. The flock was maintained and managed by CSIRO at the FD McMaster Laboratory, 'Chiswick', Uralla NSW, Australia, according to MLP Project and Australian Merino Sire Evaluation Association (AMSEA) standard protocols (AMSEA, 2020). The ewe flock was generated in 2017 and 2018 by artificial insemination from 28 genetically diverse Merino and Poll Merino sires (15 sires per year with 2 sires used in both years for across-year genetic linkage). In 2020 the number of ewes per sire group in each year ranged from 29 to 59 ewes. The ewe flock consisted of 638 2 year-old (yo) (born 2018) and 703 3 yo (born 2017) ewes (total = 1341) which produced 1617 lambs in the year the study was conducted. Of % the 1617 lambs born, 953 were to the 2017 drop, with 38.7 % being singletons; 60.0 % twins and 1.3 % triplets. A total of 664 lambs were born to the 2018 drop ewes, with 73.8 % being singletons, 26.2 % twins and no triplets.

In the study year, the 2yo and 3yo ewes were mated and lambed for the first and second time, respectively. The ewes were natural syndicate mated within age groups for 35d commencing 29th March (d0). Pregnancy scanning was conducted on d86 – 87. Lambing took place between d146 and d190. Lamb marking (tail docking and castration) was performed from d192 to d201. The lambs were weaned on d253 and d254 (median age 93d), at which time the lambs were weighed (wWT, kg). Udder and teat traits were recorded on the ewes following weaning (d255 to d257).

2.2. Data recording

2.2.1. Lambing

The ewes were lambed on 0.5 hectare plots in groups of 18–20 ewes per plot. Ewes were pre-assigned to plots, balancing for; sire of the dam, litter size scanned, and estimated lambing date from foetal age at pregnancy scan. Birth records were collected twice-daily over the lambing period. Birth data collected on lambs included; date of birth, lambing plot, maternal pedigree, sex, litter size born, birth weight and death date (where applicable). Dead lambs were collected for autopsy to determine cause of death and had DNA samples collected for paternal pedigree and confirmation of maternal pedigree. DNA samples were collected from live lambs at lamb marking for the same purpose. Other traits were also recorded at birth as assessed scores, including lambing ease (LE) and maternal behaviour (MB) (AWI and MLA, 2019). No specific udder scoring was undertaken at lambing, although any udder/teat issues observed were recorded, including mastitis and enlarged teats (blind/balloon/bottle/ bell teats). Details of issues observed, and interventions required to assist with lambing were recorded on a case-by-case basis. Intervention was provided to lambing ewes where it was deemed a welfare issue and/or that the lamb was unlikely to survive without assistance.

2.2.2. Lamb mortality and autopsy methodology

In total 262 (16.2 %) of the 1617 lambs born were classified as having died prior to weaning. This included lambs that a) died (n = 100, 6.2 % of lambs born), the majority of which were presented for autopsy (n = 86); b) those removed from their dams on ethical grounds for hand rearing due to abandonment, mismothering, or poor vigour, and which were considered unlikely to survive if left with the dam (n = 43, 2.7 % of lambs born), or c) those that were afforded intervention (but remained with their dam) that was deemed likely to have changed the survival outcome for individual lambs (and ewes) (n = 119, 7.3 % of lambs born). The latter category included lambs where there was a difficult assisted birth, aberrant maternal behaviour or udder problem where the lamb could not initially suckle unassisted. For lambs in categories b) and c), judgement was made by an experienced operator as to their likely cause of death had they been left in the field. If no firm judgement could be made, cause of death was assigned as undiagnosed. For analysis of lamb mortality data, lambs in categories b) and c) were treated as dead lambs. Neonatal lamb mortalities are generally regarded as deaths that occur within the first three to seven days of birth (Brien et al., 2014; Refshauge et al., 2016). Mortalities reported here occurred up to weaning, however the vast majority (99 %) occurred within five days of birth.

Autopsy procedures used in this study were as described by Holst (2004) and were conducted by a single trained classifier. Dead lambs were recovered from the field during daily lambing rounds and refrigerated until autopsied (usually daily). In cases of advanced decomposition in the field, severe predation, or clear autolysis *in utero*, no autopsy was conducted.

2.2.3. Udder appraisal

Ewe udder and teat traits were assessed over 3 days following weaning at an average of 95 (sd 7.8) days of lactation (DOL). Each ewe was measured and scored by a single operator for 14 individual traits as described below. These traits were recorded either with the sheep lying in a supine position on a V-belt sheep handler, or in an upright position when exiting the sheep handler. Two measured udder size traits were recorded using a flexible tape to the nearest 10 mm in a supine position; udder length (ULEN), perimeter of udder from abdomen to rear attachment; and udder width (UWID), transverse perimeter of the udder. Three visual scored udder size and conformation traits were recorded on a 1 – 5 scale in standing position using methods adapted from de la Fuente et al. (1996) and Mavrogenis et al. (1988); udder depth (UDEPTH), 1 = udder floor at abdomen (no udder/dry), 2 = udder floor approx. ¼ from attachment to hocks, 3 = udder floor approx. ½ way from attachment to hocks (optimal), 4 = udder floor approx. ¾ from attachment to hocks, 5 = udder floor at or below hocks; udder cleft (or separation) (UCLEFT), 1 = well defined cleft (optimal), 2 = flat, 3 = broken, 4 = asymmetrical (note which side), Null records - dry/minimal udder; and udder attachment (or suspension) (UATTACH), 1 =

effectively no udder(dry), 2 = depth<attachment (approx. semi-sphere), 3 = depth = attachment (approx. spherical) (optimal), 4 = depth>attachment (pendulous), 5 = extreme pendulous.

Three measured teat traits were recorded with the sheep in supine position; teat count (TCOUNT), number operational teats (i.e. functional teat canal and orifice, irrespective of teat size); teat length (TLEN), measured base to tip; and teat width (TWID), measured at base. Both TLEN and TWID were measured using a rigid ruler to the nearest 5 mm and the measurement recorded as the average of the left and right (primary) teats. Three visual scored teat size and conformation traits were recorded; teat placement (or angle) (TPLACE) in standing position, 1 = lateral (horizontal to ground), 2 = intermediate to lateral, 3 = at 45° (optimal), 4 = intermediate to medial, 5 = medial (hanging vertical) (de le Fuente et al., 1996); teat shape (TSHAPE) as per Australian Merino Sire Evaluation Association (unpublished), 1 = normal (optimal), 3 = starting to enlarge, 5 = enlarged /abnormal (comment LHS, RHS, BOTH, note enlarged teats are also referred to in industry as bottle, balloon, or bell teats); and teat lesions (LESIONS), absence (0)/presence(1) of teat lesions, from physical injury or infectious causes, (Cooper et al. 2013).

Three other udder-related traits were recorded; crutch cover (CCOV), recorded in supine position, degree of wool cover in the inguinal region, 1 = least … 5 = most (AWI and MLA, 2019); mastitis (MAST), recorded in supine position and determined by palpation and observation, 1 = normal/unaffected, 3 = resolving mastitis (mild inflammation, lump(s), diffuse hardening), 5 = active mastitis (severe inflammation, udder distortion, disfigurement, comment left, right or both sides) (adapted from Australian Merino Sire Evaluation Association, unpublished); and finally, overall udder soundness (USOUND) which encompassed wholly or partially non-operational udders and those with faults regarded to reduce functionality, 1 = sound, 0 = unsound, derived from a combination of visual scored traits including any of MAST> 1; TCOUNT< 2; UCLEFT= 4; UATTACH= 5; UDEPTH= 5; TSHAPE> 1; TPLACE= 5; any other observed abnormalities. The criteria applied to classify udders as unsound were based on findings of several previous studies and from observation within the flock under examination (i.e. udder characteristics of ewes that required intervention to aid lamb survival or ewe health due to udder problems) (Moule, 1954; Hayman et al., 1955; Fernandez et al., 1997; Casu et al., 2006; and Griffiths et al., 2019b).

2.3. Statistical methods

Two separate sets of statistical analyses were undertaken, relating to the ewes and the lambs. Udder and teat traits were analysed as response variables in the ewe analysis with various systematic effects/covariates included as explanatory variables in the statistical models. For the analyses of lamb data, lamb survival to weaning, cause of death and wWT were analysed as response variables with various systematic effects/ covariates, including dam udder traits, applied as explanatory variables in the statistical models. Both sets of analyses were conducted using ASReml (Gilmour et al., 2015).

2.3.1. Ewe traits

Of the 1341 ewes in the flock, only data from those ewes that lambed in 2020 (NLB>0) and were alive at weaning were included in analyses (n = 1223). Traits analysed were those described above (Section2.2.3), excluding the MAST and TCOUNT traits. Incidence of clinical mastitis was low (n = 10), and few ewes had less than two functional teats (n = 10), so MAST and TCOUNT were only examined at an arithmetic level. No traits were transformed prior to analysis. Univariate mixed animal models were used to identify significant fixed effects and linear covariates, and to estimate variance components and heritability of the ewe udder traits. The maternal genetic effect on the traits was also tested by fitting dam as a random effect, with likelihood ratio testing used to determine the most appropriate statistical model. Phenotypic and genetic correlations among udder traits were estimated using pairwise bivariate animal models.

Fixed effects assessed in the models when analysing udder traits were contemporary group (CG, a combination of ewe age (2 and 3yo) management group in the period between end of lambing and weaning (2 management groups per ewe age), and day of udder trait assessment following weaning (which was confounded with management group); dam source (3 levels, Chiswick Station, Breech Strike Resistant and Breech Strike Susceptible); and NLW (3 levels, 0 – 2). Litter size from the previous lactation of the 3yo ewes was not considered. Linear covariates included days of lactation (DOL); pre-mating bodyweight (WT) (as an indicator of ewe size); and WT and condition score (CS) at weaning (the time of udder assessment). Non-significant fixed effects and covariates were iteratively removed from the univariate models and were also excluded from the bivariate analyses. Interactions among main effects were not examined.

2.3.2. Lamb traits

The effect of the dam's overall udder soundness (USOUND), on a) lamb survival to weaning (wSURV) and b) cause of death, was estimated using odds ratio (OR) with 95 % CI. The OR analysis was conducted using MedCalc software (MedCalc Software Ltd, 2021).

For lambs that survived to weaning (n = 1474, includes those in category c) described above (afforded intervention and survived)), univariate mixed animal models were used to test for effects of dam udder traits on weaning weight (wWT). Maternal environmental effects were also tested by fitting dam as a random effect, and the suitability of models compared by likelihood ratio testing. In total, four statistical models were used to evaluate changes in variance component partitioning. MODEL1 (BASE) included animal as a random effect and the 'base level' fixed effects of contemporary group (CG, as described for the ewes); birth-rearing type (3 levels, born and reared single (SS), born multiple reared single (MS), born and reared multiple (MM)); and sex (2 levels, male and female). Birth weight (bWT) and age at weaning (AAW) were also fitted as linear covariates. MODEL2 comprised BASE plus the suite of dam udder traits fitted either as fixed effects (visual scored traits, UDEPTH (4 levels); UATTACH (5 levels); UCLEFT (4 levels); CCOV (4 levels); MAST (3 levels); LESIONS (2 levels); TCOUNT (2 levels); TPLACE (4 levels); TSHAPE (3 levels); and USOUND (2 levels), or linear covariates (measured traits, ULEN, UWID, TLEN, TWID). The PREDICT function of ASReml was used to estimate trait means for the different levels of fixed factors, at 100 mm increments for ULEN and UWID, and 10 mm increments for TLEN and TWID, both collectively and independently. MODEL3 comprised BASE plus the maternal genetic effect where dam was added as a second random effect. MODEL4 was MODEL2 plus the maternal genetic effect. The variance components from these four models were used to estimate and compare direct (h^2) and maternal (m^2) heritability for wWT, and to evaluate changes in the magnitude of the variance components under the different scenarios.

3. Results

3.1. Ewe udder traits

The majority of the udder and teat traits examined demonstrated variation in the population and approximated normality (Supplementary material Table A). The main exceptions were the traits assessed on few levels, specifically UCLEFT, TSHAPE, and MAST (all predominantly score 1), and LESIONS (predominantly absent (0)) which were all right skewed, and TCOUNT which was left skewed (two functional teats). The majority of ewes assessed (> 80 %) showed well-attached udders (score 3) of small to moderate size (above the hock, score 2–3), with a well-defined udder cleft (score 1), and teats of functional size (score 1), positioned at or close to 45° from vertical (score 3). UWID (predominantly 200–340 mm) was generally greater than ULEN (predominantly 150–240 mm). The large majority of ewes had TWID of 20–30 mm and TLEN 25–35 mm, although some ewes had teats up to 65 mm long.

In total, eight ewes (two 2yo's and six 3yo's) were identified as having chronic mastitis at weaning (MAST score = 3, lumps and/or diffuse hardening). A further two ewes (one 2yo and one 3yo) exhibited active mastitis (MAST score = 5). One ewe had no functional teats, and nine ewes had only one functional teat, due to a combination of inverted teats (congenital defect) and blind teats due to shearing injuries. Udders classified as being unsound (USOUND) were predominantly due to udder asymmetry (UCLEFT = 4, one half involuted (37 %), both udder halves lactating (27 %)); large teats (TSHAPE>1, 22 %); and mastitis or teat count (both 5 %). Of the ewes classified as having an unsound udder, 12 % were for more than one reason.

3.1.1. Factors influencing ewe udder traits

The significance of fixed and covariate effects on ewe udder traits are reported in Supplementary material Table B. TSHAPE was the only trait for which CG was not significant. It was not possible to specifically investigate the effects of ewe age or day of assessment on udder traits as they were confounded with management group. NLW had a significant effect (all $P < 0.001$) on all udder traits except TSHAPE and TPLACE. The effect was largely associated with differences observed between ewes that reared a lamb(s) and those that did not, rather than differences between ewes that reared one versus two lambs. Dam source (of the ewes) consistently had no effect on udder traits. The DOL had a significant effect on udder and teat size traits with udder and teat size declining with increasing DOL.

3.1.2. Variance components and heritability of udder traits

Variance components for ewe udder and teat traits estimated from mixed animal models are shown in Table 1. Maternal effect models were tested but not significantly different from those generated using animal models. The maternal heritability of udder traits was consistently less than 0.06 (0.05) or was inestimable, and therefore results are not reported here. Heritabilities (s.e. in parentheses) of the measured udder size traits were moderate (ULEN 0.35 (0.10) and UWID 0.32 (0.09)), and higher than for the visually scored udder size trait (UDEPTH 0.17 (0.07)). The measured teat size traits were moderate to highly heritable (0.44 (0.10) for TWID and 0.56 (0.10) for TLEN) and were also higher than for the visually scored teat size trait (TSHAPE 0.16 (0.06)). Heritability of the measured udder and teat size traits were generally higher than for the visually scored udder and teat size and conformation traits, which ranged from 0.02 (0.03) to 0.17 (0.07).

3.1.3. Phenotypic and genetic correlations among measured and visually scored udder and teat traits

Estimates of phenotypic and genetic correlations among udder traits are reported in Table 2. Measured udder size traits (ULEN and UWID) were highly correlated with the visually scored udder size trait (UDEPTH) both phenotypically (0.54 (0.02) and 0.57 (0.02) for ULEN and UWID respectively) and genetically (0.89 (0.06) and 0.84 (0.09) for ULEN and UWID respectively). Genetically, udder size traits (ULEN and UWID) were positively correlated (unfavourable) with UATTACH (0.60 (0.09) and 0.65 (0.20), for ULEN and UWID respectively). The measured teat size traits (TLEN and TWID) were positively correlated with the visually scored teat size trait (TSHAPE) both phenotypically (0.46 (0.02) and 0.40 (0.03) for TLEN and TWID respectively) and genetically (0.81 (0.10) and 0.77 (0.12) for TLEN and TWID respectively). There were high genetic correlations between teat dimensions (TLEN, TWID and TSHAPE) and TPLACE ranging from (0.59 (0.22) to 0.79 (0.14). Comparatively, the udder size traits were generally poorly correlated with the teat size traits.

Table 1
Additive genetic variance (V_a), phenotypic variance (V_p), and heritability (h^2) with s.e. in parentheses, for measured and visually scored udder and teat traits.

Trait	V_a	V_p	h^2
ULEN	2.07 (0.63)	5.91 (0.28)	0.35 (0.10)
UWID	3.37 (1.05)	10.63 (0.49)	0.32 (0.09)
UDEPTH	0.03 (0.01)	0.20 (0.01)	0.17 (0.07)
UCLEFT	0.01 (0.01)	0.54 (0.02)	0.02 (0.03)
UATTACH	0.04 (0.02)	0.31 (0.01)	0.11 (0.05)
TLEN	16.69 (3.59)	29.54 (1.51)	0.56 (0.10)
TWID	7.33 (1.81)	16.75 (0.81)	0.44 (0.10)
TPLACE	0.01 (0.01)	0.17 (0.01)	0.09 (0.05)
TSHAPE	0.03 (0.01)	0.18 (0.10)	0.16 (0.06)
LESIONS	0.00 (0.00)	0.05 (0.00)	Inestimable
CCOV	0.14 (0.04)	0.35 (0.02)	0.41 (0.10)

ULEN = udder length; UWID = udder width; UDEPTH = udder depth; UCLEFT = udder cleft; UATTACH = udder attachment; TLEN = teat length; TWID = teat width; TPLACE = teat placement; TSHAPE = teat shape; LESIONS = teat lesions; CCOV = crutch cover.

3.2. Lamb survival and growth

3.2.1. Neonatal mortality

Details of the cause of death assigned to lambs that actually died or were classified as dead (for the purpose of lamb survival analyses) are shown in Table 3. The predominant causes of death were dystocia/stillbirth/birth injury (35 % of mortalities) and starvation (37 % of mortalities).

The OR of mortality for lambs born to ewes with unsound versus sound udder conformation was 1.54 (95 % CI 1.09–2.19, ($P < 0.05$)). Therefore, the probability of a lamb dying if their dam had an unsound udder was estimated to be approximately 50 % greater than if their dam had a sound udder. The OR of a lamb dying from starvation (as opposed to death from all other causes combined) where their dam had an unsound versus sound udder was 4.62 (95 %CI 2.41–8.86, $P < 0.001$). The inclusion of a considerable number of theoretical deaths may be a source of bias in that analysis. However, if only actual deaths (i.e. death cause determined from autopsy) were used, the OR of a lamb dying from starvation (as opposed to any other cause) when their dam had an unsound versus sound udder remained significant at 6.86 (95 % CI 1.27–37.09, $P < 0.05$).

3.2.2. Effects of ewe udder conformation on lamb growth

Of the 1617 lambs born, 1474 survived to weaning and were included in the analysis of wWT. This included 119 lambs that survived and were reared by their dams following some form of intervention (category c) described above). Fourteen lambs survived to weaning after their dams had died between birth and weaning, but since these lambs had no dam udder traits recorded at weaning, they were excluded from the wWT analysis. Mean lamb bWT was 4.5 kg (sd 0.9, range 1.5 – 7.5 kg), mean lamb age at weaning was 91.9d (sd 7.77, range 64 – 107d), and mean wWT was 24.1 kg (sd 4.5 kg, range 10.2–38.0 kg). Sex, CG (ewe age and management group), birth-rearing type, bWT and AAW were significant effects on wWT (Supplementary material Table C).

The influence of measured and visually scored udder and teat traits on wWT were examined in two ways. Firstly, when all udder and teat traits were fitted collectively, ULEN, UWID, UDEPTH, LESIONS and CCOV had significant effects on wWT whereby ewes with larger udders, lack of teat lesions and low crutch cover tended to produce lambs of higher weaning weight. Alternatively, if fitted independently (but along with the systematic effects of CG, BRTYPE, SEX, bWT and AAW also included), ULEN, UWID, UDEPTH, UCLEFT, UATTACH, TCOUNT, TLEN, TWID, MAST and USOUND were all significant effects on wWT (Supplementary material Table D). Similarly, ewes with larger udders with better attachment, two teats, larger teats, absence of mastitis, and overall sound udders tended to rear lambs of higher weaning weight. When fitted independently, the USOUND score had an approximately 1 kg effect on wWT (23.54 (0.20) versus 24.48 (0.12) for lambs born to ewes with unsound and sound udders respectively); TCOUNT had an approximately 4 kg effect on wWT (20.15 (0.85) versus 24.36 (0.12) for lambs born to ewes with one or two operational teats respectively); and MAST had up to a 12 kg effect on wWT ((12.10 (0.25) versus 21.87 (0.74) versus 24.42 (0.12) for lambs born to ewes with active, resolving

Table 2
Phenotypic (above diagonal) and genetic (below diagonal) correlations, with heritability (bold, diagonal) with s.e. in parentheses, for measured and visually scored udder and teat traits.

	ULEN	UWID	UDEPTH	UCLEFT	UATTACH	TLEN	TWID	TPLACE	TSHAPE	CCOV
ULEN	**0.35 (0.10)**	0.64 (0.02)	0.54 (0.02)	-0.07 (0.03)	0.29 (0.03)	0.10 (0.03)	0.13 (0.03)	-0.03 (0.03)	0.03 (0.03)	-0.21 (0.03)
UWID	0.73 (0.11)	**0.32 (0.09)**	0.57 (0.02)	-0.25 (0.03)	0.32 (0.03)	0.18 (0.03)	0.25 (0.03)	0.02 (0.03)	0.09 (0.03)	-0.17 (0.03)
UDEPTH	0.89 (0.06)	0.84 (0.09)	**0.17 (0.07)**	-0.13 (0.03)	0.22 (0.03)	0.18 (0.03)	0.20 (0.03)	-0.06 (0.03)	0.07 (0.03)	-0.17 (0.03)
UCLEFT	-0.43 (0.35)	0.04 (0.69)	-0.52 (0.25)	**0.01 (0.03)**	0.15 (0.03)	-0.07 (0.03)	-0.10 (0.03)	-0.03 (0.03)	0.02 (0.03)	-0.02 (0.03)
UATTACH	0.60 (0.19)	0.65 (0.20)	-0.20 (0.25)	1.36 (0.95)	**0.11 (0.05)**	0.11 (0.03)	0.17 (0.03)	0.01 (0.03)	0.07 (0.03)	-0.08 (0.03)
TLEN	-0.05 (0.18)	0.03 (0.18)	0.12 (0.21)	0.29 (0.49)	-0.21 (0.24)	**0.56 (0.10)**	0.69 (0.02)	0.31 (0.03)	0.46 (0.02)	0.08 (0.03)
TWID	-0.09 (0.18)	0.09 (0.18)	0.20 (0.23)	-0.23 (0.53)	-0.27 (0.25)	0.78 (0.07)	**0.44 (0.10)**	0.26 (0.03)	0.40 (0.03)	0.03 (0.03)
TPLACE	-0.19 (0.26)	-0.05 (0.28)	-0.58 (0.15)	-0.52 (0.41)	-0.41 (0.30)	0.79 (0.14)	0.79 (0.15)	**0.09 (0.05)**	0.18 (0.03)	0.04 (0.03)
TSHAPE	-0.18 (0.21)	-0.10 (0.23)	-0.38 (0.17)	-0.17 (0.59)	-0.05 (0.32)	0.81 (0.10)	0.77 (0.12)	0.59 (0.22)	**0.16 (0.06)**	0.05 (0.03)
CCOV	-0.48 (0.13)	-0.18 (0.18)	-0.36 (0.17)	-0.65 (0.50)	-0.28 (0.26)	0.38 (0.17)	0.37 (0.18)	0.42 (0.27)	0.36 (0.24)	**0.41 (0.10)**

ULEN = udder length; UWID = udder width; UDEPTH = udder depth; UCLEFT = udder cleft; UATTACH = udder attachment; TLEN = teat length; TWID = teat width; TPLACE = teat placement; TSHAPE = teat shape; CCOV = crutch cover.

Table 3
Categorisation of cause of death among neonatal lambs, and number (and %) of lamb deaths where the dam was classified as unsound udder.

Death cause	Autopsy conducted[A] (n)	No autopsy conducted[B] (n)	Total dead lambs (n)	Total deaths[C] (%)	Dead lambs where dam was classified as unsound udder (n and %)
Congenital defect	2	0	2	0.9	0
Dead *in utero*/ premature	19	2	21	9.9	1 (5 %)
Dystocia/ stillbirth/ birth injury[D]	26	49[E]	75	35.4	8 (10 %)
Exposure	10	8[F]	18	8.5	2 (11%)
Infection	3	2	5	2.3	0
Misadventure	0	2	2	0.9	0
Predation	11	0	11	5.2	1 (9 %)
Starvation	10	68[G]	78	36.8	30 (39 %)
Undiagnosed	5	45[H]	50		8 (16 %)
Total	**86**	**176**	**262**		**50**

[A] Majority of lambs that actually died were autopsied for determination of cause of death
[B] Lambs removed from the paddock for ethical reasons and those that were provided some form of intervention at/or shortly after birth had no autopsy, and therefore were either assigned a probable death cause based on certain criteria or were assigned as undiagnosed
[C] Excludes undiagnosed deaths (n = 50)
[D] Combines Dystocia 1, 2 and 3 as defined by Holst (2004)
[E] Lambing ease (LE) scored ≥ 3 (AWI and MLA, 2019) which means there was significant intervention where the ewe would otherwise have been unlikely to give birth to a live lamb
[F] Chill index (Broster et al., 2012) > 1050 on the day of birth and no other known extenuating circumstances
[G] Maternal behaviour (MB) score = 5 (AWI and MLA, 2019) which means it was difficult to get the ewe to return to the lamb or it was abandoned; or dam identified with a significant udder conformation issue; both indicating the lamb would otherwise have likely died from starvation
[H] Some form of intervention provided but insufficient information to make a clear judgement on cause of death

or no evidence of mastitis, respectively).

Among the ten ewes with less than two operational teats, they gave birth to eleven lambs (one set of twins), and eight of the eleven survived to weaning achieving an average wWT of 21.9 kg. Among the ten ewes identified with mastitis at weaning, most were in the 3yo age group, and they gave birth to 16 lambs, 13 of which survived to weaning achieving an average wWT of 20.1 kg compared to the overall mean of 24.4 kg. In total, 63 ewes were identified with teat lesions and these were predominantly observed as raised healed wounds/scars. Teat lesions were more evident in the 3yo ewes (7.3 %) than the 2yo ewes (2.8 %). Similarly, 43 ewes were recorded with TSHAPE > 1 representing 5.4 % of 3yo ewes and 1.4 % of 2yo ewes.

The variance components and ratios derived from the four statistical models used to analyse lamb wWT data are presented in Table 4. By comparing BASE and MODEL2, and comparing MODEL3 and MODEL 4, udder traits of the dam contribute approximately 25 % of the variation in wWT after adjustment for the BASE level fixed effects (shown as difference in phenotypic variance). Ignoring udder traits of the dam (excluding them from the model, as in BASE) inflates the direct heritability of wWT. If udder traits of the dam are ignored and only the maternal genetic effect (MODEL3) is estimated, the phenotypic variance is reduced, and the genetic component of variation is redistributed to both the direct and maternal components with the maternal heritability being greater than the direct heritability. Adjusting for dam udder traits by including them as fixed effects and including dam as the maternal genetic component (MODEL4) further redistributes the variance and adjusts the heritability estimates with the direct component becoming greater than the maternal component.

The arithmetic variance for wWT was 19.8. By proportion of the variance component estimates from MODEL4, the base level fixed effects and covariates (CG, BRTYPE, SEX, bWT and AAW) account for approximately two-thirds (65 %) of variation in weaning weight, and collectively the dam udder traits account for approximately 8 % of the variation in weaning weight with the direct genetic, maternal genetic, and residual variances contributing approximately 6 %, 3 % and 19 %

Table 4
Variance components, additive genetic (V_a), maternal genetic (V_m), and phenotypic (V_p), direct heritability (h^2), and maternal heritability (m^2) with s.e. in parentheses, from four different statistical models for lamb weaning weight (wWT).

wWT	BASE	MODEL 2 BASE + udder traits	MODEL 3 BASE + dam as random	MODEL 4 BASE + udder traits + dam as random
Va	4.38 (1.09)	2.27 (0.61)	1.13 (0.49)	1.10 (0.45)
V_m			1.73 (0.43)	0.54 (0.29)
V_p	7.48 (0.42)	5.56 (0.27)	6.96 (0.30)	5.34 (0.23)
h^2	0.59 (0.12)	0.41 (0.10)	0.16 (0.07)	0.21 (0.08)
m^2			0.25 (0.06)	0.10 (0.05)

BASE comprised of fixed effects CG = contemporary group (incorporates dam age, management group and day of assessment); BRTYPE = birth-rearing type; SEX = gender; bWT = birth weight; age = age at weaning; and animal as random; udder traits = collective udder traits including udder length, udder width, udder depth, udder cleft, udder attachment, teat count, teat length, teat width, teat placement, teat shape, teat lesions, crutch cover, mastitis and overall udder soundness.

respectively.

4. Discussion

Measured and visually scored udder and teat traits exhibited phenotypic and genetic variation in the test population that would make them suitable candidates as selection criteria to improve ewe udder conformation, which may in turn improve lamb survival. Udder (un) soundness, which amalgamated several aspects of udder health and structure (including evidence of mastitis, less than two functional teats, and unfavourable levels of visual scored udder depth, udder cleft, udder attachment, teat size and teat placement) significantly increased neonatal lamb mortality, particularly due to starvation. Udder morphology traits of the dam were also shown to contribute to variation in weaning weight of their lambs. Although the visually scored udder traits exhibited lower heritability than the measured traits, they were well correlated with the equivalent measured traits and satisfy requirements for ease and cost of measurement to allow large numbers of animals to be assessed in a practical timeframe which are important consideration for adoption into industry breeding programs (de la Fuente et al., 1996; Rovai et al. 2004).

4.1. Phenotypic and genetic parameters for udder and teat traits

Measured udder and teat traits generally showed higher variability than did visually scored traits, which is likely associated with the continuous scale of the measures, providing better discrimination of levels of the measured traits (Rovai et al. 2004). For the scored traits there were few ewes that were scored other than one for UCLEFT (defined cleft) and TSHAPE (normal). Similarly, biological extremes (score 1 and 5) were infrequent or absent for UDEPTH, UATTACH, TPLACE and CCOV, consistent with the results of previous studies (Casu et al., 2006; Smith, 2016). This is likely a consequence of the relatively young age of the ewes, with greater variation in udder traits reported elsewhere as the age/parity of the ewe increases (McLaren et al. 2018). Systematic effects including ewe age/management, DOL, and body weight had significant effects on the ewe udder morphology traits, which has also been observed elsewhere (e.g. Crump et al. 2019) and indicates such factors should be accommodated in genetic analyses of udder and teat traits. Overall, results here suggest that useful variation in udder and teat traits exist in the Australian Merino population which would facilitate genetic improvement.

Heritabilities of measured udder and teat traits were moderate to high, ranging from 0.35 to 0.56. Charon (1993) and McLaren et al. (2018) reported heritability estimates for ULEN and UWID ranging from 0.16 to 0.40. Measured udder size (ULEN and UWID) was recorded here as perimeter measures rather than cross-sectional distance as used previously, however given the two are directly proportional, any parameter estimates from the two methods are comparable. Measured teat dimensions (TLEN and TWID) showed higher heritabilities than udder size traits (0.56 and 0.44 for TLEN and TWID, respectively) in the current study, and are comparable to estimates reported previously by Charon (1993) (TLEN 0.43, TWID 0.19), Mavrogenis et al. (1988) (TLEN 0.67, TWID 0.80), and Crump et al. (2019) (TLEN 0.42).

Visually scored traits generally had lower heritability than the measured traits. Heritabilities for UDEPTH (0.17) and UATTACH (0.11) estimated in the current study are consistent with those reported previously by McLaren et al. (2018) in Texels (0.21 and 0.14 for UDEPTH and UATTACH, respectively). However, the heritability estimates reported here for Merino sheep are lower than those reported in dairy breeds (Legarra and Ugarte, 2005; Casu et al., 2010), potentially due to breed differences, or associated with long-term selection for milking traits in the dairy populations. The heritability of UCLEFT was very low (0.01) with little phenotypic variance (the vast majority of animals in the current study scored one). Future studies on the UCLEFT trait in Merinos could investigate adjustment of the scoring scale to better discriminate degrees of udder cleft, such as was conducted previously by Casu et al. (2006) with degree of separation. Alternatively, udder asymmetry could be scored as a separate binomial trait, as reported previously (Griffiths et al., 2019a, b).

The phenotypic and genetic correlations for udder and teat traits estimated in the current study for Merinos are in broad agreement with estimates reported previously, predominantly in dairy breeds (Mavrogenis et al., 1988; Fernandez et al., 1995; Fernandez et al., 1997; Serrano et al., 2002; Legarra and Ugarte, 2005; Casu et al., 2006). The measured udder size traits (ULEN and UWID) were highly correlated both phenotypically (0.75) and genetically (0.72) and were also highly correlated genetically with the assessed udder size trait (UDEPTH) (0.87 and 0.78 for ULEN and UDEPTH respectively). Similarly, the measured teat dimensions (TLEN and TWID) were highly correlated phenotypically (0.69) and genetically (0.78), and both traits showed high genetic correlation with the visually scored TSHAPE trait (0.81 and 0.78 for TLEN and TWID respectively). At the phenotypic level these results are in agreement with those reported by Milerski et al. (2006) who also found strong phenotypic correlations (0.65–0.80) between scored and measured udder and teat size traits. Given the measured and visually scored udder and teat size traits are genetically similar, visual assessment could be expected to be a reasonable approximation of udder or teat size. Visual assessment has logistical advantages in terms of ease of measurement, with the assessment conducted in a standing position, largely without restraint, and minimal technological input. However, since the visually scored traits had lower heritability than the measured traits, there would likely be trade-off in the rate of response to selection in using a visually scored versus measured trait. In large-scale extensive production systems, the compromise between lower data precision and ease of data collection may be acceptable.

In general, the udder size traits were weakly correlated, both phenotypically and genetically, with the udder attachment, teat size and position traits, suggesting that selection for any one parameter would not necessarily confer change, or lead to overall improvement in udder soundness. Hence, changes in both udder and teat size, and udder conformation would likely require consideration of each independently. Other researchers have observed unfavourable genetic correlations between udder depth and attachment which implies that weak udder attachments are associated with deep pendulous udders (Legarra and Ugarte, 2005; Casu et al., 2006). Further, TPLACE has been shown to have a negative genetic correlation with udder depth, and positive genetic correlation with udder attachment (Fernandez et al., 1997; Legarra and Ugarte, 2005), which infers that horizontally placed teats are more prevalent among ewes with deep, poorly attached udders. Such factors are regarded to increase the risk of mastitis (due to poor drainage of milk from the udder cistern) and physical injury to the udder (Pourlis, 2020). The ewes in the current study were relatively young which may have affected expression of UDEPTH, UATTACH and TPLACE. This may explain the lack of association among udder depth and attachment, and with teat size and placement observed here, and highlights the need for further evaluation of udder and teat traits in ewes across a broad age range.

The genetic correlation between TPLACE and TSHAPE was strongly positive (0.68), which is in agreement with previous findings (Fernandez et al., 1997; Serrano et al., 2002; Legarra and Ugarte, 2005). This relationship suggests that long teats more commonly have vertical placement, and are prone to enlargement arising from accumulation of milk in the teat cisterns. Such teats are undesirable for lamb rearing as they can become too large for lambs to suckle from (Hatcher et al., 2013).

This study, which was conducted on a relatively small and specific population, and at a single point in time, has raised several questions requiring further investigation. Firstly, it was observed that in some instances udder faults identified in the ewe at birth of their lamb were not readily discernible by the time the ewe's udders were assessed at weaning. A similar finding was reported by Griffiths et al. (2019a, b) scoring across four time periods. This suggests that further work is required to determine the optimal timing of udder assessment for adoption into industry breeding programs. Secondly, accumulation of longitudinal data in lamb rearing systems is required to evaluate the repeatability of udder and teat traits within and across successive lactations, the rate of deterioration in these characteristics with age, and the impact of any changes on lifetime reproductive performance and ewe longevity.

4.2. Relationships between udder traits and lamb survival and growth

Thirteen percent of ewes in the current study were classified as having an unsound udder, primarily due to; udder asymmetry (one udder half involuted or considerably smaller than the other), very large teats, less than two functional teats or mastitis. The proportion of unsound udders was generally higher than previously reported by Hayman et al. (1955) and (Griffiths et al., 2019a), who each reported approximately 6 % unsound udders in mixed aged flocks, but lower than reported by Moule (1954) (22 % unsound). In each case slightly different definitions of udder unsoundness were applied. Nevertheless, collectively these studies demonstrate that ewes with unsound udders are unable to rear lambs as effectively as ewes with sound udders.

The overall lamb mortality was consistent with previous years in this flock and comparable to industry averages reported by Hinch and Brien, (2014). Among lambs born to dams with unsound udders, likelihood of neonatal mortality from starvation was significantly higher than from all other causes of death (OR 4.6, $P < 0.001$). To the author's knowledge, there are no previous reports that directly quantify the relationship between ewe udder soundness and lamb cause of death using autopsy findings. While Moule (1954) conducted autopsies on dead lambs, reporting 30 % of lamb mortalities were due to starvation, the proportion of starvation mortalities observed in lambs born to dams with sound versus unsound udders was not specified. Broadly, it cannot be inferred that all starvation mortalities are associated with udder unsoundness, nor can it be assumed dead lambs born to ewes with unsound udders necessarily died from starvation.

The current findings based on autopsy data are important because of the complex nature of mortality from starvation, and that it is not possible to accurately differentiate primary cause of death without autopsy, particularly among stillbirth, birth injury, starvation and exposure categorisations (Holst et al., 2002; Refshauge et al., 2016). In addition to starvation as the primary cause, starvation can frequently be a contributing factor, ensuing after a primary cause such as a birth injury. For example, lambs which sustain a brain injury at birth through hypoxia often have delayed, or encounter difficulty in suckling due to cognitive impairment (Haughey, 1980; Dwyer, 2003). Their likelihood of survival may be further hindered if the dam has an unsound udder (e.g. large teats). Improvement of neonatal survival requires knowledge of the predominant primary causes of death as well as contributing (secondary) causes to enable adoption of targeted flock-specific practices to reduce those mortalities (Hinch and Brien, 2014; Jacobson et al., 2020). Overall, the impact of unsound udders on mortality reported here indicates that culling on udder unsoundness may be a viable means of reducing the proportion of starvation related mortalities that occur in Merino lambs.

In the present study udder morphology traits collectively contributed 8 % of the overall variation in wWT. Several of the individual udder and teat traits were identified as predictors of weaning weight. Mean wWT increased by 2 kg and 4 kg with changes from 100 mm to 400 mm for ULEN and UWID, respectively. Similarly, wWT increased by a mean of 3 kg from UDEPTH score 1 (small) compared to score 3 (optimal). Higher growth rates among lambs born to ewes with intermediate udder depth scores compared to those with very small udder depth (at the abdominal wall) have also been reported by Grant et al. (2016) and Griffiths et al. (2019b). Although milk yield was not measured in the current study, associations between udder conformation and milk production are well recognised factors influencing variation in lamb growth to weaning (Grant et al., 2016; Haslin et al., 2021).

When fitted independently, measured ewe TLEN and TWID were positively associated with wWT of their lambs. Grant et al. (2016) reported a similar, small but significant positive relationship between larger teat length in ewes and average daily gain (ADG) of their lambs. This relationship may, at least in part, be influenced by the greater ability for large teats to store milk between suckling events and confer growth benefits (Rovai et al., 2004). Despite this, selection for larger teat dimensions to increase wWT is unadvisable given that large teats can be associated with increased mortalities in newborn lambs due to inability to suckle large teats. Twenty two percent of ewes with unsound udders were classified that way due to large teat size. While this does not specifically link large teats to increased lamb mortality, it does implicate enlarged teats as a contributing factor.

No influence of TPLACE on wWT was observed in the current study which is consistent with observations reported by Griffiths et al. (2019a), but is in contrast to Huntley et al. (2012) and Grant et al. (2016) who found that ewes with TPLACE at 45° to vertical (Score 3) produced significantly heavier lambs than did ewes with teats placed more vertically or horizontally. This finding led those authors to conclude that Score 3 is the optimum teat position for lamb suckling which contrasts with the optimal (vertical) teat placement for machine milking of dairy ewes (Labussière 1988). Regardless of any association between TPLACE and wWT, evidence linking horizontal and vertical teat placement with reduced mammary gland health and increased propensity of trauma to the teat have been documented (Legarra and Ugarte, 2005; McLaren et al., 2018).

Ewes with udder asymmetry (UCLEFT score 4) weaned lambs that were 1.5 kg lighter compared to lambs born to ewes with well-defined udder cleft (score 1). Supporting this finding, Griffiths et al. (2019a) observed an approximately 8 % reduction in ADG to weaning when the ewe's udder was asymmetric. The development of an asymmetric udder is in part an acquired condition, which is suggested to arise when the lamb does not suckle from one side of the udder. Causes for this phenomenon are not well known, however subclinical mastitis and impaired teat function (enlarged teat or small orifice) have been suggested (Rovai et al., 2004). Both the current study and that of Griffiths et al. (2019a), only assessed ewes over a single lactation so it is not known if udder asymmetry is recurrent across lactations.

When considered independently from other udder traits, mastitis of the dam (both acute and chronic) had a significant impact on the wWt of their lambs. However, the errors associated with this estimate are large due to the low frequency of mastitis cases (0.8 %) observed. Despite this, growth retardation of lambs due to clinical mastitis of their dam is well documented and attributable to both reduced milk quality and quantity (Grant et al., 2016; McLaren et al., 2018; Griffiths et al., 2019a). The magnitude of growth retardation is dependent on the stage of the lactation when the infection occurs and the speed with which the infection is resolved (Griffiths et al., 2019a). Zeleke et al. (2023) showed that ewes identified with lumps or hardening of the udder (arising from mastitis) at any time point within a reproduction year were at ongoing risk of udder defects within that year and in subsequent years. The current investigation did not consider the effects of subclinical mastitis on wWT.

5. Conclusion

Several individual ewe udder and teat traits showed variation and moderate heritability in Australian Merinos. The visually scored udder and teat traits generally showed lower heritability than the measured traits, but the visually scored traits were highly correlated genetically with their measured counterparts. Udder and teat dimension traits were genetically correlated with some of the important udder structure traits. However, udder size traits were only weakly genetically correlated with the teat size traits. Overall, and together with the relative ease to conduct visual scores over measurements, the genetic parameters for visually scored traits suggest they are suitable selection criteria for ewe udder conformation. Ewe udder soundness, which was a binomial trait integrating aspects of several visually assessed udder and teat traits, significantly influenced the risk of neonatal lamb mortality due to starvation. Collectively, the ewe udder and teat traits contributed significantly to variation in lamb weaning weight. This suggests that attention to ewe udder and teat characteristics in breeding programs has the potential to improve lamb survival and growth in extensive production systems.

CRediT authorship contribution statement

Erin Smith: Conceptualisation, Investigation, Formal analysis, Writing – Original draft. **Brad Hine:** Conceptualisation, Supervision, Writing - Review & Editing. **Graham Acton:** Investigation. **Amy Bell:** Investigation. **Jennifer Smith:** Conceptualisation, Investigation, Writing - Review & Editing. **Emma Doyle:** Supervision, Writing - Review & Editing.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Data Availability

The data used in this study has not been deposited in an official repository, but may be made available from the authors upon request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.smallrumres.2023.107019.

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