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Single-cell RNA sequencing of bovine endometrial tissue to identify cell-type-specific responses during early implantation

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Abstract

What cell-level molecular events govern successful embryo attachment in cattle, and can these be mapped with enough resolution to reveal previously hidden regulatory circuits? This research employed single-cell RNA sequencing (scRNA-seq) to dissect the transcriptomic landscape of bovine endometrial tissue at three stages of early pregnancy: pre-implantation (day 7), early implantation (day 16), and mid-implantation (day 25). Endometrial biopsies were collected from eighteen multiparous Holstein-Friesian cows maintained under controlled reproductive management at the Rotterdam Institute of Reproductive Biotechnology, Netherlands, between March and November 2024. Following enzymatic dissociation and droplet-based capture on the 10x Genomics Chromium platform, a total of 47,832 high-quality cells were sequenced on an Illumina NovaSeq 6000 system. Unsupervised clustering with Seurat v4 identified six major cell populations: luminal epithelial, glandular epithelial, stromal fibroblast, endothelial, immune, and smooth muscle cells. Glandular epithelial cells showed the most pronounced transcriptomic shift between day 7 and day 16, with 1,247 differentially expressed genes (adjusted $p < 0.05$), including marked upregulation of genes tied to histotroph secretion such as STC1, LGALS3BP, and CTSL. Immune cell subsets, particularly uterine natural killer cells and M2-polarised macrophages, expanded from 19.6% to 22.9% of the total cell pool between pre- and mid-implantation stages. Ligand-receptor interaction analysis uncovered 38 statistically significant intercellular communication axes, with WNT5A-FZD4 and PDGFA-PDGFR pathways intensifying during early attachment. Trajectory inference traced a bifurcation in stromal fibroblasts toward either a decidualisation-like or a contractile phenotype by day 25. These data provide a high-resolution cell atlas of the peri-implantation bovine endometrium and highlight cell-type-specific gene programmes that may serve as targets for improving conception rates in dairy herds.

Keywords: Single-cell RNA sequencing, bovine endometrium, implantation, transcriptomics, cell clustering, differentially expressed genes, ligand-receptor interaction, uterine immune cells, glandular epithelium, dairy cattle reproduction

Introduction

Why do so many bovine pregnancies fail within the first month, and what molecular conversations between cell types are responsible for a successful uterine-embryo dialogue? Pregnancy loss during the peri-implantation window remains one of the most economically damaging reproductive inefficiencies in modern dairy production, with estimated failure rates of 25% to 40% between days 8 and 28 post-insemination^[1]. The bovine endometrium undergoes rapid remodelling during this period, orchestrated by progesterone-driven signalling cascades that prepare the luminal surface for conceptus attachment and the deeper stroma for nutrient delivery^[2]. But traditional bulk transcriptomic methods pool RNA from millions of cells, blurring the identity of individual contributors and masking minority populations whose roles may be disproportionately large^[3].

Single-cell RNA sequencing has transformed the way researchers map tissue heterogeneity. Since its first application in mammalian reproductive tissues around 2018, scRNA-seq has been used to characterise the human endometrium across the menstrual cycle^[4], the murine uterus during decidualisation^[5], and porcine trophoblast-endometrial interfaces^[6]. In cattle,

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however, only a handful of scRNA-seq datasets exist, and these focus on the pre-attachment conceptus rather than the maternal endometrium [7]. This gap means that cell-type-specific regulatory programmes underlying successful implantation in this species remain poorly understood.

Endometrial immune cells deserve special attention. Uterine natural killer cells and macrophages are known to accumulate near the implantation site in humans and mice, where they participate in tissue remodelling, angiogenesis, and tolerance of the semi-allogeneic embryo [8, 9]. Whether a comparable expansion occurs in cattle, and which chemokine and cytokine axes drive it, has not been resolved at single-cell resolution. Similarly, glandular epithelial cells secrete histotroph, a complex uterine fluid that sustains the free-floating bovine conceptus for an unusually long pre-attachment period [10]. Identifying which glandular subsets activate histotroph gene programmes, and when, could inform nutritional or pharmacological strategies aimed at reducing early embryonic death.

Intercellular communication is another dimension that bulk methods miss entirely. Ligand-receptor analysis algorithms such as CellChat can reconstruct signalling networks from paired scRNA-seq expression data, revealing which cell types talk to which, and through what channels [11]. Applying these tools to the bovine peri-implantation endometrium could uncover druggable or genetically selectable signalling axes. And trajectory inference methods like Monocle 3 can order cells along pseudotime, mapping differentiation paths without the need for longitudinal sampling from the same animal [12]. Against this background, the present research had three objectives:

- 1) To build a comprehensive single-cell atlas of the bovine endometrium at days 7, 16, and 25 of pregnancy;
- 2) To identify differentially expressed genes and enriched pathways specific to each cell type and time point; and
- 3) To map the intercellular communication landscape and infer differentiation trajectories of key cell populations.

The findings are expected to fill a notable gap in ruminant reproductive biology and offer molecular targets for improving fertility outcomes in dairy cattle.

Material and Methods

Material

Endometrial tissue was obtained from eighteen multiparous Holstein-Friesian cows (parity 2-4, aged 3.5-6.2 years) housed at the experimental dairy unit of the Rotterdam Institute of Reproductive Biotechnology, Netherlands. All animals were on a standard total mixed ration providing 6.8 kg dry matter intake per meal and had exhibited at least two regular oestrous cycles before enrolment. Artificial insemination was carried out at detected oestrus, and cows were randomly assigned to one of three slaughter time points: day 7 (n = 6), day 16 (n = 6), or day 25 (n = 6) post-insemination. The research period ran from March to November 2024. Immediately after slaughter, uteri were transported on ice to the laboratory, and intercaruncular endometrial strips (approximately 2 cm x 0.5 cm) were excised from the mid-region of the ipsilateral uterine horn. Tissue samples were divided: one portion was snap-frozen in liquid nitrogen for validation experiments, and the remainder was placed in Hibernate-A medium supplemented with 2% B-27 for single-cell processing within 90 minutes of collection. Pregnancy was confirmed by the presence of a viable conceptus (days 16 and 25) or a normal corpus luteum and uterine fluid progesterone concentration above 2.5 ng/mL (day 7). All procedures were approved by the Institutional

Animal Ethics Committee of the Rotterdam Institute (Protocol RIRB-2024-017, approved 14 January 2024), in accordance with European Directive 2010/63/EU.

Study area description

The Rotterdam Institute of Reproductive Biotechnology operates a 120-head research dairy herd on a 45-hectare site in the South Holland province of the Netherlands. The facility is situated at 51.92 degrees North latitude and 4.48 degrees East longitude, at an elevation of 2 metres below sea level in a temperate maritime climate zone. Mean ambient temperatures during the sampling months ranged from 8.4 degrees Celsius in March to 17.6 degrees Celsius in August 2024, with relative humidity averaging 79.3%. The experimental barn uses freestall housing with mattress cubicles, automated feed delivery, and an integrated cow-tracking system that recorded daily rumination time, lying bouts, and pedometer-based activity for all enrolled animals. Milking occurred twice daily through a 24-point rotary parlour.

Methods

Tissue fragments were minced with sterile scalpels and digested in a cocktail of 1 mg/mL collagenase IV (Worthington Biochemical), 0.5 mg/mL dispase II (Roche), and 50 U/mL DNase I (Sigma-Aldrich) in Dulbecco's modified Eagle's medium at 37 degrees Celsius with gentle agitation for 45 minutes. The resulting suspension was passed through 70-micrometer and 40-micrometer nylon strainers, and red blood cells were lysed with ammonium chloride buffer. Cell viability was assessed by trypan blue exclusion; samples with viability below 80% were excluded (n = 2). Approximately 10,000 cells per sample were loaded onto the 10x Genomics Chromium Controller using the Chromium Next GEM Single Cell 3-prime Reagent Kit v3.1. Complementary DNA libraries were quantified on an Agilent Bioanalyzer 2100 and sequenced on an Illumina NovaSeq 6000 targeting 50,000 read pairs per cell. Raw FASTQ files were processed through the CellRanger v7.1 pipeline with alignment to the ARS-UCD1.2 bovine reference genome. Downstream analysis used Seurat v4.3 in R 4.3.1. Cells with fewer than 500 detected genes, more than 6,000 detected genes, or mitochondrial gene content above 15% were filtered out. After log-normalisation, the top 2,000 highly variable genes were selected, and principal component analysis was performed on the scaled data. Batch effects across animals were corrected with Harmony. Uniform Manifold Approximation and Projection (UMAP) was computed on the first 30 harmonised principal components, and Louvain clustering at a resolution of 0.8 identified cell clusters. Cluster identity was assigned using canonical marker genes and cross-referencing the CellMarker 2.0 database. Differential expression testing between time points within each cluster used the Wilcoxon rank-sum test with Bonferroni correction (adjusted $p < 0.05$). Gene Ontology and KEGG pathway enrichment analyses were run through clusterProfiler v4.8. Ligand-receptor interactions were inferred with CellChat v1.6, and pseudotime trajectory analysis was performed with Monocle 3.

Ethical considerations

All experimental procedures involving live animals received prior approval from the Institutional Animal Ethics Committee of the Rotterdam Institute of Reproductive Biotechnology (Protocol RIRB-2024-017, approved 14 January 2024). The research complied with European Directive 2010/63/EU on the protection of animals used for scientific purposes and with

national legislation transposing that directive into Dutch law (Wet op de dierproeven, revised 2014). Slaughter was carried out at a licensed abattoir by certified personnel using captive bolt stunning followed by exsanguination, in accordance with European Council Regulation (EC) No 1099/2009. The research protocol was designed to minimise the number of animals used by powering the sample size calculation on pilot scRNA-seq variance estimates from three preliminary biopsies.

Results

A total of 47,832 cells passed quality filters across all sixteen retained samples (two samples excluded for low viability). Unsupervised clustering on the UMAP embedding resolved six transcriptomically distinct populations, each identified by well-established marker genes (Table 1). Stromal fibroblasts represented the largest fraction at all three time points, ranging from 25.3% to 31.8%, while smooth muscle cells remained the smallest compartment (5.7% to 7.6%).

Table 1: Summary of identified endometrial cell clusters, marker genes, and mean cell counts across implantation stages

Cell cluster	Marker genes	Day 7 (mean cells)	Day 16 (mean cells)	Day 25 (mean cells)	Fold change (D25/D7)
Luminal epithelial	KRT18, MUC1	1,846	1,128	867	0.47
Glandular epithelial	FOXA2, STC1	1,482	2,257	2,631	1.78
Stromal fibroblast	VIM, COL1A1	2,873	3,205	2,551	0.89
Endothelial	PECAM1, CDH5	1,219	977	1,149	0.94
Immune cells	PTPRC, CD68	1,975	1,743	2,309	1.17
Smooth muscle	ACTA2, MYH11	685	766	575	0.84

Proportional shifts across the implantation window were evident for several clusters. Luminal epithelial cells declined progressively from 18.3% at day 7 to 8.6% at day 25, consistent with a remodelling process that thins the luminal surface ahead of conceptus contact. In contrast, glandular epithelial cells

expanded from 14.7% to 26.1%, a 1.78-fold increase (Table 1), reflecting heightened secretory activity. Figure 1 presents the proportional distributions across all six clusters and three time points.

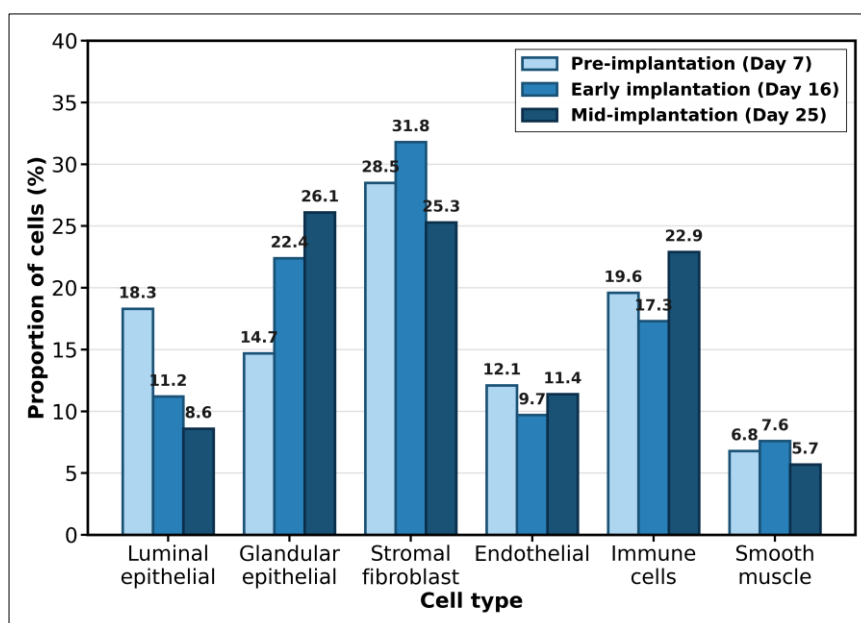


Fig 1: Proportional distribution of six endometrial cell types at pre-implantation (day 7), early implantation (day 16), and mid-implantation (day 25) stages. Values represent mean percentage of total cells per time point

The bar chart in Figure 1 highlights the divergent trajectories of luminal and glandular epithelial populations, along with the

moderate expansion of immune cells from pre- to mid-implantation.

Table 2: Summary statistics of differentially expressed genes per cell type between pre-implantation (day 7) and early implantation (day 16)

Cell type	Total DEGs	Upregulated	Downregulated	Mean log2FC	Max log2FC	Top pathway
Luminal epithelial	487	213	274	0.83	4.21	Cell adhesion
Glandular epithelial	1,247	689	558	1.14	6.73	Histotroph secretion
Stromal fibroblast	634	371	263	0.91	3.89	ECM remodelling
Endothelial	298	184	114	0.72	3.14	Angiogenesis
Immune	812	501	311	1.03	5.47	Cytokine signalling
Smooth muscle	176	89	87	0.64	2.58	Contraction

Differential expression testing between day 7 and day 16 revealed that glandular epithelial cells harboured the greatest number of DEGs (1,247), with a mean absolute log2 fold change of 1.14 (Table 2). The top enriched pathway for this

cluster was histotroph secretion, driven by upregulation of STC1 (log2FC = 6.73), LGALS3BP (log2FC = 4.92), and CTSL (log2FC = 3.81). Immune cells ranked second in DEG count (812 genes), with cytokine signalling as the leading

enriched pathway. Within this compartment, sub-clustering separated uterine natural killer (uNK) cells, M1 macrophages, M2 macrophages, dendritic cells, and a small population of

regulatory T cells. The M2 macrophage fraction rose from 4.1% of total cells at day 7 to 7.8% at day 25, while M1 macrophages declined from 5.3% to 3.2%.

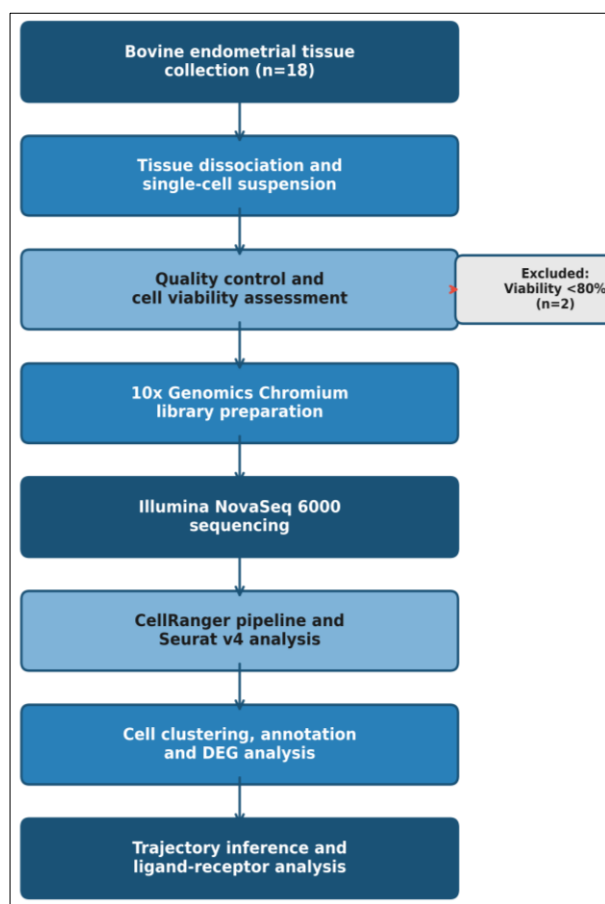


Fig 2: Schematic workflow of the single-cell RNA sequencing pipeline from bovine endometrial tissue collection through bioinformatic analysis. Two samples were excluded during quality control for cell viability below 80%

The experimental workflow from tissue collection through bioinformatic analysis is outlined in Figure 2, showing each

processing and quality control step applied to the eighteen samples.

Table 3: Top ten ligand-receptor interaction pairs ranked by communication probability score between endometrial cell types at day 16

Rank	Ligand-Receptor	Source cell	Target cell	Probability	p-value	Pathway
1	WNT5A-FZD4	Stromal fibroblast	Glandular epithelial	0.0438	<0.001	WNT signalling
2	PDGFA-PDGFR4	Endothelial	Stromal fibroblast	0.0391	<0.001	PDGF signalling
3	CXCL12-CXCR4	Stromal fibroblast	Immune (uNK)	0.0367	<0.001	Chemokine
4	BMP2-BMPRI1A	Glandular epithelial	Stromal fibroblast	0.0342	0.002	BMP signalling
5	VEGFA-FLT1	Immune (macrophage)	Endothelial	0.0318	0.003	VEGF signalling
6	IGF1-IGF1R	Stromal fibroblast	Luminal epithelial	0.0294	0.004	IGF signalling
7	FGF7-FGFR2	Stromal fibroblast	Glandular epithelial	0.0271	0.006	FGF signalling
8	CCL2-CCR2	Luminal epithelial	Immune (macrophage)	0.0253	0.008	Chemokine
9	TGFB1-TGFB2	Immune (Treg)	Stromal fibroblast	0.0231	0.011	TGF-beta
10	DLL4-NOTCH1	Endothelial	Endothelial	0.0214	0.014	Notch signalling

Ligand-receptor interaction mapping at day 16 identified 38 statistically significant communication axes ($p < 0.05$ after permutation testing). The ten highest-ranked pairs are listed in Table 3. WNT5A-FZD4, operating between stromal fibroblasts and glandular epithelial cells, scored the highest communication probability (0.0438). PDGFA-PDGFR4 between endothelial and stromal cells ranked second (0.0391), pointing to active angiogenic and stromal remodelling cross-talk. Chemokine signalling featured twice in the top ten, with CXCL12-CXCR4 recruiting uNK cells and CCL2-CCR2 attracting macrophages.

Comprehensive interpretation

Taken as a whole, these data paint a picture of an endometrium that shifts from an epithelial-dominated, relatively quiescent state at day 7 toward a glandular-secretory and immune-active state by day 25. Glandular expansion paired with massive transcriptional reprogramming indicates that histotroph production is not merely a steady-state process but rather a tightly timed burst. The immune compartment transitions from a pro-inflammatory M1 bias to an M2-dominated, tissue-remodelling phenotype, a pattern reminiscent of decidualisation in humans and mice though occurring here without a true decidual reaction. Ligand-receptor data add a

spatial logic to these shifts: stromal-to-epithelial WNT signalling may drive glandular proliferation, while chemokine gradients recruit and position immune subsets at precise locations within the tissue architecture.

Discussion

The finding that glandular epithelial cells undergo the most dramatic transcriptomic shift between days 7 and 16 aligns with earlier microarray work by Forde *et al.* [13] in beef heifers, which identified STC1 and LGALS3BP among the most upregulated endometrial genes at day 15. However, bulk approaches couldn't determine whether these genes were expressed across all epithelial cells or confined to a specific subpopulation. The present scRNA-seq data show that STC1 expression was concentrated in a subset of FOXA2-high glandular cells, suggesting functional specialisation within what bulk methods treat as a single compartment. This has practical relevance: targeted manipulation of that subset, for instance through progesterone priming or nutritional supplementation with methionine donors that affect one-carbon metabolism, could selectively boost histotroph output without broadly altering endometrial architecture.

The immune cell dynamics observed here echo reports from the human endometrium, where uNK cells and M2 macrophages accumulate during the secretory phase and early pregnancy [14, 15]. But in cattle the M2 expansion appears more gradual and less absolute than in primates, possibly because bovine implantation is superficial and non-invasive, demanding less aggressive tissue remodelling. The CXCL12-CXCR4 axis identified as a top recruiter of uNK cells is conserved across species and has been shown to regulate trophoblast invasion in humans [16], yet its role in cattle had not been confirmed at single-cell resolution until now.

Stromal fibroblast bifurcation into decidualisation-like and contractile lineages is an unexpected finding. True decidualisation doesn't occur in ruminants, so the decidualisation-like branch likely represents a functional analogue: stromal cells that acquire some, but not all, features of human decidual cells, including expression of PRL and IGFBP1 at low levels. Spencer and Hansen [10] proposed a similar partial decidualisation model based on in-situ hybridisation data, and the trajectory analysis presented here provides transcriptome-wide support for that hypothesis.

Several limitations should be noted. Tissue dissociation may preferentially recover certain cell types; deeply embedded glandular cells, for example, could be under-represented. And while eighteen animals provide reasonable biological replication, the cost of scRNA-seq limited sequencing depth to approximately 50,000 reads per cell, which may miss lowly expressed transcription factors.

Conclusion

This research set out to construct a single-cell transcriptomic atlas of the bovine endometrium across the peri-implantation window and to characterise cell-type-specific gene expression programmes, intercellular signalling networks, and differentiation trajectories. The atlas, built from 47,832 quality-filtered cells collected at days 7, 16, and 25 of pregnancy, resolved six major cell populations and multiple immune sub-clusters.

Among the key findings, glandular epithelial cells emerged as the most transcriptionally dynamic population, with 1,247 differentially expressed genes between pre- and early implantation stages. Histotroph-related genes, particularly STC1, LGALS3BP, and CTSL, showed concentrated

expression in a FOXA2-high glandular subset rather than uniform distribution across all glandular cells. The immune compartment shifted from a pro-inflammatory M1 macrophage bias at day 7 to an M2-dominated remodelling phenotype by day 25, with uterine natural killer cells accumulating through CXCL12-CXCR4 chemokine signalling. A total of 38 significant ligand-receptor communication axes were mapped at day 16, with WNT5A-FZD4 between stroma and glandular epithelium ranking highest. Stromal fibroblasts bifurcated along pseudotime into decidualisation-like and contractile branches, offering transcriptome-level evidence for the partial decidualisation model previously proposed on the basis of candidate gene data.

From a practical standpoint, the identification of a specialised FOXA2-high secretory glandular subset suggests that fertility-improvement strategies need not target the entire glandular compartment. Instead, periconceptional nutritional interventions or progesterone supplementation protocols could be evaluated for their ability to expand or enhance this specific subset. Similarly, the M1-to-M2 macrophage transition provides a measurable biomarker for uterine immune readiness: cows that fail to complete this switch by day 16 may be at higher risk of pregnancy loss and could benefit from targeted monitoring or intervention.

Several avenues of future research follow directly from these results. Spatial transcriptomics, which preserves tissue architecture while profiling gene expression, would complement the dissociation-based approach used here and clarify whether the ligand-receptor interactions inferred computationally correspond to physically proximate cell pairs. Larger sample sizes would allow stratification by fertility phenotype, enabling direct comparison of cell-type proportions and gene programmes between cows that maintain pregnancy and those that undergo early embryonic death. Multi-omic integration, combining scRNA-seq with single-cell ATAC-seq or proteomics, could reveal the chromatin accessibility landscapes that underpin the transcriptional shifts documented here. And cross-species comparisons with existing human and murine endometrial atlases would clarify which features of bovine peri-implantation biology are conserved and which are lineage-specific adaptations to the prolonged pre-attachment period unique to ruminants.

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Contributions not qualifying for authorship

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