

Genital Tract Microbiome of Cattle

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The term microbiota refers to the entire population of microorganisms that colonizes a particular location and includes not just bacteria, but also other microbes such as fungi, archaea, viruses, and protozoans. Cows have bacteria inhabiting the uterus even before calving and establish a unique endometrial microbiome within 20 min of calving where the microbiome is similar between cows that develop metritis and cows without endometritis until at least the second day postpartum.

Keywords: genital ; microbiome ; health ; cattle ; pathogens

1. The Genital Tract Contains a Dynamic Microbiota

In cattle and sheep, *Bacteroidetes*, *Fusobacteria*, and *Proteobacteria* are the most common phyla in the genital tract ^[1]. At the genera level, *Aggregatibacter spp.*, and *Streptobacillus spp.* were the most abundant. Interestingly, *Lactobacillus spp.*, the predominate microbial populations in the human genital tract, were present in 80% and 90% of vaginal samples from ewes and cows, respectively ^{[2][3][4]}. In women, where the genital microbiome is intensively investigated, there are different vaginal microbial community state types (CSTs). The CSTs are defined by the dominant *Lactobacillus* species; CST I: *Lactobacillus crispatus* (*L. crispatus*), CST II: *L. gasseri*, CST III: *L. iners*, and CST V: *L. jensenni*. The CST IV population is defined by the absence of *Lactobacilli* species and the large diversity with strict and facultative anaerobic bacteria ^[3]. Such groupings, if present in cattle, may be indicative of bacterial profiles beneficial for fertility.

2. Significance of the Genital Microbiome

The reproductive tract microbiome of cattle is relatively under-explored, particularly in terms of the specific taxonomic classification and functional aspect of the microbiome, which are beneficial for the development of diagnostic methods, such as microbial biomarkers and dysbiosis indexes. The genital microbes in humans and animals have protective functions against major pathogens. In women, *Lactobacilli* produces lactic acid, which regulates vaginal pH and inhibits the proliferation of pathogens ^[5]. In turn, symbiotic bacteria utilize the secretions of the genital tract such as mucus sugar and proteins as a source of essential nutrients ^[6]. Lactic acid also induces acidification of milieu within the vagina, which interferes with intracellular functions, leading to microbial elimination ^[5]. Results from in vitro studies revealed that *Chlamydia trachomatis* is inactivated when there are normal concentrations of lactic acid ^[7], as are *Neisseria gonorrhoeae* and *Escherichia coli* (*E. coli*) ^{[8][9]}. One of the potential benefits of the commensal bacteria in women is the protection against human immunodeficiency virus type 1 (HIV-1). It seems that *Lactobacilli* in the vagina protect women from contracting HIV-1 during sexual intercourse. Lactic acid and the resultant biofilm limit the number of free virions and thereby reduce the shedding of HIV ^{[10][11]}. In vitro, HIV-1 is irreversibly inactivated when challenged with normal concentrations of lactic acid ^[12]. This may be the mechanism by which *Lactobacilli* confers vaginal protection against pathogens.

The genital microbiome is also implicated in the sociochemical signaling in different species through the production of pheromones ^{[13][14][15]}. Pheromones are produced by the microbiome by either direct production of pheromonal cues or through the fermentation hypothesis, by which microbes metabolize existing endogenous organic compounds to produce highly volatile compounds ^[16]. Results from a study in buffalo indicated there was a repetitive Flehmen response of males exposed to vaginal mucus from females at estrus ^[17]. Interestingly, the pheromones elaborated vary with the diversity of the genital microbiome ^{[13][18]}.

3. Origin of the Genital Microbiome

The composition of the neonate microbiome is determined by the mode of birth and environment ^[19]. In humans, the general microbiome of the neonate delivered vaginally is similar to the maternal vaginal microbiome, dominated by *Lactobacillus*, *Prevotella*, or *Sneathia spp.* Neonates delivered through caesarean-section have a general microbiome

similar to the maternal skin microbiome, mainly composed of *Staphylococcus*, *Corynebacterium*, and *Propionibacterium* spp. [20] (**Figure 1**). Therefore, initial exposure to the maternal microbiome influences an individual's microbial load and diversity [20][21]. In cattle, microbes such *Bacteroides* and *Enterobacteriaceae* present in the genital tract causing reproductive diseases are thought to originate from the gut or the environment [22][23]. The results from some studies suggested that the vaginal microbiome originates from the gastrointestinal system [24], whereas others concluded that the vaginal microbial population includes methanogen species, and therefore the vaginal microbiome contributes to the establishment of the digestive tract microbiota [25]. The hematogenous route is also an important possible route for uterine contamination with pathogens [26].

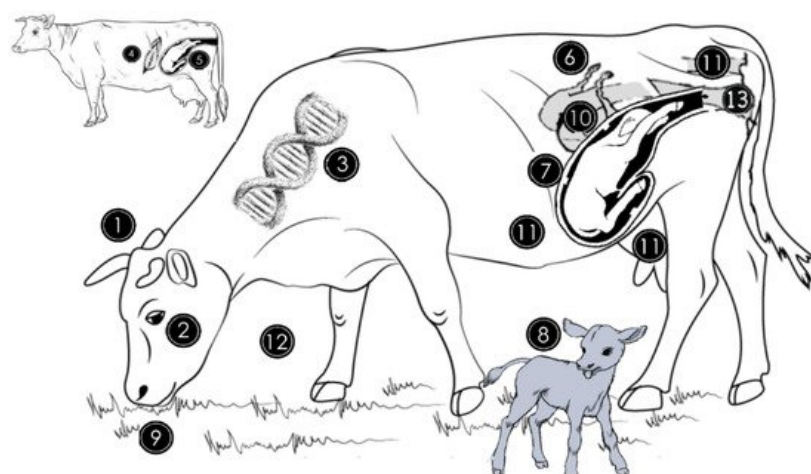


Figure 1. Origin of genital microbiome and factors that can affect the abundance and diversity of the microbial population. The genital microbiome is highly variable between species (1) and individuals of the same species (2). For instance, in cattle, genital microbiota is different between Gyr, Nellore, and Holstein breeds (3). The general microbiome of the newborn is similar to the mother's skin microbiome if the delivery method was caesarean section (4) and is similar to the vaginal microbiome if it was natural delivery (5). Estrogen and progesterone hormone concentration variations during the estrous cycle influence bacterial growth in the genitalia by favoring some species at different times (6). During pregnancy, bacterial quantity and diversity decrease while archaeal abundance increases in vaginal milieu (7). Vaginal and uterine microbiomes of cows not diagnosed with metritis during the first month postpartum are similar in cows without uterine infections but differ from those with uterine infections (8). Dietary quality and quantity peripartum alter the endometrial microbiome through the provision of energy and protein nutrients (9). The uterine microbiome between 10 and 35 days postpartum is similar in cows not diagnosed with subclinical endometritis and those that will develop subclinical endometritis (10). Rumen, skin, rectum or feces (11) contribute to the establishment of the genital microbiome, while the environment (12) and intravaginal antibiotic therapy (13) can also alter the endometrial microbiota during a female's lifetime.

4. Diversity of the Genital Microbiome

4.1. Vagina

Cows without uterine infections have in the vagina 15 taxa, predominantly *Bacteroides* (28.3%) and *Enterobacteriaceae* (17.8%), in addition to *Victivallis* (7.2%), *Streptococcus* (6.1%), *Phyromonadaceae* (5%), *Alistipes* (3.9%), *Coriobacteriaceae* (3.3%), *Clostridium* (3.3%), *Betaproteobacteria* (2.8%), *Corynebacterineae* (2.8%), *Cytophagaceae* (2.8%), *Oscillibacter* (2.8%), and *Planctomycetaceae* (2.8%) [27]. Cows with reproductive diseases such as purulent vaginal discharge have a more diverse vaginal microbiome containing 68 taxa, dominated by *Bacteroides* (35.83%), *Enterobacteriaceae* (18.62%), *Histophilus* (8.79%), *Alistipes* (4.34%), *Flavobacteriaceae* (1.77%), *Victivallis* (8.49%), *Coriobacteriaceae* (2.44%), *Streptococcus* (2.09%), *Barnesiella* (2.03%), and *Oscillibacter* (1.24%) [27]. Results from another study indicated that unclassified *Enterobacteriaceae* (21.05%), *Ureaplasma* (4.37%), and unclassified *Bacteroidaceae* (2.49%) were the most predominant [25]. At the phyla level, *Tenericutes* (36%), *Proteobacteria* (30%), *Fusobacteria* (7.6%), and *Firmicutes* (1.8%) were the most abundant [28]. In the study by Deng et al. (2019), *Firmicutes* (31.57%), *Proteobacteria* (24.08%), *Bacteroidetes* (12.96%), and *Tenericutes* (4.95%) were the most prevalent in the vagina. A comparison of the results from these two recent studies reveals that the proportions of the predominant microbial populations differ significantly between individuals.

4.2. Uterus

It is now known that cows have a natural microbiome in the uterus during the gestational period [29][30]. While the uterine microbes originate mainly from the vagina, and to a lesser extent, from the skin and gut, this microbiome is not as diverse as the vaginal microbiome [31]. Bacteria are always present in the uterus. *F. necrophorum*, *Porphyromonas Levii*, and *T. pyogenes* were detected in pregnant cows [29]. Interestingly, opportunistic microbes, such as *Histophilus* and *Mycoplasmataceae*, can become pathogenic [32][33]. Furthermore, the bacterial abundance in the uterus before calving is not associated with inflammation, which is indicative of a greater microbial tolerance during gestation [26].

5. Factors Affecting Genital Microbiome Diversity

The genital microbiome changes during the lifetime of females. Microbial populations in the reproductive tracts of animals are naturally selected because of different symbiotic functions. For example, in women, *Lactobacilli* use their small membrane extensions (for example, fimbriae) that adhere to the genital mucosa [34]. Likewise, the vaginal tissue is rich in collagen, a valuable source of nutrients for *Aggregatibacter spp.* [35][36]. There are also other factors that affect the genital microbial diversity with some being specific to the stage of the female reproductive cycle, and others are extrinsic such as nutrition. Interestingly, the vaginal microbiome could have originated from the intestinal microbiota from an evolutionary perspective because there are marked similarities between the microbial population of the two anatomical parts [24]. The thought was that this microbial similarity is due to the fact that the vagina and anus are juxtaposed, and feces are often in contact with vulva [24]. However, the prevailing thoughts at present are that the genital microbiome of the neonate initially originated from maternal tissue that is in contact with the neonate subsequent to parturition. The genital microbiome subsequently undergoes several changes during the lifetime of a female under the effect of the many factors, including the contamination by the microbiome of proximate organs such as the gastro-intestinal tract. Recent findings support the hypothesis (Figure 1) [25]. When there was a comparison of the changes in the microbial population in feces and vaginal samples collected before mating and at different stages of the gestational period, the fecal microbial diversity was the same, but the vaginal microbiome changed dynamically at different stages of the gestational period.

5.1. Intrinsic Factors

Individual variation in microbial species in the genital tract of bovids is thought to have effects of fertility outcomes [24]. This variation may explain how some animals develop resistance and others become infected with uterine diseases. Such differences are thought to be common in other mammals including humans (Figure 1) [37].

5.1.1. Species

The genital microbiome is diverse among animal species and also individual animals, which perturbs the regulation of reproductive hormones (Figure 1) [2]. For example, in two separate studies using either cows with endometritis or those administered bacterial lipopolysaccharide (LPS), estradiol concentrations were lower, and there was a relatively prolonged period to the time of ovulation during the follicular phase of the reproductive cycle [38][39]. The vaginal microbiomes of cattle were composed of a large abundance of *Enterococcus spp.*, *Staphylococcus spp.*, and *Streptococcus spp.*, which was different from the vaginal microbiome of ewes where there was a predominance of *Bacillus spp.*, *Corynebacterium spp.*, *Escherichia spp.*, *Staphylococcus spp.*, and *Streptococcus spp.* [40][41][42][43]. At the phyla level, the genital microbiomes in both cows and ewes were composed predominantly of *Proteobacteria*, *Fusobacteria*, and *Bacteroidetes*. At the genera level, *Aggregatibacter spp.* and *Streptobacillus spp.* were the predominant species [2]. While *Lactobacilli* are detected in 80% of ewes and 90% of cows, the total microbial population is less abundant, leading to the near-neutral vaginal environment compared to the acid environment in women where there is a large population of *Lactobacilli* [2]. In addition to *Lactobacilli*, cows and ewes share several genera, mainly *Sneathia spp.*, *Porphyromonas spp.*, and *Prevotella spp.* [3][2]. A small *Firmicutes* to *Bacteroidetes* ratio is an early indicator of cows that subsequently develop postpartum endometritis [44].

5.1.2. Breed (Genetic Background)

In Gyr cattle, a common dairy breed in South American countries such as Brazil, the vaginal microbiome is enriched with bacteria and fungi while there is a small population of archaea (Figure 1) [45]. Among bacteria, *Firmicutes*, *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria* were the most frequently detected. *Mycosphaerella* and *Cladosporium* were the most frequently detected fungal genera. While archaea were in low abundance, the *Methanobrevibacter* genus was the most abundant. In Nellore beef cattle, the vaginal microbiome is predominately composed of *Firmicutes*, *Bacteroidetes*, *Proteobacteria*, and up to 20% of unclassified bacteria [24]. *Mycosphaerella* was the most abundant fungal genus while *Methanobrevibacter* was the predominant archaeal genus. In Holstein Friesian cattle, the most ubiquitous dairy breed in

North Africa, Europe, and the USA, the vaginal microbiome was predominately composed of *Firmicutes*, *Tenericutes*, *Proteobacteria*, and *Bacteroidetes* phyla. Other bacteria were detected in smaller quantities such as *Actinobacteria* and *Spirochaetae* [19].

5.1.3. Delivery Mode

The type of fetal delivery at parturition is one of the major factors affecting the genital microbiome diversity [20]. The general microbiome of the neonate is similar to the maternal skin microbiome if the parturition was by cesarean section and similar to the vaginal microbiome if it was natural delivery (**Figure 1**) [20]. Early established bacterial communities provide protection against pathogenic bacteria that may be infective agents to the neonate. While the maternal vagina is the main source for the natural microbiome, a unique neonatal microbiome is established shortly after parturition with microbes from other sources. For example, neonates delivered by caesarean section have a greater prevalence of methicillin-resistant *Staphylococcus aureus* (*S. aureus*) (MRSA) skin infections (64–82%) compared to when neonates are born without complications (i.e., natural delivery) [20].

5.1.4. Estrous Cyclicity

Estrous cycles in cattle are regulated by hormonal concentration changes with relatively higher concentrations of estradiol during proestrus and estrus and relatively higher progesterone concentrations during metestrus and diestrus, having marked effects on the vaginal pH in mammals [46][47]. Microbes are very sensitive to acidic milieu; therefore, it is thought that when there are greater estradiol concentrations, there will be effects on the microbiome in the genital milieu of some species, with effects varying as a result of estradiol concentrations (**Figure 1**). Results from a recent study indicated that *Bacteroidete spp.*, *Histophilus somni*, *Actinobacillus seminis*, and unclassified *Fusobacterium* populations increase when there are relatively lower estradiol concentrations in the vaginal milieu [28]. When there are relatively higher estradiol concentrations in the vaginal milieu, unclassified *Pasteurellaceae* are the predominant microbes in the vagina. Likewise, when there are higher progesterone concentrations, the populations of microbes in the vagina are relatively larger [24][40].

5.1.5. Pregnancy

During the gestational period, there is lower microbial diversity of the vaginal microbiome and a greater archaeal population [24]. The bacterial species present in the vagina during the gestational period are less diverse due to the relatively higher progesterone concentrations that lead to suppression of the vaginal microbial population (**Figure 1**) [40]. The relatively lower microbial population in the vagina during the gestational period could lead to a greater risk of dysbiosis and abortion. Similarly, in humans, the microbial population in the vagina decreases as duration of the gestational period increases [48][49]. Unlike in humans, the vaginal microbiome of cattle is relatively stable throughout the gestational period [25]. In nonpregnant heifers, *Pasteurellaceae spp.* and *Fusobacterium spp.* were abundant in the vagina, whereas pregnant heifers had a greater prevalence of *Pasteurella multocida* [28].

5.1.6. Postpartum

Interestingly, the vaginal, and uterine microbiomes of cows without uterine inflammation during the first 50 DPP were similar and were highly enriched with *Firmicutes* [44]. This finding could be explained by the fact that soon after calving, the cervical lumen is less constricted, resulting in a mixing of the vaginal and uterine milieu with there being movement of these contents throughout the reproductive tract. It was hypothesized that in cows without uterine inflammation, the genital microbiome is not contaminated during calving by the external microbiome or at least not affected for an extended period subsequent to parturition. A comparison of the genital microbiome of pregnant cows before calving retrospectively with those that develop endometritis after 21 DPP to those that continue to have an uninfected uterus revealed that genital microbiome pre-calving was similar to the vaginal microbiome of healthy cows that did not develop uterine infections subsequent to 21 DPP [44].

5.2. Extrinsic Factors

5.2.1. Nutrition

The microbial population of the uterus of dairy cows during the postpartum period was reported to be affected by the nutrient content of the diet, especially the energy content, around the time of calving (**Figure 1**) [50]. Cows that were fed 80% of the energy requirement had uterine inflammation, and the predominant species of the uterine microbiome were *Bacteroidetes* and *Fusobacteria*. A comparison of the uterine microbiome pre-calving to that post-calving in cows that developed metritis with those that did not contract metritis indicated that cows with metritis had predominantly *Bacteroides* and *Fusobacteria* and a lower abundance of *Proteobacteria* and *Tenericutes*, which was markedly different from those that

did not have metritis [26]. Therefore, nutrition affects the genital microbiome through the modulation of general metabolism and immune functions and therefore affects the occurrence of dysbiosis and genital infections.

5.2.2. Genital Pathologies

Metritis, which is indicated by a marked inflammation of the endometrium and myometrium soon after calving and before day 21 postpartum, is characterized by relatively lower abundance of the vaginal microbiome quantities and higher relative abundance of *Bacteroides*, *Porphyromonas*, and *Fusobacterium* [26][51]. Likewise, cows with metritis had a uterine microbiome that was markedly enriched with *F. necrophorum*, *Porphyromonas levii*, and *Prevotella melaninogenica* compared with cows without metritis [52]. *E. coli* is another interesting bacterium that is detected early postpartum in most of the cows because the presence of this microbe is important for the development of *F. necrophorum*, leading to metritis, while the latter bacterium is often detected in association with *T. pyogenes* in the case of endometritis [26][53]. In women with mild or moderate vaginal atrophy, the vaginal microbial population tends to be predominantly invasive pathogens, mainly *Streptococcus* and *Prevotella* [54]. Microbiomes in cattle diagnosed with necrotic vulvovaginitis (BNVV), as compared with those not diagnosed with BNVV, are characterized by a relatively microbial diversity and a large abundance of *Bacteroidetes* [55].

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