

RESEARCH ARTICLE

Efficacy of Fecal Microbiota Transplantation Restores Antibiotic-induced Gut Microbiota Dysbiosis and Ameliorates Endotoxemia of Chickens

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ABSTRACT

The objective of this study was to explore the effect of Fecal microbiota transplantation (FMT) on restoring antibiotic-induced gut microbiota dysbiosis and ameliorating endotoxemia in chickens, as well as its impact on chicken intestinal morphology and meat quality. Although FMT has been extensively investigated in mammals, its application in poultry, which serves as a major global food source species with unique physiological characteristics, remains insufficiently studied. Thirty white feather broilers were randomly divided into three groups: The control group was fed a basal diet (Control group), the basal diet supplemented with antibiotics (Antibiotic group), and the antibiotic treatment followed by fecal microbiota transplantation (Antibiotic+FMT group). Compared to the Antibiotic group, the 16S rDNA sequencing revealed a significant recovery of microbial community in the Antibiotic+FMT group ($P<0.05$), the morphological analysis showed that the Antibiotic+FMT group significantly increased the height of small intestinal villi and the number of small intestinal glands ($P<0.05$), the serum biochemical analysis indicated that the levels of TNF- α , IL-6, and LPS decreased significantly, while IL-10 increased significantly in the Antibiotic+FMT group ($P<0.05$). Additionally, FMT also significantly enhanced meat quality parameters (color and pH) ($P<0.05$). It is concluded that FMT can significantly enhance the diversity of gut microbiota and support the restoration of intestinal structural damage, thereby ameliorating endotoxemia in chickens, and improving chicken meat quality.

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INTRODUCTION

In intensive poultry farming operations, antibiotics have been widely used for decades as growth enhancers and disease prevention measures. However, their overuse has increasingly led to dysbiosis in the gut microbiota of poultry (Ren *et al.*, 2023). Antibiotics disrupt microbial diversity by inhibiting the proliferation of commensal microbiota, promoting the abnormal colonization of opportunistic pathogens (e.g., *Escherichia coli*, *Salmonella*), and exacerbating gut microbiota dysbiosis (Peng *et al.*, 2024).

The intestinal microbiome plays a vital role in regulating metabolic processes, supporting growth and development, and maintaining overall health in animals. It regulates immune function, maintaining a balanced immune state to prevent or reduce the occurrence of

immune-related diseases. Once the intestinal flora is disordered, it will lead to endotoxemia (Zhao *et al.*, 2022; Ding *et al.*, 2024). The specific protective mechanisms are illustrated in Fig. 1. Endotoxin, which is a high-molecular-weight lipopolysaccharide (LPS), constitutes a structural component of the outer membrane in Gram-negative bacterial cell walls (Kar *et al.*, 2021; Page *et al.*, 2022; Perricone *et al.*, 2024). Endotoxemia can occur in various systemic diseases. The presence of endotoxin can activate the body's immune system and trigger a series of inflammatory reactions. This process will have adverse effects on the normal functions of multiple organs and systems. It usually causes fatal septic shock, multiple organ failure, diffuse intravascular coagulation, etc., with relatively high mortality (Prado *et al.*, 2023; Sugita *et al.*, 2024; Mráziková *et al.*, 2025).

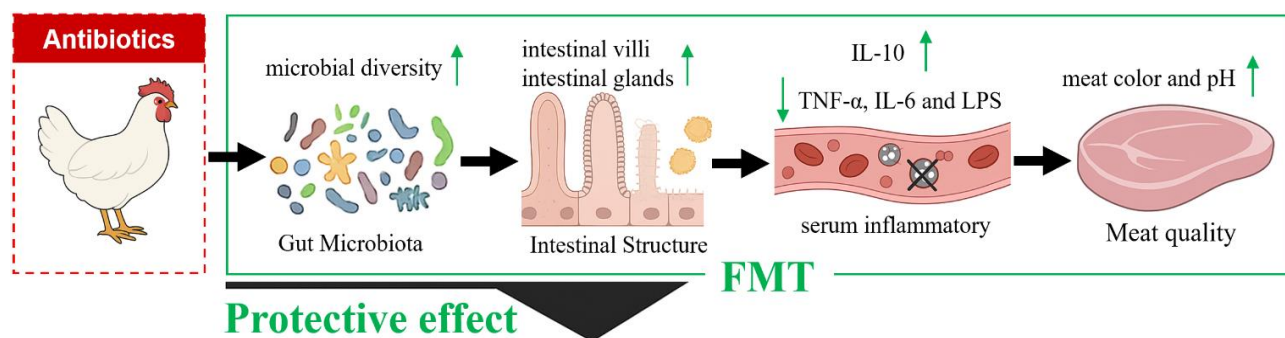


Fig. 1: Schematic Diagram of the Protective Effects of Fecal Microbiota Transplantation. An antibiotic-induced endotoxemia model in chickens was established to evaluate the protective effects of FMT comprehensively. FMT significantly restored gut microbial diversity and alleviated intestinal structural damage, regulated serum inflammatory cytokine levels, and improved meat quality. Abbreviations: FMT; Fecal microbiota transplantation, IL-6; Interleukin-6, IL-10; Interleukin-10, IL-1 β ; Interleukin-1 β , LPS; Lipopolysaccharide, TNF- α ; Tumor necrosis factor- α .

Fecal microbiota transplantation (FMT) is a therapeutic intervention that introduces the fecal microbial community from a healthy donor into a patient's gut ecosystem to restore microbial balance and manage gastrointestinal disorders (Yang *et al.*, 2024; Mooyottu *et al.*, 2025). FMT represents a unique form of biological therapy, analogous to organ transplantation. This technique has proven particularly effective in eliminating toxigenic *Clostridium difficile* and has demonstrated therapeutic potential for multiple gastrointestinal disorders (Wang *et al.*, 2022). Following its successful application in treating gastrointestinal disorders and enhancing gut health in animals, FMT has emerged as a prominent research focus for both agricultural producers and scientists. In livestock production, studies have demonstrated that FMT technology significantly enhances growth performance in juvenile animals, including increased weight gain and improved feed efficiency in piglets and chicks, while markedly reducing the incidence of diarrhea (Rahman *et al.*, 2023; Wang *et al.*, 2024; Song *et al.*, 2025). Consequently, FMT demonstrates significant potential for both clinical therapeutics and agricultural applications.

However, current research on FMT in poultry has primarily focused on its ability to restore microbial community composition or improve growth performance (Yu *et al.*, 2021; Chen *et al.*, 2024). A critical gap remains in understanding its systemic role in alleviating antibiotic-induced dysbiosis, particularly the progression from intestinal barrier disruption to endotoxemia and systemic inflammation, and how these physiological improvements ultimately translate into enhanced meat quality. Therefore, this study aims to demonstrate that FMT possesses multifaceted reparative functions comprehensively: it can not only reconstruct a healthy gut microbiota but also alleviate endotoxemia by modulating inflammatory cytokines and repair intestinal morphological damage, thereby bridging the critical knowledge gap between microbial intervention and overall production outcomes, including meat quality parameters.

MATERIALS AND METHODS

Ethical approval: This research was conducted in compliance with Chinese national guidelines (Regulations for the Administration of Affairs Concerning Experimental Animals, State Council Order No. 676) and the institution's animal welfare policies. The experimental design was

reviewed and approved by the Ethics Committee of Anhui Science and Technology University, Chuzhou, China (Ethical Approval No. AK-2022028).

Experimental animals and treatments: Thirty healthy white feather broilers (1,000–1,500g) were randomly divided into three groups (n=10 per group) and kept under controlled conditions (temperature 22–26°C, humidity 60–80%, with scheduled ventilation) with free access to water. The Control group was fed a standard diet, while the Antibiotic group and the Antibiotic+FMT group received a daily oral gavage of 200 μ L of an antibiotic mixture (neomycin sulfate 8g/L, vancomycin 4g/L, ampicillin 8g/L) for 7 consecutive days. After 7 days, the Antibiotic+FMT group underwent fecal microbiota transplantation (1,000 μ L fecal suspension via gavage, twice daily for 5 days). On day 20, all chickens were euthanized, and samples (including venous blood, duodenum/jejunum/ileum segments, intestinal contents, and breast/leg muscle) were collected for analysis.

Fecal suspension preparation: Donor chickens that were clinically normal, weighed more than 1,500g, and had no recent antibiotic exposure were selected. Pooled fecal samples from these chickens were screened and confirmed negative for major pathogens, including *Salmonella spp.*, *Campylobacter spp.*, and *Escherichia coli* (pathogenic strains), before further processing. Fresh feces were aseptically collected daily, and the white urate part was removed. They were placed in a sterile closed centrifuge tube and immediately transported on ice to the laboratory for treatment. Twenty grams of fecal samples were weighed and mixed with 60mL of 75% sterile physiological saline, thoroughly homogenized, and left on ice to settle. After complete sedimentation, the supernatant was gathered and filtered through sterile gauze to prepare a high-concentration bacterial suspension.

Gut microbiota composition and intestinal morphology: To analyze the microbial diversity and composition of the collected intestinal contents, the 16S rDNA amplicon sequencing technology (16S V3–V4 region) was applied. The sequencing work was done by Shanghai Parson Biotechnology Co., Ltd. (Shanghai, China).

Intestinal segments (duodenum, jejunum, ileum, and cecum) were harvested, flushed with sterile saline, and

processed through graded ethanol dehydration, xylene clearing, and paraffin embedding. Tissue sections were stained with hematoxylin-eosin (H&E) for microscopy. Five non-overlapping fields per section were randomly imaged under a light microscope.

Detection of endotoxemia: To detect the levels of TNF- α , IL-1 β , IL-10, IL-6, and LPS, the ELISA kits (TNF- α : H052-1-2; IL-1 β : H002-1-2; IL-10: H009-1-2; IL-6: H007-1-2; LPS: H255-1-2) were purchased from Nanjing Jiancheng Bioengineering Institute (Nanjing, China). The serum samples of chickens were collected, and the levels of the above inflammatory cytokines were detected by ELISA kits.

Determination of chicken meat quality and PH: Meat color was measured using a calibrated colorimeter (CHROMA METER CR-400) by pressing the probe against the sample surface to record the values of the lightness (L^*), redness (a^*), and yellowness (b^*).

The pH of the chicken meat was measured with a calibrated pH meter (Youke PHS-3E). A direct-insertion probe was inserted 0.5-1.0cm below the sample surface for direct reading.

Statistical methods: Statistical analyses were carried out using SPSS 22.0 software. Results are shown as mean $\pm$ standard deviation, with $P < 0.05$ considered statistically significant.

RESULTS

Effect of FMT on the diversity of gut microbiota: To investigate the effect of FMT on the diversity of gut microbiota, 16S rDNA high-throughput sequencing analysis was performed on fecal samples collected from three groups of chickens. A comprehensive analysis of the intestinal microbiota was conducted, including the number of operational taxonomic units (OTUs), a rank-abundance curve, a dilution curve, and Beta diversity. The experimental results are presented in Fig. 2.

The Venn diagram based on OTUs (Fig. 2A) showed that a total of 7105 OTUs were detected. The Control group exhibited the highest total number of OTUs, reaching 3066, with 2607 unique OTUs, which indicated the most significant microbial diversity. The total number of OTUs in the Antibiotic group significantly decreased to 1100, with only 1018 unique OTUs. The total number of OTUs in the Antibiotic+FMT group was 2965, with 2510 unique OTUs, and shared 429 OTUs with the Control group.

The rank-abundance curve (Fig. 2B) showed that the curve for the Control group extends significantly to the far right, indicating a relatively high abundance of bacterial communities in this group. In contrast, the curve for the Antibiotic group was noticeably narrower, reaching only about one-third of the width of the Control group, suggesting a significant reduction in microbiota abundance following antibiotic treatment. After fecal microbiota

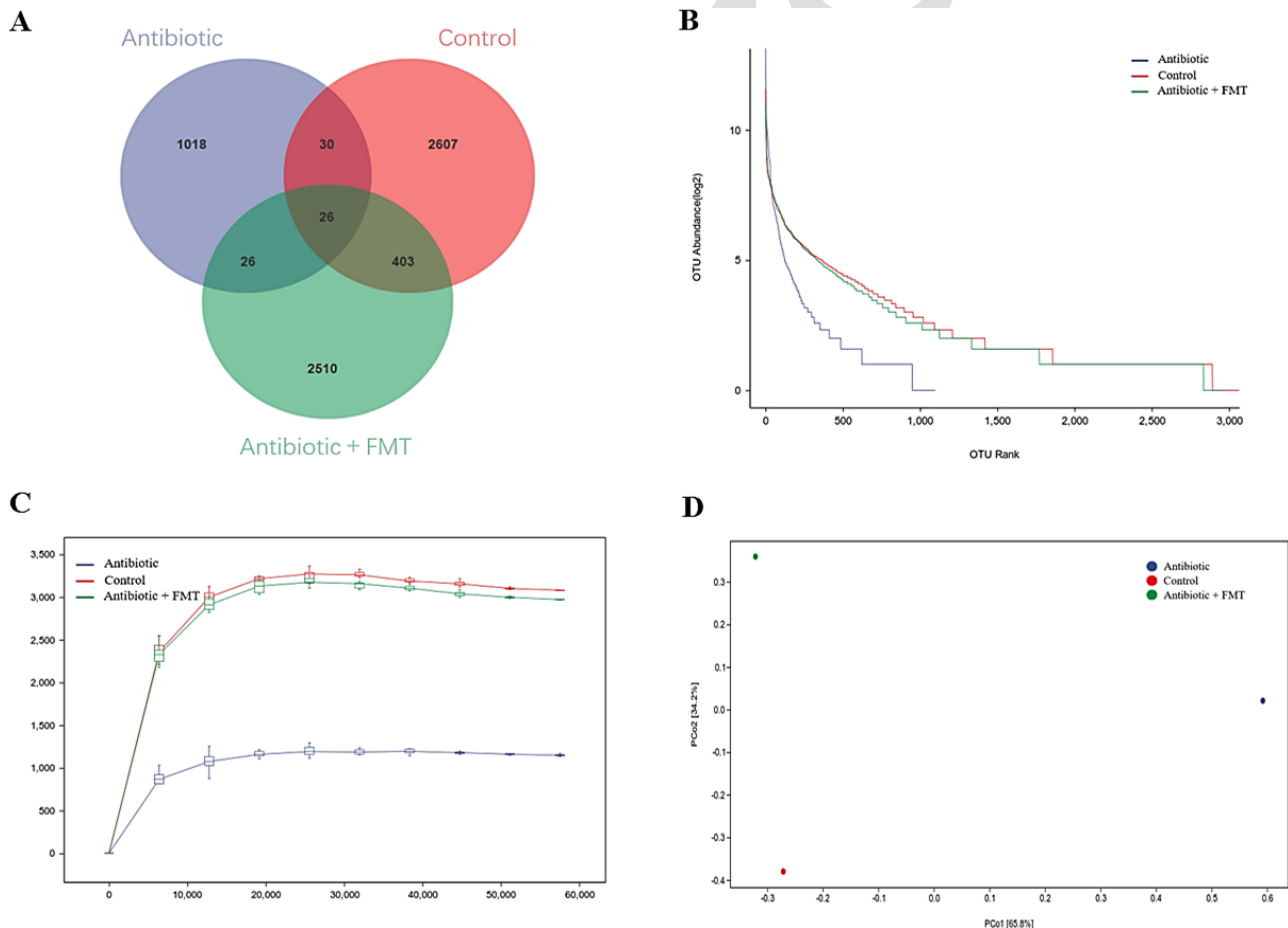


Fig. 2: Analysis of FMT on the diversity of chicken gut microbiota; A: Venn diagram illustrating the number of shared and unique OTUs among the Control, Antibiotic, and Antibiotic + FMT groups; B: Rank-abundance curve of chicken gut microbiota; C: Dilution curve of chicken gut microbiota; D: Analysis of Beta diversity of intestinal flora after fecal microbiota transplantation. Abbreviations: FMT; Fecal microbiota transplantation, OTUs; Operational taxonomic units.

transplantation in the Antibiotic+FMT group, the curve width significantly increased, indicating a recovery in microbiota abundance.

In addition, the dilution curves were plotted through the Payson Cloud analysis platform (Fig. 2C). The results demonstrated that the gut microbiota diversity in the Control group was relatively high. In contrast, it was significantly reduced in the Antibiotic group. However, the gut microbiota diversity in the Antibiotic+FMT group increased significantly, nearly restoring to normal levels.

To investigate the similarity of the gut microbiota after FMT, Beta diversity was analyzed using Principal coordinates analysis (PCoA) based on the binary-Euclidean algorithm. The principal component analysis (PCA) plot for Beta diversity is shown in (Fig. 2D), where the contribution of PC1 along the x-axis was 65.8%, and the contribution of PC2 along the y-axis was 34.2%. The graphical results showed that the data of Control group were closer to those of Antibiotic+FMT group, while the Antibiotic group was farther away, indicating that the composition of gut microbiota was obviously different from that of normal chickens after antibiotic treatment, whereas the gut microbiota after FMT was markedly restored, and the composition of its microbiota was much more similar to that of the normal chickens' intestines.

Effects of FMT on the intestinal morphology and structure: The effects of FMT on intestinal architecture were evaluated through histological examination of duodenum, jejunum, and ileum samples following paraffin section and H&E staining.

Effect of FMT on the structure of small intestinal villi: H&E staining showed that antibiotic treatment resulted in a disorganized and incomplete structure of small intestinal villi (Fig. 3B, Fig. 3E, Fig. 3H). After Fecal Microbiota Transplantation, the intestinal villi of duodenum, jejunum, and ileum segments were well arranged with a significant increase in height and length (Fig. 3C, Fig. 3F, Fig. 3I).

Effect of FMT on small intestinal glands: H&E staining indicated that antibiotic treatment markedly reduced the number of small intestinal glands in the duodenum, jejunum, and ileum segments, leading to structural disorganization and irregular cellular arrangement (Fig. 4B, Fig. 4E, Fig. 4H). After fecal microbiota transplantation treatment, the number of small intestinal glands was significantly increased, the structure was restored to be neat, and the cellular arrangement tended to be tight and orderly (Fig 4C, Fig 4F, Fig 4I).

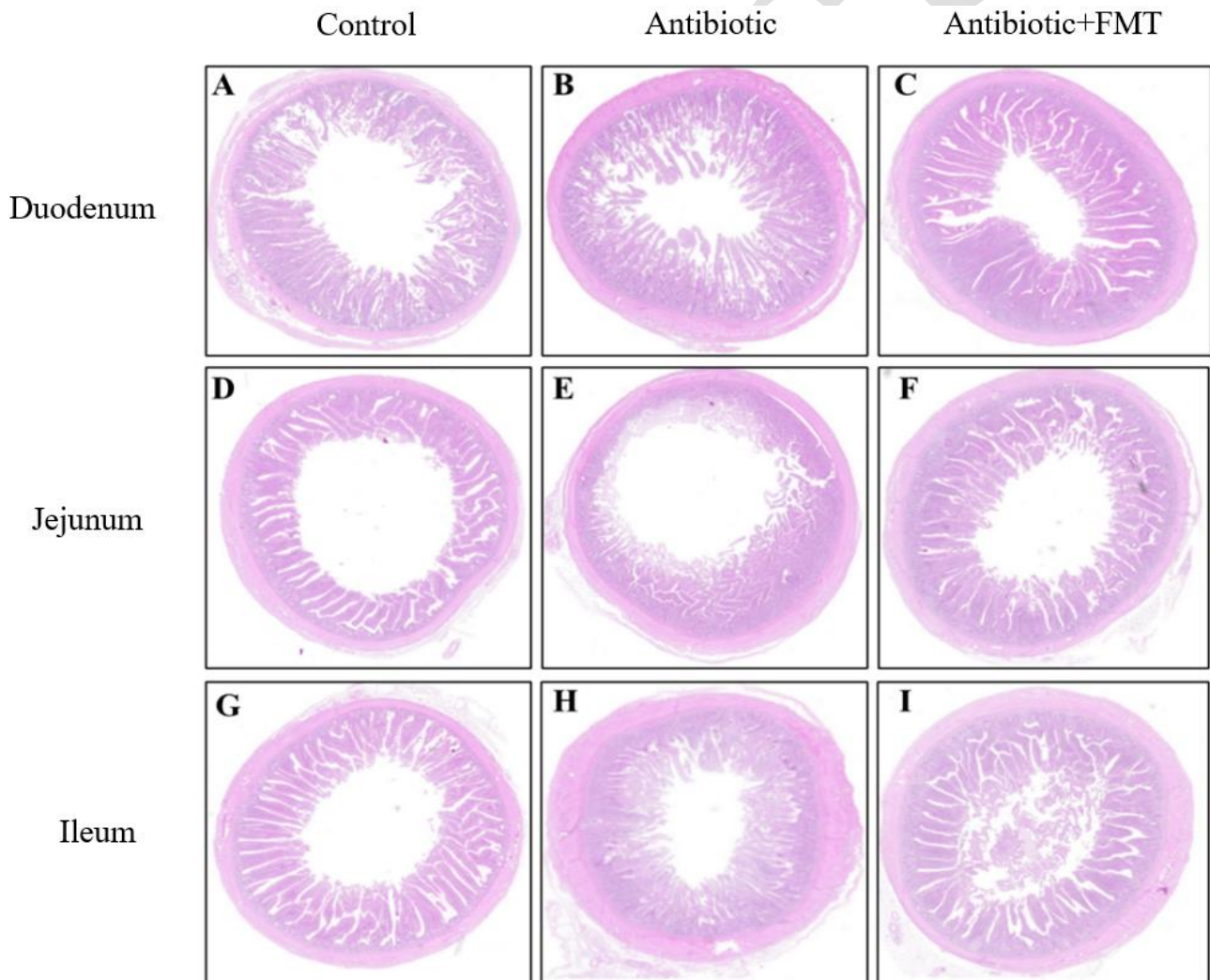


Fig. 3: The effect of fecal microbial transplantation on the small intestinal villi and overall morphological structure (H&E, 40X). Abbreviations: FMT; Fecal microbiota transplantation, H&E; Hematoxylin and Eosin.

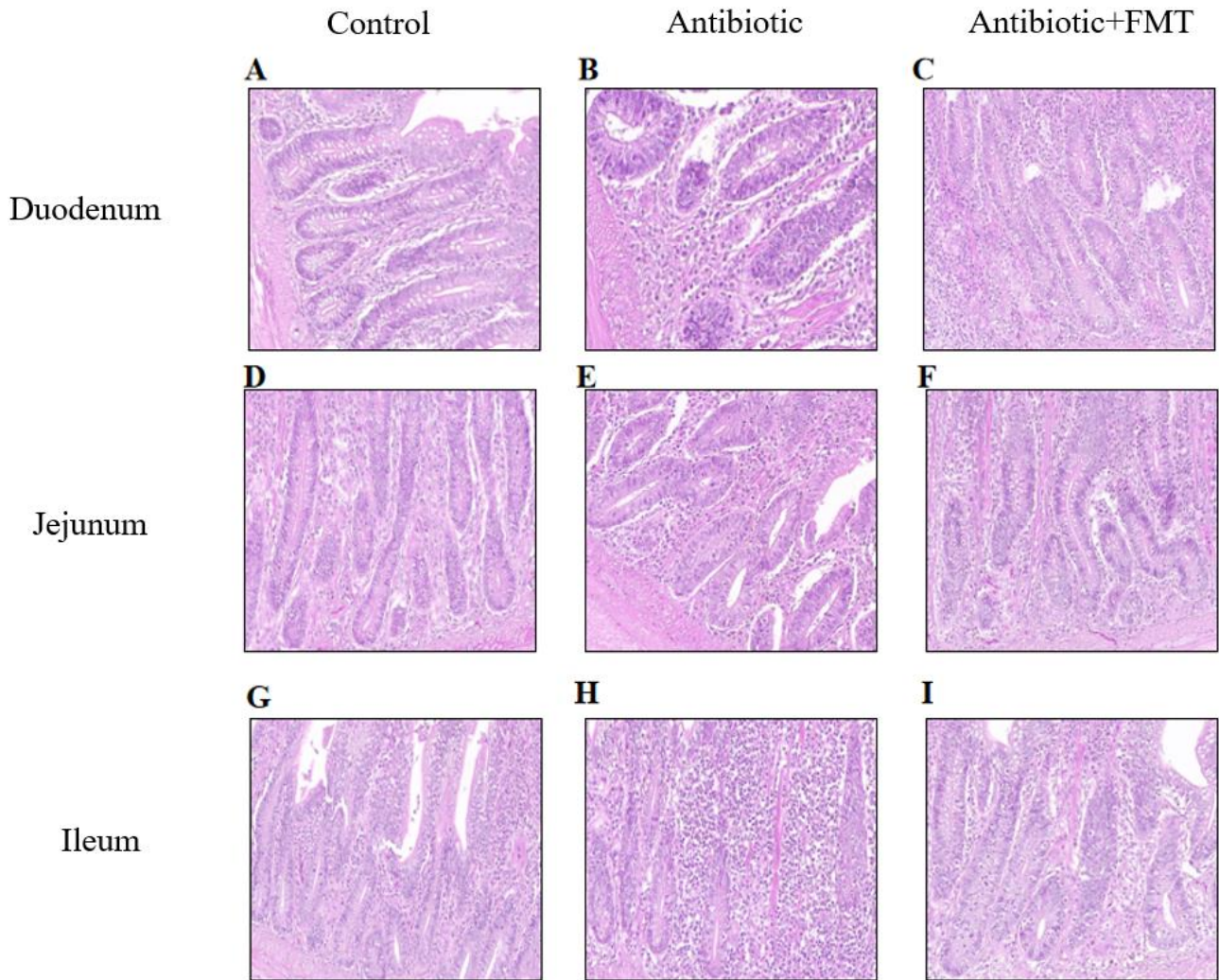


Fig. 4: The effect of fecal microbiota transplantation on the small intestinal glands (H&E, 100X). Abbreviations: FMT; Fecal microbiota transplantation, H&E; Hematoxylin and Eosin.

Effect of FMT on intestinal goblet cells: The results of H&E staining revealed that antibiotic treatment resulted in a disordered and incomplete intestinal villus structure. Specifically, the number of goblet cells in the duodenum, jejunum, and ileum of the Antibiotic group increased significantly (Fig. 5B, Fig. 5E, Fig. 5H), while the Antibiotic+FMT group exhibited the opposite findings (Fig. 5C, Fig. 5F, Fig. 5I).

Effect of FMT on serum inflammatory factors: As demonstrated in Table 1 and Fig. 6, antibiotic treatment induced significant gut microbiota dysbiosis and inflammatory responses in chickens. Relative to the Control group, the Antibiotic group exhibited significantly higher serum levels of pro-inflammatory cytokines (TNF- α , IL-6, IL-1 β) and LPS ($P<0.05$), while anti-inflammatory IL-10 levels were significantly lower ($P<0.05$). Furthermore, the levels of TNF- α , IL-6, and LPS were significantly reduced, while the IL-10 exhibited the opposite results in the Antibiotic+FMT group ($P<0.05$).

Effect of FMT on color and pH of chicken meat: The data presented in Table 2 demonstrate that the breast and leg muscle of chickens in the Antibiotic+FMT group exhibited significantly higher values of the lightness (L^*) and yellowness (b^*) ($P<0.05$), but lower redness (a^*)

values compared to the Antibiotic group ($P<0.05$). Moreover, the pH value was markedly higher in the Antibiotic+FMT group ($P<0.05$).

Table 1: Study on the effect of fecal microbiota transplantation on endotoxemia injury caused by intestinal flora disorder in chickens (pg/mL)

	Control	Antibiotic	Antibiotic + FMT	P
LPS	6.82 $\pm$ 0.95 ^c	10.29 $\pm$ 0.94 ^a	8.88 $\pm$ 0.78 ^b	0.000
IL-6	3.95 $\pm$ 0.36 ^c	5.3 $\pm$ 0.64 ^a	4.66 $\pm$ 0.61 ^b	0.000
IL-10	11.15 $\pm$ 1.12 ^{ab}	9.79 $\pm$ 0.94 ^b	12.31 $\pm$ 1.82 ^a	0.006
IL-1 β	70.25 $\pm$ 15.06 ^b	76.19 $\pm$ 12.91 ^b	82.67 $\pm$ 4.76 ^a	0.001
TNF- α	12.24 $\pm$ 1.29 ^b	14.87 $\pm$ 1.63 ^a	11.36 $\pm$ 0.86 ^b	0.000

Note: $P<0.05$ was considered significant. Abbreviations: FMT; Fecal microbiota transplantation, IL-6; Interleukin-6, IL-10; Interleukin-10, IL-1 β ; Interleukin-1 β , LPS; Lipopolysaccharide, TNF- α ; Tumor necrosis factor- α .

Table 2: Effect of fecal microbiota transplantation on breast/leg muscle color and pH determination results

	Anatomical parts	L^*	a^*	b^*	pH
Control	chest	59.93 $\pm$ 5.84 ^{ab}	3.67 $\pm$ 1.99 ^b	11.24 $\pm$ 1.6 ^b	6.56 $\pm$ 0.16 ^b
	leg	46.18 $\pm$ 5.21 ^{ab}	14.42 $\pm$ 2.35 ^b	11.05 $\pm$ 1.7 ^b	6.72 $\pm$ 0.18 ^b
Antibiotic	chest	56.50 $\pm$ 3.23 ^b	8.98 $\pm$ 4.88 ^a	11.15 $\pm$ 1.3 ^b	6.47 $\pm$ 0.25 ^b
	leg	43.49 $\pm$ 3.48 ^b	20.48 $\pm$ 1.67 ^a	11.03 $\pm$ 1.4 ^b	6.66 $\pm$ 0.22 ^b
Antibiotic + FMT	chest	62.00 $\pm$ 5.96 ^a	6.97 $\pm$ 3.77 ^{ab}	12.83 $\pm$ 1.76 ^a	6.75 $\pm$ 0.45 ^a
	leg	49.00 $\pm$ 5.01 ^a	20.15 $\pm$ 6.08 ^{ab}	12.94 $\pm$ 1.84 ^a	6.93 $\pm$ 0.43 ^a
P	chest	0.031	0.018	0.015	0.032
	leg	0.041	0.006	0.02	0.022

Note: $P<0.05$ was considered significant. L^* is the lightness of the meat, a^* is the redness, and b^* is the yellowness.

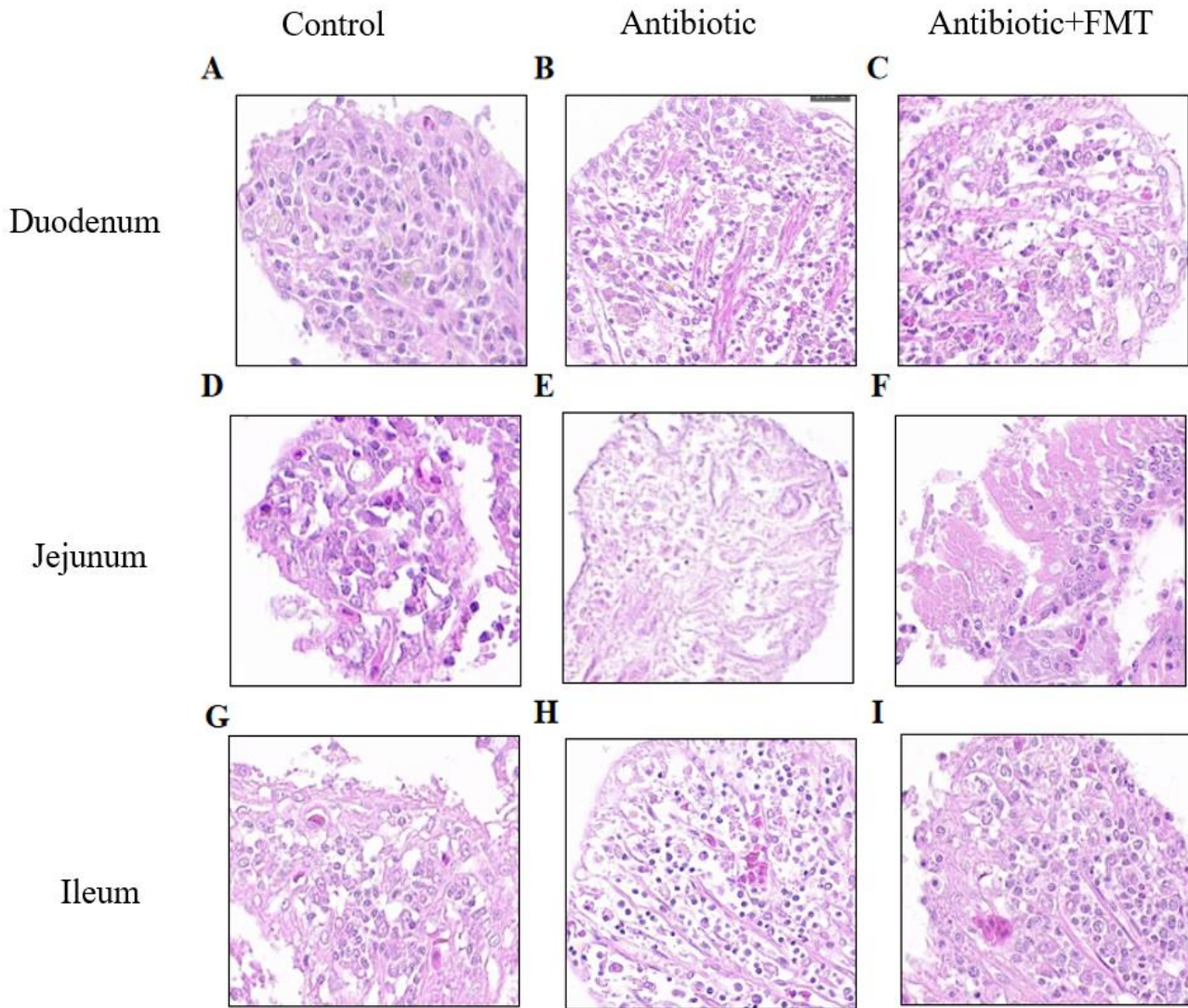


Fig. 5: The effect of fecal microbiota transplantation on small intestinal goblet cells on intestinal morphological structure (H&E, 400X). Abbreviations: FMT; Fecal microbiota transplantation, H&E; Hematoxylin and Eosin.

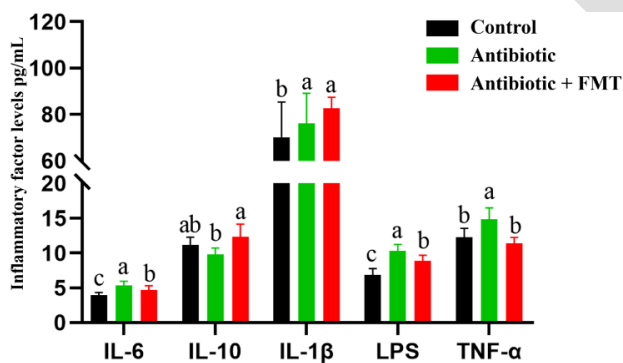


Fig. 6: FMT against endotoxemia injury caused by intestinal flora disorder in chickens. Abbreviations: FMT; Fecal microbiota transplantation, IL-6; Interleukin-6, IL-10; Interleukin-10, IL-1 β ; Interleukin-1 β , LPS; Lipopolysaccharide, TNF- α ; Tumor necrosis factor- α .

DISCUSSION

In this study on an antibiotic-induced endotoxemia model in chickens, the therapeutic effects of FMT exhibited both commonalities and species-specific differences compared with findings in mammalian studies. The cross-species common mechanism lies in the

restoration of gut microbial diversity and enhancement of intestinal barrier function. Experimental results from this study demonstrated that FMT ameliorated intestinal structural damage in chickens, consistent with findings in mouse models (Zhang *et al.*, 2024; Hu *et al.*, 2025). Additionally, the effective regulation of serum inflammatory cytokines by FMT in this chicken model aligned with observations in weaned calves and mouse models (Jiang *et al.*, 2023; Gao *et al.*, 2025). This immunomodulatory effect is achieved through cross-species conserved pathways involving microbial metabolites. However, key differences exist between avian species and mammals. The unique digestive tract structure of birds (such as the crop and ceca) shapes their distinct microbial communities, making the success of FMT dependent on microbiota adapted to such environments. The dynamics of microbial engraftment and the taxonomy of key beneficial bacteria differ from those in mammals (Gan *et al.*, 2023; Sommer *et al.*, 2025). Furthermore, meat quality is a key parameter in poultry research, but studies focusing on its fundamental mechanisms in laboratory mammalian models (e.g., rodents) remain relatively insufficient. Therefore, although the core mechanism by which FMT promotes

health through microbiota reconstruction is universal, its specific mechanisms of action and efficacy are still subject to host-specific regulation.

The intestinal microbiota, a complex symbiotic ecosystem inhabiting the gastrointestinal tract, has a fundamental influence on host physiological development and growth performance. Current research demonstrates that FMT serves as an effective microbial intervention strategy, capable of markedly improving animal productivity (Cheng *et al.*, 2022; Yang *et al.*, 2024). Furthermore, FMT has been shown to selectively suppress pathogenic bacterial proliferation while facilitating the establishment of beneficial microbial populations, thereby enhancing both ecological diversity and community resilience of the gut microbiome (Su *et al.*, 2024; Hou *et al.*, 2025). Specifically, FMT mediates microbial reconstitution through the introduction of functionally beneficial bacterial taxa, effectively reestablishing populations of probiotic microorganisms, along with bacterial species involved in vitamin biosynthesis and amino acid metabolism, while concurrently suppressing pathogenic bacterial colonization (Wen *et al.*, 2024). The efficacy of FMT in restoring gut health is supported by research. Similarly, strategies such as the use of *Streptomyces* species and probiotics serve as antibiotic alternatives to enhance poultry health (Gul and Alsayeqh, 2022; Maqbool *et al.*, 2023; Rashid *et al.*, 2023). Notably, the use of metabolites derived from specific actinomycetes, such as *Streptomyces hygroscopicus*, in treating poultry diseases further highlights the therapeutic potential of modulating the gut microbiota (Tariq *et al.*, 2025).

The functional efficiency of nutrient digestion and absorption in animals is directly influenced by intestinal villus height, whereas crypt depth governs the proliferation rate of intestinal villus epithelial cells and serves as an indicator of intestinal epithelial metabolic turnover (Abd El-Hack *et al.*, 2020). Scientific investigations demonstrate that FMT contributes to the reestablishment of intestinal microbial homeostasis, optimization of gut morphological architecture, and enhancement of nutrient utilization efficiency (Chen *et al.*, 2021; Acevedo-Román *et al.*, 2024). This restoration of intestinal integrity is crucial for mitigating the systemic consequences of dysbiosis. The histomorphological improvements provide conclusive evidence that FMT effectively reverses antibiotic-induced intestinal damage and restores mucosal architecture (Kamlárová *et al.*, 2025). The observed villus elongation substantially expands the intestinal absorptive surface area, thereby enhancing nutrient assimilation capacity and ultimately supporting enhanced organismal growth and development.

The presence of focal inflammatory reactions triggers the upregulation and release of pro-inflammatory mediators, including IL-6, which subsequently stimulates excessive TNF- α production, ultimately potentiating the severity of colonic inflammatory processes (Koureta *et al.*, 2024; Lv *et al.*, 2024). Therapeutic management of colitis primarily involves modulating the microbiota and attenuating the inflammatory response. Intestinal dysbiosis facilitates the overproliferation of pathogenic bacteria, thereby elevating luminal endotoxin concentrations. This cascade compromises mucosal barrier integrity, enhancing intestinal permeability and facilitating transmural

lipopolysaccharide translocation into the systemic circulation. The resultant endotoxemia induces persistent low-grade systemic inflammation, ultimately resulting in subclinical endotoxemia (Dmytriv *et al.*, 2024). FMT demonstrates significant immunomodulatory capacity by simultaneously downregulating pro-inflammatory mediators and enhancing the production of anti-inflammatory cytokines (Lai *et al.*, 2025).

Meat color is the most important indicator for evaluating the appearance of meat, which can reflect the tenderness, color, nutritional value, and other sensory characteristics. The formation of meat color is primarily determined by the content of myoglobin and hemoglobin in the muscle (Hoa *et al.*, 2020). The greater the loss of hemoglobin, the higher the myoglobin content, resulting in an increase in the a^* value of meat color (Wu *et al.*, 2023). Muscle with a low pH value typically appears lighter in color and exhibits better tenderness and palatability, whereas muscle with a high pH value tends to be darker and firmer in texture. This is attributed to the color changes of myoglobin and hemoglobin in response to pH variations (Fotou *et al.*, 2024).

Although the findings highlight the promise of FMT, several limitations must be acknowledged for its translation into field applications. Key challenges include biosecurity concerns regarding pathogen transmission, the need for standardization of donor screening and microbiota preparation protocols, and unresolved regulatory hurdles for widespread use in poultry production (Moreno-Sabater *et al.*, 2025; Xie *et al.*, 2025). Addressing these issues is essential for harnessing the full potential of FMT as a sustainable alternative to antibiotics.

Conclusions: Antibiotic treatment can disrupt the gut microbiota, leading to endotoxemia and negatively impacting host health. As an effective microecological intervention, FMT serves as a therapeutic approach, restoring microbial diversity, mitigating endotoxemia, and repairing intestinal damage caused by dysbiosis. Furthermore, FMT enhances meat quality in chickens, highlighting its dual role in improving both gut health and the quality of poultry products. This study provides a systematic investigation of the therapeutic effects of FMT on endotoxemia and gut dysbiosis-induced damage in chickens. The findings provide novel insights into microbiota-based strategies for managing intestinal health and preventing disease in poultry production, offering both theoretical foundations and practical applications for sustainable poultry farming practices.

Declaration of Interest statement: The authors declare that they have no conflict of interest.

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Data availability: The experimental data and materials can be obtained by contacting the corresponding author.

Authors contribution: XC, YQ and HW conceived and designed the study. XC, BY, JQ, MC, YL, WC, HZ, YW and MS executed the experiment and analyzed the sera and tissue samples. XC and BY analyzed the data. XC edited the manuscript. All authors approved the final version of the manuscript.

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