Review

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Posted Date: 11 July 2025

doi: 10.20944/preprints202507.0885.v1

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 doi:10.20944/preprints202507.0885.v1

Review

Zoonotic Risks of *Proteus mirabilis*: Detection, Pathogenicity, and Antibiotic Resistance in Animals and Animal-Derived Foods

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Abstract

Proteus mirabilis is a major uropathogen with growing concern over its presence in animal products and the associated zoonotic transmission risks. As a gut commensal in both humans and animals, it is increasingly detected in wild, farm, and companion animals, as well as in animal-derived foods and related environments. This review summarizes current evidence on its distribution across these sources and explores potential transmission routes to humans. Special attention is given to reported genomic similarities and shared antimicrobial resistance patterns between animal and human isolates. The role of *P. mirabilis* in exacerbating intestinal inflammation further highlights its relevance beyond urinary infections. By revealing the epidemiology, pathogenic traits, and resistance profiles of animal-associated isolates, this review underscores the zoonotic potential of *P. mirabilis* and emphasizes the need for enhanced surveillance and research from a One Health perspective.

Keywords: *Proteus mirabilis*; animals; transmission; antibiotic resistance; One Health

1. Introduction

Proteus mirabilis, a Gram-negative facultative anaerobic bacterium, belongs to the genus Proteus within the family Morganellaceae. Traditionally classified in the *Enterobacteriaceae* family, the taxonomy of *P. mirabilis* was reassessed with advancements in genomic analysis, leading to its reclassification under *Morganellaceae* by Adeolu et al. in 2024 based on phylogenetic studies [1]. As of December 9, 2024, the LPSN database lists *P. mirabilis* as a formally recognized species within this family, alongside other species such as *Proteus vulgaris*, *Proteus cibi*, and *Proteus faecis* [2,3]. The genus *Proteus* includes ten officially named species, with additional unnamed genomic species (genotypes 4, 5, and 6) [2,3].

Morphologically, *P. mirabilis* displays remarkable features, with a cell size ranging from 1.0 to 3.0 μm in length and 0.4 to 0.8 μm in width. The bacterium is polymorphic, appearing as short rods, spheres, and filaments, and lacks both a capsule and spore structure [4,5]. It is motile due to the presence of flagella and exhibits a characteristic swarming behavior on agar surfaces. This strong motility leads to the formation of concentric rings and visible demarcation lines—known as Dienes' lines—which are used for strain differentiation [6,7]. The bacterium also possesses pili, enabling adhesion to epithelial cells of plants and fungi [8]. *P. mirabilis* is a major uropathogen, contributing to more than 40% of catheter-associated urinary tract infections (CAUTIs) cases [9–12]. Its virulence factors, including urease, flagella, pili, hemolysins, and metalloproteases, play crucial roles in its ability to colonize the host, damage tissues, and evade immune responses [13,14]. Although typically a commensal in the intestinal tract, recent studies have linked P. mirabilis to inflammatory bowel diseases such as Crohn's disease [15]. It has been shown to exacerbate colitis by disrupting the intestinal mucus barrier and modulating host immune responses [16].

 doi:10.20944/preprints202507.0885.v1

Although the epidemiology and pathogenicity of *P. mirabilis* have been widely studied, its significance as a zoonotic pathogen remains poorly documented. This review summarizes current findings on the distribution of *P. mirabilis* in wildlife, farm animals, companion animals, and associated environments and products. We also aim to elucidate the potential transmission routes of this zoonotic pathogen between humans and animals, with a focus on reported genomic similarities and shared antibiotic resistance patterns. By highlighting the zoonotic risks associated with *P. mirabilis*, this review seeks to provide a basis for future research on its pathogenic mechanisms and its impact on human and animal health.

2. The Detection of *P. mirabilis* in Animals

As a commensal bacterium in the gastrointestinal tract of both humans and animals, *P. mirabilis* is widely distributed across diverse animal species, including wildlife, farm animals, and companion animals. This broad host range suggests potential transmission routes between domestic and wild environments, as well as between animals and humans. As shown in the Table 1, the frequent isolation of *P. mirabilis* from various animal sources underscores its widespread presence.

Wildlife has been identified as a significant reservoir for *P. mirabilis*, with the bacterium isolated from a wide range of species and their environments, underscoring its zoonotic potential. In undisturbed natural settings, Suárez-Pérez et al. detected *P. mirabilis* in 36.2% (17/47) of cloacal swabs from Egyptian vulture chicks in the Canary Islands, Spain [17]. Gao et al. isolated a single *P. mirabilis* strain (KUST-1312) from 1 out of 37 migratory bird fecal samples collected at Dianchi Lake, China, representing a detection rate of 2.7% (1/37) [18]. These findings underscore the potential role of wild birds in the transmission of *P. mirabilis*. In addition to vertebrate hosts, ectoparasites may also contribute to the transmission of *P. mirabilis* among wildlife populations. For example, Ergunay et al. reported a high isolation rate 48.5% (17/35) from ticks collected from wild animals in Kenya—including black rhinos, buffaloes, elephants, giraffes, Grevy's zebras, lions, and leopards—as well as from domestic cattle [19].

In wildlife held in controlled environments such as zoos or farms, *P. mirabilis* has also been successfully isolated. Liu et al. employed multiplex PCR to detect *P. mirabilis* in 100 fecal samples from giant pandas in Sichuan, China, reporting an isolation rate of 30% (35/100) [20]. Furthermore, in an investigation of 32 red panda deaths, three positive cases of *P. mirabilis* were found in kidney, liver, and urine samples, yielding an isolation rate of 9.38% (3/32), in the same center [21]. Lv et al. isolated 53 strains of *P. mirabilis* from the feces of foxes, raccoons, and minks, as well as from the surrounding soil in farming environments. The isolation rates were 41.51% (22/53) for foxes, 33.96% (18/53) for raccoons, and 24.53% (13/53) for minks [22]. Under controlled laboratory conditions, *P. mirabilis* has been isolated from various wildlife species. Yu et al. reported its detection in the feces of diarrheal rhesus macaques 9.5% (7/74) and ferrets 30% (4/12) [23]. As an emerging laboratory animal in biomedical research, the tree shrew harbors *Proteus* species as dominant members of its gut microbiota, with *P. mirabilis* being the most frequently isolated. Gu et al. reported that *P. mirabilis* was isolated from 34 out of 36 fecal samples, yielding a prevalence rate of 94.4% (34/36) [24].

Farm animals serve as important reservoirs for *P. mirabilis*, with the presence of this bacterium raising concerns for both animal health and public safety. As essential sources of food for humans, farm animals, particularly livestock and poultry, act as major reservoirs for this bacterium. Chinnam et al. found a 15.95% (26/163) isolation rate of *P. mirabilis* from rectal swabs of pigs in Krishna District, Andhra Pradesh, India, highlighting its widespread presence in the digestive systems of livestock [25]. In Zhejiang, China, Qu et al. reported a 5.55% (30/541) isolation rate from pigs across three cities, with the highest contamination found in the Jinhua region (8.91%) [26]. The bacterium's presence is not limited to the digestive tract, as it has also been detected in boar semen samples from an artificial insemination center in Rome, Italy. Here, *P. mirabilis* was shown to negatively impact sperm motility, which could influence reproductive success and breeding efficiency [27]. Besides pigs, Chinnam et al. reported that in Krishna District, Andhra Pradesh, India, *P. mirabilis* was isolated from cloacal swabs of healthy chickens at a rate of 21.36% (47/220), as well as from rectal swabs of cattle and sheep,

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with isolation rates of 33.33% (20/60) and 31.91% (15/47), respectively [25]. A study conducted in Shandong, China revealed an isolation rate of 7.07% (50/707) in broilers [28], while Ramatla et al. reported a lower isolation rate of 5.4% (26/480) in chicken manure from farms in the Ngaka Modiri Molema district, South Africa [29]. These findings underscore the role of farm animals as key players in the ecology of *P. mirabilis* and highlight the potential risks to animal health and food safety.

However, the association of *P. mirabilis* with disease in farm animals presents a more concerning aspect. For example, in Guangxi, China, Ge et al. found an isolation rate of 21.42% (21/98) in fecal and tissue samples from diseased pigs, highlighting the potential pathogenic role of this bacterium in compromised animal health [30]. Similarly, Sun et al. reported a higher isolation rate of 22.5% (18/80) in diarrheal poultry and 23.26% (20/86) in cattle from northeastern China, indicating that *P. mirabilis* may exacerbate disease in affected animals [31]. In ducks, Algammal et al. found an isolation rate of 14.6% (35/240) in both healthy and diseased individuals in Port-Said Province, Egypt, further suggesting the bacterium's diverse role in animal health [32].

Companion animals, which have frequent and close interactions with humans, serve as a potential source for the transmission of zoonotic pathogens, including *P. mirabilis*. This bacterium has been increasingly identified in pets, underlining its significance in the epidemiology of zoonotic diseases. Marques et al. reported that in households with companion animals, *P. mirabilis* was isolated from the feces of both humans and dogs. The isolation rate in humans was 12.5% (3/24), while in dogs, it was significantly higher at 44.4% (8/18), with no detection in cats [33]. Liu et al. isolated 75 strains of *P. mirabilis* from fecal samples of both household and stray dogs in Sichuan, China, with an overall isolation rate of 31.12% (75/241). Notably, the isolation rate 36.17% (34/94) in stray dogs was significantly higher than 27.89% (41/147) in household dogs [34]. Interestingly, exotic pets have also been identified as carriers of *P. mirabilis*. Pathirana et al. isolated the bacterium from pet turtles bought from pet shops and online stores in South Korea, with an isolation rate of 28.8% (15/52) [35].

The involvement of *P. mirabilis* in diseased companion animals has also been documented. As a well-known urinary tract infection (UTI) pathogen in humans, *P. mirabilis* similarly contributes to UTIs in dogs and cats. Fonseca et al. identified *P. mirabilis* in 22.7% (145/637) of canine urine samples, whereas its detection in feline samples was markedly lower at 2.2% (4/171), based on specimens submitted to NationWide Laboratories in the United Kingdom [36]. Similarly, Moyaert et al. found *P. mirabilis* in 11.0% (48/437) of dog and 1.1% (2/179) of cat urine samples across Europe, while *Escherichia coli* being the most common pathogen for UTI [37]. In Chiang Mai, Thailand, Amphaiphan et al. detected *P. mirabilis* in 13.6% (27/198) of dog and 16.7%.

Table 1. Isoalation of Proteus mirabilis from animals and animal-drived foods.

Category	Host	Region (Year)	Isolation Rate	Virulence Gene	Reference
Wildlife	Migratory Birds	China (2024)	2.7% (1/37)	NA	[18]
	Canarian Egyptian Vultures	Spain (2022)	36.2% (17/47)	NA	[17]
	Tick from wildlife	Kenya (2022)	48.5% (17/35)	NA	[19]
	Panda	China (2023)	30% (30/100)	NA	[20]
	Red panda	China (2022)	9.38% (3/32)	NA	[21]
	Fox	China (2022)	41.51% (22/53)	*ureC, zapA, pmfA, atfA, mrpA, atfC , hmpA, rsmA, rsbA, ucaA*	[22]
	Raccoon	China (2022)	33.96% (18/53)	*ureC, zapA, pmfA, atfA, mrpA, atfC , hmpA, rsmA, rsbA, ucaA*	[22]

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	Ferrets	China (2015)	30% (4/12)	NA	[23]
	Mink	China (2020, 2022)	24.53% (13/53)-28.7% (62/216)	*ureC, zapA, pmfA, atfA, mrpA, atfC , hmpA, rsmA, rsbA, ucaA, FliL*	[22,31]
	Rhesus Monkeys	China (2015)	9.5% (7/74)	NA	[23]
	Tree shrews	China (2020)	94.4% (34/36)	NA	[24]
	Pig	China (2021, 2022), Rome (2021), India (2021)	5.55% (30/541)-21.43% (21/98)	*ureC, hpmA, zapA, pmfA, rsbA, ucaA, mrpA, atfA, ireA , ptA*	[25–27,30]
Farm animals	Broiler	China (2020, 2022), India (2021), South Africa (2024)	5.4% (26/480)-22.5% (18/80)	*ureC, rsmA, hmpA, FliL , ireA, ptA , zapA, ucaA, pmfA, atfA , mrpA, hlyA , hpmA*	[25,28,29,31]
	Duck	Egypt (2021)	14.6% (35/240)	*atpD, ureC, rsbA , zapA*	[32]
	Cattle	China (2020), India (2021)	23.26% (20/86)-33.33% (20/60)	*ureC, zapA, rsmA, hmpA, mrpA, atfA, pmfA, FliL, ucaA*	[25,31]
	Sheep	India (2021)	31.91% (15/47)	NA	[25]
	Dog	China (2020, 2022, 2023), Egypt (2022), UK (2021), Thailand (2019), European countries (2016), Portugal (2018, 2021)	11.0% (48/437)-87.85% (94/107)	*ureC, FliL, ireA, zapA, ptA, hpmA, hpmB, pmfA, rsbA, mrpA, ucaA, rsmA, atfA*	[31,33,34,36–40,48,75]
Companion animals	Cat	UK (2021), Thailand (2020), Europe (2017), Portugal (2019, 2022)	0-16.7% (4/24)	*hmpA/hmpB, mrpA, pmfA, ucaA*	[33,36–38,48]
	Pet turtle	South Korea (2018)	28.8% (15/52)	*ureC, rsbA, zapA , mrpA*	[35]
	Pork	China (2022, 2023), Brazil (2021), India (2021)	14.38% (23/160)-65.61% (149/227)	*mrpA, pmfA, ucaA, atfA, hpmA, zapA, ptA, ireA*	[25,41,45,46]
	Beef	Brazil (2021)	27.8% (100/360)-32.73% (17/55)	*mrpA, pmfA, ucaA, atfA, hpmA, zapA, ptA, ireA*	[25,41]
Animal-derived foods	Mutton	India (2021)	25.51% (25/98)	NA	[25]
	Chicken	China (2022, 2023), Belgium (2020), Brazil (2021), India (2021), Egypt (2023)	1.51% (1/66)-100% (200/200)	*mrpA, pmfA, ucaA, atfA, hpmA, zapA, ptA, ireA*	[25,41–43,45,46]
	Duck meat	China (2023)	67.9% (84/124)	NA	[46]
	Milk/Dairy Products	India (2021), Egypt (2023)	3.45% (2/58)-22.11% (21/95)	NA	[25,42]
Other source	Aquatic products	China (2022)	7.61% (7/92)	NA	[45]

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Vegetables	**China (2023)**	**62.5% (5/8)**	***hpmA, mrpA, ptA, ireA, zapA, pmfA , atfA***	**[76]**

(4/24) of cat urine samples [38]. Beyond UTIs, *P. mirabilis* has been isolated from companion animals with gastrointestinal symptoms. Wang et al. reported a 19.35% (12/62) isolation rate from fecal samples of dogs with diarrhea in Jilin, China [39]. Furthermore, Sui et al. found *P. mirabilis* in 47.37% (9/19) of dogs infected with canine parvovirus and 10% (2/20) of dogs suffering from canine distemper [40].

3. Detection of *P. mirabilis* in Animal-Derived Foods

Animal-derived foods have become a major focus of public health concern due to their contamination with *P. mirabilis*. The prevalence of *P. mirabilis* in animal products varies significantly across different countries and regions, reflecting differences in hygiene practices and environmental conditions (as shown in table). In Andhra Pradesh, India, beef samples exhibited the highest contamination rate at 32.73% (17/55), while chicken and pork samples showed relatively lower detection rates of 19.49% (38/195) and 14.38% (23/160), respectively [25]. In Londrina-PR regions, Brazil, chicken meat displayed the contamination rate of chicken meat was the highest at 100% (200/200), that of beef was much lower at 27.8% (100/360) [41]. In Al Qalyubia Governorate, Egypt, chicken and milk samples had contamination rates of 1.51% (1/66) and 3.45% (2/58) [42]. In Ghent, Belgium, Yu et al. reported P. mirabilis in 36.25% (29/80) broiler carcasses [43], while Liu et al. reported a much higher contamination rate of 66% (66/100) in fresh chicken at Heibei, China [44]. A study by Ma et al. in wet market in Chengdu, China, isolated 89 strains of *P. mirabilis* from 347 samples of chicken, pork, and aquatic products, with an overall contamination rate of 25.65% (89/347). Among these, chicken showed the highest rate at 54.39% (62/114), followed by pork 14.18% (20/141) and aquatic products 7.61% (7/92) [45]. Lan et al. found *P. mirabilis* in 490 of 579 fresh meat samples (84.63%) from five wet markets in Zhongshan, China, with chicken 78.95% (180/228), duck 67.90% (84/124), and pork 65.61% (149/227) being the most contaminated [46]. These findings indicate that poor hygiene at poultry and meat stalls may result in significant contamination and cross-contamination, particularly affecting poultry meat. Flies associated with animal-derived food also appear to serve as potential vectors of transmission. Zaher et al. detected *P. mirabilis* from flies collected on pig carcasses [47].

Currently, *P. mirabilis* has been detected in food derived from farm animals, and its epidemiology in these animals has been well-documented. However, detection of *P. mirabilis* in game meat from wildlife has not yet been reported. This gap in the research highlights an area for further investigation, as the potential for *P. mirabilis* to be present in game meat from wildlife and contribute to zoonotic transmission remains unexplored.

4. Genomic Similarity Between Animal- and Human-Derived *P. mirabilis*

High genomic similarity has been observed between P. mirabilis isolates from hu-mans, animals, and associated products and environments (as shown in the figure). Notably, P. mirabilis isolates from companion animals have been shown to share high genomic similarity with human isolates, with some strain pairs originating from indi-viduals and pets within the same household. Marques et al. collected urine samples from 76 human patients and 107 companion animals with UTIs, and subsequently con-structed a phylogenetic tree based on PFGE genotyping to compare the genetic relat-edness of the isolates [48]. Among 39 clusters, 17 contained both human and animal isolates, with genomic similarity ranging from 80% to 100%. One canine isolate of P. mirabilis showed 100% similarity with a human isolate, while a feline isolate shared over 90% similarity with a human strain [48]. In a separate study, Marques et al. identified a human-dog pair harboring genetically related P. mirabilis strains, exhibiting 82.5% sim-ilarity to the animal-derived clinical strain FMV4938/07, which was isolated from a dog with a urinary tract infection [33]. One fecal P. mirabilis isolate from a dog in a separate household clustered with two human community-acquired UTI isolates, showing 80.9%

 doi:10.20944/preprints202507.0885.v1

and 88.9% genomic similarity, respectively [33]. Wang et al. isolated P. mirabilis (CC16012 strain) from a diarrheal dog, which was closely related to the human-derived Crl143 strain from the United States [39]. Pathirana et al. found that the mrpA gene se-quence of P. mirabilis from pet turtles showed 96.4% and 94.9% similarity to human isolates from UTI and respiratory infections, respectively [35]. In experimental animals, Yu et al. isolated P. mirabilis from diarrheal primate feces, which exhibited 99.6% simi-larity to the UTI patient-derived HI4320 strain, demonstrating a high level of genomic similarity [23].

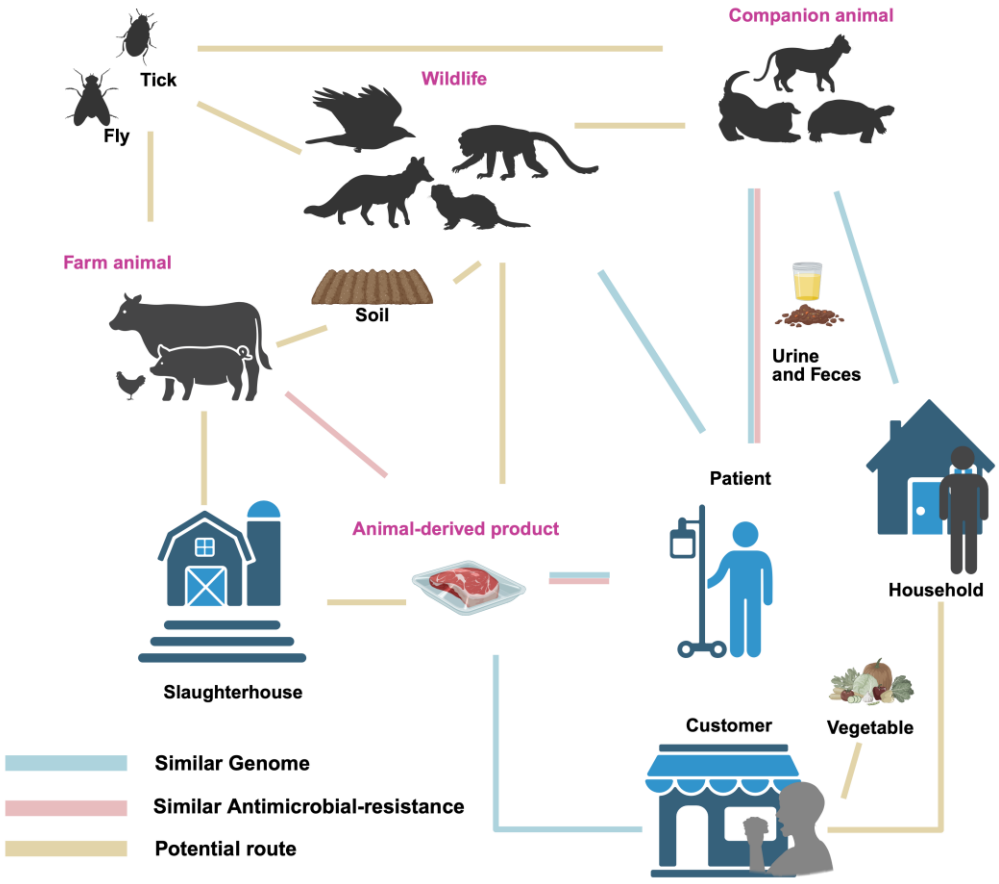

Figure 1. Transmission routes of Proteus mirabilis between animals, products, environments, and humans. Line for similar genome: Similarity of genomes between isolates from both sources has been reported; Line for similar antimicrobial resistance: Similar patterns of antibiotic resistance have been reported; Line for potential route: Potential connection between sources, but not yet studied.

Isolates from animal-derived products have shown high genomic similarity with those from human sources. Yu et al. reported that, based on PFGE analysis, the highest similarity observed between a broiler carcass isolate and a human stool isolate was 83.3%, differing by only two bands [43]. Similarly, Sanches et al. confirmed clonal rela-tionships exclusively between chicken-derived isolates and those causing communi-ty-acquired urinary tract infections (UTI-CA), particularly within cluster C01. Notably, two strains within this cluster—one from chicken meat and the other from a UTI-CA patient—exhibited 100% genomic similarity as determined by PFGE [49]. Furthermore, the blaNDM-1 gene in strain JZ109 showed 100% nucleotide identity (with only a single base difference) to SGI1-1NDM, which was the first reported clinical P. mirabilis strain from China [45].

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5. Pathogenicity of *P. mirabilis* in Humans and Animals

The *pathogenicity of P. mirabilis* has been reported in various tissues and organs of both humans and animals, with severe cases leading to death. One of the most notable associations of P. mirabilis is as a major pathogen in UTIs in both humans and companion animals [37,50]. Studies indicate that *P. mirabilis* accounts for 1-10% of all UTI cases in humans [51]. In nearly 3,000 confirmed UTI cases in North America, infections caused by *P. mirabilis* represented 4% of all cases. Furthermore, the incidence of catheter-associated urinary tract infections (CAUTIs) caused by P. mirabilis is as high as 45% or more [52]. The incidence of *P. mirabilis*-induced UTI is significantly higher in women and the elderly population [51–53]. In animals, *P. mirabilis* has been linked to recurrent urinary stones in dogs with urinary system disorders, as evidenced by Song et al. [54]. Herout et al. also reported a high infection rate of *P. mirabilis* in a murine CAUTI model, further highlighting the bacterium's role in urinary infections across species [55]. These findings highlight the role of *P. mirabilis* in UTIs in both humans and animals, with important implications for medical treatment and public health.

P. mirabilis has also been implicated in food poisoning incidents. Between 2016 and 2017, 3.61% of reported food poisoning cases in the Datong, China were caused by *P. mirabilis*, with symptoms such as abdominal pain, diarrhea, nausea, and dizziness [56]. Wang et al. reported a food poisoning incident in Beijing in 2018, where *P. mirabilis* contamination in braised meatballs led to illness among customers, with the bacterium detected on the hands of the chef and waitstaff [57]. Furthermore, between August and December 2018, Fan et al. isolated *P. mirabilis* from 49 out of 486 diarrheal pediatric samples, yielding a detection rate of 10.1% [58]. Zhang et al. compared the feces and inflamed colon samples from Crohn's disease (CD) patients and healthy individuals, finding a significant increase in the abundance of *P. mirabilis* in CD patients. The experimental results showed signs of colon shortening, and liver and spleen enlargement, indicating that *P. mirabilis* plays a critical role in inducing CD inflammation [15]. Additionally, Kitamoto et al. suggested that oral inflammation could exacerbate intestinal inflammation, and the use of proton pump inhibitors may promote the proliferation of *P. mirabilis* and other microbes in the intestines, thus triggering intestinal inflammation [59].

In animals, *P. mirabilis* has been associated with various cases of gastrointestinal diseases. In 2018, a bamboo rat farm in Guangdong, China reported the deaths of 400 bamboo rats due to vomiting and diarrhea, with *P. mirabilis* identified as the causative agent [60]. Yu et al. reported similar symptoms in 74 rhesus monkeys infected with *P. mirabilis*, including diarrhea and bloody stools [23]. In a rabbit farm in Henan, China, *P. mirabilis* (strain HN001) infection resulted in lethargy, yellow watery diarrhea, and mass fatalities, accompanied by multi-organ tissue damage [61]. In Lhasa, China, a breeding farm experienced deaths of breeding rabbits due to *P. mirabilis* (strain T2018) infection, presenting with diarrhea and subsequent fatality [62]. Moreover, Dong et al. identified *P. mirabilis* (strain 17f) as the primary pathogen responsible for diarrhea in lambs in the Hotan area of Xinjiang, China [63]. These reports underscore the significant role of *P. mirabilis* as a gastrointestinal pathogen in both humans and animals, with implications for public health, food safety, and animal welfare.

In addition to affecting the urinary and gastrointestinal systems, *P. mirabilis* has been implicated in a wide range of infections across various organs in both animals and humans. In human medicine, Mistry et al. reported the isolation of *P. mirabilis* from skin abscesses with an isolation rate of 21.6%, second only to methicillin-sensitive *Staphylococcus aureus* (24.3%) [64]. In pigs, Qin et al. and Chen et al. identified *P. mirabilis* (GX-PM1 and GX-Y9251 strains) as a cause of respiratory symptoms such as fever and difficulty breathing. They also noted that P. mirabilis could cross the placental barrier, resulting in fetal death [65,66]. Similarly in animals, Li et al. found that *P. mirabilis* caused multi-organ lesions and systemic inflammation in pigs, which progressed to septicemia and death [67]. In Northern Paraná, Brazil, Sanches et al. isolated *P. mirabilis* strains (LBUEL-A33 and LBUEL-A34) from broiler chickens, where the bacterium induced caseous exudates and hemorrhaging in the subcutaneous tissue, leading to condemnation in poultry industry. Histopathological analysis

 doi:10.20944/preprints202507.0885.v1

revealed edema, congestion, and necrosis in the pectoral muscles, along with cellulitis and infiltration of inflammatory cells [68].

Furthermore, *P. mirabilis* has been reported to cause severe infections in other animal species. Abdollahi et al. and Ghahremani et al. were the first to document *P. mirabilis*-induced pyoderma and purulent pericarditis in sheep [69,70]. Sacristán et al. identified *P. mirabilis* as a significant causative agent of neck abscesses and bacteremia in sea lions [71]. Pattanayak et al. observed *P. mirabilis*-induced hemorrhaging in the glomeruli and localized necrosis with mononuclear cell infiltration in the kidneys of infected Indian carp [72].

6. Antibiotic Resistance of *P. mirabilis* from Animals and Animal-Derived Products

Antibiotic resistance in *P. mirabilis* isolates from animal and food sources has been widely studied due to the growing concerns about public health (Figure & Supplementary Table S1). Among farmed wildlife, Lv et al. reported differences in antibiotic resistance rates of *P. mirabilis* isolates from foxes, raccoons, and minks. Fox-derived strains showed high resistance to cefotaxime (94.4%), gentamicin (83.3%), and ampicillin (88.9%), significantly higher than those from raccoons and minks. Mink-derived strains showed narrower resistance profiles, maintaining sensitivity to cefotaxime, ceftazidime and ofloxacin. Notably, most isolates were resistant to imipenem (71.70%), a carbapenem [22]. In traditionally farmed livestock, *P. mirabilis* isolates from pigs, as reported by Ge et al. and Qin et al., were found to be multi-drug resistant (MDR), exhibiting resistance to at least three classes of antibiotics [30,65]. These MDR strains exhibited 100% resistance to tetracyclines, ampicillin, and sulfonamides, with resistance rates for imipenem and kanamycin at 85.7%. Resistance to gentamicin and amikacin was 9.5%, and ciprofloxacin resistance was 38.1%, with fosfomycin resistance at 28.6% [30,65]. Qu et al. found that all 30 *P. mirabilis* strains isolated from pigs were MDR, with 100% (30/30) resistance to tetracyclines, chloramphenicol, and macrolides. Resistance to ampicillin and amoxicillin/clavulanate reached 90% (27/30), while all are sensetive to meropenem. Among quinolones, ciprofloxacin had the highest resistance 76.67% (23/30), and ofloxacin had the lowest 43.33% (13/30). For aminoglycosides, gentamicin and amikacin resistance rates were 56.67% (17/30) and 20% (6/30), respectively, with rifampicin resistance at 40% (12/30) [26].

In poultry, Li et al. found that all 50 *P. mirabilis* isolates from meat chickens in Shandong exhibited MDR. Resistance rates to β-lactams (cefazolin, ceftriaxone, and cefuroxime) and aminoglycosides (tobramycin and gentamicin) exceeded 50%, with no resistance to aztreonam. Ciprofloxacin, chloramphenicol, and trimethoprim-sulfamethoxazole resistance rates were all 98% [28]. Ramatla et al. found that 30.7% (8/26) of *P. mirabilis* strains from broilers exhibited MDR, with ciprofloxacin resistance at 61.5% (16/26), nalidixic acid resistance at 30.8% (8/26), and gentamicin resistance at 38.5% (10/26). Resistance to amoxicillin-clavulanate was 46.2% (12/26), while imipenem and ertapenem resistance was low at 7.7% (2/26) [29]. Moreover, Algammal et al. reported that *P. mirabilis* isolates from ducks showed 100% (35/35) resistance to amoxicillin, penicillin, trimethoprim-sulfamethoxazole, and doxycycline, with 31.4% (11/35) of the strains classified as extensively drug-resistant (XDR), and 8.6% (3/35) as pan-drug-resistant (PDR) [32]. In the β-lactam class, the resistance rates to piperacillin, amoxicillin-clavulanate, and ampicillin-sulbactam were 77.1% (27/35), while meropenem and imipenem resistance was 8.6% (3/35). Among the quinolones, nalidixic acid resistance reached 62.8% (22/35), while norfloxacin resistance was 8.6% (3/35). Resistance rates to erythromycin and polymyxins were 62.8% (22/35) and 40% (14/35), respectively [32]. Moreover, In the environment, Wang et al. reported the isolation of *P. mirabilis* carrying the *blaNDM-1* gene from the surface of houseflies at a sheep farm in Hubei, China [73]. Similarly, Odetoyin et al. found two *Proteus* spp. isolates from captured houseflies, both of which were multidrug-resistant and exhibited 100% (2/2) resistance to streptomycin, trimethoprim-sulfamethoxazole, and amoxicillin [74].

For companion animals, Liu et al. isolated 75 strains of *P. mirabilis* from dog feces in Chengdu, China, including 41 from pet dogs and 33 from stray dogs. Of these, 53.33% (40/75) were MDR, with pet dogs exhibiting a significantly higher proportion of MDR strains (75%) compared to stray dogs

 doi:10.20944/preprints202507.0885.v1

(25%). Pet dog strains showed resistance to β-lactam antibiotics, with 31.71% (13/41) resistance to cefotaxime, 36.59% (15/41) to ciprofloxacin, 21.95% (9/41) to gentamicin, and 51.22% (21/41) to chloramphenicol. All strains were resistant to tetracyclines 100% (75/75). In contrast, isolates from stray dogs remained susceptible to these antibiotics [34]. This contrast suggests that the use of antimicrobials in companion animal clinics may play a role in the emergence and exacerbation of antibiotic resistance.

In diseased animals, Marques et al. reported *P. mirabilis* strains from companion animals with UTIs in Portugal had significant resistance to β-lactams such as ceftazidime 5.6% (6/107), cefotaxime 9.4% (10/107), cefoxitin 9.4% (10/107), and cefovecin 9.4% (10/107), as well as to chloramphenicol 28% (30/107) [48]. Sun et al. reported that 60.22% (106/176) of *P. mirabilis* strains isolated from diarrheal animals (dogs, minks, cattle, and fowl) from a northeast farm, China, were MDR, with 16.48% (29/176) classified as XDR. High resistance rates were observed to β-lactams like ampicillin 59.09% (104/176), quinolones such as ciprofloxacin 57.39% (101/176), aminoglycosides like streptomycin 55.68% (98/176), tetracyclines such as doxycycline 63.64% (112/176), and tetracycline 55.12% (97/176). imipenem resistance was the lowest at 20.45% (36/176). Additionally, resistance was observed to sulfamethoxazole 43.19% (76/176), nitrofurantoin 42.61% (75/176), and polymyxin B 39.2% (69/176) [31]. El-Tarabili et al. found *P. mirabilis* isolates from diarrheal dogs in Egypt exhibited 100% (25/25) resistance to β-lactams like penicillin and amoxicillin, and sulfonamides such as trimethoprim-sulfamethoxazole. Resistance to cefotaxime 36% (9/25), ceftazidime 36% (9/25), amoxicillin-clavulanate 32% (8/25), aztreonam 28% (7/25), gentamicin 12% (3/25), nalidixic acid 12% (3/25), and tetracycline 32% (8/25) was also observed [75]. Pattanayak et al. reported that *P. mirabilis* isolates from diseased carp exhibited MDR and XDR properties, showing resistance to eight classes of antibiotics, including β-lactams (Penicillin G, etc.), tetracyclines (tetracycline), aminoglycosides (tobramycin), sulfonamides, erythromycin, lincomycin, polymyxin, and vancomycin [72].

Since *P. mirabilis* isolates from farm animals exhibit widespread antibiotic resistance, the presence of resistant strains in animal-derived food poses an undeniable public health concern. Sanches et al. reported high rates of MDR in *P. mirabilis* strains isolated from chicken 76.5% (153/200), pork 46% (38/83), and beef 6% (6/100). Chicken-derived strains exhibited the highest resistance to most antibiotics, except for chloramphenicol and florfenicol, with resistance levels surpassing those in beef and pork. Pork-derived strains showed higher resistance to quinolones (nalidixic acid, enrofloxacin), sulfamethoxazole-trimethoprim, florfenicol, and chloramphenicol compared to beef-derived strains [49]. In another study, Lan et al. isolated 490 *P. mirabilis* strains from meat in the Zhongshan market and found that chicken-derived strains had the highest resistance rates to doxycydine 83.33%, β-lactams 82.87%, aminoglycosides 89.81%, sulfonamides 91.67%, and quinolones 54.17%. Pork-derived strains showed resistance only to erythromycin 100%, while duck meat strains exhibited intermediate resistance profiles. Notably, 14.9% of the strains were PDR, highlighting the severe issue of antibiotic misuse [46]. Ma et al. found that 91.01% (81/89) of *P. mirabilis* strains isolated from meat and aquatic products were MDR, with resistance to β-lactams 83.15%, quinolones 79.78%, chloramphenicol 86.52%, and trimethoprim-sulfamethoxazole 94.38%. Among aminoglycosides, resistance to streptomycin 93.26% was high, while amikacin resistance was only 5.62% [45].

Interestingly, non-animal-derived foods have also shown *P. mirabilis* resistant strains. Li et al. found that *P. mirabilis* from vegetables exhibited multi-drug resistance, with resistance to at least four antibiotic classes, including β-lactams (cefotaxime, etc.), quinolones (ciprofloxacin, etc.), aminoglycosides (streptomycin, etc.), and tetracyclines. This suggests the possibility of cross-contamination between animal-derived and other food sources [76].

In addition to genomic similarities, antibiotic resistance profiles of human- and animal-derived *P. mirabilis* strains also show notable similarities. Marques et al. reported that *P. mirabilis* strains isolated from companion animals and human with UTIs in Portugal harboured common antimicrobial resistance [48]. Both companion animal and human strains were sensitive to carbapenems like imipenem, meropenem, and ertapenem. Similarly, Yu et al. found higher resistance

 doi:10.20944/preprints202507.0885.v1

rates in poultry-derived *P. mirabilis* strains compared to human patient isolates for quinolones (ciprofloxacin) and penicillins (ampicillin), with poultry strains showing 48% (25/52) resistance to ciprofloxacin and 62% (32/52) resistance to ampicillin, compared to 35% (17/48) and 44% (21/48) in human isolates. Moreover, both groups exhibited two MDR profiles, suggesting the potential for cross-transmission of resistance genes [43]. These findings indicate a risk of resistance transmission between clinical and food sources.

Furthermore, similar antibiotic resistance patterns were observed between isolates from animals and those from animal-derived food. Chinnam et al. found that 72 *P. mirabilis* strains (31.03%) from 232 animal and food sources were positive for β-lactamase production, including 60 strains confirmed to produce extended-spectrum β-lactamases (ESBLs), which were resistant to ceftazidime and cefotaxime but could be inhibited by β-lactamase inhibitors. About 42% of the sub-clusters contained strains from different hosts, indicating the potential for cross-contamination in slaughterhouse environments [25].

Antibiotic resistance genes (ARGs) contribute significantly to the resistance phenotypes of *P. mirabilis* isolates and have been identified across various animal sources and related products (see Supplementary Table S1). For β-lactam antibiotics, resistance genes *blaOXA-1*, *blaPSE*, *blaTEM*, *blaCTX-M*, and *blaNDM* have been found in isolates from farmed foxes, raccoons, and minks [22]. In farm animals such as pigs, chickens, and ducks, a wider range of resistance genes was detected, including *norA*, *acrB*, *blaOXA*, *blaTEM*, *blaCTX-M*, *blaNDM*, *blaDHA*, and *blaKPC* [25,26,28–30,32,66]. Isolates from companion animals (dogs and cats) carried *blaOXA-1*, *blaTEM*, *blaCTX-M*, and *blaDHA* [34,48,75], while foodborne isolates harbored *blaCTX-M*, *blaOXA*, *blaDHA*, *blaCMY-2*, *blaNDM*, *blaTEM*, *blaSHV*, *blaFOX*, *blaCIT*, *blaEBC*, and *bleMBL* [25,45,49,76].

For quinolones antibiotics, reistance genes *qnrA* and *qnrC* were detected in isolates from farm-rasied wild animals [22], and additional genes such as *qnrS*, *parC*, *qnrD*, and *oqxA* were reported in farm animal isolates [26,28,30]. *qnrA* and *qnrD* were also found in isolates from companion animals [34,48,75], while only *qnrD* was identified in food-derived isolates [45,49]. Aminoglycosides resistance genes including *aac(6')-Ib-cr*, *aadA*, *aadB*, *aphA6*, and *aaC2* were identified in farmed wild animal isolates [22]. Farm animals carried *aac(6')-Ib-cr*, *aph(3)-IIa*, *rmtB*, *aaC1*, and *aaC2*[26,28,30,66], while companion animals harbored *aphAI-IAB*, *aac(3')-IV*, *aac(6')-Ib*, and *aadA1*[34,48,75]. In foodborne isolates, *aac(6')-Ib-cr*, *aph(4)-Ia*, *aadA1*, *aadA2*, *aac(3')-Ia*, *aac(3)-IV*, and *aac(3)-IVa* were detected [45,49,76].

Tetracycline resistance genes such as *tetO*, *catI*, *tet(J)*, *tetA (48)*, *tetA*, *tetB*, *tet (C)*, and *tetM* were found in isolates from farm animals, companion animals, and food sources, but not in wild animal isolates [26,32,34,45,65,66,75,76]. Sulfonamide resistance genes (*sul1*, *sul2*, *sul3*, *dfrIa*) and chloramphenicol resistance genes (*floR*, *catB3*, *cml*, *cmlA*, *stcM*, cat, *cat1*, *cat2*) were widely present in isolates from farm animals (pigs, poultry)[26,28,32,65,66], companion animals (dogs, cats)[48,75], wild animals (foxes, raccoons, minks)[22], and food sources (chicken, pork, beef, vegetables, aquatic products)[45,49,76].

Resistance genes to macrolides, including *mphE*, *ermB*, *mefA*, and *mrsD*, were only reported in isolates from pigs and chickens [26,28]. The polymyxin resistance gene *mcr-1* and glycopeptide resistance gene *mecA* were exclusively found in chicken-derived isolates [29]. *fos* and *fosA3*, related to fosfomycin resistance, were identified in isolates from pigs and chickens, as well as food sources such as chicken, pork, and aquatic products [26,45,49].

Lincosamide resistance genes *cfr* and *lnu(F)* were detected by Ma et al. and Li et al. in food sources including chicken, pork, aquatic products, and vegetables. The same teams also identified the tigecycline resistance gene *tmexCD3-toprJ1* and the rifampin resistance gene *arr-3*, respectively [45,76]. In addition, the rifampin resistance gene *arr-3* and the disinfectant resistance gene *qacH* were found in pig-derived isolates [26]. The co-occurrence of *arr-3* and *qacH* may enhance resistance to rifampin and reduce sensitivity to common disinfectants, potentially compromising hygiene measures and increasing the risk of cross-contamination.

 doi:10.20944/preprints202507.0885.v1

7. Perspectives

The emergence and spread of *P. mirabilis* across diverse animal hosts and food products, coupled with its multidrug resistance and virulence, underscore its growing importance as a zoonotic and foodborne pathogen. The widespread detection of clinically relevant ARGs such as *blaNDM*, *mcr-1*, and *tmexCD3-toprJ1* in isolates from farm animals, companion animals, wildlife, and animal-derived food highlight the urgent need for integrated surveillance systems. Moreover, the identification of resistance genes in vectors such as houseflies and in contaminated slaughterhouse environments suggests overlooked transmission routes that warrant further investigation.

Moving forward, a One Health approach should be emphasized, integrating data from human, animal, food, and environmental sectors to better understand the ecology and evolution of *P. mirabilis*. Molecular epidemiology tools such as whole-genome sequencing, resistome and virulome profiling, and comparative genomics will be invaluable for tracking its transmission and adaptation mechanisms. In addition, studies exploring biofilm formation, quorum sensing, and host-pathogen interactions may offer new targets for intervention. As *P. mirabilis* continues to adapt and spread under antimicrobial selective pressure, coordinated international efforts are needed to mitigate its threat to public health and food safety.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org. Table S1: Antibiotic resistance of Proteus mirabilis from animals and animal-derived products.

Author Contributions: Conceptualization, X.L. and Z.Y.; validation, X.L. and Z.Y.; resources, X.L.; data curation, X.L.; writing—original draft preparation, X.L. and Z.Y.; writing—review and editing, Z.Y.; visualization, X.L. and Z.Y.; supervision, Z.Y.; project administration, Z.Y. All authors have read and agreed to the published version of the manuscript."

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: During the preparation of this manuscript/study, the author(s) used ChatGPT-4o for the purposes of improving readability and language. The authors have reviewed and edited the output and take full responsibility for the content of this publication.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

P. mirabilis	*Proteus mirabilis*
NDRJ	multi-drug resistant
XDR	extensively drug-resistant
PDR	pan-drug-resistant

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