

# The role of wildlife (wild birds) in the global transmission of antimicrobial resistance genes

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## ABSTRACT

Antimicrobial resistance is an urgent global health challenge in human and veterinary medicine. Wild animals are not directly exposed to clinically relevant antibiotics; however, antibacterial resistance in wild animals has been increasingly reported worldwide in parallel to the situation in human and veterinary medicine. This underlies the complexity of bacterial resistance in wild animals and the possible interspecies transmission between humans, domestic animals, the environment, and wildlife. This review summarizes the current data on expanded-spectrum  $\beta$ -lactamase (ESBL), AmpC  $\beta$ -lactamase, carbapenemase, and colistin resistance genes in *Enterobacteriaceae* isolates of wildlife origin. The aim of this review is to better understand the important role of wild animals as reservoirs and vectors in the global dissemination of crucial clinical antibacterial resistance. In this regard, continued surveillance is urgently needed worldwide.

**Keywords:** AmpC; ESBLs; IMP, *mcr-1*; NDM; Wild birds

## INTRODUCTION

Over several decades, antimicrobial resistance has become a global clinical and public health threat against the effective treatment of common infections caused by resistant pathogens, resulting in treatment failure and increased mortality (WHO, 2014). The development of bacterial resistance is a natural evolution of microorganisms, but the widespread use and misuse of antibacterial agents in humans and animals has accelerated this process (WHO, 2014). Furthermore, the increasing frequency of global travel and trade has also contributed to the rapid worldwide spread of antimicrobial resistance (Laxminarayan et al., 2013). Some resistant clones, such as *Escherichia coli* ST131, *Klebsiella pneumoniae* ST258 and ST11, and methicillin-resistant *Staphylococcus aureus* (MRSA) USA 300, which are involved in the spread of resistance to crucially significant antibiotics in human medicine,

have been widely disseminated (Lee et al., 2016; Mathers et al., 2015; Nimmo, 2012). Antimicrobial resistance is a complex and multifaceted problem involving humans, animals, and the environment. However, the role of wildlife in the emergence of antibacterial resistance might be underestimated. The first report of antibacterial resistance in wildlife revealed chloramphenicol resistance in *E. coli* isolates obtained from Japanese wild birds (Sato et al., 1978). Since then, the occurrence of resistant bacteria in wild animals has been increasingly reported within diverse animal species across different geographical areas. In addition, several important antimicrobial resistant pathogens, such as MRSA (Loncaric et al., 2013a; Porrero et al., 2014), vancomycin-resistant enterococci (Drobni et al., 2009; Sellin et al., 2000), *Salmonella* spp. (Lee et al., 2011a), *Vibrio cholerae* (Aberkane et al., 2015), and *Campylobacter* spp. (Weis et al., 2016), have been described in wild animals, highlighting the importance and complexity of wildlife, not normally exposed to antibiotics directly, in the transmission of resistant bacteria.

This review gives a brief overview of the emergence and prevalence of expanded-spectrum  $\beta$ -lactamase (ESBL), AmpC  $\beta$ -lactamase, carbapenemase, and colistin resistance genes in *Enterobacteriaceae* strains from wild animals, all of which have significant public health impact. Furthermore, this review aims to better understand the role of wildlife in the transmission of clinically significant antimicrobial resistance in *Enterobacteriaceae*.

## ESBL-PRODUCING *ENTEROBACTERIACEAE* FROM WILDLIFE

The global dissemination of ESBL-producing *Enterobacteriaceae* in human clinics is an urgent problem that poses a serious challenge to the treatment of infectious diseases, particularly the worldwide emergence of CTX-M-15-producing ST131 *E.*

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*coli* (Algoribi et al., 2015; Blanco et al., 2013; Hansen et al., 2014; Hussain et al., 2014; Mathers et al., 2015; Platell et al., 2011; Sauget et al., 2016). ESBL-producing *Enterobacteriaceae* have also been increasingly reported in livestock, companion animals, and food (Aliyu et al., 2016; Braun et al., 2016; Ewers et al., 2010; Hordijk et al., 2013; Michael et al., 2016). The CTX-M-type  $\beta$ -lactamases are the most common ESBLs among *Enterobacteriaceae* isolates of human and veterinary origin worldwide (Hordijk et al., 2013; Liu et al., 2016a; Pietsch et al., 2017; Wang et al., 2016; Wellington et al., 2013).

Since the first report on ESBL-producing *E. coli* isolates from wild animals in Portugal in 2006 (Costa et al., 2006), ESBL-producing *Enterobacteriaceae* of wildlife origin have so far been reported in Europe, Africa, Asia, South America, North America, and Australia (Table 1). Although ESBLs have been found in various *Enterobacteriaceae*, most ESBL-producing bacterial pathogens in wild animals are *E. coli*, followed by *K. pneumoniae* (Table 1). To date, at least 80 wildlife species have been found to be carriers of ESBL-producing *Enterobacteriaceae*, most being wild birds (Table 1). Similar to that among isolates from human and veterinary medicine, the CTX-M family is the most prevalent type of ESBL-producing *Enterobacteriaceae* found in wild animals (Table 1). Both *bla*<sub>CTX-M-1</sub> and *bla*<sub>CTX-M-15</sub> are commonly reported in wild animals and are the most prevalent ESBL genes, followed by *bla*<sub>CTX-M-14</sub>, *bla*<sub>CTX-M-32</sub>, *bla*<sub>CTX-M-9</sub>, *bla*<sub>CTX-M-3</sub>, *bla*<sub>CTX-M-2</sub>, and *bla*<sub>CTX-M-22</sub>. Other ESBL genes, such as *bla*<sub>CTX-M-27</sub>, *bla*<sub>CTX-M-55</sub>, *bla*<sub>CTX-M-8</sub>, *bla*<sub>CTX-M-24</sub>, *bla*<sub>CTX-M-25</sub>, *bla*<sub>CTX-M-28</sub>, *bla*<sub>CTX-M-29</sub>, and *bla*<sub>CTX-M-124</sub>, have also been detected, though infrequently (Table 1). Significant geographical differences have been observed in the occurrence of CTX-M enzymes. As summarized in Table 1, CTX-M-15 is the only reported CTX-M-type  $\beta$ -lactamase in Africa to date, and is the most common CTX-M-type enzyme reported in Bangladesh. In Canada and the US, CTX-M-14 is dominant, followed by CTX-M-15. Diversity in CTX-M  $\beta$ -lactamases has been reported in European countries, with the predominance of CTX-M-1 and CTX-M-15. Interestingly, CTX-M-15 is also reported to be the most common CTX-M enzyme in Franklin's gulls (*Leucophaeus pipixcan*) in northern Chile (Báez et al., 2015), although CTX-M-1 was previously reported to be dominant in the same gull species in central Chile (Hernandez et al., 2013). Báez et al. (2015) hypothesized that, based on their migratory habits, Franklin's gulls from the north acquired resistant CTX-M-15-producing ST131 and ST10 *E. coli* clones, which are highly prevalent in humans in the US and Canada but scarce in Chile. However, this hypothesis, though possible, needs further investigation.

In addition to CTX-M enzymes, SHV and TEM enzymes have also been reported in wildlife, especially SHV-12 and TEM-52, which accords with that found in ESBL-producing isolates from humans, livestock, and companion animals (Table 1) (Blanco et al., 2013; Carattoli et al., 2005; Hordijk et al., 2013; Michael et al., 2016; Smet et al., 2010). For example, SHV-12 has been frequently detected in wildlife in Spain (Alcalá et al., 2016; Gonçalves et al., 2012), and is highly prevalent in ESBL-producing *E. coli* obtained from 8- to 16-month-old healthy children in northern Spain (Fernández-Reyes et al., 2014) and

in raw poultry meat from southern Spain (Egea et al., 2012), as well as from hospitals (Blanco et al., 2013). Other SHV-type enzymes, such as SHV-102, SHV-1, SHV-2, and SHV-5, and TEM-type enzymes, such as TEM-19, TEM-40, TEM-176, and TEM-20, have also been sporadically reported in wild animals (Table 1).

More than 170 different sequence types (STs) have been identified in ESBL-producing *E. coli* isolates of wildlife origin (Table 1). Among them, ST131 is the most commonly detected clone. The dominant ST131 clone identified in wild animals, which has been frequently described in humans, companion animals, food products, and the environment, is involved in the international dissemination of *bla*<sub>CTX-M-15</sub> and *bla*<sub>CTX-M-14</sub> (Algoribi et al., 2015; Bogaerts et al., 2015; Ewers et al., 2010; Hu et al., 2013; Hussain et al., 2014; Kawamura et al., 2014; Kim et al., 2017; Mathers et al., 2015). Additionally, other STs described in wild animals, such as ST10, ST69, ST405, ST410, and ST648, have also been reported in various sources and are responsible for the intercontinental distribution of CTX-M (Fischer et al., 2014, 2017; Hansen et al., 2014; Hu et al., 2013; Liu et al., 2016a; Müller et al., 2016; Su et al., 2016; Wang et al., 2016). However, some STs found in wildlife, such as ST1340, ST1646, ST2687, ST3018, and ST3056, have been identified as new types and have not yet been reported in human or veterinary isolates (Bonnedahl et al., 2010; Hasan et al., 2014; Jamborova et al., 2015).

As for ESBL-producing *K. pneumoniae*, limited studies are currently available on the clonal group of *K. pneumoniae* from wildlife (Table 1). Loncaric et al. (2016) found an SHV-11-encoding *K. pneumoniae* strain from mouflon (*Ovis orientalis musimon*) in Austria belonging to the epidemic clone ST11, which is associated with carbapenemase (Hu et al., 2016; Kim et al., 2013; Lee et al., 2016; Voulgari et al., 2016) and ESBL in humans worldwide (Hu et al., 2016; Lee et al., 2011b; Lu et al., 2016; Sennati et al., 2012), and previously described in companion animals and Eurasian beaver (*Castor fiber*) (Donati et al., 2014; Pilo et al., 2015). In Algeria, all 17 *bla*<sub>CTX-M-15</sub>-bearing *K. pneumoniae* isolates found in wild boars and Barbary macaques belong to ST584, which has also been detected in silver gulls as carriers of carbapenemase IMP-4 in Australia (Dolejska et al., 2016) as well as in human in Brazil (<http://bigsd.b.pasteur.fr/klebsiella/klebsiella.html>).

Successful clones found in humans and domestic and wild animals indicate possible interspecies transmission of ESBL-producing isolates. However, horizontal transfer mediated by mobile elements, such as insertion sequences and plasmids, is also one of the main methods for ESBL dissemination worldwide (Carattoli, 2013; Partridge, 2015). Only limited (mostly European) studies are available on ESBL-encoding plasmids in wild animals (Table 1). For example, *bla*<sub>CTX-M-15</sub> is reportedly associated with IncF plasmids (mostly multiple replicons containing IncFIA and IncFIB) and IncI1 (Guenther et al., 2010a; Loncaric et al., 2016; Poirel et al., 2012; Tausova et al., 2012; Veldman et al., 2013), which agrees with previous research involving CTX-M-15-producing *Enterobacteriaceae* obtained from the environment, healthy cattle, and humans

**Table 1 Presence of extended-spectrum  $\beta$ -lactamase (ESBL)-producing *Enterobacteriaceae* in wild animals**

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Bird of prey, Deer, Fox, Owl (all unspecified)	2003-	<i>E. coli</i>	9	<i>bla</i> <sub>CTX-M-14</sub> (3)		ISEcp1-		Portugal	Costa et al., 2006
	2004			<i>bla</i> <sub>CTX-M-14</sub> + <i>bla</i> <sub>TEM-52</sub> (1)					
Common kestrel, Sparrow hawk, Seagulls (not specified)	2003-2004	<i>E. coli</i>	2	<i>bla</i> <sub>CTX-M-1</sub> (1)		<i>bla</i> <sub>CTX-M-1</sub>		Portugal	Costa et al., 2008
				<i>bla</i> <sub>SHV-12</sub> (1)					
	2007	<i>E. coli</i>	11	<i>bla</i> <sub>TEM-52</sub> (3)		ISEcp1-		Portugal	Poeta et al., 2008
				<i>bla</i> <sub>CTX-M-14</sub> (1)					
				<i>bla</i> <sub>CTX-M-14</sub> + <i>bla</i> <sub>TEM-52</sub> (1)		<i>bla</i> <sub>CTX-M-14</sub>			
Yellow-legged gulls ( <i>Larus michaëllis</i> )	Not specified	<i>E. coli</i>	16	<i>bla</i> <sub>TEM-52</sub> (8)		ISEcp1-		France	Bonedahl et al., 2009
				<i>bla</i> <sub>CTX-M-1</sub> (1)					
				<i>bla</i> <sub>CTX-M-14</sub> (1)					
				<i>bla</i> <sub>CTX-M-32</sub> (1)					
				<i>bla</i> <sub>CTX-M-14</sub> (7)					
				<i>bla</i> <sub>CTX-M-1</sub> + <i>bla</i> <sub>TEM</sub> (1)*				ST90, ST156, ST351, ST533, ST681 (2), ST746, ST1134, ST1135, ST1140 (2), ST1142, ST1143 (2), ST1144, ST1199	
				<i>bla</i> <sub>SHV-15</sub> + <i>bla</i> <sub>TEM</sub> (1)*					
				<i>bla</i> <sub>SHV</sub> + <i>bla</i> <sub>TEM</sub> (2)*					
				<i>bla</i> <sub>TEM</sub> (5)*					
Black-headed gull ( <i>Larus ridibundus</i> )	2006	<i>E. coli</i>	7	<i>bla</i> <sub>CTX-M-1</sub> (1)				Czech Republic	Dolejská et al., 2009
				<i>bla</i> <sub>CTX-M-15</sub> (2)					
				<i>bla</i> <sub>SHV-2</sub> (1)					
				<i>bla</i> <sub>SHV-12</sub> (2)					
Wild boars	2005-2007	<i>E. coli</i>	8	<i>bla</i> <sub>CTX-M-1</sub> (8)				Portugal	Poeta et al., 2009

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Common buzzards ( <i>Buteo buteo</i> )	2007-2008	<i>E. coli</i>	10	<i>bla</i> <sub>CTX-M-32</sub> (7) <i>bla</i> <sub>CTX-M-1</sub> (3)		ISEcp1- <i>bla</i> <sub>CTX-M-1</sub> (3)		Portugal	Radhouani et al., 2010
Black-headed gull ( <i>Larus ridibundus</i> )	2008	<i>E. coli</i>	3	<i>bla</i> <sub>CTX-M-14</sub> (2) <i>bla</i> <sub>CTX-M-15</sub> + <i>bla</i> <sub>TEM</sub> (1)*			ST1340, ST1646, ST1647	Sweden	Bonnedahl et al., 2010
Glaucous winged gull ( <i>Larus glaucescens</i> )	2007	<i>E. coli</i>	4	<i>bla</i> <sub>CTX-M-14</sub> (1) <i>bla</i> <sub>CTX-M-14</sub> + <i>bla</i> <sub>TEM</sub> (1) <i>bla</i> <sub>CTX-M-15</sub> + <i>bla</i> <sub>TEM</sub> (2)*			ST131, ST609 (2), ST746	Russia	Hernandez et al., 2010
Mallard, Herring gull, Waterbird	2008-2009	<i>E. coli</i>	9	<i>bla</i> <sub>CTX-M-1</sub> (6) <i>bla</i> <sub>CTX-M-9</sub> (1) <i>bla</i> <sub>CTX-M-15</sub> (1) <i>bla</i> <sub>SHV-12</sub> (1)	~35 kb IncN ( <i>bla</i> <sub>CTX-M-1</sub> ) ~90 kb IncI1 ( <i>bla</i> <sub>CTX-M-1</sub> ) ~80 kb NT ( <i>bla</i> <sub>CTX-M-1</sub> ) ~100 kb IncI1 ( <i>bla</i> <sub>CTX-M-1</sub> ) ~95 kb IncI1 ( <i>bla</i> <sub>SHV-12</sub> )			Poland	Literak et al., 2010a
Wild boar ( <i>Sus scrofa</i> )	2006-2007	<i>E. coli</i>	5	<i>bla</i> <sub>CTX-M-1</sub> (4) <i>bla</i> <sub>TEM-52b</sub> (1)	~80 kb IncI1 ( <i>bla</i> <sub>CTX-M-1</sub> )(4) ~45 kb NT ( <i>bla</i> <sub>TEM-52b</sub> )			Czech Republic, Slovakia	Literak et al., 2010b
Eurasian blackbirds ( <i>Turdus merula</i> ), Rock pigeon ( <i>Columba livia</i> ), Greater white-fronted goose ( <i>Anser albifrons</i> )	2006	<i>E. coli</i>	4	<i>bla</i> <sub>CTX-M-15</sub> (4)	>100 kb IncFII-FIA-FIB		ST648 (4)	Germany	Guenther et al., 2010a
Brown rat ( <i>Rattus norvegicus</i> )	Not specified	<i>E. coli</i>	1	<i>bla</i> <sub>CTX-M-9</sub> (1)	>100 kb FIA-FIB		ST131	Germany	Guenther et al., 2010b

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Common buzzard ( <i>Buteo buteo</i> ), Common barn owl ( <i>Tyto alba</i> ), Eurasian tawny owl ( <i>Strix aluco</i> ), Booted eagle ( <i>Hieraetus pennatus</i> ), Montagu's harrier ( <i>Circus pygargus</i> ), Black kite ( <i>Milvus migrans</i> ), Eurasian black vulture ( <i>Aegypius monachus</i> ), Bonelli's eagle ( <i>Hieraetus fasciatus</i> ), Eurasian eagle owl ( <i>Bubo bubo</i> ), Common raven ( <i>Corvus corax</i> )	2008	<i>E. coli</i>	32	<i>bla</i> <sub>CTX-M-1</sub> (27) <i>bla</i> <sub>CTX-M-1</sub> + <i>bla</i> <sub>TEM-20</sub> (1) <i>bla</i> <sub>SHV-5</sub> (3) <i>bla</i> <sub>TEM-20</sub> (1)				Portugal	Pinto et al., 2010
Seagulls ( <i>Larus fuscus</i> , <i>Larus cachinnans</i> )	2007-2008	<i>E. coli</i>	45	<i>bla</i> <sub>CTX-M-1</sub> (8) <i>bla</i> <sub>TEM-9</sub> (4) <i>bla</i> <sub>CTX-M-15</sub> (17) <i>bla</i> <sub>CTX-M-32</sub> (15)			ST10, ST43, ST58, ST69, ST86, ST131 (4), ST155, ST156, ST165, ST205, ST224 (3), ST297, ST359, ST405, ST453, ST559, ST1152, ST1163, ST1284 (4)	Portugal	Simões et al., 2010
Canada goose ( <i>Branta canadensis</i> ), Wild domestic goose ( <i>Anser anser domesticus</i> )	2010	<i>E. coli</i>	2	<i>bla</i> <sub>SHV-12</sub> (1) <i>bla</i> <sub>TEM-52</sub> (1)			ST1079 ST1844	Belgium	Garmyn et al., 2011
Iberian lynx ( <i>Lynx pardinus</i> )	2008-2010	<i>E. coli</i>	10	<i>bla</i> <sub>CTX-M-14</sub> (6) <i>bla</i> <sub>SHV-12</sub> (4)		ISEcp1- <i>bla</i> <sub>CTX-M14</sub> (6)		Spain	Gonçalves et al., 2012

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Wild rodents	2008-2010	<i>E. coli</i>	19	<i>bla</i> <sub>CTX-M-1</sub> (9) <i>bla</i> <sub>CTX-M-9</sub> (8)				Hong Kong, China	Ho et al., 2011
Blackcap ( <i>Sylvia atricapilla</i> )	2006-2010	<i>E. coli</i>	1	<i>bla</i> <sub>CTX-M-14</sub> + <i>bla</i> <sub>SHV-12</sub> (1)				Azores Archipelago / Portugal	Silva et al., 2011
Glithead Seabream ( <i>Sparus aurata</i> )	2007	<i>E. coli</i>	5	<i>bla</i> <sub>TEM-52</sub> (2) <i>bla</i> <sub>SHV-12</sub> (3)				Atlantic Ocean, West coast of Portugal	Sousa et al., 2011
Black-headed gull ( <i>Larus ridibundus</i> ), Common gull ( <i>Larus canus</i> ), Herring gull ( <i>Larus argentatus</i> ), Lesser black backed gull ( <i>Larus fuscus</i> )	2010	<i>E. coli</i>	18	<i>bla</i> <sub>CTX-M-1</sub> (16) <i>bla</i> <sub>CTX-M-14</sub> (1) <i>bla</i> <sub>SHV-12</sub> (1)				Sweden	Wallensten et al., 2011
Black kites ( <i>Milvus migrans</i> ), Red kites ( <i>Milvus milvus</i> ), Buzzard ( <i>Buteo buteo</i> )	2010	<i>E. coli</i>	9	<i>bla</i> <sub>CTX-M-1</sub> (9)				Germany	Guenther et al., 2012
Black kites ( <i>Milvus migrans</i> ), Black vultures ( <i>Aegypius monachus</i> ), Demoiselle cranes ( <i>Anthropoides virgo</i> )	2010	<i>E. coli</i>	5	<i>bla</i> <sub>CTX-M-9</sub> (4) <i>bla</i> <sub>CTX-M-55</sub> (1)				Mongolia	
Common teal ( <i>Anas crecca</i> ), Tufted duck ( <i>Aythya fuligula</i> )	2009	<i>E. coli</i>	3	<i>bla</i> <sub>CTX-M-15</sub> (3)				Bangladesh	Hasan et al., 2012

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Seagull ( <i>Larus delawarensis</i> ), Pelican	2010	<i>E. coli</i>	8	<i>bla</i> <sub>CTX-M-15</sub> (5) <i>bla</i> <sub>CTX-M-32</sub> (2) <i>bla</i> <sub>CTX-M-124</sub> (1)	FIA-FIB ( <i>bla</i> <sub>CTX-M-15</sub> ) (4), FIB ( <i>bla</i> <sub>CTX-M-15</sub> ) (1)		ST10, ST405, ST410, ST559, ST617, ST648, ST853, ST1845	Florida, USA	Poiret et al., 2012
Roe, Deer	2011	<i>E. cloacae</i> <i>E. coli</i>	2 1	<i>bla</i> <sub>SHV-7</sub> (2) <i>bla</i> <sub>CTX-M-1</sub> (1)	InclM (2)			Switzerland	Stephan & Hächler, 2012
Great cormorants ( <i>Phalacrocorax carbo</i> )	2006- 2007, 2009	<i>E. coli</i>	10	<i>bla</i> <sub>CTX-M-15</sub> (7) <i>bla</i> <sub>CTX-M-27</sub> (2)	170kb FIA-FIB ( <i>bla</i> <sub>CTX-M-15</sub> )(1) 100 kb Incl1 ( <i>bla</i> <sub>CTX-M-15</sub> ) (2) 120 kb FIA-FIB ( <i>bla</i> <sub>CTX-M-27</sub> )(1)	ISEcp1- <i>bla</i> <sub>CTX-M</sub> (9)	ST131 (2)	Czech Republic, Slovak Republic	Tausova et al., 2012
Franklin's gulls ( <i>Leucophaeus pipixcan</i> )	2009	<i>E. coli</i>	129 <sup>b</sup>	<i>bla</i> <sub>CTX-M-1</sub> (39) <i>bla</i> <sub>CTX-M-15</sub> (8) <i>bla</i> <sub>CTX-M-14</sub> (1) <i>bla</i> <sub>CTX-M-3</sub> (2)			ST10, ST34, ST38, ST48, ST54, ST58, ST69, ST70, ST127, ST131, ST155, ST167, ST216, ST349, ST367, ST405, ST617, ST641, ST847, ST1106, ST1711, ST1712, ST1714, ST1715, ST1722, ST1723, ST1724, ST1716, ST1713, ST1725	Chile	Hernandez et al., 2013

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Rooks ( <i>Corvus frugilegus</i> )	2013	<i>E. coli</i>	20	<i>bla</i> <sub>CTX-M-1</sub> (15) <i>bla</i> <sub>CTX-M-3</sub> (3) <i>bla</i> <sub>CTX-M-15</sub> (3) <i>bla</i> <sub>TEM-15</sub> (1)	Incl1-InciV ( <i>bla</i> <sub>CTX-M-1</sub> ) (3), IncN ( <i>bla</i> <sub>CTX-M-1</sub> ) (3), IncF-FIB-Incl1-IV ( <i>bla</i> <sub>TEM-15</sub> ), IncF-FIB-Incl1-IV-N ( <i>bla</i> <sub>CTX-M-1</sub> ) (2), IncF-FIB-IncN ( <i>bla</i> <sub>CTX-M-1</sub> ) (2), IncHI1 ( <i>bla</i> <sub>CTX-M-1</sub> ) (3), IncF-FIA-FIB ( <i>bla</i> <sub>CTX-M-15</sub> ) (3), IncF ( <i>bla</i> <sub>CTX-M-3</sub> )	ISEcp7- <i>bla</i> <sub>CTX-M</sub> (18)	ST23, ST34 (2), ST58(2), ST69 (2), ST90, ST131, ST162, ST491, ST744 (3), ST1683(5)	Austria	Loncaric et al., 2013b
Red fox ( <i>Vulpes vulpes</i> )	2008-2009	<i>E. coli</i>	2	<i>bla</i> <sub>SHV-12</sub> (2)			ST1086	Portugal	Radhouani et al., 2013
European herring gull, Mallard, Black-headed gull, Egyptian goose, Feral pigeon, Grey heron, Mute swan, Northern gannet, Northern lapwing, Gadwall, Common redshank, Lesser black-backed gull, Tufted duck, Common gull, Common goldeneye, Common guillemot, Black swan, Barnacle goose, Ruff	2010-2011	<i>E. coli</i>	65	<i>bla</i> <sub>CTX-M-1</sub> (14) <i>bla</i> <sub>CTX-M-15</sub> (13) <i>bla</i> <sub>CTX-M-3</sub> (8) <i>bla</i> <sub>CTX-M-14</sub> (8) <i>bla</i> <sub>CTX-M-32</sub> (3) <i>bla</i> <sub>SHV-12</sub> (3) <i>bla</i> <sub>TEM-52c</sub> (1) <i>bla</i> <sub>SHV-12</sub> + <i>bla</i> <sub>TEM-52c</sub> (1)	Incl1( <i>bla</i> <sub>CTX-M-1</sub> ) (13), IncF ( <i>bla</i> <sub>CTX-M-1</sub> ), IncB/O ( <i>bla</i> <sub>CTX-M-14</sub> ), IncF ( <i>bla</i> <sub>CTX-M-14</sub> ) (6), IncF ( <i>bla</i> <sub>CTX-M-15</sub> ) (3), IncHI2 ( <i>bla</i> <sub>CTX-M-15</sub> ), IncHI2-IncF( <i>bla</i> <sub>CTX-M-15</sub> ), Incl1 ( <i>bla</i> <sub>CTX-M-15</sub> ) (4), Incl2 ( <i>bla</i> <sub>CTX-M-15</sub> ), IncF ( <i>bla</i> <sub>CTX-M-3</sub> )(6), Incl1 ( <i>bla</i> <sub>CTX-M-3</sub> ), IncF ( <i>bla</i> <sub>CTX-M-32</sub> ), IncF ( <i>bla</i> <sub>SHV-12</sub> ), Incl1 ( <i>bla</i> <sub>SHV-12</sub> ), IncN ( <i>bla</i> <sub>SHV-12</sub> ), Incl1( <i>bla</i> <sub>SHV-12</sub> + <i>bla</i> <sub>TEM-52c</sub> ), Incl1 ( <i>bla</i> <sub>TEM-52c</sub> )			Netherlands	Veldman et al., 2013



Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Gulls (unspecified)	2010	<i>E. coli</i>	33	<i>bla</i> <sub>CTX-M-14</sub> (23) <i>bla</i> <sub>CTX-M-27</sub> (3) <i>bla</i> <sub>CTX-M-15</sub> (1) <i>bla</i> <sub>TEM-19</sub> (5)			ST10 (1), ST38 (10), ST131 (12), ST405 (3), ST2253, ST2967 (6)	Barrow, Alaska, USA	Bonnedahl et al., 2014
		<i>K. pneumoniae</i>	35	<i>bla</i> <sub>CTX-M-15</sub> (1) <i>bla</i> <sub>CTX-M-14</sub> (23) <i>bla</i> <sub>TEM-19</sub> (1) <i>bla</i> <sub>TEM-52</sub> (1) <i>bla</i> <sub>SHV-2</sub> (1) <i>bla</i> <sub>SHV-12</sub> (7) <i>bla</i> <sub>SHV-102</sub> (8) <i>bla</i> <sub>SHV-102+</sub> <i>bla</i> <sub>TEM-19</sub> (2) <i>bla</i> <sub>CTX-M-15</sub> (1)+ <i>bla</i> <sub>SHV-1</sub> (4) <i>bla</i> <sub>CTX-M-15</sub> (1)+ <i>bla</i> <sub>SHV-12</sub> (4)					
Boops boops, Sardinia pichardus, <i>Sarpa salpa</i> , <i>Trachurus trachurus</i> , <i>Pagellus acarne</i>	2012-2013	<i>E. coli</i>	22	<i>bla</i> <sub>CTX-M-15</sub> (15) CTX-M group 9 (1) <i>bla</i> <sub>TEM-24</sub> (6)			ST8, ST21, ST31 (2), ST37, ST66, ST74, ST131 (2), ST132, ST398 (3), ST471 (7), ST477 (2)	Mediterranean Sea	Brahmi et al., 2015
Brown-headed gull ( <i>Chroicocephalus brunneicephalus</i> )	2010	<i>E. coli</i>	29	<i>bla</i> <sub>CTX-M-15</sub> (28) <i>bla</i> <sub>CTX-M-14</sub> (1)			ST10, ST48, ST131, ST345, ST349, ST648, ST853, ST1727, ST2687, ST2688, ST2689,	Bengal	Hasan et al., 2014
		<i>K. pneumoniae</i>	1	<i>bla</i> <sub>CTX-M-15</sub> (1)					
		<i>E. albertii</i>	1	<i>bla</i> <sub>CTX-M-55+</sub> <i>bla</i> <sub>CTX-M-78</sub> (1)					

Continued

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Wintering rooks ( <i>Corvus frugilegus</i> )	2011	<i>E. coli</i>	82	<i>bla</i> <sub>CTX-M-1</sub> (39) <i>bla</i> <sub>CTX-M-8</sub> (1) <i>bla</i> <sub>CTX-M-14</sub> (2) <i>bla</i> <sub>CTX-M-15</sub> (25) <i>bla</i> <sub>CTX-M-24</sub> (4) <i>bla</i> <sub>CTX-M-25</sub> (1) <i>bla</i> <sub>CTX-M-28</sub> (1) <i>bla</i> <sub>CTX-M-55</sub> (2) <i>bla</i> <sub>TEM-52</sub> (4) <i>bla</i> <sub>SHV-12</sub> (2)			ST10 (7), ST48 (3), ST58 (8), ST88, ST101, ST106, ST115 (4), ST131 (11), ST154, ST155, ST167(3), ST206, ST351, ST361, ST394, ST398 (2), ST405, ST448, ST542, ST609, ST617 (5), ST641, ST669, ST746 (3), ST1011, ST1141, ST1249, ST1638 (2), ST1642, ST1725, ST1832 (2), ST2226, ST3014 (3), ST3015, ST3017, ST3018, ST3019, ST3020, ST3056, ST3223	Czech Republic, Germany, Poland, Serbia, Spain	Jamborova et al., 2015

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Franklin's gulls ( <i>Leucophaeus pipixcan</i> )	2011	<i>E. coli</i>	67	<i>bla</i> <sub>CTX-M-15</sub> (38)			ST10 (6), ST38 (6), ST44 (10), ST131 (12), ST205, ST350 (3), ST359, ST405 (2), ST540 (2), ST617 (6), ST642, ST648, ST665 (4), ST744, ST2277, ST3476, ST4184, ST4185, ST4186, ST4187 (3), ST4188, ST4189	Chile	Báez et al., 2015
				<i>bla</i> <sub>CTX-M-2</sub> (12)					
				<i>bla</i> <sub>CTX-M-22</sub> (11)					
				<i>bla</i> <sub>CTX-M-3</sub> (1)					
				<i>bla</i> <sub>TEM-40</sub> (5)					
				<i>bla</i> <sub>TEM-198</sub> (1)					
Franklin's gulls ( <i>Leucophaeus pipixcan</i> )	2010	<i>E. coli</i>	55 <sup>c</sup>	<i>bla</i> <sub>CTX-M-1</sub> (2)			ST10, ST12, ST38 (5), ST48, ST69 (5), ST131, ST167 (3), ST617, ST1304, ST1431	Canada	Bonnedahl et al., 2015
				<i>bla</i> <sub>CTX-M-3</sub> (1)					
				<i>bla</i> <sub>CTX-M-14</sub> (23)					
				<i>bla</i> <sub>CTX-M-15</sub> (16)					
				<i>bla</i> <sub>CTX-M-55</sub> (1)					
				<i>bla</i> <sub>CTX-M-14</sub> + <i>bla</i> <sub>TEM-52</sub> (1)					
<i>K. pneumoniae</i>	7	<i>K. pneumoniae</i>	7	<i>bla</i> <sub>CTX-M-14</sub> (1)					
				<i>bla</i> <sub>CTX-M-15</sub> (3)					
				<i>bla</i> <sub>SHV-2</sub> (1), <i>bla</i> <sub>SHV-2A</sub> (1)					
				<i>bla</i> <sub>SHV-11</sub> (1)					
				<i>bla</i> <sub>SHV-12</sub> (1)					

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
House crow ( <i>Corvus splendens</i> )	2010	<i>E. coli</i>	154 <sup>d</sup>	<i>bla</i> <sub>CTX-M-1</sub> <i>bla</i> <sub>CTX-M-14</sub> <i>bla</i> <sub>CTX-M-15</sub> <i>bla</i> <sub>CTX-M-55</sub> (142) <i>bla</i> <sub>CTX-M-79</sub>			ST38, ST46, ST58 (2), ST131 (6), ST354 (3), ST405, ST1664, ST1706, ST2141, ST2521, ST3486, ST3487, ST3488, ST3135, ST3482 (2), ST3780, ST3781, ST3782	Bangladesh	Hasan et al., 2015
		<i>K. pneumoniae</i>	21	<i>bla</i> <sub>CTX-M-15</sub> (17)					
		<i>E. cloacae</i>	4	<i>bla</i> <sub>CTX-M-15</sub> (3)					
		<i>Citrobacter freundii</i>	3	<i>bla</i> <sub>CTX-M-15</sub> (3)					
		<i>Proteus mirabilis</i>	1	<i>bla</i> <sub>CTX-M-14</sub>					
		<i>Raoultella terrigena</i>	14	<i>bla</i> <sub>CTX-M-15</sub> (14)					
		<i>Escherichia spp.</i>	1	<i>bla</i> <sub>CTX-M-15</sub> (1)					
Common kestrel ( <i>Falco tinnunculus</i> ), Rock dove ( <i>Columba livia</i> ), Baboon monkey (Papio hamadryas), Yemen linnet ( <i>Carduelis yemenensis</i> ), African gray parrot ( <i>Psittacus erithacus</i> )	Not specified	<i>E. coli</i> <i>E. cloacae</i> <i>K. pneumoniae</i> <i>K. oxytoca</i> <i>Citrobacter freundii</i>	5	<i>bla</i> <sub>CTX-M</sub> (5)				Saudi Arabia	Hassan & Shobrak, 2015

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Brown rats, Black rats, Indo-Chinese forest rats	2008-2013	<i>E. coli</i>	77	<i>bla</i> <sub>CTX-M-1</sub> (36) <i>bla</i> <sub>CTX-M-9</sub> (31) <i>bla</i> <sub>CTX-M-1</sub> + <i>bla</i> <sub>CTX-M-9</sub> (2)			ST10 (6), ST12, ST34, ST38 (4), ST48, ST58 (2), ST69 (3), ST75, ST88, ST117 (5), ST131 (2), ST155 (6), ST156, ST162, ST224 (4), ST226, ST366, ST405 (2), ST410, ST414, ST602, ST617, ST641, ST648 (2), ST994, ST1081, ST1380, ST2003, ST2165, ST2178, ST2253, ST2913, ST3489, ST3894, ST4375, ST4531, ST4532, ST4533, ST4534, ST4535, ST4537, ST5436	Hong Kong, China	Ho et al., 2015

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Herring gulls ( <i>Larus argentatus</i> ), Lesser-black backed gulls ( <i>Larus fuscus</i> ), Yellow-legged gulls ( <i>Larus michahellis</i> )	2009	<i>E. coli</i> <i>K. pneumoniae</i> <i>K. oxytoca</i> <i>Citrobacter</i> spp. <i>Enterobacter</i> spp.	948 <sup>b</sup>	M1 group ( <i>bla</i> <sub>CTX-M-1</sub> <i>bla</i> <sub>CTX-M-3</sub> , <i>bla</i> <sub>CTX-M-15</sub> , <i>bla</i> <sub>CTX-M-32</sub> , <i>bla</i> <sub>CTX-M-65</sub> ) (318), M2 group ( <i>bla</i> <sub>CTX-M-2</sub> ) (28), M8 group ( <i>bla</i> <sub>CTX-M-8</sub> ) (1), M9 group ( <i>bla</i> <sub>CTX-M-9</sub> , <i>bla</i> <sub>CTX-M-14</sub> , <i>bla</i> <sub>CTX-M-24</sub> , <i>bla</i> <sub>CTX-M-27</sub> , <i>bla</i> <sub>CTX-M-65</sub> ) (254), <i>bla</i> <sub>SHV</sub> (372), <i>bla</i> <sub>TEM</sub> (222)				England, Ireland, Latvia, Poland, Portugal, Spain, Sweden, Netherlands	Stedt et al., 2015
Open bill stork ( <i>Anastomus oscitans</i> )	2010	<i>E. coli</i>	2	<i>bla</i> <sub>CTX-M-15</sub> (2)			ST2689, ST4016	Bangladesh	Rashid et al., 2015
White stork ( <i>Ciconia ciconia</i> ), Black kite ( <i>Milvus migrans</i> ), Red kite ( <i>Milvus milvus</i> ), Golden eagle ( <i>Aquila chrysaetos</i> ), Griffon vulture ( <i>Gyps fulvus</i> ), Common cuckoo ( <i>Cuculus canorus</i> ), Barn owl ( <i>Tyto alba</i> ), Spotted starling ( <i>Sturnus unicolor</i> )	2013-2014	<i>E. coli</i>	14	<i>bla</i> <sub>CTX-M-1</sub> (3) <i>bla</i> <sub>CTX-M-14</sub> (2) <i>bla</i> <sub>SHV-12</sub> (9)			ST10, ST38, ST57, ST131, ST155, ST156, ST453 (3), ST744, ST877, ST1158, ST1431, ST3778	Spain	Alcalá et al., 2016
Glaucous-winged gulls ( <i>Larus glaucescens</i> ), Herring gulls ( <i>Larus argentatus</i> )	2014	<i>E. coli</i>	3	<i>bla</i> <sub>CTX-M-15</sub> (3)				Alaska, USA	Atterby, et al., 2016
Wild boars, Barbary macaques	2014-2015	<i>E. coli</i>	30	<i>bla</i> <sub>CTX-M-15</sub> (30)			ST69 (2), ST131 (3), ST226 (2), ST405 (3), ST617 (13), ST648 (4), ST1421 (2), ST1431	Algeria	Bachiri et al., 2017
		<i>K. pneumoniae</i>	17	<i>bla</i> <sub>CTX-M-15</sub> (17)			ST584 (17)		

Animal species	Year of sampling	Species	No. of ESBL-producing isolates	Detected ESBL types (no.)	Plasmid replicon typing <sup>a</sup>	Insertion sequence	MLST	Country	References
Wild boar, Gull, Rook (not specified)	Not specified	<i>E. coli</i>	8	<i>bla</i> <sub>SHV-12</sub> (2) <i>bla</i> <sub>TEM-52b</sub> (2) <i>bla</i> <sub>TEM-176</sub> (4)	40 kb IncX1, 45 kb IncX1 45 kb IncX2, 55 kb IncX2 145 kb IncX2-11 (2) 50 kb IncX3 80 kb IncX3-N			Australia, Czech Republic, Germany	Dobiasova & Dolejska, 2016
Cattle egret, Black vulture, Pigeon	2012	<i>E. coli</i>	10	<i>bla</i> <sub>CTX-M-15</sub> (6) <i>bla</i> <sub>CTX-M-32</sub> (2) <i>bla</i> <sub>CTX-M-2</sub> (1) <i>bla</i> <sub>CTX-M-22</sub> (1)				Nicaragua	Hasan et al., 2016
Kelp gull ( <i>Larus dominicanus</i> )	2012	<i>E. coli</i>	5	<i>bla</i> <sub>CTX-M-14</sub> (4) <i>bla</i> <sub>CTX-M-2</sub> (1)			ST101, ST744 (4)	Argentina	Liakopoulos et al., 2016
Mouflons ( <i>Ovis orientalis musimon</i> )	2013	<i>E. coli</i>	1	<i>bla</i> <sub>CTX-M-15</sub> (1)	FIA-FIB		ST744	Austria	Loncaric et al., 2016
		<i>K. pneumoniae</i>	1	<i>bla</i> <sub>SHV-11</sub> (1)			ST11		
		<i>Klebsiella</i> spp.	1	<i>bla</i> <sub>CTX-M-3</sub> (1)					
Crow	2014	<i>E. coli</i>	3	<i>bla</i> <sub>CTX-M-15</sub> (1) <i>bla</i> <sub>SHV-2</sub> (2)				Canada	Parker et al., 2016
Mute swan ( <i>Cygnus olor</i> ), Sea eagle, Crow, Goshawk, Buzzard, Herring gull, Sparrowhawk, Pigeon, Bean goose, Magpie, Grey heron, Marsh harrier	2011-2014	<i>E. coli</i>	24	<i>bla</i> <sub>CTX-M-1</sub> (13) <i>bla</i> <sub>CTX-M-55</sub> (8)			ST88, ST115, ST131, ST167, ST224, ST373, ST398, ST405 (2), ST410 (3), ST617 (3), ST648, ST1167, ST1204, ST1304, ST1670, ST1730, ST1968, ST4306, ST4307	Germany	Schaufli et al., 2016
		<i>E. cloacae</i>	1	<i>bla</i> <sub>CTX-M-1</sub> (1)					

\* TEM and SHV genotype not specified. <sup>a</sup> Plasmid replicons performed on original isolates are not listed in Table 1; NT, plasmid replicons not determined by PCR-based replicon typing. <sup>b</sup> 50 of 129 ESBL-producing isolates were randomly selected for further genotype and MLST analysis. <sup>c</sup> 20 of 55 ESBL-producing *E. coli* isolates were selected for MLST analysis. <sup>d</sup> Numbers of *bla*<sub>CTX-M-1</sub>, *bla*<sub>CTX-M-14</sub>, *bla*<sub>CTX-M-15</sub>, and *bla*<sub>CTX-M-79</sub> were not specified; 27 of 154 ESBL-producing isolates were selected for MLST analysis. <sup>e</sup> Numbers of *bla*<sub>TEM</sub> and *bla*<sub>SHV</sub> including *bla*<sub>TEM-1</sub>, *bla*<sub>TEM-2</sub>, and *bla*<sub>SHV-1</sub>, which were not true ESBLs.

(Zurfluh et al., 2015). IncH12 plasmids have also been reported as carriers of *bla*<sub>CTX-M-15</sub> in humans (Harrois et al., 2014; Nilsen et al., 2013), companion animals (Haenni et al., 2016), pigs (Tamang et al., 2015), and wild birds (Veldman et al., 2013). Though rare, IncI2 plasmid has also been described with *bla*<sub>CTX-M-15</sub> in the lesser black-backed gull from the Netherlands (Veldman et al., 2013) and identified in a chicken *E. coli* strain in China (Liu et al., 2015). In *Enterobacteriaceae* of human and veterinary origin, *bla*<sub>CTX-M-1</sub> has been frequently found associated with IncN and IncI1 plasmids (Carattoli, 2009; Jakobsen et al., 2015; Madec et al., 2015). Interestingly, *bla*<sub>CTX-M-1</sub> has been mainly located on IncI1 plasmids in wildlife in Europe as well (Literak et al., 2010a, b; Loncaric et al., 2013b; Veldman et al., 2013). However, IncN, IncF, and IncHI1 plasmids have also been reported as carriers of *bla*<sub>CTX-M-1</sub> (Literak et al., 2010a; Loncaric et al., 2013b; Veldman et al., 2013). Furthermore, IncI1 plasmids are also carriers of other ESBL genes in wild animals, such as *bla*<sub>CTX-M-3</sub>, *bla*<sub>SHV-12</sub>, and *bla*<sub>TEM-52</sub> (Poirel et al., 2012; Veldman et al., 2013). Similarly, IncF plasmids are also reported to be associated with *bla*<sub>CTX-M-3</sub>, *bla*<sub>CTX-M-9</sub>, *bla*<sub>CTX-M-14</sub>, *bla*<sub>CTX-M-27</sub>, *bla*<sub>CTX-M-32</sub>, and *bla*<sub>SHV-12</sub> in wildlife (Guenther et al., 2010b; Poirel et al., 2012; Tausova et al., 2012; Veldman et al., 2013). The narrow-host-range plasmid IncX has been found to carry several ESBL genes, namely *bla*<sub>TEM-135</sub>, *bla*<sub>TEM-52b</sub>, *bla*<sub>TEM-176</sub>, and *bla*<sub>SHV-12</sub>, in *E. coli* isolated from diverse sources in Australia, Czech Republic, Spain, and Poland (Dobiasova & Dolejska, 2016). Notably, plasmid replicon typing was performed on ESBL-producing isolates with multiple plasmids in several studies, thus the replicons of ESBL-carrying plasmids could not be confirmed (Gonçalves et al., 2012; Hernandez et al., 2013).

Insertion sequences also play an important role in facilitating the spread of ESBL genes (Partridge, 2015). Though few studies are available on horizontal transfer mediated by insertion sequences, associations of insertion sequence *ISEcp1* and *bla*<sub>CTX-M</sub>, including *bla*<sub>CTX-M-1</sub>, *bla*<sub>CTX-M-14</sub>, *bla*<sub>CTX-M-15</sub>, *bla*<sub>CTX-M-27</sub>, and *bla*<sub>CTX-M-32</sub>, have been observed in *E. coli* from wild animals (Costa et al., 2006; Gonçalves et al., 2012; Poeta et al., 2008; Radhouani et al., 2010; Tausova et al., 2012).

In summary, the ESBL gene types identified in wild animals are the same as those in human and veterinary medicine. Thus, interspecies transmission mediated by successful pandemic ESBL-producing clones and plasmids in humans, domestic animals, and wildlife might occur.

#### PLASMID-MEDIATED AmpC β-LACTAMASE-PRODUCING ENTEROBACTERIACEAE FROM WILDLIFE

Plasmid-mediated AmpC β-lactamases among *Enterobacteriaceae* in human and veterinary medicine are of considerable global concern because they confer resistance to clinically important cephalosporin antibiotics and β-lactamase inhibitors (Jacoby, 2009; Smet et al., 2010). CMY-2 is the most prevalent AmpC β-lactamase and has been globally disseminated among *Enterobacteriaceae* in humans, companion animals, food-producing animals, and retail meat (Bogaerts et al., 2015; Carmo et al., 2014; Hansen et al., 2016; Jacoby, 2009; Ma et al., 2012; Smet et al., 2010; Vogt et al., 2014; Wu et al., 2015). As

shown in Table 2, AmpC β-lactamases have been reported in *E. coli*, *K. pneumoniae*, and *Enterobacter cloacae* isolates of wildlife origin in Europe, North America, and Asia, and particularly in central Europe, similar to ESBL-producing *Enterobacteriaceae* (Table 2). To date, 20 different wild animal species, mostly birds, have been identified as *bla*<sub>CMY-2</sub> carriers (Table 2). Like that in human and veterinary medicine, *bla*<sub>CMY-2</sub> is the most commonly detected AmpC-type β-lactamase among wild animals, though its identification has been limited to *E. coli* isolates.

The *bla*<sub>CMY-2</sub> gene is mainly located on IncA/C and IncI1 plasmids from *Enterobacteriaceae* isolates of human and veterinary origin (Bogaerts et al., 2015; Bortolaia et al., 2014; Carattoli, 2009; Guo et al., 2014; Sidjabat et al., 2014). Among wild animals, *bla*<sub>CMY-2</sub> has been reported to be mainly associated with IncI1 plasmids in *E. coli* from Dutch wild birds and wild seagulls in the US (Poirel et al., 2012; Veldman et al., 2013). Other plasmid types, such as IncB/O, IncK, and IncF, have also been identified as carriers of *bla*<sub>CMY-2</sub> in wildlife (Poirel et al., 2012; Veldman et al., 2013), as previously reported in humans, companion animals, broiler chickens, and retail meat (Bortolaia et al., 2014; Hansen et al., 2016; Hiki et al., 2013; So et al., 2012; Vogt et al., 2014). Thus far, the IncA/C plasmid, a major carrier of *bla*<sub>CMY-2</sub>, has not yet been identified in wild animals. The absence of *bla*<sub>CMY-2</sub>-bearing IncA/C plasmids could simply reflect the limited studies on the characterization of *bla*<sub>CMY-2</sub>-carrying plasmids in wildlife, or might indicate that *bla*<sub>CMY-2</sub>-harbouring IncI1 plasmids are more successful among wildlife.

In addition to CMY-2, DHA-type AmpC β-lactamase genes have also been detected in *K. pneumoniae* from mouflons (*Ovis orientalis musimon*) in Austria, *E. coli* from hill mynah (*Gracula religiosa*) in Saudi Arabia, and *K. pneumoniae* ST11 isolates from Eurasian beaver (*Castor fiber*) in Switzerland (Hassan & Shobrak, 2015; Loncaric et al., 2016; Pilo et al., 2015). FOX-5 encoded by an IncA/C plasmid has been obtained from *K. pneumoniae* isolates in the US (Poirel et al., 2012). Furthermore, a novel variant of the ACT AmpC β-lactamase gene has been identified in an *Enterobacter cloacae* strain originating from glaucous gull (*Larus hyperboreus*) in Arctic Svalbard, Norway (Literak et al., 2014).

#### CARBAPENEMASE-PRODUCING ENTEROBACTERIACEAE FROM WILDLIFE

Carbapenemase-producing *Enterobacteriaceae* isolates pose an urgent public health threat. New Delhi metallo-β-lactamase (NDM), as one of the most widespread carbapenemases, has been increasingly reported in human clinics, foods, domestic animals, and the environment worldwide (Abdallah et al., 2015; Chandran et al., 2014; He et al., 2017; Kumarasamy et al., 2010; Lee et al., 2016; Qin et al., 2014; Toleman et al., 2015; Yaici et al., 2016; Yong et al., 2009).

The first reported carbapenemase-producing bacteria in wild animals were isolated from black kites (*Milvus migrans*) in Germany (Fischer et al., 2013). Among 184 cefotaxime-resistant *Salmonella* spp. isolates, only one *Salmonella*



**Table 2 Presence of plasmid-mediated AmpC  $\beta$ -lactamase-producing Enterobacteriaceae in wild animals**

Animal species	Year of sampling	Species	No. of AmpC-producing isolates	Detected AmpC types (no.)	Plasmid replicon typing (no. of isolates)	MLST (no. of isolates)	Country	References
Raccoons ( <i>Procyon lotor</i> )	2007	<i>E. coli</i>	3	<i>bla</i> <sub>CIMY-2</sub> (3)			Canada	Jardine et al., 2012
Seagull ( <i>Larus delawarensis</i> ), Pelican	2010	<i>E. coli</i>	16	<i>bla</i> <sub>CIMY-2</sub> (16)	Inc11(11), IncFIB (1), IncF (2)	ST38 (2), ST68 (2), ST162, ST167 (2), ST224, ST540, ST617, ST963 (6),	Florida, USA	Poirel et al., 2012
Black kite ( <i>Milvus migrans</i> )	Not specified	<i>K. pneumoniae</i> <i>Salmonella</i> Corvallis	1 1	<i>bla</i> <sub>FOX-5</sub> (1) <i>bla</i> <sub>CIMY-16</sub>	IncA/C		Germany	Fischer et al., 2013
Rooks ( <i>Corvus frugilegus</i> )	2013	<i>E. coli</i>	2	<i>bla</i> <sub>CIMY-2</sub> (2)		ST224	Austria	Loncaric et al., 2013b
European herring gull, Common redshank, Great black-backed gull, Black-headed gull, Domesticated duck, Herring gull, Lesser black-backed gull, Mute swan, Mallard	2010-2011	<i>E. coli</i>	14	<i>bla</i> <sub>CIMY-2</sub> (14)	IncB/O, IncK (2)	Inc1 (10),	Netherlands	Veldman et al., 2013
Wintering rooks ( <i>Corvus frugilegus</i> )	2011	<i>E. coli</i>	56	<i>bla</i> <sub>CIMY-2</sub> (47)		ST10 (3), ST23, ST57, ST58 (4), ST69 (2), ST93 (2), ST95, ST117 (3), ST131, ST351 (4), ST354, ST429 (3), ST453 (3), ST615 (2), ST665, ST770, ST963 (3), ST1056, ST1167 (2), ST1431, ST3274, ST3568, ST3778, ST4274, ST4275, ST4276	Czech Republic, Poland	Jamborova et al., 2015
Glaucous gull ( <i>Larus hyperboreus</i> )	2010	<i>E. cloacae</i>	1	<i>bla</i> <sub>ACT-23</sub> (1)			Norway	Literak et al., 2014
Arabian red fox ( <i>Vulpes vulpes</i> )	Not specified	<i>E. coli</i>	2	<i>bla</i> <sub>CIMY-2</sub> (1) <i>bla</i> <sub>DHA-1</sub> (1)			Saudi Arabia	Hassan & Shobrak, 2015

Animal species	Year of sampling	Species	No. of AmpC-producing isolates	Detected AmpC types (no.)	Plasmid replicon typing (no. of isolates)	MLST (no. of isolates)	Country	References
Eurasian beaver ( <i>Castor fiber</i> )	2013	<i>K. pneumoniae</i>	3	<i>bla<sub>DHA-1</sub></i> (3)		ST11 (3)	Switzerland	Pilo et al., 2015
Yellow-legged gull ( <i>Larus michahellis</i> )	2013-2014	<i>E. coli</i>	1	<i>bla<sub>CMV-2</sub></i> (1)		ST10	Spain	Alcalá et al., 2016
Glaucoous-winged gulls ( <i>Larus glaucescens</i> ), Herring gulls ( <i>Larus argentatus</i> )	2014	<i>E. coli</i>	5	<i>bla<sub>CMV-2</sub></i> (5)			Alaska, USA	Atterby et al., 2016
Gull (unspecified)	Not specified	<i>E. coli</i>	2	<i>bla<sub>CMV-2</sub></i> (2)	50 kb IncX1 (2)		Czech Republic	Dobiasova & Dolejska, 2016
Mouflons ( <i>Ovis orientalis musimon</i> )	2013	<i>K. pneumoniae</i>	1	<i>bla<sub>DHA-1</sub></i> (1)		ST11	Austria	Loncaric et al., 2016

Continued

Corvallis isolate belonging to ST1541 has shown reduced susceptibility to carbapenem, and carries the carbapenemase gene *bla*<sub>NDM-1</sub> located on ~180 kb IncA/C conjugative plasmid pRH-1738 (Fischer et al., 2013). The broad-host-range IncA/C plasmids are among the most predominant plasmids associated with *bla*<sub>NDM-1</sub> in humans (Carattoli, 2013). Fischer et al. (2013) supposed that the *bla*<sub>NDM-1</sub>-bearing *Salmonella* Corvallis isolate might have originated from non-European countries and was transferred to Germany through the black kite migratory route, since *Salmonella* Corvallis was prevalent in South-East Asia and was emerging in North Africa and Nigeria, rather than in European countries. The complete sequence of plasmid pRH-1738 further confirms this hypothesis. Plasmid pRH-1738 exhibited high relatedness with plasmid pMR0211 obtained from human *Providencia stuartii* isolate in Afghanistan, but showed distinct differences from other sequenced NDM-1-IncA/C<sub>2</sub> plasmids from Western countries (Villa et al., 2015). In addition, fosfomycin resistance gene *fosA3*, which has been rarely detected in Europe but is prevalent among CTX-M-encoding *E. coli* and *K. pneumoniae* isolates in Asia (i.e., China, Japan, and South Korea), has also been identified on NDM-1-producing plasmid pRH-1738. *bla*<sub>NDM-1</sub> transferred with *fosA3* on IncA/C plasmid has only been described in clinical *E. coli* and *Citrobacter freundii* isolates in China (Qin et al., 2014). Taken together, these findings suggest that the origin of this plasmid might be in the Asiatic region.

Large-scale transmission of IMP-producing bacteria into wildlife was first reported in 2015. In total, 120 carbapenemase-producing *Enterobacteriaceae* of 10 species were obtained from silver gulls in Australia, mainly *E. coli* (*n*=85), carrying *bla*<sub>IMP-4</sub>, *bla*<sub>IMP-38</sub>, or *bla*<sub>IMP-26</sub> (Dolejska et al., 2016). The *bla*<sub>IMP-4</sub> gene has been found in 116 isolates, and is the most commonly detected gene among carbapenemase-producing *Enterobacteriaceae* isolates in human clinics in Australia (Bell et al., 2016; Sidjabat et al., 2015). *bla*<sub>IMP-4</sub> in gulls is carried by various conjugative plasmids, mostly IncHI2-N plasmid type, followed by IncA/C plasmids, as well as IncL/M and IncI1, and is associated with a class 1 integron-containing *bla*<sub>IMP-4</sub>-*qacG*-*aacA4*-*catB3* array in most positive strains (Dolejska et al., 2016). The same array carried by IncA/C and IncL/M plasmids is also reportedly responsible for the dissemination of *bla*<sub>IMP-4</sub> in clinical isolates in Australia (Espedido et al., 2008), and by the IncHI2 plasmid in *Salmonella* Typhimurium from a cat in Australia (Abraham et al., 2016). Furthermore, 19 different STs have been detected in IMP-4-producing *E. coli* isolates, including five prevalent lineages (ST216, ST58, ST354, ST167, and ST224), in which ST58, ST354, and ST167 are clinically relevant clone lineages (Ben Sallem et al., 2015; Fernández et al., 2014; Huang et al., 2016).

Although carbapenem resistance reported in wild animals is rare, the emergence of NDM-1 and IMP carbapenemases in wild birds is of concern.

#### **COLISTIN RESISTANCE GENE *mcr-1* IN ENTEROBACTERIACEAE FROM WILDLIFE**

Colistin is widely applied in food-producing animals and is currently used as the last resort for treating infections caused

by multi-resistant gram-negative bacteria (Kaye et al., 2016). Since the first identification of the plasmid-mediated colistin resistance gene *mcr-1* in China in 2015 (Liu et al., 2016b), it has been identified in *Enterobacteriaceae* isolates from food-producing animals, companion animals, food products, the environment, and humans worldwide (Anjum et al., 2016; Doumith et al., 2016; Hasman et al., 2015; McGann et al., 2016; Xavier et al., 2016; Zhang et al., 2016; Zurfluh et al., 2016).

The role of wild birds as reservoirs and vectors for the global distribution of *mcr-1* should be considered. Recently, *mcr-1* was described in an *E. coli* strain isolated from European herring gull (*Larus argentatus*) feces collected from the Kaunas (Lithuania) city dump (Ruzauskas & Vaskeviciute, 2016). However, the emergence of *mcr-1* in wildlife could be traced back to *E. coli* strains isolated in 2012 (Liakopoulos et al., 2016). Five extended-spectrum cephalosporin-resistant *E. coli* isolates obtained from kelp gulls in Ushuaia, Argentina in 2012 were found to carry *mcr-1* and *bla*<sub>CTX-M-2</sub> (*n*=1) and *bla*<sub>CTX-M-14</sub> (*n*=4) and exhibited elevated colistin MICs (4–8 mg/L). The *mcr-1* gene was located on a ~57 kb IncI2 plasmid without *bla*<sub>CTX-M</sub> in all five isolates. IncI2 plasmids, which have been detected in *E. coli* and *Salmonella* isolates from food, food-producing animals, and humans in China, Great Britain, the US, Venezuela, and Denmark, have been reported to be associated with the transmission of *mcr-1* (Anjum et al., 2016; Delgado-Blas et al., 2016; Doumith et al., 2016; Hasman et al., 2015; Meinersmann et al., 2016; Yang et al., 2016). Notably, four *mcr-1*-carrying isolates, which belong to ST744, have been previously described in Denmark and carry the *mcr-1*-bearing IncI2 plasmid (Hasman et al., 2015; Liakopoulos et al., 2016).

#### **CONCLUSIONS**

Clinically relevant resistance, such as ESBL, AmpC cephalosporinase, carbapenemase, and colistin resistance, has been detected in wild animals, particularly wild birds, from distinct geographical areas. Thus, wild animals could serve as important reservoirs of resistant bacteria. Although the origin of bacterial resistance genes in wild animals remains unclear, as wildlife are not exposed to antibiotics directly, contact with sewage or animal manure might be one possibility (Wellington et al., 2013). Additionally, the potential of wild animals as vectors of resistant bacteria or genetic determinants should not be underestimated. Wildlife, especially migratory birds with their instinctive mobility, can carry resistant bacteria over long distances, even between continents; thus, this might be a new transmission route and partly responsible for the global dissemination of bacterial resistance. Contamination of food or water by wildlife is recognized as an important risk factor for the transmission of antimicrobial resistance or pathogens to food animals and humans (Greig et al., 2015).

Wild animals might play a vital role in the worldwide spread of clinically relevant pathogens or resistance genes. Pandemic ESBL-producing *E. coli* clones or plasmids shared by humans, domestic animals, and wildlife further strengthen this hypothesis. Thus, continued surveillance of multi-resistant bacteria in wild animals is warranted.

## REFERENCES

- Abdallah HM, Reuland EA, Wintermans BB, Al Naiemi N, Koek A, Abdelwahab AM, Ammar AM, Mohamed AA, Vandenbroucke-Grauls CMJE. 2015. Extended-spectrum  $\beta$ -lactamases and/or carbapenemases-producing *Enterobacteriaceae* isolated from retail chicken meat in Zagazig, Egypt. *PLoS One*, **10**(8): e0136052, doi: 10.1371/journal.pone.0136052.
- Aberkane S, Compain F, Barraud O, Ouédraogo AS, Bouzinbi N, Vittecoq M, Jean-Pierre H, Decré D, Godreuil S. 2015. Non-O1/Non-O139 *Vibrio cholerae* avian isolate from France co-carrying the *bla*<sub>VIM-1</sub> and *bla*<sub>VIM-4</sub> genes. *Antimicrobial Agents and Chemotherapy*, **59**(10): 6594-6596.
- Abraham S, O'Dea M, Trott DJ, Abraham RJ, Hughes D, Pang S, Mckew G, Cheong EYL, Merlino J, Saputra S, Malik R, Gottlieb T. 2016. Isolation and plasmid characterization of carbapenemase (IMP-4) producing *Salmonella enterica* Typhimurium from cats. *Scientific Reports*, **6**: 35527, doi: 10.1038/srep35527.
- Alcalá L, Alonso CA, Simón C, González-Esteban C, Orós J, Rezusta A, Ortega C, Torres C. 2016. Wild birds, frequent carriers of extended-spectrum  $\beta$ -lactamase (ESBL) producing *Escherichia coli* of CTX-M and SHV-12 types. *Microbial Ecology*, **72**(4): 861-869.
- Algoribi MF, Gibreel TM, Farnham G, Al Johani SM, Balkhy HH, Upton M. 2015. Antibiotic-resistant ST38, ST131 and ST405 strains are the leading uropathogenic *Escherichia coli* clones in Riyadh, Saudi Arabia. *Journal of Antimicrobial Chemotherapy*, **70**(10): 2757-2762.
- Aliyu AB, Saleha AA, Jalila A, Zunita Z. 2016. Risk factors and spatial distribution of extended spectrum  $\beta$ -lactamase-producing-*Escherichia coli* at retail poultry meat markets in Malaysia: a cross-sectional study. *BMC Public Health*, **16**: 699, doi: 10.1186/s12889-016-3377-2.
- Anjum MF, Duggett NA, AbuOun M, Randall L, Nunez-Garcia J, Ellis RJ, Rogers J, Horton R, Brena C, Williamson S, Martelli F, Davies R, Teale C. 2016. Colistin resistance in *Salmonella* and *Escherichia coli* isolates from a pig farm in Great Britain. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2306-2313.
- Atterby C, Ramey AM, Hall GG, Järhult J, Börjesson S, Bonnedahl J. 2016. Increased prevalence of antibiotic-resistant *E. coli* in gulls sampled in Southcentral Alaska is associated with urban environments. *Infection Ecology & Epidemiology*, **6**(1): 32334, doi: 10/3402/itee.v6.32334.
- Bachiri T, Bakour S, Ladjouzi R, Thongpan L, Rolain JM, Touati A. 2017. High rates of CTX-M-15-producing *Escherichia coli* and *Klebsiella pneumoniae* in wild boars and Barbary macaques in Algeria. *Journal of Global Antimicrobial Resistance*, **8**: 35-40.
- Báez J, Hernández-García M, Guamparito C, Díaz S, Olave A, Guerrero K, Cantón R, Baquero F, Gahona J, Valenzuela N, del Campo R, Silva J. 2015. Molecular characterization and genetic diversity of ESBL-producing *Escherichia coli* colonizing the migratory Franklin's gulls (*Leucophaeus pipixcan*) in Antofagasta, North of Chile. *Microbial Drug Resistance*, **21**(1): 111-116.
- Bell JM, Turnidge JD, Coombs GW, Daley DA, Gottlieb T, Robson J, George N. 2016. Australian group on antimicrobial resistance Australian *Enterobacteriaceae* sepsis outcome programme annual report, 2014. *Communicable Diseases Intelligence*, **40**(2): E229-E235.
- Ben Sallem R, Ben Slama K, Estepa V, Cheikhna EO, Mohamed AM, Chairat S, Ruiz-Larrea F, Boudabous A, Torres C. 2015. Detection of CTX-M-15-producing *Escherichia coli* isolates of lineages ST410-A, ST617-A and ST354-D in faecal samples of hospitalized patients in a Mauritanian hospital. *Journal of Chemotherapy*, **27**(2): 114-116.
- Blanco J, Mora A, Mamani R, López C, Blanco M, Dahbi G, Herrera A, Marzoa J, Fernández V, de la Cruz F, Martínez-Martínez L, Alonso MP, Nicolas-Chanoine MH, Johnson JR, Johnston B, López-Cerero L, Pascual Á, Rodríguez-Baño J. 2013. Four main virotypes among extended-spectrum- $\beta$ -lactamase-producing isolates of *Escherichia coli* O25b: H4-B2-ST131: bacterial, epidemiological, and clinical characteristics. *Journal of Clinical Microbiology*, **51**(10): 3358-3367.
- Bogaerts P, Huang TD, Bouchahrouf W, Bauraing C, Berhin C, El Garch F, Glupczynski Y, the ComPath Study Group. 2015. Characterization of ESBL- and AmpC-producing *Enterobacteriaceae* from diseased companion animals in Europe. *Microbial Drug Resistance*, **21**(6): 643-650.
- Bonnedahl J, Drobni M, Gauthier-Clerc M, Hernandez J, Granholm S, Kayser Y, Melhus Å, Kahlmeter G, Waldenström J, Johansson A, Olsen B. 2009. Dissemination of *Escherichia coli* with CTX-M type ESBL between humans and yellow-legged gulls in the south of France. *PLoS One*, **4**(6): e5958, doi: 10.1371/journal.pone.0005958.
- Bonnedahl J, Drobni P, Johansson A, Hernandez J, Melhus Å, Stedt J, Olsen B, Drobni M. 2010. Characterization, and comparison, of human clinical and black-headed gull (*Larus ridibundus*) extended-spectrum  $\beta$ -lactamase-producing bacterial isolates from Kalmar, on the southeast coast of Sweden. *Journal of Antimicrobial Chemotherapy*, **65**(9): 1939-1944.
- Bonnedahl J, Hernandez J, Stedt J, Waldenström J, Olsen B, Drobni M. 2014. Extended-spectrum  $\beta$ -lactamases in *Escherichia coli* and *Klebsiella pneumoniae* in gulls, Alaska, USA. *Emerging Infectious Diseases*, **20**(5): 897-899.
- Bonnedahl J, Stedt J, Waldenström J, Svensson L, Drobni M, Olsen B. 2015. Comparison of extended-spectrum  $\beta$ -lactamase (ESBL) CTX-M genotypes in Franklin gulls from Canada and Chile. *PLoS One*, **10**(10): e0141315, doi: 10.1371/journal.pone.0141315.
- Bortolaia V, Hansen KH, Nielsen CA, Fritsche TR, Guardabassi L. 2014. High diversity of plasmids harbouring *bla*<sub>CMY-2</sub> among clinical *Escherichia coli* isolates from humans and companion animals in the upper Midwestern USA. *Journal of Antimicrobial Chemotherapy*, **69**(6): 1492-1496.
- Brahmi S, Dunyach-Rémy C, Touati A, Lavigne JP. 2015. CTX-M-15-producing *Escherichia coli* and the pandemic clone O25b-ST131 isolated from wild fish in Mediterranean Sea. *Clinical Microbiology and Infection*, **21**(3): e18-e20, doi: 10.1016/j.cmi.2014.09.019.
- Braun SD, Ahmed MF, El-Adawy H, Hotzel H, Engelmann I, Weiß D, Monecke S, Ehrlich R. 2016. Surveillance of extended-spectrum beta-lactamase-producing *Escherichia coli* in dairy cattle farms in the Nile Delta, Egypt. *Frontiers in Microbiology*, **7**: 1020, doi: 10.3389/fmicb.2016.01020.
- Carattoli A, Lovari S, Franco A, Cordaro G, Di Matteo P, Battisti A. 2005. Extended-spectrum  $\beta$ -lactamases in *Escherichia coli* isolated from dogs and cats in Rome, Italy, from 2001 to 2003. *Antimicrobial Agents and Chemotherapy*, **49**(2): 833-835.
- Carattoli A. 2009. Resistance plasmid families in *Enterobacteriaceae*. *Antimicrobial Agents and Chemotherapy*, **53**(6): 2227-2238.
- Carattoli A. 2013. Plasmids and the spread of resistance. *International Journal of Medical Microbiology*, **303**(6-7): 298-304.
- Carmo LP, Nielsen LR, Costa PMD, Alban L. 2014. Exposure assessment of extended-spectrum beta-lactamases/AmpC beta-lactamases-producing

- Escherichia coli* in meat in Denmark. *Infection Ecology & Epidemiology*, **4**: 22924, doi: 10.3402/iee.v4.22924.
- Chandran SP, Diwan V, Tamhankar AJ, Joseph BV, Rosales-Klantz S, Mundayoor S, Lundborg CS, Macaden R. 2014. Detection of carbapenem resistance genes and cephalosporin, and quinolone resistance genes along with *oqxAB* gene in *Escherichia coli* in hospital wastewater: a matter of concern. *Journal of Applied Microbiology*, **117**(4): 984-995.
- Costa D, Poeta P, Sáenz Y, Vinué L, Rojo-Bezares B, Jouini A, Zarazaga M, Rodrigues J, Torres C. 2006. Detection of *Escherichia coli* harbouring extended-spectrum  $\beta$ -lactamases of the CTX-M, TEM and SHV classes in faecal samples of wild animals in Portugal. *Journal of Antimicrobial Chemotherapy*, **58**(6): 1311-1312.
- Costa D, Poeta P, Sáenz Y, Vinué L, Coelho AC, Matos M, Rojo-Bezares B, Rodrigues J, Torres C. 2008. Mechanisms of antibiotic resistance in *Escherichia coli* isolates recovered from wild animals. *Microbial Drug Resistance*, **14**(1): 71-77.
- Delgado-Blas JF, Ovejero CM, Abadia-Patiño L, Gonzalez-Zorn B. 2016. Coexistence of *mcr-1* and *bla<sub>NDM-1</sub>* in *Escherichia coli* from Venezuela. *Antimicrobial Agents and Chemotherapy*, **60**(10): 6356-6358.
- Dobiasova H, Dolejska M. 2016. Prevalence and diversity of IncX plasmids carrying fluoroquinolone and  $\beta$ -lactam resistance genes in *Escherichia coli* originating from diverse sources and geographical areas. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2118-2124.
- Dolejská M, Bierošová B, Kohoutová L, Literák I, Čížek A. 2009. Antibiotic-resistant *Salmonella* and *Escherichia coli* isolates with integrons and extended-spectrum beta-lactamases in surface water and sympatric black-headed gulls. *Journal of Applied Microbiology*, **106**(6): 1941-1950.
- Dolejska M, Masarikova M, Dobiasova H, Jamborova I, Karpiskova R, Havlicek M, Carlile N, Priddel D, Cizek A, Literak I. 2016. High prevalence of *Salmonella* and IMP-4-producing Enterobacteriaceae in the silver gull on Five Islands, Australia. *Journal of Antimicrobial Chemotherapy*, **71**(1): 63-70.
- Donati V, Feltrin F, Hendriksen RS, Svendsen CV, Cordaro G, García-Fernández A, Lorenzetti S, Lorenzetti R, Battisti A, Franco A. 2014. Extended-spectrum-beta-lactamases, AmpC beta-lactamases and plasmid mediated quinolone resistance in *Klebsiella* spp. from companion animals in Italy. *PLoS One*, **9**(3): e90564, doi: 10.1371/journal.pone.0090564.
- Doumith M, Godbole G, Ashton P, Larkin L, Dallman T, Day M, Day M, Muller-Pebody B, Ellington MJ, Pinna ED, Johnson AP, Hopkins KL, Woodford N. 2016. Detection of the plasmid-mediated *mcr-1* gene conferring colistin resistance in human and food isolates of *Salmonella enterica* and *Escherichia coli* in England and Wales. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2300-2305.
- Drobni M, Bonnedahl J, Hernandez J, Haemig P, Olsen B. 2009. Vancomycin-resistant enterococci, point barrow, Alaska, USA. *Emerging Infectious Diseases*, **15**(5): 838-839.
- Egea P, López-Cerero L, Torres E, Gómez-Sánchez MDC, Serrano L, Navarro Sánchez-Ortiz MD, Rodríguez-Baño J, Pascual A. 2012. Increased raw poultry meat colonization by extended spectrum beta-lactamase-producing *Escherichia coli* in the south of Spain. *International Journal of Food Microbiology*, **159**(2): 69-73.
- Espedido BA, Partridge SR, Iredell JR. 2008. *bla<sub>IMP-4</sub>* in different genetic contexts in Enterobacteriaceae isolates from Australia. *Antimicrobial Agents and Chemotherapy*, **52**(8): 2984-2987.
- Ewers C, Grobbel M, Stamm I, Kopp PA, Diehl I, Semmler T, Fruth A, Beutlich J, Guerra B, Wieler LH, Guenther S. 2010. Emergence of human pandemic O25: H4-ST131 CTX-M-15 extended-spectrum- $\beta$ -lactamase-producing *Escherichia coli* among companion animals. *Journal of Antimicrobial Chemotherapy*, **65**(4): 651-660.
- Fernández J, Montero I, Fleites A, Rodicio MR. 2014. Cluster of *Escherichia coli* isolates producing a plasmid-mediated OXA-48  $\beta$ -lactamase in a Spanish hospital in 2012. *Journal of Clinical Microbiology*, **52**(9): 3414-3417.
- Fernández-Reyes M, Vicente D, Gomariz M, Esnal O, Landa J, Oñate E, Pérez-Trallero E. 2014. High rate of fecal carriage of extended-spectrum- $\beta$ -lactamase-producing *Escherichia coli* in healthy children in Gipuzkoa, northern Spain. *Antimicrobial Agents and Chemotherapy*, **58**(3): 1822-1824.
- Fischer J, Schmoger S, Jahn S, Helmuth R, Guerra B. 2013. NDM-1 carbapenemase-producing *Salmonella enterica* subsp. *enterica* serovar Corvallis isolated from a wild bird in Germany. *Journal of Antimicrobial Chemotherapy*, **68**(12): 2954-2956.
- Fischer J, Rodríguez I, Baumann B, Guiral E, Beutin L, Schroeter A, Kaesbohrer A, Pfeifer Y, Helmuth R, Guerra B. 2014. *bla<sub>CTX-M-15</sub>*-carrying *Escherichia coli* and *Salmonella* isolates from livestock and food in Germany. *Journal of Antimicrobial Chemotherapy*, **69**(11): 2951-2958.
- Fischer J, Hille K, Ruddat I, Mellmann A, Köck R, Kreienbrock L. 2017. Simultaneous occurrence of MRSA and ESBL-producing Enterobacteriaceae on pig farms and in nasal and stool samples from farmers. *Veterinary Microbiology*, **200**: 107-113, doi: 10.1016/j.vetmic.2016.05.021.
- Garmyn A, Haesebrouck F, Hellebuyck T, Smet A, Pasmans F, Butaye P, Martel A. 2011. Presence of extended-spectrum  $\beta$ -lactamase-producing *Escherichia coli* in wild geese. *Journal of Antimicrobial Chemotherapy*, **66**(7): 1643-1644.
- Gonçalves A, Igrejas G, Radhouani H, Estepa V, Alcaide E, Zorrilla I, Serra R, Torres C, Poeta P. 2012. Detection of extended-spectrum beta-lactamase-producing *Escherichia coli* isolates in faecal samples of Iberian lynx. *Letters in Applied Microbiology*, **54**(1): 73-77.
- Greig J, Rajić A, Young I, Mascarenhas M, Waddell L, Lejeune J. 2015. A scoping review of the role of wildlife in the transmission of bacterial pathogens and antimicrobial resistance to the food chain. *Zoonoses and Public Health*, **62**(4): 269-284.
- Guenther S, Grobbel M, Beutlich J, Bethe A, Friedrich ND, Goedecke A, Lübke-Becker A, Guerra B, Wieler LH, Ewers C. 2010a. CTX-M-15-type extended-spectrum beta-lactamases-producing *Escherichia coli* from wild birds in Germany. *Environmental Microbiology Reports*, **2**(5): 641-645.
- Guenther S, Grobbel M, Beutlich J, Guerra B, Ulrich RG, Wieler LH, Ewers C. 2010b. Detection of pandemic B2-O25-ST131 *Escherichia coli* harbouring the CTX-M-9 extended-spectrum  $\beta$ -lactamase type in a feral urban brown rat (*Rattus norvegicus*). *Journal of Antimicrobial Chemotherapy*, **65**(3): 582-584.
- Guenther S, Aschenbrenner K, Stamm I, Bethe A, Semmler T, Stubbe A, Stubbe M, Batsajkhan N, Glupczynski Y, Wieler LH, Ewers C. 2012. Comparable high rates of extended-spectrum-beta-lactamase-producing *Escherichia coli* in birds of prey from Germany and Mongolia. *PLoS One*, **7**(12): e53039, doi: 10.1371/journal.pone.0053039.
- Guo YF, Zhang WH, Ren SQ, Yang L, Lü DH, Zeng ZL, Liu YH, Jiang HX. 2014. IncA/C plasmid-mediated spread of CMY-2 in multidrug-resistant *Escherichia coli* from food animals in China. *PLoS One*, **9**(5): e96738, doi: 10.1371/journal.pone.0096738.
- Haenni M, Saras E, Ponsin C, Dahmen S, Pettitjean M, Hocquet D, Madec

- JY. 2016. High prevalence of international ESBL CTX-M-15-producing *Enterobacter cloacae* ST114 clone in animals. *Journal of Antimicrobial Chemotherapy*, **71**(6): 1497-1500.
- Hansen F, Olsen SS, Heltberg O, Justesen US, Fuglsang-Damgaard D, Knudsen JD, Hammerum AM. 2014. Characterization of third-generation cephalosporin-resistant *Escherichia coli* from bloodstream infections in Denmark. *Microbial Drug Resistance*, **20**(4): 316-324.
- Hansen KH, Bortolaia V, Nielsen CA, Nielsen JB, Schønning K, Agersø Y, Guardabassi L. 2016. Host-Specific patterns of genetic diversity among Inc11-ly and IncK plasmids encoding CMY-2  $\beta$ -Lactamase in *Escherichia coli* isolates from humans, poultry meat, poultry, and dogs in Denmark. *Applied and Environmental Microbiology*, **82**(15): 4705-4714.
- Harrois D, Breurec S, Seck A, Delauné A, Le Hello S, Pardos de la Gándara M, Sontag L, Perrier-Gros-Claude JD, Sire JM, Garin B, Weill FX. 2014. Prevalence and characterization of extended-spectrum  $\beta$ -lactamase-producing clinical *Salmonella enterica* isolates in Dakar, Senegal, from 1999 to 2009. *Clinical Microbiology and Infection*, **20**(2): O109-O116.
- Hasan B, Sandegren L, Melhus Å, Drobní M, Hernandez J, Waldenström J, Alam M, Olsen B. 2012. Antimicrobial drug-resistant *Escherichia coli* in wild birds and free-range poultry, Bangladesh. *Emerging Infectious Diseases*, **18**(12): 2055-2058.
- Hasan B, Melhus Å, Sandegren L, Alam M, Olsen B. 2014. The gull (*Chroicocephalus brunnicephalus*) as an environmental bioindicator and reservoir for antibiotic resistance on the coastlines of the Bay of Bengal. *Microbial Drug Resistance*, **20**(5): 466-471.
- Hasan B, Olsen B, Alam A, Akter L, Melhus Å. 2015. Dissemination of the multidrug-resistant extended-spectrum  $\beta$ -lactamase-producing *Escherichia coli* O25b-ST131 clone and the role of house crow (*Corvus splendens*) foraging on hospital waste in Bangladesh. *Clinical Microbiology and Infection*, **21**(11): 1000.e1-1000.e4, doi: 10.1016/j.cmi.2015.06.016.
- Hasan B, Laurell K, Rakib MM, Ahlstedt E, Hernandez J, Caceres M, Järhult JD. 2016. Fecal carriage of extended-spectrum  $\beta$ -lactamases in healthy humans, poultry, and wild birds in León, Nicaragua-A shared pool of *bla*<sub>CTX-M</sub> genes and possible interspecies clonal spread of extended-spectrum  $\beta$ -lactamases-producing *Escherichia coli*. *Microbial Drug Resistance*, **22**(8): 682-687.
- Hasman H, Hammerum AM, Hansen F, Hendriksen RS, Olesen B, Agersø Y, Zankari E, Leekitcharoenphon P, Stegger M, Kaas RS, Cavaco L, Hansen DS, Aarestrup FM, Skov RL. 2015. Detection of *mcr-1* encoding plasmid-mediated colistin-resistant *Escherichia coli* isolates from human bloodstream infection and imported chicken meat, Denmark 2015. *Eurosurveillance*, **20**(49), doi: 10.2807/1560-7917.ES.2015.20.49.30085.
- Hassan SA, Shobrak MY. 2015. Detection of genes mediating beta-lactamase production in isolates of enterobacteria recovered from wild pets in Saudi Arabia. *Veterinary World*, **8**(12): 1400-1404.
- He T, Wang Y, Sun L, Pang MD, Zhang LL, Wang R. 2017. Occurrence and characterization of *bla*<sub>NDM-5</sub>-positive *Klebsiella pneumoniae* isolates from dairy cows in Jiangsu, China. *Journal of Antimicrobial Chemotherapy*, **72**(1): 90-94.
- Hernandez J, Bonnedahl J, Eliasson I, Wallensten A, Comstedt P, Johansson A, Granholm S, Melhus Å, Olsen B, Drobní M. 2010. Globally disseminated human pathogenic *Escherichia coli* of O25b-ST131 clone, harbouring *bla*<sub>CTX-M-15</sub>, found in Glaucous-winged gull at remote Commander Islands, Russia. *Environmental Microbiology Reports*, **2**(2): 329-332.
- Hernandez J, Johansson A, Stedt J, Bengtsson S, Porczak A, Granholm S, González-Acuña D, Olsen B, Bonnedahl J, Drobní M. 2013. Characterization and comparison of extended-spectrum  $\beta$ -lactamase (ESBL) resistance genotypes and population structure of *Escherichia coli* isolated from Franklin's gulls (*Leucophaeus pipixcan*) and humans in Chile. *PLoS One*, **8**(9): e76150, doi: 10.1371/journal.pone.0076150.
- Hiki M, Usui M, Kojima A, Ozawa M, Ishii Y, Asai T. 2013. Diversity of plasmid replicons encoding the *bla*<sub>CMY-2</sub> gene in broad-spectrum cephalosporin-resistant *Escherichia coli* from livestock animals in Japan. *Foodborne Pathogens and Disease*, **10**(3): 243-249.
- Ho PL, Chow KH, Lai EL, Lo WU, Yeung MK, Chan J, Chan PY, Yuen KY. 2011. Extensive dissemination of CTX-M-producing *Escherichia coli* with multidrug resistance to 'critically important' antibiotics among food animals in Hong Kong, 2008-10. *Journal of Antimicrobial Chemotherapy*, **66**(4): 765-768.
- Ho PL, Lo WU, Lai EL, Law PY, Leung SM, Wang Y, Chow KH. 2015. Clonal diversity of CTX-M-producing, multidrug-resistant *Escherichia coli* from rodents. *Journal of Medical Microbiology*, **64**(2): 185-190.
- Hordijk J, Schoormans A, Kwakernaak M, Duim B, Broens E, Dierikx C, Mevius D, Wagenaar JA. 2013. High prevalence of fecal carriage of extended spectrum  $\beta$ -lactamase/AmpC-producing *Enterobacteriaceae* in cats and dogs. *Frontiers in Microbiology*, **4**: 242, doi: 10.3389/fmicb.2013.00242.
- Hu LH, Liu YL, Deng LQ, Zhong QS, Hang YP, Wang ZZ, Zhan LL, Wang LX, Yu FY. 2016. Outbreak by ventilator-associated ST11 *K. pneumoniae* with co-production of CTX-M-24 and KPC-2 in a SICU of a tertiary teaching hospital in Central China. *Frontiers in Microbiology*, **7**: 1190, doi: 10.3389/fmicb.2016.01190.
- Hu YY, Cai JC, Zhou HW, Chi D, Zhang XF, Chen WL, Zhang R, Chen GX. 2013. Molecular typing of CTX-M-producing *Escherichia coli* isolates from environmental water, swine feces, specimens from healthy humans, and human patients. *Applied and Environmental Microbiology*, **79**(19): 5988-5996.
- Huang YL, Yu XN, Xie MM, Wang X, Liao K, Xue WC, Chan EWC, Zhang R, Chen S. 2016. Widespread dissemination of carbapenem-resistant *Escherichia coli* sequence type 167 strains harboring the *bla*<sub>NDM-5</sub> in clinical settings in China. *Antimicrobial Agents and Chemotherapy*, **60**(7): 4364-4368.
- Hussain A, Ranjan A, Nandanwar N, Babbar A, Jadhav S, Ahmed N. 2014. Genotypic and phenotypic profiles of *Escherichia coli* isolates belonging to clinical sequence type 131 (ST131), clinical non-ST131, and fecal non-ST131 lineages from India. *Antimicrobial Agents and Chemotherapy*, **58**(12): 7240-7249.
- Jacoby GA. 2009. AmpC  $\beta$ -lactamases. *Clinical Microbiology Reviews*, **22**(1): 161-182.
- Jakobsen L, Bortolaia V, Bielak E, Moodley A, Olsen SS, Hansen DS, Frimodt-Møller N, Guardabassi L, Hasman H. 2015. Limited similarity between plasmids encoding CTX-M-1  $\beta$ -lactamase in *Escherichia coli* from humans, pigs, cattle, organic poultry layers and horses in Denmark. *Journal of Global Antimicrobial Resistance*, **3**(2): 132-136.
- Jamborova I, Dolejska M, Vojtech J, Guenther S, Uricariu R, Drozdowska J, Papousek I, Pasekova K, Meissner W, Hordowski J, Cizek A, Literak I, Nojiri H. 2015. Plasmid-mediated resistance to cephalosporins and fluoroquinolones in various *Escherichia coli* sequence types isolated from rooks wintering in Europe. *Applied and Environmental Microbiology*, **81**(2):

648-657.

Jardine CM, Janecko N, Allan M, Boerlin P, Chalmers G, Kozak G, Mcewen SA, Reid-Smith RJ. 2012. Antimicrobial resistance in *Escherichia coli* isolates from raccoons (*Procyon lotor*) in Southern Ontario, Canada. *Applied and Environmental Microbiology*, **78**(11): 3873-3879.

Kawamura K, Goto K, Nakane K, Arakawa Y. 2014. Molecular epidemiology of extended-spectrum  $\beta$ -lactamases and *Escherichia coli* isolated from retail foods including chicken meat in Japan. *Foodborne Pathogens and Disease*, **11**(2): 104-110.

Kaye KS, Pogue JM, Tran TB, Nation RL, Li J. 2016. Agents of last resort: polymyxin resistance. *Infectious Disease Clinics of North America*, **30**(2): 391-414.

Kim SY, Shin J, Shin SY, Ko KS. 2013. Characteristics of carbapenem-resistant *Enterobacteriaceae* isolates from Korea. *Diagnostic Microbiology and Infectious Disease*, **76**(4): 486-490.

Kim YA, Kim JJ, Kim H, Lee K. 2017. Community-onset extended-spectrum- $\beta$ -lactamase-producing *Escherichia coli* sequence type 131 at two Korean community hospitals: the spread of multidrug-resistant *E. coli* to the community via healthcare facilities. *International Journal of Infectious Diseases*, **54**: 39-42.

Kumarasamy KK, Toleman MA, Walsh TR, Bagaria J, Butt F, Balakrishnan R, Chaudhary U, Doumith M, Giske CG, Irfan S, Krishnan P, Kumar AV, Maharjan S, Mushtaq S, Noorie T, Paterson DL, Pearson A, Perry C, Pike R, Rao B, Ray U, Sarma JB, Sharma M, Sheridan E, Thirunarayan MA, Turton J, Upadhyay S, Warner M, Welfare W, Livermore DM, Woodford N. 2010. Emergence of a new antibiotic resistance mechanism in India, Pakistan, and the UK: a molecular, biological, and epidemiological study. *The Lancet Infectious Diseases*, **10**(9): 597-602.

Laxminarayan R, Duse A, Watal C, Zaidi AKM, Wertheim HF, Sumpradit N, Vlieghe E, Hara GL, Gould IM, Goossens H, Greko C, So Anthony D, Bigdeli M, Tomson G, Woodhouse W, Ombaka E, Peralta AQ, Qamar FN, Mir F, Kariuki S, Bhutta ZA, Coates A, Bergstrom R, Wright GD, Brown ED, Cars O. 2013. Antibiotic resistance-the need for global solutions. *The Lancet Infectious Diseases*, **13**(12): 1057-1098.

Lee CR, Lee JH, Park KS, Kim YB, Jeong BC, Lee SH. 2016. Global dissemination of carbapenemase-producing *Klebsiella pneumoniae*: epidemiology, genetic context, treatment options, and detection methods. *Frontiers in Microbiology*, **7**: 895, doi: 10.3389/fmicb.2016.00895.

Lee K, Iwata T, Nakadai A, Kato T, Hayama S, Taniguchi T, Hayashidani H. 2011a. Prevalence of *Salmonella*, *Yersinia* and *Campylobacter* spp. in feral raccoons (*Procyon lotor*) and masked palm civets (*Paguma larvata*) in Japan. *Zoonoses and Public Health*, **58**(6): 424-431.

Lee MY, Ko KS, Kang CI, Chung DR, Peck KR, Song JH. 2011b. High prevalence of CTX-M-15-producing *Klebsiella pneumoniae* isolates in Asian countries: diverse clones and clonal dissemination. *International Journal of Antimicrobial Agents*, **38**(2): 160-163.

Liakopoulos A, Mevius DJ, Olsen B, Bonnedahl J. 2016. The colistin resistance *mcr-1* gene is going wild. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2335-2336.

Literak I, Dolejska M, Janoszowska D, Hrusakova J, Meissner W, Rzycka H, Bzoma S, Cizek A. 2010a. Antibiotic-resistant *Escherichia coli* bacteria, including strains with genes encoding the extended-spectrum beta-lactamase and QnrS, in waterbirds on the Baltic Sea Coast of Poland. *Applied and Environmental Microbiology*, **76**(24): 8126-8134.

Literak I, Dolejska M, Radimersky T, Klimes J, Friedman M, Aarestrup FM,

Hasman H, Cizek A. 2010b. Antimicrobial-resistant faecal *Escherichia coli* in wild mammals in central Europe: multiresistant *Escherichia coli* producing extended-spectrum beta-lactamases in wild boars. *Journal of Applied Microbiology*, **108** (5): 1702-1711.

Literak I, Manga I, Wojczulanis-Jakubas K, Chroma M, Jamborova I, Dobiasova H, Sedlakova MH, Cizek A. 2014. *Enterobacter cloacae* with a novel variant of ACT AmpC beta-lactamase originating from glaucous gull (*Larus hyperboreus*) in Svalbard. *Veterinary Microbiology*, **171**(3-4): 432-435.

Liu LP, He DD, Lv LC, Liu WL, Chen XJ, Zeng ZL, Partridge SR, Liu JH. 2015. *bla*<sub>CTX-M-15/91</sub> hybrid genes may have been generated from *bla*<sub>CTX-M-15</sub> on an IncI2 plasmid. *Antimicrobial Agents and Chemotherapy*, **59**(8): 4464-4470.

Liu XQ, Thungrat K, Boothe DM. 2016a. Occurrence of OXA-48 Carbapenemase and other  $\beta$ -lactamase genes in ESBL-producing multidrug resistant *Escherichia coli* from dogs and cats in the United States, 2009-2013. *Frontiers in Microbiology*, **7**: 1057, doi: 10.3389/fmicb.2016.01057.

Liu YY, Wang Y, Walsh TR, Yi LX, Zhang R, Spencer J, Doi Y, Tian GB, Dong BL, Huang XH, Yu LF, Gu DX, Ren HW, Chen XJ, Lv LC, He DD, Zhou HW, Liang ZS, Liu JH, Shen JH. 2016b. Emergence of plasmid-mediated colistin resistance mechanism MCR-1 in animals and human beings in China: a microbiological and molecular biological study. *The Lancet Infectious Diseases*, **16**(2): 161-168.

Loncaric I, Küber-Heiss A, Posautz A, Stalder GL, Hoffmann D, Rosengarten R, Walzer C. 2013a. Characterization of methicillin-resistant *Staphylococcus* spp. carrying the *mecC* gene, isolated from wildlife. *Journal of Antimicrobial Chemotherapy*, **68**(10): 2222-2225.

Loncaric I, Stalder GL, Mehinagic K, Rosengarten R, Hoelzl F, Knauer F, Walzer C. 2013b. Comparison of ESBL- and AmpC producing *Enterobacteriaceae* and methicillin-resistant *Staphylococcus aureus* (MRSA) isolated from migratory and resident population of rooks (*Corvus frugilegus*) in Austria. *PLoS One*, **8**(12): e84048, doi: 10.1371/journal.pone.0084048.

Loncaric I, Beiglböck C, Feßler AT, Posautz A, Rosengarten R, Walzer C, Ehrlich R, Monecke S, Schwarz S, Spersger J, Küber-Heiss A. 2016. Characterization of ESBL- and AmpC-producing and fluoroquinolone-resistant *Enterobacteriaceae* isolated from Mouflons (*Ovis orientalis musimon*) in Austria and Germany. *PLoS One*, **11**(5): e0155786, doi: 10.1371/journal.pone.0155786.

Lu PL, Hsieh YJ, Lin JE, Huang JW, Yang TY, Lin L, Tseng SP. 2016. Characterisation of fosfomycin resistance mechanisms and molecular epidemiology in extended-spectrum  $\beta$ -lactamase-producing *Klebsiella pneumoniae* isolates. *International Journal of Antimicrobial Agents*, **48**(5): 564-568.

Ma JY, Liu JH, Lv LC, Zong ZY, Sun Y, Zheng HQ, Chen ZL, Zeng ZL. 2012. Characterization of extended-spectrum  $\beta$ -lactamase genes found among *Escherichia coli* isolates from duck and environmental samples obtained on a duck farm. *Applied and Environmental Microbiology*, **78**(10): 3668-3673.

Maded JY, Haenni M, Métayer V, Saras E, Nicolas-Chanoine MH. 2015. High prevalence of the animal-associated *bla*<sub>CTX-M-1</sub> IncI1/ST3 plasmid in human *Escherichia coli* isolates. *Antimicrobial Agents and Chemotherapy*, **59**(9): 5860-5861.

Mathers AJ, Peirano G, Pitout JDD. 2015. The role of epidemic resistance plasmids and international high-risk clones in the spread of multidrug-

- resistant *Enterobacteriaceae*. *Clinical Microbiology Reviews*, **28**(3): 565-591.
- McGann P, Snesrud E, Maybank R, Corey B, Ong AC, Clifford R, Hinkle M, Whitman T, Lesho E, Schaecher KE. 2016. *Escherichia coli* harboring *mcr-1* and *bla<sub>CTX-M</sub>* on a novel IncF plasmid: first report of *mcr-1* in the United States. *Antimicrobial Agents and Chemotherapy*, **60**(7): 4420-4421.
- Meinersmann RJ, Ladely SR, Plumblee JR, Hall MC, Simpson SA, Ballard LL, Scheffler BE, Genzlinger LL, Cook KL. 2016. Colistin resistance *mcr-1*-gene-bearing *Escherichia coli* strain from the United States. *Genome Announcements*, **4**(5): e00898-16, doi: 10.1128/genomeA.00898-16.
- Michael GB, Kaspar H, Siqueira AK, de Freitas Costa E, Corbellini LG, Kadlec K, Schwarz S. 2017. Extended-spectrum  $\beta$ -lactamase (ESBL)-producing *Escherichia coli* isolates collected from diseased food-producing animals in the GERM-Vet monitoring program 2008-2014. *Veterinary Microbiology*, **200**: 142-150, doi: 10.1016/j.vetmic.2016.08.023.
- Müller A, Stephan R, Nüesch-Inderbilen M. 2016. Distribution of virulence factors in ESBL-producing *Escherichia coli* isolated from the environment, livestock, food and humans. *Science of the Total Environment*, **541**: 667-672.
- Nilsen E, Haldorsen BC, Sundsfjord A, Simonsen GS, Ingebretsen A, Naseer U, Samuelsen Ø. 2013. Large IncHI2-plasmids encode extended-spectrum  $\beta$ -lactamases (ESBLs) in *Enterobacter* spp. bloodstream isolates, and support ESBL-transfer to *Escherichia coli*. *Clinical Microbiology and Infection*, **19**(11): E516-E518.
- Nimmo GR. 2012. USA300 abroad: global spread of a virulent strain of community-associated methicillin-resistant *Staphylococcus aureus*. *Clinical Microbiology and Infection*, **18**(8): 725-734.
- Parker D, Sniatynski MI, Mandrusiak D, Rubin JE. 2016. Extended-spectrum  $\beta$ -lactamase producing *Escherichia coli* isolated from wild birds in Saskatoon, Canada. *Letters in Applied Microbiology*, **63**(1): 11-15.
- Partridge SR. 2015. Resistance mechanisms in *Enterobacteriaceae*. *Pathology*, **47**(3): 276-284.
- Pietsch M, Eller C, Wendt C, Hoffelder M, Falgenhauer L, Fruth A, Grössl T, Leistner R, Valenza G, Werner G, Pfeifer Y, the RESET Study Group. 2017. Molecular characterisation of extended-spectrum  $\beta$ -lactamase (ESBL)-producing *Escherichia coli* isolates from hospital and ambulatory patients in Germany. *Veterinary Microbiology*, **200**: 130-137, doi: 10.1016/j.vetmic.2015.11.028.
- Pilo P, Vogt D, Origgi FC, Endimiani A, Peterson S, Perreten V. 2015. First report of a multidrug-resistant *Klebsiella pneumoniae* of sequence type 11 causing sepsis in a free-ranging beaver (*Castor fiber*). *Environmental Microbiology Reports*, **7**(2): 351-353.
- Pinto L, Radhouani H, Coelho C, Costa PMD, Simões R, Brandão RML, Torres C, Igrejas G, Poeta P. 2010. Genetic detection of extended-spectrum  $\beta$ -lactamase-containing *Escherichia coli* isolates from birds of prey from Serra da Estrela natural reserve in Portugal. *Applied and Environmental Microbiology*, **76**(12): 4118-4120.
- Platell JL, Cobbold RN, Johnson JR, Heisig A, Heisig P, Clabots C, Kuskowski MA, Trott DJ. 2011. Commonality among fluoroquinolone-resistant sequence type ST131 extraintestinal *Escherichia coli* isolates from humans and companion animals in Australia. *Antimicrobial Agents and Chemotherapy*, **55**(8): 3782-3787.
- Poeta P, Radhouani H, Igrejas G, Gonçalves A, Carvalho C, Rodrigues J, Vinué L, Somalo S, Torres C. 2008. Seagulls of the Berlengas natural reserve of Portugal as carriers of fecal *Escherichia coli* harboring CTX-M and TEM extended-spectrum beta-lactamases. *Applied and Environmental Microbiology*, **74**(23): 7439-7441.
- Poeta P, Radhouani H, Pinto L, Martinho A, Rego V, Rodrigues R, Gonçalves A, Rodrigues J, Estepa V, Torres C, Igrejas G. 2009. Wild boars as reservoirs of extended-spectrum beta-lactamase (ESBL) producing *Escherichia coli* of different phylogenetic groups. *Journal of Basic Microbiology*, **49**(6): 584-588.
- Poirel L, Potron A, De La Cuesta C, Cleary T, Nordmann P, Munoz-Price LS. 2012. Wild coastline birds as reservoirs of broad-spectrum  $\beta$ -lactamase-producing *Enterobacteriaceae* in Miami Beach, Florida. *Antimicrobial Agents and Chemotherapy*, **56**(5): 2756-2758.
- Porrero MC, Valverde A, Fernándezllario P, Díezguerrier A, Mateos A, Lavín S, Cantón R, Domínguez L. 2014. *Staphylococcus aureus* carrying *mecC* gene in animals and urban wastewater, Spain. *Emerging Infectious Diseases*, **20**(5): 899-901.
- Qin SS, Fu Y, Zhang QJ, Qi H, Wen JG, Xu H, Xu LJ, Zeng L, Tian H, Rong LJ, Li YH, Shan LH, Xu HD, Yu YS, Feng XJ, Liu HM. 2014. High incidence and endemic spread of NDM-1-positive *Enterobacteriaceae* in Henan Province, China. *Antimicrobial Agents and Chemotherapy*, **58**(8): 4275-4282.
- Radhouani H, Pinto L, Coelho C, Gonçalves A, Sargo R, Torres C, Igrejas G, Poeta P. 2010. Detection of *Escherichia coli* harbouring extended-spectrum  $\beta$ -lactamases of the CTX-M classes in faecal samples of common buzzards (*Buteo buteo*). *Journal of Antimicrobial Chemotherapy*, **65**(1): 171-173.
- Radhouani H, Igrejas G, Gonçalves A, Estepa V, Sargo R, Torres C, Poeta P. 2013. Molecular characterization of extended-spectrum-beta-lactamase-producing *Escherichia coli* isolates from red foxes in Portugal. *Archives of Microbiology*, **195**(2): 141-144.
- Rashid M, Rakib MM, Hasan B. 2015. Antimicrobial-resistant and ESBL-producing *Escherichia coli* in different ecological niches in Bangladesh. *Infection Ecology & Epidemiology*, **5**(1): 26712, doi: 10.3402/iee.v5.26712.
- Ruzauskas M, Vaskeviciute L. 2016. Detection of the *mcr-1* gene in *Escherichia coli* prevalent in the migratory bird species *Larus argentatus*. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2333-2334.
- Sato G, Oka C, Asagi M, Ishiguro N. 1978. Detection of conjugative R plasmids conferring chloramphenicol resistance in *Escherichia coli* isolated from domestic and feral pigeons and crows. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene. Erste Abteilung Originale. Reihe A: Medizinische Mikrobiologie und Parasitologie*, **241**(4): 407-417.
- Sauget M, Cholley P, Vannier A, Thouverez M, Nicolas-Chanoine MH, Hocquet D, Bertrand X. 2016. Trends of extended-spectrum  $\beta$ -lactamase-producing *Escherichia coli* sequence type 131 and its H30 subclone in a French hospital over a 15-year period. *International Journal of Antimicrobial Agents*, **48**(6): 744-747.
- Schauffer K, Semmler T, Wieler LH, Wöhrmann M, Baddam R, Ahmed N, Müller K, Kola A, Fruth A, Ewers C, Guenther S. 2016. Clonal spread and interspecies transmission of clinically relevant ESBL-producing *Escherichia coli* of ST410-another successful pandemic clone? *FEMS Microbiology Ecology*, **92**(1): fiv155, doi: 10.1093/femsec/fiv155.
- Sellin M, Palmgren H, Broman T, Bergström S, Olsen B. 2000. Involving ornithologists in the surveillance of vancomycin-resistant enterococci. *Emerging Infectious Diseases*, **6**(1): 87-88.



- Sennati S, Santella G, Di Conza J, Pallecchi L, Pino M, Ghiglione B, Rossolini GM, Radice M, Gutkind G. 2012. Changing epidemiology of extended-spectrum  $\beta$ -lactamases in Argentina: emergence of CTX-M-15. *Antimicrobial Agents and Chemotherapy*, **56**(11): 6003-6005.
- Sidjabat HE, Seah KY, Coleman L, Sartor A, Derrington P, Heney C, Faoagali J, Nimmo GR, Paterson DL. 2014. Expansive spread of Inc11 plasmids carrying *bla*<sub>CMY-2</sub> amongst *Escherichia coli*. *International Journal of Antimicrobial Agents*, **44**(3): 203-208.
- Sidjabat HE, Townell N, Nimmo GR, George NM, Robson J, Vohra R, Davis L, Heney C, Paterson DL. 2015. Dominance of IMP-4-producing *Enterobacter cloacae* among carbapenemase-producing *Enterobacteriaceae* in Australia. *Antimicrobial Agents and Chemotherapy*, **59**(7): 4059-4066.
- Silva N, Igrejas G, Rodrigues P, Rodrigues T, Gonçalves A, Felgar AC, Pacheco R, Gonçalves D, Cunha R, Poeta P. 2011. Molecular characterization of vancomycin-resistant enterococci and extended-spectrum  $\beta$ -lactamase-containing *Escherichia coli* isolates in wild birds from the Azores Archipelago. *Avian Pathology*, **40**(5): 473-479.
- Simões RR, Poirel L, Costa PMD, Nordmann P. 2010. Seagulls and beaches as reservoirs for multidrug-resistant *Escherichia coli*. *Emerging Infectious Diseases*, **16**(1): 110-112.
- Smet A, Martel A, Persoons D, Dewulf J, Heyndrickx M, Herman L, Haesebrouck F, Butaye P. 2010. Broad-spectrum  $\beta$ -lactamases among *Enterobacteriaceae* of animal origin: molecular aspects, mobility and impact on public health. *FEMS Microbiology Reviews*, **34**(3): 295-316.
- So JH, Kim J, Bae IK, Jeong SH, Kim SH, Lim SK, Yong HP, Lee K. 2012. Dissemination of multidrug-resistant *Escherichia coli* in Korean veterinary hospitals. *Diagnostic Microbiology and Infectious Disease*, **73**(2): 195-199.
- Sousa M, Torres C, Barros J, Somalo S, Igrejas G, Poeta P. 2011. Gilthead seabream (*Sparus aurata*) as carriers of SHV-12 and TEM-52 extended-spectrum beta-lactamases-containing *Escherichia coli* isolates. *Foodborne Pathogens and Disease*, **8**(10): 1139-1141.
- Stedt J, Bonnedahl J, Hernandez J, Waldenström J, McMahon BJ, Tolf C, Olsen B, Drobni M. 2015. Carriage of CTX-M type extended spectrum  $\beta$ -lactamases (ESBLs) in gulls across Europe. *Acta Veterinaria Scandinavica*, **57**: 74, doi: 10.1186/s13028-015-0166-3.
- Stephan R, Hächler H. 2012. Discovery of extended-spectrum beta-lactamase producing *Escherichia coli* among hunted deer, chamois and ibex. *Schweizer Archiv Für Tierheilkunde*, **154**(11): 475-478.
- Su YC, Yu CY, Tsai Y, Wang SH, Lee C, Chu C. 2016. Fluoroquinolone-resistant and extended-spectrum  $\beta$ -lactamase-producing *Escherichia coli* from the milk of cows with clinical mastitis in Southern Taiwan. *Journal of Microbiology, Immunology and Infection*, **49**(6): 892-901.
- Tamang MD, Gurung M, Nam HM, Moon DC, Kim SR, Jang GC, Jung DY, Jung SC, Park YH, Lim SK. 2015. Prevalence and characterization of *Salmonella* in pigs from conventional and organic farms and first report of *S. serovar* 1, 4, [5], 12: i - from Korea. *Veterinary Microbiology*, **178**(1-2): 119-124.
- Tausova D, Dolejska M, Cizek A, Hanusova L, Hrusakova J, Svoboda O, Camlik G, Literak I. 2012. *Escherichia coli* with extended-spectrum  $\beta$ -lactamase and plasmid-mediated quinolone resistance genes in great cormorants and mallards in Central Europe. *Journal of Antimicrobial Chemotherapy*, **67**(5): 1103-1107.
- Toleman MA, Bugert JJ, Nizam SA. 2015. Extensively drug-resistant New Delhi metallo- $\beta$ -lactamase-encoding bacteria in the environment, Dhaka, Bangladesh, 2012. *Emerging Infectious Diseases*, **21**(6): 1027-1030.
- Veldman K, van Tulden P, Kant A, Testerink J, Mevius D. 2013. Characteristics of cefotaxime-resistant *Escherichia coli* from wild birds in the Netherlands. *Applied and Environmental Microbiology*, **79**(24): 7556-7561.
- Villa L, Guerra B, Schmogger S, Fischer J, Helmuth R, Zong Z, Garcia-Fernández A, Carattoli A. 2015. IncA/C plasmid carrying *bla*<sub>NDM-1</sub>, *bla*<sub>CMY-16</sub>, and *fosA3* in a *Salmonella enterica* Serovar Corvallis strain isolated from a migratory wild bird in Germany. *Antimicrobial Agents and Chemotherapy*, **59**(10): 6597-6600.
- Vogt D, Overesch G, Endimiani A, Collaud A, Thomann A, Perreten V. 2014. Occurrence and genetic characteristics of third-generation cephalosporin-resistant *Escherichia coli* in Swiss retail meat. *Microbial Drug Resistance*, **20**(5): 485-494.
- Voulgari E, Poulou A, Dimitroulia E, Politi L, Ranellou K, Gennimata V, Markou F, Pournaras S, Tsakris A. 2016. Emergence of OXA-162 carbapenemase- and DHA-1 AmpC cephalosporinase-producing sequence type 11 *Klebsiella pneumoniae* causing community-onset infection in Greece. *Antimicrobial Agents and Chemotherapy*, **60**(3): 1862-1864.
- Wallensten A, Hernandez J, Ardiles K, González-Acuña D, Drobni M, Olsen B. 2011. Extended spectrum beta-lactamases detected in *Escherichia coli* from gulls in Stockholm, Sweden. *Infection Ecology and Epidemiology*, **1**: 7030, doi: 10.3402/iee.v1i0.7030.
- Wang S, Zhao SY, Xiao SZ, Gu FF, Liu QZ, Tang J, Guo XK, Ni YX, Han LZ. 2016. Antimicrobial resistance and molecular epidemiology of *Escherichia coli* causing bloodstream infections in three hospitals in Shanghai, China. *PLoS One*, **11**(1): e0147740, doi: 10.1371/journal.pone.0147740.
- Weis AM, Storey DB, Taff CC, Townsend AK, Huang BC, Kong NT, Clothier KA, Spinner A, Byrne BA, Weimer BC. 2016. Genomic comparison of *Campylobacter* spp. and their potential for zoonotic transmission between birds, primates, and livestock. *Applied and Environmental Microbiology*, **82**(24): 7165-7175.
- Wellington EMH, Boxall ABA, Cross P, Feil EJ, Gaze WH, Hawkey PM, Johnson-Rollings AS, Jones DL, Lee NM, Otten W, Thomas CM, Williams AP. 2013. The role of the natural environment in the emergence of antibiotic resistance in gram-negative bacteria. *The Lancet Infectious Diseases*, **13**(2): 155-165.
- WHO. 2014. Antimicrobial Resistance: Global Report on Surveillance. Geneva: World Health Organization 2014.
- Wu HY, Wang Y, Wu Y, Qiao J, Li H, Zheng SJ, Xia XD, Cui SH, Wang X, Xi ML, Meng JH, Yang BW. 2015. Emergence of  $\beta$ -lactamases and extended-spectrum  $\beta$ -lactamases (ESBLs) producing *Salmonella* in retail raw chicken in China. *Foodborne Pathogens and Disease*, **12**(3): 228-234.
- Xavier BB, Lammens C, Butaye P, Goossens H, Malhotra-Kumar S. 2016. Complete sequence of an IncFII plasmid harbouring the colistin resistance gene *mcr-1* isolated from Belgian pig farms. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2342-2344.
- Yaici L, Haenni M, Saras E, Boudehouche W, Touati A, Madec JY. 2016. *bla*<sub>NDM-5</sub>-carrying IncX3 plasmid in *Escherichia coli* ST1284 isolated from raw milk collected in a dairy farm in Algeria. *Journal of Antimicrobial Chemotherapy*, **71**(9): 2671-2672.
- Yang YQ, Zhang AY, Ma SZ, Kong LH, Li YX, Liu JX, Davis MA, Guo XY,

- Liu BH, Lei CW, Wang HN. 2016. Co-occurrence of *mcr-1* and ESBL on a single plasmid in *Salmonella enterica*. *Journal of Antimicrobial Chemotherapy*, **71**(8): 2336-2338.
- Yong D, Toleman MA, Giske CG, Cho HS, Sundman K, Lee K, Walsh TR. 2009. Characterization of a new metallo- $\beta$ -lactamase gene, *bla*<sub>NDM-1</sub>, and a novel erythromycin esterase gene carried on a unique genetic structure in *Klebsiella pneumoniae* sequence type 14 from India. *Antimicrobial Agents and Chemotherapy*, **53**(12): 5046-5054.
- Zhang XF, Doi Y, Huang X, Li HY, Zhong LL, Zeng KJ, Zhang YF, Patil S, Tian GB. 2016. Possible transmission of *mcr-1*-harboring *Escherichia coli* between companion animals and human. *Emerging Infectious Diseases*, **22**(9): 1679-1681.
- Zurfluh K, Glier M, Hächler H, Stephan R. 2015. Replicon typing of plasmids carrying *bla*<sub>CTX-M-15</sub> among *Enterobacteriaceae* isolated at the environment, livestock and human interface. *Science of the Total Environment*, **521-522**: 75-78.
- Zurfluh K, Klumpp J, Nüesch-Inderbinen M, Stephan R. 2016. Full-length nucleotide sequences of *mcr-1*-harboring plasmids isolated from extended-spectrum- $\beta$ -lactamase-producing *Escherichia coli* isolates of different origins. *Antimicrobial Agents and Chemotherapy*, **60**(9): 5589-5591.