The Role of Gulls as Reservoirs of Antibiotic Resistance in Aquatic Environments: A Scoping Review

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The role of wildlife with long-range dispersal such as gulls in the global dissemination of antimicrobial resistance (AMR) across natural and anthropogenic aquatic environments remains poorly understood. Antibiotic-resistant bacteria have been detected in resident and migratory gulls worldwide for more than a decade, suggesting gulls as either sentinels of AMR pollution from anthropogenic sources or independent reservoirs that could maintain and disperse AMR across aquatic environments. However, confirming either of these roles remains challenging and incomplete. In this review, we present current knowledge on the geographic regions where AMR has been detected in gulls, the molecular characterization of resistance genes, and the evidence supporting the capacity of gulls to disperse AMR across regions or countries. We identify several limitations of current research to assess the role of gulls in the spread of AMR including most studies not identifying the source of AMR, few studies comparing bacteria isolated in gulls with other wild or domestic species, and almost no study performing longitudinal sampling over a large period of time to assess the maintenance and dispersion of AMR by gulls within and across regions. We suggest future research required to confirm the role of gulls in the global dispersion of AMR including the standardization of sampling protocols, longitudinal sampling using advanced satellite tracking, and whole-genome sequencing typing. Finally, we discuss the public health implications of the spread of AMR by gulls and potential solutions to limit its spread in aquatic environments.

Keywords: marine birds, One Health, seagulls, wildlife, bacteria, antimicrobial resistance, AMR, ESBL

INTRODUCTION

Antimicrobial resistance (AMR) is a major global health challenge affecting human, animal, and environmental health (FAO and WHO, 2019; WHO, 2019). Thus, a One Health approach is required to understand the dynamics of AMR between humans and animals (Salgado-Caxito et al., 2021). Many studies have reported the presence of antibiotic-resistant bacteria (ARB) in
wild animals, highlighting their potential role in the spread of clinically important bacteria to humans and domestic animals (Wang et al., 2017; Benavides et al., 2018; Dolejska and Literak, 2019). Wildlife such as wild birds, particularly the ones living in proximity to human settings or agriculture fields, can acquire AMR from anthropogenic sources when feeding on landfills and wastewater (Nelson et al., 2008; Wang et al., 2017). Despite several reports of wild birds carrying ARB (Wang et al., 2017), their impact on the dissemination of ARB in aquatic environments remains still poorly understood.

Gulls can impact the spread of ARB of public health concern by acting either as (i) receivers of ARB or antibiotic-resistant genes (ARGs) and acting as sentinels of human environmental pollution to natural ecosystems (Guenther et al., 2011) or as (ii) reservoirs of ARBs and ARGs, capable of dispersing ARB or ARGs to different geographic locations and to other species including humans and domestic animals. In particular, the migratory capacity of several gull species such as the Franklin’s gull (Leucophaeus pipixcan), migrating across America from Canada to Chile, could result in the dissemination of ARB and ARGs over extensive geographic areas, dispersing AMR from regions with high levels of AMR to less affected areas (Báez et al., 2015; Dolejska and Literak, 2019). Gulls are also present in most urban and rural environments, and their feces are extensively dispersed in the environment (Bonnedahl and Järhult, 2014). Several studies have detected ARGs in gulls (Oravcova et al., 2017; Ahlstrom et al., 2019b; Haenni et al., 2020). In particular, AMR has been detected in several species of seagulls, which have large breeding distributions in urban areas and feed on human waste (Bonnedahl et al., 2015; Stedt et al., 2015; Ahlstrom et al., 2019a). Thus, gulls have been suggested as potential reservoirs of ARB and ARGs, although evidence proving their role as reservoirs has not been provided (Radhouani et al., 2010; Aberkan et al., 2015; Merkeviciene et al., 2018).

In this scoping review, we summarized the current knowledge regarding the global dissemination of ARB and ARGs among gulls and assess whether there is evidence supporting the assumption that gulls can act as reservoirs of AMR. In particular, we aim to provide a comprehensive overview of the geographic location where ARB and ARGs have been found in gulls, the gull and bacteria species involved, as well as the antibiotic families and genes detected. To discuss the public health implications of gulls, we summarized whether bacteria of critical importance according to WHO have been detected in gulls. We also assessed the number of publications that had either identified the origin of AMR found in gulls or tested and concluded that gulls can disperse AMR across the landscape or to other species. Based on this current evidence, we discussed several recommendations aiming to improve our understanding of the role of gulls in the dissemination of AMR.

**MATERIALS AND METHODS**

We performed a scoping review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-ScR) checklist (Tricco et al., 2018; Supplementary Table 1). All authors defined research questions, objectives, search strategy, and inclusion/exclusion criteria through previous discussions.

**Search Strategy**

The search was performed in PubMed, Scopus, and Web of Science databases using three general queries: (antibiotic resist* OR antimicrobial resist*), (Escherichia OR Klebsiella OR Staphylococcus OR Enterococcus OR Enterobacter OR Salmonella OR Pseudomonas), and (bacteria). Each of them was merged with (marine bird* OR aquatic bird* OR gull* OR Larus).

Details of the search strategy are available as an additional file (Supplementary Table 2). Visualization, duplicate removal, and storing collected data were performed in Microsoft Excel.

**Eligibility Criteria**

We aimed to identify peer-reviewed studies on AMR in different wild species of gulls (i.e., seagulls) showing the presence and/or potential transmission of ARB and ARGs. Thus, we included only studies providing at least one of the following information: (i) wild gull species where ARB was recovered, (ii) phenotypic resistance to specific antibiotics in bacteria isolated from gulls, and/or (iii) ARGs identified in bacteria isolated from gulls. There were no restrictions related to the year of publication or geographical location. Any type of reviews or studies including in vivo experiments, samples of gulls from rehabilitation centers, or containing previously published data were excluded. Details of all inclusion and exclusion criteria are provided in Supplementary Table 3.

**Identification and Screening of Articles**

After the removal of duplicates, we identified a total of 3,475 articles published from 1964 to January 2021, including 3 additional references that were identified from reading these papers. Pre-selection by title and abstract reduced to 227 articles for full-text analysis, and 90 fulfilled the preestablished criteria and were included in the final analysis (Figure 1). The remaining 140 articles did not fit our inclusion criteria as they did not include gull samples, did not present AMR information/data, data from gulls were previously published, the study included experimental infection, the study was performed on captive gulls or in rehabilitation centers, the study sampling was conducted postmortem, or the full text of the article was not available.

**Data Extraction**

Extracted data were independently performed by three authors (DZG, MSC, and ZRS) and verified by other authors. Disagreements were resolved through discussion. The obtained data were entered into a Microsoft Excel template adapted from a previous study (Supplementary Table 4; Salgado-Caxito et al., 2021). This file included the title of the article, authorship, year of publication, gull species included in the study and whether the species was migratory or not, the number of sampled individuals, the bacteria species studied, the number of recovered isolates, the antimicrobial susceptibility tests performed, the name and family of the antibiotics tested, and the molecular typing used (i.e., PCR,
sequencing, and whole-genome sequencing) when available. To assess the current knowledge on the role of gulls as reservoirs of ARB or ARGs, we also specifically extracted from studies (i) whether the study compared gulls to other animals in the area; (ii) whether the study identified the origin (e.g., anthropogenic source) of the ARB or ARGs found; (iii) if gulls were sampled more than once, particularly in both areas of migration (origin and destination); (iv) if molecular typing of ARB was performed; and (iv) if an individual follow-up and sampling of gulls were performed, along with the method used.

Statistical Analysis
We estimated the proportion of studies filling a given criteria (e.g., studies identifying the presence of ARGs or the origin of ARB) using R. 3.1.6 (R Development Core Team).

RESULTS
Geographic Locations and Gull and Bacteria Species Studied
Our scoping review identified 90 articles published between 1981 and 2020, although only 22% of these studies were published before 2010. The number of studies published on gulls increased from 1 in 1981 to 10 per year in 2020 and peaked in 2017 with 12 articles (Figure 2B). Studies were conducted in gulls from all five continents, but the majority of publications were made in Europe (58%) followed by North America (19%) (Figure 2A). Studies were conducted in a total of 31 countries, with high-income countries such as the United States (17%), Portugal (12%) and Spain (10%) conducting the highest number of studies (Figure 2C). In contrast, in middle- and low-income countries, few publications were conducted (Morocco, 1%; South Africa, 1%; Bangladesh, 1%).

From 100 species of gulls known (IUCN, 2021), ARB or ARGs were recovered from 23 species. Most gulls studied (74%) were migratory species. The number of studies per gull species was highly heterogeneous (Figure 3B). The majority of studies focused on the herring gull (Larus argentatus, 26%), followed by the laughing gull (Chroicocephalus ridibundus, 23%) and the yellow-legged gull (Larus michahellis, 19%) (Figure 3A). These three species are widely distributed in the northern hemisphere.

Among the 90 studies, 49 ARB species were recovered from gulls. Most studies focused on Escherichia coli (59%), Salmonella enterica (23%), Campylobacter jejuni (8%), and Klebsiella pneumoniae (8%) (Figure 3C). The temporal trend of publications showed that after 2008, most studies have focused on E. coli.
Antibiotic Susceptibility in Bacteria From Gulls

Screening of ARB using selective media supplemented with antibiotics before antimicrobial susceptibility tests was performed in 43% of studies. Seventeen percent of studies performed antibiotic susceptibility tests after isolation in non-supplemented media. The remaining 40% of the studies did not present the methodology for recovering isolates. Forty-one publications had information about the number of positive individuals, and 68% of those studies were conducted in Europe. The highest proportion of animals harboring bacteria resistant to at least one antibiotic (referred as positive animals) was estimated in one study in Africa (70%) that included less than 50 individuals. The highest proportion of positive gulls was observed among Larus dominicanus (100%), while Proteus mirabilis showed the highest proportion of positive individuals (27.9%) (Table 1). Given the high heterogeneity in susceptibility methods and antibiotics tested, a comparison of ARB prevalence across studies, defined as the number of positive individuals over the total of sampled animals, could not be performed. Regarding the methodology used to test susceptibility, 68% of studies confirmed phenotypic resistance using the disk diffusion method (CLSI, 2018). Overall, resistance to 79 antibiotic agents from 21 families was tested (Supplementary Table 5), including antibiotics used in human medicine such as beta-lactams (i.e., penicillin, cephalosporins, and carbapenems), tetracyclines, fluoroquinolones, sulfonamides,
aminoglycosides, nitrofurans, macrolides, monobactam, polypeptides, glycopeptides, and lincosamides. More than 50% of studies reported at least one bacterial isolate resistant to tetracycline (58%) and ampicillin (52%), followed by chloramphenicol (47%), streptomycin (44%), trimethoprim–sulfamethoxazole (38%), gentamicin (36%), nalidixic acid (35%), and ciprofloxacin (32%) (Figure 4A). In particular, broad-spectrum beta-lactams used in human medicine such as amoxicillin with clavulanic acid and ceftazidime were reported in 20% of publications.

Among the four antimicrobial-resistant pathogens considered as a “critical priority” by the WHO (WHO, 2017), all were tested at least once in the reviewed studies. Third-generation cephalosporin-resistant Enterobacterales from gulls were the most reported (41%), followed by carbapenem-resistant Enterobacterales (10%) (Table 2). Among “high-priority”
pathogens, Campylobacter spp. (6%) and Salmonella spp. (8%) both resistant to fluoroquinolones were the most identified. No "medium-priority" pathogen has been recovered from gulls.

**Molecular Characterization of ARGs in Gulls**

ARGs were reported in 70% of studies conducted in gulls (Tables 3, 4). Mobile genetic elements (MGE) were identified in 43% of studies, with 35 studies confirming that ARGs were inserted on an MGE. Sixteen percent of studies detected ARGs using PCR alone, or in combination with sequencing (43%). Only 8% of studies characterized bacteria by whole-genome sequencing, and one study used a metagenomic approach (Figure 4B).

Most studies detecting ARGs focused on beta-lactamase genes including extended-spectrum beta-lactamasases (ESBL), AmpC-type beta-lactamasases, and carbapenemases, which were identified in all continents but Antarctica (Table 3). Among these beta-lactamasases, ESBL were the most identified genes, evenly distributed across continents, particularly the genotype blaCTX-M. Studies detected blaCTX-M-14 and blaCTX-M-15 in Asia, Europe, North and South America, and Oceania. Likewise, blaCTX-M-55 was reported in all these continents with the exception of South America. Beta-lactamasases blaCMY-2 (AmpC) were reported in Europe, North America, and Oceania, and blaOXA-48 (carbapenemase) were reported in Africa, Europe, North America, and Oceania (Table 3). Of the 15 studies that found AmpC-type beta-lactamases, 7 identified that they were inserted on an MGE, 2 identified them on the bacterial core genome, 2 detected both chromosomal and acquired AmpC, and 4 studies did not identify the location of the AmpC gene. Genes conferring resistance to other antibiotics such as fluoroquinolones, aminoglycosides, sulfonamides along with trimethoprim, polypeptides, tetracyclines, chloramphenicol, macrolides, streptogramins, glycopeptides, fosfomycin, and rifamycin were reported in 59 studies (Table 4). Asia only reported beta-lactam resistance genes.

**Origin of AMR in Gulls**

Only 19% of studies suggested a potential origin for the ARB or ARGs detected among gulls. Landfill (41%), places close to gulls nesting, and/or resting areas with high human density (29%), sewage effluents (29%), and contaminated water (6%) were suspected. Suspicions were based on potential contamination sources around the sampling area. However, only one study (Masarikova et al., 2016) carried out sampling to verify whether the gulls acquired the bacteria from a specific contamination source, comparing bacteria from gulls to bacteria isolated from

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**TABLE 1 | AMR bacteria detected in gulls by continent and gull species between 1981 and 2020.**

| Category       | Description                  | Publications | No. of individuals | % of positive animals |
|----------------|------------------------------|--------------|--------------------|-----------------------|
|                |                              | No. | %    | Positives* | Total |                      |
| Continent      |                              |     |      |            |       |                      |
| Africa         |                              | 1   | 2.4  | 28         | 40    | 70.0                  |
| Europe         |                              | 28  | 68.3 | 919        | 6,375 | 14.4                  |
| North America  |                              | 5   | 12.2 | 50         | 1,310 | 3.8                   |
| Oceania        |                              | 3   | 7.3  | 57         | 1,108 | 5.1                   |
| South America  |                              | 4   | 9.8  | 164        | 832   | 19.7                  |
| Total          |                              | 41  |      | 1,218      | 9,665 |                       |
| Gull species   |                              |     |      |            |       |                      |
| Chroicocephalus novaehollandiae | 2     | 4.9  | 4    | 1,008     | 0.4            |
| Chroicocephalus ridibundus | 2     | 4.9  | 16   | 1,025     | 1.6            |
| Larus argentatus | 4     | 9.8  | 77   | 343       | 22.5          |
| Larus audouini | 1     | 2.4  | 27   | 111       | 24.3          |
| Larus dominicanus | 1    | 2.4  | 10   | 10        | 100.0         |
| Larus hyperboreus | 1     | 2.4  | 2    | 15        | 13.3          |
| Larus michahellis | 6     | 14.6 | 260  | 814       | 31.9          |
| Larus ridibundus | 6     | 14.6 | 161  | 2,718     | 5.9           |
| Leucophaeus pipixcan | 1     | 2.4  | 91   | 124       | 73.4          |
| Larus delawarensis | 1     | 2.4  | 2    | 32        | 6.3           |
| More than one species | 16   | 39.0 | 568  | 3,465     | 16.4          |
| Total          |                              | 41  |      |            |       |                      |
| Bacteria species |                             |     |      |            |       |                      |
| Acinetobacter baumannii | 1     | 2.4  | 2    | 741       | 0.3            |
| Campylobacter spp. | 2     | 4.9  | 26   | 151       | 17.2          |
| Enterobacter cloacae | 1     | 2.4  | 2    | 15        | 13.3          |
| Escherichia coli | 21    | 51.2 | 805  | 3,395     | 23.7          |
| Proteus mirabilis | 2     | 4.9  | 98   | 351       | 27.9          |
| Salmonella enterica | 9     | 22.0 | 130  | 3,327     | 3.9           |
| More than one species | 5     | 12.2 | 155  | 1,685     | 9.2           |
| Total          |                              | 41  |      |            |       |                      |

*Positive individuals represent an individual where at least one resistant bacteria to any antibiotic researched in the study was obtained.
sewage water near their nesting sites. The same AMR phenotypic profiles were obtained in both sample types, and pulsed-field gel electrophoresis (PFGE) detected the same AMR profiles in bacterial clones from wastewater and gulls.

Evidence of Gulls Acting as Reservoirs of ARB or ARGs

Two studies (2%) tagged gulls in both the origin and final movement areas to identify whether they were capable of spreading AMR across the landscape (Palmgren et al., 2006; Ahlstrom et al., 2019a). Ahlstrom et al. (2019a) sampled individual gulls at different periods of time obtaining fecal samples at a landfill and in places where humans and seagulls gathered. Satellite telemetry was used to monitor individuals for up to 3 months, and whole-genome sequencing of bacteria was used to compare *E. coli* isolates between different locations. Their results showed that the prevalence and genetic typing of AMR isolates were highly similar between gulls and a landfill. Palmgren et al. (2006) ringed gulls and sampled 1,047 individuals for up to 3 years. This study failed to detect long-term carriage of antibiotic-resistant *Salmonella* since

![FIGURE 4](image-url)
**TABLE 2**: ARB of the “Global Priority Pathogens” list of the World Health Organization isolated from gulls reported between 1981 and 2020.

| Priority category | Pathogens | Antibiotic resistance | No. of publications | Gull species | References |
|-------------------|-----------|------------------------|---------------------|--------------|------------|
| Critical          | Acinetobacter baumannii | Carbapenem-resistant | 1% (1/90) | C. ridibundus | Łopińska et al., 2020 |
|                   | Pseudomonas aeruginosa | Carbapenem-resistant | 0% (0/90) | – | – |
|                   | Enterobacteriales* | Carbapenem-resistant | 10% (9/90) | L. glaucescens, L. argentatus, L. hyperboreus, C. novaehollandiae, L. michaelli, C. genei | Papagiannitsis et al., 2017; Vergara et al., 2017; Vittecoq et al., 2017; Ahlstrom et al., 2018, 2019a,c; Barguigua et al., 2018; Mukerji et al., 2019; Aires-De-sousa et al., 2020 |
|                   | Enterobacteriales* | Carbapenem-resistant | 1% (1/90) | C. ridibundus | – | – |
|                   | Enterobacteriales* | Third generation cephalosporin-resistant | 41% (37/90) | L. glaucescens, L. argentatus, L. hyperboreus, L. fuscus, L. michaelli, C. novaehollandiae, L. glaucescens, C. ridibundus, L. marinus, L. canus, L. c. c. c. dominicanus, Leucophaeus pipixcan, C. brunnicapillus, L. atricilla | Poeta et al., 2008; Bonnedahl et al., 2009, 2014; Rose et al., 2009; Hernandez et al., 2010; Simões et al., 2010; Veldman et al., 2014; Hernandez et al., 2010; Simões et al., 2010; Veldman et al., 2013; Hasan et al., 2014; Stedt et al., 2015; Alcalá et al., 2016; Aberkane et al., 2016, 2017; Atterby et al., 2016, 2017; Doleska et al., 2016; Liakopoulos et al., 2016; Merkeviciene et al., 2017, 2018; Papagiannitsis et al., 2017; Troxler et al., 2017; Vergara et al., 2017; Ahlstrom et al., 2018, 2019a,b, 2021; Mukerji et al., 2019, 2020; Ngaiganam et al., 2019; Aires-De-sousa et al., 2020; Haenni et al., 2020; Zendri et al., 2020 |
| High              | Enterococcus faecium | Vancomycin-resistant | 3% (3/90) | Chroicocephalus novaehollandiae, L. c. c. | Radhouni et al., 2010; Bonnedahl et al., 2014; Oravcova et al., 2017 |
|                   | Staphylococcus aureus | Methicillin-resistant | 2% (2/90) | L. argentatus | Merkeviciene et al., 2017; Aires-De-sousa et al., 2020 |
|                   | Staphylococcus aureus | Vancomycin-intermediate | 0% (0/90) | – | – |
|                   | Staphylococcus aureus | Vancomycin-resistant | 0% (0/90) | – | – |
|                   | Helicobacter pylori | Clarithromycin-resistant | 0% (0/90) | – | – |
|                   | Campylobacter spp. | Fluoroquinolone-resistant | 6% (5/90) | L. michaelli, L. audouini, C. ridibundus, L. dominicanus, Thalasseus bergii | Merkeviciene et al., 2017; Migura-Garcia et al., 2017; Moré et al., 2017; Troxler et al., 2017; Antilles et al., 2021 |
|                   | Salmonella spp. | Fluoroquinolone-resistant | 8% (7/90) | L. michaelli, L. audouini, L. dominicanus, C. novaehollandiae, C. ridibundus, Leucophaeus pipixcan, Leucophaeus modestus | Fresno et al., 2013; Antilles et al., 2015, 2021; Retamal et al., 2015; Masarkova et al., 2016; Cummins et al., 2020; Tardone et al., 2020 |
|                   | Neisseria gonorrhoeae | Third generation cephalosporin-resistant | 0% (0/90) | – | – |
|                   | Neisseria gonorrhoeae | Fluoroquinolone-resistant | 0% (0/90) | – | – |
| Medium            | Streptococcus pneumoniae | Penicillin-non-susceptible | 0% (0/90) | – | – |
|                   | Haemophilus influenzae | Ampicillin-resistant | 0% (0/90) | – | – |
|                   | Shigella spp. | Fluoroquinolone-resistant | 0% (0/90) | – | – |

*Klebsiella pneumoniae, Escherichia coli, Enterobacter spp., Serratia spp., Proteus spp., Providencia spp., and Morganella spp.

all positive individuals were negative during the sampling 2 months later.

**DISCUSSION**

AMR has been detected in resident and migratory gulls worldwide for more than a decade (Fenlon, 1981; Tsubokura et al., 1995; Smith et al., 2002). However, the role of gulls as reservoirs (i.e., having the capacity to disperse and transmit AMR to other species) remains unknown. Our review identified 90 studies on AMR in wild gulls. AMR has been widely detected across all continents including in 23 of 100 species of gulls (IUCN, 2021), 49 bacteria species with 9 of 13 ARB classified as critical priority for human health (WHO, 2017), ARGs from 13 classes, and 47 antibiotic types. Our results show that, with the exception of China, studies in middle- and low-income countries are rare. Similarly, most studies have focused on a few species of gulls from Europe (e.g., *L. argentatus* and *C. ridibundus*) and most on *E. coli* and *Salmonella spp.* Despite ARB and ARGs being widely detected in gulls, our analyses showed that the origin of these AMR remains unknown in 81% of studies, and only two studies followed gulls across time (for up to 3 years), but none has been able to prove that gulls were reservoirs...
TABLE 3 | Beta-lactamases genes identified in isolates from gulls reported between 1981 and 2020.

| Continent | AmpC | CP | ESBL | Others\(^a\) | References |
|-----------|------|----|------|------------|------------|
| Africa    | NR   | NR | NR   | NR         | Barguglia et al., 2019 |
| Antarctica| NR   | NR | NR   | NR         | Hasan et al., 2014 |
| Asia      | NR   | NR | NR   | NR         | -           |
| Europe    | _blaCMV-2_, _blaCMY-2_, _blaCMY-41_, _blaCMY-5_, _blaCMY-61_, _blaCMY-65_, _blaCMY-69_, _blaCMY-71_ | _blaACT-23_ | _blaCTX-M-14_, _blaCTX-M-15_, _blaCTX-M-55_, _blaCTX-M-79_ | - | Čížek et al., 2007; Dolejska et al., 2007; Poeta et al., 2009; Bonnedahl et al., 2009, 2010; Dolejska et al., 2010; Radhouani et al., 2009; Hernandez et al., 2010; Literak et al., 2010, 2014; Simões et al., 2010; Wallensten et al., 2011; Veldman et al., 2013; Veenendaal et al., 2014; Aberg et al., 2015, 2016, 2017; Antiles et al., 2019; Steed et al., 2015; Varela et al., 2015; Carroll et al., 2015; Masariyova et al., 2016; Alcalá et al., 2016; Atterby et al., 2017; Mekerviceni et al., 2017, 2018; Vergara et al., 2017; Vita et al., 2017 |
| North America | _blaBGC_, _blaCMY-2_, _blaCMY-61_, _blaCMY-65_, _blaCMY-69_, _blaCMY-71_ | _blaCMY-65_, _blaCMY-69_, _blaCMY-71_ | _blaCTX-M-14_, _blaCTX-M-15_, _blaCTX-M-27_, _blaCTX-M-32_, _blaCTX-M-55_, _blaCTX-M-65_, _blaCTX-M-8_, _blaTEM-14_, _blaTEM-52_, _blaTEM-52_, _blaACT-14_, _blaACT-18_, _blaACT-23_ | - | Aroy and Ellis, 2011; Martiny et al., 2011; Bonnedahl et al., 2014, 2015; Atterby et al., 2016; Ahlstrom et al., 2018, 2019a,b, 2021; Gomez-Álvarez et al., 2019 |
| Oceania   | _blaCMY-2_, _blaCMY-61_, _blaCMY-65_, _blaCMY-69_, _blaCMY-71_ | _blaCMY-65_, _blaCMY-69_, _blaCMY-71_ | _blaCTX-M-14_, _blaCTX-M-15_, _blaCTX-M-27_, _blaCTX-M-32_, _blaCTX-M-55_, _blaCTX-M-65_, _blaCTX-M-8_, _blaTEM-14_, _blaTEM-52_, _blaTEM-52_, _blaACT-14_, _blaACT-18_, _blaACT-23_ | - | Dolejska et al., 2019; Papagiannitsis et al., 2017; Mekerji et al., 2019, 2020; Cummins et al., 2020 |
| South America | NR | NR | NR | NR | Hernandez et al., 2013; Blàtz et al., 2015; Liakopoulos et al., 2016 |

\(^a\)Corresponds to beta-lactamases that are not classified as ESBL, AmpC, or CP.

(Palmgren et al., 2006; Ahlstrom et al., 2019a). Therefore, our review highlights the need for increased surveillance of AMR in gulls and design innovative studies aiming to assess their role as reservoirs, which can have major implications for public and conservation measures to limit the global spread of AMR in aquatic systems.

The detection of AMR in gulls across all continents, including critically important antibiotic-resistant pathogens such as ESBL and carbapenemase-producing *E. coli* and *S. enterica*, illustrates the potential of gulls to participate in the alarming global spread of AMR (Dolejska et al., 2016; Ahlstrom et al., 2019c; Aires-De-sousa et al., 2020; Cummins et al., 2020). The migratory capacity of gulls makes them an ideal host to spread ARB and ARGs across landscapes and ecosystems. For example, Ahlstrom et al. (2021) reported that gulls of the *Larus* genus, including *L. argentatus*, can migrate 3,000 km over a week, *L. fuscus* can migrate from Europe to Africa (Kilpi and Saurola, 1984), while *Leucophaeus pipixcan* migrates from North to South America (Hernandez et al., 2013; Barbieri et al., 2016). In contrast, other gull species such as *L. dominicanus* are resident but also carry ESBL-resistant *E. coli* with ARGs genes such as _blaCTX-M_ and _blaSHV_ and aminoglycoside-resistant *Salmonella enteritidis* with _str_ genes (Liakopoulos et al., 2016; Toro et al., 2016). Although these species might not necessarily contribute to the long-range dispersal of AMR, they could participate in local transmission to other species and humans (Vigo et al., 2011; Retamal et al., 2015; Toro et al., 2016). Overall, this review highlights that gulls are at least sentinels of ARB and ARGs spreading in the environment, calling for future research in species and countries where AMR has not yet been studied. In particular, environmental and animal health national and international authorities should consider gulls in the surveillance of AMR within the environment.

Although AMR is widely spread among gulls, there are almost no data on the origin of the observed ARB and ARGs. In fact, less than 20% of studies included in this review mentioned potential sources of AMR contamination. Given that AMR has exponentially increased with antibiotic use in humans and livestock and several gull species feed on human and agricultural waste, most studies suspect a human origin including landfills, places close to gulls nesting, and/or resting areas that have a high human density, sewage effluents, and contaminated water (Bonne Dahl et al., 2014; Atterby et al., 2016; Mekerji et al., 2019; Ahlstrom et al., 2021). This is consistent with the overall assumption that wildlife becomes contaminated with AMR from anthropogenic sources in studies suggesting transmission in areas where wildlife lives and feeds (Dolejska and Literak, 2019). However, no study has fully proven the origin of AMR in gulls, and other environmental factors such as co-selection with heavy metals and microplastics can also generate AMR.
| Continent | FQ | POLY | TET | AMG | CHL | SUL | TMP | MAC | STR | GLY | FOS | RIF | References |
|-----------|----|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----------|
| Africa    |     |      |     |     |     |     |     |     |     |     |     |     | Barguigia et al., 2019 |
| Antarctica|     |      |     |     |     |     |     |     |     |     |     |     | – |
| Asia      |     |      |     |     |     |     |     |     |     |     |     |     | – |
| Europe    |     |      |     |     |     |     |     |     |     |     |     |     | Čížek et al., 2007; Dolejska et al., 2007; Gionechetti et al., 2008; Poeta et al., 2008; Dolejska et al., 2009; Radhouani et al., 2009, 2010, 2011; Bonnedahl et al., 2009, 2010; Hernandez et al., 2010; Literak et al., 2010, 2014; Simões et al., 2010; Wallensten et al., 2011; Veldman et al., 2013; Vredenburg et al., 2014; Aberkan et al., 2015, 2016; Carroll et al., 2015; Aberkan et al., 2017; Stedt et al., 2015; Varela et al., 2015; Antilles et al., 2015; Masarikova et al., 2016; Ruzauskas and Vaskevicute, 2016; Alcâá et al., 2016; Merkevičiene et al., 2017, 2018; Vergara et al., 2017; Vittecoq et al., 2017; Atterby et al., 2017; Ngaigamam et al., 2019; Ahlstrom et al., 2019b; Haenri et al., 2020; Logórska et al., 2020; Zendri et al., 2020; Aires-De-Sousa et al., 2020; Airoy and Ellis, 2011; Marthy et al., 2011; Bonnedahl et al., 2014, 2015; Atterby et al., 2016; Ahlstrom et al., 2018, 2019a,c, 2021; Gomez-Alvarez et al., 2019 |
| North America |     |      |     |     |     |     |     |     |     |     |     |     | |
| Oceania   |     |      |     |     |     |     |     |     |     |     |     |     | |
| South America |     |      |     |     |     |     |     |     |     |     |     |     | |

FQ, fluoroquinolones; POLY, polypeptides; TET, tetracyclines; AMG, aminoglycosides; CHL, chloramphenicol; SUL, sulfonamides; TMP, trimethoprim; MAC, macrolides; STR, streptogramins; GLY, glycopeptides; FOS, fosfomycin; RIF, rifamycin; NR, not reported.
could be explained by the relatively easier collection of fecal samples compared to capturing and sampling gulls to detect other pathogens (e.g., blood bacteria). Thus, the absence of other global-priority ARB in current studies such as *Pseudomonas aeruginosa* carbapenem-resistant (critical priority), *Staphylococcus aureus* vancomycin-intermediate or -resistant (high priority), and *Shigella* spp. fluoroquinolone-resistant (medium priority) could reflect a lack of research and not necessarily that these bacteria are not circulating among gulls. In fact, one study using a metagenomic approach found 31 previously undescribed ARGs, while another detected more than 70 bacterial species and 24 ARGs (Martiny et al., 2011; Merkeviciene et al., 2017). This review identified a high diversity of ARGs including those implicated in bacterial infections of humans and animals such as ESBL and carbapenemases (Bevan et al., 2017; Li et al., 2019). The presence of ARGs inserted in MGE could facilitate the spread of these resistance genes within gulls and between humans and other animals (Loayza et al., 2020). Our review also shows a wide diversity of bacterial clones and ARGs found in gulls. Whole-genome sequencing for bacterial typing was used in 13% of studies since 2011. Thus, the more widespread use of this technique in the following years could increase the detection of ARB clones and ARGs in gulls.

Our review showed that North America and Europe had the most diverse molecular diversity among ARB, which could be associated with more available molecular typing techniques compared to low-income countries. For example, ESBL- *E. coli* ST131, previously associated with nosocomial infections in humans, has been identified in gulls mainly from the United States (Bonnedahl et al., 2014; Ahlstrom et al., 2018, 2019a, 2021) and Portugal (Simões et al., 2010; Vredenburg et al., 2014; Varela et al., 2015). Despite fewer information available, ST131 has also been reported in gulls from low- and middle-income countries (LMICs) such as Bangladesh (Hasan et al., 2014). Future research should also evaluate the pathogenic potential of the detected ARB using whole-genome sequencing to detect virulence factors and other pathogenic genetic material (e.g., biofilms).

**CONCLUSION AND FUTURE DIRECTIONS**

Our review identified an increasing interest in ARB and ARGs among gulls in the last decade, although there is a considerable lack of information in LMICs, particularly regarding migratory species. Despite the widespread detection and high diversity of ARB and ARGs worldwide, there is no evidence that gulls act as reservoirs of ARB and ARGs. Furthermore, most of the studies could not demonstrate whether ARB and ARGs in gulls came from anthropogenic sources. Finally, we could not compare ARB or ARGs prevalence across studies due to their heterogeneity in the results and methodologies to assess AMR.

Knowledge gaps identified in this review can be overcome by future research. First, the use of whole-genome sequencing
combined with sampling across different species could help assessing cross-species transmission between gulls and humans, domestic animals, or other wild species that do not usually interact with humans but share nesting sites with gulls (e.g., penguins). Secondly, future research should identify if environmental factors such as plastic and heavy metal pollution are also selecting ARB and ARGs in gulls independently of contact with humans. Thirdly, the clinical relevance and conservation implications of the detected ARB for gull’s health require further investigation. In particular, there is no evidence that the observed bacteria cause any pathogenicity to the studied gulls nor complicate treatment of gulls with antibiotics in rehabilitation centers. Finally, innovative techniques such as satellite tracking and collaborations across research teams in different countries where gulls migrate (e.g., Canada to Chile for the Franklin’s gulls) could help elucidate whether gulls are spreading ARB and/or ARGs across countries and continents during their migration.

AUTHOR CONTRIBUTIONS

JB and DZ-G: conceptualization. DZ-G: data curation. JB, DZ-G, ZR-S, and MS-C: formal analysis, investigation, and methodology. JB: funding acquisition, project administration, resources, software, supervision, validation, and visualization. DZ-G: conceptualization. DZ-G: data curation. JB, ZR-S, MS-C, CT, and PP: writing—original draft and writing—review and editing. All authors have read and agreed to the published version of the manuscript.

FUNDING

This work was funded by the National Agency for Research and Development (ANID) FONDECYT Iniciación 11181017, awarded to JB, the National Agency for Research and Development (ANID) Beca Doctorado Nacional No. 21201076, awarded by ZR-S, the Concurso de Apoyo a la Realización de Actividades de Investigación en Etapa de Pregrado (APP 2019-2) UNAB, awarded to DZ-G, and the ANID Millennium Science Initiative/Millennium Initiative for Collaborative Research on Bacterial Resistance, MICROB-R, NCN17_081.

ACKNOWLEDGMENTS

We thank members of The Monkey Lab (@themonkey_lab) for the useful comments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2021.703886/full#supplementary-material

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SUPPLEMENTARY MATERIAL

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