



Widespread antibiotic-resistant *Salmonella* in reptiles and amphibians at a global exotic pet trade hub: An emerging zoonotic threat

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ABSTRACT

Along with the rise in exotic pet ownership, the prevalence of reptile- and amphibian-associated Salmonellosis (RAAS) has increased globally. Given that a high proportion of associated strains were antimicrobial-resistant, transmission of *Salmonella* from these animals may enhance disease burden and facilitate transmission of antibiotic resistance genes (ARGs) to other critical pathogens. However, data on *Salmonella* carriage rates and associated pathogenic risks in these animals remain scarce. This study investigates the prevalence and antibiotic resistance profiles of *Salmonella* in pet reptiles and amphibians in a major hub for the exotic pet trade. Among over 160 samples from 47 reptile and six amphibian species, 54.9% shed viable *Salmonella*, with comparable rates between reptiles (55.6%) and amphibians (50.0%). Alarming, 93.3% of positive samples contained antibiotic-resistant *Salmonella*, including 1.47% multidrug-resistant (MDR) strains, predominantly from the same Cranwell's horned frog. Resistance was the highest to streptomycin (58.7%), followed by colistin (6.1%), and ampicillin (5.9%), raising critical public health concerns. This study provides evidence on MDR *Salmonella* in pet reptiles and amphibians, highlighting the underestimated zoonotic threats and public health risks posed by these animals in the global exotic pet trade. We advocate enhanced surveillance of resistant *Salmonella* in imported reptiles and amphibians and urge the enforcement of stricter regulations to mitigate pathogen transmission risks.

1. Introduction

Salmonellosis (i.e., *Salmonella* spp. infection) has been a global health problem, accounting for over 93.8 million cases annually worldwide [1]. While most salmonellosis cases originate from food-borne infections, a growing number of zoonotic cases have been documented in the last two decades, with a majority associated with pet reptiles, especially turtles, lizards and snakes [2], and some with amphibians, e.g. salamanders and frogs [3–5]. Along with the increasing popularity of exotic pets, the prevalence of reptile- and amphibian-associated salmonellosis (RAAS) has risen globally [2,4,6], with infants and young children being the most affected [7]. To this date, RAAS have been reported in multiple countries on all continents except Antarctica, including Germany, the UK, Australia, the Netherlands, and Japan [7], causing outbreaks since 2009 [5,8,9]. Importantly, clinical outcomes of RAAS can be more severe than food-borne cases [4], such that hospitalisation rates associated with these infections can be 2.5 times higher [5,10].

A wide range of commercially traded reptile and amphibian species can carry *Salmonella*, with diverse prevalence and outcomes [2]. While detection rates vary geographically and seasonally [11–13] and depend on the technique employed [7], carriage rates of higher than 80% have been documented in pet reptiles, e.g. lizards, turtles, and tortoises [14,15]. Certain risk factors are associated with *Salmonella* carriage in these animals, for example, captivity (as opposed to living in the wild) [16–18], a human-prepared diet [19,20], and a high density of conspecifics within the habitat [21]. Meanwhile, information regarding *Salmonella* prevalence and pathology among pet amphibians has been limited [22,23]. Importantly, most *Salmonella*-carrying reptiles or amphibians were subclinical carriers [22], with rare occurrences of complications, including dermatitis, osteomyelitis, and septicemia observed in infected reptiles [7,24]. Despite this, both subclinical and symptomatic animals can shed *Salmonella* [17], making it challenging for pet handlers and keepers to avoid transmission. Notably, certain serovars of public health concern have been identified in captive reptiles and amphibians, including *Salmonella enterica* ser. Typhimurium, Newport and

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Kentucky [25,26], highlighting the potential risks of salmonellosis associated with these animals.

In addition to pathogenic serotypes, antimicrobial resistant (AMR) *Salmonella* strains from reptiles and amphibians also pose critical public health concerns. Importantly, AMR and multidrug-resistant (MDR) *Salmonella* have become increasingly prevalent since the last decade [27], making treatment of salmonellosis an unprecedented challenge. In 2017, *Salmonella* was listed as one of the WHO priority organisms for antibiotic resistance surveillance, to address the increased threats, morbidity and mortality associated with resistant strains [28]. In particular, high percentages of resistant *Salmonella* have also been reported globally in captive reptiles and amphibians, especially to streptomycin, ciprofloxacin, and colistin [15,29,30], which could be a result of prevalent antibiotic use in aquaculture, the pet industry, and veterinary medicine [31,32]. For instance, the prevalence of MDR *Salmonella* isolates exceeded 64% in pet reptiles in Poland, Spain, and mainland China [12,13,15,20]. On the other hand, apart from edible frogs [29], the prevalence and pathogenicity of AMR *Salmonella* carried by captive amphibians have rarely been explored. Given the heightened severity associated with AMR salmonellosis and the transmission of mobile Antibiotic Resistance Genes (ARGs) to other pathogenic bacterial species [33], investigating the prevalence and sources of AMR *Salmonella* carried by pet reptiles and amphibians is essential.

Notably, the detection and characterisation of *Salmonella* spp. in pet reptiles and amphibians are critical in countries or regions with large populations of exotic pets. For instance, as a major trade hub and importer of exotic pets in the global market, Hong Kong has a high human-to-exotic-animal density, which poses risks in terms of zoonotic transmission associated with these animals [34]. Among nearly six million imported exotic animals (excluding cats and dogs) per year, approximately 0.17 million were pet reptiles and 4.7 million were frogs of unspecified use [34]. According to publicly available data on exotic pet ownership in 2005, approximately one in five pet-owning households kept a turtle or tortoise [34]. Given the surge in imported exotic pets in recent years, it is believed that the current local population of reptiles and amphibians is larger than past estimates [34]. Despite the associated zoonotic risks, data on the carriage rate and pathogenic risks of *Salmonella* in these animals in Hong Kong are lacking. Given that over 75% of *Salmonella* isolates obtained from clinical samples in Hong Kong each year are AMR [35], investigating the resistance profiles of pet-associated *Salmonella* is essential to understand the transmission and sources of resistant *Salmonella* within the local community. Aside from the regional level, given that most exotic animals in Hong Kong are imported from international sources [34], the detection and characterisation of *Salmonella* spp. in these captive animals can shed light on the associated risks carried by traded animals in the global pet market.

In this study, we investigated the prevalence and antibiotic resistance profiles of *Salmonella* in live reptiles and amphibians in the exotic pet market of Hong Kong, primarily aiming to identify MDR strains. Based on the high prevalence of AMR *Salmonella* in exotic pet animals in nearby regions, e.g. Beijing, Chongqing Province, and Taiwan [12,13,36], and some of the exporter countries, including the US and Indonesia [5,34,37], reported in previous studies, we hypothesise a high discovery rate of these isolates in Hong Kong. We tested the resistance of isolated *Salmonella* to eight antibiotics of diverse classes. These drugs were selected based on their importance to public health, as indicated by the WHO List of Medically Important Antimicrobials [38], and the prevalence of resistance in pet-associated *Salmonella* in other regions, as indicated by previous studies [39–44]. In addition, we hypothesise that host species, source of origin, life stage, and/or cohabitation condition are risk factors of AMR *Salmonella* carriage. Through this study, we aim to expand our understanding of public health risks and risk factors associated with *Salmonella* carried by captive reptiles and amphibians.

2. Materials and methods

2.1. Sample collection

Stool samples ($N = 162$) were collected from 47 reptile and six amphibian species from a commercial breeding/retailing facility in Hong Kong in June 2020 (Table S1). Three samples were collected from each species, except for Chahoua Gecko (*Rhacodactylus chahoua*), from which six samples were collected (three from each source of origin, respectively; Table S1). Sampled animals were housed individually or cohabited with conspecifics in the same cage or aquarium. For animals that were singly housed or in pairs, samples were collected independently from each individual. For animals housed in groups of three or more, since samples were collected from their captivity, the same individual may be sampled multiple times.

Information, including the species identity, source (wild-caught or captive-bred), cohabitation conditions (number of co-existing conspecifics), life stages (juvenile, sub-adult, or adult) and countries of origin of sampled animals, was collected during sample collection and supplemented with information provided by the pet shop owner [45,46]. All individuals of the same species shared the same living conditions, source, origin, and life stage, except for the Chahoua geckos (*Rhacodactylus chahoua*), as mentioned previously. None of the sampled individuals exhibited observable symptoms. Samples were kept on ice immediately after collection. Within two hours, 5 mL of tryptic soy broth (TSB; Soybean-Casein Digest Medium; BD, New Jersey, U.S.) was added to 10–500 mg of each sample. Samples were then incubated at 35 °C overnight. Cultured solutions were added with 25% glycerol and stored at –80 °C for subsequent steps.

2.2. *Salmonella* isolation

First, gram-negative bacteria were selectively cultured from the stored, cultured solutions of each sample ($N = 162$) using the Modified Semi-solid Rappaport Vassiliadis (MSRV) medium base (Biorad, California, U.S.) with 2% novobiocin (Thermo Fisher Scientific, Massachusetts, U.S.) at a final concentration of 1 mL/L. Cultured solutions were transferred to the media surface at three evenly distributed spots, with 50 µL at each position, as described by a previous study by Rodriguez et al. [40]. Inoculated plates were incubated at 42 °C for 24 h. Subsequently, each inoculated spot on an MSRV medium agar plate with observable microbial growth was streaked onto a Hektoen enteric (HE) agar plate (Biorad) using an inoculation loop. HE plates were incubated at 35 °C for 24 h to select for *Salmonella*. From each positive plate, two typical *Salmonella* colonies, i.e., colonies with transparent exterior and a black centre, were picked and considered presumptive *Salmonella* isolates. These isolates were then inoculated into cation-adjusted Mueller-Hinton broth (MHB; DIFCO Mueller-Hinton Broth, BD). Inoculated broths were incubated at 35 °C for 14 h. Assuming growth at each inoculation step, six isolates should have been obtained from each positive sample. Cultured solutions were added with 25% glycerol and stored at –80 °C for subsequent steps. To validate the purity of *Salmonella* spp., stored cultures of a subset of isolates originating from colonies in close proximity to other colonies on the original HE plate, and thus with a higher potential to produce a mixed culture ($n = 23$), were re-inoculated onto a second HE plate. Plates with colonies of diverse appearances indicated mixing of species and/or strains. These cultures ($n = 8$) were discarded. Eventually, a total of 495 isolates were obtained.

2.3. *Salmonella* verification

Salmonella identity of all isolates was verified by *Salmonella*-specific PCR. The *invA* gene was amplified using previously published primer pairs 139/141 or Salm3/Salm4 according to protocols documented in literatures [47,48]. *Salmonella* identity was verified by a clear band at the expected size in either reaction (Supplementary materials and

methods). On top of that, one isolate was randomly selected from each host species ($N = 53$) to be tested using antigenic agglutination tests for double confirmation of *Salmonella* identity. Agglutination tests were performed by ENVIRO LABS LTD (Hong Kong), using polyvalent antisera against O (A to S), Vi and H (H1 and H2) antigens.

2.4. Antibiotic susceptibility testing (AST)

Antibiotic susceptibility of all verified *Salmonella* isolates ($N = 477$) was tested by disk diffusion or the broth microdilution method, following guidelines from the Clinical & Laboratory Standards Institute (CLSI) for most antibiotics, and the European Committee on Antimicrobial Susceptibility Testing (EUCAST) for tigecycline only. As mentioned, eight antibiotics were chosen based on literature and the WHO List of Medically Important Antimicrobials while maximising the diversity of tested antibiotic classes [38]. For instance, antimicrobial agents with high resistance rates detected in animal-associated *Salmonella* according to previous studies [39–44], and those that were classified as critically important to human medicine by WHO [28], were prioritised. The antimicrobial agents chosen were: streptomycin and gentamycin (class aminoglycosides), tigecycline and tetracycline (class tetracyclines), colistin (class polymyxins), ampicillin (class penicillins), trimethoprim-sulphamethoxazole (class sulfonamides), and ciprofloxacin (class quinolones).

To prepare for both tests, a loopful of glycerol stock of each cultured *Salmonella* isolates was inoculated in Mueller-Hinton broth and incubated for two hours. Cell density was then measured using the NanoDrop One Microvolume UV–Vis Spectrophotometer (Thermo Fisher Scientific). Cultures were diluted to a turbidity equivalent to that of a 0.5 McFarland standard with sterile phosphate-buffered saline (PBS). For disk diffusion tests, Mueller-Hinton agar (MHA; Thermo Fisher Scientific) plates were inoculated with diluted cultures using sterile cotton swabs. Inoculated plates were then allowed to dry for five to fifteen minutes inside a Class II biological safety cabinet (BSC). Antibiotic disks (Thermo Fisher Scientific) were applied to inoculated agar plates, which were then incubated at 35 °C for 16–18 h. Antibiotic disks include streptomycin (STR, 10 µg), gentamycin (GEN, 10 µg), tigecycline (TIG, 15 µg), tetracycline (TET, 30 µg), ampicillin (AMP, 10 µg), trimethoprim-sulfamethoxazole (SXT, 1:19, 25 mg), and ciprofloxacin (CIP, 5 µg). Zone diameters were measured and interpreted according to CLSI guidelines for most drugs, and EUCAST indications for tigecycline only [49,50]. Disc diffusion tests suspected of contamination, as indicated by colonies within the clear zone(s) or multiple clear zone edges surrounding a disc (i.e., formed by lawns of bacteria with different MIC values within the mixed culture), were repeated until no signs of contamination were detected. At the same time, broth microdilution tests were conducted to determine susceptibility to colistin. Colistin stock solution (4 µg/mL) was first prepared by dissolving colistin sulphate salt (Cat #C4461, Sigma-Aldrich, Minnesota, U.S.) in UltraPure DNase/RNasefree distilled water (Thermo Fisher Scientific), and sterilised using syringe filters [0.22 µm; Millex-GP Filter Unit (Sterile), Merck KGaA, Darmstadt, Germany]. Serial dilutions of the stock solution were prepared in sterile MHB to final concentrations of 4, 2, and 1 µg/mL. For the minimum inhibitory concentration (MIC) assay, 1 µL of prepared *Salmonella* culture solutions was added to 199 µL of each colistin dilution. A positive and negative control was included in each test, with cultured isolate solution or sterile water added to MHB without any antibiotics, respectively. Each isolate was tested in duplicate. Inoculated solutions were incubated at 35 °C for 16–20 h. MICs of each isolate were determined according to the guidelines of CLSI. Tested isolates were classified as non-resistant (NR; “susceptible” or “intermediate” isolates according to CLSI and/or EUCAST guidelines) or resistant (R). Indications of contamination, including inconsistent colistin resistance levels between duplicate measurements and growth in negative control reactions, were recorded, and MIC assays were repeated until no signs of contamination were detected.

2.5. Statistical analysis

2.5.1. *Salmonella* prevalence and host factors

Regression models were constructed to investigate the influence of host-dependent factors on the presence/absence of *Salmonella* spp. in each sample/individual. Because host species identity was highly collinear with the other factors, we constructed two models with 1. host species identity and 2. Species-associated factors, i.e., class (reptile or amphibian), taxonomic categories (geckos, snakes, other lizards, tortoises, and frogs/toads), source (wild-caught or captive bred), number of co-habiting conspecifics, life stages, and country/region of origin), as the explanatory variable(s) respectively. Regarding the former model, a Firth's Penalised Likelihood Model was used to reduce bias caused by data separation, a common problem linked to binomial models [51]. ANOVA was then used to evaluate the overall effects of host species.

Subsequently, a binomial generalized linear model (GLM) was used to analyse the effects of species-associated factors. Since only one toad species (*Bufo raddei*) was sampled, toads and frogs were grouped for better model fit. Based on the variance inflation factors (VIF), the country/region of origin was highly collinear with the other variables and was therefore removed. Host class and taxonomic category were used interchangeably considering their nested nature. Model averaging was conducted on a set of models that were within seven AIC units of the top-ranked model ($\Delta\text{AICc} < 7$), to increase model reliability.

For all models, P -values were corrected using the Benjamini-Hochberg (BH) false discovery rate correction for multiple testing. All statistical analyses were conducted using R 4.4.1 [52]. Firth's Penalised Likelihood Model was constructed using *logistf* 1.26.1 [53]. GLM was conducted using *glmmTMB* v1.1.11 [54]. VIFs were calculated using *olsrr* v0.6.0 [55]. Model averaging was performed using *DHARMA* v0.4.6 [56]. Model quality was evaluated using the ‘simulateResiduals’ function of *MuMin* v1.48.4 [57].

2.5.2. Antibiotic resistance profiles and host factors

Binomial GLMs were used to test the influence of host-dependent factors on antibiotic resistance patterns. We constructed models to analyse the significance of host-dependent factors in predicting: 1. resistance to two or more classes of antibiotics; 2. resistance to any antibiotics; and 3. resistance to streptomycin, ampicillin, or colistin in isolates from each sample. P -values were corrected using the BH false discovery rate correction.

In addition, the contributions of host-associated factors in explaining antimicrobial resistance profiles were examined using distance-based redundancy analysis (db-RDA). Resistance profiles of isolates were used to calculate a pairwise distance matrix between samples with the Jaccard dissimilarity metric. To facilitate distance calculation, isolates without resistance to any of the tested antibiotics were removed.

In view of observable variability in antimicrobial resistance patterns among isolates from the same sample (Fig. S1), we also constructed a model using individual/sample ID as the only explanatory variable to assess the significance of host identity in explaining the variation in resistance patterns. The host species was used as the conditioning variable to condition for the variance contributed by the host species and other confounding factors.

Db-RDA models were constructed with *vegan* v2.6–6.1 [58]. The significance of models and each explanatory term was assessed using ANOVA with 999 permutations.

3. Results

3.1. *Salmonella* prevalence and associations with host factors

Out of 162 samples, 54.94% (89/162) tested positive for *Salmonella* (Table 1). Positive samples were obtained from 42 out of 47 reptile species and five out of six amphibian species. The prevalence of *Salmonella* was not significantly different between host species ($P = 0.43$,

Table 1
Salmonella prevalence of sampled species.

Class	Common name	Species Name	No. of positive samples	No. of samples	Prevalence (%)	CI (%) ^a
Reptiles			80	144	55.56	48.45–65.31
Lizards (exc. Geckos)			25	45	55.56	42.12–71.03
	Peninsular Horned Tree Lizard	<i>Acanthosaura armata</i>	3	3	100.00	
	Maned forest lizard	<i>Bronchocela jubata</i>	3	3	100.00	
	Central bearded dragon	<i>Pogona vitticeps</i>	3	3	100.00	
	Argentine black and white tegu	<i>Salvator merianae</i>	3	3	100.00	
	Mongolia racerunner	<i>Eremias argus</i>	2	3	66.67	
	Green iguana	<i>Iguana iguana</i>	2	3	66.67	
	Sandfish skink	<i>Scincus scincus</i>	2	3	66.67	
	Indonesian blue-tongued skink	<i>Tiliqua gigas gigas</i>	2	3	66.67	
	Wedge-snouted skink	<i>Chalcides sepsoides</i>	1	3	33.33	
	Sudan plated lizard	<i>Gerrhosaurus major</i>	1	3	33.33	
	Bell's anglehead lizard	<i>Gonocephalus bellii</i>	1	3	33.33	
	Fire skink	<i>Mochlus fernandi</i>	1	3	33.33	
	Asian Glass Lizard	<i>Ophisaurus gracilis</i>	1	3	33.33	
	Schneider's skink	<i>Eumeces schneideri</i>	0	3	0.00	
	Chameleon forest dragon	<i>Gonioccephalus Chameleontinus</i>	0	3	0.00	
Geckos			23	54	42.59	30.35–56.93
	Chahoua Gecko*	<i>Rhacodactylus chahoua</i>	5 (EUR: 3; HKG: 2)	6	83.33	
	Chinese cave gecko	<i>Goniurosaurus hainanensis</i>	2	3	66.67	
	Lichtenfelder's gecko	<i>Goniurosaurus lichtenfelderi</i>	2	3	66.67	
	Chinese leopard gecko	<i>Goniurosaurus lui</i>	2	3	66.67	
	Rough bent-toed gecko	<i>Gymnodactylus Scaber</i>	2	3	66.67	
	White-spotted wall gecko	<i>Tarentola annularis</i>	2	3	66.67	
	Cat gecko	<i>Aeluroscalabotes felinus</i>	1	3	33.33	
	Tokay gecko	<i>Gekko gecko</i>	1	3	33.33	
	Madagascar giant day gecko	<i>Phelsuma grandis</i>	1	3	33.33	
	Madagascar day geckos	<i>Phelsuma madagascariensis</i>	1	3	33.33	
	New Caledonian giant gecko	<i>Rhacodactylus leachianus</i>	1	3	33.33	
	Dune gecko	<i>Stenodactylus petrii</i>	1	3	33.33	
	Golden spiny-tailed gecko	<i>Strophurus taenicauda</i>	1	3	33.33	
	Common wall gecko	<i>Tarentola mauritanica</i>	1	3	33.33	
	Peters' bow-fingered gecko	<i>Cyrtodactylus consobrinus</i>	0	3	0.00	
	Gargoyle gecko	<i>Rhacodactylus auriculatus</i>	0	3	0.00	
	Bishari dwarf gecko	<i>Tropicolotes bisharicus</i>	0	3	0.00	
Snakes			19	24	79.17	60.11–93.82
	California kingsnake	<i>Lampropeltis getula californiae</i>	3	3	100.00	
	Honduran milk snake	<i>Lampropeltis triangulum hondurensis</i>	3	3	100.00	
	Western rat snake	<i>Pantherophis obsoletus</i>	3	3	100.00	
	Bullsnake	<i>Pituophis catenifer sayi</i>	3	3	100.00	
	Western hognose snake	<i>Heterodon nasicus</i>	2	3	66.67	
	Brown House Snake	<i>Lamprophis fuliginosus</i>	2	3	66.67	
	Corn snake	<i>Pantherophis guttatus</i>	2	3	66.67	
	Ribbon snake	<i>Thamnophis sauritus</i>	1	3	33.33	
Tortoises			13	21	61.91	41.77–81.57
	Leopard tortoise	<i>Stigmochelys pardalis</i>	3	3	100.00	
	Red-footed tortoise	<i>Chelonoidis carbonaria</i>	2	3	66.67	
	Aldabra giant tortoise	<i>Geochelone gigantea</i>	2	3	66.67	
	Hermann's tortoise	<i>Testudo hermanni</i>	2	3	66.67	
	Marginated tortoise	<i>Testudo Marginata</i>	2	3	66.67	
	African spurred tortoise	<i>Geochelone sulcata</i>	1	3	33.33	
	Russian tortoise	<i>Testudo horsfieldii</i>	1	3	33.33	
Amphibians			9	18	50.00	29.68–72.92
Frogs			8	15	53.33	30.79–77.28
	Surinam horned frog	<i>Ceratophrys cornuta</i>	3	3	100.00	
	Long-nosed horned frog	<i>Megophrys nasuta</i>	3	3	100.00	
	Australian green tree frog	<i>Litoria caerulea</i>	1	3	33.33	
	Cranwell's horned frog	<i>Ceratophrys cranwelli</i>	1	3	33.33	
	White-lipped tree frog	<i>Litoria infrafrenata</i>	0	3	0.00	
Toads			1	3	33.33	4.65–81.72
	The Mongolian toad	<i>Bufo raddei</i>	1	3	33.33	
Total			89	162	54.94	48.28–64.26

^a Confidence intervals (CI) were calculated based on Reiczigel's method, assuming a 98.4% positive detection rate of *Salmonella* using HE agar [59,60].

* This species had two country/region of origins.

Firth's Penalised Likelihood Model), nor between reptiles (55.57%; 80/144) and amphibians (50.00%; 9/18; Table S3). Among host species categories, snakes (Order Squamata, Suborder Serpentes) had the highest *Salmonella* prevalence of 79.17% (19/24), followed by tortoises (Order Testudines, Family Testudinidae; 1.91%, 13/21), lizards excluding geckos (Order Squamata, Families Agamidae, Anguidae, Gerrhosauridae, Iguanidae, Lacertidae, Scincidae, and Teiidae; 55.56%, 25/45), frogs (Order Anura, Families Ceratophryidae, Hylidae and

Megophryidae; 53.33%, 8/15), geckos (Order Squamata, Infraorder Gekkota, Families Diplodactylidae, Eublepharidae, Gekkonidae, and Phyllodactylidae; 42.59, 23/54), and lastly, toads (Order Anura, Family Bufonidae; 33.33%, 1/3; Fig. 1A; Table 1). Host category was not significantly associated with *Salmonella* carriage after correction for multiple testing (Table S2).

While *Salmonella* prevalence rate was higher in captive-bred than wild-caught individuals (Fig. 1B), such a difference was not statistically

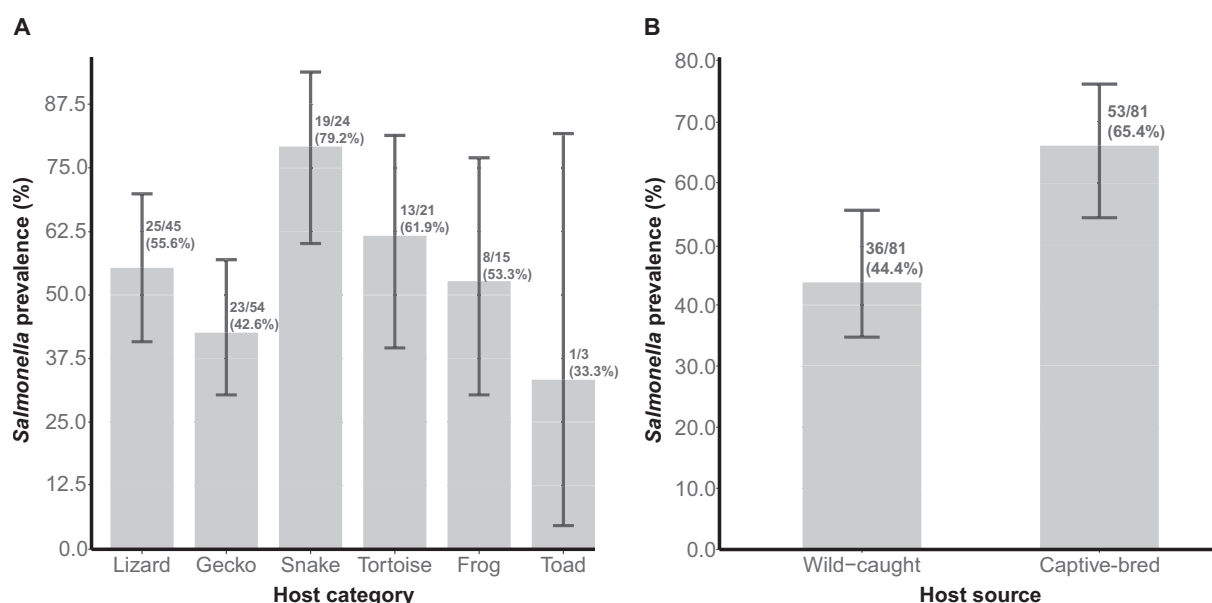


Fig. 1. Barplots showing prevalences (%) of *Salmonella*-positive samples in each (A) host species category and (B) source. Error bars represent confidence intervals (CI), which were calculated based on Reitzel's method, assuming a 98.4% positive detection rate of *Salmonella* using HE agar [59,60]. None of host category or source was significantly associated with *Salmonella* carriage according to generalized linear models.

significant after correction for multiple testing (Wild-caught: $\beta \pm \text{adj. SE} = -0.89 \pm 0.40$, $P = 0.10$). Similarly, no significant association was found between prevalence and host class or any host-dependent factors after P -value adjustment (Table S2).

3.2. AMR in *Salmonella* isolates

Of the 89 positive samples, 477 viable *Salmonella* isolates were obtained, with a maximum of six and 18 isolates from each sample and host species, respectively. Regarding antimicrobial resistance, resistant isolates could be cultured from 83 of 89 samples (Table S3). Among 477 isolates, 61.45% ($n = 293$) were resistant to at least one antibiotic (Table S4). Specifically, 63.38% of isolates from reptiles and 60.78% of isolates from amphibians were AMR. Among tested antimicrobial agents, streptomycin resistance was the most prevalent, with more than half of isolates (58.71%; $n = 299$) being resistant. Streptomycin-resistant isolates were identified across all host species categories, being the most common among lizards (excluding geckos; 70.00%, 98/140), followed by geckos (61.74%, 71/115), snakes (60.91%, 67/110), toads (60.00%, 3/5), frogs (52.17%, 24/46), and lastly, tortoises (27.87% 17/61). Other detected resistance types include resistance to colistin (6.09%; $n = 29$), ampicillin (5.88%; $n = 28$), gentamycin (1.47%; $n = 7$), tigecycline (1.47%; $n = 7$), trimethoprim/sulfamethoxazole (1.47%; $n = 7$), and tetracycline (1.26%; $n = 6$). None of the isolates were resistant to ciprofloxacin. Using GLM, we tested the associations between host-dependent variables and the resistance of isolates to streptomycin, colistin or ampicillin. Yet, none of the variables were significant predictors of resistance to these antibiotics after FDR adjustment (Table S5).

Furthermore, 1.47% ($n = 7$) of isolates were MDR, which is defined as being resistant to antibiotics of three classes or more (Fig. 2; Table S5) [61]. All of these isolates were resistant to streptomycin (class aminoglycoside), ampicillin (class penicillin) and trimethoprim (class diaminopyrimidine) / sulfamethoxazole (class sulfonamide), with five also resistant to gentamycin, tetracycline and tigecycline, and one resistant to all of the eight tested antibiotics except ciprofloxacin. One of the MDR isolates was cultured from a sample from a sandfish skink (*Scincus scincus*), while the other six were from the same Cranwell's horned frog (*Ceratophrys cranwelli*). Since most MDR isolates originated from the same sample/individual, contributions of host-related variables to MDR rate could not be determined. Meanwhile, 7.55% ($n = 36$) of isolates

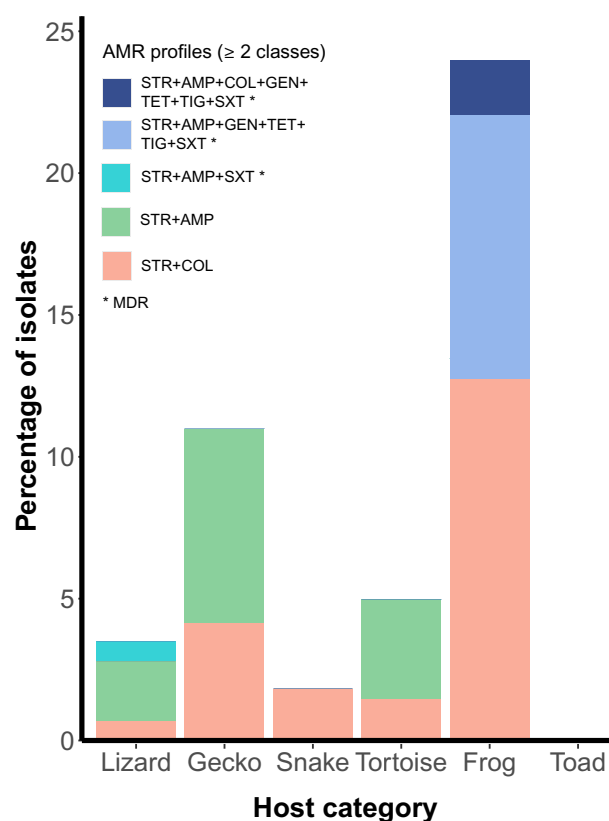


Fig. 2. Frequency of antimicrobial resistance profiles by host species categories among isolates exhibiting resistance to at least two antibiotic classes. None of the isolates obtained from toads was resistant to at least two drug classes. Multi-drug resistant (MDR) isolates, i.e., those resistant to at least three antibiotic classes, are indicated in shades of blue, denoted in the legend with asterisks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were resistant to drugs of two or more antibiotic classes. All these isolates were resistant to streptomycin. Most of these isolates were also

resistant to ampicillin (4.19%, $n = 20$) and colistin (3.56%, $n = 17$). Using GLM, we tested the associations between host-associated factors and multiple resistance. Yet, none of the tested factors were significant after FDR adjustment (Table S6).

3.3. Antibiotic resistance profiles and associations with host-dependent variables

Considering that all isolates resistant to multiple antibiotics were resistant to streptomycin and that a nested pattern exists in the resistance to different antibiotics (Fig. 3A & S1), we hypothesized that there might be interactive effects between resistance to different antibiotics, i. e. resistance to some antibiotics may increase the chance of gaining resistance to others. Therefore, we assessed the relationships between host factors and the antimicrobial resistance profiles of each isolate using a multivariate approach, instead of treating the presence/absence of resistance to each antibiotic as independent, response variables. Db-RDA was used to assess the contributions of host-dependent variables in explaining the variance in antimicrobial resistance profiles of representative isolates, i.e. isolates with resistance to the most types of antibiotics in each sample. Yet, none of the tested factors were significant (Table S7).

Despite observable variability in AMR profiles among isolates from each sample (Fig. 3B & S1), results showed that individual/sample ID was significant to explain resistance profiles (adj. $R^2 = 0.16$, $P = 0.001$; Table S8), which accounted for 19.40% of the detected variance. Approximately 46.70% of the remaining data variance can be attributed to host species, which was used as the conditioning variable, showing that a majority of variance unexplained by individual/sample ID could be attributable to the host species and other confounding host-dependent factors. Yet, animals that co-housed with multiple conspecifics might be repeatedly sampled, which could contribute to an inflation of such a detected proportion (Fig. S1). All in all, 33.90% of data variance remained unexplained by both individual/sample ID, host species, and other collinear effects.

4. Discussion

Along with the rising popularity of exotic pets, salmonellosis associated with reptiles and amphibians (RAAS) has become a global concern [2,4]. Coupled with the increasing prevalence of antimicrobial resistance, the detection and characterisation of *Salmonella* carried by pet reptiles and amphibians are essential to assess the associated risks. For the first time, this study investigates the prevalence and

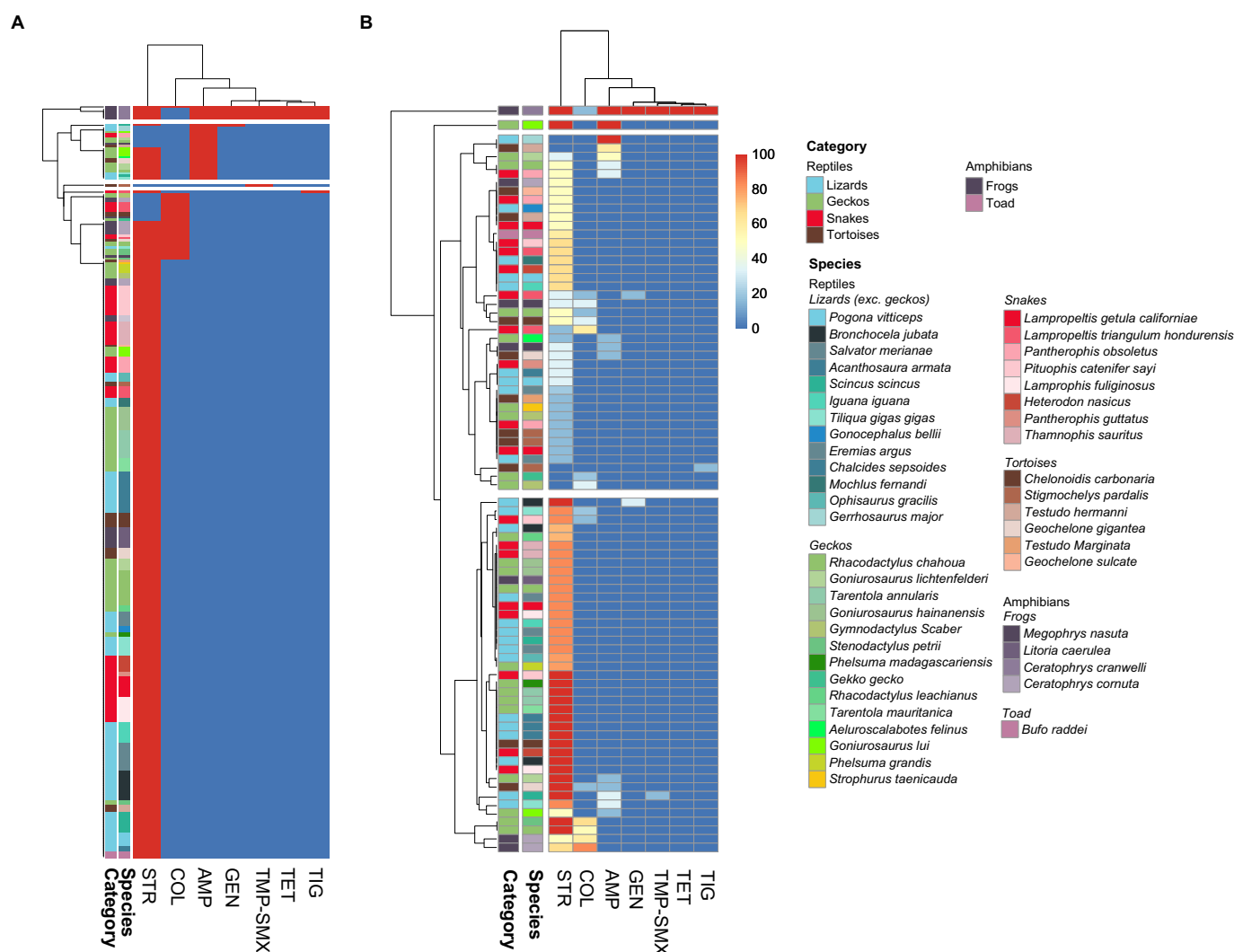


Fig. 3. Heatmaps showing (A) resistance profiles of individual *Salmonella* isolates and (B) frequency of resistant isolates from each sample. Each row denotes one isolate or one sample in (A) and (B) respectively. The two columns on the left of each plot indicate host species categories and species respectively. The remaining columns represent resistance level to each antibiotic, with red representing resistance and blue representing non-resistance (susceptible and intermediate levels in CLSI or EUCAST). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

antimicrobial resistance profiles of *Salmonella* carried by over 50 imported pet reptile and amphibian species in Hong Kong, as well as analyses their relationships with host-dependent factors. We demonstrated that most samples contained viable *Salmonella*, with comparable rates between reptiles (55.56%) and amphibians (50.00%). Importantly, a majority of the obtained isolates were AMR, of which approximately 1.47% were MDR. To our knowledge, this is also the first documentation of MDR in *Salmonella* carried by pet amphibians in Hong Kong.

Regarding reptile carriers, our identified *Salmonella* carriage rate was higher than the average of those in subclinical, captive reptiles (42.90%) reported in the last two decades [7]. In particular, nine of our sampled reptile species had a 100% *Salmonella* carriage rate, including the Central bearded dragon (*Pogona vitticeps*), one of the most popular exotic pets worldwide [62]. Among all sampled host species categories, the highest prevalence was observed in snakes (79.19%), which were also reported to be common *Salmonella* carriers in other studies (on average: 68.1%) [7]. Given the popularity of reptile pets in Hong Kong, our results indicate high risks linked to *Salmonella* shedding by these animals. Altogether, our findings contribute to the currently limited knowledge on this topic within Asia [7]. Furthermore, based on limited evidence demonstrated by previous studies, the occurrence of *Salmonella* in pet amphibians has mostly been low, if not undetectable, and therefore generally not regarded as hazardous to public health [63,64], especially in Asia [34]. In contrast to this belief, a majority of our sampled amphibians shed *Salmonella*, at a carriage rate comparable to reptiles, which have long been identified as common carriers [20,65]. In fact, our identified *Salmonella* carriage rate in pet amphibians exceeded those reported in previous studies in the last three decades [22,23,63,64], with all sampled individuals of two horned frog species (Surinam horned frog, *Ceratophrys cornuta*; and Long-nosed horned frog, *Megophrys nasuta*) being positive. Our results highlight the underestimated threats posed by *Salmonella* carried by pet frogs, especially to young children and immunocompromised individuals, who are highly susceptible to infection [64].

Furthermore, we found a higher *Salmonella* carriage rate in captive-bred than wild-caught individuals. Even though such an association was not statistically significant after correction for multiple testing, it is consistent with the higher average *Salmonella* prevalence in captive reptiles (42.90%) when compared to wild reptiles (24.30%) as reported in previous studies [7,17]. On this note, by comparing *Salmonella* occurrence and abundance in the gut microbial community between captive and wild reptiles, some researchers hypothesized that *Salmonella* colonization in captive reptiles might be largely contributed by human care, especially through the intake of artificially prepared food [7]. For instance, *Salmonella* spp. was more abundant in captive crocodile lizards, especially those with human-kept loaches as part of their diet [19]. Other studies also suggest that the food of pet reptiles, mostly of animal origin, may contribute to *Salmonella* colonization in these animals [17,20,22]. Specifically, commercial feeder mice may carry *Salmonella* serotypes that were linked to outbreaks of salmonellosis in humans in the US [20]. Along this line, prolonged feeding of artificially prepared food may enhance *Salmonella* carriage in captive-bred animals, especially snakes [64]. Yet, information about the diet of sampled animals is required to verify such associations.

Regarding antimicrobial resistance profiles of cultured *Salmonella* isolates, more than 60% were resistant to at least one of the tested antimicrobial agents, which falls within the range of those obtained in pet reptiles according to previous studies (32.00%–100.00%) [12,15,20]. A majority were resistant to streptomycin (58.71%), at a rate higher than reported in previous studies, including those from other Asian regions, e.g. 7.14% in Chongqing Province and 14.70% in Taiwan [13,36]. As one of the first discovered antibiotics, streptomycin has been commonly used in clinical, agricultural and veterinary practices since the early 1940s, which may contribute to the accumulation of resistance in a wide range of bacteria, including *Salmonella* [66]. In fact, STR-resistant *Salmonella* has become increasingly prevalent in animals,

humans and the environment, and is one of the most common forms of resistance among all antimicrobial agents [67]. Importantly, since certain mechanisms of STR-resistance can also contribute to cross-resistance, i.e., resistance to other antibiotics that may or may not be in the same class, including ampicillin (penicillin) and chloramphenicol (amphenicol), the occurrence of STR-resistant *Salmonella* may also promote multi-drug resistance [66]. That may explain the high proportion of ampicillin-resistant isolates that were also streptomycin-resistant (50.00%), and all MDR isolates identified were streptomycin-resistant. However, a relatively low prevalence of cross-resistance between aminoglycosides (0.21%), i.e., streptomycin and gentamycin, was observed, which was unexpected based on the repeated occurrence of aminoglycoside resistance genes in reptile-associated *Salmonella* demonstrated in other studies [68–70].

Furthermore, attention should be given to colistin-resistant isolates in our samples, which existed as the second-most abundant antimicrobial resistance type (6.08%; Fig. S2). Colistin-resistance in isolates can pose critical public health concerns, given that colistin is a last-resort medication to treat diseases associated with MDR bacteria and cystic fibrosis in humans [71]. While colistin is not normally used to treat *Salmonella*, plasmid-mediated Mobilised Colistin Resistance (*mcr*) genes, an increasingly prevalent ARG contributing to colistin-resistance in diverse bacterial groups, may allow the transmission of resistance between diverse genetic backgrounds, such as *Escherichia coli* and *Klebsiella pneumoniae*, which can cause severe consequences [72,73]. Alarming, the prevalence of colistin-resistant isolates in humans has been on the rise [72–74], despite the regulated usage of colistin in clinical settings in most countries or regions [75]. In particular, farm animals and domestic pets, which likely acquired resistant bacteria through repeated exposure to colistin used in agriculture and veterinary practices, are among the major potential sources of colistin-resistant bacteria [75]. Specifically, colistin has been and is still being used to treat and prevent oral and topical Enterobacteriaceae infections (e.g., as eye or ear drops) in animals in some countries in 2025 [76]. While there is no direct evidence of transmission of colistin-resistant bacteria or ARGs from pet animals to humans, colistin-resistant *Salmonella* isolated in this and other studies demonstrate that exotic pets may be an underestimated source of colistin-resistance to humans [20]. In addition, our identified prevalence of colistin-resistant *Salmonella* among amphibians (21.57%) was much higher than that in reptiles (4.23%). Such findings highlight the hazards associated with the transmission of colistin-resistance via pet amphibians in Hong Kong, and raise concerns about the potential usage of colistin in the keeping and husbandry of these animals in commercial environments. Investigation of the ARGs carried by resistant isolates will be helpful to clarify the potential impacts of colistin resistance in our sampled animals.

Out of the obtained *Salmonella* isolates, less than 2% were MDR (1.47%), and more than 7.5% were resistant to antibiotics of two classes or more. Among reptiles, the MDR rate identified in our study (0.29%) was substantially lower than those reported in the literature (more than 64%), but with different resistance types [15,20]. For instance, a larger proportion of MDR isolates identified in this study were resistant to streptomycin, whereas resistance to gentamycin, tigecycline, or ciprofloxacin was less common compared to previous studies [20]. At the same time, despite rare reports of antimicrobial resistance in captive amphibians in the literature [77], we identified isolates with resistance to antibiotics of two classes or more from amphibian samples, with some of them being MDR. Those with resistance to two or more classes of antibiotics were isolated from three horned frog species: Surinam horned frog, Cranwell's horned frog, and Long-nosed horned frog. In particular, most of the MDR isolates were obtained from the same Cranwell's horned frog. These isolates were resistant to six out of the eight tested antibiotics, indicating a high risk of antimicrobial resistance transmission from this species. While the risk factors linked to this individual are largely unclear, given that the Cranwell's horned frog was the only captive-bred frog species sampled in this study, the MDR

Salmonella may be associated with captivity. Consistent with this theory, contact with humans is a risk factor for AMR bacteria acquisition as demonstrated by higher resistance levels in captive animals when compared to wild animals based on previous studies [78,79], with differences potentially contributed by human-prepared diet and high breeding density [79]. To evaluate the potential risks associated with captive Cranwell's horned frogs, further studies of the serotype, ARG genotypes, infectivity, and virulence of co-resistant *Salmonella* isolates from this species are recommended. Our finding is not the first report of *Salmonella* shedding in Cranwell's horned frogs. There was reporting of *Salmonella* serotypes Abidjan and Wandsworth being isolated from a pet Cranwell's horned frog in Vienna more than two decades ago, yet the antibiotic susceptibility profiles of these isolates were not determined in that study [22]. Information on the prevalence and resistance profiles of *Salmonella* in pet amphibians was largely lacking. While most of the previous studies focused on reptiles as *Salmonella* carriers, our study highlights that public health risks associated with pet amphibians have been substantially underestimated and should be considered equally important as those posed by reptiles.

Interestingly, we observed a nested pattern of antimicrobial resistance in isolates: isolates with rare resistance types, e.g., gentamycin and tetracycline, also carry prevalent resistance types, e.g., streptomycin and ampicillin (Fig. 3A and B). Such an observation may imply that resistance to certain antibiotics, likely the prevalent resistant types, can increase the chance of gaining rarer resistant types. Interestingly, observed nested resistance patterns appear independent of antibiotic classes, i.e. aminoglycosides (streptomycin and gentamycin) did not share a similar hierarchy. Although such a nested pattern exists among isolates from different host species and hosts of diverse life-history backgrounds, the observed nested resistance pattern is consistent with the phenomenon of “multi-drug resistance over-representation” observed among clinical isolates of diverse bacterial species [80,81], stating that resistance to diverse antibiotics tends to be seen in the same isolate, instead of distributed randomly across a microbial population. Multiple mechanisms can lead to over-representation of multi-drug resistance [81]. For instance, diverse classes of antimicrobial agents may share the same resistance mechanism, which leads to collateral resistance. For example, efflux-pump overexpression can lead to resistance to fluoroquinolones, β -lactams, and other drug classes simultaneously [81,82]. Under exposure to diverse antibiotics, collateral resistance confers a substantial fitness advantage and therefore enhances the competitiveness of bacterial strains among non-resistant strains and those with less resistance types [83]. So far, multi-drug resistance over-representation has been documented in a wide range of clinically relevant bacteria species, but not *Salmonella* [80]. Our results suggest that a positive correlation between resistance phenotypes also exists in animal-associated *Salmonella*. Yet, although our analyses did not provide evidence to support the significance of host-dependent factors in explaining variations of AMR profiles, one should note that the observed nested resistance patterns may be contributed by variations in species-associated factors that were not surveyed in this study such as life history, husbandry, and antibiotic exposure.

While individuality or sample ID was significant to explain antimicrobial resistance profiles in our isolates, it accounted for only approximately 20% of total variation. With an additional 46.7% of remaining variation attributable to host species and its confounding variables, these results show that a substantial proportion of variation (~34%) remained unexplained, and that variations in resistance profiles within the same individual or sample can be prevalent. This observation reflects the coexistence of resistant and sensitive *Salmonella* strains within the same host, as shown in previous studies [75–77]. Furthermore, our results imply potential biases associated with using antimicrobial resistance profiles of less than three isolates per individual/sample to represent each individual or animal species, which has been a common practice [20].

This study has a few limitations. Firstly, since only one facility was

sampled, we were unable to investigate risk factors of *Salmonella* carriage and antimicrobial resistance that were linked to husbandry practices (e.g. diet) and living conditions (e.g. hygiene, source and quality of water in aquatic environments), which were significant according to previous studies [20,36,84]. Accordingly, single-source sampling also constrains the representativeness of our findings to animals from other commercial sources in Hong Kong. However, given that our sampled facility served as both a breeding facility and a supplier to multiple retail pet shops, we believe that the detection and characterisation of *Salmonella* at this facility offer significant and valuable insights to understand the potential risks of *Salmonella* dissemination within the local pet industry. Secondly, the small sample size in each host species limited our ability to analyse the associations between host species and carriage of AMR *Salmonella*. Similarly, the nested structure of host-associated factors, e.g. source and origin, within each host species prevented us from assessing the linkages between these factors and *Salmonella* carriage when conditioning for the effects of host species. Furthermore, the absence of serotype information and whole-genome sequences for the obtained isolates prevented us from analysing the prevalence of *Salmonella* serotypes and the potential contributions of ARGs to the observed AST patterns. Such information is critical for assessing the transmission risks and virulence of the recovered strains. Moreover, whole-genome sequencing would have facilitated the detection of contamination in cultures and inoculum prior to AST, which was otherwise addressed through the removal of contaminated isolates based on re-plating results and avoided by strict practices of aseptic techniques. By identifying the carriage of AMR *Salmonella* in a majority of sampled animals, our results indicate substantial zoonotic risks associated with *Salmonella* spp. in the pet trade of reptiles and amphibians. Given that most sampled animals were imported from international sources, we also highlight the potential hazards linked to exotic animals in the global market. Although pathogenic risks related to the sampled isolates cannot be assessed without serotype and strain information, considering that numerous types of antimicrobial resistance can be attributed to mobile gene elements (MGE) that are subject to horizontal gene transfer (HGT) [85], the transmission of resistance to pathogenic bacteria by the AMR *Salmonella* is of important concern. Pet handlers, including owners and pet shop attendants, especially children and immunosuppressed individuals, are at the highest risk of RAAS and infections associated with AMR *Salmonella* [64]. Currently, testing for *Salmonella* carriage is not mandatory for imported pet reptiles and amphibians in Hong Kong, except for pet turtles [34]. The high prevalence of AMR *Salmonella* identified in this study, especially MDR isolates among the Cranwell's horned frog, indicates that risks associated with *Salmonella* carriage in pet reptiles and amphibians have been largely underestimated. To clarify infection risks and pathogenicity of AMR *Salmonella* carried by imported, exotic pet animals, we urge investigations on the genetic components of resistance patterns, and virulence gene elements in these bacteria using genome-based approaches [12,86].

CRedit authorship contribution statement

Jackie Cheuk Kei Ko: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Cactus Ling Ling Tam:** Investigation, Formal analysis. **Mengdan Tian:** Investigation. **Ken Wing Ho Lee:** Investigation. **Aixin Yan:** Methodology. **Simon Yung Wa Sin:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.onehlt.2026.101567>.

Data availability

I have included the data in supplementary materials.

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