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Short Communication

Bats and birds as viral reservoirs: A physiological and ecological perspective



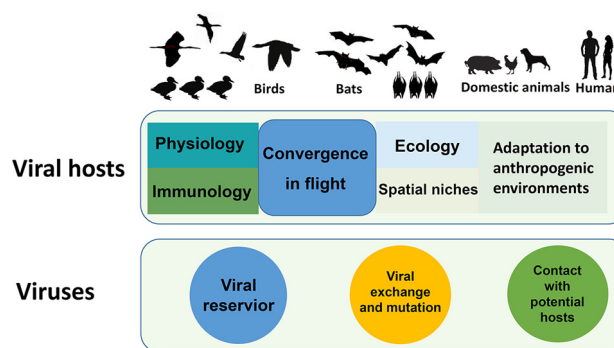
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HIGHLIGHTS

- Bats and birds are the natural hosts of many zoonotic pathogens.
- Similar ecological and physiological traits predispose them to be viral reservoirs.
- Some birds and bats close to urban areas increase the chance of zoonotic outbreaks.

GRAPHICAL ABSTRACT



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ABSTRACT

The birds (class Aves) and bats (order Chiroptera, class Mammalia) are well known natural reservoirs of a diverse range of viruses, including some zoonoses. The only extant volant vertebrates, bats and birds have undergone dramatic adaptive radiations that have allowed them to occupy diverse ecological niches and colonize most of the planet. However, few studies have compared the physiology and ecology of these ecologically, and medically, important taxa. Here, we review convergent traits in the physiology, immunology, flight-related ecology of birds and bats that might enable these taxa to act as viral reservoirs and asymptomatic carriers. Many species of birds and bats are well adapted to urban environments and may host more zoonotic pathogens than species that do not colonize anthropogenic habitats. These convergent traits in birds and bats and their ecological interactions with domestic animals and humans increase the potential risk of viral spillover transmission and facilitate the emergence of novel viruses that most likely sources of zoonoses with the potential to cause global pandemics.

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1. Introduction

The coronavirus disease 2019 (COVID-19) caused by the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) was characterized as a global pandemic on 11th March 2020 (World Health

Organization, 2020). The COVID-19 pandemic has had a dramatic socio-economic impact due to its exceptionally rapid spread and higher number of deaths (Cash and Patel, 2020; Weiss and Murdoch, 2020), particularly among older age groups (Mahase, 2020). Epidemiological research has revealed that free-living bats are likely the native host of the SARS-CoV-2 (Zhou et al., 2020). Other recent viral epidemics are also believed to have originated from either bats or birds (Calisher et al., 2006; Chan et al., 2015; Olival et al., 2017; Nabi et al., 2020). Indeed, bats or birds are thought to host many pathogens (Morse et al.,

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2012; Chan et al., 2013; Hayman, 2016; Olival et al., 2017; Woolhouse and Brierley, 2018).

The relatively high number of zoonoses carried by birds and mammals is highly correlated with their diversity at the order level (Mollentze and Streicker, 2020). Birds (class Aves) and bats (order Chiroptera, class Mammalia) have both undergone dramatic adaptive radiations; there are over 10,000 bird species (Avibase; <https://avibase.bsc-eoc.org/>) and 1400 bat species, and both taxa have a global distribution (Wilson and Mittermeier, 2019). The high diversity of birds and bats provides an abundance of potential reservoirs for a diverse range of viruses (Calisher et al., 2006; Hayman, 2016), especially recently emerging, high-profile zoonoses (Olival et al., 2017; Woolhouse and Brierley, 2018).

Why are birds and bats reservoirs of so many zoonotic viruses (Chan et al., 2013; Chen et al., 2014; Hayman, 2016; Olival et al., 2017; Mířek and Blicharz-Domańska, 2018; Venkatesh et al., 2018; Wong et al., 2019)? One explanation lies in their many shared, convergent features, such as small body size, high population densities, close social interaction, spatial mobility, and the ability to colonize anthropogenic environments (Chan et al., 2013; Chan et al., 2015). These features predispose birds and bats to act as viral reservoirs and to transmit viruses to other vertebrates, including humans. However, few studies have compared the physiology and immunology of these ecologically, and medically, important taxa (Caviedes-Vidal et al., 2007; Mollentze and Streicker, 2020; Song et al., 2020). This paper reviews convergent traits in the physiology, immunology and flight-related ecology of birds and bats with the aim of a better understanding of why these species are such important reservoirs of viral zoonoses, and the potential risk of bat and bird viruses infecting humans.

2. Birds and bats as natural reservoirs of viruses

Wild birds are reservoirs of many emerging zoonotic viruses (Reed et al., 2003; Abulreesh et al., 2007). For example, a large variety of influenza A viruses are hosted by wild aquatic birds in the orders of Anseriformes and Charadriiformes (Olsen et al., 2006). Approximately 300 avian species have been confirmed to carry the West Nile virus (CDC, 2019) and also others *gamma*- and *delta*-CoVs have been detected in multiple avian orders on all continents (Hughes et al., 2009; Chu et al., 2011; Chamings et al., 2018). The majority of viral infections in birds are either typically of low pathogenicity or asymptomatic (Olsen et al., 2006; Kuiken, 2013; Lycett et al., 2019). However, in recent years, several birds-borne viruses, such as the highly pathogenic avian influenza virus (HPAIV) A (e.g., H5N1 and H7N9) and infectious bronchitis viruses (IBV), have caused major epidemics and mortality among humans or domestic animals (Alexander, 2007; Bui et al., 2016; Wang et al., 2020).

Bats, primates, and rodents not only have the greatest viral richness among mammals but also harbor a higher proportion of zoonotic viruses than other mammalian taxa (Olival et al., 2017; Mollentze and Streicker, 2020). Bats host a greater diversity of viruses than non-flying mammals, including the paramyxoviruses (Drexler et al., 2012), the rhabdoviruses (Rupprecht et al., 2017), the hepaciviruses, the pegiviruses (Quan et al., 2013), and the influenza A viruses (Tong et al., 2013). The updated bat-virus database indicates that 301 bat species host viruses with all known viral genomic structures and replication strategies according to the Baltimore classification system (<http://www.mgc.ac.cn/DBatVir/>; Chen et al., 2014; Hayman, 2016). Bats are believed to host the ancestors of all major mammalian paramyxoviruses (Drexler et al., 2012; Hayman, 2016); those hosted by non-flying mammals and birds originated from bats (Drexler et al., 2012). In the past two decades, domestic mammals and humans have contracted several viruses from bats including SARS-CoV-2 (Zhou et al., 2020), the virus that is causing the current global pandemic, but also SARS-CoV, the Middle East respiratory syndrome coronavirus (MERS-CoV), the Ebola virus, the Marburg virus, and the rabies virus (Cui et al., 2019; Hayman, 2016).

Compared with mammals, birds had significantly lower viral and zoonosis richness, but the proportion of zoonotic viruses was comparable between classes (Mollentze and Streicker, 2020). Avian CoVs are believed to be the ancestors of *gamma*- and *delta*-CoVs, whereas bat CoVs are thought to be the ancestors of the *alpha*- and *beta*-CoVs (Woo et al., 2012). Birds (particularly aquatic birds) are natural hosts of the influenza A virus (Olsen et al., 2006; Webster et al., 1992), but bats also host influenza A-like viruses (Tong et al., 2013; Zhu et al., 2013) and the conventional influenza A virus can infect bat cells (Zhou et al., 2014). The fact that they are both capable of flight means that birds and bats have coexisted within a broad range of spatial niches for over 50 Myr (Veselka et al., 2010). It is therefore unclear whether coronaviruses and influenza A virus were transmitted from birds to bats or vice versa (Brunotte et al., 2016). It is worth noting that the human influenza A virus is thought to have come from an avian ancestor, with pigs as an immediate host, approximately 100 years ago (Gammelin et al., 1990; Scholtissek, 1996).

3. Convergences in ecology, physiology and immunology between birds and bats

Because they are both endothermic vertebrates, birds and bats should be subject to similar selective pressures on flight-related morphological and physiological traits (McGuire and Guglielmo, 2009). The convergent traits of miniaturized body size, enhanced metabolic rate and antioxidant capacity, prolonged lifespan, a short but efficient digestive tract, and possessing some specific immunological features relative to non-flying mammals are thought to be the result of functional constraints on evolution imposed by the demands of powered flight (Thomas and Suthers, 1972; Norberg, 1990; Caviedes-Vidal et al., 2007; Costantini, 2008; Munshi-South and Wilkinson, 2010; Song et al., 2020).

Unlike non-flying mammals which tend to increase in size over evolutionary time (Cope's rule; Laurin, 2004), the evolutionary trend in birds and bats has been towards miniaturization; the mass of flying birds ranges from 1.5 g to 15 kg, and for bats from 1.5 g to 1.5 kg (Fig. 1; Norberg, 1990). In the volant groups, although the energetic costs (per unit body weight) can vary with the type of flight (e.g., sustained flapping flight, short flight, and gliding flight; Guigueno et al., 2019), in general, the energetic cost (per unit body weight) of flight is approximately comparable in birds and bats (Thomas and Suthers, 1972; Munshi-South and Wilkinson, 2010). Compared with non-flying mammals, both birds and bats have significantly higher metabolic demands for volant flight (Norberg, 1990; Guigueno

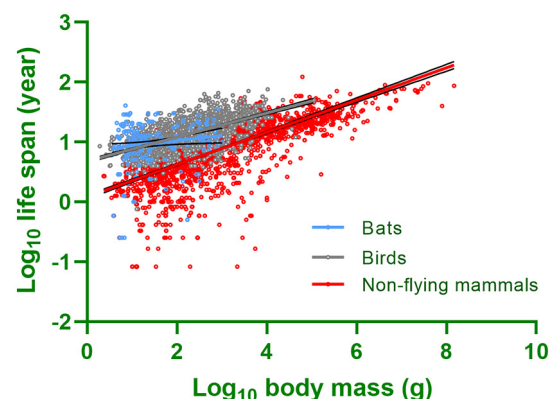


Fig. 1. The relationships between body mass and life span in birds ($n = 1660$), bats ($n = 260$), and non-flying mammals ($n = 2293$). Birds ($P < 0.001$) and bats ($P < 0.001$) have significantly longer lifespans than non-flying mammals when controlled for body mass in a general linear model. Black lines around the fitted line are the 95% confidence intervals for each taxon. Body mass and lifespan data for each group were taken from Myhrvold et al. (2015).

et al., 2019). The enhanced metabolic demands for powered flight in birds and bats are thought to have driven the evolution of reduced cell and genome sizes (Gregory, 2001, 2002; Organ et al., 2007). For example, bats have the smallest genome size (~1.6 to 3.5 Gb) of all mammals, and their DNA loss/gain ratio is ~4.3-fold greater than that of other mammals (Kapusta et al., 2017; Teeling et al., 2018). Similarly, birds have the smallest genome size of all vertebrates (Tiersch and Wachtel, 1991; Gregory et al., 2009). Furthermore, the reduction in DNA in both birds and bats has proceeded mostly through the deletion of large segments (>10 kb) events and gene loss (Zhang et al., 2014; Kapusta et al., 2017). The acquisition of powered flight and the evolution of smaller genome size in birds and bats is believed to have been achieved by streamlining genomic structure and reducing genomic redundancy (Teeling et al., 2018).

In endotherms, body size is positively correlated with life span (Speakman, 2005). However, bats and birds have a substantially longer life span than non-flying mammals of similar body size (Fig. 1; Austad and Fischer, 1991; Prinzinger, 1993; Healy et al., 2014). On average, birds live up to four times longer than similar-sized mammals (Lindstedt and Calder, 1981; Holmes and Ottinger, 2003), and bats live 3.5 times longer than similar-sized, non-flying, placental mammals (Austad and Fischer, 1991; Wilkinson and South, 2002). The mechanisms underlying the relatively long life spans of birds and bats are associated with their enhanced capability for preventing oxidative damage to mitochondria and nuclear DNA (Costantini, 2008; Munshi-South and Wilkinson, 2010). Because of their longer life spans, widespread distributions and population connectivity, both bats and birds are exposed to a broader range of environments which may increase the probability of these taxa accumulating zoonotic pathogens over time (Figueroa and Green, 2000; Munshi-South and Wilkinson, 2010; Lucas, 2016).

In both birds and bats, the size and mass of the digestive tract have been minimized to reduce weight during the flight (Caviedes-Vidal et al., 2007). However, both birds and bats have more efficient digestive systems than non-flying mammals (Caviedes-Vidal et al., 2007). There has also been a striking convergence in the gut microbiomes of birds and bats that tends to be independent of diet or phylogeny (Song et al., 2020). Despite their smaller body size, the capacity of bats and most birds to fly allows them to easily escape from unfavorable conditions and predation (Healy et al., 2014).

Given that the immune system is highly conserved in amniotes, the basic structure and function of responses to viruses are broadly similar in mammals and birds (Schat and Kaiser, 2014; Wigley, 2017). However, birds and bats as volant groups, some specific immunological features absent in non-flying mammals have enabled them to coexist with viral pathogens (Table 1; Zhang et al., 2013; Schat and Kaiser, 2014) and act as natural reservoirs for emerging viruses (Brook and Dobson, 2015; Chan et al., 2013). Birds lack lymph nodes but have a specific primary lymphoid organ, the bursa of Fabricius. Birds have heterophil in their white blood cells that is the functional equivalent of mammalian neutrophil (Schat and Kaiser, 2014; Wigley, 2017). Compared to mammals, birds have different repertoires of Toll-like receptors (TLRs), inflammatory cytokines and other immune molecules (Kaiser, 2010). Genes related to innate immunity in birds are initiated immediately during antiviral responses. For example, the duck major histocompatibility complex type I (MHC-I) and interferon-induced protein with 5 tricopeptide repeats (IFIT5) are initiated in response to H₅N₁ virus inoculation (Vandervan et al., 2012). Avian immunoglobulin Y (IgY) is a functional counterpart of mammalian IgG and IgE, providing defense against infections. However, IgY cannot activate the complement system and promote hemagglutination inhibition (Warr et al., 1995; Zhang et al., 2017). These specific features of the avian immunological system enable birds to be tolerant of many viruses (Chan et al., 2013). Such notion has been validated by previous studies, e.g., some species can survive H5N1 virus infections and shed the virus (Sturm-Ramirez et al., 2004; Hulse-Post et al., 2005; Chen et al., 2006) and can be

partially immune owing to previous exposures to the virus (Seo et al., 2002).

Among mammalia groups, bats possess very similar virus-sensing pattern recognition receptors (PRRs) and conserved immune systems. However, bats appear to control viral replication by initiating an innate immune response earlier than non-flying mammals (Baker et al., 2013; Brook and Dobson, 2015). There are other critical differences in the adaptive immune response between bats and non-flying mammals. First, bats have a diverse antibody repertoire with relatively lower avidity and a weaker association with antigens (Baker et al., 2010). Second, bats exhibit a delayed, or differential, peak of primary antibody response and a slow secondary antibody response relative to rodents, primates, and ungulates (Baker et al., 2013; Chan et al., 2013; Pavlovich et al., 2018). In bat genomes, genes in the type I interferon family, the MHC-I, and natural killer-cell receptors, are known to be highly expanded (Zhang et al., 2013). It has recently been suggested that the low expression of C-1-tetrahydrofolate synthase in the cells and tissues of bats compared to humans is due to antiviral replication (Anderson et al., 2020). Notably, several genes, such as c-REL (a vital gene for maintaining lymphoid cell function) and the ataxia-telangiectasia mutated gene (ATM) in the DNA damage checkpoint-DNA repair pathway, were positively selected in bat ancestors (Zhang et al., 2013). Compared with non-flying mammals, these special immunological features allow bats to mount efficient immune responses against a diverse range of viruses (Banerjee et al., 2020).

4. Convergences in flight-related ecology between birds and bats

The ability to fly not only significantly reduces the risk of predation but also significantly increases the ability to colonize new niches and habitats (Norberg, 1990). This enhanced mobility also means that birds and bats transport viruses over hundreds, even thousands of kilometers during migration (Hill et al., 2012; Prosser et al., 2013). Approximately 20% of birds are migratory (Kirby et al., 2008; Newton, 2008). The migrations of billions of birds worldwide also transport viruses to stopover sites, overwintering and breeding habitats (Hill et al., 2012), although migrations can also lower infection risks by escaping from habitats where pathogen stages have accumulated and eliminating infected individuals during strenuous journey (Satterfield et al., 2018). Wild birds are associated with the dispersal of CoVs (Georgopoulou and Tsiouris, 2008; Chamings et al., 2018), the Influenza A virus (Hill et al., 2012), the Arboviruses (West Nile virus), the Usutu virus, the Newcastle disease virus, the avian pox virus, and the duck plague virus (Georgopoulou and Tsiouris, 2008; Verhagen et al., 2015; Satu et al., 2017). Fewer bats migrate (Krauel and McCracken, 2013) but some undertake migrations of over 1000 km (Plowright et al., 2015; Allocati et al., 2016). Such migrations allow bat viruses, such as CoVs, the rabies virus, the Hendra, and Nipah viruses, to spread over long distances (Calisher et al., 2006). Although migratory bird and bat species have different migration patterns, their movements, particularly during intercontinental migration, contribute to viral dissemination and also facilitate viral recombination, mutation and evolution (Bahl et al., 2013; Hill et al., 2016; Plowright et al., 2017; Lycett et al., 2019).

Given that bats and birds have evolved to compete for spatial niches such as roosting sites they may interact with each other, either directly or indirectly. The bird-bat interactions include co-occurrence in the same nest (e.g., between starling *Sturnus vulgaris* and noctule bats *Nyctalus noctule*) (Myczko et al., 2016), the predation of eggs, nestlings, or adult birds by bats (Medellín, 1988; Ibáñez et al., 2001; Perrella et al., 2020) and the predation of bats by birds (Fenton and Fleming, 1976; Camargo and Laps, 2016; Mikula et al., 2016). Perrella et al. (2020) found about 8% of bird nests were preyed by bats and 2% by reptiles. Both bats and birds species richness increases in proximity to the equator due to higher ecological productivity (Brown, 2014; De Oliveira et al., 2018). Similarly, pathogen diversity is also greater in tropical areas compared to temperate regions, and therefore, pathogen richness

Table 1
Comparison of the structure and function of the immunological systems of birds, bats, and non-flying mammals.

Structure and function	Birds	Non-flying mammals	Bats	References
Lymph node	No peripheral or mesenteric lymph nodes, but have the bursa of Fabricius	Peripheral or mesenteric lymph nodes	Peripheral or mesenteric lymph nodes	Schat and Kaiser, 2014; Wigley, 2017
White blood cells	Heterophil, eosinophil, basophil, lymphocyte, and monocytes	Neutrophils, eosinophil, basophil, lymphocyte, and monocyte	Neutrophils, eosinophil, basophil, lymphocyte, and monocyte	Schat and Kaiser, 2014; Wigley, 2017
Immunoglobulins	Three classes: IgY, IgA, IgM	Five classes: IgG and IgE, IgA, IgM, IgD	Five classes: IgG and IgE, IgA, IgM, IgD	Schat and Kaiser, 2014; Wigley, 2017
Innate or adaptive immune response	Early and quick innate antiviral immune response	Delayed innate antiviral immune response. Higher avidity and weaker association with antigens; Quick primary and secondary antibody responses	Early and quick innate antiviral immune response; Lower avidity and weaker association with antigens; Delayed, or differential, peaks of primary antibody response and a slow secondary antibody response	Baker et al., 2010, 2013; Kaiser, 2010; Chan et al., 2013; Brook and Dobson, 2015; Pavlovich et al., 2018

in birds and bats could be higher near the equator compared to temperate regions (Guernier et al., 2004). This coexistence could allow the mixing of bats and birds viruses for the generation of recombinant, novel mutant, or reassortment of RNA viruses (Chan et al., 2013; Perrella et al., 2020). Furthermore, a large number of birds and bats are gregarious with high population densities. For example, colonies of the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) can contain up to one million individuals per roost at an average density of about 4000 bats/m² (McCracken and Gustin, 1991). Indirect bird-bat interactions include competition for food, and for temporal, and spatial, niches (Fenton and Fleming, 1976; Goldingay, 2009). Therefore, these convergent features of small body size, high population densities, and spatial mobility, and the bird-bat social interactions provide the opportunity for exchanging viruses, thereby facilitating the emergence of highly pathogenic, new viruses.

5. Adaptation of birds and bats to anthropogenic environments

Human activity, such as agriculture and urban development, is causing significant degradation, loss and fragmentation of bird and bat habitat (Voigt and Kingston, 2016; Walsh et al., 2017). Although the majority of the birds and bats are susceptible to anthropogenic change, some flourish in anthropogenic environments, including cities (Duchamp and Swihart, 2008; Johnson and Munshi-South, 2017) and are well adapted to urban environments by exhibiting a suite of phenotypic traits in morphology, physiology, and behavior (MacGregor-Fors et al., 2012; Magle et al., 2012; Jung and Threlfall, 2016; Afelt et al., 2018; Isaksson, 2018). Anthropogenic environments provide some human commensal species with an abundance of food and reduced numbers of parasites and predators, thereby increasing reproductive output and winter survival (Minias, 2016). The often high densities of birds and bats in anthropogenic environments facilitate viral transfer to humans (Plowright et al., 2015; Afelt et al., 2018). Domestic fowl and livestock are often also at high density in anthropogenic environments, in some countries close to captive wild game. This juxtaposition of domestic and wild animals provides an abundance of immediate hosts for bird and bat-derived viruses, many of which can become pathogenic once transmitted to humans (Chan et al., 2015). Furthermore, many birds and bats are caught and transported to markets to be sold for food, traditional medicine, ornamentation, as pets or for sport hunting (Mildenstein et al., 2016). For example, at least 167 species of bats (92 species of large-bodied fruit bats and 75 insectivorous species) are reported to be hunted in Africa, Asia, Central and South America, and across the islands of Oceania (Mildenstein et al., 2016). Similarly, 4561 bird species (45.7% of all species) are caught by humans for different purposes (Butchart, 2008). Generally, these captured bats and birds are sold and kept in close contact with humans and other taxa in

overcrowded and unhygienic wet markets that have become epicenters for the mixing and transmission of viral pathogens (Chan et al., 2013; Aguirre et al., 2020). The high human population density in cities increases the risk of humans becoming infected with recombinant viruses from intermediate hosts, some of having already caused global pandemics (Sehgal, 2010). The risk of cross-species transmission depends on the spatio-temporal network connecting viral reservoirs to intermediate, and final, hosts (Hassell et al., 2017; Plowright et al., 2017). Anthropogenic environments can, therefore, be regarded as a viral nexus where bird and bat-derived viruses, a diverse range of potential intermediate hosts, and humans, all exist in close proximity. Because their primary and secondary hosts are either mildly symptomatic or asymptomatic, many bird and bat-derived viruses may spread and diversify unnoticed in anthropogenic environments (Afelt et al., 2018).

6. Conclusions

The occasional transmission of viral pathogens from asymptomatic host species to new hosts can lead to either asymptomatic infection, severe disease, or death. Birds and bats share a variety of flight-related physiological and ecological traits that predispose them to harbor, disperse, and transmit viruses. Special features of their immune systems enable them to function as asymptomatic carriers of a diverse range of viruses. Close interactions between birds and bats in the course of competition for spatial niches, further increases the probability of viral transmission, recombination, and mutation, while the migrations undertaken by many birds and bats disperse viruses over long distances. The ability of some birds and bats to flourish in anthropogenic environments increases the probability of the viral transmission to domestic animals or captive wild game, which facilitates the emergence of novel viruses pathogenic to humans. By bringing together birds, bats, domestic animals, wild game and humans, urban environments provide the ideal conditions for acquiring new viral genes, and harboring high viral burden with strains of higher transmission efficiency, thus facilitating transmission of the viruses to humans. Considering that many ongoing bird and bat-derived zoonotic viruses are probably circulating, diversifying, and spreading unnoticed, the risk of such pandemics is ongoing. More transdisciplinary and interdisciplinary investigations are warranted to unravel the complex interactions connecting bat and bird-derived viruses to immediate hosts and to humans and shed light on the origin of the current COVID-19 pandemic and reduce the risk of future pandemics.

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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CRediT authorship contribution statement

Nabi G. and Wang Y., literature search and writing the original draft; Lv L., Jiang C., Ahmad S., and Wu Y., literature search and discussion; Li D., study design and writing the final manuscript.

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