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Reverse zoonosis of SARS-CoV-2: literature review

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Abstract:

Introduction: SARS-CoV-2, the causative agent of COVID-19, was initially considered primarily a pathogen transmitted between humans. As the pandemic unfolded, attention turned to the phenomenon of reverse zoonosis—that is, the transmission of the virus from humans to animals—which may have significant epidemiological and environmental implications.

Objective: The aim of this study was to analyze available data on SARS-CoV-2 reverse zoonosis, with particular emphasis on the susceptibility of various animal species, mechanisms of infection, and potential public health implications.

Materials and methods: An analysis was conducted of the scientific literature cited in the study, encompassing experimental and observational studies as well as clinical reports. The analysis included results from molecular (RT-PCR) and serological tests, phylogenetic analyses, and data on ACE2 receptor homology across various animal species.

Results: It was demonstrated that SARS-CoV-2 can infect numerous animal species, including domestic, farmed, and wild animals. The highest susceptibility is observed in felids, minks, and ferrets. In many cases, transmission of the virus from humans to animals has been confirmed, and sporadically also between animals and from animals to humans. The course of infection is most often asymptomatic or mild, although severe complications are possible.

Conclusions: Reverse zoonosis of SARS-CoV-2 is a significant issue that requires further research and monitoring. Animals may serve as reservoirs for the virus and sources of new variants. It is essential to implement biosecurity measures and foster interdisciplinary collaboration to minimize the risk of interspecies transmission.

Keywords: SARS-CoV-2; COVID-19; zoonosis; reverse zoonosis; ACE2; receptor; host-pathogen interactions

Introduction:

The COVID-19 pandemic, caused by the SARS-CoV-2 virus, has drawn attention not only to the transmission of the pathogen between humans but also to its ability to infect animals.

The phenomenon of reverse zoonosis, involving the transmission of the virus from humans to animals, can lead to the emergence of new reservoirs and promote its further evolution.

The ACE2 receptor plays a key role in the infection process, and its interspecies variation influences animals’ susceptibility to infection. Reports indicate that SARS-CoV-2 can infect numerous animal species, which has significant epidemiological implications and requires further research.

Materials and methods:

A comprehensive search of the PubMed, Scopus, SpringerLink, and Web of Science databases identified relevant literature on reverse zoonosis caused by the SARS-CoV-2 virus, with particular emphasis on the mechanisms of infection, the role of the ACE2 receptor, and cases of virus transmission from humans to animals. The research material included scientific publications, review articles, and experimental and clinical reports from 2020–2024, cited in this article. Data on natural and experimental infections in various animal species were analyzed, including the results of molecular (e.g., RT-PCR), and phylogenetic analyses of the viral genome. Studies on the homology of ACE2 protein sequences across species were also included, as they allow for the assessment of animals' susceptibility to SARS-CoV-2 infection. The selection of sources was based on their thematic relevance to the issue of reverse zoonosis and the recency of the data, covering the period from the onset of the COVID-19 pandemic to the latest available studies.

Literature review:

Characteristics of SARS-CoV-2

SARS-CoV-2 coronavirus (severe acute respiratory syndrome coronavirus 2), which is the causative agent of COVID-19 (coronavirus disease 2019), triggered a pandemic in 2019. The virus belongs to the *Coronaviridae* family, which consists of enveloped viruses that contain single-stranded positive-sense RNA (ssRNA) as their genetic material. The family derives its name from the spike projections surrounding the virion surface, which are composed of the S glycoprotein. Virions are composed of four types of structural proteins: envelope protein E, membrane protein M, nucleocapsid protein N, and spike protein S. This glycoprotein consists of two subunits: S1 and S2. The first subunit contains the receptor-binding domain (RBD), which plays a crucial role in recognizing and binding the virus to the host receptor. The second subunit is responsible for the fusion of the viral lipid envelope with the host cell membrane or the endocytic vesicle membrane. The spikes surrounding the virions significantly influence viral tropism [1][2]. The S glycoprotein can adopt different conformational states: closed and open. In the closed state, the RBD is hidden, making it less accessible for receptor binding on the cell surface. This helps the virus evade immune detection by concealing critical epitopes targeted by antibodies. In the open state, the RBD is positioned "up," exposing the receptor-binding site. When the virus approaches the receptor, conformational changes occur in the S protein, transitioning it from the closed to the open state. This transition is essential for the virus to attach to the host cell membrane [3]. The receptor for SARS-CoV-2 is the angiotensin-converting enzyme 2 (ACE2), which is present on the membranes of various host cells.

ACE2 receptor

Angiotensin-converting enzyme 2 (ACE2) is an enzyme that converts angiotensin I into angiotensin (1-9) and angiotensin II into angiotensin (1-7). Angiotensins (1-9) and (1-7) participate in the nonclassical pathway of angiotensinogen metabolism. As a result, they exert effects opposite to those of angiotensin II, causing vasodilation through the stimulation of nitric oxide (NO) and prostacyclin synthesis. They influence the cardiovascular system and can also regulate other components of the renin-angiotensin-aldosterone system [4]. ACE2 is expressed in many human tissues and cells. The highest expression of this protein is observed in enterocytes of the small intestine, whereas lower expression is found in the endothelium of the coronary arteries, cardiomyocytes, and kidneys. Low expression has also been observed in the liver [5]. Although SARS-CoV-2 spreads primarily through the respiratory system, only minimal expression of ACE2 has been detected in this system at protein and mRNA levels [5]. The structure of the ACE2 protein can be divided into three parts: an intracellular tail, a short transmembrane region, and an extracellular portion consisting of two domains. Starting from the N-terminus of the protein, the first domain is a zinc-containing metallopeptidase. This enzymatic domain is responsible for angiotensin conversion and also serves as the binding site for the receptor-binding domain (RBD) of the SARS-CoV-2 virus. The second domain is similar to collectrin, a protein involved in the regulation of renal amino acid transport and insulin secretion by pancreatic beta cells [6].

Interaction between ACE2 and SARS-CoV-2

For the coronavirus to enter a cell, two cleavage events involving the spike protein are required. The first event is the separation of the S protein into two subunits: S1 and S2, while the second involves cleavage at the S2' site within the S2 subunit. In the case of SARS-CoV-2, the cleavage of the sequence between the S1 and S2 subunits and their separation occurs while the virus is still inside the infected cell that produces it, during the maturation process. This process takes place in the Golgi apparatus and is carried out by furins or furin-like proprotein convertases. Cleavage at the S2' site occurs after the virus binds to the ACE2 protein on the surface of the target cell. Binding of the virus to ACE2 induces structural changes in the S1 subunit, exposing the cleavage site of S2 in the S2 subunit. The cleavage at the S2' site is carried out by the serine protease TMPRSS2, which is located on the cell surface. However, if the expression of this protease in the target cell is insufficient or if the virus-ACE2 complex does not encounter TMPRSS2, the complex undergoes clathrin-mediated endocytosis. Subsequently, cleavage at the S2' site occurs within endolysosomes by cathepsin L. In both cases, after cleavage at the S2' site, fusion occurs between the viral membrane and the cell membrane or the endosomal membrane, leading to the release of viral RNA into the cell [7]. After the release of the viral genetic material from the endosome or nucleocapsid, the synthesis of viral proteins and the replication of the viral genome take place. The virus replicates within the cytoplasm of infected cells. Once viral RNA and proteins are synthesized, these components are transported to the membranes of the endoplasmic reticulum and the Golgi apparatus, where viral proteins undergo modifications. The virions are then assembled within these organelles. The viral RNA is enclosed in protein capsids. The fully formed virions are transported to the host cell membrane in transport vesicles. This process is known as budding. Upon reaching the membrane, they fuse with it, and the contents of the vesicles—newly formed virions—are released outside the cell. The newly created virions can then infect other susceptible cells that possess the ACE2 receptor.

ACE2 in animals

The ACE2 protein is present in many animal species, mainly in mammals, but its expression levels and amino acid sequence can vary among them. ACE2 has been well studied in mammals, including mice, rats, monkeys, rabbits, and pigs. However, not all animal forms of ACE2 exhibit the same similarity to human ACE2, which may be significant in the context of SARS-CoV-2 infection. Using bioinformatics analyzes, it is possible to predict which animal species are more susceptible to natural SARS-CoV-2 infection [8]. To achieve this, a comparative analysis of the variability in the full coding sequence of ACE2 has been conducted, with a particular focus on the receptor-binding domain (RBD) of the S protein of SARS-CoV-2 across different animal species. Based on the homology of these sequences, the highest susceptibility to infection is predicted in humans and other primates, followed by carnivores, rodents, and ungulates [9].

COVID-19 – symptoms

As mentioned above, COVID-19 is a respiratory disease caused by the SARS-CoV-2 virus. The virus spreads primarily via droplets in the form of aerosols expelled during coughing, sneezing, or speaking. When binding to the respiratory tract epithelial cells, SARS-CoV-2 initiates replication and migration to deeper parts of the respiratory system, eventually reaching the alveolar epithelial cells. The main symptoms of the disease include fever, cough, especially dry and nonproductive, and shortness of breath. Other flu-like symptoms may also occur, such as muscle aches, headaches, sore throat, and, less frequently, hemoptysis or confusion. However, these symptoms are not highly specific. One of the most characteristic symptoms reported by some patients at the beginning of the pandemic was loss of taste and smell. The type and severity of symptoms depend on the SARS-CoV-2 variant. SARS-CoV-2 infection may present without any symptoms in the early stages of the disease or throughout its course. Mild respiratory symptoms may also occur. Rapid replication of SARS-CoV-2 in the lungs can trigger a strong immune response. Cytokine storm syndrome can lead to severe pneumonia with acute respiratory distress syndrome (ARDS), which may further progress to multiorgan failure. ARDS-induced respiratory failure is considered the leading cause of death in cases of COVID-19 [10][11]. These symptoms can occur not only in humans, but also in animals infected with the SARS-CoV-2 virus.

Zoonosis and reverse zoonosis

According to the World Health Organization, zoonosis (also known as zoonotic disease) refers to a disease or infection that is naturally transmitted from vertebrates to humans. Zoonotic diseases can be classified based on their etiology, such as bacterial, viral, fungal, or parasitic infections, or based on the mode of transmission. They may be transmitted through direct contact with an infected vertebrate (contact with the pathogen), through an intermediate vertebrate host, as seen in human taeniasis. Another type includes zoonoses that require both vertebrate and invertebrate hosts to complete their infectious cycle, such as Lyme disease. These are known as ferozoonoses, where the infectious agent reproduces or develops in an invertebrate before being transmitted to a vertebrate. The fourth type of zoonosis, known as saprozoonosis, involves a vertebrate host, as well as an inanimate developmental reservoir, such as organic matter, food, or soil [12]. Research indicates that COVID-19 is one of many known zoonotic diseases. Despite four years having passed since the outbreak of the pandemic, the origin of the SARS-CoV-2 virus has not been definitively determined. Although there have been speculations about a possible laboratory origin, genomic studies suggest that the virus emerged by natural selection in an animal environment before being transmitted to humans. Phylogenetic analyzes show that SARS-CoV-2 is closely related to coronaviruses detected in bats, particularly RaTG13 and SARSr-CoV, suggesting that bats may be its primary hosts.

The recent discovery of SARSr-CoV in *Rhinolophus shameli* bats further supports the close relationship with SARS-CoV-2, indicating that bats probably played a crucial role in the evolution of the virus before its transmission to humans. Regarding the intermediate hosts of SARS-CoV-2, they have not yet been fully identified. Some hypotheses suggest that pangolins could serve as intermediate hosts. Studies have found viruses related to SARS-CoV-2 in Malayan pangolins, with genetic material showing 100%, 98.6%, 97.8%, and 90.7% similarity to the E, M, N, and S proteins of SARS-CoV-2, respectively. This suggests that pangolins may potentially act as an intermediate host for the virus; however, further research is needed to confirm this hypothesis [13]. Other potential intermediate hosts considered in the studies include snakes such as *Bungarus multicinctus* and *Naja atra,* as well as turtles such as *Chrysemys picta bellii*, *Chelonia mydas* and *Pelodiscus sinensis*. However, it was ultimately concluded that the ACE2 proteins of these animals had lost their ability to bind with the S protein of the virus, thereby excluding them as possible intermediate hosts [14].

Reverse zoonosis (also known as anthropozoonosis) refers to the phenomenon in which diseases are transmitted from humans to animals. Similarly to zoonotic diseases, reverse zoonosis can have bacterial, viral, fungal, or parasitic origins. It can result from direct contact with an infected human or indirect factors such as parasites, vectors, or environmental contamination. Recent examples of pathogens transmitted from humans to animals include *Staphylococcus aureus*, influenza A virus, *Cryptosporidium parvum*, *Ascaris lumbricoides*, and SARS-CoV-2.

Reverse zoonosis of the SARS-CoV-2 virus

Serological and molecular studies, as well as infection experiments, have demonstrated the possibility of SARS-CoV-2 infecting various animal species across different regions of the world. Both domestic and wild animals, such as cats, dogs, tigers, lions, pumas, snow leopards, minks, and domestic ferrets, have been naturally infected with SARS-CoV-2, primarily due to potential transmission from humans to animals. Cases of virus transmission between animals within the same species have also been observed. Furthermore, in vivo inoculation experiments have shown the susceptibility of cats, ferrets, hamsters, Egyptian fruit bats, and nonhuman primates to the virus. It has also been found that these experimentally infected species can transmit the virus to other animals of the same species kept in households. However, SARS-CoV-2 has demonstrated a low replication capacity in livestock animals such as pigs, chickens, and ducks, with no viral RNA detected after intentional infection or exposure to infected individuals [15].

Domestic animals

Dogs

The first reported case of a dog infected with SARS-CoV-2 occurred in Hong Kong in February 2020. Viral RNA was detected in five nasal swabs collected from a neutered 17-year-old male Pomeranian between February 26 and March 9. The genetic material of the virus was identified using quantitative RT-PCR. Additionally, rectal and fecal swabs were collected but tested negative for SARS-CoV-2. After the virus was detected, the dog was isolated from its household members and placed in quarantine. Throughout the quarantine period, no symptoms or clinical changes were observed in the animal. The dog had several pre-existing health conditions, including systemic and pulmonary hypertension, chronic kidney disease, hypothyroidism, and adrenal hyperactivity. Heart murmurs were also detected. On March 16, 2020, the dog passed away; however, it is not clear to what extent the virus contributed to its death. The dog's pre-existing conditions and advanced age may have played a significant role in the sudden deterioration of its health. COVID-19 was diagnosed in the dog’s 60-year-old owner on February 24, 2020, with symptoms appearing approximately two weeks earlier. Other household members also reported COVID-19 symptoms, and all were quarantined. The viral RNA from nasal swabs taken from the dog on February 26 and 28 was sequenced directly from the clinical sample and compared to the virus detected in the dog's owner and another member of the household. Viral sequences were identical in all cases, indicating transmission from human to animal [16][19]. However, not all SARS-CoV-2 infections in dogs are asymptomatic, as seen in the above case. Symptomatic infections in dogs with the British variant B.1.1.7 of the virus have been reported in southeastern England. Additionally, it was observed that many of the owners or caretakers of these animals experienced COVID-19 symptoms 3–6 weeks before their pets developed illness, and they also tested positive for SARS-CoV-2 via PCR tests. In particular, all dogs infected with the B.1.1.7 variant exhibited unusual clinical symptoms, such as severe heart function disorders caused by myocarditis and a significant decline in overall health. However, they did not show primary respiratory symptoms. None of the infected dogs had a history of heart disease, and their clinical presentation was similar. The presence of SARS-CoV-2 in dogs was confirmed by oral, nasopharyngeal, and rectal swabs. The presence of viral genetic material was analyzed using RT-PCR. The clinical condition of infected dogs was assessed by laboratory tests and imaging studies, including blood troponin levels, echocardiography, chest radiographs, and ECG [17]. However, the symptoms described above are not specific to SARS-CoV-2 infection; more commonly reported symptoms include flu-like signs such as fever, respiratory issues, and gastrointestinal symptoms.

The reported prevalence of SARS-CoV-2 infections in dogs varies significantly depending on the target population, test characteristics, geographic location, and time period. The infection rate in dogs has been studied in various populations since the beginning of the pandemic, with close contact with SARS-CoV-2-positive owners being a significant factor.

To demonstrate this, the researchers examined infection rates among two different groups: dogs living in households where at least one person was infected with SARS-CoV-2 and dogs visiting veterinary clinics for sample collection. Among households with COVID-19-positive individuals, 23.6% (46 out of 195) had infected pets. In contrast, among dogs brought to veterinary clinics, the infection rate was significantly lower at 4.6%. Excluding dogs with known exposure to COVID-19-positive owners further reduced the infection rate to 1.8%. Additionally, the study found that the prevalence of SARS-CoV-2 in dogs was significantly higher in households with multiple COVID-19-positive individuals than in those with only one confirmed case. Another finding of the study was the reported seroprevalence in Dutch dogs, which ranged from 0.2% in pets without documented contact with infected owners to as high as 53% in households with confirmed SARS-CoV-2 cases. This clearly indicates that reverse zoonotic transmission from humans to dogs occurs. Studies also suggest a very low risk of virus transmission from infected pets to humans within the household, a lack of severe clinical symptoms in dogs, and minimal transmission between pets [18].

Cats

The first documented instance of natural transmission of SARS-CoV-2 from a human to a cat was reported in Belgium on March 6, 2020, after the animal's owner had been diagnosed with COVID-19. This marked the third known case of the virus spreading from humans to animals, following two prior infections identified in dogs in Hong Kong. [19] SARS-CoV-2 RNA was detected in samples collected from the cat's nasopharynx, vomit and feces, and specific immunoglobulins for the virus were identified in serum samples collected during the recovery phase. Later, in France, an RT-PCR test conducted on a rectal swab from a cat confirmed the presence of the virus. This was the first reported case of natural SARS-CoV-2 infection in a cat in France, likely transmitted from its infected owners. Phylogenetic analysis showed that the virus infecting the cat was identical to most coronaviruses found in the French human population. Genome sequencing of the virus collected from the cat revealed eight nucleotide mutations compared to the reference Wuhan strain, covering 94% of the genome. Additionally, the sequenced genome contained a mutation causing an amino acid substitution (D614G) in the S glycoprotein, a mutation characteristic of the virus circulating in the French population at that time [19]. Another case of a cat infected with SARS-CoV-2 was reported on May 8, 2020, in Spain. The virus was detected in a 4-year-old cat from a household where a human COVID-19 case had been confirmed and the owner had died from the disease. After the owner's death, the cat was taken to a veterinary clinic due to severe respiratory distress. Imaging studies and cardiac failure markers indicated circulatory and respiratory failure caused by hypertrophic cardiomyopathy and secondary thromboembolic disease. A post-mortem examination of the cat revealed significant histological changes in lung tissues, indicating severe pulmonary edema, congestion, and capillary thrombosis.

Hemorrhages were also observed in the nasal turbinates, as well as abnormalities in the heart muscle, liver, and kidneys. Samples were collected to test for the presence of SARS-CoV-2, and viral RNA was confirmed by RT-PCR in nasal swabs and mesenteric lymph nodes. It was likely that the infection resulted from exposure to the virus from the infected owner [19][20]. This case demonstrates that the symptoms of SARS-CoV-2 infection can vary greatly. It is important to consider the animal’s pre-existing health conditions before infection. The cat had been diagnosed with hypertrophic cardiomyopathy and thrombocytopenia, indicating that SARS-CoV-2 infection in animals can exacerbate pre-existing chronic conditions, leading to life-threatening complications even in the absence of typical disease symptoms caused by the virus.

Other cases of domestic animal infections with SARS-CoV-2 have been reported worldwide, including in Europe, the United States, and Hong Kong [20]. Studies have investigated how often pets are exposed to the virus through their owners.

Samples were taken from 34 cats whose owners had confirmed COVID-19 infections. Only one cat from the study group exhibited mild clinical symptoms, such as nasal congestion. Swabs were taken to detect viral genomes using RT-PCR, revealing an RNA detection rate of 14.7%. This suggests that approximately 15% of cats in infected households may contract the virus from their COVID-19-positive owners [21]. To prevent SARS-CoV-2 infection in their domestic animals, owners should avoid close contact, such as kissing or sharing food with their pets [22].

Cases of cat-to-cat transmission of SARS-CoV-2 have also been documented. Experimental studies have shown that this transmission is possible when cats are in close contact for a sufficient duration [23]. A naturally occurring case of cat-to-cat transmission was reported when a missing cat returned home after two weeks with flu-like respiratory symptoms. The presence of SARS-CoV-2 was confirmed by RT-qPCR from a nasal swab. The owner tested negative for the virus, ruling them out as the source of infection. A second cat in the household initially tested negative for the virus but later tested positive despite having no documented contact with other animals or humans outside the household [24].

According to the World Organization for Animal Health (WOAH), from the start of the pandemic until the end of 2023, a total of 114 outbreaks of the disease in cats were reported in 21 countries, while 105 outbreaks in dogs were reported in 16 countries. However, since these data are based on voluntary reporting, there is a high likelihood of underreporting, particularly in free-ranging or stray cats and dogs with limited human contact. Comparing studies on dogs and cats, it can be concluded that SARS-CoV-2 infections in both species typically present asymptomatically or with mild respiratory or gastrointestinal symptoms. However, severe complications can occur in some cases. The likelihood of transmission of human to animal within the same household is approximately 15%. When SARS-CoV-2 is transmitted from humans to animals, the virus can undergo mutations that could improve its adaptation to a new host or environment. Furthermore, the virus could potentially spread back from animals to humans, raising concerns about the emergence of new viral variants. Therefore, it is crucial to prevent the transmission of SARS-CoV-2 from owners to pets [22].

Livestock

Due to the phenomenon of reverse zoonosis, concerns have been raised about the potential transmission of SARS-CoV-2 from humans to livestock, which live in close proximity to human and could establish a persistent viral reservoir in animals. This issue is of particular interest because of the frequent close contact between humans and livestock, especially in certain parts of the world where high densities of farmed animals are maintained.

Such a transmission could also pose a threat to food supply chains, as infected animals cannot be sent to slaughterhouses. This could have significant implications, for example, in large-scale beef cattle farms [25].

Cattle

Studies have shown that chickens, ducks, and pigs are not susceptible to SARS-CoV-2 infection [26]. However, the situation is different for cattle. Cattle are known to be susceptible to bovine coronavirus (BCoV), raising concerns that they might also be vulnerable to SARS-CoV-2 infection [27]. An experiment was conducted in which six calves were inoculated intranasally with SARS-CoV-2 particles. These infected calves were then housed together with three uninfected calves. Before the experiment, nasal, oral, and rectal swabs were collected from all animals and no viral presence was detected. In addition, no SARS-CoV-2 antibodies were found in their serum. After experimental infection, the veterinarians conducted daily physical examinations. None of the animals exhibited clinical symptoms of infection.

However, viral RNA was detected by RT-PCR in nasal swabs from two calves on the 2nd and 3rd days after infection. Serum analysis revealed that from day 12 after inoculation, one of the calves developed antibodies against the virus, indicating seroconversion. The results of this study suggest that cattle exhibit a low susceptibility to SARS-CoV-2 infection under experimental conditions. This aligns with the expected moderate susceptibility predicted by computational modeling of the ACE2 protein, the virus receptor, in cattle species. No intraspecies transmission was observed among the calves housed together, indicating that cattle are unlikely to play a significant role in the human pandemic. Moreover, there have been no reports of naturally infected cattle. However, in regions with large cattle populations and a high incidence of SARS-CoV-2 infections in humans—such as the United States or countries in South America—close contact between livestock and infected farmers or caretakers could increase the risk of anthropozoonotic transmission to cattle [27].

Horses

To date, no official SARS-CoV-2 outbreaks in domestic horses have been reported to the World Organization for Animal Health (WOAH). However, isolated cases of horse infection have been documented after contact with humans infected with SARS-CoV-2. One such case occurred in the United States in October 2021, when a woman caring for two horses contracted COVID-19. Despite exhibiting symptoms of the infection, she maintained daily contact with the animals. No horses had clinical symptoms of the disease and viral genetic material was not detected in blood, nasal secretions, or feces using RT-qPCR. However, seven days after the onset of symptoms in the owner, antibodies against the receptor-binding domain (RBD) of the SARS-CoV-2 spike protein were detected in one of the horses through an ELISA blood test. This suggests that horses can become infected with SARS-CoV-2 after close contact with infected humans [28]. A serological study conducted in the United States found that 5.9% of 587 tested horses had developed antibodies against the SARS-CoV-2 RBD after close contact with asymptomatic SARS-CoV-2-infected individuals [29].

Minks

American minks (*Neovison vison*) have shown a high susceptibility to SARS-CoV-2 infection, both through experimental inoculation and natural infections. Minks are the only non-human species in which large-scale SARS-CoV-2 outbreaks have been reported at the population level. In mink farms across Europe and North America, cases of reverse zoonosis and mink-to-mink virus transmission have been observed, leading to clinical symptoms and high mortality rates within populations. Minks are also the first animal species for which the transmission of the virus back to humans and other animals has been documented. Natural infections of farmed minks with SARS-CoV-2 have been reported in several countries worldwide, including the United States, France, Italy, the Netherlands, Sweden, Canada, Greece, and Poland [30]. The first signs of SARS-CoV-2 infection in minks were observed on April 19 and 20, 2020, on two farms in the Netherlands. In most cases, symptoms were limited to watery nasal discharge, although some animals exhibited severe respiratory distress. Tests were conducted to detect the presence of SARS-CoV-2, influenza A virus, adenovirus infection, *Escherichia coli*, and *Pseudomonas aeruginosa*. These tests confirmed SARS-CoV-2 infection, with the first cases officially confirmed on April 23 and 25, 2020. Autopsies performed on deceased minks revealed significant pulmonary fibrosis in 16 out of 18 cases, indicating interstitial pneumonia. In the affected farms, COVID-19 symptoms were reported among farm workers before symptoms were observed in minks. One hospitalized worker tested positive for SARS-CoV-2; however, the viral concentration in the collected sample was too low for sequence analysis. Sequencing was performed on samples from infected minks, revealing that viral sequences were closely related to human-origin isolates viruses [31]. The spread of SARS-CoV-2 on mink farms was rapid, with the estimated duration of outbreaks lasting approximately one month. On farms, minks were typically kept individually in wire mesh cages with solid dividers arranged in long rows. Consequently, direct contact between the minks was limited, and transmission occurred primarily through food contamination or aerosol droplets. Evidence from mink farms confirmed the presence of SARS-CoV-2 in dust samples and in air exhaled by minks at a distance of up to three meters from cages [32]. Based on these studies, it can be concluded that the most likely cause of widespread infection in mink farms is the mechanism of reverse zoonosis, followed by mink-to-mink virus transmission.

Ferrets

Ferrets are commonly used as laboratory model animals. Experimental SARS-CoV-2 infections have demonstrated their susceptibility and ability to transmit the virus to other ferrets [33]. Infected ferrets typically do not show any symptoms of infection; however, flu-like symptoms, such as elevated body temperature and loss of appetite, may occur. A study conducted in Spain included 71 ferrets owned by seven different individuals and tested for the presence of the novel coronavirus between August and November 2020. Oral, throat, and rectal swabs were collected to isolate and detect viral RNA using the qRT-PCR method. Viral genetic material was detected in 6 out of 71 samples, with infected animals belonging to four different owners. Phylogenetic analysis revealed that the spike protein gene sequences found in the infected ferrets closely resembled the SARS-CoV-2 genomes circulating in the human population in Spain at the time. This confirms that natural ferret infections result from human-to-animal transmission of the virus. Ferrets have a lower potential for large-scale infections compared to minks [34].

Wild animals

Felids

Reverse zoonosis of SARS-CoV-2 in wild animals raises concerns globally due to the potential emergence of new virus variants that could be pathogenic to humans and spread through secondary zoonotic transmission. At the Bronx Zoo in New York, clinical signs of infection, such as dry cough and wheezing, were observed in a Malayan tiger on March 27, 2020. A week later, nasal, oral, and throat swabs, as well as tracheal wash samples, were collected from the tiger. On April 3, similar symptoms were observed in three other tigers: a Malayan tiger and two Amur tigers. These animals were subsequently isolated, and no other animals in the zoo exhibited respiratory symptoms. All samples collected from the first infected tiger tested positive for SARS-CoV-2 by qRT-PCR and genetic sequencing. On April 15, tests conducted on a lion that had been in contact with the infected tiger also confirmed SARS-CoV-2 infection. All animals experienced mild illness and recovered. It is believed that the infections were caused by an asymptomatic zoo worker [19]. In July 2020, two pumas and three lions at a zoo in South Africa were diagnosed with SARS-CoV-2. The pumas exhibited gastrointestinal symptoms such as diarrhea, as well as respiratory symptoms like dry cough. Almost a year later, similar symptoms appeared in lions at the same zoo. RT-PCR tests confirmed SARS-CoV-2 infection in all affected animals. The symptoms in these animals ranged from mild signs similar to flu, including eye and nasal discharge, to more severe cases such as respiratory distress and bronchopneumonia in a lion. Antibiotic treatment was ineffective, but significant improvement was observed after administering nonsteroidal anti-inflammatory drugs (NSAIDs) and corticosteroids. The infected animals also received vitamin supplements and doxycycline to address secondary bacterial infections. Despite prolonged virus shedding, all infected felids recovered within 15–25 days. An epidemiological investigation found that two zoo employees had tested positive for SARS-CoV-2 around the same time the lions fell ill. Genetic sequencing and phylogenetic analysis confirmed that the viral samples from the staff and lions were nearly identical, indicating human-to-animal transmission. However, identifying the exact source of infection was challenging as none of the staff in direct contact with the infected cats presented COVID-19 symptoms [35]. A similar scenario occurred on October 12, 2020, at Knoxville Zoo in Tennessee, involving three Malayan tigers. Initially, the tigers exhibited mild symptoms such as coughing, lethargy, and loss of appetite, but they gradually recovered [19]. In late November 2020, SARS-CoV-2 infections were reported in three snow leopards at the Louisville Zoo. One leopard initially exhibited wheezing, followed by a dry cough in the second animal. A week later, mild symptoms were also observed in the third snow leopard. On December 4, fecal samples were tested using RT-PCR, and all were positive for SARS-CoV-2. Subsequently, the leopards were quarantined. Initially, they were housed in separate enclosures but had access to a shared outdoor space. A week before symptoms appeared in the first leopard, a zookeeper responsible for their care tested positive for SARS-CoV-2, confirming human-to-animal transmission. Since then, numerous cases of infections and fatalities associated with SARS-CoV-2 have been reported in snow leopards in zoos across four U.S. states: California, Nebraska, South Dakota, and Illinois. Transmission in these cases was attributed to human-to-animal contact. The virus variants found in zoo animals evolved alongside the pandemic, with both the original strain (in Kentucky and California zoos) and the Delta variant (in Nebraska, South Dakota, and Illinois zoos) infecting snow leopards. During the Delta wave of the pandemic (August 2021–January 2022), this variant dominated both human and animal infections in the U.S. Several snow leopards succumbed to the Delta variant, though the reasons for the severe course of the disease and poorer outcomes remain unclear, especially in snow leopards [36]. In Poland, Warsaw Zoo reported the death of a snow leopard in 2022 after exposure to SARS-CoV-2. Despite exhibiting respiratory symptoms, RT-PCR tests on samples of the animal’s mouth and nose returned negative results. The female snow leopard ultimately died due to respiratory failure, with a human presumed to be the source of infection [37].

Primates

On January 11, 2021, the presence of SARS-CoV-2 was detected in three gorillas at the San Diego Zoo Safari Park in California. After two of the primates developed a cough, fecal samples were collected from them and other gorillas to confirm the infection with the novel coronavirus. Ultimately, SARS-CoV-2 infection was confirmed in eight gorillas at the zoo. A 48-year-old adult male gorilla exhibited severe respiratory symptoms, while the younger animals experienced mild symptoms of infection. Despite the precautions taken by the zoo, it is suspected that the gorillas were infected by an asymptomatic staff member with COVID-19 [38][39]. Between 2020 and 2023, a study was conducted in Spain to examine non-human primates for SARS-CoV-2 infection by collecting serum samples. A total of 127 animals from 30 different species, housed in 17 zoos, were tested. Between February and May 2022, fecal samples were also collected. SARS-CoV-2 infection was detected in two western lowland gorillas in 2020 and 2022. Serum samples from these two gorillas contained antibodies against both nucleocapsid and spike proteins from SARS-CoV-2. The first infected gorilla exhibited a dry cough, while the second gorilla showed no symptoms of infection. These findings emphasize the need for active screening and monitoring efforts to prevent the emergence of unknown viral reservoirs and potential viral evolution. Based on these cases, it can be concluded that reverse zoonosis from asymptomatic zoo staff poses a risk to large cats and primates living in zoos. The potential transmission of the Delta variant of the coronavirus could result in more severe symptoms in these animals. Furthermore, prolonged viral shedding may facilitate the spread of the virus to other nearby animals [40].

Deer species:

White-tailed deer (*Odocoileus virginatus)*

From November 2021 to April 2022, studies were conducted in the United States to investigate SARS-CoV-2 infections in wild white-tailed deer. Samples were collected from 8,830 animals and viral genetic material was detected in 944 samples. The primary mode of infection was found to be human-to-deer transmission, as evidenced by the identification of precursor virus sequences originally found in humans within samples collected from the deer population. Phylogenetic analyses indicated that reverse zoonotic transmission occurred at least 109 times among the tested animals. Additionally, cases of deer-to-deer transmission were observed, as well as the transmission of the virus from an infected deer back to humans [41].

Prevention of infections

To prevent the transmission of infections from humans to animals, personal protective measures such as face masks, disposable gloves, and protective suits should be used. Hand and footwear disinfection is also crucial, which can be ensured through the use of special disinfectant mats. A subunit vaccine for animals has been developed using the SARS-CoV-2 spike protein. This vaccine works similarly to the Novavax vaccine, which was conditionally approved for human use by the European Medicines Agency on December 20, 2021.

The vaccine consists of the S1 spike protein and the receptor-binding domain (RBD) protein. The efficacy and safety of the vaccine were tested on Beagle dogs. [42] The animals were divided into three groups: a negative control group and two experimental groups. The first experimental group received an adjuvant-containing vaccine, while the second experimental group received a vaccine containing both the adjuvant and a stimulant. In the negative control group, PBS (phosphate-buffered saline) was administered instead of the vaccine. Each vaccine was injected subcutaneously on the first day, with a second dose administered in the same way after three weeks. Blood samples were collected for analysis on the day of the first and second vaccinations and two weeks after the second dose. The animals' weight and body temperature were also monitored. No side effects were observed after vaccination. Serum antibody tests showed that antibody titers significantly increased in both experimental groups after the second vaccination. The group that received the vaccine exhibited a six-fold higher antibody production rate. Although no challenge tests involving exposure to the virus were conducted, antibody levels suggest a protective potential against SARS-CoV-2 infection.

Thus, the application of this vaccine in pets could help reduce the risk of reverse zoonosis [42].

Proper implementation of biosafety measures and use of personal protective equipment are crucial to preventing future transmission of SARS-CoV-2 from animals to humans.

Conclusion

Cases of SARS-CoV-2 reverse zoonosis have been identified in many animal species across different countries worldwide. Studies suggest that the SARS-CoV-2 can infect domestic, wild and farmed animals. It has been confirmed that dogs, cats, tigers, lions, pumas, snow leopards, primates, minks, ferrets, and even cattle are susceptible to SARS-CoV-2 infection and can contract the virus through contact with humans. Research indicates that pets living in households with COVID-19 positive individuals are at increased risk of infection, which can be transmitted to other animals. Genetic analyzes of viral material have shown that, in some cases, the virus genome was identical in both animals and humans with whom they had contact, confirming human-to-animal transmission. To better understand how the virus spreads among host populations, guidelines should be established for the monitoring and intervention of wild, captive, and domestic animals infected with SARS-CoV-2. The COVID-19 pandemic has presented a global challenge and highlighted the importance of cooperation between global healthcare systems. It has also led to significant changes in social habits and professional practices. To address widespread concerns related to environmental and public health issues, effective collaboration between medical doctors and veterinarians, supported by biologists and ecologists, is essential for both research and practical applications.

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