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How one pandemic led to another: was African swine fever virus (ASFV) the disruption contributing to severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) emergence?

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Abstract

The spillover of a virus from an animal reservoir to humans requires both molecular and ecological risk factors to align. While extensive research both before and after the emergence of SARS-CoV-2 in 2019 implicates horseshoe bats as the significant animal reservoir for the new human coronavirus, it remains unclear why it emerged at this time. One massive disruption to animal-human contacts in 2019 is linked to the on-going African swine fever virus (ASFV) pandemic. Pork is the major meat source in the Chinese diet. We hypothesize that the dramatic shortage of pork following large-scale culling and restrictions of pig movement (resulting in marked price increases) led to alternative sources of meat and unusual animal and meat movements nationwide, e.g., involving wildlife, and thus greatly increased opportunities for human-sarbecovirus contacts. Pork prices were particularly high in southern provinces (Guangdong, Guangxi, Fujian, Jiangxi, Hunan, and Hubei), where wildlife is farmed and more frequently consumed. Major wildlife farming provinces are spread from Northern to Southern China, which overlaps with horseshoe bat host ranges, potential hosts of the proximal SARS-CoV-2 ancestor, and wildlife sourcing provinces of Wuhan Huanan market and possibly other markets. Trading of SARS-CoV-2 susceptible wildlife in these markets, such as minks, raccoon dogs, foxes and palm civets in Wuhan markets, could have increased the risk of SARS-CoV-2 from an intermediary host. Moreover, large quantities of animals raised for fur could have entered the human food chain undetected and significantly increased risks of animal-human contact. Performing retrospective testing of stored susceptible animals and their meat sold before December 2019 may be helpful in the next stage of tracing the animal origin of SARS-CoV-2 as spillover events are more likely to have taken place in 2019 when China was experiencing the worst effects of the ASFV pandemic.

Keywords

African swine fever virus (ASFV); Pork shortage; Alternative meat consumption; Human-wildlife contact; Zoonotic spillover; SARS-CoV-2

Introduction

SARS-CoV-2, a sister lineage of SARS-CoV from the *Sarbecovirus* subgenus of *Betacoronavirus*, emerged in Wuhan city, China, in late 2019 with many cases associated with the Huanan Seafood Market(World Health Organization, 2021). While it is ambiguous whether the Seafood market is the only source of spillover events (due to early COVID-19 cases not linked to the market), epidemiological data categorically confirm Hubei province as the probable epicentre of the SARS-CoV-2 pandemic. Although there are numerous studies exploring the natural origins of the new coronavirus(Andersen, Rambaut, Lipkin, Holmes, & Garry, 2020; Boni et al., 2020; Latinne et al., 2020; Wacharapluesadee et al., 2021; Y.-Z. Zhang & Holmes, 2020; H. Zhou et al., 2020; P. Zhou et al., 2020), it remains unknown from where and how SARS-CoV-2 was introduced to Wuhan city(Holmes et al., 2021). We propose that uncovering the origins of zoonotic pathogen emergence like SARS-CoV-2 should have a socio-economic perspective, i.e., it is important to consider the broader societal factors that contribute to virus emergence and any changes that might have increased the probability of spillover.

There are several important barriers to be overcome for a successful zoonotic spillover event: sufficient opportunities for animal-human transmission, environmental and demographic barriers linked to ecological factors and host receptors and other molecular factors determined by host biology and immunity(Parrish et al., 2008; Plowright et al., 2017). Assuming a human-adapted or generalist zoonotic pathogen already capable of circumventing human-host barriers, ecological factors will play a key role in the chance of viral emergence. The interaction between the zoonotic pathogen and a susceptible human population with sufficient density for onward transmission, such as a mega city like Wuhan, is an important precondition for successful spillover and subsequent epidemic/pandemic. Human-induced changes can promote increased animal-human contact: human behavioral change, e.g., choosing alternative meat sources or travel to remote locations, and land-use changes, which can be compounded as a result of socio-economic disruptions(Tong Wu et al., 2016).

Prior to the COVID-19 pandemic in 2019, the pork crisis has resulted in a change in animal meat consumption in China, which has significantly increased animal-human contact particularly of wildlife(Mason-D’Croz et al., 2020; Maria Cristina Rulli, D’Odorico, Galli, & Hayman, 2021). The changes in meat availability in China is a consequence of another ongoing pandemic, driven by African swine fever virus (ASFV) infections in pigs and wild boars. It first reached Liaoning, Northeast of China on 3 August 2018, roughly one year before the current COVID-19 pandemic(Blome, Franzke, & Beer, 2020; Vergne et al., 2017), likely via infected wild boars or pork products. ASFV outbreaks in pigs have appeared several times in Europe since 1955 as a result of spread from Africa, where ASFV is endemic. ASFV was first described in East Africa where it has predominantly a sylvatic cycle (only infecting wildlife)(Eustace Montgomery, 1921). The current ASFV pandemic appears to have begun in Georgia, Europe in 2007 linked to travel to Africa (where ASFV is endemic) and since then has spread globally. China was the first country in Asia to report ASFV cases, but subsequently many more farmed and wild pigs in Asian countries have been infected. ASFV is a double stranded DNA virus of the genus *Asfivirus* in the *Asfiviridae* family and it causes, African swine fever (ASF), is a viral hemorrhagic disease with almost 100% lethality for which there is currently no vaccine or effective treatment. Culling is the only effective way to contain ASFV transmissions in pigs(Blome et al., 2020).

Here we demonstrate that large-scale domestic pork shortages in China due to the nationwide ASFV epidemic, resulted in culling and provincial control measures abruptly breaking the regular meat supply chain and meat consumption structure, likely triggering massive and unusual animal and meat movements through food supply and cold chains. This disruption will have significantly increased the risks of human contact with the infected wildlife animals, their meat, contaminated meat and/or other susceptible animals. Additionally, human encroachment into once rural areas in China have increased significantly in recent years due to urbanisation and poverty reducing programs(Department of Transport of Yunnan Province, 2019). The significantly expanded transportation network with nationwide links has placed once remote locations in much closer proximity to mega cities, increasing contact opportunities between reservoir hosts, such as bats and other potential intermediate animals, and humans(Tong Wu et al., 2016). Coupled with farming in rural areas, the trading of these live animals or live trapped animals in city markets increases the risk of animal to human spillover of respiratory viruses. We hypothesise these frequent movements of alternative meat sources, their cold/supply chain workers and consumers, via well-connected high-speed road and railway networks, resulted in a successful spillover transmission of the SARS-CoV-2 progenitor in Wuhan possibly on more than one occasion.

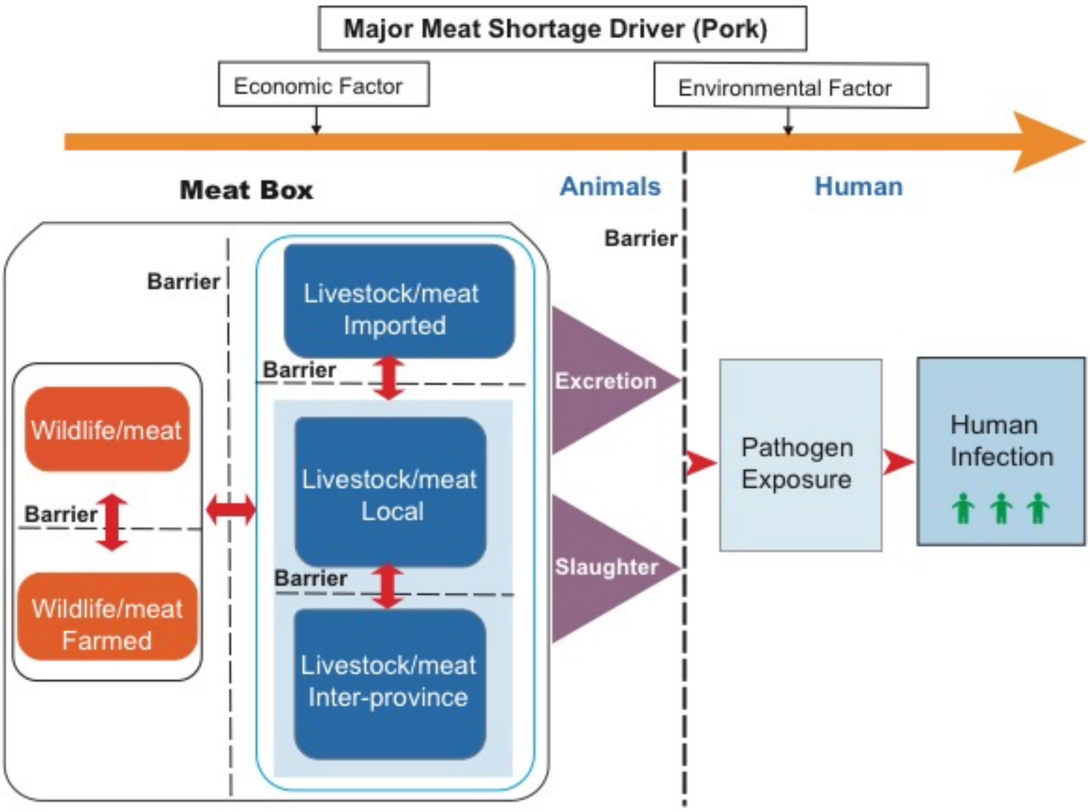

Figure 1. Major pork shortage increased human contact opportunities with SARS-CoV-2 infected wildlife or farmed animals. This illustration shows that a major meat shortage with significant cultural and economic importance, such as pork in China, may reduce the barriers at many levels that usually stop spillovers and sustained animal-human zoonotic transmissions. These barriers usually restrict the zoonotic pathogens from reaching more susceptible or larger human populations. Alternative meat through supply/cold chains, such as wildlife animals, can frequently 'break' the barrier between animals and humans, increasing zoonotic spillover(Plowright et al., 2017).

Results and Discussion

Pigs are economically and culturally important in China(Dong, Brown, Waldron, & Zhang, 2018; G. Zhou, Zhang, & Xu, 2012) (Supplementary Notes and Supplementary Figures 1-6). Here, we propose four drivers that may explain how the ASFV's introduction to China may have contributed to SARS-CoV-2's emergence in Wuhan, a city in Central China >1500 Km from Yunnan where its closest evolutionary related horseshoe bat coronavirus was sampled in China(Lytras, Hughes, Xia, Jiang, & Robertson, 2021) and a distance of >1800 Km for the closest virus outside of China in Laos(Temmam et al., 2021). Note, the divergence of these closest bat *Sarbecoviruses* from the SARS-CoV-2 progenitor (corresponding to many decades of evolution) indicates the viruses that emerged in Wuhan is not necessarily from Yunnan and that sampling should be widened to other areas horseshoe bat species reside in China(Zhiqiang Wu et al., 2021), and neighboring Southeast Asian countries(Zhiqiang Wu et al., 2021; H. Zhou et al., 2021). It is also possible there were multiple spillover events in Wuhan or just at the Huanan Seafood market as SARS-CoV-2 is inferred to have been circulating prior to its first association with the Huanan Seafood Market(Holmes et al., 2021; Pekar, Worobey, Moshiri, Scheffler, & Wertheim, 2021). This is indicative of infected live animals or infected carcasses or meat being introduced into Wuhan multiple times from a single source under the influence of pork meat shortage. The ASFV infections profoundly changed the structure of the Chinese meat market in the following ways: (1) causing a dramatic drop of pork supply, (2) a sharp rise and volatility in the pork prices, (3) new governmental regulations on pig and pork transportation, and (4) increased use of wildlife. These drastic changes triggered the unusual movement of animals and their products, either live, chilled, frozen or processed, which indirectly increased the contact probability between humans and SARS-CoV-2 infected animal hosts or contaminated products.

Dramatic drop of pork supply in China since 2018

China produces approximately 50% of the world's pigs. This corresponds to over 700 million hogs and ~55 million metric tons of pork annually, forming an industry worth over $128 billion(Mason-D'Croz et al., 2020; Woonwong, Do Tien, & Thanawongnuwech, 2020). ASFV infections had spread to 31 provinces/regions, almost the entire country, by the fourth quarter of 2019. Immediately before the Wuhan SARS-CoV-2 outbreak, there were 160 reported ASFV outbreaks nationwide, among which 157 were domestic pig herds and the other three were in wild boars, according to the Ministry of Agriculture and Rural Affairs (MARA)(MARA, 2019a) (Figure 2a). Since the first case in August 2018, the Chinese governments culled pigs within a 3 km radius of any infected farms and adopted more stringent quarantine procedures, fast testing and reporting systems, and strict regulations on across-province transportation of live pigs and pork products (more regulation details in Supplementary Table S1)(T. Wang, Sun, & Qiu, 2018).

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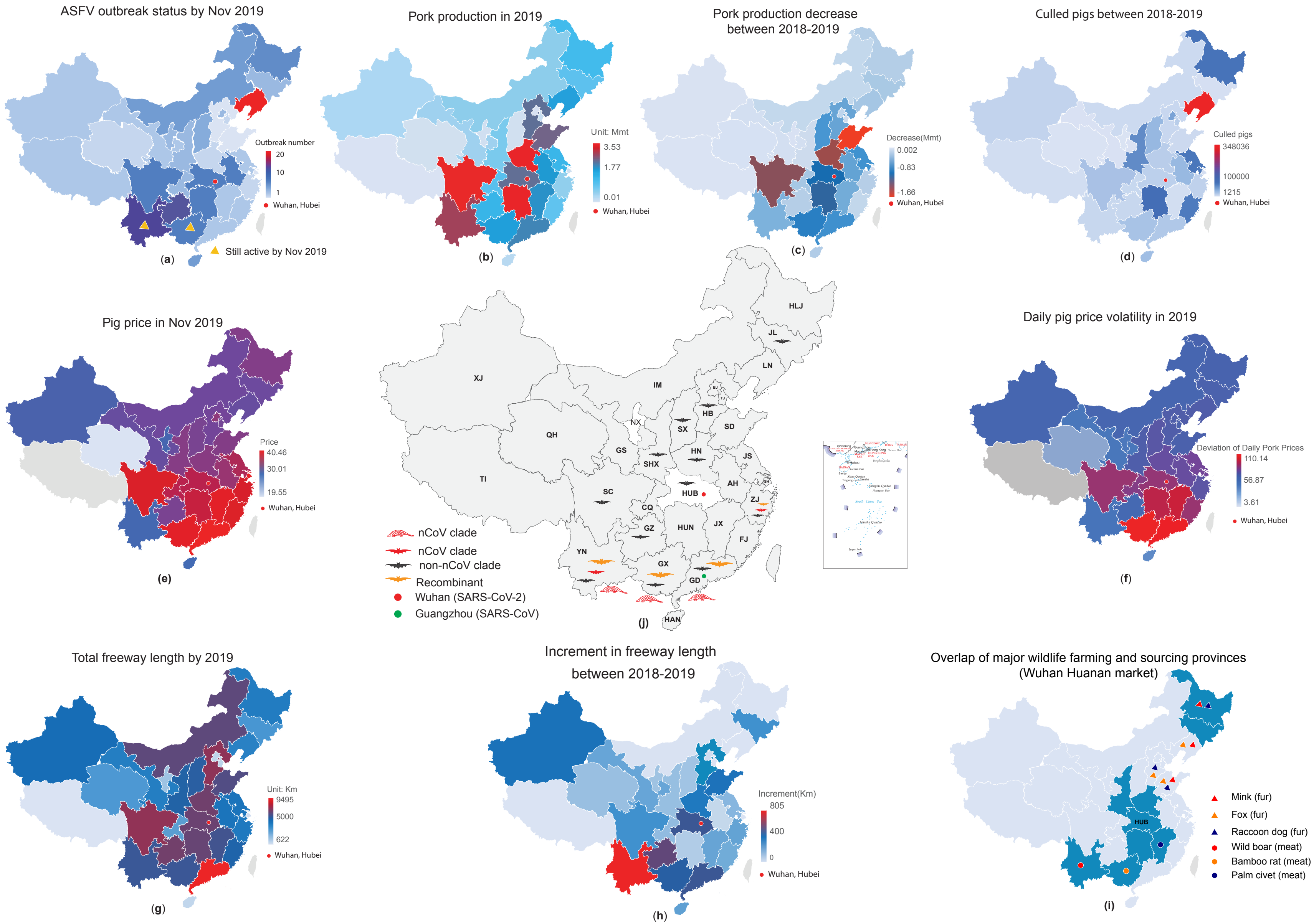

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Figure 2. Linking ASFV outbreaks, pig production/reduction/culling/prices, freeway network length, wildlife farming and trading, and sampling locations of sarbecovirus genomes (some of which are identifiably recombinants) among provinces in 2019 right before the SARS-CoV-2 emergence in Wuhan. Data for Hongkong, Macao, and Taiwan are not included. (a) The number of ASFV outbreaks and status as of November 2019 with Yunnan and Guangxi province still active; red and purple indicate more outbreaks. (b) Pork production in million metric tons (Mmt) in 2019; Hubei province located in the center with the three largest pig producers. (c) Decrease of pork production in million metric tons (Mmt) in 2019 compared to 2018. (d) The culled infected pigs between August 2018 and November 2019. (e) The average pig price in November 2019. (f) Price volatility in each province in 2019, an indicator for the stability of the pork market and prices, calculated by deviation of daily prices. (g) Total freeway length in each province in kilometers by the end of 2019. (h) Increment in freeway length in each province in kilometers in 2019. (i) Overlap of major wildlife farming and Wuhan Huanan market wildlife sourcing provinces; triangle and circle symbols denote major provinces farming for fur (mink, fox and racoon dog) and meat (wild boar, bamboo rat and palm civet), respectively. Huanan market wildlife sourcing provinces are colored in dark blue(World Health Organization, 2021; Xiao, Newman, Buesching, Macdonald, & Zhou, 2021). (j) Sampling locations of sarbecovirus genomes of SARS-CoV-2 related ('nCoV') or non-related (non-nCoV) lineages. Pangolin (red) and Bat (red) indicate the nCoV linages, Bat (black) indicates non-nCoV related lineages and Bat (orange) indicates recombinants between nCoV and non-nCoV lineages(Lytras et al., 2021). XJ: Xinjiang, TI: Tibet, GS: Gansu, QH: Qinghai, SC: Sichuan, YN: Yunnan, IM: Inner Mongolia, NX: Ningxia, SHX: Shaanxi, CQ: Chongqing, GZ: Guizhou, GX: Guangxi, SX: Shanxi, HN: Henan, HUB: Hubei, HUN: Hunan, GD: Guangdong, HLJ: Heilongjiang, JL: Jilin, LN: Liaoning, BJ: Beijing, TJ: Tianjin, HB: Hebei, SD: Shandong, JS: Jiangsu, AH: Anhui, SH, Shanghai, ZJ: Zhejiang, JX: Jiangxi, FJ: Fujian, HAN: Hainan.

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Consequently, the Chinese pork industry has suffered a great loss as a result of the ASFV epidemic (Figure 2b-c)(T. Wang et al., 2018). A total of ~1.2 million infected pigs had been culled by the end of November 2019 (including Hongkong SAR) (Figure 2d). Government data indicate a decrease between 118 and 175 million pig inventories in 2019, i.e., 27.6% to 41% year-on-year and 11.5 million metric tons reduction of pork output(MARA, 2019b; National Bureau of Statistics of China, 2020). The scale of reduction in pork production varied greatly among provinces, which was significantly worse in large production provinces (Figure 2b-c). Interestingly, although Shandong was not the largest producer in 2019 (Figure 2b), it suffered the largest reduction in pork production (Figure 2c), followed by Henan, Sichuan, Hunan and Hubei. Meanwhile, Yunnan, as a large pig producer, experienced more ASFV outbreaks than others but had a relatively small decrease in the pork output. Nevertheless, the scale of the ASFV outbreaks and pig losses are considered to be underestimated(Costard, Zagmutt, Porphyre, & Pfeiffer, 2015; Inouye, 2020). The pig industries estimated that the number of infected pigs could be as high as 200-400 million heads, equivalent to ~40-60% of the total pig population(Rabobank, 2019).

The Chinese government enacted a series of policy tools to restore the domestic pig production with strong fiscal supports and favorable policies for large-scale pig farms. However, the life-cycle constraints of pig growth and losses in the breeding sow weakened the ability to secure the short-term pork market supply. The government also released frozen pork stock to the markets during holiday seasons or in response to extraordinary disparity between the actual and target PGR (pork-grain-price ratio) and expanded the international meat and seafood imports as well (Supplementary Notes). But the increase from pig restoration, other livestock and aquatic food production, and international imports only covered a fraction of the ASFV-associated pork losses in the short term. Consequently, China, especially the southern and

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eastern provinces as traditional large pork consumers, were experiencing a severe pork supply shortage in the wintertime of 2019 (Figure 2b).

Major meat shortages, such as pork crisis in a large market in China in 2019, have significant ecological, socio-economic and zoonotic consequences, which likely contributed to the use alternative animal meat either farmed or trapped entering the human food chain. The introduction and spread of ASFV in China resulted in tremendous damage to the pig industry. Containment measures in line with the World Organisation for Animal Health (OIE) guidelines, such as pig culling and regional blockades(Ding & Wang, 2020) exacerbated regional imbalance in the pork supply and pork prices. Under this circumstance, alternative animal and meat movements across provinces and national borders were difficult to avoid. Banning hog movements and promoting cold chain meat supply had been proven to be an effective way for curtailing persistent ASFV transmission and easing the pork crisis. Is it coincidental that another zoonotic spillover SARS-CoV-2 has emerged as the wholesale pig price reached a historic peak between mid-October and mid-November 2019(Pekar et al., 2021)?

Sharp rise in pork price and strong geographical imbalance

The price of pork rose strikingly, more than doubling, between January and October, coincidently before the SARS-CoV-2 outbreak. Prior to 2019, the mean national wholesale pig price was below 20 Yuan/kg on average (Figure 3) and the price disparity among provinces was minimal (grey shading in Figure 3). After ASFV infections spreading from Northern to Southern China from August 2018, the disparity in the wholesale pig prices among provinces increased sharply (Figure 2f and Figure 3).

In October 2019, average wholesale pig prices rose by ~150% from the previous year ago (Figure 3). Between mid-October and mid-November 2019, which was the likely

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period when the first case contracted SARS-CoV-2 in Hubei(Pekar et al., 2021), the average wholesale pig price nationwide had risen to ~35.4 Yuan/kg, the highest in history, compared to ~13.6 Yuan/kg in 2018(Ministry of Commerce, 2021). On average, a fattened live pig weighing 100kg was priced ~3500 Yuan in the wholesale market. To put this in context, the average annual per capita disposable income for Chinese rural residents was ~14,600 Yuan in 2018(National Bureau of Statistics of China, 2019a). Facing tough inflation pressure, the Chinese government has been releasing strong market signals that governmental pork reserves and imported pork would enter the market. In response, pork prices kept going down rapidly. By the end of November, the average pig price dropped to 32.1 Yuan/kg, i.e., 10% drop in just two weeks. This represents at least ~300 Yuan loss in net profit per pig, a large margin compared to the average Chinese household income level. This led to the expectation that pork prices would drop dramatically. Stakeholders along the pig supply chain rushed to slaughter fattened pigs and to sell their frozen inventory(Patton & Gu, 2019).

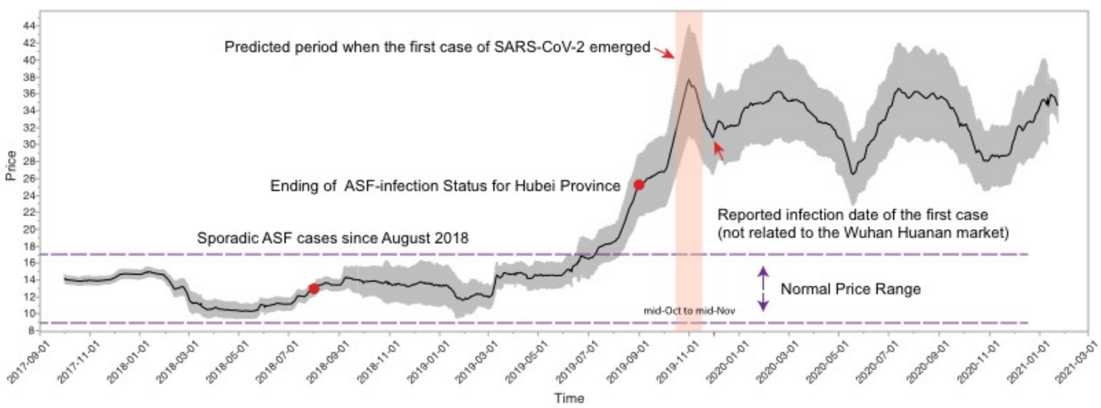

Figure 3. Dramatic increase in wholesale pig price among provinces in China, 2017-2020. Red arrow on the left side of the price peak pointing to the light red bar indicate the predicted period (mid-October 2019 to mid-November 2019) of the first case emerged in Hubei(Pekar et al., 2021). Red arrow on the right of the peak shows the reported date of the first confirmed SARS-CoV-2 case contracting the virus that is not linked to the Huanan market in Wuhan(Q. Li et al., 2020). The black line indicates the average price, and the grey bars indicate standard deviation of the prices in all provinces. By the end of November, Yunnan and Guangxi were the only two

provinces still in ASFV-infection list with blockade measures for outwards pig movements while the other 29 provinces/cities were officially ASFV-free and free for hog and pork movements. Data source: China Pig Web, https://hangqing.zhuwang.cc/shengzhu/list-63-83.html.

Before the ASFV outbreak, the pig prices were relatively similar among provinces as indicated by smaller price standard deviation (Figure 3). However, in 2019, pig prices showed strong geographical disparity, especially in November (Figure 2f and Figure 3). Prices were double in Southern (Guangxi and Guangdong), Eastern (Fujian and Zhejiang), Central (Hunan, Jiangxi and Hubei) and Western China (Sichuan) than in the rest of China (Figure 2f). Daily hog price fluctuated intensely throughout 2019 (Figure 3). Strikingly, pig price fluctuated more dramatically in southern China (Guangxi, Guangdong), extending to part of Western (Sichuan), Central (Jiangxi, Hunan and Hubei) and Eastern (Fujian) China, compared to the rest of China (Figure 2f). Importantly, these provinces (e.g., Guangxi and Guangdong) with much higher pig prices and volatility traditionally consumed much more wildlife than the rest of China(China Development Brief, 2020; Meng, Lu, Yin, & Xu, 2009). Moreover, these provinces overlap with the host range of the four potential hosts of the proximal SARS-CoV-2 ancestor, *R.affinis*, *R.sinicus*, *R. ferrumequinum*, *R. malayanus and R. pusillus* (Lytras et al., 2021; H. Zhou et al., 2021). It is notable that in Yunnan, a major pig producer in Southern China, which were still under the government ASFV restrictions for shipping out pigs and pork products due to two ASFV outbreaks by the end of October 2019, pig prices stayed among the lowest range, 8-9 Yuan/kg cheaper than the surrounding Sichuan and Guangxi (Figure 2a-f). It is conceivable that illegal movements of meat to other regions of China from Yunnan have taken place.

Regulation on pig and pork transportation across provinces

After confirming the first ASFV outbreak in Shenyang on 3rd August 2018, MARA launched the Level-II emergency response and issued several policies and regulations in the hope to halt further ASFV transmission(Food and Agriculture Organization, 2018; MARA, 2018; T. Wang et al., 2018). One of the most important measures was movement restrictions on live hogs, pork, and pork products from affected areas or regions (Supplementary Table S1). MARA also announced intensified requirements and inspections on pig and pork product transportation vehicles(Food and Agriculture Organization, 2018). At first, authorities primarily suspended the movement of hogs and related pork products from the epidemic zone Shenyang City(MARA, 2018). This measure may not have been sufficient to control ASFV transmission from Northeastern China to the rest of the country.

Regional controls/blockades have tremendous influences on regional pork supply and demand balance, especially on the mega cities with a large population but limited pig farming.(Sun, Li, & He, 2020). Due to rapid economic development, urbanization and governmental interventions for environmental protection and industrial development since 2016 (details in the Supplementary Notes), China's pork production has gradually shifted from southern and eastern regions towards northeast and southwest parts (Figure 2b)(Z. Bai et al., 2020; D. Han, Jin, Hu, Wu, & Chen, 2019; Sun et al., 2020). However, south China traditionally consumes a larger volume of pork than north China(Mason-D'Croz et al., 2020). Hence, long distance transportation of live pigs and pork products is unavoidable[36]. Prior to 2019, inter-provincial pig trade was largely in the form of live pig shipment due to the limited capacity of agricultural cold supply chain(Zhao, Liu, Tian, Yan, & Wang, 2018). There were 100~102 million (14~19%) live pigs transported across provinces before the ASFV outbreaks in 2018(Sun et al., 2020). Sudden restrictions and bans on inter-provincial transportation of live pigs inevitably worsened the imbalance of local pork supply and demand.

In seeking to contain ASFV spread and protect pork supplies, central Chinese government promoted chilled and frozen pork through cold chain rather than shipping live pigs. Pig transportation benefited from the Green Channel policy with discounted freeway toll fees, which extends the span of the pig supply chain across provinces(Z. Bai et al., 2018; Zhao et al., 2018). However, during ASFV outbreak period, the Green Channel policy for pigs and pork products had been deactivated since October 26th, 2018. Not until 10th September 2019, did the Chinese government release an announcement that piglets and chilled pork were officially permitted to enjoy the Green Channel policy again, while frozen pork and breeding sows would have the freeway toll-fee waived between 1 September 2019 and 30 June 2020(China State Council, 2019) (Supplementary Notes and Supplementary Table S1).

Long distance transportation of live animals and meat products mostly relies on ground transportation, especially the freeway network. During 2010 and 2015, the registered number of refrigerated trucks increased from 26 to 81 thousand(Zhao et al., 2018). As of 2019, the total length of China's freeway network measured ~150 thousand kilometers (Figure 2g), the world longest by length(National Bureau of Statistics of China, 2020). Around 42% of the increase compared to 2018 were from Southern China, including Yunnan, Guizhou, Guangxi, Guangdong and Hubei (Figure 2h). Importantly, Yunnan ranked at the top with an increase of 805 Km reaching a total length of 6003 Km in 2019. This increase in the road network connects once remote areas with modern cities(Chu, 2014; Department of Transport of Yunnan Province, 2019), and forms a transportation network with seven inter-provincial and five trans-national freeways, connecting Myanmar, Vietnam, Thailand and India(Yunnan Government, 2019).

The regulatory policies tackling ASFV outbreaks and the rapidly expanding of national freeway network jointly facilitate the development of meat cold chains. Cold chains successfully extend the storage time and transportation distances. Previous studies found that third-party cold chain logistic companies transport fresh agricultural products in a mixed way suggesting cross-contamination is possible if SARS-CoV-2 infected animal carcasses or their products are also transported(J. Han, Zhang, He, & Jia, 2020; Zhao et al., 2018), as this can reduce transportation cost(Huang, 2020). Inspired by the favorable policies for frozen pork meat waiving off the toll fees since the middle September 2019, cold chain service providers likely run pork meat or any other meat business including farmed/illegal wildlife at the same time. Intensive new freeway constructions nationwide in recent years, especially in Central and Southwest China, such as Hubei, Yunnan, Guangdong, and Guizhou provide infrastructure for meat cold chain movements (Fig 2h). Road construction stretching to remote and isolated areas, in pursuit of poverty reduction and economic development connects these impoverished rural areas to modern and population-dense regions, leading to extensive human encroachment into these regions and potentially increased contact with new pathogens like SARS-CoV-2.

Wildlife farming, consumption and trafficking

To understand whether wildlife or farmed animals could be a potential source for alternative meat during pork shortage and price rises, the legal and economic status of wildlife market in recent years in China are investigated.

The basic principle of China's laws regarding wildlife issues is a dual track of necessary protection and rational utilization(M. You, 2020). Wildlife Protection Law (2018) before the COVID-19 pandemic focused on the protection of endangered and precious terrestrial and aquatic wildlife, and wildlife with important ecological, scientific and social values(NPC Standing Committee, 2018). It was illegal to hunt, kill, purchase, transport and sell these strictly state protected species. Meanwhile, it was legal to hunt, slaughter, trade and consume wildlife other than these two protected categories with relevant legitimate licenses and proofs abiding by the requirements of the Wildlife Protection Law (M. You, 2020). Various wildlife had been legally permitted to be artificially bred and farmed for commercial purpose with a special wildlife breeding or farming license, and to be traded in the markets with a special business license issued by the Domestic or National Forestry Administration Office before 2020(M. You, 2020). In 2016, workers engaged in wildlife farming nationwide was reported around 14.09 million, generating an industry worth 520 billion RMB or 80 billion US dollars approximately (Supplementary Table S2)(Chinese Academy of Engineering, 2017). Wildlife farming industry contributes to domestic economy, rural livelihoods, and poverty reduction(F. Bai, 2020; Jiangxi Newspaper, 2019). Therefore, licensed wildlife farming was encouraged in many provinces, especially in low-income provinces with rich natural forest and wildlife resources, such as Shandong, Guangxi, Jiangxi, Guizhou, Yunnan, Jilin, Liaoning and Heilongjiang(F. Bai, 2020; Jiangxi Newspaper, 2019; H. Liu, Li, Li, & Gong, 2020).

Palm civets (*Paguma larvata*), minks (*Neovison vison*), bamboo rats (*Rhizomys sp.*), deer (*Cervus nippon*), raccoon dogs (*Nyctereutes procyonoides*) are the most popular wildlife widely farmed in China. Raccoon dogs, minks, foxes (*Vulpes vulpes/ Alopex lagopus/Vulpes vulpes fulva*) are farmed for furs in northern China, mostly in Shandong, Hebei, Liaoning, Jilin, and Heilongjiang Provinces. According to estimates by the Chinese Leather Industry Association, there has been a steady decrease in pelt production since 2015 (Table 1). The decrease was mostly attributed to mink pelts due to weak demand from the international market(D. Wang & Qing, 2020a). Nevertheless, Shandong province ranked the top with 56.79% pelt production for minks and 40.2% for foxes, and second with 22% for raccoon dogs in 2019(H. Liu et al., 2020). Bamboo rats have been farmed for meat in many southern provinces, with a large volume in

Guangxi province(F. Bai, 2020), while palm civets have also been widely farmed, at large scale in Jiangxi, Guangdong and Guangxi provinces(Zhu, Tian, & Wu, 2017). These wildlife farms were running with poor hygiene conditions and weak epidemic prevention measures with insufficient immunization(H. Liu et al., 2020). Bamboo rats and palm civets have been sold for foods mostly alive. Unfortunately, there were no strict sanitary and quarantine standards, inspection systems, regulatory authorities for processing, transporting and selling of farmed wildlife like those for livestock animals, placing unprecedented risks for emerging zoonotic pathogens and animal-human transmission(F. Bai, 2020; Xue, 2020).

Table 1. National pelt production number in China between 2015 and 2019(D. Wang & Qing, 2020b). Population size for these three farmed fur animals can be roughly estimated from their pelt numbers.

Unit: Millions

	2015	2016	2017	2018	2019
Mink	44.5	26.2	20.6	20.7	11.7
Fox	14.5	12.7	14.1	17.4	14.4
Raccoon Dog	16.1	14.7	12.4	12.3	13.6
Total	75.1	53.6	47.1	50.4	39.7

Source: China Leather Industry Association statistical reports(D. Wang, 2016, 2017, 2018, 2019; D. Wang & Qing, 2020a).

Consumption of wildlife (including farmed wildlife) is active in China and expanding at high speed due to the combined effects of increasing household income, a culture of medicinal use and commercial cultivation and utilization of regulated wild animals(Liang, Hu, Hu, Zhao, & Lee, 2020). China has become one of the largest wildlife consumers and wildlife trafficking destinations in the global wildlife supply chain. Wild animal trade and consumption takes place more frequently in Southern China, such as Guangdong, Guangxi, Fujian, Hainan and Jiangxi(Meng et al., 2009). A recent joint online survey by several nonprofit organizations in March 2020, on previous experiences of wildlife consumption, suggests that the primary consumption is for eating, followed by raising as pets, decoration, and medical uses(China Development Brief, 2020). Wild birds, snakes, turtles, salamanders, bamboo rats, squirrels, porcupines, deer, and wild boars are popular for food. Most of them were traded as live animals rather than processed products. Due to the rapid development of online shopping platforms in recent years, wildlife consumption has also shifted from traditional wet markets to online trading. These online shopping behaviors were difficult to discover, trace and monitor.

The pork shortage likely broke the barrier between wildlife and regularly consumed animals. Extremely high pork price and other main livestock meats (e.g., red meat such as beef and mutton) make the price of wildlife for foods relatively cheaper than normal periods and wildlife meat substitutes were more favorable in a region where there is already a culture of consuming wildlife. Although the WHO report showed no farmed fur wildlife like raccoon dogs, minks or foxes sold in the Wuhan Huanan market(World Health Organization, 2021), a recently published survey of Wuhan wet markets immediately prior to the December 2019 outbreak showed that all these fur animals and palm civets, all susceptible to sarbecoviruses (e.g., SARS-CoV-1 and SARS-CoV-2), were sold alive for foods(Xiao et al., 2021). They were caged and stacked in poor conditions, sometimes mixed up with different species and could be butchered on site upon request(Xiao et al., 2021). Our analysis shows that there is significant overlap of major wildlife farming and sourcing provinces of Wuhan Huanan market (Figure 2i), which includes wildlife farmed for fur (mink, fox and racoon dog) and meat (wild boar, bamboo rat and palm cat). The population size of these fur animals can be roughly estimated using the annual pelt production number. These are reported for Shandong, Liaoning, Heilongjiang and Hebei in Supplementary Table S3 between 2015-2019.

Although the sourcing provinces for other Wuhan wet markets selling wildlife are currently unknown(World Health Organization, 2021; Xiao et al., 2021), if known this can further increase the current range of the sourcing provinces (Figure 2i).

Table 2. Potential meat quantity from farmed fur animals in 2019.

Species	Carcass weight (kg/head)	Pelt number (million)	Total weight (million kg)	Estimated quantity (million kg)				
				5%	10%	30%	50%	70%
Mink	1	11.7	11.7	0.6	1.2	3.5	5.8	8.2
Fox	10	14.4	144	7.2	14.4	25.8	43.2	100.8
Raccoon dog	3.6	13.6	49	2.5	4.9	14.7	24.5	34.3
Total	/	39.7	204.7	12.3	24.5	61.4	102.3	143.3

Note: (1) Data of the average carcass weight of raccoon dogs are from a previous study(R. Zhang, 2015), taken as the minimum carcass weight, weights from other data source at 5.6-6 kg per individual; Data of mink and fox are from a previous study(M. Xu, Liang, & Liu, 2016); (2) The pelt number were from China Leather Industry Association statistical reports(D. Wang, 2016, 2017, 2018, 2019; D. Wang & Qing, 2020a); (3) The hypothetical quantity range is set between 5%-70%(Y. Zhang, 2015).

The price hike of pork and livestock meat due to severe pork shortages and associated economic losses(S. You et al., 2021) also provides strong incentives of adulterating cheap fur animal meat into the food supply chain, along the major zoonotic risk from live wildlife trade, posing another direction for further investigation. The carcasses of these fur animals are legislated to be safely destroyed. However, in practice some of them were processed into pet foods, or into meat and bone meal as additives, or even were processed into foods for human consumption illegally(H. Liu et al., 2020; Zhaomin Wu et al., 2019; Yang, Zhou, Qu, Lian, & Wan, 2014). The farmed wildlife like raccoon dogs is expensive when sold alive in the wet market, but their carcasses sold at fur farms are much cheaper, ~1.1-2.2 Yuan/kg (~0.17-0.34 USD/kg) according to various surveys(China Daily, 2015; B. Li, 2018; K. Zhang, 2020). Due to pork shortage and the low fur prices in global fur market, there is strong incentive for fur farmers to sell these fur animal carcasses as by-products for extra income. Some of these carcasses were found to be illegally sold as foods(Y. Zhang, 2015), and some of their meats were used as adulterated beef, lamb, donkey, dog meats or mixed into sausages for human consumption before 2019(China Daily, 2015; M. Xu et al., 2016; K. Zhang, 2020). For instance, in June 2014, mink and fox contents were found from mutton products in Shandong by the inspection and quarantine authority of Shandong province(K. Zhang, 2020). To understand potential animal-human contact through these meats, we estimated the quantity of the three farmed fur animal meats entering the human food chain in 2019 (Table 2).

The dramatic pork shortage interrupted the regular meat supply chain and increased risks for zoonotic virus spillovers difficult to observe and manage. The shortage could be as large as ~40-60% of the total pig population. For Wuhan City, slaughtered fattened hogs decreased by ~46%, 770,000 pig head losses with 89,000 tons of pork meat reduction in 2019, while the outputs of other regular meats (livestock, poultry and aquatic products) remained relatively stable(National Bureau of Statistics of China, 2019b). It encourages food producers/sellers to supply wild animals either wild caught or farmed(Xiao et al., 2021), or commit food fraud by producing/selling adulterated livestock meat for higher profit margins(China Daily, 2015; M. Xu et al., 2016; K. Zhang, 2020). As early SARS-CoV-2 cases in Wuhan had exposure to both wet markets that are known to sell susceptible animals for food and modern supermarkets such as RT-market (Dayunfa)(World Health Organization, 2021), testing meat products for adulteration of SARS-CoV-2 susceptible farmed wildlife animals from Wuhan's biggest wholesale agri-food market Baishazhou, which supplies 70% frozen food to Wuhan including individuals, restaurants and traditional wet markets, such as Huanan market(World Health Organization, 2021), could have provided further information regarding the animal origin of SARS-CoV-2. However, this has not been performed(World Health Organization, 2021). Retrospective testing of meat products of remaining stock or unconsumed customer products from early cases sold prior to December 2019 would still provide valuable information. Finally, the pork shortage and extremely high pork price not only change the supply side, but also consumption behavior. Increase in pork price drove consumers to substitute expensive pork meat with alternative meat varieties. National statistics showed that per capita pork consumption in 2019 dropped by 9.1%, while per capita consumption for urban consumers of beef, lamb, poultry, and aquatic products increased by 7.4%, -6.7%, 16.3%, and 16.8% respectively (National Bureau of Statistics of China, 2020). The statistics of meat consumption for Hubei residents or Wuhan residents are unavailable, but the retail price index of the livestock meat in Wuhan rose 30% up in 2019(National Bureau of Statistics of China, 2019b), indicating potential consumption choices for alternative meats or processed meat products whose prices may remain relatively stable, such as frozen meats (e.g., frozen mutton mixed with other meats), and these can be adulterated with cheap wildlife meat from fur farms by sellers(China Daily, 2015; M. Xu et al., 2016; K. Zhang, 2020).

Potential cheap wildlife meats may come from major fur farming provinces (Figure 2i and Supplementary Table S3) and these could be transported nationwide to reach regional hub cities, such as Wuhan. For example, Shandong experienced the largest decline (~1.7 million metric tons) in pork production and indirect economic losses(S. You et al., 2021) among provinces in 2019 (Fig 2c) and it is the largest producer of minks, foxes, and second largest of raccoon dogs in China. A survey in County Changli in Hebei province finds that 70% of the local fur animal carcasses had been reported sold to Shandong province(Y. Zhang, 2015), showing a potential industry of wildlife meat processing in Shandong. Crucially, these active wildlife farming/trafficking regions also overlap with the known horseshoe bat host ranges of the proximal SARS-

CoV-2 ancestor (figure 2j)(Boni et al., 2020; Lytras et al., 2021; Temmam et al., 2021; H. Zhou et al., 2021) and all with well-connected freeway networks for supply/cold chains to reach Central China (figure 2g). Although Shandong is not generally considered in the horseshoe bat host range of the proximal SARS-CoV-2 ancestor, due to climate change, slight expansion of host range of these bat species to include Shandong is not unexpected(Beyer, Manica, & Mora, 2021; H. J. Han et al., 2017), particularly *R. pusillus*, which is known to have a range including Southeast Asia and Southern China, harbouring the closest known SARS-related coronavirus (SARSr-CoV) of SARS-CoV-2(Temmam et al., 2021; H. Zhou et al., 2021). The meats of these domesticated animals, such as minks and racoon dogs in fur farms, which are known to transmit SARS-CoV-2(Freuling et al., 2020; Oude Munnink et al., 2021), or palm civets and bamboo rats farmed for meat, could conveniently act as alternative meat sources, particularly those considerably cheap meats from fur farms(M. Xu et al., 2016).

It is also interesting that SARS-CoV and SARS-CoV-2 emerged at a similar time between November and early December of the year. In China, October is the starting month of the traditional peak season for meat consumption due holiday effects. It is the traditional period for preparing Chinese sausage and other preserved meat from November. In winter, wildlife is also fattened naturally and traded more as luxury meat in Chinese culture. Hence, the outbreak of two sarbecoviruses around the same time of a year may not be a coincidence(Feng et al., 2009; Q. Li et al., 2020). Moreover, November in 2019 was unique. Pig farms and slaughterhouses rushed to sell out their fattened pigs, including frozen meat stock, due to strong expectation of futural price drop. The fur animals like foxes and raccoon dogs are also traditionally slaughtered at large scale from November and the cold chain warehouse nearby are found fully occupied with fresh carcasses(Zheng, 2015). Although coronavirus has potential seasonality for outbreak/transmission(Merow & Urban, 2020), the timing of this ecological/economic disturbance due to severe pork shortage is critical.

All these significantly increased the probabilities of spillover and transmission from horseshoe bat species and other potential intermediate animal hosts to humans. Moreover, China's recent development in globalization, urbanization, and transportation networks further magnify the effect of spillovers(Tong Wu, 2021). Due to significantly increased animal-human contact probability for alternative meat, any animal host or contaminated meat from its place of origin can conveniently reach any mega city with an immunologically naive population to initiate a successful zoonotic transmission and subsequent pandemic(Parrish et al., 2008; Ruan, Wen, He, & Wu, 2020), especially in a dense urban setting like Wuhan.

Conclusion

A highly contagious animal virus infection like ASFV focused on a major livestock, such as pigs, can have dramatic consequences for food security. Our analysis shows that the ASFV epidemic and associated pork shortage likely changed the meat market structure, human/consumption behavior and wildlife/hosts contact leading to an increased risk of zoonoses. The meat supply/cold chains and well-connected high-speed transportation networks may have contributed to spilloverby transporting SARS-CoV-2-infected live animals or carcasses into a large immunologically naive population and densely populated area. Importantly, pork consumption continues to increase in China and Southeast Asia in recent years and takes up an important proportion of the daily diet. According to the recent estimation of global poverty by the economist group of WorldBank, COVID-19 pandemic generates 119-224 million new poor, out of which 60% are living in Southeast Asia, reversing a decade of poverty reduction(Lakner, Yonzan, Mahler, Aguilar, & Wu, 2021). As the global grain prices continue to rise and the size of impoverished population prone to food shortage increases, hunting and trading of wildlife tend to intensify either for consumption or commercial purposes(M.

C. Rulli, D 'Odorico, Galli, & Hayman, 2021). Moreover, ASF, a major livestock pandemic with 100% lethality, is currently sweeping through Southeast Asia likely causing similar meat shortages in a region where the sarbecovirus from the nCoV clade is also endemic in horseshoe bat species(Wacharapluesadee et al., 2021). These conditions enable the emergence of another pandemic SARS-2.1 or SARS-3 in this region.

Methods

Supply and price

Cobweb theorem based on pig cycle theory is still widely used as the analytic tool in recent economic studies(Chen, Abler, Zhou, Yu, & Thompson, 2016; He, Quan, & Ma, 2013; Tan & Zeng, 2019) . According to the pig cycle theory in economics, cyclical fluctuations are normal for agricultural commodities with long time lags from breeding decisions to output for sale(Ezekiel, 1938). Low price and large supply in one period will make the market saturated, followed by a smaller supply along with price rises in the next period. In return, high market price simulates larger pig supply, but drags down pig price in the succeeding period. This process repeats and forms a drifting pig cycle in the long run like a cobweb(Harlow, 1960). There are strong biological constraints for expansion in hog production when prices continually increase, but no biological constraint in response to decreasing pork prices. Hence, slaughtering and selling promptly for cash is a typical choice for most pig farmers and butcher houses.

Demand for pork and alternative meats

The economic analysis for how pork demand reacts to the price increase is based on consumer behavior theories in microeconomics. Demand is primarily driven by price and income. Price elasticities, the marginal consumption volume changes due to the price changes, of foods are generally much smaller than other products as daily necessities(Andreyeva, Long, & Brownell, 2010). Pork and pork products are the

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traditional major sources of animal protein in China. Pork demand is observed to be robustly inelastic to price changes in most studies, with elasticity between -1.3 to 1.2, the mean at -0.67, most robust with smallest variance across studies out of livestock and seafoods(Chen et al., 2016), as the absolute value of the price elasticity less than unity indicates price inelasticity.

Analysis of the potential changes in consumption of alternative meats as substitution due to dramatic increase of pork prices is based on the theory of consumer choices(Elzerman, Hoek, Van Boekel, & Luning, 2011; Lattin & McAlister, 1985). According to the theory, with a fixed expenditure budget, taking pork is a normal good in China, not luxury or inferior, if pork price increases, substitution effects and income effects will take place. Consumers will eat less pork(Green et al., 2013), alternatively cheaper meats to maintain the previous meat protein levels (Mason-D'Croz et al., 2020). Both the relative price and absolute price differences matter to the substitution choice(Azar, 2011). The sizes of substitution effects depend on whether alternative meats are perfect substitutes or imperfect substitutes for pork. A wider range of varieties leads to greater substitution possibilities(Chen et al., 2016). Chicken is frequently found a closer substitute for pork in the Chinese diet(Z. Liu, 2014). Wildlife/domesticated animals appear to be imperfect substitutes but provide a wider range of varieties. The likelihood of substitution may vary depending on various factors, such as income level, relative prices, diet culture, geographic locations, variety availability, and consumer preference, etc. Since August 2019, pork prices had risen far from its normal price range, the probability of consuming wildlife and their products increased in the areas with diet culture and market access to wildlife varieties.

Government frozen pork reserve effects

Government storage is supposed to help the supply and expectations and thus reduce dramatic price fluctuations(Serra & Gil, 2013). The competitive storage model is frequently used for analyses(Serra & Gil, 2013; Tan & Zeng, 2019). To analyze the market effects of government emergency pork reserves, this study adopts the analytic paradigm of augmented Competitive Storage model proposed by Tan&Zeng (2018). Following their theory, marginal costs of pork reserve is considered at zero since costs were not an important consideration factor during the stockpiling period(Tan & Zeng, 2019). Moreover, asymmetric information effects of price transmission should be taken into consideration. When supply exceeds demand and prices (expect to) go down, hogs are slaughtered and stored frozen for future release. Afterwards, when prices went up, these frozen meats were released and transported. Hence, there was strong market expectation prior to important Chinese holidays or in the face of incredibly high market prices, which coincides exactly with the predicted period of the first COVID-19 case contracted SARS-CoV-2 (Figure 3).

Data

Pig production and import

Annual provincial pig, pork production and pig inventory data are derived from China Rural Statistical Yearbook (2020) and (2019)(National Bureau of Statistics of China, 2019a, 2020).

Annual meat import data including pork, beef, mutton, poultry, and seafood were obtained from the trade database of the United Nation: https://comtrade.un.org/data/.

Pig prices

Average weekly prices for pork meat nationwide from 2010 to 2019 were obtained from the Ministry of Commerce. To analyse the price distribution, fluctuation and dynamics, daily hog prices were obtained from China Pig Web by a custom Python script: https://hangqing.zhuwang.cc. Hog prices rather than pig prices were used due to the concerns as follows. First, there is no open official data for daily pork prices for all provinces. MOC releases historical daily data for some provinces, but do not include Hubei province. Second, China Pig Web is a relatively credible and authoritative data provider which is a listed company on Shanghai Stock Exchange Centre. It provides continual daily provincial pig price data. The liaison of the website stated that the data are derived comprehensively from diverse sources, including regional investigating staff, slaughterhouse, hog wholesale market, and official statistics. Third, the pork price is also available on the China Pig Web, but they are imbalanced and unstable. Fourth, studies on China's pig supply chain indicate that there is no time lag to transmit the pig prices to the pork prices. Finally, there are bilateral transmission between pork price and pig price. It is found that fluctuation in pork price immediately passed to pig prices(Dong et al., 2018; S.-w. XU et al., 2012).

ASF outbreaks

The records of African Swine Fever outbreaks in China and in Southeast Asia countries were obtained from OIE: https://www.oie.int/wahis_2/public/wahid.php/Diseaseinformation/WI.

Freeway status

The freeway construction data was obtained from Statistical Yearbooks (2020) from 31 provinces.

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Competing interests

The authors declare no competing interests.

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