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ASSESSING RISK FACTORS FOR VIRAL DISEASE EMERGENCE WITHIN THE WILDLIFE TRADE

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Front Cover photo: A gibbon (Hylobatidae) inside a cage in Central Java, Indonesia,
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Back cover photo: Pigs and chicken on a family farm in Calamar, Guaviare, Colombia.
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INTRODUCTION

The COVID-19 pandemic has changed the world. We are now more aware than ever of the risks we impose upon ourselves due to the current unsustainable ways in which we manage and use nature. As we have experienced over the course of the COVID-19 pandemic, these risks are not just related to our health, but also have deep repercussions for global economies, local livelihoods and society in general.

Much has been written about the rise of pathogens - especially in regard to rapidly changing environments. Rising ocean temperatures, changing salinities and rising pollution in the marine environments (Erken et al. 2013) increase the risk of human exposure to pathogens. Human population growth and increased, often unsustainable consumption have driven global warming, and deforestation and fragmentation, resulting in intensified proximity/interaction between people, their livestock and nature, increasing risk of exposure and spillover (Dobson et al 2020, WWF 2020). Legal international wildlife trade has risen 500% since 2005 (IPBES 2020, UN Comtrade Database 2020), and there is considerable evidence that illegal and unregulated trade also have increased over time. Unregulated trade and unsustainable consumption of wildlife, especially birds and mammals, are believed to be a greater risk of disease emergence than the legal, regulated trade, although diseases have emerged from all forms of wildlife trade (IPBES 2020).

The rise of emerging infectious diseases (EIDs) of zoonotic origin (Jones et al. 2008) has understandably caused widespread concern and underscores the need to prevent future spillover events and avoid potential pandemics. Wildlife trade bans and closure of markets selling live wildlife have been proposed, but such approaches are considered impractical by many and would provide a partial solution at best to the problem. Domestic animals, for example, have been identified as the source of many infectious diseases of zoonotic origin affecting people and account for 96% of mammalian biomass on Earth (Bar-on et al. 2018). The vast majority of meat traded and consumed is from domestic rather than wild animals. When considering these differences in scale of production and consumption, the high levels of human-domestic species interactions, and the fact that domestic species can be disease hosts themselves, the risk of contracting a food-borne illness from domestic animals in trade has been estimated to be ~3,000 times greater than from wild animals in trade (Koch et al., in prep). However, it should be noted that wildlife health is not being adequately monitored and managed with the same diligence as domestic animal health (OIE 2020).

While not all emerging infectious disease (EID) events have occurred within the context of the wildlife trade, SARS, Ebola, and monkeypox, are examples of spillover events with their origins most probably - although not conclusively - linked to wildlife consumption, wildlife farms, and/or markets selling live wildlife (Karesh et al. 2005). The SARS Cov-2 virus that causes the COVID-19 disease is suspected to use horseshoe bats as reservoir hosts and may have entered humans via an intermediary animal associated with the wildlife trade. However, no intermediary, wild or domestic, has been unambiguously identified (Koch et al. in prep). Significant gaps remain in our knowledge as to exactly how and when these diseases emerge.

What we do know for certain is that one EID is one too many. Every pandemic begins with a single infection event and while these events may occur frequently around the world, most infections are unable to spread (IPBES 2020). In the not unlikely event that an infection spreads into an urban human community (coupled with airborne transmission), pandemics can result. Dobson et al. (2020) showed that costs of preventing a pandemic can be measured in hundreds of billions of dollars while the economic and social costs of dealing with a pandemic (e.g. Covid-19) are measured in tens of trillions of dollars.

While the probability of wildlife trade resulting in future devastating pandemics may be lower than other contributing drivers, it cannot be ignored. We need a holistic approach to reducing risk for emerging diseases that could spillover from animals to humans (Petrovan et al. 2020), including those risks associated with wildlife trade.

In this review, we attempt to identify factors that contribute to risk and combinations of those factors that create high, medium and lower risk situations within the wildlife trade. Risk encompasses both the likelihood of an undesirable event occurring and the severity of such an event were it to occur (Bing et al. in review). The factors contributing to risk are multiple, can be found in numerous combinations, and are poorly quantified, making it difficult to tease apart the relative effects of one variable over another. Many factors are not linear and in some cases we cannot demonstrate clear causal relationships. We structure our review around three dimensions of threat generally used to evaluate risks related to climate change: hazard, vulnerability and exposure. In the context of wildlife trade, hazard relates to the threat of infected wildlife, vulnerability relates to the threat of weak governance and poor market infrastructure, and exposure relates to the exposure of humans to pathogens (Figure 1, Supplemental Materials).

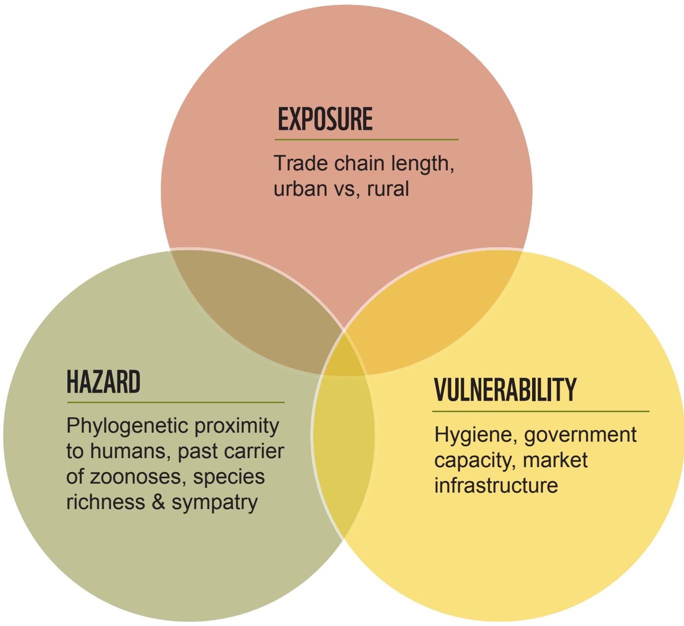

Figure 1. *The risk of pandemic emergence and spillover is a function of hazard, vulnerability and exposure.*

We explore the risks of zoonotic viral transmission in the wildlife trade, with a specific focus on mammals. While we recognize the potential role of birds in disease transmission (poultry and waterfowl are especially important sources for novel influenza viruses; Kaplan and Webby 2013), mammals form the majority of animals identified as potential reservoirs of other emerging viral pathogens (Han et al. 2016, Cupertino et al. 2020) and those that have been linked to the wildlife trade whether via farmed, captive bred or wild sourced animals (IPBES 2020). At least 1,441 mammal species are legally traded internationally with an additional unknown number of illegally traded species (Scheffers et al. 2019). Large volumes of legal and illegal trade also occur within countries, cumulatively, this likely exceeds international trade flows (IPBES 2020). Our review is not intended to be exhaustive but rather to provide sufficient relevant information to help evaluate risk levels and where they lie across the wildlife trade sector, and to assist in guiding advocacy. We highlight areas where there is a lack of consensus and identify gaps where insufficient data are available to make firm conclusions.

In addition, we provide in the supplemental materials an interactive tool to qualitatively assess hazard, vulnerability and exposure associated with wildlife species and markets. The tool is not meant to be used in any way as a certification but rather to promote dialogues and debates, and assist governments, NGOs, and other stakeholders in differentiating between broad categories of risk in wildlife trade until more reliable and consistent data become available.

EVALUATING RISK: HAZARD, VULNERABILITY AND EXPOSURE

HAZARD: THE THREAT OF INFECTED WILDLIFE

A hazard can be defined as a dangerous phenomenon, substance, human activity or condition that may cause loss of life, injury or other health impacts, loss of livelihoods, social and economic disruption, or environmental damage (Viner et al. 2020). We define the hazards of concern to wildlife trade risk as the biological attributes of the taxa being traded, the state of wildlife (alive or dead) and the conditions under which they are being held.

TAXA IN TRADE

The phylogeny, socio-ecology and life history patterns of traded taxa are thought to influence their probabilities of carrying pathogens, the levels of virulence of any pathogens carried, and therefore the risk of spillover to and infection of humans.

Phylogenetic relatedness to humans is believed to play a key role in determining those species which pose a high risk for disease spillover. In general, the more closely related a species is to humans, the more likely that the diseases they carry have the ability to adapt to human hosts (Davies and Pedersen 2008). Based on time since common ancestry (in millions of years) apes (gorillas, chimps, orangutans and gibbons) would pose the greatest risks of disease transmission to humans followed by old world monkeys (baboons, macaques and vervets), new world monkeys (capuchins, squirrel monkeys and marmosets) and prosimians (tarsiers, lemurs and bushbabies). Phylogenetically, we would expect amphibians, reptiles and birds to pose little risk to humans, with bats, pigs, ungulates, carnivores and rodents falling in between these extremes.

Disease risk also appears to be correlated with s*pecies richness* within orders. Han et al. (2016) note that the number of zoonotic hosts in an animal order increases with the species richness, and as a result, there is a higher prevalence of potentially zoonotic pathogens. Orders with high levels of species richness include rodents, bats, shrews, primates, carnivores, and even-toed ungulates. Mollentze and Streicker (2020) likewise found that the number of human-infecting viruses scales positively with the total number of viruses maintained within an order, which in turn is correlated with the number of animal species within each order.

Another key intrinsic factor related to viral disease transmission risk is the *number of zoonotic pathogens that a single species is known to harbor*. Johnson et al. (2020) found that the number of zoonotic viruses detected in mammalian species scales positively with global abundance. Luis et al. (2013) found higher viral richness in orders sharing species with greater sympatric distribution, i.e. species whose populations shared higher degrees of overlap with related species. They compared the abundance of zoonotic viruses in bats and rodents and found a stronger effect of sympatry and viral richness in co-occurring bat species than rodent species, suggesting that interspecific transmission is more prevalent among bats than among rodents. Sympatric bats are more likely to occur in multi-species roosts; sympatric rodents are more solitary and rarely share enclosed spaces such as the caves and hollow trees favoured by bats.

Olival et al. (2017) also found that sympatry within mammalian orders was the most biologically relevant measure associated with total virus richness. Bats, rodents, primates, and ungulates had higher mean viral richness than predicted by the other ecological, life history and taxonomic traits. They argue that these taxa may be important targets for finding new zoonotic viruses in wildlife. Pangolins and carnivores (e.g. Canidae and Mustelidae) also have been found to carry viruses with zoonotic potential but we lack conclusive data on most mammalian species in trade (IPBES 2020; Lam et al. 2020; Munnink et al. 2020).

All of the above argues for the development of a Global Virome Project to classify and quantify the diversity of viruses and other pathogens. There may be ten times as much parasitic diversity as free-living biodiversity; as we develop a better understanding of the key roles that pathogens play in regulating abundance and enhancing coexistence in their hosts then it is increasingly apparent that we have to include this missing 90% of biodiversity within conservation planning.

STATE OF THE PRODUCT (ALIVE OR DEAD)

Live animals are more likely to harbor and transmit viral pathogens than dead animals. Greatorex et al. (2016) note that "smoked, dried, fermented and frozen carcasses," have not been shown to transmit pathogens. However, they argue for the inclusion of freshly dead carcasses in viral surveillance, as studies have noted the possibility of viral contamination in fresh meat/carcasses (Amonsin et al. 2008).

CAPTIVE CONDITIONS

The diversity and abundance of species within the trade chain and in markets appears to play a large role in viral disease transmission. Childs (2004) recognized various steps required for the emergence of a zoonotic virus from a wildlife reservoir: 1) interspecies contact, 2) cross-species virus transmission (i.e., spillover), 3) sustained transmission, and 4) virus adaptation within the spillover species. High species diversity and abundance of both wild and farmed animals increases the rate of interspecies contact along the trade chain and in wildlife markets, facilitating all four of these transition events (Huong et al. 2020). Contact among specimens of the same species from different locations (whether wild or domestic) also facilitates transition events.

The four transition events described above occurred during the SARS outbreak in 2003 and contributed to the rapid spread of the disease around the world (Wang et al. 2006). Given that horseshoe bats were found to be the most probable reservoir for SARS (Lau et al. 2005), interspecies cross-contamination and unhygienic marketplace conditions are thought to be the reason the virus found a route to invade humans. Guan et al. (2003) proposed civets as an amplifying species which allowed the virus to adapt to human systems, and further demonstrated that animal handlers had a significantly higher prevalence of SARS-CoV antibodies than vegetable sellers in the same markets. Tu et al. (2004) suggest that infection of civets in the marketplace was associated with "post-farm transport, handling, and sale under concentrated conditions with people and live wild animal species in the permanent live animal markets."

BOX 1 WHAT'S DIFFERENT ABOUT BATS?

Bats appear to act as major reservoirs for emerging viruses (Li et al. 2005, Calisher et al. 2006, Han et al. 2015). Researchers have identified more than 200 viruses in less than 10 % of bat species surveyed. Most are RNA viruses that adapt rapidly to changing environmental conditions. The ability of bats to host and transmit large numbers of viruses is generally attributed to life history patterns: long evolutionary history, ability to fly, "super-charged" immune systems, long life span, roosting behavior, and high levels of sociality (Calisher et al. 2006).

Bat viruses tend to exhibit higher pathology in humans than those from non-volant mammals. This seems to be associated with bats having a limited inflammatory response, so their viruses express themselves in a very different way in novel hosts. In addition to high numerical estimates of viruses, this higher virulence makes bat viruses more of a concern than pathogens found in many other mammals (Pavlovich et al. 2018, Ahn et al. 2019). For example, most COVID-19 patients that die suffer from an extreme inflammation response to tissue damage in the lungs or other organs (Shi et al. 2020). Wang et al. (2020) note that six of the past 25 emerging zoonotic viruses have confirmed or suspected bat origin: Hendra (1994), Nipah (1998-99), SARS (2002-03), MERS (2012), and Ebola (2014), and COVID-19 (2019-20).

Mixing live wild, peridomestic and domestic species, at any point along the trade chain, but particularly associated with conditions in live animal markets increases risk of transmission. Studies replicating market conditions have found that stacking cages of species on top of other species and sharing water sources can facilitate direct or indirect viral transmission of influenza A viruses between species (Achenbach & Bowen 2011; Bosco-Lauth, Bowen, & Root 2016). In live wildlife markets, the combination of mixed species in close proximity and at high density, high human traffic through a market, unhygienic conditions, and on-site butchering all increase the risk of transmission from wildlife to humans (IPBES 2020).

VULNERABILITY: WEAK GOVERNANCE AND POOR MARKET INFRASTRUCTURE

Vulnerability encompasses a variety of concepts and elements including sensitivity or susceptibility to harm and lack of capacity to cope and adapt (Viner et al. 2020). In the context of wildlife trade, susceptibility to harm (spillover of diseases to humans) may be created by poor market infrastructure and hygiene conditions, as well as lack of capacity within governments to monitor, evaluate or regulate trade and market conditions.

HYGIENE REGULATIONS AND FACILITIES

Lack of hygiene from source to consumer - whether in markets, restaurants, or food stalls - is a significant risk for human health. In Africa and Asia much of the food industry is informal, poorly regulated, and subject to corrupt actors (Oloo et al 2018), resulting in wide variation in hygienic practices. Poor hygiene practices have been linked to viral, bacterial and parasite infections through improper handling and processing of live or dead animals, improper storage of carcasses, and use of polluted water or proximity to other contaminants (Wu et al. 2006, Lo et al 2019). In Africa for example, about 2,000 food-borne related deaths - primarily from domestic livestock - occur each day (FAO/WHO 2015). While most countries have hygiene regulations for markets, restaurants and food handlers, knowledge of regulations and compliance varies widely among vendors and handlers of live animals and meat (Bamidele et al. 2015, Chukwuocha et al. 2009). In many developing countries, hygiene guidelines are legislated centrally (FAO/WHO 2005), often ignoring the informal sector where most wildlife trade and consumption occurs (Oloo et al. 2018). Enforcement of regulations also varies widely due to limited staffing, resourcing and other capacity constraints as well as corruption among market inspectors. Hand washing, protective apparel, routine cleaning practices, clean water sources and separation of fruits and vegetables from animals, and separation of wild and domestic animals are widely recommended (FAO/WHO 2005), but implementation is very spotty, even when people understand the regulations (Bamidele et al. 2015). Greatorex et al. (2016), in their study of wildlife markets in Lao PDR, defined a number of parameters upon which to assess good hygiene: market layout that separates different species of live animals and carcasses; substrates that are easy to clean and kept free of blood or entrails (e.g. cement or tile); access to running water, hand washing facilities and refrigeration; and no on-site butchering of live animals.

Following the SARS outbreak of the early 2000s, civets in markets in the Guangdong Province of China tested positive for presence of SARS-CoV antibodies (~80% of the animals from one animal market in Guangzhou contained high levels of antibodies to SARS-CoV), whereas civets in the wild and on farms (that sold to the markets) tested negative (Tu et al. 2004, Kan et al. 2005). Tu et al. suggest that this infection of civets in the marketplace was associated with "post-farm transport, handling, and sale under concentrated conditions with people and live wild animal species." Given that horseshoe bats were found to be the most probable reservoir (Lau et al. 2005), interspecies cross-contamination and poor marketplace conditions are generally thought to be the highest risk for viral spillover.

The same can be said for various live poultry markets and avian flu outbreaks. In a US study, Senne et al. (2003) demonstrated that the H5N2 virus was not present in poultry entering the marketplace but was present in a sizable number of the poultry within the marketplace. Another study of New York City markets showed that healthy birds were contracting forms of avian influenza virus upon arrival to the market (Trock et al. 2003). However, Kung et al. (2003) found that the institution of a monthly cleaning in live poultry markets decreased the prevalence of certain diseases (though not all -- in this case H9N2 decreased but there was no change in Newcastle Disease Virus).

MONITORING AND SURVEILLANCE

Monitoring hygiene practices along the trade chain is difficult in practice and often insufficient, even in developed countries. In the USA, the FDA investigated 16 instances of food-borne illnesses in 2019 (https://www.fda.gov/food/recalls-outbreaks-emergencies/outbreaks-foodborne-illness), while in the EU in 2018, member states reported 5,146 food-borne outbreaks (https://www.ecdc.europa.eu/en/news-events/salmonella-most-common-cause-foodborne-outbreaks-european-union). Often the supply chain is composed of the informal sector which is unregulated. Many countries do not have standards for the preparation and trade of indigenous foods, including bushmeat. In addition, food quality inspections fail to be carried out due to lack of authority, inadequate logistical support, and overworked inspectors (Oloo et al. 2018). Food inspectors often neglect rural communities where wildlife is initially sourced. IPBES (2020) points out that there are few mandates for disease surveillance in the wildlife trade.

GOVERNANCE CAPACITY

The ability of international and national agencies to regulate wildlife trade is exceedingly complex. Most references to wildlife trade focus on the international trade regulations and illegal international trade, whereas the roots of international trade suffer from weak governance in wildlife source countries. CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) is the body governing international trade but much trade occurs within national borders. Many countries have regulations regarding importation and exportation of wildlife (e.g. USA - Lacey Act, EU ban on wild bird imports) and regional bodies to regulate trade (Convention for Regulation of Migratory Birds, Convention on Regulation of Whaling; Couzens 2013). Unfortunately, seizures of wildlife products at ports of egress and entry do little to protect wildlife, and only seizures of live animals will reduce pandemic risk.

Geographically, Sheffers et al. (2019) show that wildlife trade is concentrated in the tropics of Africa, Asia and Latin America, and IPBES (2020) notes that within-border trade dominates wildlife trade in these regions. A national government's capacity to set and enforce quotas, regulate trade, and the rural population's attitudes toward wildlife all affect the impact of local trade in wildlife ('t Sas-Rolfes et al. 2019). In many of these countries, lack of resources limits the ability to enforce legislation on wildlife trade (Wilkie et al. 2005). Rowcliffe et al. (2004) show that species protection laws have no effect on hunting of large mammals in the DRC. Similar results are reported for Cameroon (Ntungfor and Atanga 2017).

A typical urban wildlife market might result from the convergence of a large number of small supply chains (hunters, wildlife farms, transporters, marketers) providing a mix of legally and illegally harvested wildlife (Cowlishaw et al. 2005; 't Sas-Rolfes et al. 2019). Regulations controlling such a chain may be contradictory, confusing, ignored, or subject to informal taxes (bribes) and corrupt practices. Furthermore, centrally mandated legislation may ignore street vendors and small wildlife markets, as well as the supply chain supporting this informal sector.

Wildlife protection is also compromised by spatial jurisdiction and taxonomic confusion. For instance, it may be illegal to take a species within a protected area while the same species may be legally taken outside a protected area. Under such circumstances, a legally harvested animal is indistinguishable from an illegally harvested animal once it enters the trade chain. In Cameroon, duikers species span three classes of wildlife: fully protected, partially protected and not protected. Duiker species are hard to distinguish by law enforcement officers, especially when processed to skins and bushmeat (Djeukam et al. 2007).

Weak centralized governance and conservation regulations that lack resources for implementation can result in: personnel and resource shortages; low detection of illegal activity; low prosecution rates; ignorance by public regarding wildlife law; lack of wildlife law expertise within the judiciary, low status of wildlife crime perceived by courts and public; slow judicial proceedings; weak penalties awarded by courts; low execution rate of judicial decisions; failure to arrest and prosecute high level poaching; pressure from politically powerful people; and limited government will and corruption within the law enforcement systems (Ntungfor and Atanga 2017).
van Uhm and Moreto (2017) argue that corruption associated with wildlife trade occurs at all levels of regulation and facilitates the progression of wildlife products along the supply chain from source to consumers. Wyatt et al. (2018) concur that wildlife trafficking chains operate within already corrupt structures (criminal justice system, political environment, economic environment) that facilitate crime more generally. Poaching of wildlife is often

associated with low Corruption Perceptions Index (CPI) scores (Williams et al. 2016). The global average CPI Score in 2019 is a disappointing 43 (range 9 - 87) out of a possible 100 points. Sub-Saharan Africa and Southeast Asia score 32 and 33 respectively, indicating widespread corruption among major wildlife source regions (Transparency International 2020). "When the rule of law, political economy and societal/cultural attitudes fail to value or recognise wildlife and do not recognise that wildlife crime is a serious crime, wildlife trafficking and other wildlife crimes continue largely unchallenged" (Wyatt et al. 2018).

EXPOSURE
(HUMAN EXPOSURE TO PATHOGENS)

Exposure is a measure of possible future loss (or losses) which may result from interacting with an activity or occurrence. The presence of people, livelihoods, species, economic, social, or cultural assets in places and settings may interact to increase exposure (Viner et al.2020).

TRADE CHAIN

Supply chain length appears to pose a significant risk within the wildlife trade, associated with the prolonged mixing and close confinement of stressed live animals. The risk of human exposure to wildlife pathogens starts at the source of harvest and hypothetically increases with the length of the trade chain due to the increasing numbers of actors and interactions and the prolonged mixing and close confinement of stressed live animals (Karesh et al. 2005, 2012). Exposure risk may be least at the source, especially if animals are captured live and quickly passed into the trade. If animals are butchered on site, risk increases because the handlers may be exposed to blood and other body fluids containing pathogens, and peridomestic rodents and other wildlife may consume the cast aside entrails and blood (Karesh et al. 2005). Processing of wildlife at the site by cooking, smoking, freezing may reduce the risk of pathogen transmission further up the trade chain.

Huong et al. (2020) determined that the presence of coronavirus in field rats (*Rattus* spp., *Bandicota* sp.) in Vietnam increased significantly with length of supply chain. Field rats being sold for consumption in restaurants were 10 times more likely to test positive for presence of a coronavirus than their counterparts tested in the wild or other segments of the trade chain, including markets. Huong et al. also detected the presence of avian and bat coronaviruses in farmed rodents and Malayan porcupines (*Hystrix brachyura*). Lee et al. (2020) found no sign of coronavirus in Malayan pangolins (*Manis javanica*) seized in the country of origin, whereas Malayan pangolins seized at the end of the trade route contained coronaviruses closely related to SARS-CoV-2, and other viruses likely of pangolin origin (Xiao et al 2020). They speculate that these animals were infected with recombinant viruses that may have evolved due to contact with other species during prolonged trade routes. Based on these


Photo credit: © WWF / Margaret Kinnaird

Sulawesi market in Tomohon, Indonesia

results, the authors hypothesized that "observed viral amplification along the wildlife trade supply chain for human consumption likely resulted from the mixing and close confinement of stressed live animals and sheds light on the potential for coronavirus shedding in other wildlife supply chains (e.g., civets, pangolins) where similarly large numbers of animals are collected, transported, and confined."

Bats at guano mines and household roosts have tested positive for coronaviruses illustrating a potential risk of bat to human transmission (Huong et al. 2020). They note however that it was unclear whether coronavirus transmission occurred as a result of live animal contact or due to contaminated guano. They posit the two as "equally likely explanations" for the cross-species infection, further noting that both possibilities constitute forms of interspecies "mixing."

The absence of SARS-CoV antibodies in farmed civets vs those being sold in markets following the SARS outbreak described above supports the indications that viral loads increase along the supply chain.

HIGH-RISK SITES

While certain locations have been linked to zoonotic disease and spillover (Jones et al. 2008, Gibb et al. 2020), it is difficult to generalize the nature of "high-risk" sites from which traded wildlife are encountered or sourced. However, EIDs are associated with regions where habitat is being destroyed, and may pose an elevated threat as populations of wildlife are accessed (Han et al. 2016; Scheffers et al. 2019). Regions in which there is both a high amount of habitat destruction, dense and/or growing human populations, and a large volume of trade may pose a particular risk for EID events (Karesh et al. 2012). More localized high-risk sites include wildlife farms (civet, raccoon dogs, mink), guano mining sites, and caves or mines inhabited by *Rousettus* bat colonies (https://www.who.int/health-topics/marburg-virus-disease/#tab=tab_1).

Additionally, Luis et al. (2013) found more zoonotic viruses where species have greater sympatric distribution. Certain taxa may represent a higher risk if sourced from congeneric species-dense sites. Huong et al. (2020) identified bat guano mines in Vietnam as risky sites. Calisher et al. (2006) note that the generally high densities of bat populations and their crowded roosting behavior increase the likelihood of intra- and interspecies transmission of viral infections. Maganga et al. (2020) found that the two most significant factors driving CoV positivity in cave-dwelling bats in Gabon were seasonality and location (i.e. specific roost site). Their study indicates that high-risk sites may be species specific as opposed to following broader patterns such as sympatry or density, which may make it difficult to generalize the relative risk of different source sites.

Where an animal is killed determines the risk of viral amplification and also determines the number of handlers with which the animal will come into contact. While there is less evidence for viral amplification in animals killed in the bush, several studies have indicated that hunters, wildlife handlers, and others who come into contact with live animals in the bush are at higher risk of viral infection as a result of this contact. With specific regard to the bushmeat trade, there seems to be a higher likelihood of viral contact, where hunters are the main interface with live animals (Wilkie & Carpenter 1999, Bowen-Jones et al. 2003, Cowlishaw et al. 2004).

A number of zoonoses (SARS, avian flu, etc.) have been contracted primarily by food-handlers (Guan et al. 2003, Xu et al. 2004). Studies of SARS indicated that early case-patients were more likely than later case-patients to report living near a produce market but not near a farm, and ~40% of early patients were food handlers with probable animal contact. Mounts et al. (1999) showed that transmission of H5N1 to humans was significantly correlated to proximity to live poultry markets.

Guan et al. (2003) proposed civets as an amplifying species which allowed SARS to adapt to human systems, and further demonstrated that animal handlers had a significantly higher prevalence of SARS-CoV antibodies than vegetable sellers in the same markets. Additionally, Wang et al. (2005) showed that 2 human cases of SARS were contracted due to proximity to caged civets in a restaurant setting. Huong et al. (2020) found highest coronavirus loads in field rats in restaurants.

Further research is required to determine whether market size (related to number of individuals frequenting and/or physical space occupied) holds a specific relationship to viral pathogen shedding, as opposed to other factors such as relative density or hygiene practices. Small roadside markets in rural areas may sell live and dead wildlife, risk exposure to relatively few customers, but are likely subject to less hygiene oversight. Large urban wildlife markets have higher species density and interspecies contact, and may risk exposure to many more customers but may also have more stringent hygiene monitoring and enforcement.

Temminck's ground pangolin

CONCLUSIONS

- Significant gaps remain in our knowledge as to exactly how and when emerging infectious diseases (EIDs) arise.
- While evidence points to deforestation, habitat conversion and fragmentation and other drivers (wild and domestic animal farming) playing a greater role in viral disease spread, wildlife trade nonetheless presents a risk and strategies are needed to better understand that risk and to address it.
- The SARS Cov-2 virus that causes the COVID-19 disease is suspected to have originated in horseshoe bats and entered humans via an intermediary animal associated with the wildlife trade. However, no intermediary, wild or domestic, has been unambiguously identified.
- When evaluating the wildlife trade sector for its role in potential spillover events, it is difficult to tease out the individual effects of many risk factors, as they are multiple, non-linear, and do not always demonstrate clear causal relationships. However, important factors are believed to include: the presence of high risk taxa; lengthy trade supply chains; unhygienic practices; interspecies contact (especially at high densities); and lack of government capacity or will to regulate trade.
- High-risk taxa are those that have a high level of species diversity and/or close taxonomic relation to humans. While much remains to be done on identifying high risk species for now, we know bats, rodents and primates are of concern.
- While sweeping trade bans may seem immediately appealing, responses to Covid-19 that seek to avoid repeat pandemics should additionally focus on a holistic approach to mitigating key drivers of disease, such as those delineated in this review, to be most effective.
- There is no one-size-fits-all solution to disease outbreaks that might be associated with wildlife trade. Appropriate solutions for Africa may not be useful for Europe or Asia. Any efforts to mitigate disease risk, however, should be based on the best science available, be responsive to local context, and be adaptive as new information becomes available.

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SUPPLEMENTAL MATERIALS

QUALITATIVE RISK REGISTER

We offer a simple yet robust scoring system that assesses the threat of pandemic emergence and spillover in three threat dimensions: hazard (the threat of infected wildlife); vulnerability (the threat of weak governance and poor market infrastructure); and exposure (the exposure of humans to pathogens) (Figure1).

Method

The composite risk assessment system is a linear spreadsheet model that provides a 13-point score for each of the three dimensions (hazard, vulnerability and exposure), respectively, with a total risk score of 39 (3x13).

The three risk dimensions are made up of 3-4 sub-variables each, which allowed us to add up sub-scores between 1 and 3, or 1 and 4 in some instances (Figure 2). Some sub-scores which were deemed more influential or relevant than others were assigned a weighting coefficient which the user can control to evaluate the model's sensitivity to various factors and parameters.

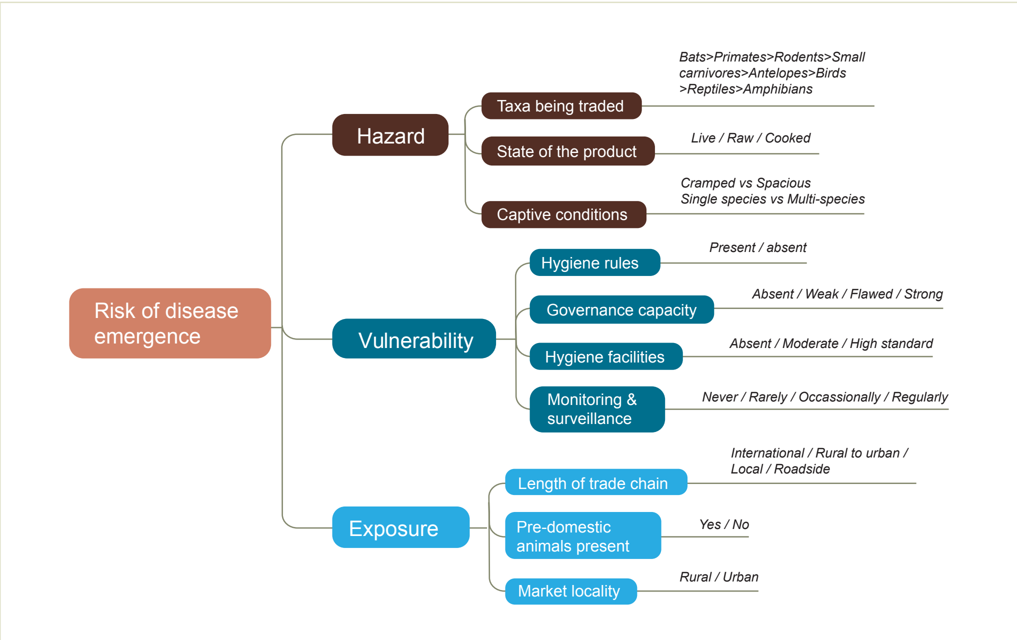

Figure 2. *Risk of disease emergence and spillover is a function of three dimensions: hazard, vulnerability and exposure. Each of the three dimension has 3-4 sub-variables, resulting in a composite risk score*

Hazard:

Hazard (cells AC1-AG6) is a function of 1) the wildlife taxa being traded, 2) whether the animals are traded live, as raw meat or as cured meat; and 3) the captive conditions under which animals are kept. The wildlife taxa (cells AC1-AC6) were assigned a hazard score in the "Taxa" tab, based on a) genetic proximity to humans (see histogram); b) the taxonomic richness of the group; c) whether there was historical evidence of spillover to other animals and humans; d) pathogenicity, i.e. ability to host pathogens that can spread rapidly and lethally; and d) co-habitation with other species in the same roost site or hiding place. This enabled us to identify a 'hazard hierachy' of species (Figure 3). Changeable weighting factors (cells AC7-AG7) allow the users to arbitrarily change weightings to evaluate the sensitivity of the model for such changes.

Vulnerability:

Vulnerability (cells AH1-AO6) is linked to market conditions and mitigation capacity. Four factors: a) the presence of hygiene rules; b) governance capacity; c) availability of hygiene infrastructure & facilities; and d) availability of testing, surveillance, monitoring and evaluation. Each of these factors were scored on a 3-point scale, with 3 representing the highest risk. Weighting factors (cells AH7-AO7) can be changed to evaluate sensitivity.

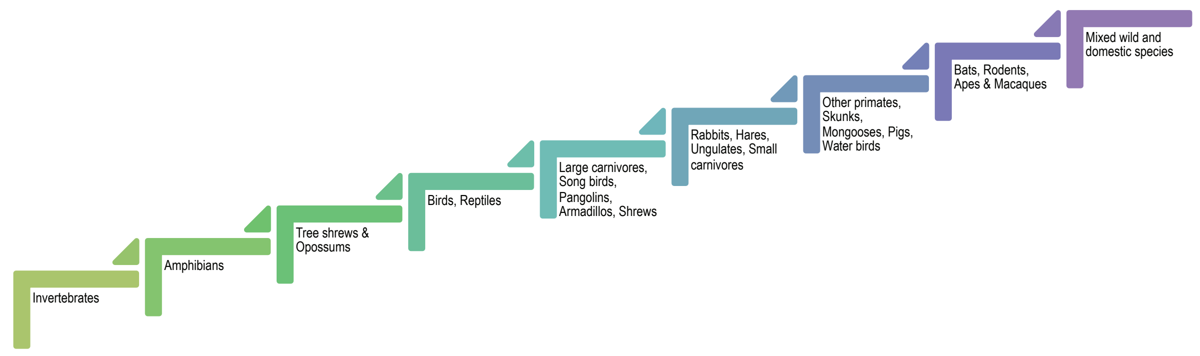

Figure 3. *Proposed hazard hierarchy of species, scored according to the literature (cf "Taxa" tab in the spreadsheet)*

Exposure:

Exposure (cells AP1-AO6) is a composite of a) trade chain length (whether trade was international, national, in local markets or at roadside); b) whether species were taken from deforestation frontiers; and c) whether the market was rural or urban. Scores ranged from 0-4 and trade chain length and deforestation frontiers scores were weighted by a factor of 2. All weighting factors (cells AP7-AU7) can be changed by the user. Weighting factors of 2 were assigned to trade chain length, and deforestation frontiers, partly because the literature points to these being influential, and partly to equalize the relative contribution of exposure to total risk, commensurate with hazard and vulnerability.
The spreadsheet has three tabs: "Taxa"; "Multiple cases"; and "Single case".

Single case:

Single case analysis consists of 10 questions in 3 categories (hazard, vulnerability and exposure):
Hazard questions (brown):

Hazard questions (brown):

1. Which kinds of animals are being sold?
2. Is the product alive, raw, cooked or a mixture of these?
3. Under what conditions are animals being kept?

Vulnerability questions (dark blue):

4. Are there hygiene rules at the market?
5. How good is the governance capacity - to fairly enforce policies, rules and regulations?
6. What is the standard of ablution facilities at the market?
7. How often does disease testing, surveillance, monitoring & evaluation take place?

Exposure questions (cyan):

8. How long is the trade and transport chain?
9. Were any of the species taken from a deforestation frontier zone?
10. Is it a rural or an urban market?

Drop-down menus

Each question is associated with a drop-down menu of choices which, if selected, automatically provides a score derived from cells AC1-AU8 in the "Multiple cases" tab. These scores take weighting factors into account. There is also a dop-down menu for the type of market (cell B3).

Risk categories

Over-all risk of disease emergence and spillover (cell B17) is automatically calculated from hazard (B14), vulnerability (B15) and exposure (B16). Instead of percentage risk which can be misleadingly accurate, over-all risk is categorized as "Very High" (red); "High" (orange); "Moderate" (yellow) or "Low" (green). The same categories apply to hazard, vulnerability and exposure levels (cells B14-16).

Multiple cases:

The "Multiple cases" tab allows the user to create a collection of case studies and their associated risk scores within the same spreadsheet for comparative analysis. Drop-down menus are the same as those in the "Single case" tab and scores are calculated in cells AC1-AO7, as explained earlier.

"What if" analysis

"What if" simulation is useful to understand potential for mitigation. The spreadsheet is useful to assess the sensitivity or risk to various interventions. Hazard reduction can for example be simulated by changing captive conditions or state of produce. Similarly, vulnerability reduction can be simulated by considering the probability of changing governance factors, market conditions or surveillance and testing.

When risk remains "High" or "Very High", notwithstanding the implementation of mitigating factors, or the probability of mitigation is low, then market closure would be the main solution to recommend or consider.

Way forward

The risk assessment system proposed here, while the product of significant expert consultation, literature review and iterative consensus seeking, is only the beginning. There are many potential tools, all contributing to our understanding of what constitutes risky wildlife trade, how to objectively assess it, and how to use this information in decision making. Next steps should be to collect a large sample of case studies, gain consensus on their parameters, and use the larger sample to calculate and refine probabilities based on fuzzy logic rather than empirical statistical analysis. Rule-based models, using 'if-then-else' rules derived by experts, could be additional instruments in the toolkit. It should also be borne in mind that while it is WWF's responsibility as an honest broker to identify risks at various dimensions, as well as options for intervention, this does not mean that we have an obligation or mandate to address those risks ourselves.

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