







# Post COVID-19: a solution scan of options for preventing future zoonotic epidemics

Silviu O. Petrovan<sup>1,2\*</sup> , David C. Aldridge<sup>1,2</sup>, Harriet Bartlett<sup>2,3</sup> , Andrew J. Bladon<sup>1,2</sup> , Hollie Booth<sup>4</sup>, Steven Broad<sup>5</sup>, Donald M. Broom<sup>1,3</sup> , Neil D. Burgess<sup>6,7</sup>, Sarah Cleaveland<sup>8</sup>, Andrew A. Cunningham<sup>9</sup>, Maurizio Ferri<sup>10</sup> , Amy Hinsley<sup>11</sup>, Fangyuan Hua<sup>12</sup>, Alice C. Hughes<sup>13</sup>, Kate Jones<sup>14</sup> , Moira Kelly<sup>15</sup>, George Mayes<sup>16</sup>, Milorad Radakovic<sup>3</sup>, Chinedu A. Ugwu<sup>17</sup>, Nasir Uddin<sup>13</sup>, Diogo Verissimo<sup>4,18</sup>, Christian Walzer<sup>19,20</sup>, Thomas B. White<sup>2</sup>, James L. Wood<sup>3</sup> and William J. Sutherland<sup>1,2</sup>

<sup>1</sup>*BioRISC (Biosecurity Research Initiative at St Catharine's), St Catharine's College, Cambridge, CB2 1RL, U.K.*

<sup>2</sup>*Department of Zoology, University of Cambridge, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, U.K.*

<sup>3</sup>*Department of Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge, CB3 0ES, U.K.*

<sup>4</sup>*Interdisciplinary Centre for Conservation Science, Department of Zoology, University of Oxford, Oxford, OX1 3SZ, U.K.*

<sup>5</sup>*TRAFFIC, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, U.K.*

<sup>6</sup>*UNEP-WCMC, 219 Huntington Road, Cambridge, CB3 0DL, U.K.*

<sup>7</sup>*GLOBE Institute, University of Copenhagen, Oester Voldgade 5-7, Copenhagen, 1350, Denmark*

<sup>8</sup>*Institute of Biodiversity, College of Medical, Veterinary and Life Sciences, Animal Health & Comparative Medicine, University of Glasgow, Glasgow, G12 8QQ, U.K.*

<sup>9</sup>*Institute of Zoology, Zoological Society of London, London, NW1 4RY, U.K.*

<sup>10</sup>*Italian Society of Preventive Veterinary Medicine (Simevep), Via Nizza 11, Rome, 00198, Italy*

<sup>11</sup>*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford, OX1 3SZ, U.K.*

<sup>12</sup>*Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing, P.R. China*

<sup>13</sup>*Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna, Yunnan, 666303, P.R. China*

<sup>14</sup>*Centre for Biodiversity and Environment Research, University College London, Gower Street, London, WC1E 6BT, U.K.*

<sup>15</sup>*Wildlife Health Ghent, Department of Pathology, Bacteriology and Poultry Diseases, Faculty of Veterinary Medicine, Ghent University, Salisburylaan 133, Merelbeke, B-9820, Belgium*

<sup>16</sup>*MacArthur Barstow & Gibbs Veterinary Surgeons, 36 Hanbury Road, Droitwich, WR9 8PW, U.K.*

<sup>17</sup>*Africa Centre of Excellence for Genomics of Infectious Disease, Redeemers' University Ede, Osun State, Nigeria*

<sup>18</sup>*Institute for Conservation Research, San Diego Zoo Global, Escondido, CA, 92027, U.S.A.*

<sup>19</sup>*Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Savoyenstraße 1, Vienna, A-1160, Austria*

<sup>20</sup>*Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY, U.S.A.*

## ABSTRACT

The crisis generated by the emergence and pandemic spread of COVID-19 has thrown into the global spotlight the dangers associated with novel diseases, as well as the key role of animals, especially wild animals, as potential sources of pathogens to humans. There is a widespread demand for a new relationship with wild and domestic animals, including suggested bans on hunting, wildlife trade, wet markets or consumption of wild animals. However, such policies risk ignoring essential elements of the problem as well as alienating and increasing hardship for local

\* Address for correspondence (E-mail: [sop21@cam.ac.uk](mailto:sop21@cam.ac.uk))

communities across the world, and might be unachievable at scale. There is thus a need for a more complex package of policy and practical responses. We undertook a solution scan to identify and collate 161 possible options for reducing the risks of further epidemic disease transmission from animals to humans, including potential further SARS-CoV-2 transmission (original or variants). We include all categories of animals in our responses (i.e. wildlife, captive, unmanaged/feral and domestic livestock and pets) and focus on pathogens (especially viruses) that, once transmitted from animals to humans, could acquire epidemic potential through high rates of human-to-human transmission. This excludes measures to prevent well-known zoonotic diseases, such as rabies, that cannot readily transmit between humans. We focused solutions on societal measures, excluding the development of vaccines and other preventive therapeutic medicine and veterinary medicine options that are discussed elsewhere. We derived our solutions through reading the scientific literature, NGO position papers, and industry guidelines, collating our own experiences, and consulting experts in different fields. Herein, we review the major zoonotic transmission pathways and present an extensive list of options. The potential solutions are organised according to the key stages of the trade chain and encompass solutions that can be applied at the local, regional and international scales. This is a set of options targeted at practitioners and policy makers to encourage careful examination of possible courses of action, validating their impact and documenting outcomes.

*Key words:* emerging infectious disease, zoonotic risk, zoonotic spillover, SARS-CoV-2, coronavirus, pandemic prevention, wildlife trade

## CONTENTS

I. Introduction	3
II. Major transmission pathways for zoonotic disease transfer	3
(1) Importance of zoonotic pathogens, including COVID-19	3
(2) Disease transfer pathways	4
(3) Disease transfer involving wild animals	4
(4) Disease transfer involving domestic animals	7
(5) Disease transfer involving wild or exotic pets	7
(6) State of knowledge on coronaviruses – origins and transfer	7
III. Solution scanning: identifying options for minimising zoonotic disease transfer	8
(1) The need for solution scanning	8
(2) Interpreting the list of options	9
IV. The list of options	9
(1) Supply side	9
(a) <i>Area-based management (e.g. protected areas)</i>	10
(b) <i>Hunter/collector behaviour change, for wild-sourced species</i>	10
(c) <i>Ensure wildlife farming is safe and legal</i>	10
(d) <i>Reduce wildlife–livestock–human interfaces in and around farms and wild places</i>	11
(e) <i>Increase animal hygiene and health standards for livestock and farmed wild animal production</i>	12
(f) <i>Farm biosecurity</i>	12
(2) Transport and sale	13
(a) <i>Reduce disease transmission risk during transport</i>	13
(b) <i>Reduce disease risks during slaughtering, processing and at place of sale</i>	14
(3) Consumption	14
(a) <i>Coercive measures to change consumer demand</i>	15
(b) <i>Promoting voluntary behaviour change in consumers</i>	15
(4) Enabling environment (applies to all)	15
(a) <i>Capacity</i>	15
(b) <i>Government commitments</i>	16
V. Discussion	16
(1) Using options to make decisions	16
(a) <i>Identifying risks</i>	16
(b) <i>Assessment, review and testing</i>	17
(c) <i>Cost–benefit and trade-offs</i>	17
(d) <i>Choosing interventions / developing and modifying strategies</i>	17
(2) High-level options currently proposed in the response to COVID-19	17
VI. Further unanswered questions	17
VII. Future directions	18

VIII. Conclusions .....	18
. Acknowledgements .....	19
IX. References .....	19

## I. INTRODUCTION

The COVID-19 pandemic has alerted the world to the risks of emerging diseases of zoonotic origin and has prompted widespread concern and interest in acting to prevent future similar pandemics. Many solutions have been proposed, in particular related to complete bans of wildlife trade and wildlife markets, but such solutions are considered impractical by some and, if implemented, could cause major socio-economic shocks and food insecurity (Booth *et al.*, 2021) and would only cover part of the problem. Thus, more holistic solutions should be examined to understand additional mechanisms that could drive spillover from other animals to humans. There is a need for larger scale rethinking of the means of reducing risk for emerging diseases that could spill over from animals into humans, and especially those diseases that could spread rapidly due to high transmission rates from human to human (Dobson *et al.*, 2020; Morens, Daszak & Taubenberger, 2020).

Herein we (i) review the risks posed by different transmission pathways for zoonotic disease spillover, and (ii) use solution scanning as a methodological approach to consider and collate the possible options for reducing these risks. We also identify important outstanding questions and pragmatic approaches for the future.

Solution scanning, which involves listing all the known options for addressing a particular problem, represents a more transparent and rigorous strategy for assessing possible policy options than the traditional approach of selecting a subjective subset of policies from a combination of the experience and beliefs of practitioners and politicians (Sutherland *et al.*, 2014). While a complete review of the evidence base for all available policy options would be preferable, especially for complex policy problems where outcomes may be location or context specific, the scale and duration of such reviews are often impractical. Solution scanning can be a valuable first step in this decision-making process, by creating a comprehensive and transparent basis for subsequent assessment of evidence, effectiveness and contextualised considerations for the practical implementation of different options (Sutherland *et al.*, 2014; Sutherland & Burgmann, 2015). This approach has been used successfully for a range of topics including agro-forestry, options for the conservation of marine biodiversity, and sustainable intensification of agricultural practices or place-based food networks (Jacquet *et al.*, 2011; Hernandez-Morcillo *et al.*, 2018; Plieninger *et al.*, 2018; Dicks *et al.*, 2019). Solution scanning is also the first stage of subject-wide evidence synthesis, for example to assess the effectiveness

of biodiversity conservation interventions (Sutherland *et al.*, 2019).

## II. MAJOR TRANSMISSION PATHWAYS FOR ZOOBOTIC DISEASE TRANSFER

### (1) Importance of zoonotic pathogens, including COVID-19

The pandemic potential of zoonotic pathogens is strictly linked to their ability to generate sustained human-to-human transmissibility. This is the case with SARS-CoV-2 (the virus responsible for COVID-19) which caused a global pandemic affecting over 200 countries and territories in under 100 days and resulting in over 175 million known infections and 3811561 assigned human deaths by 15th June 2021 [WHO Coronavirus Disease (COVID-19) Dashboard covid19.who.int]. Although there is debate about its exact source and infection pathway, COVID-19 appears to have been the result of zoonotic transmission from an original wildlife host, possibly *via* an intermediate animal host, following close contact with people (Andersen *et al.*, 2020; Wu *et al.*, 2020). While the direct reservoir of SARS-CoV-2 might never be identified, it is clear that close proximity of different wild and domestic animal species in a wildlife market setting (often conflated with ‘wet market’, which may, or may not, have wildlife and simply refers to the existence of fresh produce) may enable recombination between more distant coronaviruses and the emergence of recombinants with novel phenotypes (Li *et al.*, 2020). This is particularly relevant given that multiple relatives of SARS-CoV-2 and SARS-CoV (the cause of the 2003 SARS epidemic) circulate in wildlife species in Southeast Asia and southern China (Zhou *et al.*, 2021). Preventing such situations as well as reducing direct human contact with wild animals appears critical for preventing new coronavirus zoonoses.

Several other major recent pandemic and epidemic disease outbreaks have zoonotic origins including HIV-AIDS, Ebola and SARS (Wang & Eaton, 2007; Allen *et al.*, 2017); 60% of human emerging disease events are caused by zoonotic pathogens, with most (72%) originating in wildlife (Jones *et al.*, 2008). Furthermore, most known human pathogens are zoonotic (80% of viruses, 50% of bacteria, 40% of fungi, 70% of protozoa and 95% of helminths) (Taylor, Latham & Woolhouse, 2001). Although most zoonotic pathogens are not capable of sustained human-to-human transmission, some can cause major disease outbreaks; thus, preventing the transfer of pathogens from other animal species into humans is a key societal challenge. Predicting and reducing the risk of such outbreaks is imperative if we are

to avoid future detrimental impacts on human health and the global economy, such as those caused by the COVID-19 pandemic.

## (2) Disease transfer pathways

Transfer of pathogens from animals to humans can occur through diverse pathways involving interactions with free-living or captive wildlife, livestock or other domesticated animals (Table 1; Fig. 1). It is important to note that, in practice, the distinctions between these categories of animals are often poorly understood and category differentiation may be imprecise but differences have significant implications for exposure to various pathogens.

The rate of zoonotic pathogen emergence is increasing globally, and human population density is a strong predictor of emerging disease events (Jones *et al.*, 2008), indicating that pathogen emergence is driven by human-induced changes bringing wildlife, livestock and humans into closer and more frequent contact (Morse *et al.*, 2012). The risk of disease transmission depends on both intrinsic factors (e.g. pathogen life history, host availability and immunity and transmission route) and external factors (e.g. land-use, human population changes, socio-economic provisions) such that the nature of risks varies among locations and over time (Becker *et al.*, 2020), and influences both the probability of pathogen transmission from animal to human, and the probability of an infected person developing the disease (Han, Kramer & Drake, 2016).

The spillover of a pathogen from animals requires a series of stages, including the reservoir host being at sufficient density to retain the pathogen, pathogen release, human exposure to the pathogen, and the pathogen overcoming structural barriers, innate immune responses and molecular compatibility (Plowright *et al.*, 2017). The global connectivity of human society greatly increases the movement of humans, disease vectors (Tatem, Hay & Rogers, 2006) and various pathogen-infected animals (Can, D’Cruze & Macdonald, 2019), magnifying the likelihood of the spillover and spread of a pathogen, particularly in areas of high human population size and density.

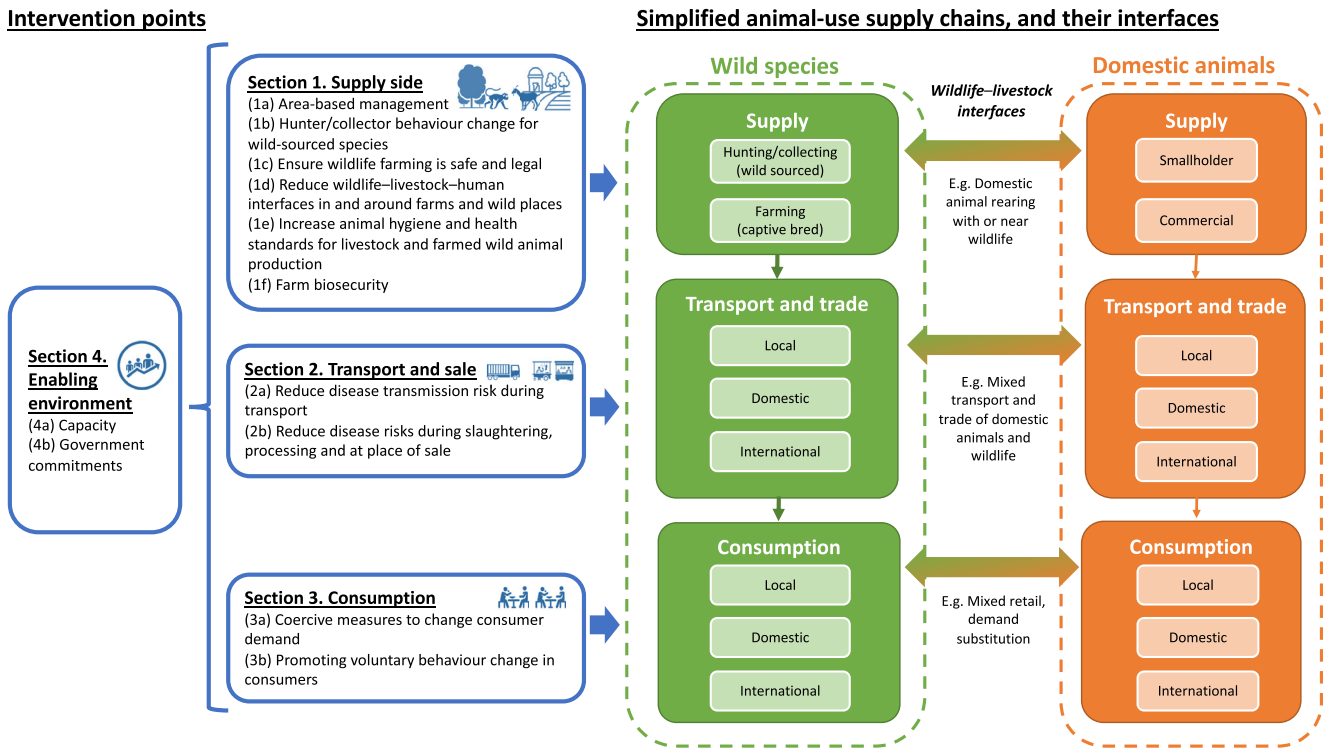
## (3) Disease transfer involving wild animals

Most emerging infectious diseases are thought to have originated in wild animals, especially non-human primates, rodents and bats (Wolfe, Dunavan & Diamond, 2007; Jones *et al.*, 2008; Han *et al.*, 2016), although many of these were transmitted to humans *via* intermediate hosts, such as companion, farmed or feral animals (Wolfe *et al.*, 2007). As an example, there is a broad consensus that human viruses responsible for HIV-AIDS resulted from multiple cross-species spillovers of simian immunodeficiency viruses involving the chimpanzee *Pan troglodytes*, western gorilla *Gorilla gorilla* and sooty mangabey *Cercocebus atys*. Lentiviruses, such as HIV, penetrate mucous membranes; therefore contact with non-human primate body fluids associated with the hunting,

Table 1. Terminology used herein to describe animal categories

Term	Description
Wildlife	We use the IUCN terminology to define wildlife as “living things that are neither human nor domesticated”, but due to the nature of our review we focus on both terrestrial and aquatic animals, especially mammals and birds, and exclude fish, plants, fungi and aquatic invertebrates (e.g. molluscs and crustaceans) due to lower opportunity for disease transmission that would result in human–human infections.
Wild sourced	Animals taken from the wild directly for trade, which may include legal or illegal trade in live wild animals (e.g. for food or exotic pets) or their parts and derivatives (e.g. for food or medicine). This includes ranched or captive-raised animals, where eggs or young were taken from the wild and then reared in captivity for commercial purposes.
Farmed and captive wildlife	We consider wild animals bred in captivity as distinct from wild-sourced animals. We define farmed wild animals as those with a phenotype not significantly affected by human selection and raised in controlled conditions and productive farm systems (e.g. mink <i>Neovison vison</i> for fur; bears, primarily <i>Ursus thibetanus</i> , or Tokay geckos <i>Gekko gekko</i> for traditional medicine; tigers <i>Panthera tigris</i> in tiger farms; bamboo rats, often <i>Rhizomys sinensis</i> , raised for food) and use ‘captive wildlife’ for those in zoological and other collection types (e.g. tigers in zoos).
Domesticated species	We consider domesticated species as those whose phenotype is driven by long-term human selection. Within this category we use the terms ‘livestock’ for animals raised primarily for meat and other animal products (e.g. pigs, poultry, cattle, sheep, goats, some camelids such as dromedary and llamas), ‘pets’ to refer to animals such as cats and dogs kept as companions or ornamentally, and ‘feral’ or ‘unmanaged and free roaming’ as per the OIE–World Organisation for Animal Health definition to refer to domestic animals normally kept as pets or livestock but which are living without direct human supervision or control, often in areas where they are not native (e.g. stray dogs, cats and goats).

butchering and consumption of animals likely led to spillovers. One transmission event, probably occurring between 1910 and 1930, gave rise to the HIV strain behind pandemic AIDS (Sharp & Hahn, 2011). Ebola has been suggested to



**Fig. 1.** A conceptual diagram of animal-use supply chains and their interfaces, identifying different intervention points and intervention options at different stages in the supply chain.

have been transmitted from bats (Leroy *et al.*, 2005; Saéz *et al.*, 2015), either directly or *via* an intermediate host, while MERS (Middle-East Respiratory Syndrome) most probably originated in a species of bat, with the dromedary camel *Camelus dromedarius* as an intermediate host (Mohd, Al-Tawfiq & Memish, 2016).

Our knowledge of pathogen prevalence in wildlife populations is heavily biased by host species, pathogen type and sample availability, but studies can provide deep insights into the diversity of potential zoonotic pathogens (e.g. for bat-borne coronaviruses; Anthony *et al.*, 2017). Species are defined as being capable of harbouring a particular zoonotic pathogen following the detection of that pathogen, but only pathogens that can be reliably detected and identified are recognised. In the natural host, however, infection loads may be low and not readily detectable even with modern molecular methods; testing might also be conducted on samples that are suboptimal for certain viruses that then could be missed. Furthermore, most host taxa have not been included in such studies and remain completely untested. Fewer than 300 viruses from 25 high-risk viral families are known to infect people, yet it is estimated that there are around 1.7 million viruses from these same viral families that have not yet been discovered in mammals and birds. Of these, some 700000 are considered to have zoonotic potential (Carroll *et al.*, 2018).

Zoonotic diseases can emerge from a wide variety of wild species, including marine turtles (Aguirre *et al.*, 2006) and

marine mammals (Waltzek *et al.*, 2012), but the risk appears variable, with the highest risk taxa being rodents (Han *et al.*, 2015, 2016), non-human primates (Pedersen *et al.*, 2005) and bats (Luis *et al.*, 2013). Transmission in this context can occur through a range of direct and indirect pathways (e.g. infected faeces, urine, saliva, invertebrate vectors), from interactions with species in natural habitats or during the supply, transport and use of wildlife or wildlife products.

Based on the number of different infected host species, as well as phylogenetic relatedness among hosts, zoonotic pathogens can be characterised as specialists (a single wildlife host species) or generalists (multiple wildlife host species). The latter often can persist by being maintained in multiple wildlife species. Understanding pathogen ecology and evolution offers many advantages in terms of strengthening surveillance programs aimed at preventing or reducing human exposure and zoonotic infection, as well as informing early warning systems for outbreak detection.

Many host species characteristics contribute to a heightened risk of zoonotic transfer. Several zoonoses of high impact for humans originated from non-human primates, probably in part because the phylogenetic barrier to transmission to humans is low (Wolfe *et al.*, 2007). In rodents, reservoir species are associated with a fast-paced life-history strategy, rapid maturation and high fecundity (Han *et al.*, 2015); these characteristics mean that some species carry multiple pathogens, increasing the probability of a

rodent being infected with a pathogen with zoonotic potential. The high population size and density of many rodents is probably also an important factor. It is hypothesised that pathogen-prone rodent species may have low investment in immune defences, but ‘outrun’ the risk of a lethal infection by producing offspring quickly (Han *et al.*, 2015).

The comparatively high zoonotic disease risk from bats (Luis *et al.*, 2013) has been linked to large colony sizes and high mobility due to flight, resulting in even larger effective population sizes and many bat species having the capacity to host a wide range of pathogens. The highest predictor of zoonotic viral richness in bats was the distribution overlap with sympatric species, suggesting that interspecific transmission probably plays a key role in the pathogen complement harboured by bats (Luis *et al.*, 2013). Evolved physiological adaptations to flight might also have enabled bats to harbour a larger range of pathogens in the absence of disease (O’Shea *et al.*, 2014), as their immune systems seem to have been modified to enable protective cellular mechanisms, a dampened interferon response, and a key innate defence pathway that is functionally different from non-bat mammals, implying that bats may be more effective at co-existing with a large number of viruses (Xie *et al.*, 2018). The rigours of flight mean that bat metabolisms can increase by up to 16 times the basal rate, producing sufficient heat to kill most mammals (Speakman & Thomas, 2003; O’Shea *et al.*, 2014). As a consequence of these costs, bats have adapted mechanisms to prevent degradation of cellular mechanisms by heat or oxygen radicals, affecting their ability to withstand infections (Healy *et al.*, 2014; Huang *et al.*, 2019). Together, these properties allow them to be asymptomatic reservoirs of multiple viruses, thus enabling these viruses to persist within bat populations. Stress responses in most mammals are shown to increase the probability of spillover (Hara *et al.*, 2011), yet such studies in bats are only now being conducted (Subudhi, Rapin & Misra, 2019). Understanding how the role of habitat loss and degradation combines with natural stressors (e.g. reproduction and migration) is urgently needed. However, studies show that at least some mechanisms of physical stress in bats do increase viral shedding; for example, bats infected with the fungal pathogen *Pseudogymnoascus destructans* can have a viral load that is increased by up to 60 times that of bats without this fungal infection (Davy *et al.*, 2018).

In addition to these hypotheses, a simpler explanation is that both rodents and bats are also highly diverse vertebrate orders (2361 rodent species and 1420 bat species) and more species-rich reservoir groups host more virus species and therefore a larger number of zoonotic pathogens (Letko *et al.*, 2020; Mollentze & Streicker, 2020).

Other, non-taxon-specific characteristics also contribute to zoonotic pathogen risk. For example, migratory species can have a profound effect on pathogen dispersal, but these effects are complex and context dependent (Altizer, Bartel & Han, 2011; Poulin & de Angeli Dutra, 2021). Migration can play a key role in introducing disease to populations naïve to the pathogen, and the heavy toll of migration can

reduce immune function, so increasing infection burden. Conversely, migration can allow individuals to escape infected areas and, hence, reduce host population pathogen levels. The unsuccessful migration of infected individuals might also lead to overall reductions in pathogen prevalence (Huber *et al.*, 2020).

Where pathogens are thought to be of wildlife origin, their emergence is often associated with a high diversity of pathogens in a wide range of host species (Jones *et al.*, 2008; Allen *et al.*, 2017; Anthony *et al.*, 2017), and many emerge in biodiverse tropical regions. However, the role of biodiversity in zoonotic disease emergence is complex. Studies have identified a general trend, known as the ‘dilution effect’, where increasing host diversity can reduce a given parasite abundance in both wild animals and humans (Civitello *et al.*, 2015; Huang *et al.*, 2017), although this effect depends on specific conditions, context and on the metrics used (Salkeld, Padgett & Jones, 2013; Roberts & Heesterbeek, 2018). While empirical evidence exists for the dilution effect in several multi-host pathogen systems, the mechanism is often unclear, for example whether it is due to actual dilution or to reduced host density (Begon, 2008).

Pathogen transmission from wildlife to humans is influenced by extrinsic factors, such as land-use change (Allen *et al.*, 2017) and agricultural intensification (Jones *et al.*, 2013). Such factors play a particularly important role in driving the emergence of zoonotic diseases in biodiverse tropical forest regions (Keesing *et al.*, 2010), where expanding human populations (and associated agriculture or other activities) into natural habitats leads to increased opportunities for human-to-wildlife contact (Han *et al.*, 2016; Bloomfield, McIntosh & Lambin, 2020) and increased pathogen transmission at human–livestock–wildlife interfaces (Gebreyes *et al.*, 2014). Multi-host pathogen models indicate that pathogen transmission between species inhabiting intact and converted habitat is highest when rates of habitat conversion are intermediate (Johnson *et al.*, 2020). However, the potential severity of epidemics increases at higher rates of habitat conversion (Faust *et al.*, 2018). Land-use change that reduces local biodiversity may increase spillover risk (Civitello *et al.*, 2015), as exemplified by Lyme disease in North America (Ostfeld & Keesing, 2000, 2012). While the diversity of wildlife species declines with habitat degradation, it has been shown that those species more able to live in human-modified habitat tend to have a higher rate of carriage of zoonotic pathogens than those that decline or disappear (Gibb *et al.*, 2020).

Hunting, whether commercially or for subsistence, and the transport, sale, preparation and use of wild animals and wild animal products are also important points of human–wildlife contact. Direct wildlife use, especially for human consumption, is most commonly an issue for zoonotic emergence in the ‘paleotropics’, where high species diversity of high-risk taxa (e.g. of bats and primates) is combined with subsistence hunting and use (Han *et al.*, 2016). Harvesting rates of wild meat in tropical areas

are currently primarily driven by an increase in demand in fast-growing urban centres (Coad *et al.*, 2019). Interactions between wildlife and humans can have complex and hard-to-predict effects, by increasing both stress and movement of species and therefore increased spread of disease and spillover risk. For example, the culling of badgers *Meles meles* is known to increase the movement of surviving animals and, hence, the spread of bovine tuberculosis (Woodroffe *et al.*, 2006).

It seems likely that it is human interactions with, and destruction of, biodiversity that leads to increased likelihood of zoonotic disease emergence. However, the pathways to overcome this are likely to be complex. It has been suggested that protecting ecosystems not currently posing a major threat of disease to humans or wildlife might prevent increases in disease emergence, yet when managing a specific disease for which the ecology is reasonably well understood, it might be more effective to manage the particular species (vectors or amplifying or diluting hosts) or habitats that are known to decrease or increase the likelihood of pathogen spillover, for example, through vaccination, culling, predator supplementation or habitat manipulation (Rohr *et al.*, 2019).

#### (4) Disease transfer involving domestic animals

Many zoonotic outbreaks result from pathogen transmission from domestic animals. Human pathogens considered to originate from the domestication process of animals include diphtheria, influenza A, measles, mumps, pertussis, rotavirus, and smallpox (Wolfe *et al.*, 2007) and contacts between humans and domestic animals have led to recent zoonotic emergence events, such as the H1N1 (Swine Flu) pandemic in 2009 and MERS in 2012. The emergence of many of these diseases has been facilitated by the increased human population size and the development of commercial agriculture and livestock domestication (Wolfe *et al.*, 2007; Jones *et al.*, 2013), as well as agricultural encroachment leading to increased livestock–wildlife interactions and more opportunities for livestock acting as bridging species for novel zoonotic pathogens such as Nipah (Pulliam *et al.*, 2011). Due to thousands of years of domestication, high contact rates and significant amounts of study, ungulates are the mammalian group with which humans are known to share the most pathogens (Cleaveland, Laurenson & Taylor, 2001). In temperate regions, the majority of the heaviest-burden zoonotic diseases impact humans through domestic livestock. Transmission routes of pathogens from livestock are facilitated by poor hygiene and biosecurity measures, such as lack of protective equipment for farm workers (Ramirez *et al.*, 2006), and can occur through a variety of direct and indirect interactions during the rearing of livestock. Numerous other zoonotic diseases involve a vector stage, such as Rift Valley fever or Crimean-Congo haemorrhagic fever (CCHF), where the host is a tick and the vector is a mammal (Wilson *et al.*, 1991).

#### (5) Disease transfer involving wild or exotic pets

Although information is comparatively scarce, wild or exotic pets (i.e. not domesticated animal pets) are another possible source of novel zoonoses with epidemic potential. For example, in 2003 six states in the USA experienced an outbreak of monkeypox, the first cases of human monkeypox reported outside the African continent. This outbreak resulted from prairie dogs *Cynomys* sp. sold as pets after being housed in close proximity to infected rodents recently imported from Ghana (Centers for Disease Control and Prevention, 2003). In 1999, an Egyptian rousette bat *Rousettus aegyptiacus* sold in a pet shop in France was diagnosed with Lagos bat lyssavirus encephalitis, resulting in the treatment of 120 exposed persons (Chomel, Belotto & Meslin, 2007). Variegated squirrels *Sciurus variegatoides* imported from Latin America as exotic pets were the identified host of a novel zoonotic Bornavirus (VSBV-1) that infected, and led to fatal progressive encephalitis or meningoencephalitis, in three squirrel breeders in Germany in 2011–2013 (Hoffmann *et al.*, 2015).

Some actions to combat zoonotic disease depend on an understanding of links between animal welfare and pathogen transmission, including the immune response, which is directly influenced by welfare (Broom & Fraser, 2015). For example, poor welfare during the transport of cattle or sheep can result in the opportunistically pathogenic bacterium *Mannheimia (Pasteurella) haemolytica* causing disease (Broom & Kirkden, 2004). Disease and mortality rates are higher in farm animals that have poor levels of welfare, and in wild animals if stressed when brought into captivity (EFSA, 2006; Leday *et al.*, 2018). If wild animals are captured and kept, capture stress as well as transport stress and other stressors (e.g. being caged with or next to conspecifics or other species; close proximity to people; rough handling; inadequate food or water; exposure to the elements; poor hygiene, etc.) increases their susceptibility to infection with pathogens and the likelihood that they will shed pathogens with or without the development of clinical disease, perhaps thereby infecting humans or other animals (Broom & Kirkden, 2004; Broom & Johnson, 2019).

#### (6) State of knowledge on coronaviruses – origins and transfer

Seven coronaviruses (CoVs) are currently known to infect humans (Andersen *et al.*, 2020), four of which are regularly found in human populations in which they cause only mild symptoms (Corman *et al.*, 2018). However, the betacoronaviruses, SARS-CoV-1, MERS and SARS-CoV-2, have been associated with fatalities and, in the case of MERS, with high fatality rates (Zhou *et al.*, 2020b). There is evidence that CoVs that infect humans have their origins in either bat or rodent species (Salata *et al.*, 2019). Intermediate species have included both domestic and captive wild animals (including cattle and swine), masked palm civets *Paguma larvata* and dromedaries (Drexler, Corman & Drosten, 2014; Corman *et al.*, 2018). Diverse CoVs have been found in bats in

China, with 6.5% of all bats in one study testing positive for at least one coronavirus (Tang *et al.*, 2006), and with SARS-like viruses confirmed in horseshoe bats *Rhinolophus* spp. in 2005 (Li *et al.*, 2005). Since then, further betacoronaviruses have been detected in wild-caught rhinolophid bats across the Old World (Gouilh *et al.*, 2011). Over 200 novel coronaviruses have been identified in bats and approximately 35% of the sequenced bat virome is composed of coronaviruses (Banerjee *et al.*, 2019).

Although many CoVs are limited to bats, some are found in a more diverse selection of mammals. Coronavirus studies have predominantly focused on non-bat hosts, which include both mammals (alpha and betacoronavirus) and birds (gamma and deltacoronavirus), yet few betacoronaviruses have been detected outside bats in the wild. In bats, CoVs have been found in bat families across the globe (Drexler *et al.*, 2014), with groups such as Hipposideridae known to host these viruses asymptotically for extended periods. Typically, CoVs have a highly restricted host range: even bats within the same cave often show different viruses in different species, with only those detected in *Miniopterus* spp. known to be capable of jumping between hosts (Gouilh *et al.*, 2011), normally as a consequence of roosting in direct physical contact with other bat species. The destruction or disturbance of caves by people can lead to different species and taxa being forced to share caves and, given their different abilities to host or pass on betacoronaviruses, this increases the risk of virus spread across species. Furthermore, as rhinolophid bats (in which SARS-like viruses have been detected) can develop clinical coronaviral disease, spillover risk may be higher from this group (Wong *et al.*, 2019). The shared use of bat caves by non-bat hosts, such as Viverridae (civets and genets), increases the risk of spillover into new host species (Song *et al.*, 2005), especially as betacoronaviruses are most commonly detected in faeces (Wong *et al.*, 2019). Rapid adaptation of SARS-CoVs has been observed to occur between hosts (such as masked palm civets and humans) and host shifts have also been observed to occur amongst bat species in wild populations (Cui *et al.*, 2007; Latinne *et al.*, 2020; Zhou *et al.*, 2020a).

The wildlife trade, both legal and illegal, has received enormous global media attention for its potential role in the emergence of novel zoonoses like SARS and COVID-19. Illegal wildlife trade alone is estimated to be a multibillion-dollar industry, comparable to the international trades in narcotics and weapons, and which raises significant human and animal health concerns, especially given its volume, the complete lack of regulation and the fact that the origins of wildlife sometimes match recognised emerging infectious disease hotspots (Smith *et al.*, 2017). However, there remains considerable uncertainty around which species have been involved in the transfer of the causative coronaviruses to humans, as well as exactly when such transfers occurred (Corman *et al.*, 2018; Salata *et al.*, 2019). The virus with the closest match to SARS-CoV-2 has been found in several species of horseshoe bat *Rhinolophus* spp., which likely represent the ancestral or evolutionary (natural) host of the virus

(Zhou *et al.*, 2020a), although the ability of this closest known relative of SARS-CoV-2 to infect humans is poor (Wan *et al.*, 2020). A related virus has been detected in Malayan pangolin *Manis javanica* (Zhang, Wu & Zhang, 2020). While different overall from any known bat CoV, the pangolin CoV receptor binding domain part of the spike protein (which allows the virus to infect a new host) is almost identical to that found in the human virus (Zhou *et al.*, 2020a), but a polybasic cleavage site in SARS-CoV-2 is absent from both known pangolin and bat CoVs, so the origin and route to human infection of SARS-CoV-2 remains unknown (Andersen *et al.*, 2020). The potential for the transmission of zoonotic CoVs through wildlife markets and farm systems, however, has been clearly noted for SARS-CoV (Wong *et al.*, 2019) and actions to prevent such zoonotic spillover risk in future have been widely discussed (e.g. Kelly *et al.*, 2020; Nabi *et al.*, 2020; Ribeiro *et al.*, 2020; Wang *et al.*, 2020).

### III. SOLUTION SCANNING: IDENTIFYING OPTIONS FOR MINIMISING ZOOONOTIC DISEASE TRANSFER

#### (1) The need for solution scanning

Creating a future in which society is more resilient to zoonotic diseases will require coordination and planning among different professionals, considering a broad range of prevention options related to wild, feral and domestic animals, all of which have potential to be the source of future epidemics in humans. These will range from medical and veterinary interventions to simple behavioural and societal interventions that could greatly reduce the risk of pathogen transfer (Morse *et al.*, 2012). Solution scanning uses published research and guidance, the experience of experts and practitioners, and brainstorming to identify a range of potential solutions to a specific problem (Sutherland *et al.*, 2014). This includes solutions that have not been reviewed, might not have evidence of effectiveness or may indeed be ineffective, inconvenient, controversial or have negative side effects. It is therefore important that practitioners and policy makers identify possible interventions as a starting point in decision-making before evidence synthesis and consideration of each option's advantages and disadvantages are conducted. The need for this is illustrated by previous research that showed that 92 conservation practitioners responsible for addressing a problem were only aware of 57% of the possible actions (Walsh, Dicks & Sutherland, 2015).

We conducted a solution scan to identify options for reducing the animal-human transfer of zoonotic pathogens with high potential for human-to-human transmission, such as COVID-19. The solution scan was compiled by documenting our own experience of actions, consulting guidance and scientific literature, and contacting a number of experts and practitioners working in different countries, contexts and institutions in order to explore the range of options available. The approach is based on methods developed as part of



subject-wide evidence synthesis (Sutherland *et al.*, 2020). This solutions scan was initiated as a collaboration between BioRISC (the Biosecurity Research Initiative at St Catharine's College, Cambridge), Conservation Evidence based in the Department of Zoology, University of Cambridge, and numerous other researchers worldwide. The options considered here are diverse, reflecting the variety of possible transmission pathways at the wildlife–livestock–human interface that are discussed in Section II from wildlife, domesticated and captive animals (Table 1). Our review excludes other sources of potential zoonotic disease emergence which could be responsible for future pandemics including (i) the evolution of antimicrobial resistance (AMR), (ii) pathogen release from laboratories, or (iii) the intentional creation of life. It is important to note that AMR is a topic of enormous importance: AMR could be responsible for 10 million deaths per year by 2050 if left unchecked (O'Neill, 2014). However, we exclude AMR from this study due to differences in the type of pathways of disease emergence, including pathogen selection in effluent pollution and the overuse and misuse of antibiotics in farming and medical settings. Nevertheless, many of the animal husbandry options considered herein, in particular those related to improvements in hygiene and health standards, are directly relevant to enabling reduced use of antimicrobials on farms and thus avoiding the selection of resistant strains.

## (2) Interpreting the list of options

We stress that the list provided below is a list of options for consideration and testing, not a list of recommendations or prescriptions. Many options listed may not be feasible, practical or affordable in some situations. For example, the options available to small-scale subsistence farmers will differ from those available to large-scale commercial farms. Similarly, options available in countries with poor animal health and hygiene infrastructure, weak governance and low capacity to regulate or control the local wild meat trade, international wildlife trade, and few available medical testing facilities, will differ from those available to countries with state-of-the-art facilities, diagnostic equipment or strict law enforcement.

It should be recognised that solution scanning is a dynamic process which means that the current list should not be viewed as exhaustive. While effort has been made to compile as complete a list as possible using expert opinion and international collaboration, the vast literature available on specific livestock groups has not been systematically searched, and there may be further options available. This is also true for the wildlife trade literature given the diversity of ways in which animals are used across the globe (e.g. wild meat, exotic pets, medicines, curios, medical research, etc.). Additions to the list are welcome and can be sent to [biorisc@caths.cam.ac.uk](mailto:biorisc@caths.cam.ac.uk), and will be added to an updated list of options available at <https://covid-19.biorisc.com>.

## IV. THE LIST OF OPTIONS

The options outlined below are split into four main sections, (1) supply-side measures, (2) transport and sale, (3) measures to tackle consumption, and (4) measures to create appropriate enabling environments (Fig. 1). Measures are focussed on the diverse categories of animals defined in Table 1. The options listed here need to be assessed for the local context of implementation (e.g. likely effectiveness, costs, feasibility, acceptability), including for their broader implications for the local human communities potentially affected.

### (1) Supply side

Supply-side measures are any that are applied to the production or sourcing of animals (i.e. rearing of farmed wildlife or livestock or hunting – endeavouring to kill or capture wild animals). They focus on preventing or reducing production, or altering the production process to reduce risk (t'Sas-Rolfes *et al.*, 2019).

Supply-side interventions to prevent zoonotic emergence from wildlife may focus on: (i) entirely preventing hunting and collection of high-risk species (area-based or species-based restrictions); (ii) controlling the rate of hunting and collection through limits to numbers or specific characteristics of the animals taken; or (iii) regulating hunting, consolidation and trade through enforced standards. Preventing or reducing hunting, collecting and disturbance of wild species, especially of high-risk species, should decrease the transmission of zoonotic diseases to livestock and people (Johnson *et al.*, 2020). For example, it can reduce the rate of contact between hunters and animals in the wild, and therefore reduce direct animal-to-human transmission. It can also reduce the movement of wild animals out of natural habitats, to places where they have more contact with people and other animals (e.g. markets and other vendors) (Swift *et al.*, 2007). For species that are lower risk for direct transmission, regulated harvesting, with licensing, standards and health or hygiene checks at critical control points, could reduce high-risk practices that cause transmission (e.g. unhygienic slaughter, interaction of domestic and non-domestic animals), and in some cases may be more effective than complete bans (e.g. Fournié *et al.*, 2013).

For livestock, supply-side interventions to prevent zoonotic emergence may focus on: (i) improving animal welfare, health and immune function in farms by limiting density, ensuring veterinary care and reducing long-distance transport or practices that involve large-scale and long-distance live animal movements (e.g. by promoting ranching instead of nomadism); (ii) preventing the mixing of domesticated and wild-sourced or farmed wildlife animals in farms; or (iii) improving the biosecurity of farming practices (e.g. *via* the use of disposable protective clothing and introduction of health surveillance for farm workers as well as controlled slaughter and hygiene conditions).

*(a) Area-based management (e.g. protected areas)*

The emergence of infectious diseases is elevated in high-biodiversity areas experiencing land-use changes (Allen *et al.*, 2017) as well as in landscapes that have been degraded (Bloomfield *et al.*, 2020; Gibb *et al.*, 2020). Well-enforced area-based management can reduce land-use change (Bruner *et al.*, 2001) but further measures may be needed to directly address illegal hunting (Geldman *et al.*, 2019; see Section IV.1*b*).

- Identify and protect unprotected areas with high biodiversity or important habitat features that are at risk from land-use change, particularly those with high-risk species (e.g. bat roosts).
- Strengthen the boundaries of existing protected areas (PAs) using clear demarcation to reduce illegal hunting.
- Establish and reinforce regulation for buffer zones around PAs to reduce human–wildlife–livestock interfaces at the boundaries.
- Increase efficiency of patrols to detect and prevent hunting, collection or disturbance of high-risk wildlife species through increasing patrol effort, targeting key times (e.g. breeding season when potential stress is highest), places (e.g. boundaries and high-risk areas), and offenders (e.g. using acoustic monitoring, drones and surveillance aircraft, thermal cameras, human detection software, satellite data).
- Build capacity for wildlife stewardship amongst hunter/collector communities, or communities living with wildlife (e.g. local community ranger groups), especially for high-risk wildlife species.
- Integrate indigenous peoples and local hunter/collector communities into early warning systems of disease emergence that link to national and international public health reporting systems.
- Establish a strong monitoring system on buying, selling, storage and disposal of hunting equipment (e.g. guns, traps and nets) and/or chemicals/poisons in the vicinity of the PA to reduce illegal hunting, especially of high-risk species (e.g. bats, rodents and non-human primates plus any additionally identified species).

*(b) Hunter/collector behaviour change, for wild-sourced species*

Interventions to change hunter behaviour can target intrinsic motivations (e.g. social norms) or extrinsic motivations (e.g. incentives/disincentives). Most effective examples of interventions to change hunter/harvester behaviour typically combine several intrinsic and extrinsic approaches, and are based on a sound understanding of local context and culture (Travers *et al.*, 2011; DeWan *et al.*, 2013; Wright *et al.*, 2016; Salazar, Mills & Verissimo, 2019; McDonald *et al.*, 2020).

- Conduct community engagement activities and co-design of interventions to strengthen perceived fairness and legitimacy of new laws or standards.

- Identify high-risk species for zoonotic emergence and disincentivise their hunting/collecting and possession, either alive or as body parts and products.
- Introduce licenses and training in risk reduction and hygiene for licensed hunters/suppliers to regulate harvesting and possession of high-risk species and their body parts.
- Introduce bans for sales and possession of certain equipment (e.g. nets or snares), or license their use and sale to prevent hunting or collection of high-risk species.
- Strengthen disincentives for hunter/collector non-compliance with existing wildlife protection and licensing laws for high-risk taxa or products (e.g. larger fines and prison sentences, or enhanced capacity within judicial systems to increase prosecution rates of collectors/hunters of high-risk species, whilst ensuring people dependent upon wild-meat for subsistence can still access resources at minimal risk).
- Incentivise switching to lower-risk hunting/harvesting, either by promoting lower-risk species alternatives (e.g. by improving access) and/or an alternative hunting/collecting method that is less damaging or lower risk.
- Incentivise alternative occupations to subsistence hunting to reduce the need to harvest high-risk species (e.g. community ranger).
- Build awareness regarding laws, penalties and risk of getting caught, and risks of disease transmission associated with specific wildlife hunting/collecting (e.g. *via* signage around PAs, events, media attention on disease risks, highly publicised prosecutions).
- Highlight beneficial ecosystem services provided by specific targeted taxa (e.g. role of bats in pest control in farmland, or in seed dispersal in forests), through informational interventions.
- Provide benefits/decrease costs of living with wildlife (e.g. performance-based monetary incentives for wildlife stewardship, compensation for damage caused by wildlife, or general financial benefits for people living in proximity to wildlife, such as a conservation-based income).
- Work with local communities and leaders to reinforce cultural taboos around hunting of high-risk species or the creation of new negative norms around the harvesting of high-risk species.
- Develop hygienic animal-handling guidelines for licensed hunters/suppliers, and modes to enforce them or, where guidelines already exist, provide training and incentives for implementation.

*(c) Ensure wildlife farming is safe and legal*

- Develop procedures and certification standards for low-risk non-domesticated animals that can be kept and harvested sustainably and legally (i.e. with high confidence of traceability) in captivity for consumption or other uses.
- Develop laws preventing the farming of new wildlife species except where the practice is demonstrably low risk and its products are traceable.

- Develop centrally administered or licensed tracing systems for farmed wild species to ensure illegally sourced specimens are not added from the wild.
- Develop certification for registered farms that demonstrate enforcement of guidelines on safe production standards.
- Develop and enforce minimum welfare and sanitary standards for animal rearing, which minimise stress-induced immunosuppression and reduce infection and spread of disease among captive individuals (e.g. maximum stocking limits and density of wildlife farming).

(d) Reduce wildlife–livestock–human interfaces in and around farms and wild places

There are many mechanisms by which pathogens can transmit from wildlife to humans; thus there are multiple means of reducing contact between wildlife, livestock and humans. Transmission routes may rely upon direct contact between wild animals and domestic herds or flocks, for example in periodic avian influenza outbreaks (FAO, 2007). Thus, designing suitable enclosures for domestic animals that preclude the entry of wild animals, as well as preventing domestic animals from accessing wildlife habitat, can reduce the risk of such events. This is particularly relevant for intensive livestock production in biodiverse areas, where biosecurity standards are sometimes not as strict as elsewhere. Examples include Nipah emergence in Malaysia in 1999 (Pulliam *et al.*, 2011), swine and avian flu epidemics (Koopmans *et al.*, 2004) and swine acute diarrhoea syndrome coronavirus (SADS-CoV) emergence in China in 2016 due to a coronavirus spilling over from bats into an intensive pig farm, then spreading amongst farms (Zhou *et al.*, 2018).

Wildlife–livestock interfaces are also relevant for backyard farming practices, with highly variable biosecurity implementations; contact rates between pigs and wild boar was demonstrated in the recent African Swine Fever epidemic (Chenais *et al.*, 2019) but is also a factor in the complex Influenza A virus transmission pathways (Artois *et al.*, 2009; Osbjer *et al.*, 2017).

Indirect transmission pathways, such as contamination of domestic animal feed or bedding by wild animal urine, faeces or corpses (Crump, Griffin & Angulo, 2002; Daniels, Hutchings & Greig, 2003) can be reduced by excluding entry of wild animals into feedstores. Contamination of human water sources and food pre- or during harvesting also presents a risk, particularly for fresh and raw produce that undergoes little processing (Jay-Russell, 2013), with examples including emerging infectious disease epidemics such as the Nipah virus outbreaks linked to bats contaminating date palm-sap collection vessels (Islam *et al.*, 2016). Once again, preventing access of wild animals to fields with livestock, and preventing access to vessels such as sap collection containers can reduce risks. A reciprocal approach would prevent livestock and poultry from encroaching on wildlife habitat.

Nipah virus also directly infected pigs in open facilities, which subsequently served as intermediary hosts and infected

humans (Yob *et al.*, 2001). Other outbreaks have unknown bat-to-human transmission pathways (Luby *et al.*, 2009).

For insect-vector-borne pathogens the interactions may be more complex, requiring the presence of wild animals and humans/livestock within a vector range, but also influenced by factors altering vector populations. For example, deforestation can lead to increased standing water and reduced shade, increasing the reproductive success of some mosquito species. By contrast, urbanisation can remove anopheline mosquito habitat, thus reducing vector populations (Kilpatrick & Randolph, 2012). For many such known risks, various prevention methods may have been tried (Nahar *et al.*, 2010; Clausen *et al.*, 2012), but the costs of such measures may be restrictive, and their effectiveness limited by climate change-related events such as droughts or floods, which can be hard to anticipate.

- Increase understanding of pathogen hosts and potential transmission mechanisms among wildlife and livestock, captive-bred animals and humans.
- Reduce contact and possible pathogen transmission among wildlife, humans and livestock (e.g. by improving crop protection using fencing).
- Introduce legislation to reduce and control the spread of animal agriculture and overlap/proximity to tropical forest/‘undisturbed ecosystems’, e.g. *via* legally required buffer zones.
- Limit the spread of urbanisation into natural areas with high potential for disease transmission (e.g. by protecting and patrolling forest edges near towns and villages in tropical areas).
- Protect, fence-off and signpost areas used by target wildlife species (e.g. important roosting trees, caves) near and inside farmland or urban areas.
- Create and enforce protocols for maintaining biosafety during caving, such as the use of waterproof coveralls and masks, in caves or other areas with high bat density.
- Reduce contact between wild and farmed or domestic animals (e.g. by separating grazing or watering areas using fencing to increase biosecurity of farmed animals).
- Provide alternative areas for target wildlife species, away from human settlements or farms (e.g. alternative roosting areas for bats or birds).
- Develop mechanisms to reduce the interaction of wild birds with domestic birds and humans (e.g. prevent object and food contamination with faeces from wild birds).
- Develop guidelines for mining, logging and other activities likely to disturb important wildlife habitats to reduce risks and disturbance to wildlife species with high disease transmission risk, especially at particular times of year (e.g. breeding, tree fruiting season, etc.).
- Influence social norms of local communities and visitors around behaviours leading to close contact with high-risk species and specific activities (e.g. keeping primates as pets; disturbance or destruction of bat roosting areas) leading to contact with people or livestock.

- Ensure good hygiene when visiting places with high wild animal densities, in particular for high-risk species (i.e. disinfect footwear after visiting caves, wear protective equipment in caves, etc.).
- Store and protect human and animal feed in areas where they cannot be accessed and potentially contaminated by wildlife (e.g. by bat or rodent faeces or urine).
- Protect food collection/harvesting processes such as sap tapping (e.g. date palm sap) from contamination from wildlife.

(e) Increase animal hygiene and health standards for livestock and farmed wild animal production

Interactions between livestock (all farmed animals), humans and wildlife risks pathogen spillover. Livestock can become hosts (intermediate or amplifier) allowing pathogen evolution before spillover into humans. Expanding and intensifying livestock production is creating more intensive interactions among livestock, people and wildlife, contributing to emerging disease events (Jones *et al.*, 2013). Proposed solutions involve improved farm hygiene and livestock health standards, including separation of species and age groups in farms (Henning *et al.*, 2009) and should be complemented by demand-side measures (like reduced livestock production, especially in areas encroaching on wild habitats). For many intensive farming systems there are detailed and comprehensive biosecurity guidelines and insurance schemes (Hovi, Mcleod & Gunn, 2005). However, these are often only feasible in countries with sufficient infrastructure and trained personnel. Increasing global standards of production systems for animals should be a major concern for preventing future zoonotic pandemics, especially in low- and middle-income countries (LMICs) that are often at the highest risk of zoonotic epidemics. Many options listed here require veterinary infrastructure for health, hygiene and surveillance efforts and this must be a target of development programmes.

Intensive livestock systems generally have fewer direct farm workers, which reduces the number of people in contact with livestock but also contain high-density populations of low genetic diversity, which may favour increased transmission and likelihood of adaptations if pathogens are introduced (Jones *et al.*, 2013). High animal density can increase the frequency of outbreaks; for example, a higher density of pig farms and higher numbers of trucks entering the farms was associated with an increased frequency of pig respiratory disease outbreaks (Rose & Madec, 2002)

- Develop and enforce minimum health, welfare and sanitary standards for animal rearing that minimise stress-induced immunosuppression and reduce the spread of disease into and among captive individuals.
- Develop a veterinary health plan.
- Ensure regular veterinary visits and preventative care.
- Seek veterinary care at the first sign of illness in an animal.
- Develop standards for limiting animal population densities where biosecurity cannot be ensured.

- House sick animals in isolated areas.
- Enforce animal health monitoring, especially for notifiable and emerging diseases and implement regular animal health surveillance programs and early warning systems to detect zoonotic pathogens promptly.
- Conduct risk assessment at the wildlife–livestock–human interfaces to inform the type of emergency response or longer term planning for prevention and control of zoonotic pathogens.
- Provide clean, fresh drinking water for animals.
- Ensure that water sources are not contaminated by manure or slurry (stored and freshly spread).
- Dispose of farm waste products (bedding, slurry) away from livestock, humans and watercourses.
- Spread slurry on arable land rather than land for grass/silage for grazing animals or let slurry rest for several months before spreading on pasture.
- Dispose of fallen stock quickly and in approved, bio-safe ways.
- Educate and train workers to identify early signs of diseases and have action protocols when symptoms are detected.
- Engage in industry-wide assurance schemes, so health plans are generic rather than farm specific.
- Reduce animal density both within and among farms.
- Take measures to reduce stress in farmed animals including maximum permissible stocking densities and other basic welfare standards.
- Separate poultry and pigs by age and species.
- Use all-in, all-out, single-species management strategies for growing or ‘fattening’ meat animals of all species.

(f) Farm biosecurity

The FAO defines biosecurity as the implementation of measures to reduce the risk of the introduction and spread of disease agents (FAO, 2007). There is no standardised way of classifying biosecurity measures but measures can be grouped into bioexclusion (preventing diseases from entering the farm) and biocontainment (preventing diseases from leaving the farm). Key notions of farm biosecurity are: (i) isolation, to ensure no contamination through housing or personal protective equipment; (ii) traffic control, to restrict movement of products, stocks and people; (iii) sanitation, to maintain cleanliness (Conan *et al.*, 2012). Resources sometimes limit the ability to apply biosecure measures, but where possible good practice includes:

- Introduce licensing and monitoring of sanitary practices, especially where high-risk species are involved.
- Clean and disinfect clothing, equipment and vehicles before and after contact with animals.
- Use disposable protective clothing, and shower in and out of farms.
- Provide clean protective clothing and footwear for visitors.
- Keep external vehicles outside the perimeter of the farm, and configure farms so vehicles can carry out their tasks (e.g. transport loading) as far from the farm as possible. If

not possible, use an antiseptic vehicle shower at the entrance of all domestic farms.

- Use personal protective equipment and strict sanitary measures wherever possible for all farm workers and in particular for personnel in direct contact with livestock.
- Introduce and enforce health surveillance protocols for farm workers and promote good hygiene such as regularly brushing and disinfecting footwear.
- Use adequate ventilation, waste disposal and compartments inside farm systems to minimise disease transmission.
- Choose farm facilities (flooring, gates, walls) that can be disinfected easily.
- Limit and control farm visitors, including provision of clear guidance at all access points, and a bell/horn for visitors to attract attention without having to enter the farm.
- Introduce and enforce nominal registers for any farm visitors to allow traceability.
- Enforce a minimum period visitors must have not had contact with relevant livestock species.
- Introduce footbaths/mats with disinfectant at every farm entrance and exit.
- Prevent symptomatic people from entering farms (e.g. people with flu-like symptoms on pig farms) and enforce a minimum symptom-free period before entering.
- Introduce a minimum period between visits to high-stocking-density livestock units that house similar species or species with high disease transmission risks.
- Provide sheltered (i.e. protected access or, if possible, indoors) drinking water and food to avoid contamination by wild animals, especially for poultry.
- Provide feed for animals in free-ranging systems to minimise the risk of foraging behaviours leading to introduction of a pathogen.
- Minimise new animal introductions (both number of sources and individuals), check their health status, isolate them (by keeping them at least 3 m away) and use separate equipment for these animals before introducing them to others on the farm.
- Minimise the animal's exposure to people, animals and wildlife by purchasing directly rather than through markets.
- Use the same isolation and health-checking procedure for animals returning from contact with others (such as shows, markets etc.).
- Prevent mixing of domesticated and wild-sourced or farmed wildlife animals in farms.
- Discourage or make more secure the backyard farming system of semi-wild animals (e.g. use fencing to avoid regular contact with humans).
- Enforce laws to ensure mandatory quarantine for exported and imported domestic and wild animals.
- Disinfect farm areas between production batches, and if possible employ an all-in, all-out system.
- Configure farms to minimise livestock exposure to humans, agricultural pests (e.g. rodents, crows, etc.), neighbouring livestock and wildlife.
- Control the presence of birds in domestic animal farms, for example by reducing visits of wild birds (crows, seagulls, pigeons) and rodents (rat, mice etc.).
- Create means to bring outdoor animals indoors if necessary in periods of high risk of disease transfer (especially poultry).
- Use fenced or indoors-only farming systems (in particular where there are risks of interaction with wildlife species) or have double fencing to provide a buffer between wildlife and livestock.
- Keep bedding stores covered and shut to prevent access by cats, dogs, agricultural pests and wildlife.
- Establish clear land zoning for human settlements and the farming of domestic animals to avoid unexpected overlap between settlements and farmland that could create human–animal interfaces.
- Promptly wash and disinfect any bites and scratches inflicted by animals.
- Avoid contact with sick animals (e.g. with diarrhoea).

## (2) Transport and sale

Transactional interventions focus on any points in the supply chain between source and consumer, for the transport or sale of animals and their products. Broadly, transactional interventions involve regulation and legislative control (e.g. <https://www.nfacc.ca/codes-of-practice>), and tracking and detection of products as they move through the supply chain, and these can be applied during transit or sale. Here we present a series of options varying in the strength of restrictions.

### (a) Reduce disease transmission risk during transport

- Ban the long-distance and/or cross-border transport of high-risk species, or increase enforcement and penalties for these activities if they are already restricted.
- Restrict the long-distance transport of high-risk species by using species quotas, licensing traders, or export certification.
- Ban the international transport of live wild animals except for licenced conservation and scientific programmes.
- Minimise international transport of live livestock and introduce detailed health status checks.
- Improve awareness of laws and penalties for the transport of high-risk species at transit stations (e.g. displays at airports and seaports), and on board international transport services (e.g. announcements on aeroplanes, ships and trains).
- Improve detection of wild-caught high-risk species by building capacity for local enforcement officers and customs regulators to identify regulated species and derivative products (e.g. visually, or using forensic traceability methods such as DNA barcoding, stable isotope analysis) to check source and species are as reported.

- Introduce mandatory quarantine for all exported live wild-life and domestic animals to destination countries to prevent diseases crossing borders.
  - Ban species mixing and introduce measures to decrease animal stress during (i) live animal transport and/or (ii) at trade consolidation points after collecting.
  - Improve enforcement of safety and hygiene standards during transit by training local enforcement and customs regulators in the legal requirements for transporting high-risk species.
  - Apply whole-supply-chain traceability methods (e.g. tamper-proof boxes, electronic tags, physical marking with barcodes, blockchain) to show that shipments have undergone quarantine/pathogen detection/disinfection at each step.
  - Introduce technology-based reporting systems to trace disease outbreaks to source, including in domestic animal farms.
  - Introduce licencing or certification systems for the transport of live animals or animal parts, to ensure adherence to hygiene and welfare standards.
  - Avoid transportation of (i) different domestic species, (ii) both wildlife and domestic animals, and (iii) animals from different sources, in the same cages and/or vehicles to prevent disease transmission among live animals during transit.
  - Regulate maximum allowed animal density for animals simultaneously housed or transported.
  - Introduce standards for regular checking and safe removal of dead or sick individuals during transport, including their bedding materials.
  - Build the capacity of airport, seaport, border and cargo personnel for safe, secure and scientific handling of wildlife and domestic animals and animal products during transit checks.
  - Introduce safe and hygienic animal handling and slaughter standards (e.g. for waste disposal of slaughter by-products), and training for licensed processors of both live animals and animal products (e.g. tannery and wool industries).
  - Increase verification checks at critical control points in the trade chain, and verify stocks present against inventories in central databases.
- (b) Reduce disease risks during slaughtering, processing and at place of sale
- Identify and introduce bans on sales of high-risk species and products.
  - Establish or increase penalties for sales of high-risk species.
  - Introduce a licencing or certification system for any vendor or processor of live animals or animal parts, with regular checks and training, to ensure laws and standards are adhered to and that quotas can be monitored.
  - Ensure all places of sale that deal with live animals, raw meat or animal parts have standardised sanitary control measures and regular inspections.
- Introduce mandatory pasteurisation methods for raw animal products from non-domesticated animals (e.g. for traditional medicine or food).
  - Introduce mandatory separation at markets or shops between live animals of different species, between live domesticated and wild animals, and between live animals and animal parts.
  - Introduce laws to prevent consumption of raw animal products (e.g. raw meat in restaurants, raw animal parts used in traditional medicine).
  - Enhance hygiene standards, such as daily disinfection of market environments, and traders' vehicles and equipment.
  - Introduce legal requirements for quarantine control of live animal movements in markets selling wild animals and meat.
  - Establish set maximal prices for specific high-risk wildlife products to influence both supply and demand for that product.
  - Introduce mandatory separation of animals and derivative products from different sources, thus any contamination is limited to single products and sources rather than dispersed throughout entire trade chain of harvests.
  - Ensure that trade hygiene standards for wild animals match those for livestock.
  - Increase awareness of laws and penalties for trade of high-risk species at places of sale (e.g. posters at known wildlife markets).
  - Build enforcement capacity and forensic accounting ability to audit marketplaces and vendors.
  - Increase enforcement, monitoring and detection for all wildlife trade, including for banned species, separation of animals and hygiene.
  - Enable easy anonymous modes of reporting of wildlife for sale or violations of restrictions in hygiene regulations, e.g. through reporting hotlines etc., and make such rules widely visible.
  - Keep premises free of animals between events (e.g. 27 days in the UK: Animal Gatherings Order, 2010) where animals are brought together (e.g. live animal shows, wholesale or retail markets) to allow sufficient time to disinfect between uses.
  - Burn or otherwise appropriately dispose of used or soiled bedding and other waste.
  - Ensure that water, including from fish and amphibian tanks, goes into drainage facilities for treatment and not directly into water courses.
  - Introduce mandatory testing (additional screening of viral pathogens in high-risk taxa or those utilised in high volumes) and health surveillance of species considered for human consumption or use.

### (3) Consumption

Demand-side interventions can reduce the frequency or the quantity of a given high-risk product being used or shift demand away from high-risk products and towards lower risk

ones (UNEP, 2019). These interventions can take the form of either coercive measures, such as laws or law enforcement aimed at dictating consumer behaviour, or closer engagement with consumers to identify interventions that promote voluntary behaviour change (tSas-Rolfes *et al.*, 2019). Demand-side measures can target consumers directly or indirectly, through the use of key influencers such as peers, doctors, or religious leaders (tSas-Rolfes *et al.*, 2019).

(a) Coercive measures to change consumer demand

These include interventions of a legal nature that aim to regulate purchase and consumption behaviours.

- Ban the purchase, sale, possession or use of high-risk products.
- Establish or increase penalties for the purchase, sale or use of high-risk products.
- Improve enforcement of regulations around purchase or use to increase perceived risk of penalties for sellers and consumers breaking the law.
- Increase consumer awareness of regulations and related penalties of illegal purchase or use of high-risk products.

(b) Promoting voluntary behaviour change in consumers

Opportunities exist to encourage behaviour change among consumers given the enhanced awareness of the risks of trade in high-risk animal species and various types of animal farming as well as increased concern of current environmental challenges, including biodiversity loss. Progress is likely to entail engagement with consumers to develop a shared understanding of drivers of demand and potential barriers to change, along with co-development of interventions based around voluntary behaviour change (Verissimo *et al.*, 2020). Engagement of key influencers may be critical, with the most appropriate figure types (e.g. local leaders) varying across demographic and psychographic consumer groups.

Further interventions that could affect demand include an increase in the costs of purchasing or consuming high-risk products or an increase in the benefits of purchasing or consuming lower-risk products, while preserving consumer choice. These include outreach campaigns aimed at influencing social norms and consumer behaviour, economic incentives and improved access to substitutes (Chaves *et al.*, 2018; Wicander & Coad, 2018; Salazar *et al.*, 2019) and can target both traditional information channels as well as social media, especially when target audiences are very active online. While all of these ideas have been discussed in the literature for decades, the evidence base around their effectiveness is still sparse (Wicander & Coad, 2018; Verissimo & Wan, 2019). The mainstreaming of social media and other digital communication platforms opens up new avenues for interventions to manage demand for wildlife products, such as the use of online advertising to reach consumers (Doughty *et al.*, 2020).

- Influence social norms to reduce social acceptability of the purchase, possession or use of high-risk animals and products, including as pets.
- Promote the development and commercialisation of synthetic alternatives (e.g. synthetic fur, leather or laboratory-created meat).
- Influence consumer attitudes to increase acceptability of lower-risk substitute products (e.g. plants or synthetic substitutes for food, clothing or medicine instead of animal products, particularly those from high-risk species).
- Tax high-risk products in order to decrease the financial gains of trading such products.
- Subsidise or lower taxes on lower-risk substitutes of high-risk products (e.g. certified captive-bred disease-free products, use of different species or plant/synthetic material instead of wild animals), to reduce the relative financial cost of purchasing substitutes.
- Increase the availability of lower-risk substitutes of high-risk products at the points of sale most relevant to consumers of high-risk products.
- Increase knowledge of the existence and availability of lower-risk products that can act as substitutes to high-risk products and guide consumer choice towards such products.
- Develop certification systems for high-value species that cannot be removed from trade but for which laundering of wild individuals, and thus disease transmission, remains a risk.
- Increase recognition and trust of certification schemes amongst consumers of high-risk products.

**(4) Enabling environment (applies to all)**

(a) Capacity

Increase effectiveness of animal health, enforcement and customs workers (e.g. by increasing numbers, motivation, training and equipment of custom officers, focusing enforcement on key airports and seaports, and tackling corruption).

- Create markets for sustainable/low-risk products and certification.
- Streamline collaboration among agencies to develop and enforce trade regulations.
- Introduce training of relevant agencies within government.
- Increase effectiveness and independence of the legal system.
- Involve community in justice initiatives that improve transparency and enforcement.
- Provide amnesty in exchange for cessation and/or information for tackling illegal or sanctionable activities concerning animal health and zoonotic risk.
- Ensure appropriate biosafety level of all educational and research laboratories dealing with samples and pathogens.
- Increase capacity of all laboratories dealing with animal samples to include trade forensics.

- Improve zoonotic disease surveillance and public health preparedness.
- Provide simple tests [e.g. Rapid diagnostic tests (RDTs)] to be used on farms for high-risk zoonotic pathogens and which can be applied without expert skills (i.e. by the farmer).
- Build capacity of law enforcement officials for identification of regulated species and standards, and rescue and release of wildlife where appropriate and safe.

(b) Government commitments

- Ensure international multilateral agreements are fit for purpose.
- Increase governmental buy-in/backing for trade agreements.
- Increase the number of countries signed up to multilateral agreements.
- Ensure clear screening and checks for all meat and animal products.
- Increase multi-agency collaboration within countries to strengthen law enforcement against wildlife criminals.
- Increase trans-boundary collaboration to dismantle criminal networks and product flows in international markets.
- Establish hygiene and safety standards at critical control points, such as developing safe and hygienic animal handling and slaughter guidelines and cleanliness standards.
- Ensure legislative framework and prosecutorial capacity for enforcing regulations.
- Tackle wider criminal networks involved in illegal wildlife trade including empowering the media, reducing corruption, prosecuting corrupt officials and rewarding and protecting whistleblowers.
- Financially support the provision and installation of adequate storage facilities for food and farm produce to minimise contacts with wildlife and their excreta.

## V. DISCUSSION

### (1) Using options to make decisions

COVID-19 has demonstrated the rapid capacity of a virus to transform human lives globally. In an interconnected world such events cause mass mortality and overload health systems, yet without systemic change the rate of emergence of zoonotic diseases with pandemic potential will continue to increase and we need to learn lessons not only on how to moderate and control pandemics post-emergence, but to minimise the risk of their emergence by reducing the likelihood of animal–human disease spillover. To cause spillover infections in humans, all zoonotic pathogens must overcome a hierarchical series of barriers. Understanding and targeting these barriers (e.g. *via* integrating studies of animal ecology, landscape ecology, microbiology, disease ecology, immunology and others) could substantially improve our ability to

predict or prevent spillover events, for instance by reducing human exposure (Plowright *et al.*, 2017).

We herein present a list of options, not conservation or sustainability focused, but specifically to achieve a reduced risk of disease transmission from animals to humans. These are not reactive strategies for use during a disease outbreak, but a set of proactive options to change the way society currently operates and to prevent disease emergence in humans at the outset. These options can be used in the design of strategies to minimise risks of zoonotic disease transfer by inter-governmental, governmental, corporate or non-governmental organisations or individuals. We emphasise that our solution scan does not provide a list of recommendations or prescriptions. It instead provides a starting point for discussion and analysis of the available options for intervention with different decision-making and regulation bodies at global, regional, national and local scales.

When deciding on which measures should be adopted, policy-makers and practitioners should first determine the context, the pathways of zoonotic disease transfer to be addressed and the risks associated with them. This will then allow relevant and practical options to be prioritised, assessed and tested. Once this has occurred, decisions can be made on which interventions to deploy, feeding into strategies to reduce the risks of zoonotic disease transfer.

### (a) Identifying risks

Our solution scan considers a wide range of threats and potential pathways of disease transmission, but it should be noted that these pathways will, in practice, have different levels of risk associated with them. Based on the results of risk assessments, specific interventions may be more or less applicable and important for different reservoir species, types of disease, transmission pathways or socio-ecological contexts. Where a specific risk is being considered, a policy-maker will be required to choose those options that are relevant to their context and to discount those that are not appropriate or may be harmful. Importantly, focusing solely on a set of options, for instance dealing with livestock systems, will not reduce the substantial risks that are related to emerging diseases from wildlife; thus priorities and context are critical.

Decision-makers, regulatory bodies and organisations involved with monitoring or guiding trade, international movement, or environmental policy (e.g. CITES, WTO, various national health, trade, agriculture and environment agencies) should therefore begin identifying transmission pathways for disease(s) that are to be tackled, the pathogen(s) of interest and the levels of risk associated with each pathway. In addition, private sector companies that facilitate the trade of animals (e.g. airlines: <https://routespartnership.org/>) should work closely with regulators to identify and address gaps and vulnerabilities in enforcement and regulation that may lead to the spread of disease (e.g. illegal wildlife trade *via* domestic flights: Utermohlen, 2020). Doing so will help determine which groups of interventions should be assessed. For example,



many of the interventions in the list above focus on high-intensity farming systems, and thus selecting appropriate interventions will necessarily have to adapt to the farming systems present and the potential for interactions between wildlife and livestock, as well as transmission of novel pathogens between other livestock and humans. Interdisciplinary engagement, such as between biomedical researchers and invasion scientists, can offer novel insights and approaches for the modelling, risk assessment, monitoring and management of future zoonoses (Ogden *et al.*, 2019; Nuñez, Pauchard & Ricciard, 2020).

(b) Assessment, review and testing

Once context and transmission pathways have been assessed, the long list of options presented above can be scanned, and candidate options selected based on their relevance and practicality. Deciding on their use will require consideration of a wide range of variables including evidence of effectiveness, cost, practicality, equity/fairness, social acceptability and the interventions already in place.

Ideally effectiveness and possible harms of an intervention (both for reducing zoonotic disease transfer, and other off-target effects) would be assessed using robust evidence from the scientific literature including systematic reviews (Donnelly *et al.*, 2018) and subject-wide evidence synthesis (Sutherland *et al.*, 2019). However, in many cases it is likely that the evidence base is lacking. In these instances, expert experience and knowledge (Sutherland & Burgmann, 2015) should be used to assess likely effects and harms and make pragmatic decisions. Where evidence is lacking, careful testing of interventions is important to promote learning and prevent harmful or unintended consequences.

(c) Cost–benefit and trade-offs

The costs of these interventions should also be assessed, including not just the direct costs of an intervention but also changes in future income (opportunity costs) to different stakeholder groups. Further, it is important to consider equity in decision-making. The costs and benefits of an intervention may not be borne equally by all members of society, or all stakeholder groups. For example, an intervention to ban the hunting of wild animals may detrimentally impact indigenous peoples and local communities who rely on that resource, whilst bearing minimal costs to other stakeholders.

(d) Choosing interventions/developing and modifying strategies

Using the relevant options identified (Step a) and an assessment of their feasibility, benefits and harms (Step b), practitioners and policy makers can create strategies for tackling the transmission pathways of interest. Strategies can involve a combination of measures tackling different environments and pathways of disease transmission. Where possible, actions should be carefully monitored after implementation

to ensure they are achieving intended outcomes, whilst avoiding unintended off-target harms.

## (2) High-level options currently proposed in the response to COVID-19

There have been numerous calls for radical changes, primarily for complete bans on hunting, wildlife trade, wildlife trade for consumption or so-called ‘wet markets’. Such calls may sound reasonable but miss the important roles of fisheries and sustainable products, wildlife’s contribution to global diets and that wet markets are an important source of affordable fresh produce, where wildlife generally has a minor role (Ribeiro *et al.*, 2020; Wang *et al.*, 2020).

Whilst acknowledging the need and appetite for change, we believe such broad measures are unlikely to be enacted or obeyed. The solution seems likely to be a broader, more pragmatic and realistic approach that considers the variety of disease pathways, the different mechanisms by which interventions can act, the complexity of options that can target such mechanisms and the likely on- and off-target effects of those actions. This solution scan can help in the early stages of designing such approaches, presenting a wide range of options, including stronger enforcement on illegal wildlife trade and bans on high-risk wildlife trade, which can be considered to tackle the transfer of emerging zoonotic diseases with epidemic potential into humans.

## VI. FURTHER UNANSWERED QUESTIONS

To help set an agenda for future research we have collaboratively identified 10 important questions. These questions were identified by the authors following the construction of the lists in Section III and relate to unanswered questions around implementation and effectiveness that arose during the solution scan.

- (1) What are the most cost-effective ways of achieving long-term consumer behaviour change, particularly in areas where the use of high-risk wildlife species (e.g. bats, rodents, primates or other species identified as high risk for disease transmission) is deeply culturally embedded?
- (2) What are the most cost-effective ways for protecting natural habitat areas that harbour high-risk species and for reducing contact of such species with humans?
- (3) What are the most cost-effective measures to prevent contact between wildlife and livestock or farmed wildlife in different settings?
- (4) For small-scale livestock kept in/under houses with human residents how can disease transmission risks be minimised, or can we find central communal alternatives?

- (5) How can adequate standards for hygiene and health of farm animals be applied in LMICs given the lack of infrastructure, the need for trained personnel and the increased production costs?
- (6) Is there any disease risk associated with animal dung used for cooking or building materials and, if so, would simple treatments be effective for sterilisation?
- (7) For wildlife farming facilities (e.g. fur farming) how can prevention of laundering of wildstock be ensured cost effectively?
- (8) In LMIC where wild meat is both a subsistence livelihood and core food supply, would restricting consumption of meat to 'low-risk' species be sufficient to minimise disease risk, does risk vary over the annual cycle so that hunting should be limited to certain periods, and how can we understand relative risk in such situations?
- (9) How can we manage natural systems to maintain healthy wild populations and reduce the chance of spillover due to host immunosuppression?
- (10) When are the key times of year where, due to natural stressors, spillover events are more likely, and how can such periods and the areas where they occur be avoided?

## VII. FUTURE DIRECTIONS

To understand which activities risk zoonotic emergence and spread and how they should be changed to minimise the risk of future zoonotic spill-over events requires a joined-up approach that combines expertise across a range of social, environmental, veterinary and medical sciences. Such a holistic approach to environmental sustainability, livestock health and human health combined is often termed 'One-Health' (<https://www.cdc.gov/onehealth/index.html>), and aims to understand how environmental health influences spillover probability, and to act to reduce those impacts and therefore risk. There is a pressing need to unite research investigating public health and domestic animal health threats from wildlife, but also to link this with the biodiversity crisis and improve our understanding of the drivers of environmental change and how these lead to disease emergence and pandemic threat (Dobson *et al.*, 2020).

Our list is a starting point for collating the evidence, identifying research gaps and building policies. We need further research into the potential sources of zoonotic diseases, risks of different transmission pathways and the effectiveness of different measures. The appropriateness of different measures will vary depending according to the scale of the operation and the extent to which it can be regulated. As just one example, measures for markets depend on whether electricity is widespread or whether animals need to be purchased live and killed before cooking to keep meat fresh. Although some intensive livestock systems are highly controlled and biosafety measures well researched, less work has been done in less-

intensive systems, or in parts of the world where standards may be lower or less rigorously enforced. Ensuring that appropriate biosafety is implemented at all levels and intensities, and developing provisions to ensure biosafety protocols are followed through supply chains, is critical to creating a robust future society.

Furthermore, reducing the opportunities for zoonotic diseases to transmit into captive animals or humans requires further work both to reduce the risk of exposure and to manage landscapes effectively to reduce the chance of spillover events occurring.

In addition to human impacts, epidemics resulting from zoonotic diseases have been a major cause of wild species population declines, thus understanding how to reduce transmission at all scales is key for both human health and wildlife conservation. Our need for animal companions, and for the products generated by animal rearing, therefore requires sufficient safeguards at low costs and at all scales, although this may be especially challenging to enact in LMICs where the risk of transmission due to proximity to wildlife and captive animals may be high, hygiene conditions poor, and veterinary screening challenging or inaccessible.

## VIII. CONCLUSIONS

- (1) The COVID-19 pandemic alerted the world to the serious nature of pandemics and created demand for change. As a consequence, there have been calls for, and debates around the relative merits of, the banning of international trade of wild animals. However whilst the current debate has focussed on the consumption of wild animals in south-east Asia, evidence from the emergence of other zoonotic pathogens suggests that transmission pathways are diverse and we also need to address disease emergence risks from (i) direct contact with and use of wild animals and their products (e.g. wild meat hunting), (ii) the export and commercial trade of wild animal products, (iii) the breeding, rearing and trade of wild animals, and (iv) the breeding, rearing and trade of domesticated animals. Although not tackled herein, zoonotic pathogens can also emerge from (v) the evolution of AMR, (vi) pathogen release or escape from laboratories, including bioterrorism, or perhaps even (vii) the intentional creation of life.
- (2) Given the diversity of possible transmission pathways, and the complexity of the socio-ecological systems in which interventions are to be put in place to reduce risk, single interventions may not address the pathways of highest risk, and may create unintended, difficult-to-predict outcomes. To design the most feasible and effective strategies for reducing the likelihood of zoonotic disease outbreaks and for predicting and preventing future pandemics, it is necessary to take a holistic, context-specific, systems-based approach and

work collaboratively across borders and disciplines. Strategies will need to implement a package of measures, tackling multiple transmission pathways of greatest risk, with actions assessed and monitored as to their effectiveness and feasibility.

- (3) Our solution scan has identified 161 options for reducing the risk of emergence which can serve as a starting point in the design of such holistic strategies. Further work should be undertaken on transmission pathways not tackled herein to identify options that could reduce the likelihood of disease emergence.

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## IX. REFERENCES

- AGUIRRE, A. A., GARDNER, S. C., MARSH, J. C., DELGADO, S. G., LIMPUS, C. J. & NICHOLS, W. J. (2006). Hazards associated with the consumption of sea turtle meat and eggs: a review for health care workers and the general public. *EcoHealth* **3**, 141–153.
- ALLEN, T., MURRAY, K. A., ZAMBRANA-TORRELIO, C., MORSE, S. S., RONDININI, C., DI MARCO, M., BREIT, N., OLIVAL, K. J. & DASZAK, P. (2017). Global hotspots and correlates of emerging zoonotic diseases. *Nature Communications* **8**, 1–10.
- ALTIZER, S., BARTEL, R. & HAN, B. A. (2011). Animal migration and infectious disease risk. *Science* **331**, 296–302.
- ANDERSEN, K. G., RAMBAUT, A., LIPKIN, W. I., HOLMES, E. C. & GARRY, R. F. (2020). The proximal origin of SARS-CoV-2. *Nature Medicine* **26**, 1–3.
- ANTHONY, S. J., JOHNSON, C. K., GREIG, D. J., KRAMER, S., CHE, X., WELLS, H., HICKS, A. L., JOLY, D. O., WOLFE, N. D., DASZAK, P., KARESH, W., LIPKIN, W. I., MORSE, S. S., PREDICT CONSORTIUM, MAZET, J. A. K. & GOLDSTEIN, T. (2017). Global patterns of coronavirus diversity. *Virus Evolution* **3**, vex012.
- ARTOIS, M., BICOUD, D., DOCTRINAL, D., FOUCHIER, R., GAVIER-WIDEN, D., GLOBIG, A., HAGEMEIJER, W., MUNDKUR, T., MUNSTER, V. & OLSEN, B. (2009). Outbreaks of highly pathogenic avian influenza in Europe: the risks associated with wild birds. *Revue Scientifique et Technique* **28**, 69–92.
- BANERJEE, A., KULCSAR, K., MISRA, V., FRIEMAN, M. & MOSSMAN, K. (2019). Bats and coronaviruses. *Viruses* **11**, 41.
- BECKER, D. J., ALBERY, G. F., KESSLER, M. K., LUNN, T. J., FALVO, C. A., CZIRJAK, G. Á., MARTIN, L. B. & PLOWRIGHT, R. K. (2020). Macroimmunology: the drivers and consequences of spatial patterns in wildlife immune defence. *Journal of Animal Ecology* **89**, 972–995.
- BEGON, M. (2008). Effects of host diversity on disease dynamics. In *Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems* (eds R. S. OSTFELD, F. KEESING and V. T. EVINER), pp. 12–29. Princeton University Press, Princeton.
- BLOOMFIELD, L. S., MCINTOSH, T. L. & LAMBIN, E. F. (2020). Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa. *Landscape Ecology* **35**, 985–1000.
- BOOTH, H., CLARK, M., MILNER-GULLAND, E. J., AMPONSAH-MENSAH, K., ANTUNES, A. P., BRITTAIN, S., CASTILHO, L. C., CAMPOS-SILVA, J. V., CONSTANTINO, P. DE A. L., LI, Y., MANOLOMA, L., NNEJI, L. M., IPONGA, D. M., MOYO, B., MCNAMARA, J., et al. (2021) Investigating the risks of removing wild meat from global food systems. *Current Biology* **31**, 1788–1797.e3. <http://dx.doi.org/10.1016/j.cub.2021.01.079>.
- BROOM, D. M. & FRASER, A. F. (2015). *Domestic Animal Behaviour and Welfare*, Fifth Edition, p. 472. CABI, Wallingford.
- BROOM, D. M. & JOHNSON, K. G. (2019). *Stress and Animal Welfare: Key Issues in the Biology of Humans and Other Animals*, Second Edition, p. 230. Springer Nature, Cham.
- BROOM, D. M. & KIRKEDEN, R. D. (2004). Welfare, stress, behavior, and pathophysiology. In *Veterinary Pathophysiology* (eds R. H. DUNLOP and C.-H. MALBERT), pp. 337–369. Blackwell, Ames.
- BRUNER, A. G., GULLISON, R. E., RICE, R. E. & DA FONSECA, G. A. (2001). Effectiveness of parks in protecting tropical biodiversity. *Science* **291**, 125–128.
- CAN, Ö. E., D'CRUZE, N. & MACDONALD, D. W. (2019). Dealing in deadly pathogens: taking stock of the legal trade in live wildlife and potential risks to human health. *Global Ecology and Conservation* **17**, e00515.
- CARROLL, D., DASZAK, P., WOLFE, N. D., GAO, G. F., MOREL, C. M., MORZARIA, S., PABLOS-MENDEZ, A., TOMORI, O. & MAZET, J. A. (2018). The global virome project. *Science* **359**, 872–874.
- CENTRES FOR DISEASE CONTROL AND PREVENTION (2003). Update: multistate outbreak of monkeypox—Illinois, Indiana, Kansas, Missouri, Ohio, and Wisconsin. *Morbidity and Mortality Weekly Report* **52**, 561–564.
- CHAVES, W. A., VALLE, D. R., MONROE, M. C., WILKIE, D. S., SIEVING, K. E. & SADOWSKY, B. (2018). Changing wild meat consumption: an experiment in the Central Amazon, Brazil. *Conservation Letters* **11**, e12391.
- CHENAIS, E., DEPNER, K., GUBERTI, V., DIETZE, K., VILTROP, A. & STÄHL, K. (2019). Epidemiological considerations on African swine fever in Europe 2014–2018. *Porcine Health Management* **5**, 1–10.
- CHOMEL, B. B., BELOTTO, A. & MESLIN, F. X. (2007). Wildlife, exotic pets, and emerging zoonoses. *Emerging Infectious Diseases* **13**, 6–11.
- CIVITELLO, D. J., COHEN, J., FATIMA, H., HALSTEAD, N. T., LIRIANO, J., MCMAHON, T. A., ORTEGA, C. N., SAUER, E. L., SEHGAL, T., YOUNG, S. & ROHR, J. R. (2015). Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 8667–8671.
- CLAUSEN, J. H., MADSEN, H., MURRELL, K. D., VAN, P. T., THU, H. N. T., DO, D. T., THI, L. A. N., MANH, H. N. & DALSGAARD, A. (2012). Prevention and control of fish-borne zoonotic trematodes in fish nurseries, Vietnam. *Emerging Infectious Diseases* **18**, 1438–1445.
- CLEAVELAND, S., LAURENSEN, M. K. & TAYLOR, L. H. (2001). Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **356**, 991–999.
- COAD, L., FA, J. E., ABERNETHY, K., VAN VLIET, N., SANTAMARIA, C., WILKIE, D., EL BIZRI, H. R., INGRAM, D. J., CAWTHORN, D. M. & NASI, R. (2019). *Towards a Sustainable, Participatory and Inclusive Wild Meat Sector*. CIFOR (Center for International Forestry Research), Bogor.
- CONAN, A., GOUTARD, F. L., SORN, S. & VONG, S. (2012). Biosecurity measures for backyard poultry in developing countries: a systematic review. *BMC Veterinary Research* **8**, 1–10.
- CORMAN, V. M., MUTH, D., NIEMEYER, D. & DROSTEN, C. (2018). Hosts and sources of endemic human coronaviruses. *Advances in Virus Research* **100**, 163–188.
- CRUMP, J. A., GRIFFIN, P. M. & ANGULO, F. J. (2002). Bacterial contamination of animal feed and its relationship to human foodborne illness. *Clinical Infectious Diseases* **35**, 859–865.
- CUI, J., HAN, N., STREICKER, D., LI, G., TANG, X., SHI, Z., HU, Z., ZHAO, G., FONTANET, A., GUAN, Y., WANG, L., JONES, G., FIELD, H. E., DASZAK, P. & ZHANG, S. (2007). Evolutionary relationships between bat coronaviruses and their hosts. *Emerging Infectious Diseases* **13**, 1526–1532.
- DANIELS, M. J., HUTCHINGS, M. R. & GREIG, A. (2003). The risk of disease transmission to livestock posed by contamination of farm stored feed by wildlife excreta. *Epidemiology and Infection* **130**, 561–568.
- DAVY, C. M., DONALDSON, M. E., SUBUDHI, S., RAPIN, N., WARNECKE, L., TURNER, J. M., BOLLINGER, T. K., KYLE, C. J., DORVILLE, N. A. S. Y., KUNKEL, E. L., NORQUAY, K. J. O., DZAL, Y. A., WILLIS, C. K. R. & MISRA, V. (2018). White-nose syndrome is associated with increased replication of a naturally persisting coronavirus in bats. *Scientific Reports* **8**, 1–12.
- DEWAN, A., GREEN, K., LI, X. & HAYDEN, D. (2013). Using social marketing tools to increase fuel-efficient stove adoption for conservation of the golden snub-nosed monkey, Gansu Province, China. *Conservation Evidence* **10**, 32–36.
- DICKS, L. V., ROSE, D. C., ANG, F., ASTON, S., BIRCH, A. N. E., BOATMAN, N., BOWLES, E. L., CHADWICK, D., DINSDALE, A., DURHAM, S., ELLIOT, J., FIRBANK, L., HUMPHREYS, S., JARVIS, P., JONES, D., et al. (2019). What agricultural practices are most likely to deliver “sustainable intensification” in the UK? *Food and Energy Security* **8**, e00148.
- DOBSON, A. P., PIMM, S. L., HANNAH, L., KAUFMAN, L., AHUMADA, J. A., ANDO, A. W., BERNSTEIN, A., BUSCH, J., DASZAK, P., ENGELMANN, J. & KINNAIRD, M. F. (2020). Ecology and economics for pandemic prevention. *Science* **369**, 379–381.
- DONNELLY, C. A., BOYD, I., CAMPBELL, P., CRAIG, C., VALLANCE, P., WALPORT, M., WHITTY, C. J. M., WOODS, E. & WORMALD, C. (2018). Four principles to make evidence synthesis more useful for policy. *Nature* **558**, 361–364.
- DOUGHTY, H., WRIGHT, J., VERISSIMO, D., LEE, J. S., OLIVER, K. & MILNER-GULLAND, E. J. (2020). Strategic advertising of online news articles as an intervention to influence wildlife product consumers. *Conservation Science and Practice* **2**, e272.

- DREXLER, J. F., CORMAN, V. M. & DROSTEN, C. (2014). Ecology, evolution and classification of bat coronaviruses in the aftermath of SARS. *Antiviral Research* **101**, 45–56.
- EUROPEAN FOOD SAFETY AUTHORITY (EFSA) (2006). Animal health and welfare risks associated with the import of wild birds other than poultry into the European Union. *EFSA Journal* **410**, 1–55.
- FAUST, C. L., MCCALLUM, H. I., BLOOMFIELD, L. S., GOTTDENKER, N. L., GILLESPIE, T. R., TORNEY, C. J., DOBSON, A. P. & PLOWRIGHT, R. K. (2018). Pathogen spillover during land conversion. *Ecology Letters* **21**, 471–483.
- FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS (2007). *FAO Biosecurity Toolkit*. FAO, Rome. <https://www.fao.org/3/a1140e/a1140e00.htm>.
- FOURNIÉ, G., GUITIAN, J., DESVAUX, S., CUONG, V. C., PFEIFFER, D. U., MANGTANI, P. & GHANI, A. C. (2013). Interventions for avian influenza A (H5N1) risk management in live bird market networks. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 9177–9182.
- GEBREYES, W. A., DUPOUY-CAMET, J., NEWPORT, M. J., OLIVIER, C. J. B., SCHLESINGER, L. S., SAIF, Y. M., KARIUKI, S., SAIF, L. J., SAVILLE, W., WITTM, T., HOET, A., QUÉSSY, S., KAZWALA, R., TEKOLA, B., SHRYOCK, T., et al. (2014). The Global One Health Paradigm: challenges and opportunities for tackling infectious diseases at the human, animal, and environment interface in low-resource settings. *PLoS Neglected Tropical Diseases* **8**, e3257.
- GELDMANN, J., MANICA, A., BURGESS, N. D., COAD, L. & BALMFORD, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 23209–23215.
- GIBB, R., REDDING, D. W., CHIN, K. Q., DONNELLY, C. A., BLACKBURN, T. M., NEWBOLD, T. & JONES, K. E. (2020). Zoonotic host diversity increases in human-dominated ecosystems. *Nature* **584**, 398–402.
- GOUILH, M. A., PUECHMAILLE, S. J., GONZALEZ, J. P., TEELING, E., KITTAYAPONG, P. & MANUGUERRA, J. C. (2011). SARS-Coronavirus ancestor's foot-prints in South-East Asian bat colonies and the refuge theory. *Infection, Genetics and Evolution* **11**, 1690–1702.
- HAN, B. A., KRAMER, A. M. & DRAKE, J. M. (2016). Global patterns of zoonotic disease in mammals. *Trends in Parasitology* **32**, 565–577.
- HAN, B. A., SCHMIDT, J. P., BOWDEN, S. E. & DRAKE, J. M. (2015). Rodent reservoirs of future zoonotic diseases. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 7039–7044.
- HARA, M. R., KOVACS, J. J., WHALEN, E. J., RAJAGOPAL, S., STRACHAN, R. T., GRANT, W., TOWERS, A. J., WILLIAMS, B., LAM, C. M., XIAO, K., SHENOY, S. K., GREGORY, S. G., AHN, S., DUCKETT, D. R. & LEFKOWITZ, R. J. (2011). A stress response pathway regulates DNA damage through  $\beta$  2-adrenoreceptors and  $\beta$ -arrestin-1. *Nature* **477**, 349–353.
- HEALY, K., GUILLERME, T., FINLAY, S., KANE, A., KELLY, S. B., MCCLEAN, D., KELLY, D. J., DONOHUE, I., JACKSON, A. L. & COOPER, N. (2014). Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140298.
- HENNING, K. A., HENNING, J., MORTON, J., LONG, N. T., HA, N. T. & MEERS, J. (2009). Farm- and flock-level risk factors associated with highly pathogenic avian influenza outbreaks on small holder duck and chicken farms in the Mekong Delta of Viet Nam. *Preventive Veterinary Medicine* **91**, 179–188.
- HERNANDEZ-MORCILLO, M., BURGESS, P., MIRCK, J., PANTERA, A. & PLEININGER, T. (2018). Scanning agroforestry-based solutions for climate change mitigation and adaptation in Europe. *Environmental Science & Policy* **80**, 44–52.
- HOFFMANN, B., TAPPE, D., HÖPER, D., HERDEN, C., BOLDT, A., MAWRIN, C., NIEDERSTRASSER, O., MÜLLER, T., JENCKEL, M., VAN DER GRITEN, E., LUTTER, C., ABENDROTH, B., TEIFKE, J. P., CADAR, D., SCHMIDT-CHANASIT, J., et al. (2015). A variegated squirrel bornavirus associated with fatal human encephalitis. *New England Journal of Medicine* **373**, 154–162.
- HÖVI, M., MCLEOD, A. & GUNN, G. (2005). Assessing UK farmer attitudes to biosecurity on sheep and cattle farms. *Research in Veterinary Science* **78**, 24.
- HUANG, Z., WHELAN, C. V., FOLEY, N. M., JEBB, D., TOUZALIN, F., PETTIT, E. J., PUECHMAILLE, S. J. & TEELING, E. C. (2019). Longitudinal comparative transcriptomics reveals unique mechanisms underlying extended healthspan in bats. *Nature Ecology & Evolution* **3**, 1110–1120.
- HUANG, Z. Y., YU, Y., VAN LANGEVELDE, F. & DE BOER, W. F. (2017). Does the dilution effect generally occur in animal diseases? *Parasitology* **144**, 823–826.
- HUBER, N., CANOINE, V., CORNILS, J. S., MAGGINI, I., CARDINALE, M., RUF, T. & FUSANI, L. (2020). Leukocyte coping capacity as a complementary stress metric in migrating birds. *Journal of Ornithology* **161**, 909–913.
- ISLAM, M., SAZZAD, H., SATTER, S., SULTANA, S., HOSSAIN, M., HASAN, M., RAHMAN, M., CAMPBELL, S., CANNON, D. L., STRÖHER, U., DASZAK, P., LUBY, S. P. & GURLEY, E. S. (2016). Nipah virus transmission from bats to humans associated with drinking traditional liquor made from date palm sap, Bangladesh, 2011–2014. *Emerging Infectious Diseases* **2**, 664–670.
- JACQUET, J., BOYD, I., CARLTON, J. T., FOX, H., JOHNSON, A. E., MEE, L., ROMAN, J., SPALDING, M. & SUTHERLAND, W. J. (2011). Scanning the oceans for solutions. *Solutions* **2**, 46–55.
- JAY-RUSSELL, M. (2013). What is the risk from wild animals in food-borne pathogen contamination of plants? *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* **8**, 040.
- JOHNSON, C. K., HITCHENS, P. L., PANDIT, P. S., RUSHMORE, J., EVANS, T. S., YOUNG, C. C. & DOYLE, M. M. (2020). Global shifts in mammalian population trends reveal key predictors of virus spillover risk. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192736.
- JONES, B. A., GRACE, D., KÖCK, R., ALONSO, S., RUSHTON, J., SAID, M. Y., MCKEEVER, D., MUTUA, F., YOUNG, J., McDERMOTT, J. & PFEIFFER, D. U. (2013). Zoonosis emergence linked to agricultural intensification and environmental change. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 8399–8404.
- JONES, K. E., PATEL, N. G., LEVY, M. A., STOREYGARD, A., BALK, D., GITTELMAN, J. L. & DASZAK, P. (2008). Global trends in emerging infectious diseases. *Nature* **451**, 990–993.
- KEESING, F., BELDEN, L., DASZAK, P., DOBSON, A., HARVELL, C. D., HOLT, R. D., HUDSON, P., JOLLES, A., JONES, K. E., MICHELL, C. E., MYERS, S. S., BOGICH, T. & OSTFELD, R. S. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**, 647–652.
- KELLY, T. R., MACHALABA, C., KARESH, W. B., CROOK, P. Z., GILARDI, K., NZIZA, J., UHART, M. M., ROBLES, E. A., SAYLORS, K., JOLY, D. O., MONAGIN, C., MULEMBAKANI MANGOMBO, P., MBALA KINGEBENI, P., KAZWALA, R., WOLKING, D., SMITH, W. & MAZET, J. A. K. (2020). Implementing One Health approaches to confront emerging and re-emerging zoonotic disease threats: lessons from PREDICT. *One Health Outlook* **2**, 1–7.
- KILPATRICK, A. M. & RANDOLPH, S. E. (2012). Drivers, dynamics, and control of emerging vector-borne zoonotic diseases. *The Lancet* **380**, 1946–1955.
- KOOPMANS, M., WILBRINK, B., CONYN, M., NATROP, G., VAN DER NAT, H., VENNEMA, H., MEIJER, A., VAN STEENBERGEN, J., FOUCHIER, R., OSTERHAUS, A. & BOSMAN, A. (2004). Transmission of H7N7 avian influenza A virus to human beings during a large outbreak in commercial poultry farms in The Netherlands. *The Lancet* **363**, 587–593.
- LATINNE, A., HU, B., OLIVAL, K. J., ZHU, G., ZHANG, L., LI, H., CHMURA, A. A., FIELD, H. E., ZAMBRANA-TORRELIO, C., EPSTEIN, J. H., LI, B., ZHANG, W., WANG, L. F., ZHENG-LI, S. & DASZAK, P. (2020). Origin and cross-species transmission of bat coronaviruses in China. *Nature Communications* **11**, 1–15.
- LEDAY, G. R., VÉRTÉS, P. E., RICHARDSON, S., GREENE, J. R., REGAN, T., KHAN, S., HENDERSON, R., FREEMAN, T. C., PARIANTE, C. M., HARRISON, N. A., PERRY, V. H., DREVETS, W. C., WITTENBERG, G. M. & BULLMORE, E. T. (2018). Replicable and coupled changes in innate and adaptive immune gene expression in two case-control studies of blood microarrays in major depressive disorder. *Biological Psychiatry* **83**, 70–80.
- LEROY, E. M., KUMULUNGUI, B., POURRUT, X., ROUQUET, P., HASSANIN, A., YABA, P., DÉLICAT, A., PAWESKA, J. T., GONZALEZ, J. P. & SWANEPOEL, R. (2005). Fruit bats as reservoirs of Ebola virus. *Nature* **438**, 575–576.
- LETKO, M., SEIFERT, S. N., OLIVAL, K. J., PLOWRIGHT, R. K. & MUNSTER, V. J. (2020). Bat-borne virus diversity, spillover and emergence. *Nature Reviews Microbiology* **18**, 461–471.
- LI, W., SHI, Z., YU, M., REN, W., SMITH, C., EPSTEIN, J. H., WANG, H., CRAMER, G., HU, Z., ZHANG, H., ZHANG, J., McEACHERN, J., FIELD, H., DASZAK, P., EATON, B. T., ZHANG, S. & WANG, L. F. (2005). Bats are natural reservoirs of SARS-like coronaviruses. *Science* **310**, 676–679.
- LI, X., GIORGI, E. E., MARICHANNEGOWDA, M. H., FOLEY, B., XIAO, C., KONG, X. P., CHEN, Y., GNANAKARAN, S., KORBER, B. & GAO, F. (2020). Emergence of SARS-CoV-2 through recombination and strong purifying selection. *Science Advances* **6**, eabb9153.
- LUBY, S. P., HOSSAIN, M. J., GURLEY, E. S., AHMED, B. N., BANU, S., KHAN, S. U., HOMAIRA, N., ROTA, P. A., ROLLIN, P. E., COMER, J. A. & KENAH, E. (2009). Recurrent zoonotic transmission of Nipah virus into humans, Bangladesh, 2001–2007. *Emerging Infectious Diseases* **15**, 1229–1235.
- LUIS, A. D., HAYMAN, D. T., O'SHEA, T. J., CRYAN, P. M., GILBERT, A. T., PULLIAM, J. R., MILLS, J. N., TIMONIN, M. E., WILLIS, C. K., CUNNINGHAM, A. A., FOOKS, A. R., RUPPRECHT, C. E., WOOD, J. L. & WEBB, C. T. (2013). A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proceedings of the Royal Society B: Biological Sciences* **280**, 20122753.
- MCDONALD, G., WILSON, M., VERISSIMO, D., TWOHEY, R., CLEMENCE, M., APISTAR, D., BOX, S., BUTLER, P., CADIZ, F. C., CAMPBELL, S. J., EFFRON, M., GAINES, S., JAKUB, R., MANCAO, R. H., ROJAS, P. T., TIRONA, R. S. & VIANNA, G. (2020). Catalyzing sustainable fisheries management through behavior change interventions. *Conservation Biology* **34**, 1176–1189.

- MOHD, H. A., AL-TAWFIQ, J. A. & MEMISH, Z. A. (2016). Middle East Respiratory Syndrome Coronavirus (MERS-CoV) origin and animal reservoir. *Virology Journal* **1**, 1–7.
- MOLLENTZE, N. & STREICKER, D. G. (2020). Viral zoonotic risk is homogenous among taxonomic orders of mammalian and avian reservoir hosts. *Proceedings of the National Academy of Sciences of the United States of America* **117**, 9423–9430.
- MORENS, D. M., DASZAK, P. & TAUBENBERGER, J. K. (2020). Escaping Pandora's box—another novel coronavirus. *New England Journal of Medicine* **382**, 1293–1295.
- MORSE, S. S., MAZET, J. A., WOOLHOUSE, M., PARRISH, C. R., CAROLL, D., KARESH, W. B., ZAMBRANA-TORRELIO, C., LIPKIN, W. I. & DASZAK, P. (2012). Prediction and prevention of the next pandemic zoonosis. *The Lancet* **380**, 1956–1965.
- NABI, G., SIDDIQUE, R., ALI, A. & KHAN, S. (2020). Preventing bat-born viral outbreaks in future using ecological interventions. *Environmental Research* **185**, 109460.
- NAHAR, N., SULTANA, R., GURLEY, E. S., HOSSAIN, M. J. & LUBY, S. P. (2010). Date palm sap collection: exploring opportunities to prevent Nipah transmission. *EcoHealth* **7**, 196–203.
- NUÑEZ, M. A., PAUGHARD, A. & RICCIARD, A. (2020). Invasion science and the global spread of SARS-CoV-2. *Trends in Ecology & Evolution* **35**, 642–645.
- O'NEILL, J. (2014). *Tackling Drug-Resistant Infections Globally: Final Report and Recommendations. The Review on Antimicrobial Resistance*, p. 80. Government of the United Kingdom.
- O'SHEA, T. J., CRYAN, P. M., CUNNINGHAM, A. A., FOOKS, A. R., HAYMAN, D. T., LUIS, A. D., PEEL, A. J., PLOWRIGHT, R. K. & WOOD, J. L. (2014). Bat flight and zoonotic viruses. *Emerging Infectious Diseases* **20**, 741–745.
- OGDEN, N. H., WILSON, J. R., RICHARDSON, D. M., HUI, C., DAVIES, S. J., KUMSGHICK, S., LE ROUX, J. J., MEASEY, J., SAUL, W. C. & PULLIAM, J. R. (2019). Emerging infectious diseases and biological invasions: a call for a One Health collaboration in science and management. *Royal Society Open Science* **6**, 181577.
- OSBJER, K., BERG, M., SOKERYA, S., CHHENG, K., SAN, S., DAVUN, H., MAGNUSSON, U., OLSEN, B. & ZOHARI, S. (2017). Influenza A virus in backyard pigs and poultry in rural Cambodia. *Transboundary and Emerging Diseases* **64**, 1557–1568.
- OSTFELD, R. S. & KEESING, F. (2000). Biodiversity and disease risk: the case of Lyme disease. *Conservation Biology* **14**, 722–728.
- OSTFELD, R. S. & KEESING, F. (2012). Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution, and Systematics* **43**, 157–182.
- PEDERSEN, A. B., ALTIZER, S., POSS, M., CUNNINGHAM, A. A. & NUNN, C. L. (2005). Patterns of host specificity and transmission among parasites of wild primates. *International Journal for Parasitology* **35**, 647–657.
- PLIENINGER, T., KOHSAKA, R., BIELING, C., HASHIMOTO, S., KAMIYAMA, C., KIZOS, T., PENKER, M., KIENINGER, P., SHAW, B. J., STOEN, G. B., YOSHIDA, Y. & SAITO, O. (2018). Fostering biocultural diversity in landscapes through place-based food networks: a “solution scan” of European and Japanese models. *Sustainability Science* **13**, 219–233.
- PLOWRIGHT, R. K., PARRISH, C. R., MCCALLUM, H., HUDSON, P. J., KO, A. I., GRAHAM, A. L. & LLOYD-SMITH, J. O. (2017). Pathways to zoonotic spillover. *Nature Reviews Microbiology* **15**, 502–510.
- POULIN, R. & DE ANGELI DUTRA, D. (2021). Animal migrations and parasitism: reciprocal effects within a unified framework. *Biological Reviews*. <https://doi.org/10.1111/brv.12704>.
- PULLIAM, J. R. C., EPSTEIN, J. H., DUSHOFF, J., RAHMAN, S. A., BUNNING, M., JAMALUDDIN, A. A., HYATT, A. D., FIELD, H. E., DOBSON, A. P. & DASZAK, P. (2011). Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. *Journal of the Royal Society Interface* **9**, 89–101.
- RAMIREZ, A., CAPUANO, A. W., WELLMAN, D. A., LESHAR, K. A., SETTERQUIST, S. F. & GRAY, G. C. (2006). Preventing zoonotic influenza virus infection. *Emerging Infectious Diseases* **12**, 997–1000.
- RIBEIRO, J., BINGRE, P., STRUBBE, D. & REINO, L. (2020). Coronavirus: why a permanent ban on wildlife trade might not work in China. *Nature* **578**, 217–217.
- ROBERTS, M. G. & HEESTERBEEK, J. A. P. (2018). Quantifying the dilution effect for models in ecological epidemiology. *Journal of the Royal Society Interface* **15**, 20170791.
- ROHR, J. R., CIVITELLO, D. J., HALLIDAY, F. W., HUDSON, P. J., LAFFERTY, K. D., WOOD, C. L. & MORDECAI, E. A. (2019). Towards common ground in the biodiversity–disease debate. *Nature Ecology and Evolution* **4**, 1–10.
- ROSE, N. & MADEC, F. (2002). Occurrence of respiratory disease outbreaks in fattening pigs: relation with the features of a densely and a sparsely populated pig area in France. *Veterinary Research* **33**, 179–190.
- SAÉZ, A. M., WEISS, S., NOWAK, K., LAPEYRE, V., ZIMMERMANN, F., DÜX, A., KÜHL, H. S., KABA, M., REGNAUT, S., MERKEL, K., SACHSE, A., THIESEN, U., VILLANYI, L., BOESCH, C., DABROWSKI, P. W., RADONIC, A., NITSCHKE, A., et al. (2015). Investigating the zoonotic origin of the West African Ebola epidemic. *EMBO Molecular Medicine* **7**, 17–23.
- SALATA, C., CALISTRI, A., PAROLIN, C. & PALU, G. (2019). Coronaviruses: a paradigm of new emerging zoonotic diseases. *Pathogens and Disease* **77**, fta006.
- SALAZAR, G., MILLS, M. & VERISSIMO, D. (2019). Qualitative impact evaluation of a social marketing campaign for conservation. *Conservation Biology* **33**, 634–644.
- SALKELD, D. J., PADGETT, K. A. & JONES, J. H. (2013). A meta-analysis suggesting that the relationship between biodiversity and risk of zoonotic pathogen transmission is idiosyncratic. *Ecology Letters* **16**, 679–686.
- SHARP, P. M. & HAHN, B. H. (2011). Origins of HIV and the AIDS pandemic. *Cold Spring Harbor Perspectives in Medicine* **1**, a006841.
- SMITH, K. M., ZAMBRANA-TORRELIO, C., WHITE, A., ASMUSSEN, M., MACHALABA, C., KENNEDY, S. & KARESH, W. B. (2017). Summarizing US wildlife trade with an eye toward assessing the risk of infectious disease introduction. *EcoHealth* **14**, 29–39.
- SONG, H. D., TU, C. C., ZHANG, G. W., WANG, S. Y., ZHENG, K., LEI, L. C., CHEN, Q. X., GAO, Y. W., ZHOU, H. Q., XIANG, H., ZHENG, H. J., CHERN, S. W., CHENG, F., PAN, C. M., XUAN, H., et al. (2005). Cross-host evolution of severe acute respiratory syndrome coronavirus in palm civet and human. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 2430–2435.
- SPEAKMAN, J. R. & THOMAS, D. W. (2003). Physiological ecology and energetics of bats. In *Bat Ecology* (eds T. H. KUNZ and M. B. FENTON), pp. 430–490. University of Chicago Press, Chicago.
- SUBUDHI, S., RAPIN, N. & MISRA, V. (2019). Immune system modulation and viral persistence in bats: understanding viral spillover. *Viruses* **11**, 192.
- SUTHERLAND, W. J. & BURGMANN, M. (2015). Use experts wisely. *Nature* **526**, 317–318.
- SUTHERLAND, W. J., DICK, L. V., PETROVAN, S. O. & SMITH, R. K. (2020). *What Works in Conservation 2020*. Cambridge, UK: Open Book Publishers.
- SUTHERLAND, W. J., GARDNER, T., BOGICH, T. L., BRADBURY, R. B., CLOTHIER, B., JONSSON, M., KAPOS, V., LANE, S. N., MÖLLER, I., SCHROEDER, M., SPALDING, M., SPENCER, T., WHITE, P. C. L. & DICKS, L. V. (2014). Solution scanning as a key policy tool: identifying management interventions to help maintain and enhance regulating ecosystem services. *Ecology and Society* **19**, 3.
- SUTHERLAND, W. J., TAYLOR, N. G., MACFARLANE, D., AMANO, T., CHRISTIE, A. P., DICKS, L., LEMASSON, A. J., LITTLEWOOD, N. A., MARTIN, P. A., OCKENDON, N., PETROVAN, S. O., ROBERTSON, R. J., ROCHA, R., SHACKELFORD, G. E., SMITH, R. K., et al. (2019). Building a tool to overcome barriers in research-implementation spaces: the Conservation Evidence database. *Biological Conservation* **235**, 93–101.
- SWIFT, L., HUNTER, P. R., LEES, A. C. & BELL, D. J. (2007). Wildlife trade and the emergence of infectious diseases. *EcoHealth* **4**, 25–30.
- TANG, X. C., ZHANG, J. X., ZHANG, S. Y., WANG, P., FAN, X. H., LI, L. F., LI, G., DONG, B. Q., LIU, W., CHEUNG, C. L., XU, K. M., SONG, W. J., VJAYKRISHNA, D., POON, L. L. M., PEIRIS, J. S. M., et al. (2006). Prevalence and genetic diversity of coronaviruses in bats from China. *Journal of Virology* **80**, 7481–7490.
- TATEM, A. J., HAY, S. I. & ROGERS, D. J. (2006). Global traffic and disease vector dispersal. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6242–6247.
- TAYLOR, L. H., LATHAM, S. M. & WOOLHOUSE, M. E. (2001). Risk factors for human disease emergence. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **356**, 983–989.
- TRIVERS, H., CLEMENTS, T., KEANE, A. & MILNER-GULLAND, E. (2011). Incentives for cooperation: the effects of institutional controls on common pool resource extraction in Cambodia. *Ecological Economics* **71**, 151–161.
- \*T SAS-ROLFES, M., CHALLENGER, D. W., HINSLEY, A., VERISSIMO, D. & MILNER-GULLAND, E. J. (2019). Illegal wildlife trade: scale, processes, and governance. *Annual Review of Environment and Resources* **44**, 201–228.
- UNEP (2019). *Policy Brief. Effectiveness of Policy Interventions Relating to the Illegal and Unsustainable Wildlife Trade*. United Nations Environment Programme, Nairobi. <http://wedocs.unep.org/bitstream/handle/20.500.11822/29394/IWTBrief.pdf?sequence=1&isAllowed=y>.
- UTERMOHLEN, M. (2020). *Runway to extinction: airports and airlines in every region of the world can assist with fighting wildlife trafficking*. <https://www.traffic.org/publications/reports/runway-to-extinction/>
- VERISSIMO, D., VIEIRA, S., MONTEIRO, D., HANCOCK, J. & NUNO, A. (2020). Audience research as a cornerstone of demand management interventions for illegal wildlife products: demarketing sea turtle meat and eggs. *Conservation Science and Practice* **2**, e164.
- VERISSIMO, D. & WAN, A. K. (2019). Characterizing efforts to reduce consumer demand for wildlife products. *Conservation Biology* **33**, 623–633.
- WALSH, J. C., DICKS, L. V. & SUTHERLAND, W. J. (2015). The effect of scientific evidence on conservation practitioners' management decisions. *Conservation Biology* **29**, 88–98.
- WALTZEK, T. B., CORTÉS-HINOJOSA, G., WELLEHAN, J. F. X. JR. & GRAY, G. C. (2012). Marine mammal zoonoses: a review of disease manifestations. *Zoonoses and Public Health* **59**, 521–535.

- WAN, Y., SHANG, J., GRAHAM, R., BARIC, R. S. & LI, F. (2020). Receptor recognition by the novel coronavirus from Wuhan: an analysis based on decade-long structural studies of SARS coronavirus. *Journal of Virology* **94**, e00127-20.
- WANG, L. F. & EATON, B. T. (2007). Bats, civets and the emergence of SARS. In *Wildlife and Emerging Zoonotic Diseases: The Biology, Circumstances and Consequences of Cross-Species Transmission* (eds J. E. CHILDS, J. S. MACKENZIE and J. A. RICHT), pp. 325–344. Springer, Berlin, Heidelberg.
- WANG, H., SHAO, J., LUO, X., CHUAI, Z., XU, S., GENG, M. & GAO, Z. (2020). Wildlife consumption ban is insufficient. *Science* **367**, 1435–1435.
- WICANDER, S. & COAD, L. (2018). Can the provision of alternative livelihoods reduce the impact of wild meat hunting in West and Central Africa? *Conservation and Society* **16**, 441–458.
- WILSON, M. L., GONZALEZ, J. P., CORNET, J. P. & CAMICAS, J. L. (1991). Transmission of Crimean-Congo haemorrhagic fever virus from experimentally infected sheep to *Hyalomma truncatum* ticks. *Research in Virology* **142**, 395–404.
- WOLFE, N. D., DUNAVAN, C. P. & DIAMOND, J. (2007). Origins of major human infectious diseases. *Nature* **447**, 279–283.
- WONG, A. C., LI, X., LAU, S. K. & WOO, P. C. (2019). Global epidemiology of bat coronaviruses. *Viruses* **11**, 174.
- WOODROFFE, R., DONNELLY, C. A., COX, D. R., BOURNE, F. J., CHEESEMAN, C. L., DELAHAY, R. J., GETTINBY, G., MCINERNEY, J. P. & MORRISON, W. I. (2006). Effects of culling on badger *Meles meles* spatial organization: implications for the control of bovine tuberculosis. *Journal of Applied Ecology* **43**, 1–10.
- WRIGHT, J. H., HILL, N. A., ROE, D., ROWCLIFFE, J. M., KÜMPPEL, N. F., DAY, M., BOOKER, F. & MILNER-GULLAND, E. (2016). Reframing the concept of alternative livelihoods. *Conservation Biology* **30**, 7–13.
- WU, F., ZHAO, S., YU, B., CHEN, Y. M., WANG, W., SONG, Z. G., HU, Y., TAO, Z. W., TIAN, J. H., PEI, Y. Y. & YUAN, M. L. (2020). A new coronavirus associated with human respiratory disease in China. *Nature* **579**, 265–269.
- XIE, J., LI, Y., SHEN, X., GOH, G., ZHU, Y., CUI, J., WANG, L. F., SHI, Z. L. & ZHOU, P. (2018). Dampened STING-dependent interferon activation in bats. *Cell Host and Microbe* **23**, 298–301.
- YOB, J. M., FIELD, H., RASHDI, A. M., MORRISSY, C., VAN DER HEIDE, B., ROTA, P., BIN ADZHAR, A., WHITE, J., DANIELS, P., JAMALUDDIN, A. & KSIAZEK, T. (2001). Nipah virus infection in bats (order Chiroptera) in peninsular Malaysia. *Emerging Infectious Diseases* **7**, 439–441.
- ZHANG, T., WU, Q. & ZHANG, Z. (2020). Probable pangolin origin of SARS-CoV-2 associated with the COVID-19 outbreak. *Current Biology* **30**, 1346–1351.
- ZHOU, H., CHEN, X., HU, T., LI, J., SONG, H., LIU, Y., WANG, P., LIU, D., YANG, J., HOLMES, E. C., HUGHES, A. C., BI, Y. & SHI, W. (2020a). A novel bat coronavirus closely related to SARS-CoV-2 contains natural insertions at the S1/S2 cleavage site of the spike protein. *Current Biology* **30**, 2196–2203.
- ZHOU, H., JI, J., CHEN, X., BI, Y., LI, J., WANG, O., TAO HU, T., SONG, H., ZHAO, R., CHEN, Y., CUI, M., ZHANG, Y., HUGHES, A. C., HOLMES, E. C. & SHI, W. (2021). Identification of novel bat coronaviruses sheds light on the evolutionary origins of SARS-CoV-2 and related viruses. *Cell* **2021**, 12082. <https://doi.org/10.1016/j.cell.2021.06.008>.
- ZHOU, P., FAN, H., LAN, T., YANG, X.-L., SHI, W.-F., ZHANG, W., ZHU, Y., ZHANG, Y.-W., XIE, Q.-M., MANI, S., ZHENG, X.-S., LI, B., LI, J.-M., GUO, H., PEI, G.-Q., et al. (2018). Fatal swine acute diarrhoea syndrome caused by an HKU2-related coronavirus of bat origin. *Nature* **556**, 255–258.
- ZHOU, P., YANG, X., WANG, X., HU, B., ZHANG, L., ZHANG, W., SI, H. R., ZHU, Y., LI, B., HUANG, C. L., CHEN, H. D., CHEN, J., LUO, Y., GUO, H., JIANG, R. D., LIU, M. Q., CHEN, Y., SHEN, X. R., WANG, X., et al. (2020b). A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* **579**, 270–273.

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