

REVIEW



Impacts of the COVID-19 pandemic on mammals at tourism destinations: a systematic review

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ABSTRACT

1. The COVID-19 outbreak is having an unprecedented effect on human society, but how is it affecting the mammals that people live with? Mammals that were part of tourism experiences are of concern, because they impact on people's health and livelihoods and, since many of them are now dependent on people, we urge consideration of the status of these mammals as a result of the pandemic.
2. We provide a systematic review of the impacts the COVID-19 outbreak has had on mammals in tourism venues. We examine reports of diverse species in various settings responding to changes in their environments that are occurring because of the pandemic.
3. We searched the scholarly literature, preprints, and online news sources using combinations of the search terms 'tourism', 'animals', 'wildlife', 'coronavirus', and 'COVID-19'. We searched Web of Science, SCOPUS, EBSCOHost, JSTOR, bioRxiv, OSFPREPRINTS, GDELT, Google News, and National Public Radio, and analysed a total of 39 news articles, one peer-reviewed article, and six preprints.
4. In total, we identified 92 distinct animal reports representing 48 mammal species. We used an existing tourism classification schema to categorise each article based on the situation reported, with the new addition of one context. We classified 92 separate animal reports in 46 articles into four (of six possible) contexts: mammals as attractions ($n = 40$ animal reports), mammals as commodities ($n = 33$), mammals as threats ($n = 2$), and unusual sightings of mammals ($n = 17$). Shortage of food, in danger of losing home, having an enriched/relaxed environment, spatial expansion, disease transmission, and poaching are the major impacts or events reported in these contexts.
5. We suggest changes for each context with respect to how people interface with mammals, with the goal of improving the lives of mammals and the people dependent on them.

INTRODUCTION

Since the first cases of COVID-19 were identified in Wuhan, Hubei, China, in December 2019, the SARS-CoV-2 virus has spread rapidly around the world. In March 2020, the World Health Organization (WHO) declared the COVID-19 outbreak a global pandemic. At the time of writing (January 2021), there are over 88 million confirmed cases, and the worldwide death toll has exceeded 1.9 million, affecting almost all countries and territories in the world (World Health Organization 2020b).

This is not the first such emerging infectious disease we humans have faced, but in comparison with the last two global disease outbreaks occurring in the 21st Century, the COVID-19 outbreak is characterised by large numbers of people infected, high mortality rates, and an unprecedented economic impact, leaving millions of people unemployed. In the last two decades, we have already witnessed severe acute respiratory syndrome (SARS) and the Middle East respiratory syndrome (MERS), both of which are caused by coronaviruses, as COVID-19 is caused by SARS-CoV-2. In 2002 and 2003, the cumulative number of SARS cases reported was 8096 from 29 countries, and 774 cases resulted in death (World Health Organization 2003). MERS has affected 2494 people from 27 countries since its outbreak in 2014, taking the lives of 858 people to date (World Health Organization 2020a).

Human mobility is a major factor contributing to the spread of infectious diseases in the 21st Century (Labonté et al. 2011). Opportunities to see wildlife and unique habitats are primary motivators of many tourists (Curtin & Kragh 2014), and the travel associated with nature-based tourism contributes to the rapid spread of diseases to the world's most remote places (Enk et al. 2010, Köndgen et al. 2008). For example, Bhutan is a Himalayan kingdom that shares borders with India and China. Seven cases of COVID-19 have been reported there; the first case was documented in a tourist from the USA who was visiting Bhutan (Ongmo & Parikh 2020). Bhutan, like many developing countries, has insufficient medical personnel and facilities to respond to outbreaks of the severity that have occurred in other parts of the world. Countries like Bhutan underscore how our modern ability to travel quickly to virtually any country in the world, which resulted from the widespread existence of the low-cost carriers and more open borders, has fuelled this pandemic and put people and other mammals living in previously inaccessible regions at risk.

People concerned with the conservation of natural resources view this pandemic as a call to action (Gillespie & Leendertz 2020). It provides opportunities to consider more carefully how humans interface with nature. This review responds to the call by focusing on the lives of

mammals in tourism venues. We focus on mammals because they are usually the most visible representatives of a given habitat, and they are often integral to nature-based tourism – defined as a type of tourism that pertains to activities occurring outdoors (Fredman & Tyrväinen 2011).

As COVID-19 becomes increasingly widespread, numerous research papers have been published, mainly addressing its impact on human lives (e.g. Baldwin & Tomiura 2020, Chinazzi et al. 2020, Zheng et al. 2020). Non-human mammals are interconnected with human societies through tourism and nature-based activities, among other mechanisms. Large numbers of people are already returning to tourism destinations in China (Westcott & Culver 2020), underscoring the need to address the impact this global crisis is having on mammals. We urge the implementation of changes now, before other countries follow China's lead in reopening nature-focused tourism venues.

Rutz et al. (2020) coined the term 'anthropause' to describe the reduction in human activities as a result of the COVID-19 pandemic. While the anthropause has had unprecedented impacts on human societies, it has also been an opportunity for researchers to examine how human activities affected other animals at a global level, which, in turn, has allowed us to develop novel strategies to coexist with other species on the planet (Rutz et al. 2020). Likewise, consideration of how COVID-19 affects non-human mammals provides a more holistic understanding of mammals' position in tourism, as well as tourism's roles in their lives, which will aid in planning and implementing appropriate risk measures in the future. While some scholars have already published studies that discuss the impact of the COVID-19 pandemic on wildlife in general or at wildlife tourism destinations (Linsey et al. 2020, Manenti et al. 2020, Newsome 2020), they capture a fraction of the pandemic's impact geographically and methodologically. Yet, tourism–animal interactions are varied and ubiquitous (Markwell 2015). How the reduction of tourism in response to the COVID-19 outbreak affected other mammals in different tourism settings and different countries remains unknown. Therefore, in this paper, we systematically reviewed the impacts of the pandemic on mammals, in order to highlight the position of mammals in the COVID-19 environment without international tourism.

METHODS

Rationale

The aim of the present study is to identify how the COVID-19 outbreak affected non-human mammals at tourism destinations. To investigate its impacts, we systematically searched academic literature, preprints, and

online news articles. We relied on secondary data sources so we could extensively characterise what happened to mammals at the start of the pandemic, when travel restrictions were imposed. Travel restrictions halted all but the most urgently needed field research, making it impossible to collect data on mammals in their natural settings. Our systematic review of scientific papers and online news articles provides coverage of a wide geographical range of diverse species in varied tourism contexts. Fig. 1 shows the step-by-step process of our systematic review.

Search strategy

The aim of our search strategy was to produce a general list of research and online news articles published after the start of the COVID-19 outbreak that were focussed on tourism. Although the specific date of the outbreak is unknown, the first confirmed cases were reported in December 2019 (Ying et al. 2020); therefore, we limited the articles to those that were published after 1 January 2020. The keywords we used in our searches were ‘tourism’, ‘animals’, ‘wildlife’, ‘COVID-19’, and ‘coronavirus’. We used the word combinations: 1) tourism, animals, COVID-19; 2) tourism, animals, coronavirus; 3) tourism, wildlife, COVID-19; and 4) tourism, wildlife, coronavirus to search for relevant literature and online news articles.

Databases

We searched the following databases for preprints and peer-reviewed articles: SCOPUS, Web of Science, EBSCOhost, JSTOR, bioRxiv, and OSFPREPRINTS. We collected online news articles by searching GDELT, National Public Radio (NPR), and Google News. We conducted all the searches between 22 April and 28 July 2020. Using Google Translate to interpret key words and article titles, we included in our news stories searches articles published in English, Spanish, Portuguese, French, Russian, Croatian, Polish, and German.

Screening process for article validity and topic

To check the validity of the news articles, two authors independently screened the news sources. We followed the criteria available in Reuter’s media fact check (www.mediabiasfactcheck.com) and NPR guidelines (www.npr.org/sections/alltechconsidered/2016/12/05/503581220/fake-or-real-how-to-self-check-the-news-and-get-the-facts). We included articles that were assessed as ‘very high’, ‘high’, or ‘mostly factual’ on NPR’s factual reporting, based on authority, URL domain, and whether the purpose of the source was to provide news content. We considered all scholarly publications to be valid, based on the fact that they had already undergone peer review. We considered preprints to be valid in that they are intended for peer

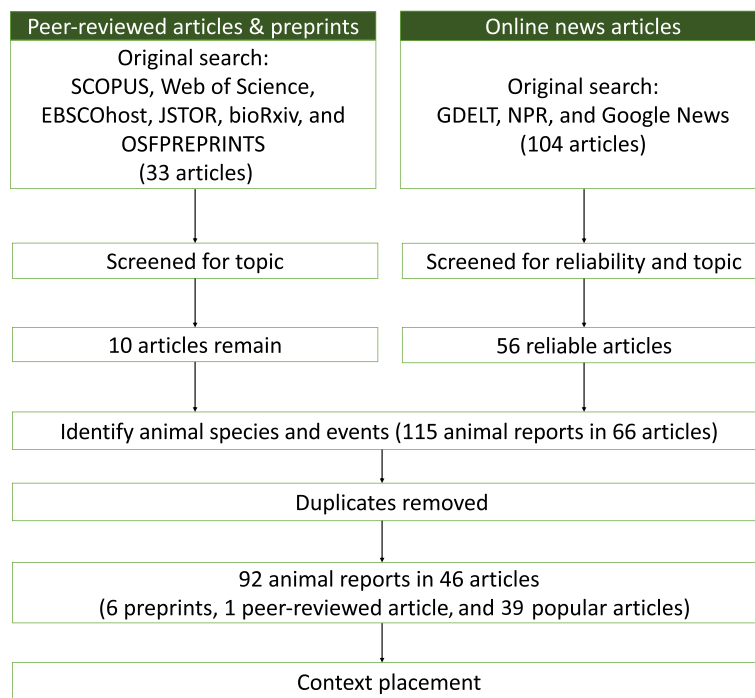


Fig. 1. The review process used. [Colour figure can be viewed at wileyonlinelibrary.com]

review. We used Cohen's kappa (κ) to assess the two raters' reliability, with alpha at 0.05. We excluded articles from further analysis if the two raters disagreed on whether the articles were valid (e.g. cases where one rater felt the article was valid, but the other rater did not). Articles excluded on this basis were ones that met only one of NPR's or Reuter's validity criteria. All but one non-English news article was eliminated from our database through application of these validity criteria. Additionally, some news outlets carried false reports of animal–human interactions (e.g. <https://www.nationalgeographic.com/animals/2020/03/coronavirus-pandemic-fake-animal-viral-social-media-posts/>) during the early stages of quarantine, so we decided to include in our analysis only those articles that both raters agreed were valid, in order to reduce the likelihood of including false reports.

At this stage in our classification, we also eliminated from further consideration articles that referred to mammals in non-tourism contexts (e.g. an article on COVID-19 and mammal genomes) and articles that referred to non-mammal species (e.g. an article that discussed unusual sightings of pythons Pythonidae).

Identifying animal species and events

We identified animal reports (species and events) for each article. Some articles reported several mammal species in one article. In those articles, we treated each novel mammal species as a separate account and included it as a distinct occurrence in our dataset. For example, a single article might describe wild boar *Sus scrofa* and cougars *Puma concolor* in urban settings. We considered these as two distinct reports of animals and classified each species account into the most appropriate context for it based on the article's narrative.

Removing duplicates

The potential for pseudo-replication existed in our context dataset, because different articles sometimes reported the same story of the same species in the same location – that is, an identical species account. If we found multiple articles with identical species accounts, we used a random number generator (www.random.org) to choose a number. We then used the article with that number to represent that species account in our analysis. For example, two articles carried an identical story of Asian elephants *Elephas maximus* in Thailand. We numbered the articles one and two. Next, we used the random number generator to select one number in that sequence; in this example, one was the randomly generated number. We used the article numbered one to represent in our analysis elephants in Thailand at this specific location, and removed article two

from further consideration. Through this process, we attempted to avoid over-representation of species accounts in our analysis.

Data classification into tourism contexts

After we removed the duplicates from the dataset, two of us read each article and separately categorised the animals described therein into a context. For this classification, we used Markwell's (2015) model of tourism–animal relationships (Fig. 2). Markwell categorised tourists' destination experiences into five broad contexts: animals as attractions, animals as commodities, animals as threats, animals as companions, and animals as shared encounters. We created a new context that appears to be specific to the pandemic situation that is now occurring, which we called 'unusual sightings of mammals' (Manenti et al. 2020). We therefore classified each mammal mentioned into one of the six contexts.

We classified each species into only one context, but a single article could describe species that we classified into different contexts. For example, a single article might describe poaching of lions *Panthera leo* (commodity context) and wild boar in a city centre (unusual sightings context). Consequently, the number of mammal accounts in our dataset is larger than the number of articles. For the mammal references that remained after this winnowing process, we tested the hypothesis that mammals were evenly distributed across six contexts using a chi-square goodness-of-fit test, with alpha set at 0.05.

RESULTS AND DISCUSSION

Our search generated 104 popular articles and 33 scientific articles and preprints, a total of 137 articles. For the 33 scientific articles and preprints, we removed 23 from further analysis because they did not focus on mammals and/or did not describe mammals in a tourism context.

For the 104 popular articles, two of us rated their validity using NPR's and Reuter's validity criteria. We ran Cohen's κ to determine whether there was agreement on the articles' validity. We found there was moderate agreement between the two raters ($\kappa = 0.484$, $P < 0.0005$). Both raters agreed to exclude 24 articles and to include 56 articles. The raters disagreed on the validity of 24 articles. Discussion of those disagreements showed that those articles met only one of NPR's and Reuter's validity criteria. We excluded all 24 of those popular articles to reduce the probability of including false animal sightings in our analysis.

We reviewed the 56 remaining popular articles and 10 remaining scientific articles and preprints to check for duplicate reports. We removed 20 duplicate reports,

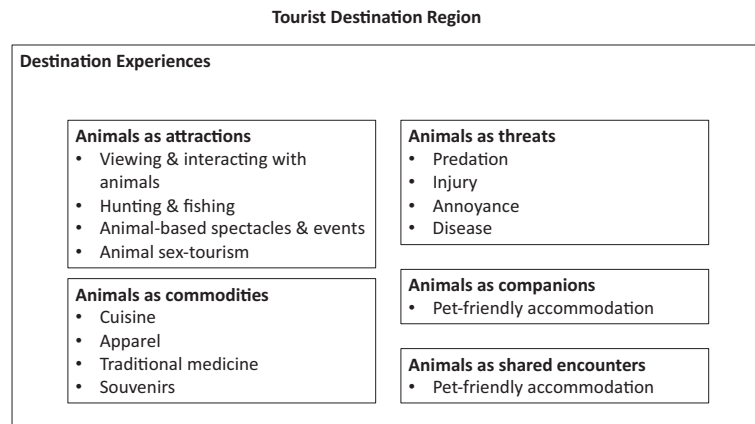


Fig. 2. Markwell's (2015, p.7) tourism–animal relationship model (modified).

leaving 46 articles in our database for context assignment (Appendix S1). Thirty-nine of these were popular articles, one was a scientific article, and six were preprints. Forty-five articles were written in English, and one was written in Portuguese. These articles represented 23 different locations. The five most frequently cited locations were Africa (including separate mentions of Kenya, South Africa, Democratic Republic of Congo, and Botswana), Thailand, USA, China, and global. We found 92 separate animal reports in these 46 articles. The mammals most frequently referenced were Asian and African elephants *Elephas* and *Loxodonta* (11 references), deer (Cervidae; five references), lions (four references), great apes *Gorilla*, *Pan*, and *Pongo* (four references), tigers *Panthera tigris* (three references), and wild boar (three references).

Classification of each event generated four contexts of human–mammal interface: mammals as attractions ($n = 40$ animal reports), mammals as commodities ($n = 33$), mammals as threats ($n = 2$), and unusual sightings of mammals ($n = 17$). We found no events reported for the contexts mammals as companions and mammals as shared encounters. The context unusual sighting of mammals, an addition to Markwell's (2015) original schema, appears to be a unique outcome of the 'shelter-at-home' orders placed in many countries around the world. Mammal events were not evenly distributed across the six contexts ($\chi^2 = 102$, $df = 5$, $P < 0.001$). Based on standardised residuals (std. res.), only the context unusual sightings of mammals (std. res. = +0.43) occurred at the expected frequency. The contexts mammals as companions (std. res. = -3.41), mammals as shared encounters (std. res. = -3.92), and mammals as threats (std. res. = -3.92) occurred at lower than expected frequencies, while mammals as attractions (std. res. = +6.30) and mammals as commodities (std. res. = +4.51) occurred at higher than expected frequencies. Table 1 summarises the results and includes a list

of all mammal species identified in each context and the impacts or events reported.

Context 1: mammals as attractions

Reports of mammals as attractions are mostly targeted for viewing and interactions. The settings in which these mammals are found range from natural settings to captivity, and the setting influences how the COVID-19 outbreak is impacting the mammals. We found seven impacts: shortage of food, in danger of losing home, spatial expansion, enriched/relaxed, lack of enrichment, disease transmission, and reprieved from being hunted.

SHORTAGE OF FOOD

Several news reports indicate that the COVID-19 outbreak brought hunger to some mammals. For instance, Japanese sika deer *Cervus nippon* in Nara Park, Japan, are hungry due to the decrease in the number of tourists visiting and feeding them the deer crackers sold in the park (Kretchmer 2020). Similarly, hundreds of long-tailed macaques *Macaca fascicularis* in Thailand have been affected, as the tourists who usually offer them food have nearly disappeared from the country (Kretchmer 2020, Newsflare 2020). In both of these cases, the animals are free ranging, so they have freedom to move around in search of food. While both reports indicated that some people do not believe these animals would suffer from hunger (Kretchmer 2020, Rodrigo 2020), there is scarce information on the proportion of their food that is provided by tourists, especially in the unregulated settings that characterise sika deer in Japan and the long-tailed macaques in Thailand. Therefore, it is too soon to draw any conclusion on how dependent these animals are on food they are given by tourists. The deer in Nara Park are unlikely to find enough food to sustain their population without tourists, because the deer population density is extremely high at more than 200

Table 1. Impacts and events reported about mammals after the start of the COVID-19 outbreak

| Context | Mammal taxa mentioned | Location (country/region) | Impacts/events |
|-------------------|--|-------------------------------|---|
| Attractions | Apes | Africa, global, DRC | a. Shortage of food |
| | Black bears <i>Ursus americanus</i> | USA | b. In danger of losing home |
| | Beluga whales <i>Patadonian mara</i> | USA | c. Enriched/relaxed |
| | Boars <i>Sus scrofa</i> | Thailand | d. Lack of enrichment |
| | Buffalo <i>Bubalus bubalis</i> | Thailand | e. Spatial expansion |
| | Donkey <i>Equus asinus</i> | Canada | f. Disease transmission |
| | Elephants <i>Elephas maximus</i> , <i>Loxodonta africana</i> | Thailand, Sri Lanka, Botswana | g. Reprieved from being hunted (sports hunting) |
| | Horses <i>Equus</i> | Thailand | |
| | Leopards <i>Panthera pardus</i> | Sri Lanka | |
| | Lions <i>Panthera</i> | South Africa, USA | |
| | Llama <i>Lama</i> | Canada | |
| | Long-tailed macaques <i>Macaca fascicularis</i> | Thailand | |
| | Pandas <i>Ailuropoda melanoleuca</i> | China | |
| | Patagonian mara <i>Dolichotis paragonum</i> | USA | |
| | Polar bear <i>Ursus maritimus</i> | USA | |
| | Primates | | |
| | Sika deer <i>Cervus nippon</i> | Japan | |
| | Spotted hyena <i>Crocuta crocuta</i> | USA | |
| | Sun bears <i>Helarctos malayanus</i> | Malaysia | |
| | Tigers <i>Panthera tigris</i> | India, USA | |
| | Vervet <i>Chlorocebus pygerythrus</i> | Caribbean | |
| | Wolves <i>Canis lupus</i> | USA | |
| | Zoo animals | Australia | |
| Commodities | African rhinos <i>Diceros bicornis</i> | Africa, South Africa | a. Poaching |
| | Bamboo rat <i>Rhizomys</i> | China | b. Meat consumption |
| | Bats <i>Rhinolophus</i> | China, global | |
| | Boars <i>Sus scrofa</i> | China | |
| | Civets (Viverridae) | China, global | |
| | Dik dik <i>Madoqua</i> | Tanzania | |
| | Dogs <i>Canis</i> | China | |
| | Elephants <i>Elephas maximus</i> , <i>Loxodonta africana</i> | Africa, Kenya, Thailand | |
| | Exotic animals | China | |
| | Foxes <i>Vulpes</i> | China | |
| | Impalas <i>Aepyceros melampus</i> | Tanzania | |
| | Indian rhinos <i>Rhinoceros unicornis</i> | India | |
| | Leopards <i>Panthera pardus</i> | Kenya | |
| | Lions <i>Panthera leo</i> | Kenya | |
| | Moon bears <i>Ursus</i> | Vietnam | |
| | Mountain gorillas <i>Gorilla beringei beringei</i> | Rwanda | |
| | Pangolins <i>Manis</i> | China, global | |
| | Sika deer <i>Cervus nippon</i> | China | |
| | Wildebeest <i>Connochaetes</i> | Tanzania | |
| | Zebra <i>Equus</i> | Tanzania | |
| Threats | Rats <i>Rattus norvegicus</i> | USA | a. Spatial expansion |
| | Animals | Global | b. Animals as a reservoir for the virus |
| Unusual sightings | Boars <i>Sus scrofa</i> | Israel, Spain | a. Venture into cities |
| | Coyotes <i>Canis latrans</i> | USA | b. Return to undisturbed space |
| | Deer (Cervidae) | Austria, Sri Lanka | |
| | Dolphins (Cetacea) | Ecuador, Italy | |
| | Dugongs <i>Dugong dugon</i> | Thailand | |
| | Elk <i>Cervus canadensis</i> | Austria | |
| | Fallow deer <i>Odocoileus</i> | UK | |
| | Goats <i>Capra aegagrus hircus</i> | UK, Austria | |
| | Nilgai <i>Boselaphus tragocamelus</i> | India | |
| | Red foxes <i>Vulpes vulpes</i> | Israel | |
| | Sea lions <i>Zalophus wollebaeki</i> | Argentina | |
| | Whales (Cetacea) | Ecuador | |

individuals/km² (Usui & Funck 2017), and habitat with naturally occurring foods may have disappeared.

Presumably, there are more mammals in similar situations, as feeding mammals is a common tourist activity around the world (Orams 2002). Feeding by tourists can be regulated or unregulated. Regulated feeding usually means that food provided by tourists is supplemental to the animals' usual diet (Smith et al. 2008, Thomson et al. 2017). Supplemental food provisioning is typically implemented to increase the chance of tourists sighting animals (Knight 2011, Usui et al. 2014), or to provide tourists with close contact with animals (Orams 2002). Thus, it is unlikely that these mammals will starve as an immediate response to the COVID-19 outbreak, as long as there is food available in nature and/or their staple diet is still supplied by park staff or volunteers.

However, the absence of tourism operation – meaning there is no provisioned food or baited food – could alter mammals' behaviour, particularly in cases where the foods provided by tourists are nutrient- or calorie-dense, such as occurs with monkeys *Macaca* living at temple or tourist sites. If the lack of tourists continues for a long time, animals may move from one place to another in search of food and, as a consequence, they may no longer be sighted at particular tourism destinations, which will be detrimental to some tourism operators. Monkeys change their ranging patterns and their group sizes and increase their density in the context of provisioning for tourism (golden snub-nosed monkeys *Rhinopithecus roxellana*, Xia et al. 2016; Assamese macaques *Macaca assamensis*, Adhikari et al. 2018; rhesus macaques *Macaca mulatta*, Sengupta & Radhakrishna 2018). Tourism often results in degradation of the surrounding habitat, and natural resources may be insufficient to support large numbers of monkeys, should provisioning lapse. One news source reported that free-ranging elephants in Sri Lanka returned to the wild to forage naturally, rather than relying on human food handouts, once the country's lockdown kept tourists from visiting (Rodrigo 2020). Furthermore, their search for food may lead to an increase in the frequency of interactions between mammals and local people and could generate conflicts between them. In Ōita, Japan, provisioning of Japanese macaques *Macaca fuscata* was intended to prevent or reduce their reliance on local people's crops (Knight 2017). On the other hand, decreasing tourism pressure might be beneficial for mammals, as numerous studies have reported tourism's negative impacts on them (e.g. Berman et al. 2007, Szott et al. 2019).

Where feeding is unregulated, as with the Nara Park sika deer and some groups of long-tailed macaques, the amount of food given to the animals varies for each animal, and by day. Some animals – most likely to be the dominant individuals – may rely more than others on

food from tourists, and as a result, they can be greatly affected by the absence of tourists. There is scarce information on the amount of food taken by mammals that are fed intermittently by tourists, and the data that exist are predominantly based on primate species. Studies of food competition in some wild primate groups show that dominant individuals tend to monopolise food, especially if the amount of food available is low relative to the number of individuals in a group (brown capuchins *Cebus apella*, Jason 1985; olive baboons *Papio anubis*, Barton & Whiten 1993; Japanese macaques, Saito 1996). Efforts to monopolise food sources may lead to increased rates of aggression in these animal groups (Tibetan macaques *Macaca thibetana*, Berman et al. 2007).

Whereas regulated feeding seems to have a minimal impact on mammals during this global crisis because the food provided is supplemental, unregulated feeding should be terminated. If feeding is considered as a tourist attraction at a site, it is important to designate certain groups or organisations to control the amount of food provided so that animals do not rely too much on the food tourists provide. However, this solution is likely to require financial investments, and may not be feasible in some countries, especially if it requires additional paid staff. At some sites, particularly those with little infrastructure, the food provided by visitors is likely to reduce the financial costs associated with keeping mammals in restricted settings. Scholars should continue working to develop effective means to monitor or control tourists feeding wildlife.

Like free-ranging mammals, those kept in captivity are negatively affected by the COVID-19 outbreak, particularly when their lives are linked to the profits made from the business of keeping them. For instance, a thousand captive Asian elephants in Thailand are seriously affected by the drop in the country's tourism (CNW Group 2020, Hatton 2020, Jones 2020, Kongrut 2020, Kuhakan 2020, Robbins 2020, Sullivan 2020). Asian elephant tourism generates income by offering tourists the opportunity to ride and feed the animals (Norkaew et al. 2019). In the absence of tourists, facility income drops, reducing funds needed to feed Asian elephants. Foraging in their natural environment is difficult, since there is inadequate food available due to habitat degradation and food scarcity, especially during the dry season (Fitz-Gibbon 2020). Other mammals are reported to be in a similar situation as are Asian elephants. The food for sun bears *Helarctos malayanus* in the Bornean Sun Bear Conservation Centre in Malaysia is supported by donations from international visitors, mainly European and American tourists (Gilhooly 2020). Due to the travel restrictions, international tourism has dropped by more than 50% (Gössling et al. 2020). It is difficult to predict when or whether international tourists will return to

these destinations where the economy depends heavily on foreign currency.

IN DANGER OF LOSING HOME

In association with food shortage, we found that some zoos and wildlife rescue centres are facing closure as a result of COVID-19. For instance, St. Augustine Wild Reserve, Florida, USA, is home to 50 rescued mammals, including tigers and lions (Gardner 2020). The monthly cost of running the facility is estimated to be USD 5000. The financial gain from regular tours provided to the public contributes to facility management. However, when the reserve was temporarily required to close in order to prevent the spread of the coronavirus, its financial source was completely cut off. Without reopening the facility, staff cannot maintain their expenditures. In situations such as this one, relocating the resident animals would be extremely difficult.

Finding a solution to mitigate or overcome the current global economic recession is not an easy task when it comes to mammals in captivity, as their lives are dependent on well-functioning human societies. If the society that they rely on is negatively impacted by disease and other social upheavals such as widespread unemployment, these animals will be affected as well. Still, it is our responsibility to make sure that the lives of captive animals will be protected. Donations might provide some support. Previous research found that caring and trust in the reputation of the facility or organisation are important factors affecting visitors' willingness to donate money (Sgalitzer et al. 2016). However, under the current circumstance with the COVID-19 economic crisis (Blustein et al. 2020), we feel that it is premature to conclude that donations can provide the solution to this particular issue. Data are needed on how the mammals and people involved in these businesses are coping with the current situation at a local level. It is possible that, in places where captive mammals are the main source of economic support for a family, efforts will be made to feed and care for these animals during this crisis, in hope that both humans and non-humans will be able to return to work soon.

ENRICHED/RELAXED

The lives of some animals in captivity may be enriched or relaxed during the COVID-19 outbreak. One report describes that two captive pandas *Ailuropoda melanoleuca* in Hong Kong mated, apparently due to the absence of visitors to the park (Sparks 2020). This story became news, as the zookeepers had hoped they would mate for ten years prior to the pandemic (Sparks 2020). Some studies

indicate that human visitations cause stress to many species of mammals (primates, Hosey 2005; Tibetan macaques, Matheson et al. 2007; Barbary macaques *Macaca sylvanus*, Maréchal et al. 2011). The absence of stressors associated with daily visitors apparently created the environment the pandas needed to mate.

In the midst of the COVID-19 outbreak, a penguin *Aptenodytes* sp. seems to have replaced the visitors' role at an aquarium in Chicago, USA, where the penguin was allowed to roam freely in the facility to meet his neighbours (Kretchmer 2020). The penguin's presence in an unusual space appeared to be enriching for marine mammals at the facility, who showed interest in this unusual visitor. Moreover, his adventure in the aquarium was shared on social media, which, based on the number of shares and likes it received, was an entertainment opportunity for humans who stayed at home. In this time of social distancing, zoos seek new ways to entertain and educate people by holding live streams for the public, and they seem to be creating a new platform for human-animal encounters.

The COVID-19 outbreak appears to have created a more relaxing environment for some wild mammals, too, where they reportedly lounge in unusual locations within their normal environment without being disturbed by tourists. For example, leopards *Panthera pardus* in Wilpattu National Park in Sri Lanka were reported to spend time relaxing out in the open (Rodrigo 2020). Lions in Kruger National Park in South Africa were found napping on the road.

LACK OF ENRICHMENT

Some captive animals are found to be deprived of enrichment without tourists. For instance, Puppe, a Sumatran orangutan *Pongo abelii* living at Toronto Zoo, Canada, is reported to be missing her favourite interaction with visitors (Jones 2020). She likes to watch visitors, especially children (Jones 2020). However, with the zoo closed, she is not getting her daily entertainment by the visitors.

SPATIAL EXPANSION

Due to spatial expansion of their ranges, mammals were seen in unusual numbers and/or unusual spaces or places once COVID-19 'shelter-at-home' orders were imposed in many countries. Note that we differentiate this case from the context of unusual sightings of mammals (see Table 1). Essentially, the mammals in the spatial expansion category already inhabit the area, so their presence is not a surprise to people living nearby. Nonetheless, it is rare to spot animals with the presence of tourists, so an increase in frequency of viewing the animals is unusual. Yosemite National Park, California, USA, was

intermittently closed to visitors beginning on 20 March 2020, when its residential animals, such as black bears *Ursus americanus*, began roaming without human disturbance (Srikanth 2020).

DISEASE TRANSMISSION

The COVID-19 outbreak physically threatens some animals that are often viewed by tourists, either in the wild or in captivity. Great apes – orangutans *Pongo* spp., chimpanzees *Pan troglodytes*, bonobos *Pan paniscus*, and gorillas *Gorilla* spp. – are genetically similar to humans, which makes them vulnerable to infection (Gillespie & Leendertz 2020), and SARS-CoV-2 infection has been confirmed in western lowland gorillas *Gorilla gorilla* at San Diego Zoo Safari Park, USA (Gibbons 2021). After the COVID-19 outbreak spread globally, some experts recommended suspending primate viewing in nature and in captivity. For instance, primate tourism in habitat countries was discouraged, as viewing endangered primates such as gorillas and chimpanzees in the wild could increase the risk of disease transmission (Gillespie & Leendertz 2020).

The level of contact between visitors and great apes can be controlled in zoos and sanctuaries, but human–primate encounters in the wild can put the endangered great ape populations at risk. In the case of great ape tourism, guidelines have been implemented to prevent disease transmission (Williamson & Macfie 2014). It includes rules such as requiring that visitors are vaccinated prior to joining tours. Even though a visitor might have been vaccinated, if she/he is sick on the day of the tour, she/he should not be allowed to go on a tour (Williamson & Macfie 2014). While these regulations are essential in protecting the health of both humans and non-humans and provide a model for other wildlife tourism operators to follow, until there is widespread vaccination and verification of its efficacy and durability, these primate species are at risk if they are in contact with humans. The risk of disease transmission in the tourism context has been studied extensively among primate species (e.g. non-human primates, Sapolsky 2014; Barbary macaques Carne et al. 2017; non-human primates, Muehlenbein 2017), but zoonotic disease transmission between humans and other species is an under-studied topic as these diseases are usually difficult to track (Odeniran et al. 2018).

Outside of mammals, nine penguin species endemic to Antarctica – formerly geographically isolated animals – have been found to be more exposed to new pathogens as the popularity of Antarctic tourism grew (*Pygoscelis adeliae*, *Pygoscelis antarctica*, *Pygoscelis papua*, *Eudyptes chrysocome*, *Eudyptes chrysolophus*, *Eudyptes schlegeli*, *Eudyptes moseleyi*, *Aptenodytes patagonicus*, *Aptenodytes*

forsteri, Grimaldi et al. 2015). In fact, tourism is reported to be the most frequent catalyst of pathogen transmissions, especially when feeding of animals is involved (Murray et al. 2016). Feeding can create a situation for animals to aggregate, which in turn increases the chance of transmitting diseases. Travel restrictions as a result of the COVID-19 outbreak have reduced the frequency of human–animal contacts at tourism destinations, and this may have reduced the potential for pathogen transmissions for now. Yet, according to a survey conducted by Japan Institute of Tourism Research (2020), tourism researchers expect nature-based tourism to be the most popular tourism style after COVID-19. If this occurs, then tourism management and planning officials must address the potential spread of inter- and intraspecific infection.

Some researchers suspect that COVID-19 may be infectious to more animals than we currently know (Wong et al. 2020). In the second half of 2020, we began seeing COVID-19-positive cases reported for some non-human animals (Gryseels et al. 2021). One news article reported that a female tiger at the Bronx Zoo, USA, was found to be infected by COVID-19 (Wamsley 2020), indicating that the virus can be transmitted to other mammals. However, it is unclear how and where she got the virus. Although we do not know the severity of viral impacts on non-human animals at this point, many animals in captivity are endangered species and, therefore, the spread of the virus in zoos would be detrimental to conservation. The Association of Zoos and Aquariums has assembled on its webpage a list of COVID-19 resources (<https://www.aza.org/covid-19-resources>) in order to share information with animal husbandry staff, many of whom are working at reduced numbers.

REPRIEVED FROM BEING HUNTED (SPORTS HUNTING)

Thousands of African bush elephants *Loxodonta africana* in Botswana are reprieved from being hunted for sports hunting, as the country has banned tourists entering from countries such as the USA, the UK, Italy, and Spain, where the majority of international trophy hunters come from (Jones 2020). Consumptive wildlife tourism such as sports hunting and fishing is controversial, and it is beyond the scope of this review to discuss its sustainability or its risks and benefits to conservation. Yet, travel restrictions have spared the lives of those elephants targeted for hunting.

Context 2: mammals as commodities

In the context of mammals as commodities, we identified two themes: poaching and meat consumption. While

poaching is discussed as an impact of the COVID-19 outbreak and may be related to decreased protection of mammals in wildlife reserves, meat consumption is a topic discussed as a potential cause of this emerging infectious disease. Additionally, the two topics are sometimes linked. For example, some articles describe how a lack of tourism revenue might lead local people who were formerly economically dependent on that tourism to hunt wild mammals for subsistence.

POACHING

Pausing tourism activities in endangered animals' habitats could help prevent them from being infected with COVID-19 and other diseases. However, some news articles indicate that the absence of tourism would put the animals in protected areas in danger of being poached. Asian and African elephants *Elephas* and *Loxodonta*, impala *Aepyceros melampus*, leopards, lions, rhinoceros *Diceros bicornis*, and zebras *Equus* spp. are reportedly facing increased risk of being poached (Deliso 2020, Maron 2020) – some of them are endangered species.

Wildlife tourism often occurs in the countries with rich natural resources. Countries such as Botswana, Democratic Republic of Congo, Kenya, South Africa, Rwanda, and Tanzania are popular wildlife tourism destinations, as they are places to see the 'big five' game species (Stumpf 2010). Poaching could be a particular risk in countries whose economies rely on wildlife tourism. When tourism is suspended, local people have no alternative way of sustaining their lives other than hunting the animals for meat consumption or selling the animals illegally at local and national markets. One news source reports: "The conservancy (...) has depended heavily on money from wildlife safari tourism, a cornerstone of Kenya's economy. In normal times, travel and tourism provide more than a million jobs nationwide, but now that industry is at a standstill. Meshemi and many conservationists worry that one consequence will be increased wildlife poaching – either to provide food for hungry families or for illegal sales – putting him and his fellow rangers in even greater danger" (Maron 2020).

However, there are mixed reports with regard to poaching. One article reports that the global travel restriction has reduced the poaching rate of South African rhinos by half, as international flights have largely been halted (The Guardian 2020).

MEAT CONSUMPTION

Causes of infectious diseases are often linked to human–animal interfaces (Travis et al. 2011, Dixon et al. 2014). For example, SARS and MERS are now known to be

transmitted from wild animals to humans (Bell et al. 2004, Azhar et al. 2014). There has been much speculation about the origin of COVID-19, but it is likely to have been transmitted from wild animals. Early COVID-19 cases of patients confirmed with pneumonia were linked to a 'wet market' – a local seafood market – in the city of Wuhan, China (Li et al. 2020, Zhou et al. 2020, Zhu et al. 2020). A study that compared genomic characteristics of SARS-CoV-2 with alpha- and betacoronaviruses further supports COVID-19's zoonotic origin (Andersen et al. 2020). The initial animal host species has yet to be identified, but an early study reported two snake species *Bungarus multicinctus* and *Naja atra* as potential reservoirs of COVID-19 (Ji et al. 2020). Other researchers have questioned this, claiming that mammals or birds are more likely hosts (Callaway & Cyranoski 2020). Among mammals, the bat species *Rhinolophus sinicus* has been implicated as the potential host of COVID-19 (Biscayart et al. 2020, Zhou et al. 2020).

Current available information indicating that the SARS-CoV-2 virus was probably transmitted from wildlife has generated heated discussion about the consumption of wild-caught meat in China (Ying et al. 2020), where the virus presumably originated. Tourism could contribute to transmission of the disease, as there are a growing number of tourists who are eager to try novel foods (Ying et al. 2020). Their motivations for consuming wild animals include, for example, flaunting their socioeconomic status (Zheng & Sun 2005, cited in Ying et al. 2020, Drury 2011), satisfying their curiosity, and meeting nutritional needs (Zheng & Sun 2005, cited in Ying et al. 2020). Globally, many wildlife markets meet tourists' demands to experience exotic foods (Hoffman et al. 2005, Travis et al. 2011, Marescotti et al. 2019).

In response to the COVID-19 outbreak, the wet market in Wuhan was closed, although it soon reopened (Impelli 2020, Young 2020). Some reports call for a complete ban of wet markets (e.g. Shaheen 2020). Another report says that in Shenzhen, a city located in Guangdong Province, China, where eating wild animals was originally practiced (Yang et al. 2007), the consumption of domestic cats *Felis catus* and dogs *Canis familiaris* has been banned in the wake of COVID-19 (BBC News 2020). The Chinese government also banned the sales and trade of wildlife (Wong et al. 2020). Yet, more recent report indicated that these bans are not entirely effective (Ledger 2020).

Raising tourists' awareness of the ethics of wildlife consumption and its health risks has been suggested (Ying et al. 2020), and we urge that this suggestion be heeded. In addition to considering the ethical issues associated with wildlife consumption and markets, we need to re-evaluate and improve the conditions under which all animals, domestic and wild, are kept for food consumption. In the wildlife market environment, where animals – either dead

or alive – are kept in cages with close contact between species, the chance of virus mutation and transmission may increase. Moreover, animals – especially those traded illegally – are reportedly kept in unsanitary conditions, which further increases a risk of disease transmission (Bell et al. 2004, Weldon et al. 2004, Borm et al. 2005). While it is beyond the scope of this paper to address the cultural, political, and financial reasons for operating wet markets and the types of animals involved, the COVID-19 outbreak must bring a change in regulatory systems and people's attitudes towards wild meat consumption and the treatment of food animals in general.

Context 3: mammals as threats

SPATIAL EXPANSION

If spatial expansion occurs, it may involve those mammals typically considered as threats or nuisances. Rats *Rattus norvegicus* in the USA that usually fed on the garbage produced by tourists or tourism-related businesses have lost their food source since the pandemic outbreak (Garcia 2020). While these city-dwelling rats may be desperate to find food, people find this an opportunity to control the pests because, more than ever, they are attracted by the pest-control baits (Garcia 2020). However, the same news raises a concern that rats may flood into cities, just as long-tailed macaques have moved into urban settings in Thailand.

This context also includes concerns of COVID-19 appearing in domesticated, laboratory, and companion animals, as described in one preprint report of a dog apparently catching the disease from its infected owner in China (Malik et al. 2020). The possibility of disease transfer between people and animals with which they have frequent contact may be contributing to the rapid and wide spread of the disease.

Context 4: unusual sightings of mammals

Unusual sightings of mammals are a new category we added to Markwell's (2015) original schema characterising animal-focused tourism. It applies when mammals were almost never seen in an area prior to the pandemic. Seeing the mammals themselves, rather than the place the animals are in, is the key point that differentiates this category from the spatial expansion of mammals. The events reported in this context are mainly divided into two: 1) mammals venturing into cities; and 2) mammals returning to spaces that are now less disturbed as humans live in quarantine.

One of the impacts described under this context is that mammals are appearing in quiet and deserted cities. Wild boar, coyotes *Canis latrans*, foxes *Vulpes vulpes*,

nilgai *Boselaphus tragocamelus*, and pumas *Puma concolor*, mammals that are typically wary of humans, are being observed in human-made and human-modified spaces. In Barcelona, Spain, for instance, a wild boar reportedly came down from the mountains to the city's empty streets (Kretchmer 2020). Likewise, with few cars on the roads, coyotes in San Francisco, USA, explore deep into the city (Garcia 2020). A group of fallow deer *Odocoileus* sp. were seen lying on the grass in residential areas near Dagnam Park, London, UK (CBC News 2020). Deer are regularly seen in the park that is adjacent to humans' living spaces, but now deer utilise roads and plazas, areas that are typically exclusively occupied by humans. Similarly, goats *Capra aegagrus hircus* in North Wales, UK, and sea lions *Zalophus wollebaeki* in Mar del Plata, Argentina are reported to be filling up spaces that used to be dominated by humans. A field study conducted in Italy after the start of the pandemic also documented changes in sightings and behaviours of some species (Manenti et al. 2020).

Marine mammals have reportedly returned to environments that were too polluted and disturbed to live in before the COVID-19 outbreak, but now provide suitable habitat. For example, endangered species have been spotted in some parts of Thailand, including 30 dugongs *Dugong dugon* that were seen feeding on sea grass in an area formerly frequented by tourists and boats (Khunsong & Harmer 2020). Similarly, 10–15 false killer whales *Pseudorca crassidens* were seen in that region for the first time (Khunsong & Harmer 2020).

It is difficult to determine whether these unusual sightings of mammals are positive or negative for animals and humans. However, in the case of terrestrial mammals, humans compete for space with them to a greater extent than typically occurs with aquatic mammals. Thus, with species such as boar and puma, more human–animal conflicts are likely to be generated as a consequence of human–animal boundary transgression. We assume that some of the mammals reported in the news can be dangerous if humans encounter them, as they are predators (e.g. coyotes and pumas) or could harm humans in self-defence (e.g. boars and nilgai).

Disease transmission due to extensive overlapping of space is a serious consequence that could occur with some mammals. According to Navarro-Gonzalez et al. (2013), wild boars in Barcelona feed and defecate in places humans normally utilise, such as parks and private gardens. They also drink water from fountains and swimming pools. While this occurred before the pandemic, zoonotic disease could be transmitted to humans or back to non-humans, if people come into contact with contaminated water or places. It seems likely that COVID-19 is transmissible to other mammals, and perhaps to many other animals, too,

such as birds and reptiles (Wong et al. 2020). This could make overlap between people, domestic animals, and wild animals a concern with respect to interspecies transmission of COVID-19.

WHAT'S NEXT?

In a world where the SARS-CoV-2 virus currently dominates, we are still in a battle with an uncertain outcome until COVID-19 vaccines are widely confirmed to be safe and effective. It is unclear when or if the virus will be contained, and when or if our lives will return to normal. In a similar way, the lives of mammals are affected through their interplay with human society. Thus far, the impact on non-human mammals has been overshadowed by more immediate human-related issues, but if people are to make a change in a previously neglected area, we argue that attention must be paid to mammals in the current outbreak. Therefore, our aim in this review was to map out the impacts of the pandemic on mammals in tourist destinations.

Given the current situation, it is difficult to obtain first-hand observations of COVID-19's impacts on different mammals. For this reason, we relied on news articles in writing this paper. While the reports presented here can indicate the possible effects of the global health crisis on mammals involved in tourism, it should be noted that these cases do not represent the whole picture. Our study is also limited in that we reviewed stories that had global or nearly global reach, rather than news reported at a local level. In addition, we searched the articles using English keywords, which is likely to have limited our search results primarily to English articles. Another point is that while GDELT, one of the search engines we used, is the largest news database, and aggregates news in more than 100 languages from across the world (<https://www.gdeltproject.org>), the sources of information could have country-specific heterogeneities, as some countries restrict access to certain kinds of information.

Whether the pandemic has affected mammals positively or negatively is difficult to determine, as our findings showed that effects of the reduction in tourism varied by species and the contexts that they are in. Mixed impacts have been reported in the study conducted in Italy as well (Maneti et al. 2020). Just as some people are impacted more than the others by the COVID-19 outbreak, some mammal species or mammal groups are affected more than others. Once travel restrictions are eased and we are able to travel without concern about spreading of the virus, researchers will need to obtain more site-specific evidence of effects of the COVID-19 outbreak on mammals and people involved in tourism businesses. With this paper, we hope to open the discussion about the positions that mammals are in, and how to make positive changes for each context.

REFERENCES

- Adhikari K, Khanal L, Chalise M (2018) Status and effects of food provisioning on ecology of Assamese monkey (*Macaca assamensis*) in Ramdi area of Palpa, Nepal. *Journal of Institute of Science and Technology* 22: 183–190.
- Andersen KG, Rambaut A, Lipkin WI, Holmes EC, Garry RF (2020) The proximal origin of SARS-CoV-2. *Nature Medicine* 26: 450–452. <https://doi.org/10.1038/s41591-020-0820-9>
- Azhar EI, El-Kafrawy SA, Farraj SA, Hassan AM, Al-Saeed MS, Hashem AM, Madani TA (2014) Evidence for camel-to-human transmission of MERS coronavirus. *New England Journal of Medicine* 370: 2499–2505.
- Baldwin R, Tomiura E (2020) Thinking ahead about the trade impact of COVID-19. In: Baldwin R, Weder di Mauro B (eds) *Economics in the Time of COVID-19*, 59–71. CEPR Press, London, UK.
- Barton RA, Whiten A (1993) Feeding competition among female olive baboons, *Papioanubis*. *Animal Behaviour* 46: 777–789.
- BBC News (2020) Shenzhen becomes first Chinese city to ban eating cats and dogs. <https://www.bbc.com/news/world-asia-china-52131940>
- Bell D, Robertson S, Hunter PR (2004) Animal origins of SARS coronavirus: possible links with the international trade in small carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 1107–1114.
- Berman C, Li JH, Ogawa H, Ionica CS, Yin H (2007) Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *International Journal of Primatology* 28: 1123–1141.
- Biscayart C, Angeleri P, Lloveras S, Chaves TSS, Schlagenhaut P, Rodríguez-Morales AJ (2020) The next big threat to global health? 2019 novel coronavirus (2019-nCoV): what advice can we give to travelers? Interim recommendations January 2020, from the Latin-American society for Travel Medicine (SLAMVI). *Travel Medicine and Infectious Disease* 33: 1–4.
- Blustein DL, Duffy R, Ferreira JA, Cohen-Scali V, Cinamon RG, Allan BA (2020) Unemployment in the time of COVID-19: a research agenda. *Journal of Vocational Behavior* 119: 1–4. <https://doi.org/10.1016/j.jvb.2020.103436>
- Borm SV, Thomas I, Hanquet G, Lambrecht B, Boschmans M (2005) Highly pathogenic H5N1 influenza virus in smuggled Thai eagles, Belgium. *Emerging Infectious Diseases* 11: 702–705.
- Callaway E, Cyranoski D (2020) Why snakes probably aren't spreading the new China virus. *Nature*. <https://doi.org/10.1038/d41586-020-00180-8>
- Carne C, Semple S, MacLarnon A, Majolo B, Maréchal L (2017) Implications of tourist-macaque interactions for disease transmission. *EcoHealth* 14: 704–717.
- CBC News (2020) Wildlife take to the streets as people stay indoors. <https://www.cbc.ca/news/world/photos-wildl>

- ife-animals-take-to-streets-as-people-take-shelter-indoors-1.5519538
- Chinazzi M, Davis JT, Ajelli M, Gioannini C, Litvinova M, Merler S et al. (2020) The effect of travel restrictions on the spread of the 2019 novel coronavirus (COVID-19) outbreak. *Science* 368: 395–400.
- CNW Group (2020) World Animal Protection launches emergency appeal for elephants in Thailand facing starvation due to COVID-19. <https://ca.finance.yahoo.com/news/world-animal-protection-launches-emergency-100000004.html>
- Curtin S, Kragh G (2014) Wildlife tourism: reconnecting people with nature. *Human Dimensions of Wildlife* 19: 545–554.
- Deliso M (2020) Conservationists fear African animal poaching will increase during COVID-19 pandemic. <https://abcnews.go.com/International/conservationists-fear-african-animal-poaching-increase-covid-19/story?id=70118142>
- Dixon MA, Dar OA, Heymann DL (2014) Emerging infectious diseases: opportunities at the human-animal-environment interface. *Veterinary Record* 174: 546–551.
- Drury R (2011) Hungry for success: urban consumer demand for wild animal products in Vietnam. *Conservation and Society* 9: 247–257.
- Enk MJ, Amaral GL, Silveira-Lemos D, Teixeira-Carvalho A, Martins-Filho OA, Correa-Oliveira R et al. (2010) Rural tourism: a risk factor for schistosomiasis transmission in Brazil. *Memorias do Instituto Oswaldo Cruz* 105: 537–540.
- Fitz-Gibbon J (2020) Elephants in Thailand face starvation as coronavirus knocks out tourism. <https://nypost.com/2020/03/31/elephants-in-thailand-facing-starvation-as-covid-19-kills-tourism/>
- Fredman P, Tyrväinen L (2011) Introduction. In: Fredman P, Tyrväinen L (eds) *Frontiers in Nature-based Tourism: Lessons from Finland, Iceland, Norway and Sweden*, 5–17. Routledge, New York, USA.
- Garcia S (2020) When humans are sheltered in place, wild animals will play. <https://www.nytimes.com/2020/04/01/science/coronavirus-animals-wildlife-goats.html>
- Gardner S (2020) Coronavirus: animal attractions seek help as tourism dwindles in St. Johns County. <https://www.staugustine.com/news/20200331/coronavirus-animal-attractions-look-for-help-as-tourism-dwindles-in-st-johns-county>
- Gibbons A (2021) Captive gorillas test positive for coronavirus. <https://www.sciencemag.org/news/2021/01/captive-gorillas-test-positive-coronavirus>
- Gilhooly L (2020) The tragic intersection of the coronavirus and ecotourism. <https://www.sapiens.org/culture/coronavirus-and-ecotourism/>
- Gillespie TR, Leendertz FH (2020) Great-ape health in human pandemics. *Nature* 579: 497.
- Gössling S, Scott D, Hall C (2020) Pandemics, tourism and global change: a rapid assessment of COVID-19. *Journal of Sustainable Tourism* 29: 1–20. <https://doi.org/10.1080/09669582.2020.1758708>
- Grimaldi WW, Seddon PJ, Lyver POB, Nakagawa S, Tompkins DM (2015) Infectious diseases of Antarctic penguins: current status and future threats. *Polar Biology* 38: 591–606.
- Gryseels S, de Bruyn L, Gyselings R, Calvignac-Spencer S, Leendertz FH, Leirs H (2021) Risk of human-to-wildlife transmission of SARS-CoV-2. *Mammal Review* 51. <https://doi.org/10.1111/mam.12225>
- Hatton C (2020) Coronavírus: elefantes da Tailândia podem morrer de fome com o colapso do turismo. <https://www.terra.com.br/noticias/coronavirus-elefantes-da-tailandia-podem-morrer-de-fome-com-o-colapso-do-turismo,9d5e9376119d030459eaf058d13bdf5a9cqt14.html>
- Hoffman LC, Muller M, Schutte DW, Calitz FJ, Crafford K (2005) Consumer expectations, perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research* 35: 33–42.
- Hosey GR (2005) How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* 90: 107–129.
- Impelli M (2020) What is a wet market? Calls for crackdown on selling live animals amid coronavirus pandemic. <https://www.newsweek.com/what-wet-market-amid-pandemic-crackdown-called-selling-live-animals-china-1495278>
- Japan Institute of Tourism Research (2020) Tourist behavioural change after COVID-19: a survey. https://7b05b3a1-8d6b-4ddf-af18-739a3d423c5e.filesusr.com/ugd/17484f_1c3d58c6d1dc4bd7b72ee64ebd39253a.pdf [in Japanese]
- Jason C (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology* 18: 125–138.
- Ji W, Wang W, Zhao X, Zai J, Li X (2020) Cross-species transmission of the newly identified coronavirus 2019-nCoV. *Journal of Medical Virology* 92: 433–440. <https://doi.org/10.1002/jmv.25682>
- Jones D (2020) The coronavirus pandemic has halted tourism, and animals are benefiting from it. <https://www.washingtonpost.com/travel/2020/04/03/coronavirus-pandemic-has-halted-tourism-animals-are-benefiting-it/>
- Khunsong PT, Harmer J (2020) Coronavirus travel restrictions in Thailand allow shy wildlife to emerge. <https://www.usatoday.com/story/travel/news/2020/04/23/coronavirus-travel-restrictions-thailand-let-shy-wildlife-emerge/3010338001/>
- Knight J (2011) *Herding Monkeys to Paradise: how Macaque Troops are Managed for Tourism in Japan*. Brill, Leiden, the Netherlands.
- Knight J (2017) Wildlife tourism as crop protection? Double-goal provisioning and the transvaluation of the

- macaque in postwar Japan. *Human-Wildlife Interactions* 11: 217–230.
- Köndgen S, Kühl H, N’Goran PK, Walsh PD, Schenk S, Ernst N et al. (2008) Pandemic human viruses cause decline of endangered great apes. *Current Biology* 18: 260–264.
- Kongrut A (2020) Covid-19 claims unlikely victims. <https://www.bangkokpost.com/thailand/special-reports/1888995/covid-19-claims-unlikely-victims>
- Kretchmer H (2020) These lock-down cities are being reclaimed by animals. <https://www.weforum.org/agenda/2020/04/covid-19-cities-lockdown-animals-goats-boar-monkeys-zoo/>
- Kuhakan J (2020) Hungry times at Thailand’s elephant sanctuaries as coronavirus hits tourism. <https://www.reuters.com/article/us-health-coronavirus-thailand-elephants/hungry-times-at-thailands-elephant-sanctuaries-as-coronavirus-hits-tourism-idUSKBN2100OQ>
- Labonté R, Mohindra K, Schrecker T (2011) The growing impact of globalization for health and public health practice. *Annual Review of Public Health* 32: 263–283.
- Ledger E (2020) Conservationists warn that violation of China’s wildlife trade ban is ‘rampant’. <https://www.independent.co.uk/world/conservationists-warning-china-wildlife-trade-ban-violation-b1367444.html>
- Li J, Li J, Xie X, Cai X, Huang J, Tian X, Zhu H (2020) Game consumption and the 2019 novel coronavirus. *The Lancet Infectious Diseases* 20: 275–276. [https://doi.org/10.1016/S1473-3099\(20\)30063-3](https://doi.org/10.1016/S1473-3099(20)30063-3)
- Linsey P, Allan J, Brehony P, Dickman A, Robson A, Begg C et al. (2020) Conserving Africa’s wildlife and wildlands through the COVID-19 crisis and beyond. *Nature Ecology & Evolution* 4: 1300–1310.
- Malik YS, Kumar N, Sircar S, Kaushik R, Bhatt S, Dhama K et al. (2020) Pandemic coronavirus disease (COVID-19): challenges and a global perspective. *Pathogens* 9: 519. <https://doi.org/10.20944/preprints202004.0469.v1>
- Manenti R, Mori E, Canio VD, Mercurio S, Picone M, Caffi M et al. (2020) The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: insights from the first European locked down country. *Biological Conservation* 249: 108728. <https://doi.org/10.1016/j.biocon.2020.108728>.
- Maréchal L, Semple S, Majolo B, Qarro M, Heistermann M, MacLarnon A (2011) Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. *Biological Conservation* 144: 2188–2193.
- Marescotti ME, Caputo V, Demartini E, Gaviglio A (2019) Discovering market segments for hunted wild game meat. *Meat Science* 149: 163–176.
- Markwell K (2015) *Animals and Tourism: Understanding Diverse Relationships*. Channel View Publications, Bristol, UK.
- Maron DF (2020) Poaching threats loom as wildlife safaris put on hold due to COVID-19. <https://www.nationalgeographic.com/animals/2020/04/wildlife-safaris-halted-for-covid-boost-poaching-threat/#close>
- Matheson MD, Hartel J, Whitaker C, Sheeran LK, Li JH, Wagner RS (2007) Self-directed behavior correlates with tourist density in free-living Tibetan macaques (*Macaca thibetana*) at the Valley of the Wild Monkeys, Mt. Huangshan, China. *American Journal of Primatology* 69: 41–42.
- Muehlenbein MP (2017) Primates on display: potential disease consequences beyond bushmeat. *American Journal of Physical Anthropology* 162: 32–43.
- Murray MH, Becker DJ, Hall RJ, Hernandez SM (2016) Wildlife health and supplemental feeding: a review and management recommendations. *Biological Conservation* 204: 163–174.
- Navarro-Gonzalez N, Casas-Díaz E, Porrero CM, Mateos A, Domínguez L, Lavín S, Serrano E (2013) Food-borne zoonotic pathogens and antimicrobial resistance of indicator bacteria in urban wild boars in Barcelona, Spain. *Veterinary Microbiology* 167: 686–689.
- Newsflare (2020) Starving monkeys fed with watermelon as coronavirus halts tourism in Thailand. https://uk.news.yahoo.com/starving-monkeys-fed-watermelon-coronavirus-150000828.html?guccounter=1&guce_referrer=aHR0cHM6Ly9hcGkuZ2RlbHRwcm9qZWNO0Mm9yZy9hcGkvZjIvZG9jL2RvYz9mb3JtYXQ9aHRtbCZzdGFydGRhdGV0aWw1IPTIwMTcwMTAxMDAwMDAwJmVuZGRhdGV0aWw1IPTIwMjAwNDI3MjM1OTU5JnF1ZXJ5PXRvdXJpc20lMjBhbmlltYWxzJTlIwJTlYQ09WSUQtMTk1MjBhbm9kZT1hcnRsaXN0Jm1heHJlY29yZHM9NzUmc29ydD1oeWJyaWRyZWw&guce_referrer_sig=AQAAALH7FWBnRXwIA226s3Ivetg7Fs7cCcfvz1sZEowgpPMzPdNZu_QKSkG86AI-VhXsQ0vQDO5VqgL6h1AjJR1rLF4cV7eX6Ca-rfnv6wXz2IrlwG6TUUQtmAtwm-qrNN_vgJka5Jo5F3TOVdqjo8Pdo9lWzSpBRbhx5SVHS6l2qZ
- Newsome D (2020) The collapse of tourism and its impact on wildlife tourism destinations. *Journal of Tourism Futures* 1–8. <https://doi.org/10.1108/JTF-04-2020-0053>
- Norkaew T, Brown JL, Thitaram C, Bansiddhi P, Somgird C, Punyapornwithaya V et al. (2019) Associations among tourist camp management, high and low tourist seasons, and welfare factors in female Asian elephants in Thailand. *PLoS One* 14: e0218579. <https://doi.org/10.1371/journal.pone.0218579>
- Odeniran P, Ademola I, Jegede H (2018) A review of wildlife tourism and meta-analysis of parasitism in Africa’s national parks and game reserves. *Parasitology Research* 117: 2359–2378.
- Ongmo S, Parikh T (2020) What explains Bhutan’s success battling COVID-19? <https://thediplomat.com/2020/05/what-explains-bhutans-success-battling-covid-19/>

- Orams MB (2002) Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management* 23: 281–293.
- Robbins S (2020) Coronavirus: one thousand Thai elephants could starve as COVID-19 hits tourism. <https://news.sky.com/story/coronavirus-one-thousand-thai-elephants-could-starve-as-covid-19-hits-tourism-11975079>
- Rodrigo M (2020) Sri Lanka's COVID-19 lockdown sets wildlife free but raises poaching threat. <https://news.mongabay.com/2020/04/sri-lankas-covid-19-lockdown-sets-wildlife-free-but-raises-poaching-threat/>
- Rutz C, Loretto MC, Bates AE, Davidson SC, Duarte CM, Jetz W (2020) COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology & Evolution* 4: 1156–1159.
- Saito C (1996) Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Animal Behaviour* 51: 967–980.
- Sapolsky RM (2014) Some pathogenic consequences of tourism for nonhuman primates. In: Russon AE, Wallis J (eds) *Primate Tourism: a Tool for Conservation?*, 147–154. Cambridge University Press, Cambridge, UK.
- Sengupta A, Radhakrishna S (2018) The hand that feeds the monkey: mutual influence of humans and rhesus macaques (*Macaca mulatta*) in the context of provisioning. *International Journal of Primatology* 39: 817–830.
- Sgalitzer HA, Brownlee MTJ, Zajchowski C, Bricker KS, Powell RB (2016) Modelling travellers' philanthropy: tourists' motivations to donate at Sweetwater Chimpanzee Sanctuary. *Journal of Ecotourism* 15: 1–20.
- Shaheen T (2020) The Chinese wild-animal industry and wet markets must go. <https://www.nationalreview.com/2020/03/the-chinese-wild-animal-industry-and-wet-markets-must-go/>
- Smith H, Samuels A, Bradley S (2008) Reducing risky interactions between tourists and free-ranging dolphins (*Tursiops* sp.) in an artificial feeding program at Monkey Mia, Western Australia. *Tourism Management* 5: 994–1001.
- Sparks H (2020) 3 ways the coronavirus is helping the environment. <https://nypost.com/2020/04/07/3-ways-the-coronavirus-is-a-boon-to-the-environment/>
- Srikanth A (2020) As coronavirus wipes out tourism, wildlife rules Yosemite again. <https://thehill.com/changing-america/sustainability/environment/493738-as-coronavirus-wipes-out-tourism-wildlife-rules>
- Stumpf BG (2010) Africa on the matrix: the Cape buffalo. <http://on-the-matrix.co.uk/africa/buffalo.asp>
- Sullivan M (2020) Thailand, growing concern for elephants as coronavirus pummels tourism. <https://www.npr.org/2020/04/11/828017452/in-thailand-growing-concern-for-elephants-as-coronavirus-pummels-tourism>
- Szott I, Pretorius Y, Koyama N (2019) Behavioural changes in African elephants in response to wildlife tourism. *Journal of Zoology* 308: 164–174.
- The Guardian (2020) South African rhino poaching halves in six months thanks to COVID-19 lockdown. <https://www.theguardian.com/environment/2020/aug/01/south-african-rhino-poaching-halves-in-six-months-thanks-to-covid-19-lockdown>
- Thomson J, Araujo G, Labaja J, McCoy E, Murray R, Ponzo A (2017) Feeding the world's largest fish: highly variable whale shark residency patterns at a provisioning site in the Philippines. *Royal Society Open Science* 4: 1–15.
- Travis DA, Watson RP, Tauer A (2011) The spread of pathogens through trade in wildlife. *Revue Scientifique et Technique (International Office of Epizootics)* 30: 219–239.
- Usui R, Funck C (2017) Not quite wild, but not domesticated either: contradicting management decisions on free-ranging sika deer (*Cervus nippon*) at two tourism sites in Japan. In: Lima IB, Green RJ (eds) *Wildlife Tourism, Environmental Learning and Ethical Encounters: Geoheritage, Geoparks and Geotourism*, 247–261. Springer, Cham, Switzerland.
- Usui R, Sheeran LK, Li JH, Sun L, Wang X, Pritchard AJ, DuVall-Lash AS, Wagner RS (2014) Park rangers' behaviors and their effects on tourists and Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. *Animals* 4: 546–561.
- Wamsley L (2020) A tiger has coronavirus. Should you worry about your pets? <https://www.npr.org/2020/04/06/828517076/a-tiger-has-coronavirus-should-you-worry-about-your-pets>
- Weldon C, du Preez LH, Hyatt AD, Muller R, Speare R (2004) Origin of the amphibian chytrid fungus. *Emerging Infectious Diseases* 10: 2100–2105.
- Westcott B, Culver D (2020) Chinese tourist sites packed as country comes out of lockdown, but experts say risk still high. <https://edition.cnn.com/2020/04/06/asia/china-coronavirus-tourist-warning-intl-hnk/index.html>
- Williamson EA, Macfie EJ (2014) Guidelines for best practice in great ape tourism. In: Russon AE, Wallis J (eds) *Primate Tourism: a Tool for Conservation?*, 292–310. Cambridge University Press, Cambridge, UK.
- Wong G, Bi Y, Wang Q, Chen X, Zhang Z, Yao Y (2020) Zoonotic origins of human coronavirus 2019 (HCoV-19): why is this work important? *Zoological Research* 41: 213–219.
- World Health Organization (2003) Summary of probable SARS cases with onset of illness from 1 November 2002 to 31 July 2003. https://www.who.int/csr/sars/country/table_2004_04_21/en/
- World Health Organization (2020a) Middle East respiratory syndrome coronavirus (MERS-CoV). Accessed April 2020. <https://www.who.int/emergencies/mers-cov/en/>
- World Health Organization (2020b) Weekly epidemiological update -12 January 2021. Accessed January 2021. <https://www.who.int/publications/m/item/weekly-epidemiological-update---12-january-2021>

- Xia W, Ren B, Li Y, Hu J, He X, Krzton A, Li M, Li D (2016) Behavioral responses of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) to tourists in a provisioned monkey group in Baimaxueshan Nature Reserve. *Folia Primatologica* 87: 349–360.
- Yang D, Dai X, Deng Y, Lu W, Jiang Z (2007) Changes in attitudes toward wildlife and wildlife meats in Hunan Province, central China, before and after the severe acute respiratory syndrome outbreak. *Integrative Zoology* 1: 19–25.
- Ying T, Wang K, Liu X, Wen J, Goh E (2020) Rethinking game consumption in tourism: a case of the 2019 novel coronavirus pneumonia outbreak in China. *Tourism Recreation Research*. <https://doi.org/10.1080/02508281.2020.1743048>.
- Young J (2020) Shockingly, China's wet markets are reopening; will we ever learn? <https://www.ccn.com/shockingly-chinas-wet-markets-are-reopening-will-we-ever-learn/>
- Zheng Y, Goh E, Wen J (2020) The effects of misleading media reports about COVID-19 on Chinese tourists' mental health: a perspective article. *Anatolia* 31: 1–4.
- Zhou P, Yang XL, Wang XG, Hu B, Zhang L, Zhang W et al. (2020) A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* 579: 270–273.
- Zhu N, Zhang D, Wang W, Li X, Yang B, Song J et al. (2020) A novel coronavirus from patients with pneumonia in China, 2019. *The New England Journal of Medicine* 382: 727–733.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. A list of online news articles and a scientific study used for analysis.