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Abstract

Worldwide, wild birds are frequently suspected to be involved in the occurrence of outbreaks of different diseases in captive-bred birds although proofs are lacking and most of the dedicated studies are insufficiently conclusive to confirm or characterize the roles of wild birds in such outbreaks. The aim of this study was to assess and compare, for the most abundant peridomestic wild birds, the different exposure routes for avian influenza and Newcastle disease viruses in conservation breeding sites of Houbara bustards in the United Arab Emirates.

To do so, we considered all of the potential pathways by which captive bustards could be exposed to avian influenza and Newcastle disease viruses by wild birds, and ran a comparative study of the likelihood of exposure via each of the pathways considered. We merged data from an ecological study dedicated to local wild bird communities with an analysis of the contacts between wild birds and captive bustards and with a prevalence survey of avian influenza and Newcastle disease viruses in wild bird populations. We also extracted data from an extensive review of the scientific literature and by the elicitation of expert opinion.

Overall, this analysis highlighted those captive bustards had a high risk of being exposed to pathogens by wild birds. This risk was higher for Newcastle disease virus than avian influenza virus, and House sparrows represented the riskiest species for the transmission of both viruses through direct exposure from direct contact with an infectious bird that got inside the aviary and indirect exposure from consumption of water contaminated from the faeces of an infected bird that got inside the aviary for Newcastle disease virus and avian influenza virus, respectively. These results also reaffirm the need to implement biosecurity measures to limit contacts between wild and captive birds and highlight priority targets for a thoughtful and efficient sanitary management strategy.

1 | INTRODUCTION

Within the field of One Health, there is a deep interest in the role of wildlife–livestock interfaces in disease ecology (Hassell et al., 2017; Okello et al., 2011). The interface between wild birds and domestic poultry is studied in particular (Wiethoelter et al., 2015) as wild birds frequently are suspected to be involved in the occurrence of outbreaks of different diseases in captive-bred birds. While many studies are insufficiently conclusive to confirm or characterize the roles of wild birds in such outbreaks (Caron et al., 2017; Gaidet & Caron, 2016), limiting contact between wild and captive-bred birds is usually advocated in poultry breeding biosecurity guidelines as precautionary measures to prevent sanitary and economic consequences of epizootic events.

Avian influenza (AIV) and Newcastle disease viruses (NDV), two of the most important avian pathogens worldwide (D. J. Alexander, 2008; Dennis J. Alexander, 2007; Capua & Alexander, 2004), have been responsible for mass mortalities and severe economic losses over recent decades (McElwain & Thumbi, 2017; Ramos et al., 2017; Thompson et al., 2019). In most of the associated epizootic events, the question of the epidemiological role of wild birds has been raised (Bodewes & Kuiken, 2018; V. R. Brown & Bevins, 2017; Chatziprodromidou et al., 2018).

In particular, populations of waterfowl and shorebirds are known to be natural reservoirs of AIV and NDV (Gavier-Widén et al., 2012; Munster & Fouchier, 2009; Olsen et al., 2006), and their role in the global spread of these viruses has been proven (Lisovski et al., 2018; Marks et al., 2014; Mase & Kanehira, 2015; Mine et al., 2019; The Global Consortium for H5N8 & Related Influenza Viruses, 2016). However, these populations are mainly restricted to wetlands and sea shores, their natural habitats, and thus are not usually in close contact with captive-bred birds. Given the ubiquity of these two viruses and the extent of their host range, the absence of classical maintenance populations in some environmental contexts suggests that other bird species may play a role in the epidemiological framework (Caron et al., 2017).

In the Middle East, despite the arid environment, unfavourable weather conditions and limited populations of wild waterfowl, AIV and NDV are regularly detected in poultry (Aamir et al., 2007; Al Shekaili et al., 2015; Al-Azemi et al., 2008; Alkhalaf, 2010; A. A. Alsahami et al., 2018; A. Alsahami et al., 2018; Haroun et al., 2015; Hirschinger et al., 2019; Kent et al., 2006; Khan et al., 2009; Mohran et al., 2011; Nagy et al., 2017; Naldo & Samour, 2004; Obon et al., 2009; Wernery et al., 2013). In the United Arab Emirates (UAE), the poultry industry is an important sector, especially broiler and layer chickens (Seifarth & Tarraf, 2018). Numerous wildlife conservation initiatives also are regularly implemented in the country. A prime example involves the endangered Asian Houbara Bustard (*Chlamydotis macqueenii*) ('Vulnerable' IUCN Red List of Threatened Species, 39), a semi-desertic avian species inhabiting the Middle East and Central Asia. In the UAE, this bird is captive-bred in dedicated breeding stations to maintain a self-sustaining captive population and to produce individuals for reinforcement programmes (around 20,000 birds are released into their natural home range every year).

On these breeding stations, captive bustards are housed in outdoor netted aviaries to prepare them to be released in the wild and maximize their chances of survival. Such facilities create an oasis in the middle of the desert, and are a godsend for wild birds, offering vital resources (water, food and shelter) that allow them to establish flourishing communities (Bock et al., 2008). Due to the combined effect of these two factors (outdoor housing and oasis effect), captive bustards are highly exposed to wild birds and whatever pathogens may accompany them. Furthermore, those breeding stations are surrounded by poultry farms (several within a perimeter of 15 km) which may act as reservoirs of pathogens.

Due to the conservation status of Houbara bustards, conventional poultry sanitary control strategies, especially 'stamping out', cannot be considered, and all efforts are focused on preventing the introduction and spread of pathogens. This is particularly important as the high density of captive flock could lead to mass mortality in case of pathogen introduction. Moreover, the release of Houbara bustards in their whole home range for reinforcement programs dictates to release birds free of major pathogens to prevent their spread in pathogens-free areas. Thus, prevention of pathogens introduction is critical and achieved through the implementation of risk-based biosecurity measures, which are based primarily on an assessment of the probability of pathogens exposure from wild birds.

The aim of this study was to assess and compare, for the most prevalent resident peridomestic wild birds, the different exposure routes of Houbara bustards for AIV and NDV to recommend preventive measures. To do so, we considered all of the potential pathways by which captive bustards could be exposed to AIV and NDV by wild birds, and ran a comparative study of the likelihood of exposure via each of the pathways considered. We merged data from an ecological study dedicated to local wild bird communities with an analysis of the contacts between wild birds and captive bustards and with a prevalence survey of AIV and NDV in wild bird populations (Hirschinger, 2020). We also extracted data from an extensive review of the scientific literature and by the elicitation of expert opinion. Finally, we identified the most significant wild bird species and pathways of exposure, representing priority targets for a thoughtful and efficient sanitary management strategy.
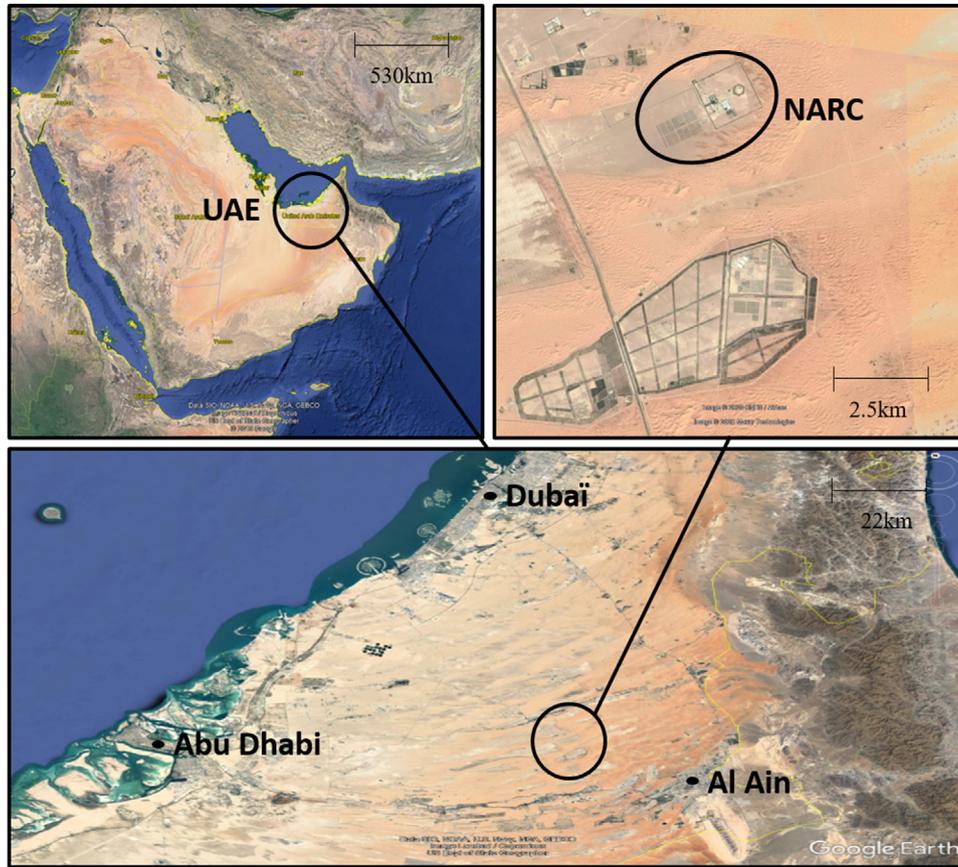
FIGURE 1 Satellite view of the United Arab Emirates. On the top right, the breeding site of the National Avian Research Center (NARC). This figure was produced on the basis of satellite views from Google Earth

2 | MATERIALS AND METHODS

This study, which is part of a research project dedicated to the evaluation of the sanitary risks associated with the exposure of poultry farms to wild birds, was conducted at the National Avian Research Center (NARC, N24.39600 E55.43630), a Houbara bustard conservation breeding project in the UAE (Figure 1).

2.1 | Scenario tree and pathways of exposure

Following the methodological framework of the World Organisation of Animal Health (OIE) for risk analysis (Office international des épizooties, 2005a, b), we investigated the likelihood of exposure of captive Houbara bustards to AIV and NDV from the four peridomestic species identified as dominant in this ecosystem and involved in the majority of contacts with captive bustards (captures results, Hirschinger, 2020): the House sparrow (*Passer domesticus*, PASDOM), the White-eared bulbul (*Pycnonotus leucotis*, PYCTIS), the Laughing dove (*Spilopelia senegalensis*, STRSEN) and the Collared dove (*Streptopelia decaocto*, STRDEC). As previously described (Hernández-Jover et al., 2015; Scott et al., 2018), we used scenario trees to consider all of the potential exposure pathways by which bustards housed in outdoor

aviaries can be in contact with AIV and NDV by target species to estimate exposure probabilities.

The exposure pathways considered in this study were divided into two groups due to the nature of the contacts between wild birds and captive bustards according to literature review and field observations. The first group considered all pathways of exposure resulting from the presence of wild birds perched on an aviary including exposure through the falling of contaminated faeces or contaminated feathers from the horizontal upper nets (Figure 2). The second group considered all pathways resulting from the presence of wild birds inside an aviary including exposure through contaminated faeces, contaminated feathers, contaminated aerosols and contaminated carcasses (Figure 3). See Figure S1 in Supporting information for the global picture.
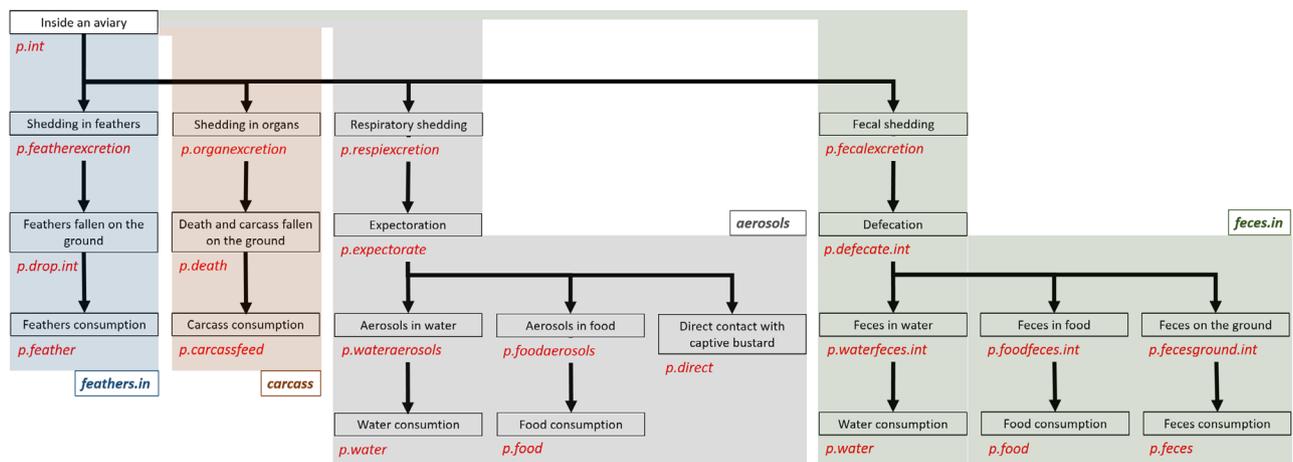
2.2 | Exposure probabilities

All of the probabilities and their definitions are summarised in Table 1.

The overall probability of exposure P_i that we aimed to estimate was the daily probability of exposure to the virus (AIV or NDV) of at least one captive bustard by at least one wild bird of each species i (i = PASDOM, PYCTIS, STRSEN and STRDEC), accounting for all
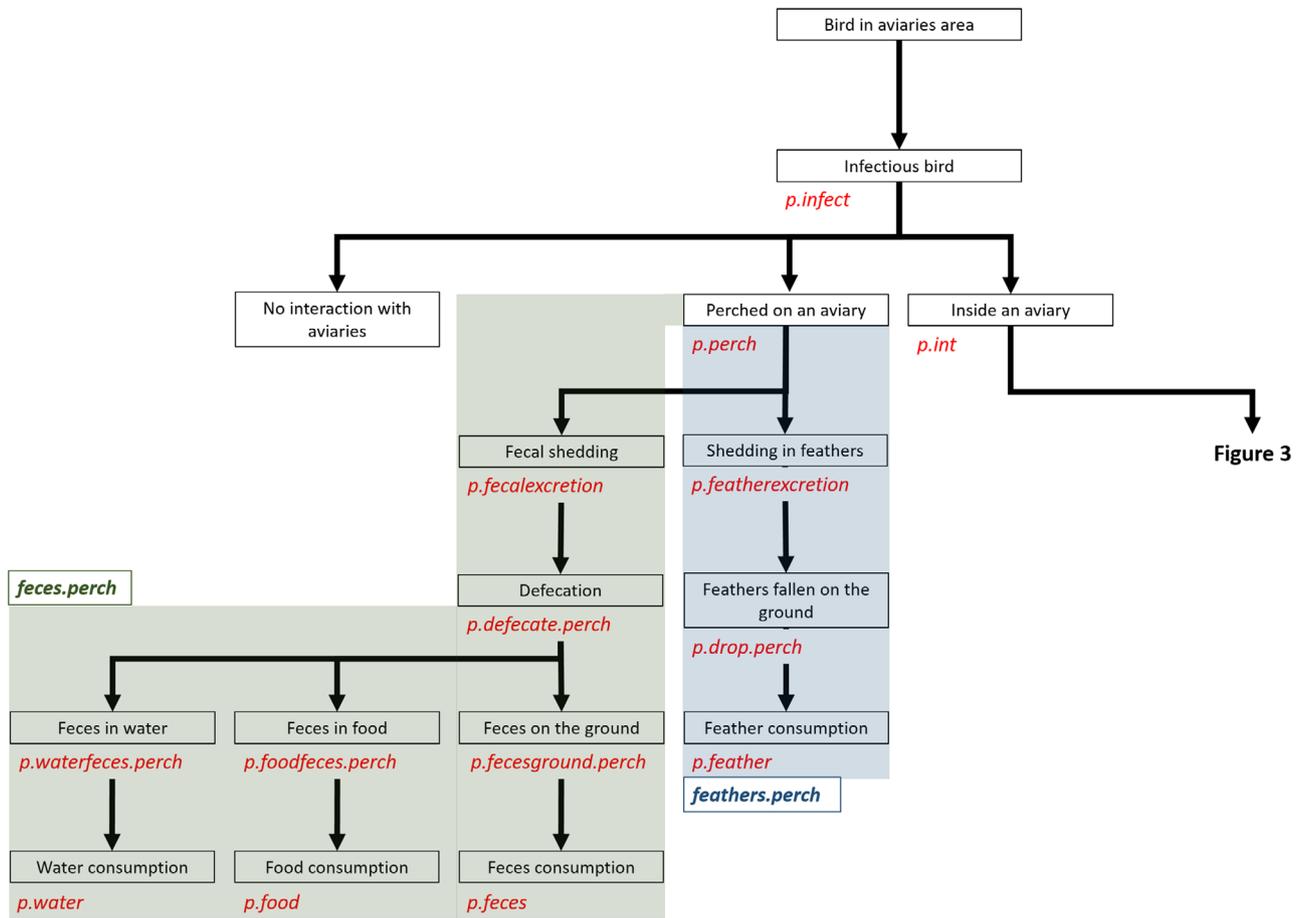
FIGURE 2 Scenario tree representing all of the potential pathways by which at least one captive bustard can be exposed to AIV and NDV by one wild bird. Details of the pathways leading to the exposure of at least one captive bustard by one infectious bird perched on an aviary are presented. Each black rectangle represents an event and each red wording represents the probability of the event to occur (all probabilities are defined in Supporting information Table S1). Dark arrows represent the succession of events. Each coloured block represents a pathway of exposure

FIGURE 3 Scenario tree representing details of the pathways leading to the exposure of at least one captive bustard by one wild bird inside an aviary. Each black rectangle represents an event and each red wording represents the probability of the event to occur (all probabilities are defined in Supporting information Table S1). Dark arrows represent the succession of events. Each coloured block represents a pathway of exposure

TABLE 1 Parameters associated with the events of the scenario trees

Parameter	Definition
n_i	Number of wild birds of species i present in aviaries areas
p.infect$_i$	Daily probability of a bird of species i to be infectious
p.perch$_i$	Daily probability of a bird of species i to be perched on an aviary
p.int$_i$	Daily probability of a bird of species i to get inside an aviary
p.fecalexcretion	Probability of an infectious bird of species i to shed virus through faecal route
p.featherexcretion	Probability of an infectious bird of species i to shed virus in its feathers
p.organexcretion	Probability of an infectious bird of species i to shed virus in its organs
p.respiexcretion	Probability of an infectious bird of species i to shed virus through respiratory route
p.defecate.perch	Probability of an infectious bird of species i to defecate when perched on an aviary
p.defecate.int	Probability of an infectious bird of species i to defecate when inside an aviary
p.drop.perch	Probability of an infectious bird of species i to drop feathers on the ground when perched on an aviary
p.drop.int	Probability of an infectious bird of species i to drop feathers on the ground when inside an aviary
p.death	Probability of an infectious bird of species i to die and of its carcass to rest on the ground when inside an aviary
p.expectorate	Probability of an infectious bird of species i to expectorate
p.waterfeces.perch	Probability of faeces from an infectious bird of species i to contaminate water when perched on an aviary
p.foodfeces.perch	Probability of faeces from an infectious bird of species i to contaminate food when perched on an aviary
p.fecesground.perch	Probability of faeces from an infectious bird of species i to fall on the ground when perched on an aviary
p.waterfeces.int	Probability of faeces from an infectious bird of species i to contaminate water when inside an aviary
p.foodfeces.int	Probability of faeces from an infectious bird of species i to contaminate food when inside an aviary
p.fecesground.int	Probability of faeces from an infectious bird of species i to fall on the ground when inside an aviary
p.wateraerosols	Probability of aerosols from an infectious bird of species i to contaminate water when inside an aviary
p.foodaerosols	Probability of aerosols from an infectious bird of species i to contaminate food when inside an aviary
p.direct	Probability of a least one bustard to be exposed through direct contact with an infectious bird of species i when inside an aviary
p.feather	Probability of at least one bustard to consume feathers on the ground
p.carcassfeed	Probability of at least one bustard to consume a carcass on the ground
p.water	Probability of at least one bustard to consume water
p.food	Probability of at least one bustard to consume food
p.feces	Probability of at least one bustard to consume faeces on the ground

exposure pathways. It was calculated as follows:

$$P_i = 1 - (1 - p_i)^{n_i}$$

with n_i being the number of wild birds of species *i* present in aviaries areas and p_i being the daily probability of exposure to the virus of at least one captive bustard by one wild bird of species *i* present in aviaries areas.

Assuming the exposure pathways are mutually exclusive, p_i was calculated as the sum of the probability of each exposure pathway (*feces.perch, feathers.perch, feathers.in, carcass, aerosols* and *feces.in*) for species *i*. More specifically, p_i was given by:

$$p_i = p.infect_i * (p.perch_i * p_a + p.int_i * p_b)$$

with *p.infect$_i$*, *p.perch$_i$* and *p.int$_i$* being the daily probabilities of a bird of species *i* to be infectious, to be perched on an aviary, and to get inside

an aviary, respectively, and p_a and p_b defined as the probability of exposure of at least one captive bustard by at least one wild bird perched on an aviary, and as the probability of exposure of at least one captive bustard by at least one wild bird inside an aviary, respectively, and given by:

$$p_a = 1 - (1 - p.fecal. perch) * (1 - p.feather.perch)$$

and

$$p_b = 1 - (1 - p.fecal.int) * (1 - p.respi) * (1 - p.feather.int)$$
$$* (1 - p.organ)$$

with probabilities *p.fecal.perch, p.feather.perch, p.fecal.int, p.feather.int, p.respi* and *p.organ* defined in Table 1 and calculated as detailed in the Supporting information.

2.3 | Model calibration

To calibrate the model, we used field observations, a literature review and an elicitation of expert opinion. Table S1 in Supporting information summarizes all of the parameters, their estimation method and the estimated range of values for both AIV and NDV in the four target species.

Briefly, the average daily number of wild birds of species i present in aviaries areas (n_i) was estimated by on-site experts using data from bird censuses in aviaries areas and population size estimates. The probability $p.infect_i$ was estimated from the viroprevalences observed on the field for AIV and NDV (Hirschinger et al, 2019). Probabilities $p.perch_i$ and $p.int_i$ were estimated from bird census in aviaries areas (Hirschinger, 2020).

Probabilities of excretion in the faeces, the feathers, the organs and the aerosols, which contribute to the computation of the above-mentioned probabilities, were estimated from published experimental infections with AIV and NDV on House sparrows and related species and on Feral rock pigeons (*Columba livia)* and related species (Supporting information Table S1). Due to the lack of available data, data on viral excretion in White-eared bulbuls were extrapolated from House sparrows, and in Laughing and Collared doves from Feral rock pigeons.

Probabilities $p.waterfeces.perch$, $p.foodfeces.perch$ and $p.fecesground.perch$ were estimated from the ratio between the surface area of the aviaries and the surface area occupied by water and food dishes.

Finally, we elicited expert opinion to estimate the remaining 17 probabilities using a semi-quantitative approach, as the required detailed information was not available to run a fully quantitative assessment (Fournié et al., 2014). The experts consulted (n = 10) were selected based on their expertise in one or several of the following fields: avian virology, epidemiology of animal diseases, avian medicine or poultry biosecurity. They were asked by email to answer a multiple-choice questionnaire regarding the probability of occurrence of 17 events leading to the release of viruses in the environment of captive birds in this specific outdoor bustards-breeding context (Supporting information Table S2). The response choices for each question consisted of probability intervals. The experts were asked to select all of the probability intervals that were considered as credible for a given event. The final interval that was considered for a given parameter was the concatenation of the smallest number of intervals that were selected by at least 50% of respondents (Supporting information Table S2). Thus, each pathway step was assigned one or more probability categories, by aggregating the opinions of individual experts. The minimum, median and maximum numerical probabilities of these aggregated results were used as model input variables.

The probability $p.infect_i$ was given a beta distribution that was calibrated based on prevalence estimations given in Hirschinger et al. (2019) while $p.perch_i$ and $p.int_i$ were also given beta distributions that were parameterized based on field observations as reported in Hirschinger (2020). Probabilities of excretion were associated with Pert distributions with minimum, mode and maximum values defined by a literature review. When no values were available, they were associated with a uniform distribution from 0 to 1. Finally, all probabilities estimated by the expert opinion elicitation were associated with Pert distributions defined by the lower, the median and the upper value of the concatenated intervals defined by the expert opinion elicitation (Supporting information Table S1).

2.4 | Model run

The distribution of the probabilities P_i was simulated by sampling randomly the parameter values in their corresponding probability distributions (Supporting Information Table S1) and combining them as detailed above. To do so, we ran 100,000 simulations using R software (R Core Team, 2019). Figures were generated using the R software and the libraries *ggplot2* (Wickham H., 2016), *readxl* (Wickham H. and Bryan J., 2019), *stringr* (Wickham H., 2019) and *gridExtra* (Auguie B., 2017).

Pairwise *t*-tests were used to analyze differences between the outcome probabilities, and a *p*-value < .05 was used to determine significance.

2.5 | Sensitivity analysis

Two sensitivity analyses were run to evaluate the effect of individual variations of the parameters calibrated using the expert opinion elicitation on the outputs of the model. The first sensitivity analysis considered the overall daily probabilities Pi to evaluate the effect of the uncertain parameters on the relative contribution of each wild bird species separately. The second considered the probabilities of exposure via the different exposure pathways for the riskiest wild bird species to evaluate the effect of the uncertain parameters on the relative contribution of the exposure pathways for that species. To do so, we changed the value of the uncertain parameters one at a time to their minimal and maximal expected values as presented in Supporting information Table S1. Meanwhile, the other uncertain parameters were set to their median values and those of the other parameters were sampled in their respective distributions as defined in Supporting information Table S1. We used 100,000 iterations for each parameter combination.

3 | RESULTS

3.1 | Probability of exposure

Model results highlighted that the risk of exposure to NDV was on average 1.65 times (95% CI: 1.63–1.66) higher than that of AIV, irrespective of the species. Indeed, the average daily probability of exposure to NDV for at least one captive bustard by at least one wild bird was estimated between $0.9*10^{-3}$ and $92.6*10^{-3}$, while for AIV this probability ranged between $0.3*10^{-3}$ and $58.3*10^{-3}$.

For both viruses, the wild bird species representing the highest mean risk of exposure was the House sparrow (PASDOM). This species was associated with an average daily probability of exposure of at least one captive bustard of $3.8*10^{-2}$ (95% CI: $0.6*10^{-2}$–$13.4*10^{-2}$) and $2.6*10^{-2}$ (95% CI: $0.5*10^{-2}$–$8.4*10^{-2}$) for NDV and AIV, respectively (Figure 4). The risk of exposure to NDV was on average 2.61
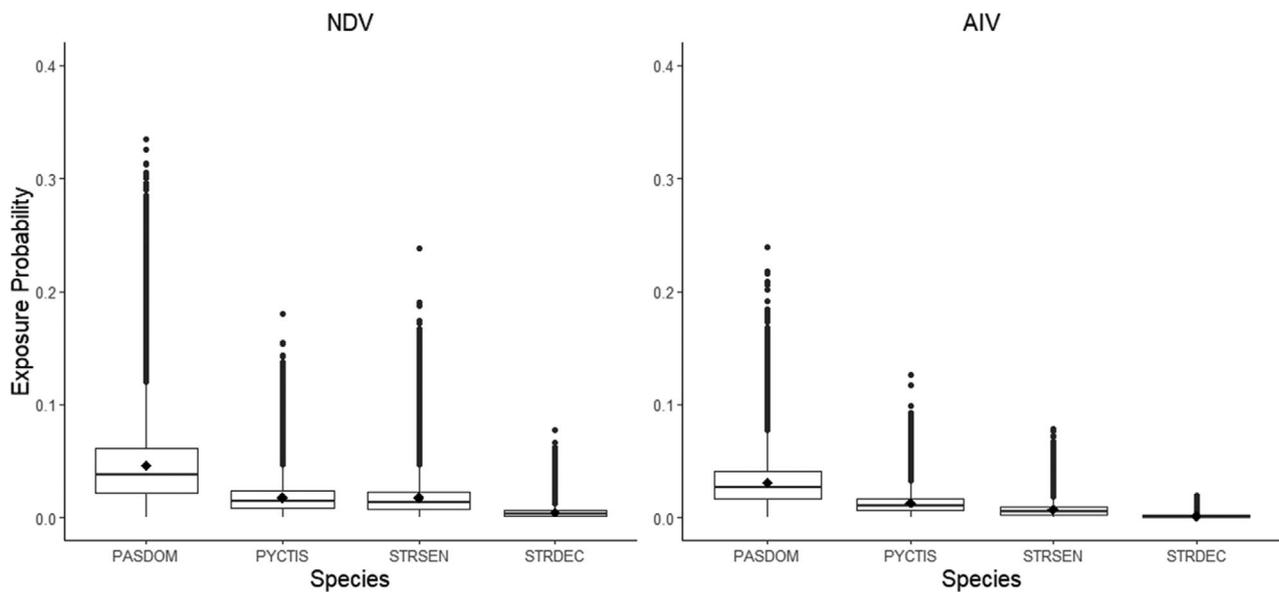
FIGURE 4 Daily probability of exposure to NDV and AIV of at least one captive bustard by one wild bird from the different species. PASDOM = House sparrow, PYCTIS = White-eared bulbul, STRSEN = Laughing dove, STRDEC = Collared dove

(95% CI: 2.59–2.63), 2.63 (95% CI: 2.61–2.65) and 9.72 (95% CI: 9.65–9.78) times lower in White-eared bulbuls, Laughing doves and Collared doves compared to House sparrows, respectively. For AIV, this risk of exposure was on average 2.41 (95% CI: 2.39–2.42), 4.41 (95% CI: 4.38–4.44) and 21.67 (95% CI: 21.53–21.81) times lower in White-eared bulbuls, Laughing doves and Collared doves compared to House sparrows, respectively. Observed inter-species differences were statistically significant (p-value < .001).

3.2 | Pathways of exposure

House sparrows were identified as the riskiest species for exposing captive bustards to both AIV and NDV. For NDV, the pathway of exposure that contributed the most to the risk was the exposure from the aerosols excreted by an infectious bird that got inside the aviary. This pathway was associated with an average daily probability of $1.4*10^{-2}$ (95% CI: $0.4*10^{-2}$–$3.2*10^{-2}$) (Figure 5). The risk of exposure was on average 1.77 (95% CI: 1.76–1.78), 2.90 (95% CI: 2.89–2.92), 2.99 (95% CI: 2.96–3.00), 3.08 (95% CI: 3.07–3.09) and 41.9 (95% CI: 41.7–42.1) times lower through the faeces of an infectious bird inside the aviary, the faeces of an infectious bird perched on the aviary, the feathers of an infectious bird perched on the aviary, the feathers of an infectious bird inside the aviary and the carcass of an infectious bird inside the aviary, respectively. For AIV, the pathway of exposure that contributed the most to the risk was the exposure from the faeces excreted by an infectious bird that got inside the aviary. This pathway was associated with an average daily probability of $1.7*10^{-2}$ (95% CI: $0.5*10^{-2}$–$3.6*10^{-2}$) (Figure 5). The risk of exposure was on average 1.36 (95% CI: 1.35–1.36), 1.64 (95% CI: 1.63–1.65), 2.29 (95% CI: 2.28–2.30), 2.36 (95% CI: 2.36–2.37) and 33.7 (95% CI: 33.6–33.8) times lower through the aerosols of an infectious bird inside the aviary, the faeces
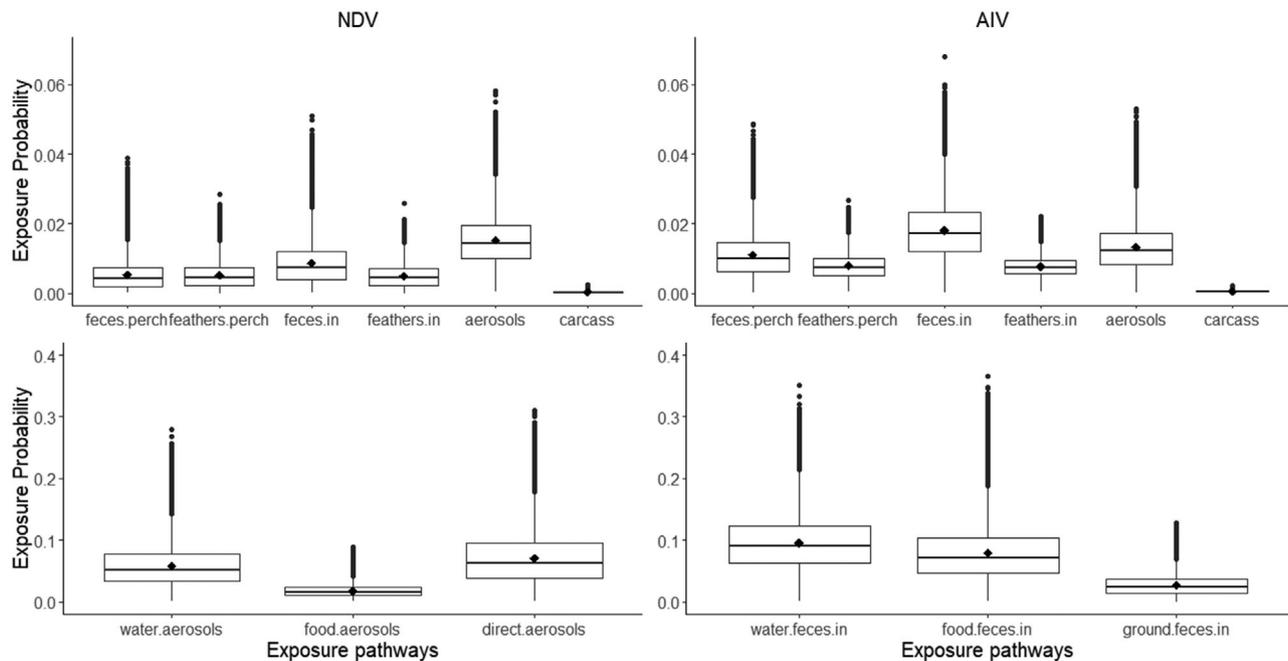
of an infectious bird perched on the aviary, the feathers of an infectious bird perched on the aviary, the feathers of an infectious bird inside the aviary and the carcass of an infectious bird inside the aviary, respectively. Observed differences between pathways were statistically significant (p-value < .001).

Delving more deeply, the pathway that contributed the most to the risk of exposure of a least one captive bustard to NDV was the exposure via direct contact with an infectious bird that got inside the aviary. This pathway was associated with an average daily probability of $7.3*10^{-2}$ (95% CI: $1.5*10^{-2}$–$19.2*10^{-2}$) (Figure 5). The risk of exposure was on average 1.21 (95% CI: 1.20–1.21) and 3.99 (95% CI: 3.97–4.01) times lower through the consumption of contaminated water and the consumption of contaminated food, respectively. For AIV, the pathway that contributed the most to the risk of exposure of a least one captive was the exposure via the consumption of water contaminated by the faeces of an infectious bird that got inside the aviary. This pathway was associated with an average daily probability of $9.1*10^{-2}$ (95% CI: $2.4*10^{-2}$–$19.6*10^{-2}$) (Figure 5). The risk of exposure was on average 1.21 (95% CI: 1.21–1.22) and 3.51 (95% CI: 3.49–3.52) times lower through the consumption of contaminated food and the consumption of faeces on the ground, respectively. Observed differences between pathways were statistically significant (p-value < .001).

For all other species, the pathway of exposure that contributed the most to the risk of exposure of a least one captive bustard to both AIV and NDV was the indirect exposure via the consumption on the ground of faeces excreted by an infectious bird perched on the aviary.

3.3 | Sensitivity analysis

The sensitivity analysis showed that the ranking of species according to their level of exposure risk was not modified when the values of the

FIGURE 5 Daily probability of exposure of at least one captive bustard to NDV and AIV from at least one House sparrow (*Passer domesticus*) according to the different exposure pathways. feces.perch = exposure through the faeces of an infectious bird perched on an aviary, feathers.perch = exposure through the feathers of an infectious bird perched on an aviary, feces.in = exposure through the faeces of an infectious bird inside an aviary, feathers.in = exposure through the feathers of an infectious bird inside an aviary, aerosols = exposure through the aerosols of an infectious bird inside an aviary, carcass exposure through the carcass of an infectious bird inside an aviary, water.feces.in = exposure from consumption of faeces contaminated water, food.feces.in = exposure from consumption of faeces contaminated food, ground.feces.in = exposure from consumption of faeces on the ground, water.aerosols = exposure from consumption of aerosols contaminated water, food.aerosols = exposure from consumption of aerosols contaminated food, direct.aerosols = exposure from direct contact

parameters estimated from experts' opinions varied between the lowest value and the highest. House sparrows remained the species contributing the most to the risk of exposure to both viruses (Supporting information Figures S2 and S3).

Moreover, the analysis showed that the variation of parameters values had little or no effect on the ranking of the pathways of exposure for the riskiest species. Thus, direct exposure from the aerosols of an infectious House sparrow that got inside the aviary contributed the most to the risk of exposure for NDV and indirect exposure from the faeces of an infectious House sparrow that got inside the aviary contributed the most to the risk of exposure for AIV in almost all cases (Supporting information Figures S4 and S5).

Similarly, direct exposure from direct contact and indirect exposure from consumption of contaminated water contributed the most to the risk of exposure in almost all cases for NDV and AIV, respectively (Supporting information Figures S6 and S7).

4 | DISCUSSION

By combining for the very first time several tried-and-tested methods, this study presents a comprehensive risk assessment framework of pathogens exposure from wild to captive birds.

Overall, this analysis highlighted those captive bustards, considering the large captive-bred flock, had a relatively high risk of being exposed to pathogens by wild birds (average daily probability of exposure for at least one captive bustard by at least one wild bird estimated between $0.9*10^{-3}$ and $92.6*10^{-3}$ and between $0.3*10^{-3}$ and $58.3*10^{-3}$ for NDV and AIV, respectively). This risk was higher for Newcastle disease virus than for AIV virus, and House sparrows represented the riskiest species for the transmission of both viruses through direct exposure from direct contact with an infectious bird that got inside the aviary and indirect exposure from consumption of water contaminated from the faeces of an infectious bird that got inside the aviary for NDV and AIV, respectively. Results from the sensitivity analysis strongly suggested robustness to parameter uncertainty.

Exposure probabilities presented in this study are comparatively higher than the ones presented in other studies (Hernández-Jover et al., 2015; Scott et al., 2018). This can likely be explained by the system considered, that is, one in which a strong oasis effect converged with a need for outdoor housing to prepare bustards for release into the wild. Indeed, outdoor breeding is usually considered as a major risk factor for pathogens exposure (Gonzales et al., 2013; Scott et al., 2018; Sims et al., 2016).

As demonstrated in similar studies, direct contact with infectious wild birds and indirect exposure from consumption of contaminated water are the riskiest pathways (Scott et al., 2018; Sims et al., 2016).

Indeed, even if bustards are housed in netted aviaries that protect them from direct contacts, these aviaries are not fully bird proof (e.g., holes in the nets, improper seals of the doors, human mistakes). Thus, some birds (sparrows especially) succeed to enter those aviaries to take advantage of the food and water, putting a risk of direct contact with the bustards as well as a risk of contaminating the food and water.

For this analysis, we had to make several assumptions. First, the estimated exposure probabilities were considered representative of an 'average' AI and ND virus. However, some of the experimental infection studies compiled to extract the probabilities of shedding of the viruses in the different biological matrices ($p.fecalexcretion$, $p.featherexcretion$, $p.respiexcretion$, $p.organexcretion$) mentioned important variations in shedding according to the strain considered (sub-type, pathogenicity) (Hayashi et al., 2011; Hiono et al., 2016; Isoda et al., 2006; Jia et al., 2008; Shriner et al., 2016; Susta et al., 2018; Xiang et al., 2017). Considering the diversity of AIV and NDV would sharpen the analysis. This holds particularly true with regard to AIV, as shedding probabilities in feathers and organs are likely to vary according to the pathogenicity of the strain considered. This is because only highly pathogenic strains present a systemic replication whereas low pathogenic strains are restricted to the digestive and respiratory tracts (Swayne et al., 2017).

In this analysis, we can consider that data from the field are more likely related to low pathogenic viruses, at least for AIV (absence of clinical signs, viral loads below the detection limit and low seroprevalence) (Hirschinger et al., 2019). In contrast, most of the data from the literature are related logically to highly pathogenic viruses. Finally, data drawn from experts' opinions depend greatly on the field of expertise of each expert, but a bias toward highly pathogenic viruses may be assumed. Therefore, it would be interesting to conduct separate analyses of low and highly pathogenic viruses. Ideally, the analysis would target strains circulating in the UAE.

Moreover, the viral load excreted often depends on the inoculated one (Abolnik et al., 2018; J. D. Brown et al., 2009; Kapczynski et al., 2006), and the viral loads used in experimental infections are usually higher than the ones faced by birds in the wild. Therefore, we may have overestimated shedding probabilities in our epidemiological context and artificially increased the exposure risk. The extrapolation of shedding data from related species, although justified in our case, also may represent an important limitation for this analysis as some studies mentioned important shedding variations according to the infected species, even with regard to closely related species (Ayala et al., 2019; Carrasco et al., 2008; Dortmans et al., 2011; Nemeth et al., 2010).

The estimation of virus excretion in the environment based on expert's elicitation may be considered to be subjective. However, the sensitivity analysis showed that neither the rank of the species nor the rank of the pathways of exposure was significantly modified when the input values of these parameters were varied along with their estimated intervals, suggesting these estimates were realistic.

Overall, the outcomes of the analysis seem trustworthy and show a high exposure risk from wild birds to captive bustards. However, despite this large exposure probability, the real number of captive bustards clinically infected by AIV or NDV is very low (Hirschinger, 2020).

We ended this analysis at the exposure step, but exposure does not lead inevitably to infection. To assess the risk of infection, one should consider a probability of transmission (i.e., pathogen passing from contaminated matrix to bustard) and a probability of infection (i.e., effective spread of the pathogen in the organism after transmission). The limited number of diseased captive bustards may simply be the result of the efficient vaccine protection set up (inactivated vaccine against LP and HPAIV plus inactivated vaccine against NDV with a first shot at 10 days old, a first booster at 30 days old, then booster every year). It also may be due to the limited efficiency of the transmission and infection since morbidity, mortality and seroprevalence rates are very low even in sentinel bustards (non-vaccinated birds) (Hirschinger, 2020). This result suggests that even with a strong exposure pressure, contamination is limited.

Several explanations are worth considering. First, environmental and climatic conditions are clearly unfavourable to the environmental persistence of the viruses (high temperatures, low humidity, high UV index) and likely prevent the contamination of bustards (Stallknecht & Brown J., 2009). We can also assume a limited susceptibility of bustards for the strains carried by wild birds, but this hypothesis seems unlikely as shared strains have already been highlighted (Hirschinger et al., 2019). Nevertheless, in the case of the circulation of a highly pathogenic strain in wild birds, exposure probabilities suggest that an outbreak in captive bustards is of real concern.

Overall, the absolute values presented in this analysis may only have a relative significance because they are directly associated with a specific epidemiologic context. However, they are of great interest for the sanitary management of the breeding site presented in this study, allowing a hierarchization of risk levels between viruses, species and pathways of exposure. Specifically, this study has made it possible to target House sparrows for sanitary surveillance of AIV and NDV, and direct contacts and water contamination by wild birds' faeces appear as priority targets for sanitary control. For example, improvement of protection from wild birds using nets with smaller meshing and use of covered feeders may reduce contacts.

Like previous studies on the role of some peridomestic species in the transmission of AIV and NDV (Abolnik, 2014; Nemeth et al., 2010, 2013), some of them being experimental ones, this analysis reveals that, on the field, also in this specific environmental context, wild peridomestic birds especially House sparrow should not be neglected. This result is of great importance considering the existence of numerous conservation breedings and private collections in the Arabian peninsula.

These results also confirm the importance of known pathways of exposure for outdoor poultry (direct contacts and faeces-contaminated water) and reaffirm the need to implement sanitary measures to limit exposure of captive birds to wild birds. Considering the global development of agroforestry and free-range breeding (Jose, 2012; Miao et al., 2005), these results are of great interest.

They also highlight the need for further research dedicated to the pathogens circulating in the Middle East and to the role of poultry farms as a reservoir of pathogens for wild birds. Finally, despite the current uncertainties associated with probabilities, this study offers an

efficient tool that may be used by decision-makers to implement a sanitary management strategy.

To conclude, such a risk assessment, based on the best data available with the use of a multimodal approach merging ecological, epidemiological and virological data, although resource and time-consuming, appears to be the most appropriate approach to assess the risk of pathogen exposure at the interface between wildlife and domestic animals.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supplementary Materials of this article.

ETHICS

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. All birds used in this study have been captured, handled and sampled by skilled ornithologists graduated from the Centre de Recherches par le Baguage des Populations d'Oiseaux (CRBPO, Natural History Museum Paris) and trained veterinarians from the NARC according to international ethical standards (Fair, J., E. Paul, and J.Jones, Eds. 2010. Guidelines to the Use of Wild Birds in Research. Washington, D .C.: Ornithological Council).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.