Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

# Disentangling wildlife–cattle interactions in multi-host tuberculosis scenarios: systematic review and meta-analysis

Eduardo M. FERREIRA* *MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE – Global Change and Sustainability Institute, University of Évora, Mitra, 7006-554 Évora, Portugal and IIFA – Institute for Advanced Studies and Research, University of Évora, Palácio do Vimioso, Largo Marquês de Marialva, 7002-554 Évora, Portugal and Conservation Biology Lab, Department of Biology, University of Évora, Évora, Portugal. Email: ferreiraeduardo.mr@gmail.com*
Elsa L. DUARTE *MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE – Global Change and Sustainability Institute, University of Évora, Mitra, 7006-554 Évora, Portugal. Email: emld@uevora.pt*
Mónica V. CUNHA *cE3c-Centre for Ecology, Evolution and Environmental Changes & CHANGE – Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal and Biosystems & Integrative Sciences Institute (BioISI), Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal. Email: mscunha@fc.ul.pt*
António MIRA *MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE – Global Change and Sustainability Institute, University of Évora, Mitra, 7006-554 Évora, Portugal and Conservation Biology Lab, Department of Biology, University of Évora, Évora, Portugal. Email: amira@uevora.pt*
Sara M. SANTOS *MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE – Global Change and Sustainability Institute, University of Évora, Mitra, 7006-554 Évora, Portugal and IIFA – Institute for Advanced Studies and Research, University of Évora, Palácio do Vimioso, Largo Marquês de Marialva, 7002-554 Évora, Portugal and Conservation Biology Lab, Department of Biology, University of Évora, Évora, Portugal. Email: smsantos@uevora.pt*

**Keywords**
bovine TB *Mycobacterium bovis* transmission, camera-trapping, Global Positioning System (GPS) collars, multi-host pathogens, proximity loggers, wildlife–livestock interface, wild mammals

*Correspondence

Received: 10 January 2023
Accepted: 12 June 2023
Editor: DR

doi: 10.1111/mam.12324

## ABSTRACT

1. Ecological interactions involving wildlife (wild mammals) and cattle *Bos taurus* are considered fundamental drivers of animal tuberculosis (TB) caused by *Mycobacterium bovis* at the wildlife–livestock interface. Despite recent insights about the role of direct and indirect interactions on TB dynamics, a mechanistic evaluation of studies addressing patterns of wildlife–cattle interaction at the global level is lacking, and the most likely factors explaining interaction rates under different epidemiological scenarios remain poorly understood.
2. We began by reviewing the main criteria used to define a wildlife–cattle interaction relevant to *Mycobacterium bovis* transmission under different methodological approaches (camera-trapping, proximity loggers and Global Positioning System collars). Secondly, we applied a generic framework to estimate and characterise interaction patterns between susceptible wildlife and cattle hosts worldwide, testing the effect of potential ecological and methodological factors on interaction rates.
3. We synthesise two main criteria to define direct interactions and five criteria to define indirect interactions between wildlife and cattle. Using data from 31 studies, our meta-analysis showed that wildlife–cattle direct interaction rates were low (mean = 0.03 interactions/month per species pair, range: 0.00–0.12). In contrast, indirect interaction rates were 154 times higher than the

mean of direct interaction rates (mean = 4.63 interactions/month per species pair, range: 0.16–30.00).

4. To prevent TB transmission to cattle, attention should be given to indirect interactions between wildlife and cattle in shared environments. Indirect interactions significantly increase with increasing wildlife density, which, hypothetically, could result in a higher TB transmission risk for cattle. We outline recommendations to achieve harmonised integration and comparison of results in future studies. Consolidation of knowledge in this field will contribute towards guiding control and biosecurity measures, also applicable to other infectious diseases at the wildlife, domestic species and human interfaces.

## INTRODUCTION

The emergence of infectious diseases at the wildlife–livestock–human interfaces has become a significant concern worldwide (Alexander et al. 2018, White & Razgour 2020, Hassell et al. 2021). Animal tuberculosis (TB), caused by *Mycobacterium bovis*, a member of the *Mycobacterium tuberculosis* complex, is among the most widespread zoonotic diseases (Palmer et al. 2012, Fitzgerald & Kaneene 2013). Interspecific transmission of this pathogen occurs in complex socio-ecological contexts, potentially affecting humans, livestock and a wide range of wildlife (wild mammal) species (Duarte et al. 2008, Palmer et al. 2012, Gortázar et al. 2015), with economic, animal and public health implications (Cunha et al. 2011, Palmer et al. 2012, Hardstaff et al. 2014). Despite considerable efforts and long-standing programmes to control TB in livestock, eradication has not yet been achieved in many countries (Cunha et al. 2012, Pereira et al. 2020, Ramos et al. 2020). Wildlife reservoir hosts are considered to be the main obstacle to eradication worldwide (Palmer 2013, Gortázar et al. 2015), with recent data evidencing a high TB burden in non-bovine hosts (Santos et al. 2020). *Mycobacterium bovis* infection is maintained within intra- and interspecific wildlife populations, contributing to the geographical expansion of animal TB and *Mycobacterium bovis* dissemination to other species, and thus increasing the risk of spill-back to livestock under extensive husbandry (Duarte et al. 2008, Santos et al. 2012, Fitzgerald & Kaneene 2013, Van Tonder et al. 2021). In this context, spatial–temporal interactions between (and within) wildlife species and livestock have been recognised as a central driver of inter-specific transmission (Kukielka et al. 2013, Barasona et al. 2014, Cowie et al. 2016, Wilber et al. 2019).

*Mycobacterium bovis* transmission between individuals can occur either through direct host-to-host interaction or through indirect interaction via contaminated environments and asynchronous space-use overlap (Humblet et al. 2009, Fitzgerald & Kaneene 2013, Pereira et al. 2020). Historically, *Mycobacterium bovis* transmission was believed to occur primarily through aerosols during direct interactions that require close proximity or physical contact between infected and susceptible hosts (Morris et al. 1994, Palmer et al. 2012). However, recent studies focusing on spatial ecology of wildlife and livestock suggest that this mode of transmission is infrequent, even rare, in different epidemiological scenarios. Direct interactions between wildlife and cattle *Bos taurus* have been infrequently documented in England (e.g. badger *Meles meles* as a case study; Drewe et al. 2013, Woodroffe et al. 2016), in North America (e.g. white-tailed deer *Odocoileus virginianus* as a case study; Lavelle et al. 2016) and even in the Iberian Peninsula (Kukielka et al. 2013, Cowie et al. 2016) where TB is maintained in a multi-host system (Cunha et al. 2011, Santos et al. 2012, Reis et al. 2021). Even if direct interactions are infrequent, they should be considered in disease dynamics because, when occurring, they increase the risk of disease transmission (Wilber et al. 2019).

High rates of indirect interactions have been reported in Spain, France and the USA, involving ungulate reservoir hosts (e.g. red deer *Cervus elaphus*, wild boar *Sus scrofa* and white-tailed deer) and suspected spillover hosts (e.g. red fox *Vulpes vulpes*), where farming typically occurs close to wildlife habitats (Barasona et al. 2016, Payne et al. 2016, Wilber et al. 2019, Martínez-Guijosa et al. 2021). Indirect transmission can take place via shared space use at different times and common exposure to an infectious off-host environment. Inter-species transmission may occur when livestock or wildlife come into contact with *Mycobacterium bovis*-contaminated fomites, such as badger latrines (e.g. Drewe et al. 2013, Campbell et al. 2019), although the use by wildlife of farm and cattle-related resources, such as food and water sites, seems to be more frequent (Carrasco-Garcia et al. 2016, Payne et al. 2016, Balseiro et al. 2019, Campbell et al. 2019). This mode of transmission might be particularly relevant in agroforestry and pastoral landscapes, where abundant wildlife occurs in sympatry with extensively reared livestock (Payne et al. 2017, Caron et al. 2021), or has access to potentially contaminated farm resources (Tolhurst et al. 2009, Campbell et al. 2019). Mycobacteria are considerably resistant to adverse environmental conditions (Fine et al.

2011, Allen et al. 2021), and widespread bacterial contamination can occur at different sites (e.g. water sites; Santos et al. 2015, Barasona et al. 2016) used by a variety of hosts, therefore, increasing transmission risk in shared environments.

Despite recent insights about the role of direct and indirect interactions on TB dynamics (Gortázar et al. 2015, Wilber et al. 2019), differences in interaction patterns derived from multiple studies hamper inferences on the underlying transmission processes. Interaction type and frequency may vary according to host species (White et al. 2018a, Wilber et al. 2019). Depending on their behavioural and ecological traits, different species, and even individuals of the same species, could contribute differently to epidemiologically meaningful interactions (Craft 2015, Silk et al. 2017, Triguero-Ocaña et al. 2020). In turn, species' traits considered relevant for disease dynamics (e.g. social behaviour and habitat selection) are shaped by environmental factors, such as resource availability and landscape patterns (Morris et al. 2016, Albery et al. 2021, Triguero-Ocaña et al. 2021).

Also, the different methods employed to study host interactions in TB epidemiology raise several issues (Bacigalupo et al. 2020). Technology-based approaches applied to this theme range from non-invasive and cost-effective methods, such as camera-trapping (e.g. Barasona et al. 2013, Kukielka et al. 2013), to proximity loggers that enable researchers to record animals' social interactions (Wilber et al. 2019). Additionally, the use of high-resolution Global Positioning System (GPS)-tracking devices capable of co-locating individuals at fine spatial–temporal scales has been reported as being useful (e.g. Triguero-Ocaña et al. 2019), although their use requires animal capture and handling (Barasona et al. 2014). Those methods tend to provide information at distinct spatial and temporal resolutions, wherein standardisation of experimental approaches (within and between methods) is significantly lacking. Furthermore, criteria used to define and evaluate animal interactions vary widely and need harmonisation (Bacigalupo et al. 2020), as different methodologies and study goals may lead to different research outputs. This poses significant constrains for comparisons of research results, thus hampering inferences on global transmission pathways and on wildlife hosts' relative importance in TB dynamics. Despite recent improvements in this direction (see Bacigalupo et al. 2020), generic mechanistic evaluations to characterise animal interactions at the wildlife–cattle interface on a global level remain a key challenge in TB epidemiology. Specifically, to date, a comprehensive comparison between studies addressing the type and frequency of interactions between wildlife hosts of *Mycobacterium bovis* and cattle has not been attempted. Moreover, obtaining estimates of wildlife–cattle interaction rates would allow us to identify the factors that are most likely to be responsible for variation in interaction patterns, an aspect that, until now, has not been assessed.

We systematically review the main criteria used to define wildlife–cattle interactions relevant to *Mycobacterium bovis* transmission and examine the main interaction patterns between *Mycobacterium bovis's* wild mammal hosts and cattle worldwide. Specifically, we aimed to: 1) synthetise the main criteria used to define wildlife–cattle interactions relevant to TB epidemiology; 2) assess the geographical and temporal trends of the studies addressing wildlife–cattle interactions; 3) assess the most frequent host species and the methods used in studies addressing wildlife–cattle interactions; 4) quantify rates of direct and indirect wildlife–cattle interactions; and 5) identify which factors influence interaction rates.

Based on our findings, we propose recommendations for future studies that will enable an improved integration and comparison of interaction results across studies. This knowledge is key for quantifying the overall relative importance of direct and indirect transmission routes and the ecological mechanisms underlying TB epidemiology at the wildlife–cattle interface on a broad scale.

## MATERIALS AND METHODS

### Literature search

A literature search was conducted through the ISI's Web of Science focusing on all English language published studies (with no year restrictions) and following the PRISMA (preferred reported items for systematic reviews and meta-analyses; Moher et al. 2009) statement. The query used was as follows: ((*Mycobacterium bovis* OR tuberculosis OR TB) AND (interactions OR contact OR movement OR visit OR spatial ecology) AND (Wildlife)), retrieving 381 studies (Appendix S1). Additionally, we examined the reference list of a systematic review on a similar topic (Dougherty et al. 2018), yielding 70 further studies. This initial list was then expanded by adopting a 'snowball' approach (e.g. Prugh & Sivy 2020), where relevant literature cited there was scanned, yielding 28 additional studies (Appendix S1). The result was 479 studies in total. Our final search took place on 13 August 2020. Although the terms 'interaction' and 'contact' are used as synonyms in TB related literature, we chose to use 'interaction' throughout the text for consistency.

### Inclusion and exclusion criteria

After removing duplicates ($n = 31$), the titles and abstracts of the remaining 448 studies were screened for study goals, target species, region, methods and TB context to meet our research goals (screening stage). This resulted in the selection of 128 relevant studies that were afterwards fully examined by one person. Hereafter, two distinct frameworks of inclusion/exclusion criteria were conducted, producing two datasets. For the systematic review of criteria defining an interaction (objective 1), we specifically focused on peer-reviewed studies that: 1) assessed interaction patterns between *Mycobacterium bovis's* wildlife hosts and cattle, and 2) included a definition of interaction by the authors in the context of TB transmission (Criteria Dataset including 13 studies; Appendix S1).

For the analysis of the interaction patterns (objectives 2–5), we examined the bulk of studies identified in the screening stage ($n=128$). Studies that explicitly investigated interaction patterns between wildlife and cattle were retained. Moreover, we included studies that, despite not addressing ecological interactions or where the authors adopted different terminologies (e.g. visit, spatial occurrence), still provided informative spatial–temporal metrics regarding shared space use at the wildlife–cattle interface. Only studies using technology-based methods such as remote cameras (hereafter termed as camera-trapping), proximity loggers and GPS tracking devices, which focused on *Mycobacterium bovis* wildlife hosts, were included. Exclusion criteria were as follows: 1) studies neither applicable to the animal TB context nor focusing on wildlife hosts; 2) experimental studies (e.g. not free-ranging animals and animal translocations) or studies not based on technological methods (e.g. observational studies and questionnaires); 3) studies not reporting raw counts or means of interactions; and 4) studies based on the same data as other studies already included in the dataset (Patterns Dataset including 31 studies; Appendix S1).

## Data extraction

For each study included in the systematic review of interaction definitions (Criteria Dataset), the following information was recorded: first author, year of publication, continent, country where the study took place, year of publication, method, wildlife host(s), criteria defining interactions and type of interaction evaluated. For each study included in the meta-analysis of interaction patterns (Patterns Dataset), the following data were extracted: first author, year of publication, continent, country where the study took place, wildlife species and study period. Additionally, data regarding 10 predictors that could potentially explain variation in interaction patterns were extracted: species pair (wildlife host species – cattle), host taxonomic family, host type (reservoir vs. susceptible), method (camera-trapping, GPS collars and proximity loggers), dominant habitat, study area range, farm size, number of farms, cattle density and wildlife density (Appendix S2).

## Calculation of interaction rates

Raw counts and means (e.g. daily/weekly means) of wildlife–cattle interactions and presence/absence of interactions (when exact quantification was unavailable) were extracted. Each observation in our Patterns Dataset corresponded to a particular species pair, that is, to a potential interaction (≥0) between one wildlife host species and cattle. Whenever a study reported results on interaction values for multiple wildlife species or for different landscapes that study contributed with more than one observation in the dataset. Interaction values for each species pair were standardised to allow data comparisons. For each species pair combination, the number of interactions per month (*RatesInt*) was calculated as a function of reported number of interactions (nr of interactions), sampling effort (sampEffort) and study period in months (time) as:

$$\mathit{RatesInt} = \text{nr of interactions}/\text{sampEffort}^{*}\ \text{time}.$$

*RatesInt* was calculated separately for direct and indirect interactions. Since the experimental design of the studies in the review varied according to the methods used to assess wildlife–cattle interactions, sampEffort corresponds to different quantifications of observation effort: 1) the number of monitoring points (direct and indirect interactions with camera-trapping); 2) the number of collared individuals, including wildlife and cattle (direct interactions with proximity loggers and indirect interactions with GPS collars); 3) the mean number of collared individuals (including wildlife and cattle) plus the number of monitoring points (indirect interactions with proximity loggers); or 4) the mean number of collared wild individuals plus the number of monitoring points (indirect interactions through environment with GPS collars). Monitoring points are defined as potential fomites sites with high-frequency use by wildlife and/or cattle (badger latrines, water sites and cattle feeding sites), as defined *a priori* in each study, more frequently in studies using camera-trapping and proximity loggers.

We also included interaction measurements estimated directly from embedded Figures (eight observations from two studies; potential reading error standard deviation ± two interactions) and considered the studies that only provided the number of days with occurrence of interactions as a proxy to the number of interactions (17 indirect observations from 5 studies). To assess the potential effect of pooling these observations on the *RatesInt*, we applied generalised linear models (GLMs) using data source as a predictor (numbers of interactions reported by authors vs. numbers estimated from Figures and proxies). No significant differences between direct and indirect *RatesInt* obtained from authors' values and estimates were recorded (direct GLM: coefficient –

coef = 0.015, 95% confidence intervals – CI 95% [−0.186; 0.216]; indirect GLM: coef = −0.363, CI 95% [−0.925; 0.200]). We also performed GLM models to inspect variation on *RatesInt* between methods (direct *RatesInt*: camera-trapping and proximity loggers; indirect *RatesInt*: camera-trapping, GPS collars and proximity loggers). No differences in *RatesInt* between methods were observed, either for direct interactions (coef = 0.094, CI 95% [−0.046; 0.234]) or for indirect interactions (coef = −1.040, CI 95% [−3.361; 1.281]; coef = −1.530, CI 95% [−6.014; 2.955]). Therefore, all observations were pooled in further analyses.

## Statistical analyses of factors influencing patterns of interaction rates

A meta-analysis was conducted to identify factors influencing estimated interaction rates. We used general linear mixed models (GLMMs) with study identification number as a random effect to account for dependence among observations (e.g. multiple observations from the same study) and detectability artefacts inherent to each study design. For direct interactions, we used the binomial family, with presence/absence of interactions as the response variable (function glmer, R package 'lme4'; Bates et al. 2015); for indirect interactions, the response variable was *RatesInt* and models were fitted with a Gaussian family (function lme, R package 'nlme'; Pinheiro et al. 2018). However, if a likelihood ratio test between a GLMM and a corresponding reduced model (without random structure) showed no improvement by adding a random effect, we opted for GLMs (Zuur et al. 2009). Host species, taxonomic family (those with high numbers of observations), host type (reservoir/susceptible host), dominant habitat, study area range, farm size, number of farms, cattle density and wildlife density were tested as predictors (Appendix S3). Numeric predictors with skewed distributions were transformed (square root/logarithmic) to reach normality and reduce the influence of outliers (Zuur et al. 2009).

The number of observations (<25) in the Patterns Dataset was insufficient for building models with multiple predictors and for multi-model inference (Jenkins & Quintana-Ascencio 2020). Thus, univariate models were applied, testing one predictor at a time, ensuring a plausible number of observations to explore data patterns adequately in the context of mixed-regression analysis (Zuur et al. 2009, Jenkins & Quintana-Ascencio 2020). Fitted univariate models were compared with their corresponding null models using AICc, Akaike's Information Criterion adjusted for small sample sizes (Burnham & Anderson 2002). A statistically informative model was considered when: 1) a delta AIC ($\Delta$AICc) > 2 was obtained between the null model and the model testing one predictor; and 2) the 95% confidence intervals (CI 95%) of predictor coefficients (coef) did not include zero (Burnham & Anderson 2002, Zuur et al. 2009). Only models with $\Delta$AICc >2 were considered for discussion in this study.

# RESULTS

## Review of criteria used to define wildlife–cattle interactions relevant to TB transmission risk

Considering the 128 eligible studies, only 10% (*n* = 13; Criteria Dataset) stated the criteria used to define a wildlife–cattle interaction. Among these, seven studies investigated and defined both direct and indirect interactions, whereas five studies were focused exclusively on direct interactions and one study only on indirect interactions (Appendix S4). We summarised two criteria used to define direct interactions between wildlife and cattle (using data obtained from camera-trapping and proximity loggers) and five main criteria to define indirect interactions (through camera-trapping, proximity loggers and GPS collars; Table 1).

### DIRECT INTERACTIONS

To assess direct interactions that could potentially increase *Mycobacterium bovis* transmission risk between wildlife and cattle, researchers reported the simultaneous presence of two individuals at a given time at a specific location (Table 1). A first criterion identified was related to data from proximity loggers (Appendix S4). Proximity loggers deployed on animals automatically record contact frequency and duration of contact between devices (Woodroffe et al. 2016). Accordingly, a direct interaction is defined (first criterion) when two collared animals (wildlife and cattle) come within a predefined short distance of one another (up to 20 metres, but most often set up to 1.5–2 metres), triggering a contact (Böhm et al. 2009, Drewe et al. 2013, Triguero-Ocaña et al. 2020). These events are considered direct interactions since short distances detected by loggers are likely to be epidemiologically meaningful due to possible aerosol transmission of *Mycobacterium bovis* (Sauter & Morris 1995). A second criterion to generate disease-relevant interactions involved the use of camera-trapping: infrared motion-triggered cameras are deployed near key resources (e.g. water sites and cattle feeding sites) used by wildlife and/or cattle, where *Mycobacterium bovis* contaminated fomites could endure (Campbell et al. 2019). Cameras are set up to operate 24 h a day, recording multiple and successive images (Kukielka et al. 2013) or short videos (Payne

**Table 1.** Synthesis of the main criteria used to define a wildlife–cattle interaction in the context of tuberculosis transmission, according to the interaction type (direct and indirect) and method (camera-trapping, proximity loggers and global positioning system [GPS] collars). Monitoring points are potential fomites sites with high use frequency by wildlife and/or cattle (badger latrines, water sites and cattle feeding sites), as defined *a priori* in each study

| Method | Direct interaction | Indirect interaction |
|---|---|---|
| Camera-trapping | When two individuals of different species (wildlife and cattle) are recorded in the same images or video (in some cases including only individuals within a pre-established close distance or making physical contact). | When two animals of different species (wildlife and cattle) are recorded in the same monitoring point within a critical time window (CTW).<br>When a wildlife species occurs at a monitoring point. |
| Proximity loggers | When two collared animals of different species establish a contact within a pre-defined proximity (frequently set up to 1.5–2 m) at a given time. | When two collared animals of different species contact a base station deployed at a potential fomites site within a given critical time window (CTW) or spatial-time window (STW).<br>When a collared animal contacts a base station deployed at potential fomites site. |
| GPS collars | | When a pair of spatial locations of wildlife and cattle fall within a pre-defined spatial–temporal window (STW). |

et al. 2016). The simultaneous presence of cattle and wildlife in the same images or video (in some cases including only individuals within a pre-established close distance or making physical contact) is defined as a direct interaction (Tolhurst et al. 2009, 2011, Barasona et al. 2016). Overall, these recorded events are assumed as proxies of closeness between species, possibly leading to an infected and a susceptible host physically interacting with one another within the same time and space frame.

### INDIRECT INTERACTIONS

Proximity loggers combined with base stations (static devices in the field that record connections to the loggers) deployed at key resources (e.g. food sites) have also been used to evaluate indirect wildlife–cattle interactions. An indirect interaction (first criterion) via environment is defined when two collared individuals (wildlife and cattle) contact a base station at different times but within a pre-established critical time window (CTW) or spatial temporal window (STW; Table 1; Appendix S4). The CTW and STW are chosen according to *Mycobacterium bovis's* environmental survival time and device specificities (e.g. positional error; Cowie et al. 2016, Lavelle et al. 2016, Wilber et al. 2019, Triguero-Ocaña et al. 2020). A second criterion defining indirect interaction through proximity loggers was implemented by Drewe et al. (2013). They defined an indirect interaction after a collared animal (wildlife or cattle) contacted a base station specifically deployed at a site that was potentially contaminated with *Mycobacterium bovis* (e.g. a badger latrine), regardless of sequential use by other animals.

For studies using camera-trapping, there are two main criteria to define an indirect wildlife–cattle interaction. One study – focused on the multi-host ungulate community in Spain – defined an indirect interaction as the occurrence of wildlife and cattle at the same monitoring point at different times, but within a CTW that was consistent with *Mycobacterium bovis's* environmental survival (Kukielka et al. 2013). A second criterion, defined as the simple occurrence (often called a 'visit') of a wildlife species at a site used by cattle (farm building and pastures), was implemented by Payne et al. (2016) in a TB-infected area in France.

Despite providing high-resolution spatial–temporal data on animal locations, GPS collars were used exclusively to assess indirect patterns of wildlife–cattle interactions within a TB hotspot area. A single criterion to define an indirect interaction was identified in two studies, both conducted in the same multi-host system in Mediterranean Spain (Triguero-Ocaña et al. 2019, 2020). An indirect interaction was defined when a given pair of GPS spatial locations of wildlife and cattle fell within a pre-defined STW, related to the mean positioning error of the GPS devices and the time lag between successive spatial locations. In contrast to camera-trapping and proximity loggers, indirect interaction events from GPS data are registered independently of potential fomites sites (e.g. water and food sites) under monitoring.

## Global patterns of wildlife–cattle interactions

### GENERAL SCOPE AND GEOGRAPHIC AND TEMPORAL TRENDS OF THE STUDIES

A total of 31 studies on wildlife–cattle interactions concerning animal TB epidemiology (Patterns Dataset) were scrutinised (Appendix S5). Most studies were conducted in Europe (84%; $n=26$), with the highest percentage in England (34%; $n=11$) and Spain (25%; $n=8$), followed by Northern Ireland (9%; $n=3$), France (6%; $n=2$), Ireland

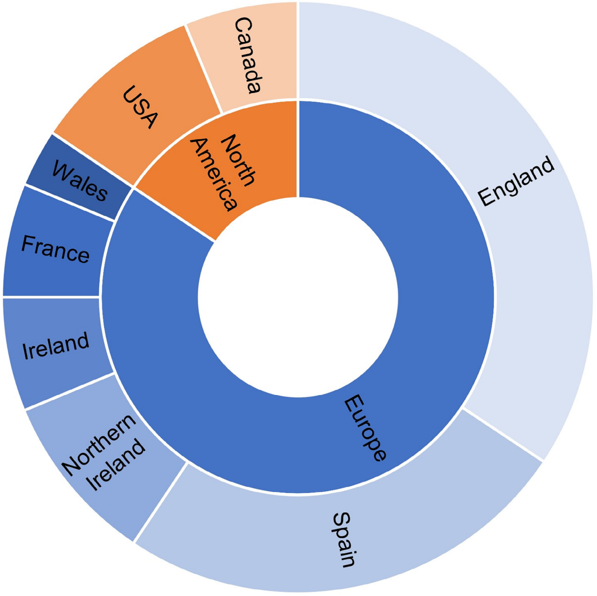

**Fig. 1.** Locations of study sites used in research included in the meta-analysis of wildlife–cattle interactions and tuberculosis ($n=31$ studies): continent (inner circle) and country (outer circle).

(6%; $n=2$) and Wales (3%; $n=1$; Fig. 1). The few studies from North America (16%; $n=5$) were from the USA (9%; $n=3$) and Canada (6%; $n=2$). All studies are relatively recent ranging between 2002 and 2020 (Fig. 2). A growing number of studies was recorded since 2008 with a peak in 2016, slightly decreasing thereafter. Overall, the studies covered a wide range of *Mycobacterium bovis* wildlife hosts. Four wildlife species were described as reservoirs depending on the ecosystem: European badger, wild boar, red deer and white-tailed deer; while another six, comprising red fox, roe deer *Capreolus capreolus*, raccoon *Procyon lotor*, fallow deer *Dama dama*, opossum *Didelphis virginiana* and wapiti *Cervus elaphus canadensis*, were defined as susceptible spillover hosts (Fig. 3). A significant percentage of the studies (42%; $n=13$) addressed multiple hosts. The European badger (31%) was the most frequently studied host, followed by the wild boar (17%), the red deer (14%) and the red fox (10%). The remaining wildlife species were less commonly represented (<7% of the studies). Camera-trapping was the most frequently used method (61%; $n=19$). Proximity loggers and GPS collars came in second, equally represented (16% each, $n=5$; Fig. 2). Additionally, 6% of the studies were multi-method ($n=2$: camera-trapping/GPS collars; GPS collars/proximity loggers).

### RATES OF WILDLIFE–CATTLE INTERACTIONS

We counted 35 records of direct interactions involving nine species pairs from 18 studies. Additionally, 59 records of indirect interactions comprising nine species pairs from 26 studies were recorded. The overall mean of direct *RatesInt* was 0.03 interactions/month [range: 0.00–0.12] per species pair, while indirect *RatesInt* was 4.63 interactions/month [range: 0.16–30.00] per species pair, representing 154 times more than the mean of direct interactions (Fig. 4).

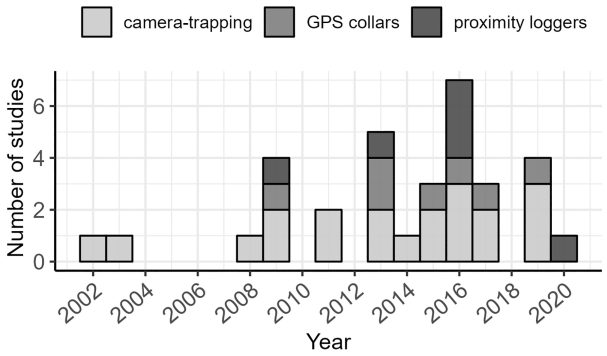

**Fig. 2.** Publication year of the studies included in the meta-analysis according to type of method used.

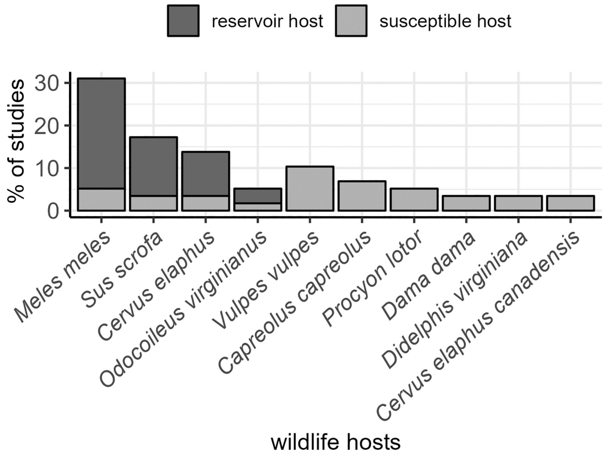

**Fig. 3.** Percentage of studies ($n=31$) included in the meta-analysis according to wildlife hosts and considering their presumed epidemiological role in the citing study.

Badger–cattle (MM) and fallow deer–cattle (DD) were the species pairs showing the highest rates of direct interactions, ranked as first and second respectively (Table 2, Fig. 5). The remaining species pairs had mean interaction rates lower than the overall mean. Wild boar–cattle (SS) presented the highest rate of indirect interactions. The pairs raccoon–cattle (PL) and red fox–cattle (VV) had moderate rates of indirect interactions, yet lower than the overall mean. The remaining species pairs made a lower contribution to the bulk of indirect interaction rates (less than two interactions/month per species pair).

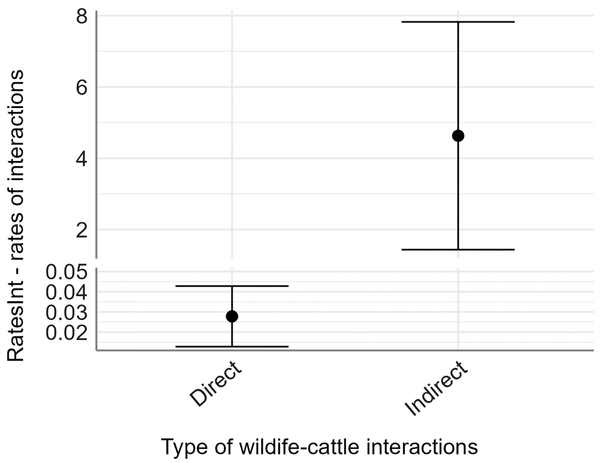

**Fig. 4.** Overall rates of wildlife–cattle interactions (*RatesInt* [interactions/month]). Weighted means (dots) and standard errors (bars) of rates are displayed by interaction type (direct or indirect). Note the broken Y-axis.

### FACTORS INFLUENCING INTERACTION RATES

Two models regarding the influential factors on the occurrence of direct interactions presented ΔAICc >2 and statistically significant coefficients: farm size (coef = 1.323, CI 95% = [0.501; 2.780]) and cattle_dens (coef = −1.606, CI 95% = [−3.743; −0.537]; Appendix S6). According to the models, direct interactions were more likely to occur in larger farms and at low cattle densities (Fig. 6a,b). Only one model concerning factors influencing indirect interaction rates had ΔAICc >2 and a significant coefficient: wild_dens (coef = 0.912, CI 95% = [0.350; 1.474]; Appendix S6). Rates of indirect interactions significantly increased with higher wildlife density (Fig. 6c). Regardless of the type of interactions considered, we found no evidence of significant effects of the remaining predictors we tested.

## DISCUSSION

Ecological interactions between disease hosts have been widely acknowledged as determinants of pathogen transmission, from domestic species to wildlife and *vice versa*. In this sense, understanding the underlying biological processes that are responsible for the transmission of infectious agents between susceptible animal hosts is becoming an important research area (Gortázar et al. 2016, Dougherty et al. 2018, Bacigalupo et al. 2020, Caron et al. 2021).

Of the studies explored in this work, only a few used specific criteria for the definition of wildlife–cattle interactions. By providing a synthesis of the main criteria used to express wildlife–cattle interactions across different methods, we hope to encourage future researchers to adopt improved integration and harmonisation of interaction data, especially in terms of frequency and interaction type. To the best of

**Table 2.** Summary of the rates of wildlife–cattle interactions (*RatesInt*) described for species pairs. For each species pair, we provide detailed information on numbers of records (*n*), means, standard errors (se) and range values (min-max) displayed by type of interactions (* is used to mark means, se and min-max based on <3 records; NA = not applicable)

| | | | Direct interactions per month | | | | Indirect interactions per month | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species pair | Scientific name – wildlife host | Species pair acronym | *n* | Mean | SE | Min–max | *n* | Mean | SE | Min–max |
| Badger–cattle | *Meles meles* | MM | 12 | 0.12 | 0.09 | [0.00–1.08] | 26 | 1.90 | 0.96 | [0.00–22.33] |
| Fallow deer–cattle | *Dama dama* | DD | 2 | 0.09* | 0.09* | [0.00–0.18]* | NA | NA | NA | NA |
| Opossum–cattle | *Didelphis virginiana* | DV | 1 | 0.00* | NA | [0.00–0.00]* | 2 | 0.30* | 0.29* | [0.02–0.59]* |
| Raccoon–cattle | *Procyon lotor* | PL | 1 | 0.01* | NA | [0.01–0.01]* | 4 | 4.24 | 2.76 | [0.02–12.11] |
| Red deer–cattle | *Cervus elaphus* | CE | 6 | 0.02 | 0.01 | [0.00–0.08] | 5 | 1.29 | 0.79 | [0.03–4.33] |
| Red fox–cattle | *Vulpes vulpes* | VV | 2 | <0.01* | <0.00* | [0.00–0.01]* | 6 | 2.26 | 1.33 | [0.13–8.46] |
| Roe deer–cattle | *Capreolus capreolus* | CC | 4 | <0.01 | 0.00 | [0.00–0.00] | 4 | 0.84 | 0.72 | [0.03–3.00] |
| Wapiti–cattle | *Cervus elaphus canadensis* | CCA | NA | NA | NA | NA | 2 | 0.16* | 0.16* | [0.00–0.31]* |
| White-tailed deer–cattle | *Odocoileus virginianus* | OV | 1 | 0.00* | NA | [0.00–0.00]* | 3 | 0.72 | 0.66 | [0.00–2.03] |
| Wild boar–cattle | *Sus scrofa* | SS | 6 | 0.00 | 0.00 | [0.00–0.03] | 7 | 29.97 | 29.28 | [0.11–205.63] |

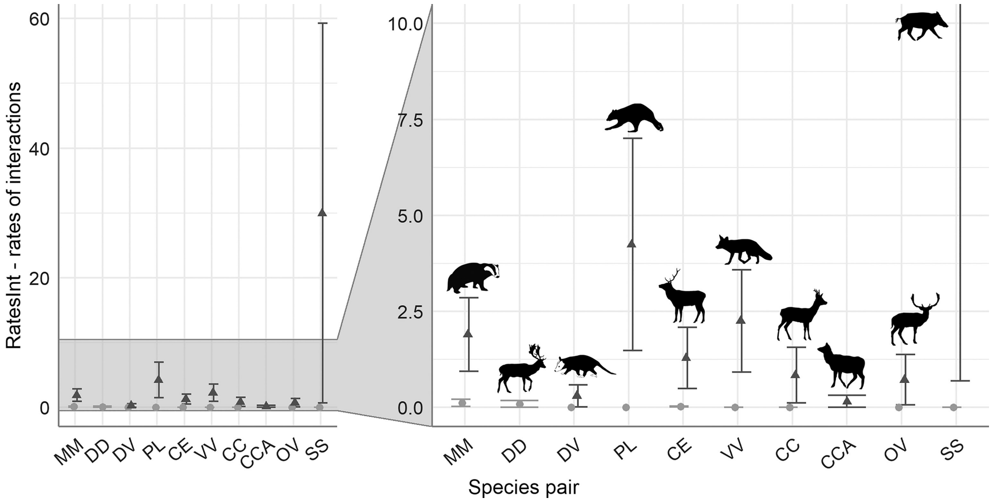

**Fig. 5.** Rates of wildlife–cattle interactions (*RatesInt* [interactions/month]) summarised by species pairs. Weighted means and standard errors of rates are displayed by interaction type. Grey dots and dark triangles represent direct and indirect interactions, respectively. Species pair acronyms are (MM) badger – cattle, (DD) fallow deer – cattle, (DV) opossum – cattle, (PL) raccoon – cattle, (CE) red deer – cattle, (VV) fox – cattle, (CC) roe deer – cattle, (CCA) wapiti – cattle, (OV) white-tailed deer – cattle and (SS) wild boar – cattle. Silhouette images of animals are from http://phylopic.org/ (*Meles meles*, *Dama dama* and *Vulpes vulpes* photos by: Anthony Caravaggi; *Didelphis virginiana* by Gabriela Palomo-Munoz).

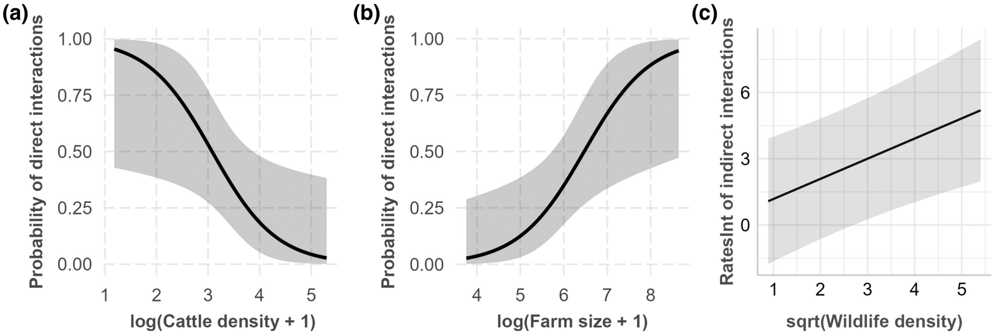

**Fig. 6.** Effect of cattle density (a) and farm size (b) on the probability of occurrence of direct interactions (±95% confidence intervals). Image c represents the effect of wildlife density on indirect interaction rates (±95% confidence intervals).

our knowledge, this study applies for the first time a framework to estimate wildlife–cattle interaction rates, allowing the comparison of the relative weight of direct and indirect inter-specific interactions on TB transmission at a global level. Regardless of the study context and wildlife host considered, direct rates of interaction between wildlife and cattle are infrequent. In contrast, special attention should be given to indirect interactions that occur frequently through shared environments, wherein wildlife density may play a key role.

## When and where do species interact? – Criteria used to define disease-relevant interactions

Despite adopting a variety of criteria, only a small number of studies used explicit standards to define direct and/or indirect interactions pertinent to *Mycobacterium bovis* transmission. This is in agreement with the only study available on cattle diseases (Bacigalupo et al. 2020), in which the authors identified a wide range of definitions used in wildlife–livestock interaction studies, and reported conflicting or overlapping definitions of direct and indirect interactions, highlighting the need for a common generic framework. We found no conflicting criteria between interaction types, although some overlapping criteria for indirect interactions existed. Moreover, Bacigalupo et al. (2020) demonstrated that interaction definitions were highly dependent on the study context, specifically on the species considered and demographic parameters. However, our results suggest that the criteria employed to define interactions vary with the type of interaction and data collection method, rather than with the species or ecosystems studied.

The criteria adopted to define direct interactions included physical contact between animals, as well as close proximity between individuals as a surrogate of that interaction, since spatial proximity may lead to biologically meaningful interaction, considering that aerosol transmission is possible between animal hosts 1–2 m apart (Sauter & Morris 1995, Humblet et al. 2009, Corner et al. 2011). For indirect interactions, a general baseline considered the use of shared environments by individuals at different times, meaning that shared contaminated sites could be high-risk locations by intermediating indirect transmission of *Mycobacterium bovis* between hosts (e.g. Cowie et al. 2016, Lavelle et al. 2016, Payne et al. 2016). We did not find any criteria based on GPS collars for measuring direct interactions. This could be explained by the inherent spatial location error, which can be high (e.g. 26 m, Triguero-Ocaña et al. 2019), resulting in insufficient precision to co-locate individuals at close contact (<2 metres; but see Cooper et al. 2010).

## Do wild hosts and study context shape TB interactions?

### GENERAL TRENDS OF THE STUDIES

Most of studies covered in our meta-analysis were relatively recent and from Europe, with badger and ungulates – particularly wild boar and red deer – as the most represented. These findings are in agreement with the previous work of Reis et al. (2020a) who found that European countries contributed the most to wildlife TB epidemiology knowledge, suggesting that the ecological field is growing alongside the epidemiological area (see also Gortazar et al. 2011, Reis et al. 2020b). In European industrialised countries, TB is a notifiable disease for which eradication programmes and surveillance are mandatory for cattle production and trade (Hardstaff et al. 2014, Gortázar et al. 2015); surveillance programmes also exist in non-European countries. Improved infrastructure and financial resources are available in countries where surveillance and related research are in place. Additionally, on a global scale, some of the best-studied wildlife TB reservoirs occur in Europe, such as in the UK, Ireland, and the Iberian Peninsula (Palmer 2013, Pereira et al. 2020). The absence of interaction-based studies in our review from South Africa and New Zealand is notable given the occurrence of wildlife TB hosts in both countries (see Pereira et al. 2020). This deficit in research could be related to: 1) different socio-economic contexts, particularly the case of South Africa, with the allocation of resources to other research areas (e.g. Di Minin et al. 2021) or to other more affordable studies to assess wildlife–cattle interfaces (e.g. questionnaires, Meunier et al. 2017); or 2) eligibility rules, as the few studies carried out in these countries did not meet our inclusion criteria (e.g. New Zealand; Ramsey et al. 2002, Rouco et al. 2018).

Regarding the methods applied to assess wildlife–cattle interactions, camera-trapping was the most widely used. This was also reported by Bacigalupo et al. (2020), highlighting its considerable versatility to monitor different species, and its applicability across different study types and ecosystems (Caravaggi et al. 2017, Niedballa et al. 2019). Furthermore, novel applications of camera-trapping have proven useful for generating animal density data and for measuring risky behaviour (e.g. Cadenas-Fernández et al. 2019, Palencia et al. 2021). These applications could be highly useful for the further evaluation of disease-relevant interactions across multi-species interfaces.

### RATES OF WILDLIFE–CATTLE INTERACTIONS

We developed a novel framework to estimate interaction rates, considering different sampling efforts inherent to data collection methods, enabling multi-studies comparison. Our findings show that direct interactions are rare, suggesting that cattle are seldom approached by wildlife (or the reverse). In contrast, indirect interactions are significantly more frequent, with a mean estimated frequency 154 times higher than the mean of direct interactions. These findings underpin the idea that a shared environment should be considered an important risk factor for TB transmission at the wildlife–cattle interface (Drewe et al. 2013, Kukielka et al. 2013, Lavelle et al. 2016, Woodroffe et al. 2016, Wilber et al. 2019, Triguero-Ocaña et al. 2020).

Transmission risk depends not only on the extent of disease-relevant interactions among individuals but also on the probability of infection during a particular interaction event (McCallum et al. 2017). In this context, the likelihood of infection involved in direct host-to-host interactions, even if such interactions occur in low numbers, should not be considered negligible in disease transmission (Wilber et al. 2019). Still, obtaining sufficient empirical evidence to quantify the relative importance of different transmission modes constitutes, to date, a real challenge (Craft 2015, Fenton et al. 2015, Webster et al. 2017), which explains the use of interaction patterns as a proxy to evaluate the risk of pathogen transmission (Triguero-Ocaña et al. 2020, Yang et al. 2021). This risk can be estimated by quantifying and modelling fine-scale movement patterns undertaken by host individuals, to elucidate how pathogens can permeate among individuals of different species, and to improve estimates of transmission risk in multi-host systems (Wilber et al. 2022).

Overall, only three predictors significantly influenced the occurrence and abundance of interaction rates. A first model showed that direct interactions are more probable in larger farms. Those areas often hold a higher number of cattle-related resources (e.g. feeding and water sites) that are attractive for wildlife species, enhancing the opportunities for wildlife and cattle to engage in the same spatial site at the same time (Herrera & Nunn 2019). On the other hand, the negative relationship between the occurrence of direct interactions and cattle density may be a behavioural effect, reflecting the local avoidance by wildlife of areas that are often occupied by cattle (see Schieltz & Rubenstein 2016). Mullen et al. (2013) and Woodroffe et al. (2016) demonstrated that badgers actively avoid cattle while foraging in Ireland and England. A similar pattern was found in Portugal by Curveira-Santos et al. (2017), where cattle presence had a negative influence on space use by the red fox. Conversely, in Spain, Carrasco-Garcia et al. (2016) found that cattle presence was positively associated with wild boar presence and, to a lesser extent, with that of red deer. Moreover, on farms in Northern Ireland, the presence of badgers was positively associated with cattle herd size, yet negatively associated with cattle presence (Campbell et al. 2019). None of these studies specifically explored the role of cattle density on direct inter-species interactions (but see Yang et al. 2021), but they did demonstrate that host behaviour is highly relevant for the co-occurrence of species, and might determine potential close interactions between hosts (Craft 2015, Herrera & Nunn 2019) and thus contribute to transmission risk.

The positive relationship between wildlife density and rates of indirect interaction in this study is consistent with previous research (Carrasco-Garcia et al. 2016, Campbell et al. 2019, Robertson et al. 2019). This pattern is compatible with a density-dependent mechanism, usually applied to exploring relations between social contact rates and animal densities, and relationships with parasite transmission (Hu et al. 2013, Hopkins et al. 2020). Specifically, this mechanism involves an increase in contact rates with higher animal density. However, to date, the limited knowledge on this theme hinders the identification of general principles that explicitly point out the density-dependent wildlife–cattle relationship and its extent. Nevertheless, patterns of interactions resulting from different density contexts might significantly affect pathogen spread, as previously acknowledged (White et al. 2018a, b, Hopkins et al. 2020, Manlove et al. 2022). Thus, regardless of the type of mechanism underlying inter-specific animal interactions, the role of wildlife density in TB epidemiology at the wildlife–cattle interface must be seriously considered (Fofana & Hurford 2017). Furthermore, animal density must be integrated with the factors driving indirect TB transmission, such as environmental persistence of pathogens (Fine et al. 2011, Santos et al. 2015, Dougherty et al. 2018, Manlove et al. 2022). For instance, high-quality habitats tend to attract a higher variety of wildlife species and support larger host densities, increasing contamination levels of indirectly transmitted pathogens (Leach et al. 2016). In those areas, high concentration of hosts enables pathogens to accumulate in spatial reservoirs, which can be viewed as ecological traps. Accordingly, by selecting such areas, individuals can be exposed to an increased infection risk and are more likely to form consistently infected populations (Leach et al. 2016).

## STUDY LIMITATIONS

Limitations of systematic reviews and meta-analyses affect researchers' ability to broach specific questions or topics. Our results in the review of interaction criteria mirror what we found in the meta-analysis process (estimates of interactions). Variation in experimental design (e.g. criteria adopted, device settings, camera operational days and frequency of fixes with GPS collars) and reporting inconsistency pose significant difficulties: first, summary statistics of interactions (raw counts and means) were often difficult to extract or were not reported at all; second, information regarding potential predictors were also often poorly reported and inconsistently detailed across studies, leading to the use of simplified models. This detailed information should be provided in fine-scale studies since it might be relevant for interpreting interaction rates and for comparing studies.

The conclusions on factors influencing interaction rates should be viewed as preliminary since our sample size was limited. However, despite these limitations, our findings offer major insights into understanding animal TB transmission risk through an ecological perspective, even if our framework and modelling approach are a simplification of a complex system. The results highlight the complex ecological links that help us to understand how animals interact at a global scale and thus are a key addition to the present body of knowledge.

## WHAT'S NEXT? GUIDELINES FOR FUTURE STUDIES

Within an ecological–epidemiological perspective of animal TB, a key focus should be wildlife surveillance through harmonised approaches. We propose that several key points should be considered in future studies targeting wildlife–cattle interactions. We encourage researchers to:

1. Adopt the main criteria summarised here, to standardise approaches, allowing comparison of results with previously published studies and easing the integration of new ones.
2. Adopt the terms interaction or contact in studies instead of other nomenclature (e.g. spatial visit and occurrence).

3. Standardise rates of interaction as a function of the sampling effort (e.g. number of camera stations, monitoring sites or collared animals) and study duration, enabling comparison of studies differing in duration and survey effort; rigorous study duration estimates must take into account the number of active camera days for camera-trapping studies; in the case of GPS collars and proximity loggers, accurate tracking periods of the collared animals are essential (discriminated by species, i.e. the number of tracking days considering the total number of collared individuals for a given species).
4. Guarantee that important predictors (e.g. seasons and sites) are properly surveyed, accommodating balanced spatial and temporal variabilities, because it is important to know when and where species are interacting, and thus when and where actions should be prioritised.
5. Consider CTWs on estimated rates of indirect interactions. Since transmission depends on the pathogen's survival time in the environment, the use of CTW is important for generating reliable estimates in the case of *Mycobacterium bovis* transmission.
6. Information on the study area (proportion of land uses and geographical coordinates), cattle herd size, TB prevalence, wildlife abundance (even if only proxies are available), raw counts of interactions and rates of interaction should be made available.
7. Evaluate both intra- and inter-wildlife species' interactions in order to improve our understanding of TB transmission dynamics in multi-host communities.

## CONCLUSIONS

Quantifying interaction patterns between disease hosts through harmonised approaches is critical for inferring key drivers of differentiation across species and ecological features responsible for interaction rate variations. Our synthesis applied to animal TB highlights that only a few studies used specific criteria to define wildlife–cattle interactions, although different criteria were available. Regardless of the study context and host species considered, direct rates of interactions between wildlife and cattle were proven to be very infrequent. In contrast, the focus is on the indirect interactions that occur frequently in shared environments, wherein wildlife density may play a key role. In this sense, the classical direct aerosol transmission might be of minor importance in inter-species disease transmission, underlining the importance of assessing whether or not indirect interactions are the main driver of wildlife–cattle TB transmission. By dissecting, for the first time, patterns of wildlife–cattle interaction at a global scale and their potential connections with ecological and methodological factors, we draw a path for future studies regarding shared interfaces and ecology of animal diseases. Ultimately, this could be the cornerstone to support initiatives for a successful reduction of disease-relevant interactions that have been proven to be relevant for disease epidemiology.

## ACKNOWLEDGEMENTS

We thank Ana Sampaio for helping with the design of the graphical abstract and Fig. 5. We acknowledge two anonymous reviewers for constructive and insightful comments, which greatly improved the manuscript. We also thank Dr. Nancy Jennings for her clarity and suggestions.

## FUNDING

This work was funded by the Fundação para a Ciência e a Tecnologia (FCT), namely with a PhD grant (SFRH/BD/146037/2019) to EMF and MOVERCULOSIS project (2022.06014.PTDC). EMF was also financed by MED funds to PhD students. We also acknowledge funding from Fundação para a Ciência e a Tecnologia, IP (FCT)/MCTES through national funds (PIDDAC) and co-funding by the European Regional Development Fund (FEDER) of the European Union, through the Lisbon Regional Operational Program and the Competitiveness and Internationalization Operational Program for Portugal 2020 or other programmes that may succeed in the scope of project 'Colossus: Control Of tubercuLOsiS at the wildlife/livestock interface uSing innovative natUre-based Solutions' (references PTDC/CVT-CVT/29783/2017, LISBOA-01-0145-FEDER-029783 and POCI-01-0145- FEDER-029783). Strategic fundings from FCT to cE3c and BioISI Research Units (UIDB/00329/2020 and UIDB/04046/2020) and the associate laboratory CHANGE (LA/P/0121/2020) are gratefully acknowledged.

## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## REFERENCES

Albery GF, Kirkpatrick L, Firth JA, Bansal S (2021) Unifying spatial and social network analysis in disease ecology. *Journal of Animal Ecology* 90: 45–61.

Alexander KA, Carlson CJ, Lewis BL, Getz WM, Marathe MV, Eubank SG, Sanderson CE, Blackburn JK (2018) The ecology of pathogen spillover and disease emergence at the human-wildlife-environment interface. In: Hurst C (ed) *The Connections between Ecology and Infectious Disease*, 267–298. Springer, Cham, Switzerland.

Allen AR, Ford T, Skuce RA (2021) Does *mycobacterium tuberculosis* var. *bovis* survival in the environment confound bovine tuberculosis control and eradication? A literature review. *Veterinary Medicine International* 2021: 1–19.

Bacigalupo SA, Dixon LK, Gubbins S, Kucharski AJ, Drewe JA (2020) Towards a unified generic framework to define and observe contacts between livestock and wildlife: a systematic review. *PeerJ* 8: 1–39.

Balseiro A, Oleaga Á, Álvarez Morales LM, González Quirós P, Gortázar C, Prieto JM (2019) Effectiveness of a calf-selective feeder in preventing wild boar access. *European Journal of Wildlife Research* 65: 1–6.

Barasona JA, VerCauteren KC, Saklou N, Gortazar C, Vicente J (2013) Effectiveness of cattle operated bump gates and exclusion fences in preventing ungulate multi-host sanitary interaction. *Preventive Veterinary Medicine* 111: 42–50.

Barasona JA, Latham MC, Acevedo P, Armenteros JA, Latham ADM, Gortazar C, Carro F, Soriguer RC, Vicente J (2014) Spatiotemporal interactions between wild boar and cattle: implications for cross-species disease transmission. *Veterinary Research* 45: 1–11.

Barasona JA, Vicente J, Díez-Delgado I, Aznar J, Gortázar C, Torres MJ (2016) Environmental presence of *mycobacterium tuberculosis* complex in aggregation points at the wildlife/livestock interface. *Transboundary and Emerging Diseases* 64: 1148–1158.

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Böhm M, Hutchings MR, White PCL (2009) Contact networks in a wildlife-livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. *PLoS One* 4: e5016.

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, New York, USA.

Cadenas-Fernández E, Sánchez-Vizcaíno JM, Pintore A, Denurra D, Cherchi M, Jurado C, Vicente J, Barasona JA (2019) Free-ranging pig and wild boar interactions in an endemic area of African swine fever. *Frontiers in Veterinary Science* 6: 1–9.

Campbell EL, Byrne AW, Menzies FD, McBride KR, McCormick CM, Scantlebury M, Reid N (2019) Interspecific visitation of cattle and badgers to fomites: a transmission risk for bovine tuberculosis? *Ecology and Evolution* 9: 8479–8489.

Caravaggi A, Banks PB, Burton AC, Finlay CMV, Haswell PM, Hayward MW, Rowcliffe MJ, Wood MD (2017) A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation* 3: 109–122.

Caron A, Barasona JA, Miguel E, Michaux J, De Garine-Wichatitsky M (2021) Characterization of wildlife-livestock interfaces: the need for interdisciplinary approaches and a dedicated thematic field. In: Vicente J, Vercauteren KC, Gortázar C (eds) *Diseases at the Wildlife – Livestock Interface*, 339–367. Springer, Cham, Switzerland.

Carrasco-Garcia R, Barasona JA, Gortazar C, Montoro V, Sanchez-Vizcaino JM, Vicente J (2016) Wildlife and livestock use of extensive farm resources in south Central Spain: implications for disease transmission. *European Journal of Wildlife Research* 62: 65–78.

Cooper SM, Scott HM, de la Garza GR, Deck AL, Cathey JC (2010) Distribution and interspecies contact of feral swine and cattle on rangeland in South Texas: implications for disease transmission. *Journal of Wildlife Diseases* 46: 152–164.

Corner LAL, Murphy D, Gormley E (2011) *Mycobacterium bovis* infection in the Eurasian badger (*Meles meles*): the disease, pathogenesis, epidemiology and control. *Journal of Comparative Pathology* 144: 1–24.

Cowie CE, Hutchings MR, Barasona JA, Gortázar C, Vicente J, White PCL (2016) Interactions between four species in a complex wildlife: livestock disease community: implications for *Mycobacterium bovis* maintenance and transmission. *European Journal of Wildlife Research* 62: 51–64.

Craft ME (2015) Infectious disease transmission and contact networks in wildlife and livestock. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 370: 20140107.

Cunha MV, Monteiro M, Carvalho P, Mendonça P, Albuquerque T, Botelho A (2011) Multihost tuberculosis: insights from the Portuguese control program. *Veterinary Medicine International* 2011: 1–10.

Cunha MV, Matos F, Canto A, Albuquerque T, Alberto JR, Aranha JM, Vieira-Pinto M, Botelho A (2012) Implications and challenges of tuberculosis in wildlife ungulates in Portugal: a molecular epidemiology perspective. *Research in Veterinary Science* 92: 225–235.

Curveira-Santos G, Marques TA, Björklund M, Santos-Reis M (2017) Mediterranean mesocarnivores in spatially structured managed landscapes: community organisation in time and space. *Agriculture, Ecosystems & Environment* 237: 280–289.

Di Minin E, Slotow R, Fink C, Bauer H, Packer C (2021) A pan-African spatial assessment of human conflicts with lions and elephants. *Nature Communications* 12: 2978.

Dougherty ER, Seidel DP, Carlson CJ, Spiegel O, Getz WM (2018) Going through the motions: incorporating movement analyses into disease research. *Ecology Letters* 21: 588–604.

Drewe JA, O'Connor HM, Weber N, McDonald RA, Delahay RJ (2013) Patterns of direct and indirect contact between cattle and badgers naturally infected with tuberculosis. *Epidemiology and Infection* 141: 1467–1475.

Duarte EL, Domingos M, Amado A, Botelho A (2008) Spoligotype diversity of *Mycobacterium bovis* and *Mycobacterium caprae* animal isolates. *Veterinary Microbiology* 130: 415–421.

Fenton A, Streicker DG, Petchey OL, Pedersen AB (2015) Are all hosts created equal? Partitioning host species contributions to parasite persistence in multihost communities. *American Naturalist* 186: 610–622.

Fine AE, Bolin CA, Gardiner JC, Kaneene JB (2011) A study of the persistence of *Mycobacterium bovis* in the environment under natural weather conditions in Michigan, USA. *Veterinary Medicine International* 2011: 1–12.

Fitzgerald SD, Kaneene JB (2013) Wildlife reservoirs of bovine tuberculosis worldwide: hosts, pathology, surveillance, and control. *Veterinary Pathology* 50: 488–499.

Fofana AM, Hurford A (2017) Mechanistic movement models to understand epidemic spread. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372: 1–11.

Gortazar C, Vicente J, Boadella M, Ballesteros C, Galindo RC, Garrido J, Aranaz A, de la Fuente J (2011) Progress in the control of bovine tuberculosis in Spanish wildlife. *Veterinary Microbiology* 151: 170–178.

Gortázar C, Che Amat A, O'Brien DJ (2015) Open questions and recent advances in the control of a multi-host infectious disease: animal tuberculosis. *Mammal Review* 45: 160–175.

Gortázar C, Ruiz-Fons JF, Höfle U (2016) Infections shared with wildlife: an updated perspective. *European Journal of Wildlife Research* 62: 511–525.

Hardstaff JL, Marion G, Hutchings MR, White PCL (2014) Evaluating the tuberculosis hazard posed to cattle from wildlife across Europe. *Research in Veterinary Science* 97: S86–S93.

Hassell JM, Newbold T, Dobson AP, Linton YM, Franklinos LHV, Zimmerman D, Pagenkopp Lohan KM (2021) Towards an ecosystem model of infectious disease. *Nature Ecology and Evolution* 5: 907–918.

Herrera J, Nunn CL (2019) Behavioural ecology and infectious disease: implications for conservation of biodiversity. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 374: 1–11.

Hopkins SR, Fleming-Davies AE, Belden LK, Wojdak JM (2020) Systematic review of modelling assumptions and empirical evidence: does parasite transmission increase nonlinearly with host density? *Methods in Ecology and Evolution* 11: 476–486.

Hu H, Nigmatulina K, Eckhoff P (2013) The scaling of contact rates with population density for the infectious disease models. *Mathematical Biosciences* 244: 125–134.

Humblet MF, Boschiroli ML, Saegerman C (2009) Classification of worldwide bovine tuberculosis risk factors in cattle: a stratified approach. *Veterinary Research* 40: 1–24.

Jenkins DG, Quintana-Ascencio PF (2020) A solution to minimum sample size for regressions. *PLoS One* 15: e0229345.

Kukielka E, Barasona JA, Cowie CE, Drewe JA, Gortazar C, Cotarelo I, Vicente J (2013) Spatial and temporal interactions between livestock and wildlife in south Central Spain assessed by camera traps. *Preventive Veterinary Medicine* 112: 213–221.

Lavelle MJ, Kay SL, Pepin KM, Grear DA, Campa H, VerCauteren KC (2016) Evaluating wildlife-cattle contact rates to improve the understanding of dynamics of bovine tuberculosis transmission in Michigan, USA. *Preventive Veterinary Medicine* 135: 28–36.

Leach CB, Webb CT, Cross PC (2016) When environmentally persistent pathogens transform good habitat into ecological traps. *Royal Society Open Science* 3: 1–11.

Manlove K, Wilber M, White L, Bastille-Rousseau G, Yang A, Gilbertson MLJ, Craft ME, Cross PC, Wittemyer G, Pepin KM (2022) Defining an epidemiological landscape that connects movement ecology to pathogen transmission and pace-of-life. *Ecology Letters* 25: 1760–1782.

Martínez-Guijosa J, Lima-Barbero JF, Acevedo P, Cano-Terriza D, Jiménez-Ruiz S, Barasona JÁ, Boadella M, García-Bocanegra I, Gortázar C, Vicente J (2021) Description and implementation of an on-farm wildlife risk mitigation protocol at the wildlife-livestock interface: tuberculosis in Mediterranean environments. *Preventive Veterinary Medicine* 191: 1–11.

McCallum H, Fenton A, Hudson PJ, Lee B, Levick B, Norman R, Perkins SE, Viney M, Wilson AJ, Lello J (2017) Breaking beta: deconstructing the parasite transmission function. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372: 20160084.

Meunier NV, Sebulime P, White RG, Kock R (2017) Wildlife-livestock interactions and risk areas for cross-species spread of bovine tuberculosis. *Onderstepoort Journal of Veterinary Research* 84: 1–10.

Moher D, Liberati A, Tetzlaff J, Altman DG, Altman D, Antes G et al. (2009) Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Medicine* 6: e1000097.

Morris RS, Pfeiffer DU, Jackson R (1994) The epidemiology of *Mycobacterium bovis* infections. *Veterinary Microbiology* 40: 153–177.

Morris LR, Proffitt KM, Asher V, Blackburn JK (2016) Elk resource selection and implications for anthrax management in Montana. *Journal of Wildlife Management* 80: 235–244.

Mullen EM, MacWhite T, Maher PK, Kelly DJ, Marples NM, Good M (2013) Foraging Eurasian badgers *Meles meles* and the presence of cattle in pastures. Do badgers avoid cattle? *Applied Animal Behaviour Science* 144: 130–137.

Niedballa J, Wilting A, Sollmann R, Hofer H, Courtiol A (2019) Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote Sensing in Ecology and Conservation* 5: 1–14.

Palencia P, Rowcliffe JM, Vicente J, Acevedo P (2021) Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology* 58: 1583–1592.

Palmer MV (2013) *Mycobacterium bovis*: characteristics of wildlife reservoir hosts. *Transboundary and Emerging Diseases* 60: 1–13.

Palmer MV, Thacker TC, Waters WR, Gortázar C, Corner LAL (2012) *Mycobacterium bovis*: a model pathogen at the interface of livestock, wildlife, and humans. *Veterinary Medicine International* 2012: 1–17.

Payne A, Chappa S, Hars J, Dufour B, Gilot-Fromont E (2016) Wildlife visits to farm facilities assessed by camera traps in a bovine tuberculosis-infected area in France. *European Journal of Wildlife Research* 62: 33–42.

Payne A, Philipon S, Hars J, Dufour B, Gilot-Fromont E (2017) Wildlife interactions on baited places and waterholes in a French area infected by bovine tuberculosis. *Frontiers in Veterinary Science* 3: 1–11.

Pereira AC, Reis AC, Ramos B, Cunha MV (2020) Animal tuberculosis: impact of disease heterogeneity in transmission, diagnosis, and control. *Transboundary and Emerging Diseases* 67: 1828–1846.

Pinheiro J, Bates D, DebRoy S, Sarkar D; R Core Team (2018) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.

Prugh LR, Sivy KJ (2020) Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters* 23: 902–918.

Ramos B, Pereira AC, Reis AC, Cunha MV (2020) Estimates of the global and continental burden of animal tuberculosis in key livestock species worldwide: a meta-analysis study. *One Health* 10: 100169.

Ramsey D, Spencer N, Caley P, Efford M, Hansen K, Lam M, Cooper D (2002) The effects of reducing population density on contact rates between brushtail possums: implications for transmission of bovine tuberculosis. *Journal of Applied Ecology* 39: 806–818.

Reis AC, Ramos B, Pereira AC, Cunha MV (2020a) The hard numbers of tuberculosis epidemiology in wildlife: a meta-regression and systematic review. *Transboundary and Emerging Diseases* 68: 3257–3276.

Reis AC, Ramos B, Pereira AC, Cunha MV (2020b) Global trends of epidemiological research in livestock tuberculosis for the last four decades. *Transboundary and Emerging Diseases* 68: 333–346.

Reis AC, Salvador LCM, Robbe-Austerman S, Tenreiro R, Botelho A, Albuquerque T, Cunha MV, Boschiroli L (2021) Whole genome sequencing refines knowledge on the population structure of *Mycobacterium bovis* from a multi-host tuberculosis system. *Microorganisms* 9: 1–15.

Robertson A, Judge J, Wilson GJ, Vernon IJ, Delahay RJ, McDonald RA (2019) Predicting badger visits to farm yards and making predictions available to farmers. *PLoS One* 14: 1–20.

Rouco C, Jewell C, Richardson KS, French NP, Buddle BM, Tompkins DM (2018) Brushtail possum (*Trichosurus vulpecula*) social interactions and their implications for bovine tuberculosis epidemiology. *Behaviour* 155: 621–637.

Santos N, Correia-Neves M, Almeida V, Gortázar C (2012) Wildlife tuberculosis: a systematic review of the epidemiology in Iberian Peninsula. In: Epidemiology Insights (ed) *Cunha MLRS*. InTech, Rijeka.

Santos N, Santos C, Valente T, Gortázar C, Almeida V, Correia-Neves M (2015) Widespread environmental contamination with *Mycobacterium tuberculosis* complex revealed by a molecular detection protocol. *PLoS One* 10: e0142079.

Santos N, Richomme C, Nunes T, Vicente J, Alves PC, de la Fuente J, Correia-Neves M, Boschiroli ML, Delahay R, Gortázar C (2020) Quantification of the animal tuberculosis multi-host community offers insights for control. *Pathogens* 9: 1–11.

Sauter CM, Morris RS (1995) Behavioural studies on the potential for direct transmission of tuberculosis from feral ferrets (*Mustela furo*) and possums (*Trichosurus vulpecula*) to farmed livestock. *New Zealand Veterinary Journal* 43: 294–300.

Schieltz JM, Rubenstein DI (2016) Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environmental Research Letters* 11: 1–18.

Silk MJ, Weber N, Steward LC, Delahay RJ, Croft DP, Hodgson DJ, Boots M, McDonald RA (2017) Seasonal variation in daily patterns of social contacts in the European badger *Meles meles*. *Ecology and Evolution* 7: 9006–9015.

Tolhurst BA, Delahay RJ, Walker NJ, Ward AI, Roper TJ (2009) Behaviour of badgers (*Meles meles*) in farm buildings: opportunities for the transmission of *Mycobacterium bovis* to cattle? *Applied Animal Behaviour Science* 117: 103–113.

Tolhurst BA, Ward AI, Delahay RJ (2011) A study of fox (*Vulpes vulpes*) visits to farm buildings in Southwest England and the implications for disease management. *European Journal of Wildlife Research* 57: 1227–1230.

Triguero-Ocaña R, Barasona JÁ, Carro F, Soriguer RC, Vicente J, Acevedo P (2019) Spatio-temporal trends in the frequency of interspecific interactions between domestic and wild ungulates from Mediterranean Spain. *PLoS One* 14: e0211216.

Triguero-Ocaña R, Martínez-López B, Vicente J, Barasona JA, Martínez-Guijosa J, Acevedo P (2020) Dynamic network of interactions in the wildlife-livestock interface in Mediterranean Spain: an epidemiological point of view. *Pathogens* 9: 1–16.

Triguero-Ocaña R, Laguna E, Jiménez-Ruiz S, Fernández-López J, García-Bocanegra I, Barasona JÁ, Risalde MÁ, Montoro V, Vicente J, Acevedo P (2021) The wildlife-livestock interface on extensive free-ranging pig farms in Central Spain during the “montanera” period. *Transboundary and Emerging Diseases* 68: 2066–2078.

Van Tonder AJ, Thornton MJ, Conlan AJK, Jolley KA, Goolding L, Mitchell AP et al. (2021) Inferring *Mycobacterium bovis* transmission between cattle and badgers using isolates from the randomised badger culling trial. *PLoS Pathogens* 17: 1–24.

Webster JP, Borlase A, Rudge JW (2017) Who acquires infection from whom and how? Disentangling multi-host and multimode transmission dynamics in the ‘elimination’ era. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372: 1–16.

White RJ, Razgour O (2020) Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change. *Mammal Review* 50: 336–352.

White LA, Forester JD, Craft ME (2018a) Dynamic, spatial models of parasite transmission in wildlife: their structure, applications and remaining challenges. *Journal of Animal Ecology* 87: 559–580.

White LA, Forester JD, Craft ME (2018b) Disease outbreak thresholds emerge from interactions between movement behavior, landscape structure, and epidemiology. *Proceedings of the National Academy of Sciences of the United States of America* 115: 7374–7379.

Wilber MQ, Pepin KM, Campa H, Hygnstrom SE, Lavelle MJ, Xifara T, VerCauteren KC, Webb CT (2019) Modelling multi-species and multi-mode contact networks: implications for persistence of bovine tuberculosis at the wildlife–livestock interface. *Journal of Applied Ecology* 56: 1471–1481.

Wilber MQ, Yang A, Boughton R, Manlove KR, Miller RS, Pepin KM, Wittemyer G (2022) A model for leveraging animal movement to understand spatio-temporal disease dynamics. *Ecology Letters* 25: 1290–1304.

Woodroffe R, Donnelly CA, Ham C, Jackson SYB, Moyes K, Chapman K, Stratton NG, Cartwright SJ (2016) Badgers prefer cattle pasture but avoid cattle: implications for bovine tuberculosis control. *Ecology Letters* 19: 1201–1208.

Yang A, Boughton RK, Miller RS, Wight B, Anderson WM, Beasley JC, VerCauteren KC, Pepin KM, Wittemyer G (2021) Spatial variation in direct and indirect contact rates at the wildlife-livestock interface for informing disease management. *Preventive Veterinary Medicine* 194: 105423.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, New York, USA.

## SUPPORTING INFORMATION

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

**Appendix S1.** Flow diagram of literature search and selection which followed the preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol.

**Appendix S2.** Source of the predictors and additional information used in the modelling process for the Patterns Dataset.

**Appendix S3.** Details of the predictors used in the modelling of the Patterns Dataset.

**Appendix S4.** Summary of the studies identified in the literature wherein researchers adopted criteria to define a wildlife–cattle interaction in animal tuberculosis (TB) context.

**Appendix S5.** Estimates of wildlife–cattle interaction rates used in the modelling of Patterns Dataset, and predictor values extracted of each species pair.

**Appendix S6.** Summary of generalised linear models (GLMs), liner mixed models (LMMs) and generalised linear mixed models (GLMMs), performed on direct and indirect interactions.