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Towards a unified generic framework to define and observe contacts between livestock and wildlife: a systematic review

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ABSTRACT

Wild animals are the source of many pathogens of livestock and humans. Concerns about the potential transmission of economically important and zoonotic diseases from wildlife have led to increased surveillance at the livestock-wildlife interface. Knowledge of the types, frequency and duration of contacts between livestock and wildlife is necessary to identify risk factors for disease transmission and to design possible mitigation strategies. Observing the behaviour of many wildlife species is challenging due to their cryptic nature and avoidance of humans, meaning there are relatively few studies in this area. Further, a consensus on the definition of what constitutes a 'contact' between wildlife and livestock is lacking. A systematic review was conducted to investigate which livestock-wildlife contacts have been studied and why, as well as the methods used to observe each species. Over 30,000 publications were screened, of which 122 fulfilled specific criteria for inclusion in the analysis. The majority of studies examined cattle contacts with badgers or with deer; studies involving wild pig contacts with cattle or with domestic pigs were the next most frequent. There was a range of observational methods including motion-activated cameras and global positioning system collars. As a result of the wide variation and lack of consensus in the definitions of direct and indirect contacts, we developed a unified framework to define livestock-wildlife contacts that is sufficiently flexible to be applied to most wildlife and livestock species for non-vector-borne diseases. We hope this framework will help standardise the collection and reporting of contact data; a valuable step towards being able to compare the efficacy of wildlife-livestock observation methods. In doing so, it may aid the development of better disease transmission models and improve the design and effectiveness of interventions to reduce or prevent disease transmission.

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INTRODUCTION

The interface where livestock and wildlife may come into contact with each other is an area of growing scientific interest, particularly as wildlife can act as a 'reservoir' for diseases of livestock (*Wiethoelter et al., 2015*). Disease transmission between livestock and wildlife can have marked economic impact, such as African swine fever outbreaks in domestic pigs and wild boar (*Sus scrofa*) in Europe and Asia (*Dixon et al., 2019*), where the loss of 12–20% of the global pig herd in 2019 led to a 10% increase in the food price index of pork (*Pitts & Whitnall, 2019*). The impact of disease transmission on wildlife can be seen in the loss of around half the global saiga (*Saiga tatarica*) antelope population in 2015 to *Pasteurella multocida*, a pathogen harboured by livestock (*Fereidouni et al., 2019*). Contact between wildlife and livestock may also lead to conflict between humans and wildlife, with compensation for large carnivore predation and other damage costing 28.5 million euros annually in Europe (*Bautista et al., 2019*). The proximity of agricultural land to wildlife habitats is a key factor in human-wildlife conflicts and in the spill-over of pathogens from wildlife to livestock and humans (*Jones et al., 2013*). The emergence of diseases from wildlife that infect humans via livestock intermediaries, such as bat-borne Hendra virus (affecting humans via horses) and Nipah virus (affecting humans via pigs) (*Field et al., 2001*), further highlight the importance of contacts between wildlife, livestock and people. These contacts are seldom recorded, however, because many wildlife species are cryptic and therefore difficult to observe, capture and sample.

Observing wildlife-livestock contacts is becoming easier with advances in remote technologies such as motion-activated cameras, global positioning system (GPS) collars and proximity loggers (*Böhm, Hutchings & White, 2009*; *Drewe et al., 2013*; *Barasona et al., 2014*). These methods are usually (but not always) used to monitor one species at a time. They are not standardised, however, meaning there are many variations in monitoring protocols, often depending on basic practicalities such as battery life, people-hours, cost and the aims of the study. The methods used to monitor livestock-wildlife contacts may influence (or be influenced by) the kind of contact to be monitored, the context of the study and what the data will be used for.

Livestock-wildlife contact data is needed to inform the simulation and modelling of diseases that have multiple host species, but information on the types of contact needed for transmission and the rates at which these occur is lacking (*Craft, 2015*). Knowledge of livestock-wildlife contact data can be used to identify risk factors and predict where these contacts are more or less likely to occur, for example predicting the likelihood of badger (*Meles meles*) visits to cattle farms in the context of bovine tuberculosis transmission (*Robertson et al., 2019*). It could also be used to implement and improve mitigation strategies to prevent unwanted livestock-wildlife contacts. To mitigate wolf (*Canis lupus*) predation on sheep, for example, the effectiveness of prevention programs needs to be evaluated in ways that do not depend on livestock attacks alone, using methods such as GPS monitoring of wolf movements around sheep farm bio-fences (*Bautista et al., 2019*; *Ausband et al., 2013*). Similarly, the effectiveness of measures taken to prevent disease transmission can also be evaluated such as by comparing deer-cattle contact rates between farms with and without deer fences installed (*Lavelle et al., 2015*; *Lavelle et al., 2016*; *Wilber et al., 2019*). Knowledge of livestock-wildlife contacts can be used in these contexts to limit the economic loss associated with disease and predation. Given these multiple ways of gathering and using livestock-wildlife contact data, the definition of what constitutes a relevant contact will vary depending on the aim of the study.

In the context of disease transmission, defining contact is challenging and while types of contact are often broadly grouped into being 'direct' or 'indirect', there are no standardised definitions (*Eames et al., 2015*). Direct contacts are usually thought of as representing physical contact or being in close proximity over a short period of time, and so may include fighting, mating between feral and domestic animals of the same species, or being face-to-face or nose-to-nose. Indirect contacts are more difficult to define due to issues of long-distance aerosol transmission, environmental persistence of pathogens in spores and fomites, and intermediate insect vectors (*Craft, 2015*). Other ecological definitions of livestock-wildlife contacts could also include avoidance behaviour or competition for resources between species. This variation in definitions means it is difficult to make meaningful comparisons between studies and to apply findings from one study to different contexts. Therefore, a standardised generic template for defining livestock-wildlife contacts would be useful.

The aim of this study was to systematically review the reasons for, and observational methods used in, studies investigating livestock-wildlife contacts, and to propose a generalised framework for defining contacts between livestock and wildlife.

METHODS

Literature search and data extraction

We defined livestock as 'farmed domesticated mammals' (*FAO, 2020*), wild animals as 'free-ranging non-domesticated mammals', and contact as 'activity implying an interaction or association between species including the shared use of resources such as farmland'. The terms interaction and contact were used synonymously within the literature, but contact is used here for consistency. The systematic review question was "Which methods have been used to assess the frequency of, and types of, contacts between wild animals and livestock or livestock farms worldwide?".

Search terms for wildlife, livestock and type of contact were combined by the Boolean operators 'OR' and 'AND' to identify publications that investigated contact between any wild and domestic mammal (Table S1). Search terms were based on common species names, and generic terms such as 'feral', 'wildlife', 'livestock' and 'farm'. Searches were conducted in CAB Abstracts, Scopus and Pubmed. CAB Abstracts is a comprehensive database of life science research with broad coverage of veterinary literature in particular, and Scopus has a broad coverage of interdisciplinary journals (*Grindlay, Brennan & Dean, 2012*; *Aghaei Chadegani et al., 2013*).

Search results were consolidated into Microsoft Excel and duplicates were identified and removed using queries followed by manual inspection. Titles, abstracts and full texts of the retrieved publications were evaluated by SAB against pre-specified exclusion and inclusion criteria (Table 1). Any papers for which the criteria were not clear were also evaluated by JAD. In all such cases both authors agreed on the final decision. We wished to capture publications that collected, used or analysed data to investigate direct or indirect

Table 1 Exclusion and inclusion criteria to select studies for the systematic review of livestock-wildlife contact.

Exclusion Criteria
1. Study does not involve a wild mammal species where adults are typically heavier than 5 kg.
2. Study does not involve a farmed mammal species where adults are typically heavier than 5 kg, or farmland associated with such livestock.
3. Study does not attempt to collect, use or analyse data to investigate contacts between wild animals and livestock or livestock farms.
4. Study does not attempt to collect, use or analyse data to establish at least one of the following: characterisation of, the nature of, frequency of, or risk factors for, contacts between wildlife and livestock.
5. Full text not available in English.
6. Full text not accessible to reviewers.
7. The method of recording livestock-wildlife contacts relies solely on predation events where the only observations are livestock kills or scat analysis
8. Wild animals were non-free-living, pre-tamed or relocated for the purpose of the study.

Inclusion Criteria
The study aims to collect, use, or analyse data to establish at least one of the following:
1. A quantifiable measure of direct contact between wildlife and livestock, where direct contact is defined as physical contact between at least one wild animal and one farm animal.
2. A quantifiable measure of indirect contact between wildlife and livestock, where indirect contact is defined as contact between at least one wild animal and a resource used by at least one farm animal including, but not limited to, food, water and space
3. Characterise and establish the type of, or risk factors for, direct or indirect contact between wildlife and livestock, as defined above.

contacts between farmed livestock and terrestrial wild mammals whose adult bodyweight is typically >5 kg. Specifically, publications were included if they attempted to quantify, characterise, or identify risk factors for livestock-wildlife contacts. Only articles in English and those accessible to researchers were included. All reasonable efforts were made to access papers that passed abstract screening. We excluded studies in which predation events were the sole indicator of livestock-wildlife contacts, and studies of wild animals that were not free-living, were tamed or were relocated for the purpose of the study. Publications until 11 November 2019 were included, and no time restrictions were applied to the start of the search. Working definitions of direct and indirect contact were developed before performing the literature search and used to avoid ambiguity when evaluating publications for inclusion.

Direct contact was provisionally defined prior to reviewing the papers as physical contact between at least one wild animal and one farm animal. Indirect contact was provisionally defined as contact between at least one wild animal and a resource used by at least one farm animal including, but not limited to, food, water and space. Therefore, studies that investigated wildlife and livestock shared resource use, but did not explicitly investigate contacts, were included. These definitions were used throughout the process of identifying and analysing the papers in this review. Study data was extracted and livestock and wildlife species, observation methods and definitions were categorised. Where available, the power of each study, defined as the likelihood of detecting contacts, was recorded. Themes that emerged during data extraction were grouped into seven broad study themes, namely behavioural, competition, conservation, disease, human-wildlife conflict, methods papers and wildlife management (Fig. S1). Where studies had more than one theme, themes were subjectively allocated as dominant (primary) or secondary based on the aims of the study. Results were visualised and plotted using R (version 3.6.3 (*R Core Team, 2020*)) and R packages listed in Table S2.

Development of a generic unified framework

Following categorisation of definitions, a generic unified framework was developed by grouping and identifying commonalities in definitions of 'direct' and 'indirect' contact, namely relating to space and time. The spatial and temporal limits separating relevant contacts from inconsequential contacts and non-contact events were identified for each study, and a framework was developed based on defining contacts in relation to both space and time. Using this framework, relevant contacts were defined using the parameters of critical space (S_C) and critical time (T_C). We defined S_C as the critical space (distance or area) between animals below which a contact relevant to the study is considered to have occurred, and T_C as the critical time window within which a relevant contact is considered to have occurred.

RESULTS

During data categorisation and analyses, many publications were categorised into more than one group due to studying multiple species, using multiple detection methods and having multiple themes, and therefore the number of studies exceed 122 (100%) in several instances reported below.

Search results, quality appraisal and themes

A total of 43,032 papers were identified by the search terms across all three databases, of which 30,080 were unique results. After screening using the exclusion and inclusion criteria in Table 1, 122 publications remained in the final analysis (Fig. 1). Publication date ranged from 1980 to 2019, with 117 (96%) published in the last 20 years (Fig. 2). Studies conducted in Europe, North America and Africa made up 89% of the results (Table S3) with the USA and UK producing the most publications (21% and 18%, respectively).

Low study power was mentioned briefly in only 11 (9%) publications and statistical power calculations were not performed. The level of uncertainty was acknowledged in 64 (53%) publications.

Disease was the dominant theme and featured in 80 of 122 studies (66%), followed by human-wildlife conflict (22/122; 18%), competition between wildlife and livestock (17/122; 14%), conservation (16/122; 13%), wildlife management (11/122; 9%), behavioural studies (3/122; 2%) and methods validation (2/122; 2%) (Fig. S1). Within the disease-themed papers, *Mycobacterium bovis* was the most studied pathogen (49/80; 61%) followed by foot-and-mouth disease virus (8/80; 10%) (Tables S4 and S5). Wildlife-cattle contacts were the focus of 98 of the 122 studies (80%) and a further 22 studies (18%) focussed on sheep, pigs, farmed deer and camelids. The most studied wildlife species were deer (30/122;

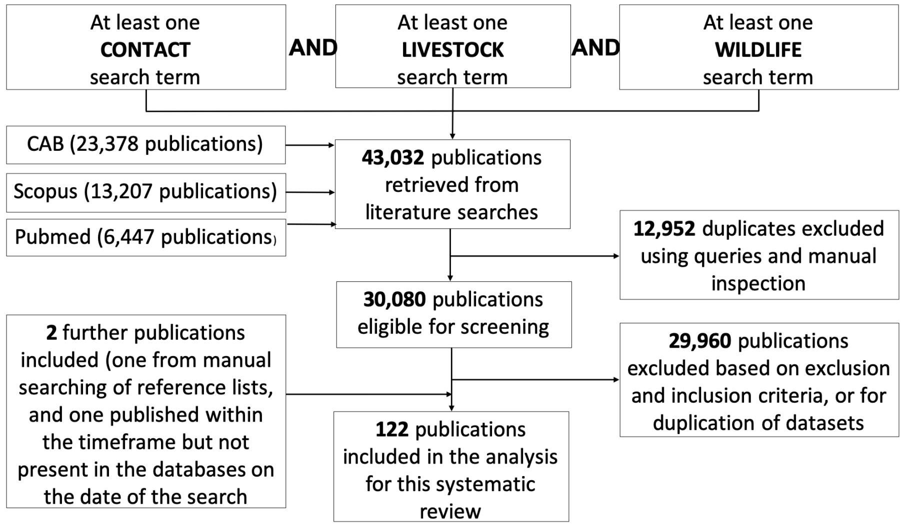

Figure 1 Flow chart documenting literature retrieval and criteria used to select articles for inclusion in the systematic review of direct and indirect contacts between wildlife and livestock. Search categories (contact term, livestock and wildlife) were combined by the Boolean operator 'AND' to identify publications containing all three terms. Databases were searched up to 11 November 2019 with no historic limit.

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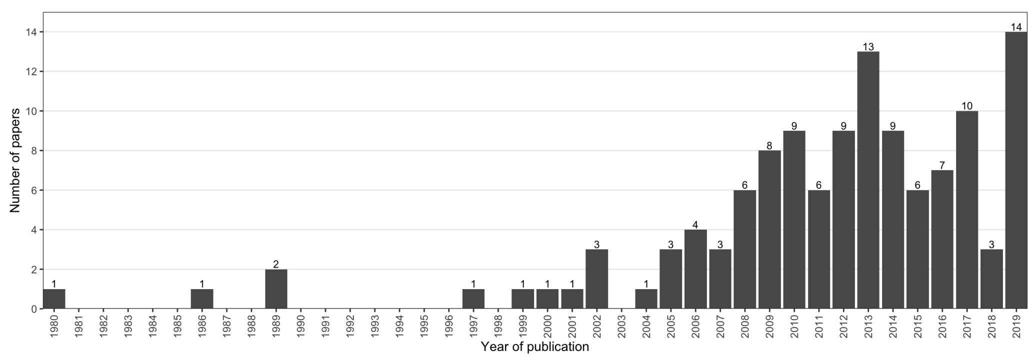

Figure 2 Distribution of the publication year of 122 publications included in the systematic review. Publication date ranged from 1980 to 2019, with 117 (96%) published in the last 20 years.

Full-size DOI: 10.7717/peerj.10221/fig-2

25%), wild pigs [including wild boar] (26/122; 21%) and badgers (25/122; 20%: Figs. S2 and S3). The wildlife species were not specified in 11 papers, some of which studied wild ungulates competing for livestock grazing (*Mizutani, Kadohira & Phiri, 2012*; *Sitters et al., 2009*; *Crawford et al., 2019*), others that concerned wildlife as hosts of cattle diseases such as bovine tuberculosis (*Munyeme et al., 2010*; *Witmer et al., 2010*; *Katale et al., 2013*) and foot-and-mouth disease (*Brahmbhatt et al., 2012*; *Molla et al., 2013*), and the remainder that were completely unspecified.

Methods used to observe livestock-wildlife contacts

Methods that monitored both livestock and wildlife species were used in 88 publications (72%) whereas 34 studies (28%) monitored wildlife only. Camera trapping was the most

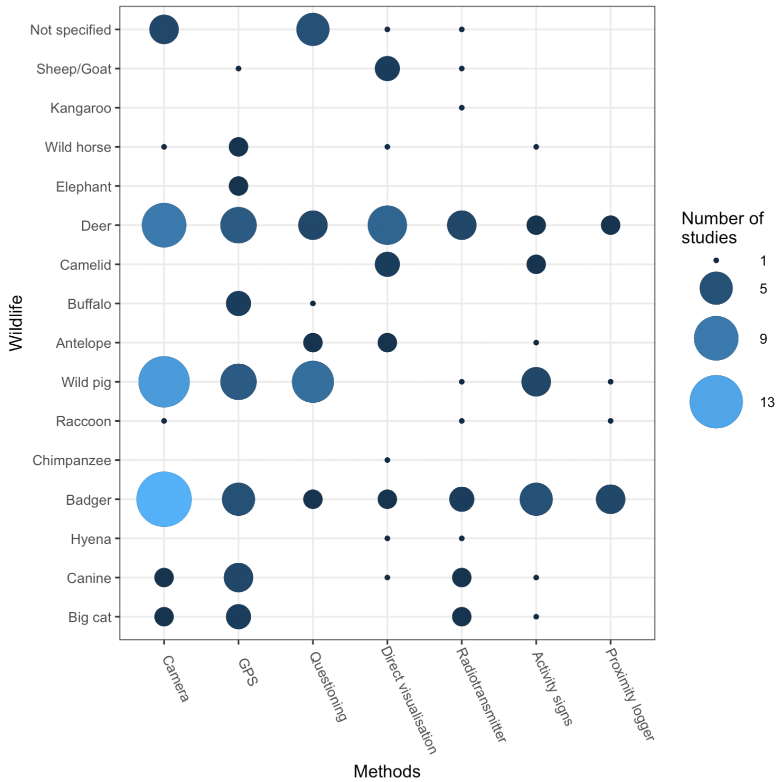

Figure 3 Observation methods used to monitor wildlife. Data from 122 publications included in the systematic review. The size and shade of circles indicate the number of studies in each category. Many publications used more than one method to monitor contacts, and therefore the number of studies exceeds 122 (100%) for some groups.

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frequent method of monitoring wildlife (37 studies, 31%), and was most prominently used in badgers, deer and wild pigs (Fig. 3). GPS collars were the second most used method to monitor wildlife (29 studies, 24%), and while they were also used predominantly on badgers, deer and wild pigs, they were used proportionally more than cameras to monitor predators such as big cats and wolves and large herbivores such as buffalo, wild horses and elephants. Other methods used to monitor wildlife were direct visualisation (21; 17%), farmer questioning (20; 16%), radio-transmitters (17; 14%), activity signs (15; 12%) and proximity loggers (7; 6%). Some studies utilised more than one observation method, and therefore the numbers of studies exceed 122 (100%) Studies that monitored livestock tended to use the same methods as for wildlife, although 10 studies dedicated fewer resources to monitor livestock; for example (*Pruvot et al., 2014*) used GPS collars to monitor wild deer and farmer questioning to monitor cattle behaviour. Studies that did not monitor livestock tended to infer wildlife-livestock contact from monitoring only the activities of wildlife on or around livestock holdings, such as on pasture, in buildings and the shared use of resources such as livestock feed.

A variety of methods were used to observe different types of contact data (Fig. S4). Methods such as GPS collars and radio-tracking (telemetry) were used to collect the locations of wildlife (e.g., *Barasona et al., 2014*; *Raizman et al., 2013*; *Cooper et al., 2008*), whereas proximity loggers were used to detect close proximity contacts between livestock and wildlife or with postulated high-risk disease transmission areas such as badger latrines (e.g., *Drewe et al., 2013*). Camera traps and direct visualisation were used to observe behavioural activity, such as nose-to-nose contacts between cattle and badgers (*Tolhurst et al., 2009*), foxes taking piglets from farrowing huts (*Fleming et al., 2016*) and wild boar eating from cattle troughs (*Kukielka et al., 2013*). Some methods were used to detect the presence of wild animals on farms or on pasture only, such as surveys of activity signs to detect wild boar rooting on sheep pasture (*Guillermo Bueno et al., 2010*) and GPS collars to demonstrate the avoidance of livestock pasture by lions (*Oriol-Cotterill et al., 2015*). Thirty studies combined more than one method to monitor wildlife, such as (*Wyckoff et al., 2012*) which combined activity signs, GPS collar data and camera traps to monitor feral swine activity at and around domestic pig pens. The majority of studies, however, used only one method and were able to collect information about the type of contact defined by the study.

Definitions of direct and indirect contacts

Definitions for both direct contact and indirect contact were provided by 27 studies, with a further four defining direct contact only and 54 defining indirect contact only (Tables 2 and 3). Definitions of direct contact tended to focus on the spatial distance between wildlife and livestock at one point in time (Table 2). Definitions of indirect contact tended to focus on the use of space or resources by wildlife in a location previously or subsequently occupied by livestock, within a certain time frame (Table 3). There were some variations to these trends: two studies specified a time frame longer than one time point to define direct contact (*Lavelle et al., 2016*; *Cooper et al., 2010*). The amount of time was usually determined by the context of the study, such as the survival time of a specified pathogen in the environment, known as the critical time window of a contact (*Cowie et al., 2016*). Contacts were also defined in 15 studies as the shared use of resources between livestock and wildlife, such as feed and water. There were large variations between studies in the defined distances and time windows, with direct contact distances ranging from physical contact (seven studies) to within 120 metres of each other (one study), and indirect definitions ranging from within the same camera image (two studies) to within 50 kilometres of a location (one study). There was less variation in definitions between studies with similar contexts and aims. For example, among *M. bovis* transmission studies in cattle and badgers, the definition of direct contact ranged from physical contact to within two metres (six studies), and indirect contacts were defined as presence on farmland, sharing of resources and visits to badger latrines by cattle (20 studies). Importantly, no definition of contact was provided in 25 studies (44%) that reported direct contacts, and 34 studies (29%) that reported indirect contacts.

Regardless of the contact definitions or methods used to observe contacts, direct contacts were detected much less frequently than indirect contacts. For example, one study (*Lavelle et al., 2016*) found no instances of cattle within two metres of deer, compared to over 40,000 indirect contacts of deer with cattle via shared feed. Overall, the median number of direct contacts between wildlife and livestock was in single figures, whereas the median number

Table 2 Definitions of direct contact from a systematic review of studies of livestock and wildlife. Parameters are listed in ascending order of distance and time. Definitions that have been used for both direct and indirect contacts are shaded grey. Percentages are rounded to the nearest integer.

'Direct contact' definition	Number (%) of publications using this definition	% Cumulative	References
At least two individuals making physical contact	9 (16)	16	*Tolhurst et al. (2009)*; *Brook et al. (2013)*; *Hockings et al. (2012)*; *Campbell et al. (2019)*; *Tolhurst, Ward & Delahay (2011)*; *Vercauteren et al. (2007a)*; *Vercauteren et al. (2007b)*; *Jori et al. (2017)*; *Trabucco et al. (2013)*
Individuals close enough to inhale expired breath	1 (2)	18	*Benham & Broom (1989)*
Individuals within one metre of the same location within one second	1 (2)	20	*Lavelle et al. (2016)*
Individuals within two metres of each other	5 (9)	29	*Drewe et al. (2013)*; *Cowie et al. (2016)*; *Drewe et al. (2012)*; *Garnett, Delahay & Roper (2002)*; *Woodroffe et al. (2016)*
Individuals within five metres of each other	3 (5)	34	*Böhm, Hutchings & White (2009)*; *Walter et al. (2012)*; *Hill (2005)*
Individuals within the same camera image	5 (9)	43	*Kukielka et al. (2013)*; *Balseiro et al. (2019)*; *Barasona et al. (2017)*; *Cadenas-Fernández et al. (2019)*; *Payne et al. (2016)*
Individuals within 20 metres of each other	1 (2)	45	*Richomme, Gauthier & Fromont (2006)*
Individuals within 20 metres of the same location within 15 min	1 (2)	46	*Cooper et al. (2010)*
Individuals within same farm building	1 (2)	48	*Fleming et al. (2016)*
Individuals within holding (farm) boundary	1 (2)	50	*Wu et al. (2012)*
Individuals within 100 metres of each other	2 (4)	54	*Wyckoff et al. (2009)*; *Dion, VanSchalkwyk & Lambin (2011)*
Individuals within 120 metres of each other	1 (2)	55	*Kukielka et al. (2016)*
Studies that reported the frequency of, types of, or risk factors for, direct contacts without first defining them	25 (45)	100	*Ausband et al. (2013)*; *Mizutani, Kadohira & Phiri (2012)*; *Munyeme et al. (2010)*; *Witmer et al. (2010)*; *Molla et al. (2013)*; *Pruvot et al. (2014)*; *Mattiello et al. (2002)*; *Arzamendia & Vilá (2015)*; *Colman et al. (2012)*; *Kolowski & Holekamp (2006)*; *Laporte et al. (2010)*; *Mattiello et al. (1997)*; *Steyaert et al. (2011)*; *Rüttimann, Giacometti & McElligott (2008)*; *Schroeder et al. (2013)*; *Stahl et al. (2002)*; *Anderson et al. (2019)*; *Barasona et al. (2013)*; *Carrasco-Garcia et al. (2016)*; *Carusi, Beade & Bilenca (2017)*; *Howe et al. (2000)*; *Meunier et al. (2017)*; *Ward et al. (2008)*; *Weise et al. (2019)*; *Zarco-González & Monroy-Vilchis (2014)*
Total	56 (100)		

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Table 3 Definitions of indirect contact from a systematic review of studies of livestock and wildlife. Parameters are listed in ascending order of distance and time. Definitions that have been used for both direct and indirect contacts are shaded grey. Percentages are rounded to the nearest integer.

'Indirect contact' definition	Number (%) of publications using this definition	% Cumulative	References
Individuals within the same camera image	2 (2)	2	*Payne et al. (2016)*; *Kaczensky et al. (2019)*
Two individuals photographed by the same camera trap within a specific time interval	1 (1)	3	*Kukielka et al. (2013)*
Latrine (faecal pits) visits	5 (4)	7	*Drewe et al. (2013)*; *Drewe et al. (2012)*; *Scantlebury et al. (2004)*; *Smith et al. (2009)*; *Hutchings & Harris (2009)*
Individuals visiting the same food or water source at the same time	2 (2)	9	*Munyeme et al. (2010)*; *Jori et al. (2017)*
Individuals visiting the same food and water sources at unspecified time intervals	13 (11)	20	*Lavelle et al. (2016)*; *Katale et al. (2013)*; *Brook et al. (2013)*; *Trabucco et al. (2013)*; *Garnett, Delahay & Roper (2002)*; *Walter et al. (2012)*; *Balseiro et al. (2019)*; *Barasona et al. (2013)*; *Carrasco-Garcia et al. (2016)*; *Brook (2010)*; *O'Mahony (2014)*; *Atwood et al. (2009)*; *Tsukada et al. (2010)*
Individuals in the same space at the same time	2 (2)	22	*Maleko et al. (2012)*; *Mullen et al. (2013)*
Individuals in the same space at different times	3 (3)	24	*Raizman et al. (2013)*; *Campbell et al. (2019)*; *Barth et al. (2018)*
Individuals in the same space at unspecified time interval	3 (3)	27	*Barasona et al. (2014)*; *Robertson et al. (2019)*; *Hill (2005)*
Individuals using the same food or water source within six hours	1 (1)	28	*Cowie et al. (2016)*
Individuals within 20 metres of the same location within six hours	1 (1)	28	*Cooper et al. (2010)*
Individuals within 30 metres of livestock or feed	1 (1)	29	*Ribeiro-Lima et al. (2017)*
Presence in farm buildings at unspecified time interval	5 (4)	34	*Witmer et al. (2010)*; *Tolhurst et al. (2009)*; *Tolhurst, Ward & Delahay (2011)*; *Robertson et al. (2017)*; *Woodroffe et al. (2017)*

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Table 3 (*continued*)

'Indirect contact' definition	Number (%) of publications using this definition	% Cumulative	References
Individuals within 50 metres of each other	1 (1)	34	*Rüttimann, Giacometti & McElligott (2008)*
Individuals within 52 metres of the same location within one hour	1 (1)	35	*Triguero-Ocaña et al. (2019)*
Individuals within 120 metres	1 (1)	36	*Brahmbhatt et al. (2012)*
Individuals using the same space with seven days	2 (2)	38	*Crawford et al. (2019)*; *Cadenas-Fernández et al. (2019)*
Individuals using the same space within 15 days	1 (1)	39	*Richomme, Gauthier & Fromont (2006)*
Presence on pasture at the same time	5 (4)	43	*Clifford et al. (2009)*; *Benham & Broom (1989)*; *Carusi, Beade & Bilenca (2017)*; *Weise et al. (2019)*; *Zarco-González & Monroy-Vilchis (2014)*
Presence on pasture at unspecified time interval	8 (7)	50	*Pruvot et al. (2014)*; *Fleming et al. (2016)*; *Guillermo Bueno et al. (2010)*; *Woodroffe et al. (2016)*; *Bromen et al. (2019)*; *Chavez & Gese (2006)*; *Ham et al. (2019)*; *Muhly et al. (2010)*
Presence on pasture at different times	1 (1)	51	*Odadi et al. (2017)*
At holding boundary and on pasture at unspecified time interval	1 (1)	52	*Gehring et al. (2010)*
Presence on farm at unspecified time interval	12 (10)	62	*Mullen et al. (2015)*; *Sleeman, Davenport & Fitzgerald (2008)*; *O'brien et al. (2014)*; *O'Mahony (2015)*; *Anderson et al. (2019)*; *Ward et al. (2008)*; *Braz et al. (2019)*; *Judge et al. (2011)*; *Kamler et al. (2019)*; *Van Der Weyde et al. (2017)*; *Viggers & Hearn (2005)*; *Berentsen et al. (2014)*
At holding (farm) boundary	3 (3)	65	*Vercauteren et al. (2007a)*; *Vercauteren et al. (2007b)*; *Tolhurst et al. (2008)*
Individuals within 120 metres of the same location at different times	1 (1)	66	*Kukielka et al. (2016)*

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Table 3 (*continued*)

'Indirect contact' definition	Number (%) of publications using this definition	% Cumulative	References
Individuals within 300 metres of the same location within 15 days	2 (2)	67	*Miguel et al. (2013)*; *Miguel et al. (2017)*
Individuals within 500 metres of the same location within six weeks	1 (1)	68	*Meunier et al. (2017)*
Individuals within 500 metres from holding (farm) boundary	2 (2)	70	*Wu et al. (2012)*; *Wyckoff et al. (2009)*
Individuals within 50 kilometres of the same location within three months	1 (1)	71	*Beauvais et al. (2019)*
Studies that reported the frequency of, types of, or risk factors for, indirect contacts without first defining them	34 (29)	100	*Mizutani, Kadohira & Phiri (2012)*; *Sitters et al. (2009)*; *Molla et al. (2013)*; *Cooper et al. (2008)*; *Oriol-Cotterill et al. (2015)*; *Mattiello et al. (2002)*; *Arzamendia & Vilá (2015)*; *Colman et al. (2012)*; *Kolowski & Holekamp (2006)*; *Laporte et al. (2010)*; *Mattiello et al. (1997)*; *Steyaert et al. (2011)*; *Barasona et al. (2013)*; *Howe et al. (2000)*; *Abade et al. (2018)*; *Acebes, Traba & Malo (2012)*; *Atickem & Loe (2014)*; *Borgnia, Vilá & Cassini (2008)*; *Coe et al. (2001)*; *Cohen et al. (1989)*; *Dohna et al. (2014)*; *Engeman, Betsill & Ray (2011)*; *Jori et al. (2009)*; *Kitts-Morgan et al. (2015)*; *Knust, Wolf & Wells (2011)*; *Kuiters, Bruinderink & Lammertsma (2005)*; *Loft, Menke & Kie (1986)*; *Moa et al. (2006)*; *Pearson et al. (2014)*; *Salter & Hudson (1980)*; *Shrestha (2007)*; *Valls-Fox et al. (2018)*; *Wronski et al. (2015)*; *Anonymous (2013)*
Total	116 (100)		

of indirect contacts occurred in the order of hundreds or even thousands. The types of contacts reported between livestock and wildlife, and the methods used to observe contacts, are summarised in Table 4. Low study power was acknowledged, but not calculated, by 11 studies (9%), and is likely to be a feature of many more which did not report it. No studies reported adequate power. The low power of studies to observe rare contacts, coupled with the variation in, or lack of, contact definitions, makes it very difficult to compare the effectiveness of the methods used to observe wildlife-livestock contacts.

Proposed unified framework to define direct and indirect contacts

Space (area or distance between animals) and time were crucial components of the varied definitions of direct and indirect contact in this review. In an effort to unify these parameters, a novel generic framework to categorise wildlife-livestock contacts is proposed in Fig. 4, based on the locations of individuals in space and time. Using this framework, we propose that the contact type (direct or indirect) is defined using the two parameters S_C and T_C. Multiple critical thresholds can be used within the framework to differentiate between definitions of direct contact (S_{C1} and T_{C1}) and indirect contact (S_{C2} and T_{C2}). For a direct contact to occur, two individuals are within the same pre-specified critical space (distance or area: S_{C1}) within a pre-specified critical time window (T_{C1}). Similarly, for an indirect contact to occur, animals are within another pre-specified critical space (S_{C2}) within another pre-specified critical time window (T_{C2}). The reader is directed to Fig. 4 for examples from the literature of possible combinations of S_C and T_C. T_{C2} may be the same as T_{C1} (if S_{C2} is larger than S_{C1}: compare example A with example B in Fig. 4) or T_{C2} may be different from T_{C1}(in which case T_{C2} will usually, but not always, be larger than T_{C1}: compare example A with examples C, D, E and F in Fig. 4). Similarly, S_{C2} may be the same as S_{C1} (if T_{C2} is larger than T_{C1}: compare example A with examples C and E in Fig. 4) or S_{C2} may be different from S_{C1} (in which case S_{C2}will usually, but not always, be larger than S_{C1}: compare example A with examples B, D and F in Fig. 4). Same, near and different are used here to illustrate spatial and temporal differences between examples. These terms are relative and will vary along with S_C and T_C depending on the system being studied, the objectives of the study and other factors such as host behaviour and the biology of the pathogen, in the case of disease studies; therefore, values for T_{C1}, T_{C2}, S_{C1} and S_{C2} should be decided in advance of a study being conducted, and they should be clearly reported when data are presented.

Although the exact values of the critical distance between animals and the critical time window over which this happens will depend on the system being studied as well as the specific objectives of each study, the adoption of this generic framework to define direct and indirect contacts will help identify studies with similar definitions where results are more easily comparable.

DISCUSSION

The need for a generic unified framework

This review has found that definitions of contact are wide-ranging and highly dependent on the context of the study. Definitions can vary depending on the species and demographics

Table 4 A summary of the types of contact(s) reported between livestock and wildlife, and the method(s) used to observe contacts, from a systematic review of 122 studies.

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
Camelid	Antelope	Multiple (d,k,q)	Yes	Yes	Shared space use	*Beauvais et al. (2019)*
	Camelid	Direct visualisation	Yes	Yes	Wild camelids grazing with domestic llamas	*Arzamendia & Vilá (2015)*
		Multiple (a,d)	No	Yes	Shared forage	*Borgnia, Vilá & Cassini (2008)*
Cattle	Antelope	Activity signs	No	Yes	Shared space use	*Atickem & Loe (2014)*
		Direct visualisation	No	Yes	Unspecified contact	*Wronski et al. (2015)*
		Model[b]	No	Yes	No contacts observed	*Howe et al. (2000)*
		Multiple (a,k,q)	Yes	Yes	Shared space use	*Beauvais et al. (2019)*
		Questioning	Yes	Yes	Shared space use. Shared grazing and water source	*Meunier et al. (2017)*
	Badger	Activity signs	No	Yes	Cattle investigating or grazing at badger latrines and setts on pasture	*Scantlebury et al. (2004)*
		Camera	Yes	Yes	Badgers and cattle being within two metres of each other. Cattle investigating badger setts and latrines. Badgers visiting farms, feed stores and cattle houses and foraging on cattle pasture. Shared use of water and feed troughs	*O'Mahony (2015)*; *Campbell et al. (2019)*; *Payne et al. (2016)*; *O'Mahony (2014)*; *Tsukada et al. (2010)*; *Judge et al. (2011)*; *Anonymous (2013)*
		Direct visualisation	Yes	Yes	Badgers foraging on cattle pasture	*Benham & Broom (1989)*
		GPS	No	Yes	Badger visits to cattle farms. Badgers and cattle being present on pasture at the same time, and at different times	*Mullen et al. (2015)*; *Mullen et al. (2013)*; *Ham et al. (2019)*
		Model	No	Yes	Cattle grazing at or investigating badger latrines	*Smith et al. (2009)*; *Hutchings & Harris (2009)*
		Multiple (a,c,m)	Yes	Yes	Badgers and cattle being within two metres of each other. Badgers visiting feed stores and shared use of feed and water troughs	*Garnett, Delahay & Roper (2002)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
		Multiple (a,c,r)	No	Yes	Badgers in and around cattle buildings	*Robertson et al. (2017)*
		Multiple (a,q)	No	Yes	Badgers visiting cattle housing, feed stores and feed and water troughs	*Robertson et al. (2019)*
		Multiple (a,c)	No	Yes	Badgers visiting farmyards	*Sleeman, Davenport & Fitzgerald (2008)*
		Multiple (d,c,r)	No	Yes	Badgers visiting farm boundaries	*Tolhurst et al. (2008)*
		Multiple (c,g)	Yes	Yes	Nose to nose contact. Badgers visiting farmyards, farm buildings and feed stores and eating cattle feed	*Tolhurst et al. (2009)*
		Multiple (c,q)	Yes	Yes	Nose to nose contact. Badgers visiting, urinating and defecating in farmyards, farm buildings and feed stores and eating cattle feed	*Ward et al. (2008)*
		Multiple (c,r)	Yes	Yes	Shared space use	*Woodroffe et al. (2016)*
		Multiple (c,l)	Yes	Yes	Shared use of feed troughs	*Woodroffe et al. (2017)*
		Proximity logger	Yes	Yes	Badgers and cattle being within one to two metres of each other. Cattle visits to badger latrines	*Böhm, Hutchings & White (2009)*; *Drewe et al. (2013)*; *Drewe et al. (2012)*
	Big cat	Camera	No	Yes	No contacts observed	*Abade et al. (2018)*
		GPS	No	Yes	Lion presence on cattle pasture. Cheetah visits to cattle farms	*Weise et al. (2019)*; *Van Der Weyde et al. (2017)*
		Multiple (a,c)	Yes	Yes	Predation events and wild felid presence oncattle pasture	*Zarco-González & Monroy-Vilchis (2014)*
	Buffalo	GPS	No	Yes	Shared space and water sources	*Miguel et al. (2013)*; *Miguel et al. (2017)*; *Valls-Fox et al. (2018)*
		Model	Yes	No	Cattle and buffalo being within 100 metres of each other	*Dion, VanSchalkwyk & Lambin (2011)*
		Literature review	No	Yes	Young buffalo joining cattle herd and 'contact' (unspecified) between cattle and buffalo	*Jori et al. (2009)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
		Questioning	Yes	Yes	Shared grazing and water source	*Meunier et al. (2017)*
	Camelid	Activity signs	No	Yes	No contacts observed	*Acebes, Traba & Malo (2012)*
		Direct visualisation	Yes	No	No contacts observed	*Arzamendia & Vilá (2015)*; *Schroeder et al. (2013)*
		Multiple (a,d)	No	Yes	Shared forage	*Borgnia, Vilá & Cassini (2008)*
	Canine	Camera	Yes	Yes	Cattle and foxes being within two metres of each other. Foxes visiting farm buildings, foraging and hunting on farmland and defecating on stored feed	*Tolhurst, Ward & Delahay (2011)*
		GPS	Yes	Yes	Wolf visits to cattle pasture	*Laporte et al. (2010)*; *Steyaert et al. (2011)*; *Muhly et al. (2010)*
		Multiple (a,d)	No	Yes	Wolf and coyote presence on cattle pasture	*Gehring et al. (2010)*
		Radio-telemetry	No	Yes	Wolf visits to cattle pasture. Jackal visits to cattle farms	*Chavez & Gese (2006)*; *Kamler et al. (2019)*
	Deer	Activity signs	No	Yes	Deer presence on pasture previously grazed by cattle	*Kuiters, Bruinderink & Lammertsma (2005)*
		Camera	Yes	Yes	Shared use of feed and water troughs	*Kukielka et al. (2013)*; *Payne et al. (2016)*; *Barasona et al. (2013)*; *Carrasco-Garcia et al. (2016)*; *Tsukada et al. (2010)*
		Direct visualisation	Yes	Yes	Aggression between deer and cattle, and deer and cattle being within five metres of each other. Deer visits to cattle feed stores and deer presence on pasture at the same time and at different times to cattle. Deer licking cattle urine	*Mattiello et al. (2002)*; *Hill (2005)*; *Mattiello et al. (1997)*; *Carusi, Beade & Bilenca (2017)*
		GPS	No	Yes	Deer visits to cattle pastures and feeding areas	*Cooper et al. (2008)*; *Ribeiro-Lima et al. (2017)*; *Berentsen et al. (2014)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
		Literature review	Yes	Yes	No contacts observed	*Walter et al. (2012)*
		Multiple (a,c)	Yes	Yes	Cattle and deer at water sources at the same time	*Barasona et al. (2017)*
		Multiple (d,c)	Yes	Yes	Unspecified contact	*Brook et al. (2013)*
		Multiple (c,p)	Yes	Yes	Cattle and deer within 1.5 metres of each other. Shared use of water and food points	*Cowie et al. (2016)*
		Multiple (g,l)	No	Yes	Deer presence on cattle pasture	*Gehring et al. (2010)*
		Multiple (g,q)	Yes	Yes	Unspecified direct contact. Deer visits to cattle feed stores	*Pruvot et al. (2014)*; *Kitts-Morgan et al. (2015)*
		Proximity logger	Yes	Yes	Deer visits to stored feed	*Lavelle et al. (2016)*
		Questioning	No	Yes	Deer presence on cattle farms, and visiting and damaging feed stores	*Brook (2010)*; *Knust, Wolf & Wells (2011)*
		Radio-telemetry	No	Yes	Deer visits to cattle pasture and shared salt licks	*Coe et al. (2001)*; *Cohen et al. (1989)*; *Dohna et al. (2014)*; *Loft, Menke & Kie (1986)*
	Elephant	GPS	No	Yes	Elephant home range overlapping with cattle grazing. Elephants using same water source at the same time and at different times to cattle	*Raizman et al. (2013)*; *Valls-Fox et al. (2018)*
	Hyena	Multiple (d,r)	Yes	Yes	Predation events	*Kolowski & Holekamp (2006)*
	Kangaroo	Radio-telemetry	No	Yes	Kangaroo presence on cattle farms	*Viggers & Hearn (2005)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
	Not specified	Camera	Yes	Yes	Raccoons licking salt lick less than thirty centimetres away from cattle, and sharing water sources. Savannah wildlife grazing at the same and at different times to cattle	*Crawford et al. (2019)*; *Witmer et al. (2010)*; *Odadi et al. (2017)*
		Direct visualisation	Yes	Yes	Cattle and savanna wildlife sharing water sources at the same and at different times	*Mizutani, Kadohira & Phiri (2012)*
		Questioning	Yes	Yes	Wildlife and cattle sharing water sources and grazing at the same and at different times	*Munyeme et al. (2010)*; *Katale et al. (2013)*; *Brahmbhatt et al. (2012)*; *Molla et al. (2013)*; *Maleko et al. (2012)*
		Radio-telemetry	No	Yes	No contacts observed	*Sitters et al. (2009)*
	Raccoon	Multiple (c,l,r)	No	Yes	Shared space use. Shared food and water sources	*Atwood et al. (2009)*
	Sheep/Goat	Direct visualisation	Yes	Yes	Chamois and ibex in close proximity to cattle. Shared use of cattle pasture	*Richomme, Gauthier & Fromont (2006)*
		Multiple (g,m)	No	Yes	No contacts observed	*Clifford et al. (2009)*
	Wild horse	GPS	No	Yes	Spatial overlap of zebra home ranges with cattle grazing areas. Shared use of water source	*Raizman et al. (2013)*
		Multiple (a,d)	No	Yes	Feral horses grazing in close proximity to cattle, and using pasture prior to cattle	*Salter & Hudson (1980)*
	Wild pig	Activity signs	No	Yes	Wild boar presence on pasture previously grazed by cattle	*Guillermo Bueno et al. (2010)*; *Kuiters, Bruinderink & Lammertsma (2005)*
		Camera	Yes	Yes	Wild boar and cattle sharing water sources and feed troughs at the same time and at different times	*Kukielka et al. (2013)*; *Balseiro et al. (2019)*; *Payne et al. (2016)*; *Barasona et al. (2013)*; *Carrasco-Garcia et al. (2016)*; *Tsukada et al. (2010)*
		GPS	No	Yes	Shared space and water sources	*Barasona et al. (2014)*; *Triguero-Ocaña et al. (2019)*
		Multiple (c,g)	Yes	Yes	Wild boar and cattle sharing water source at the same time	*Barasona et al. (2017)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
		Multiple (c,p)	Yes	Yes	Feral pigs and cattle being within 20 metres of the same location at different times	*Cooper et al. (2010)*
		Multiple (g,l)	Yes	Yes	Wild boar and cattle being within 1.5 metres of each other. Shared use of food and water points	*Cowie et al. (2016)*)
		Questioning	Yes	Yes	Shared water sources	*Anderson et al. (2019)*; *Meunier et al. (2017)*
Farmed deer	Big cat	Radio-telemetry	No	Yes	No contacts observed	*Moa et al. (2006)*
	Deer	Camera	Yes	Yes	Sparring and nose to nose contact, and presence of wild deer at fence-line of farmed deer	*Vercauteren et al. (2007a)*; *Vercauteren et al. (2007b)*
Goat	Antelope	Multiple (d,k,q)	Yes	Yes	Shared space use	*Beauvais et al. (2019)*
	Big cat	Camera	No	Yes	No contacts observed	*Abade et al. (2018)*
		Multiple (a,c)	Yes	Yes	Predation events and wild felid presence on goat pasture	*Zarco-González & Monroy-Vilchis (2014)*
	Camelid	Direct visualisation	Yes	Yes	Shared forage sources at different times	*Arzamendia & Vilá (2015)*; *Schroeder et al. (2013)*
		Multiple (a,d)	No	Yes	Shared forage	*Borgnia, Vilá & Cassini (2008)*
	Canine	Radio-telemetry	No	Yes	Jackal visits to goat farms	*Kamler et al. (2019)*
	Chimpanzee	Direct visualisation	Yes	No	No contacts observed	*Hockings et al. (2012)*
	Deer	Camera	Yes	Yes	No contacts observed	*Carrasco-Garcia et al. (2016)*
	Hyena	Multiple (d,r)	Yes	Yes	Predation events	*Kolowski & Holekamp (2006)*
	Not specified	Camera	No	Yes	Presence on pasture of predators not associated with livestock predation	*Bromen et al. (2019)*
	Wild pig	Camera	Yes	Yes	No contacts observed	*Carrasco-Garcia et al. (2016)*
		Questioning	Yes	Yes	Predation and presence on farm	*Anderson et al. (2019)*
Not specified	Big cat	GPS	No	Yes	No contacts observed	*Oriol-Cotterill et al. (2015)*
	Sheep/Goat	Direct visualisation	No	Yes	Shared space use and forage	*Shrestha (2007)*
	Wild horse	Multiple (c,g)	Yes	Yes	Livestock within photographing distance of khulan horses	*Kaczensky et al. (2019)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
Pig	Canine	Camera	Yes	Yes	Foxes approaching and entering farrowing huts and taking piglets. Fox presence in pig paddocks	*Fleming et al. (2016)*
	Deer	Camera	Yes	Yes	Shared water sources	*Kukielka et al. (2013)*; *Carrasco-Garcia et al. (2016)*
		Multiple (g,l)	Yes	Yes	Deer and pigs within 1.5 metres of each other. Shared use of food and water	*Cowie et al. (2016)*
	Wild pig	Camera	Yes	Yes	Shared food and water sources. Wild boar visiting acorn fields used by domestic pigs	*Kukielka et al. (2013)*; *Carrasco-Garcia et al. (2016)*
		GPS	No	Yes	No contacts observed	*Pearson et al. (2014)*
		Multiple (a,c,g)	No	Yes	Wild boar home range overlap with domestic pigs and shared space use	*Barth et al. (2018)*
		Multiple (a,c,q)	No	Yes	No contacts observed	*Braz et al. (2019)*
		Multiple (c,m)	Yes	Yes	Pigs and wild boar present in the same camera trap image. Shared use of water	*Cadenas-Fernández et al. (2019)*
		Multiple (c,q)	Yes	Yes	Wild boar and pigs within 1.5 metres of each other. Shared use of food and water	*Cowie et al. (2016)*
		Multiple (g,l)	No	Yes	Feral swine presence around pig farms	*Engeman, Betsill & Ray (2011)*
		Multiple (m,q)	Yes	Yes	Evidence of mating (cross-bred piglets). Wild boar within two metres of pig enclosure	*Wu et al. (2012)*
		Multiple (p,r)	Yes	Yes	Feral and domestic swine in contact through fences. Feral pigs within 500 metres of pig farm	*Wyckoff et al. (2009)*
		Questioning	Yes	Yes	Wild and domestic pigs fighting and mating. Shared use of water, food and space at different times	*Jori et al. (2017)*; *Trabucco et al. (2013)*; *Kukielka et al. (2016)*; *Anderson et al. (2019)*

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Table 4 (*continued*)

Livestock	Wildlife	Method(s)[a]	Type of contact recorded		Examples of the types of contact(s) reported between each livestock and wildlife species	References
			Direct	Indirect		
Sheep	Antelope	Multiple (d,k,q)	Yes	Yes	Shared space use	*Beauvais et al. (2019)*
	Badger	GPS	No	Yes	Badger visits to sheep farms	*Mullen et al. (2015)*
	Big cat	Radio-telemetry	Yes	Yes	Predation	*Stahl et al. (2002)*; *Moa et al. (2006)*
	Camelid	Direct visualisation	Yes	Yes	Shared forage sources at different times	*Arzamendia & Vilá (2015)*; *Schroeder et al. (2013)*
		Multiple (a,d)	No	Yes	Shared forage	*Borgnia, Vilá & Cassini (2008)*
	Canine	GPS	Yes	No	No contacts observed	*Ausband et al. (2013)*
		Radio-telemetry	No	Yes	Jackal visits to sheep farms	*Kamler et al. (2019)*
	Chimpanzee	Direct visualisation	Yes	No	No contacts observed	*Hockings et al. (2012)*
	Deer	Camera	Yes	Yes	No contacts observed	*Carrasco-Garcia et al. (2016)*
		Direct visualisation	Yes	Yes	Deer and sheep within five metres of each other	*Colman et al. (2012)*
	Hyena	Multiple (d,r)	Yes	Yes	Predation events	*Kolowski & Holekamp (2006)*
	Kangaroo	Radio-telemetry	No	Yes	Kangaroo visits to sheep farms	*Viggers & Hearn (2005)*
	Not specified	Camera	No	Yes	Presence on pasture of predators not associated with livestock predation	*Bromen et al. (2019)*
	Sheep/Goat	Direct visualisation	Yes	Yes	Chamois and ibex in close proximity to domestic sheep and sharing pasture	*Richomme, Gauthier & Fromont (2006)*; *Rüttimann, Giacometti & McElligott (2008)*
		Radio-telemetry	No	Yes	Unspecified contact	*O'brien et al. (2014)*
	Wild pig	Activity signs	No	Yes	Wild boar foraging on sheep pasture	*Guillermo Bueno et al. (2010)*
		Camera	Yes	Yes	No contacts observed	*Carrasco-Garcia et al. (2016)*
		Questioning	Yes	Yes	Predation and presence on sheep farms	*Anderson et al. (2019)*

Notes.
[a]Some studies used multiple methods combining variations of activity signs (a), cameras (c), Direct visualisation (d), GPS (g), literature review and expert knowledge elicitation (k), models (m), pathogen monitoring (p), proximity loggers (l), questioning (q) and radio-telemetry (r).
[b]Where modelling alone is reported, empirical data was used that was not specifically wildlife-livestock contact data. For example, using data on cattle grazing habits to model the frequency of contact with badger faeces on pasture.

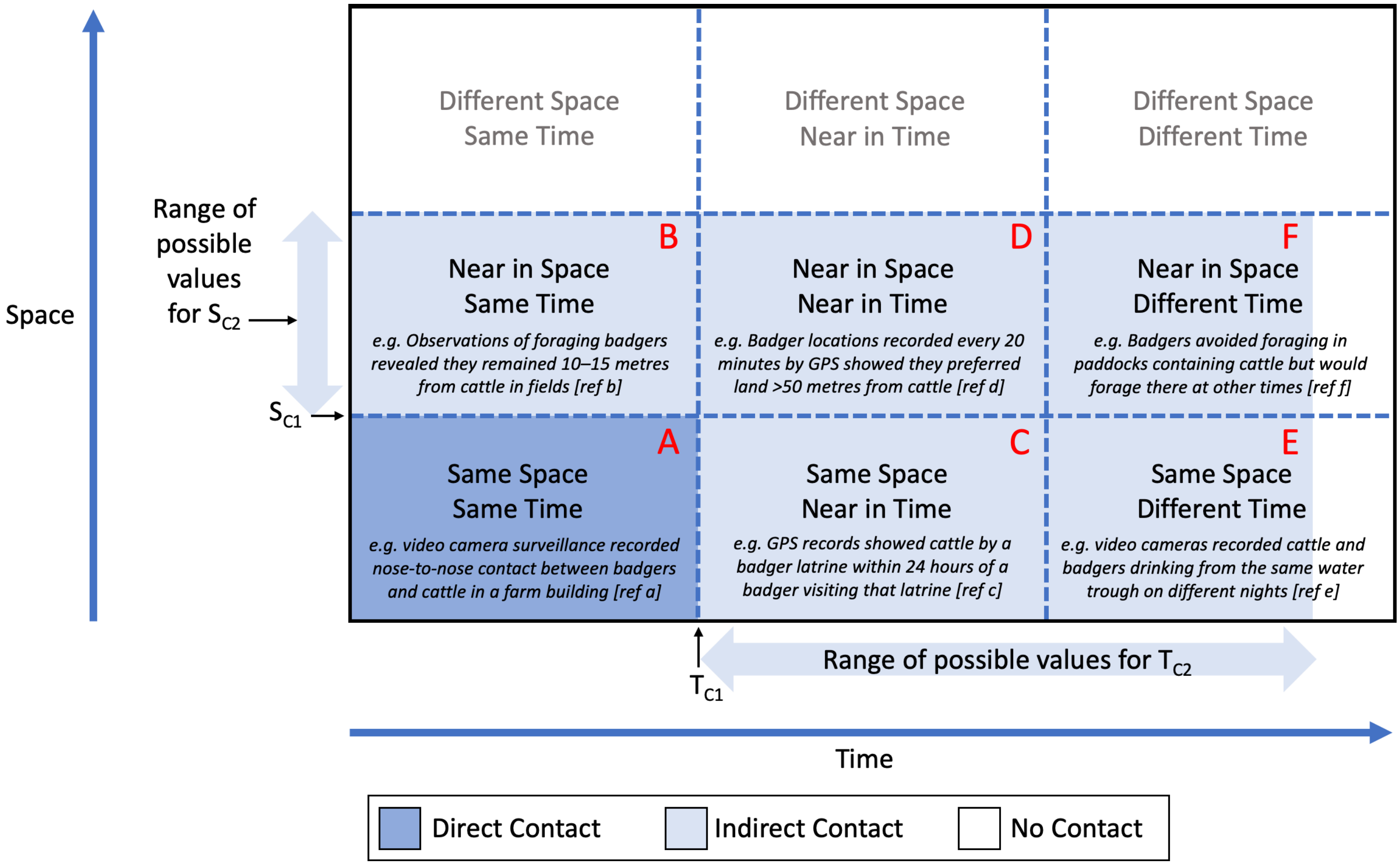

Figure 4 A proposed generic framework for describing and categorising contacts between livestock and wildlife. Examples from studies of contacts between badgers and cattle are provided to demonstrate the use of the framework. S_{C1} represents 'critical space 1', the maximum amount of space (distance or area) within which direct contact may occur; and T_{C1} represents 'critical time 1', the maximum duration of time within which direct contact may occur. Similarly, S_{C2} represents 'critical space 2', the maximum amount of space (distance or area) within which indirect contact may occur; and T_{C2} represents 'critical time 2', the maximum duration of time within which indirect contact may occur. Same, near and different are used here to illustrate spatial and temporal differences between examples (see Tables 2–4 for values and ranges for these parameters from published studies). Note that the lighter blue shading does not extend all the way to the right of the diagram because there is an upper limit to the value of time which T_{C2} can take: beyond this value, animals in the same (or nearby) space will not be in contact. Ref a = *Tolhurst et al. (2009)*, ref b = *Benham & Broom (1989)*, ref c = *Drewe et al. (2013)*, ref d = *Woodroffe et al. (2016)*, ref e = *O'Mahony (2015)*, ref f = *Mullen et al. (2015)*.

Full-size DOI: 10.7717/peerj.10221/fig-4

of the wildlife and livestock involved, the methods used to detect contacts and the system being studied such as the environmental conditions and pathogen characteristics in studies where contacts are representative of disease transmission. Definitions of direct contact were extremely diverse, ranging from direct physical contact to animals being merely within a hundred metres of each other. Indirect contact ranged from animals sharing resources, being within five kilometres of each other or overlapping in home ranges, and the time window that these events occurred in varied from hours to weeks.

The aim of this generic unified framework is to promote consistent reporting of definitions of contacts enabling comparisons to be made between the approaches of wildlife-livestock contact studies, regardless of the species or pathogen studied or the context of the study. This is needed because our systematic review found that while wildlife-livestock contact data was collected in terms of space and time, some studies omitted space or time in their definitions, or there was a complete lack of a definition. Conflicting and overlapping definitions of direct and indirect contact were also identified. Making any sort of meaningful comparison between such studies is challenging. For example it is difficult to assess what, if any, implications there are for deer-cattle disease transmission from a behavioural study showing deer avoid cattle despite similar habitat preferences (*Mattiello et al., 2002*), without knowing what types of contact (e.g., direct or indirect; what specific types) were likely to be meaningful. It is even difficult to compare studies within the same system, for example establishing the relevance of cattle-badger contacts for bovine tuberculosis transmission when some studies define a contact as 'presence on farm' (*Mullen et al., 2015*; *Sleeman, Davenport & Fitzgerald, 2008*) and others define it as 'presence in buildings', and neither study defines the time window. Use of the generic unified framework would enable consistent reporting of definitions between studies and is an important step if the results of wildlife-livestock contact studies are to be comparable.

Applications of a generic unified framework

Models that incorporate empirical rather than theoretical information on the frequency and duration of contacts important for disease transmission are more likely to be useful for disease mitigation (*Craft, 2015*). The use of a standardised definition framework in future studies of livestock-wildlife contacts would enable consistency in datasets and enable the retrospective selection of contact data relevant to a particular model, which could then be incorporated in a similar way to the data used in recent bovine tuberculosis transmission models (*Wilber et al., 2019*; *Silk et al., 2018*). The generic unified framework proposed in this current paper could also be useful in designing livestock-wildlife contact studies, since defining the type of contact to be detected—in addition to practical considerations, such as an area's signal strength affecting the viability of GPS device use—helps with the choice of detection method. The framework is also flexible and applicable to different contexts, species and diseases since it allows for the variation in definitions seen in this review, and it is hoped it will broaden the range of future livestock-wildlife contact studies.

To resolve human-wildlife conflicts usually requires robust livestock-wildlife contact studies. At least 120 studies that only used predation events to infer livestock-wildlife contacts were excluded from the review, yet predators –particularly wolves –were the second most commonly studied group of wild mammals. Given that predation studies appear to form a large proportion of wildlife-livestock contact studies, this is an area where adoption of the generic framework could help design meaningful contact studies to evaluate preventive measures without relying solely on predation events.

Further development of the generic unified framework

The generic unified framework does not provide an overall consensus on definitions of direct and indirect contact, but does provides a structure with which to start this process. While using the generic unified framework provides a standardised definition of contact in time and space, identifying the types of contact that are relevant to the study, and thus the values of S_C and T_C, will vary depending on the objectives and context of each study. While a universally accepted set of definitions for contacts is difficult to devise, we hope that by defining Sc and Tc here we will encourage the start of the debate around (and between) studies of similar contexts, and perhaps then acceptable ranges for these values will emerge. Developing a framework for deriving S_C and T_C, based upon the species studied, environment, pathogen and methodology is beyond the scope of this review, and would be a necessary next step so that wildlife-livestock contact rates could be comparable between studies of similar contexts. For example, for disease studies, it would be advisable that S_C and T_C were based on values below which transmission is likely to occur, such as aerosol dispersion distance and environmental survivability. For any system, there may be a range of appropriate values for S_C and T_C.

The generic unified framework presented in this paper is a step towards being able to compare observation methods and contact data in order to standardise and evaluate different monitoring methods. This is important as our systematic review revealed that the methods used to observe livestock-wildlife contacts to date have often had low detection rates and therefore been of low power due to the difficulty of monitoring cryptic wildlife species, and the rarity of some types of wildlife-livestock contacts, particularly direct contacts. Further considerations for the comparison of observation methods are the representativeness of individuals monitored, especially with methodologies that require the marking of individuals such as GPS and proximity loggers, and a standardised system for relativizing the number of contacts with regards to the total observation effort. For example, two studies will not be comparable if study A only uses 3 camera traps and study B uses 100 camera traps, or if study C collects GPS locations every hour when study D collects only one GPS fix per day. Reporting representativeness of individuals and relativizing contact rates in terms of total population will go some way to establishing the power of wildlife-contact studies. Furthermore, it may be useful for studies to indicate the detection limits of the methodology used, in terms of space and time.

Scope of existing wildlife-livestock contact studies

This review has identified the narrow scope and limited geographic range of livestock-wildlife contact studies, which means the data summarised in this review should not be considered representative of all wildlife-livestock contacts worldwide. The majority of studies focussed on cattle-wildlife contacts and diseases of cattle. Bovine tuberculosis (infection with *M. bovis*) featured prominently, indicative of the economic and potentially zoonotic importance of this disease to the USA and UK, where the most livestock-wildlife contact studies were conducted (*De la Rua-Domenech, 2006*; *O'Brien et al., 2011*). Foot-and-mouth-disease was the most studied viral pathogen and this is most likely explained by its broad geographical spread and high economic impact (*Knight-Jones & Rushton, 2013*). This demonstrates the human-centric view of the wildlife-livestock interface, with most focus on the impacts on humans and domestic animals, and very little (if any) focus on the value of wildlife (*Chardonnet et al., 2002*). There were, however, some livestock-wildlife contact studies of high impact conservation importance such as infection with Mannheimia spp. in bighorn sheep (*Ovis canadensis*) and Pasteurella spp. in saiga antelope (*Clifford et al., 2009*; *O'brien et al., 2014*; *Beauvais et al., 2019*). If we are to collect more (and better) wildlife-livestock contact data that include a broader range of species and contexts, careful consideration must be used when selecting the most effective and practical observational method for monitoring cryptic wildlife species.

This review highlights that observing contacts between multiple species is possible and can yield high quality information. Increasing the efficiency of monitoring methods would justify their use for more applications. Health surveillance systems at livestock-wildlife interfaces have been suggested as a method to detect and control emerging diseases along with preventing contact between wildlife and livestock (*Gortazar et al., 2015*). Preventing high-risk contacts may be more cost-effective than surveillance, but the effectiveness of prevention strategies will need to be evaluated by monitoring contacts, or lack thereof. More efficient monitoring will also allow for quantitative risk assessments of wildlife-livestock contacts which are presently difficult to conduct due to a limited understanding of potential contacts leading to pathogen transmission (*Miller, Farnsworth & Malmberg, 2013*). Some observation methods such as camera traps are likely to have the ability to identify new potential transmission routes between livestock and wildlife (e.g., the use of cattle salt licks by raccoons (*Witmer et al., 2010*)), and may identify livestock-wildlife contacts previously not considered (e.g., observing farm visits by foxes during a study focussing on badgers (*O'Mahony, 2015*)). Identifying wildlife species that may be the origin of rapidly emerging human diseases is a priority to prevent future pandemics (*Morse et al., 2012*). In situations where human infections are mediated by livestock, rapid implementation of observational methods to detect contacts between wildlife and livestock could more quickly identify wildlife hosts and risky behaviours. In order to determine the efficiency and efficacy of different observational methods, the methods used and data collected by them must be comparable, hence the need for a unified framework.

Limitations of this review

Our study has some limitations which we summarise here. At present, our generic unified framework does not explicitly account for disease transmission via vectors or fomites, although the latter will to some extent be captured within our definition of indirect contact. In order that observation methods were likely to be comparable between species, we focussed on terrestrial mammals so did not address diseases primarily hosted by birds or bats such as avian influenza, Nipah virus and Hendra virus. Small terrestrial mammals (<5 kg) were also not included for this reason, and because a disproportionate number of rodent studies focus on their roles as laboratory animals or farm pests, and not on contacts with livestock. While the generic unified framework may be applicable to these types of wildlife, it is unclear which observational methods seen in this review would be most effective or efficient, and the conclusions drawn from this review may not be reflective of systems that involve other taxa.

CONCLUSION

As human populations continue to expand and agriculture encroaches further on wildlife habitats, disease spill-over (in both directions) between wildlife, livestock and humans is becoming more frequent (*Wiethoelter et al., 2015*). As a result, the study of contacts between livestock and wildlife is receiving ever increasing attention. This systematic review of the observational methods used to study contacts, and the subsequent proposal of a generic unified framework for defining contacts, are two steps towards ensuring that data are collected and reported in a standardised way at a time of increasingly urgent need.

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Author Contributions

- Sonny A. Bacigalupo conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Linda K. Dixon, Simon Gubbins and Adam J. Kucharski conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Julian A. Drewe conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

Details of the publications included in the review and the raw data extracted are available as Supplemental Files.

Supplemental Information

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