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

Sonny A Bacigalupo Corresp., 1 , **Linda K Dixon** 2 , **Simon Gubbins** 2 , **Adam J Kucharski** 3 , **Julian A Drewe** 1

1 Royal Veterinary College, Hatfield, United Kingdom
2 The Pirbright Institute, Woking, Surrey, United Kingdom
3 London School of Hygiene & Tropical Medicine, University of London, London, United Kingdom

Corresponding Author: Sonny A Bacigalupo
Email address: sbacigalupo@rvc.ac.uk

Wild animals are the source of many pathogens of livestock and humans. The current global pandemics of both COVID-19 (affecting people) and African swine fever (affecting pigs) are likely to have originated in wildlife. Concerns about the potential for the transmission from wildlife of diseases of economic and zoonotic importance 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, and perhaps surprisingly, 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 43,000 publications were screened, of which 122 fulfilled specific criteria for inclusion in the analysis. The majority of studies examined contacts between cattle and badgers or deer, with studies involving wild pigs being 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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Sonny A. Bacigalupo[1], Linda K. Dixon[2], Simon Gubbins[2], Adam J. Kucharski[3], Julian A. Drewe[1]

[1]Royal Veterinary College, University of London, Hatfield, UK

[2] The Pirbright Institute, Woking, Surrey, UK

[3] London School of Hygiene & Tropical Medicine, London, UK

Corresponding Author

Sonny Bacigalupo[1]

Royal Veterinary College, Hawkshead Lane, Brookmans Park, Hatfield, AL9 7TA, UK

Email address: sbacigalupo@rvc.ac.uk

Abstract

Wild animals are the source of many pathogens of livestock and humans. The current global pandemics of both COVID-19 (affecting people) and African swine fever (affecting pigs) are likely to have originated in wildlife. Concerns about the potential for the transmission from wildlife of diseases of economic and zoonotic importance 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, and perhaps surprisingly, 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 43,000 publications were screened, of which 122 fulfilled specific criteria for inclusion in the analysis. The majority of studies examined contacts between cattle and badgers or deer, with studies involving wild pigs being 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.

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 [1]. 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 [2], 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 [3]. 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 [4]. 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 [5]. 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 [6]. 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) [7], 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 [8-10]. 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 [11]. 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 [12]. 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 [5, 13]. 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 [14-16]. 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 meaningful contact will vary depending on the aim of the study.

In the context of disease transmission, defining a contact is challenging and while types of contact are often broadly grouped into being ‘direct’ or ‘indirect’, there are no standardised definitions [17]. 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 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 [11]. 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' [18], *wild animals* as 'free-ranging non-domesticated mammals', and *contact* as 'activity implying an interaction or association between species'. 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, types of, and risk factors for, 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 [19, 20].

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. There were no disagreements. We wished to capture publications that collected, used or analysed data to investigate direct or indirect contacts between farmed livestock and wild mammals whose adult bodyweight is typically >5kg (thus excluding studies on small rodents). 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 agreed by the researchers to avoid ambiguity when evaluating publications for inclusion. Direct contact was provisionally defined 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. Study data was extracted and livestock and wildlife species, observation methods and definitions were categorised. Studies were grouped into seven themes that emerged during data extraction and were agreed upon by the authors (Fig. S1). Results were visualised and plotted using R (version 3.6.3 [21]) and R packages listed in Table S2.

The quality of the selected papers was appraised against a set of criteria based on the study objectives, definitions of contact, certainty of results and robustness of conclusions (Table 1). Each criterion contributed equally to the overall quality score for each paper.

Development of a Generic Unified Framework

The generic unified framework was developed by grouping and identifying commonalities in definitions of ‘direct’ and ‘indirect’ contact. The spatial (distance) and temporal (time) limits separating meaningful contacts from non-contact events were identified for each study. These data informed the development of a generic framework for defining direct and indirect contact.

Results

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).

Study aims were reported in 120 (98%) publications, of which 100 (83%) studies aimed specifically to investigate contact between livestock and wildlife. Contacts were observable, and not simply alluded to, in 100 (82%) publications. Direct or indirect contact, or both, were defined in 86 (70%) publications. Study power was mentioned in only 11 (9%) publications and the level of uncertainty was acknowledged in 64 (53%) publications. Conclusions were robust and directly derived from the results in 109 (89%) publications. The overall quality scores of the papers ranged from 0 (one study) to 7 (eight studies), and 91 (75%) publications scored between 4 and 6 out of 7 (Fig. S2).

Disease was the dominant theme and featured in 80 of 122 studies (66%), followed by human-wildlife conflict (22/122 studies; 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; 25%), wild pigs (26/122; 21%) and badgers (25/122; 20%: Fig. S3 and S4). The wildlife species were not specified in 11 papers concerning wild ungulates competing for livestock grazing [22-24] or as hosts of cattle diseases such as bovine tuberculosis [25-27] and foot-and-mouth disease [28, 29].

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 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 and large herbivores such as buffalo, wild horses and elephants. Other methods used to monitor wildlife were direct observation (21; 17%), farmer questionnaires (20; 16%), radio-transmitters (17; 14%), activity signs (15; 12%) and proximity loggers (7; 6%). 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 and co-authors [30] used GPS collars to monitor wild deer and farmer questionnaires 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. S5). Methods such as GPS collars and radio-tracking (telemetry) were used to collect location and proximity data on a broad scale (e.g. [10, 31, 32]), 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. [9]). Camera traps and direct observation were used to observe wildlife and livestock activity, such as nose-to-nose contacts between cattle and badgers [33], foxes taking piglets from farrowing huts [34] and wild boar eating from cattle troughs [35]. 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 [36] and GPS collars to demonstrate the avoidance of livestock pasture by lions [37]. Thirty studies combined more than one method to monitor wildlife, such as [38] 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 (Table 2; Table 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 spatial distance of wildlife to a location that livestock had previously occupied, within a certain time frame (Table 3), although there were two studies that used time to define direct contact [15, 39]. 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 [40]. 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 (7 studies) to within 120m of each other (1 study), and indirect definitions ranging from within the same camera image (2 studies) to within 50 kilometres of a location (1 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 (6 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 [15] 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 median indirect contacts occurred in the order of hundreds or even thousands of contacts (Table 4). Low study power was acknowledged by 11 studies (9%), and is likely to be a feature of many more which did not report it. 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 the two recurring parameters in the definitions in this review, albeit interpreted in a wide variety of ways. In an effort to unify these themes, a novel generic framework to categorise wildlife-livestock contacts is proposed in Fig. 4, based on the locations of individuals in space and over time. 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. Using this framework, we propose that the contact type (direct or indirect) is defined using the two parameters S_C and T_C. For *direct contact*, two individuals are within a pre-specified critical space (distance or area: S_{C1}) within a pre-specified critical time window (T_{C1}). For *indirect contact* animals are within another pre-specified critical space (S_{C2}) within a pre-specified critical time window (T_{C2}). T_{C2} may be the same as T_{C1} (if S_{C2} is larger than S_{C1}) or T_{C2} may be different to T_{C1} (in which case T_{C2} will usually, but not always, be larger than T_{C1}). Similarly, S_{C2} may be the same as S_{C1} (if T_{C2} is larger than T_{C1}) or S_{C2} may be different to S_{C1} (in which case S_{C2} will usually, but not always, be larger than S_{C1}). The reader is directed to Fig. 4 for examples from the literature of possible combinations of S_C and T_C. Although these critical values will likely vary between studies (depending on, for example, the animal species, the purpose of the study and the critical time window of a contact), the adoption of this generic framework to define direct and indirect contacts will help ensure results between studies are more easily comparable.

Discussion

The generic unified framework was developed to promote consistent definitions of contacts and enable meaningful comparisons between studies regardless of the species studied or the context of the study. This is needed because our systematic review found definitions describing contacts between livestock and wildlife to be wide-ranging. Direct contact was 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. 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 [41], 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' [42, 43] and others define it as 'presence in buildings', and neither study defines the time window.

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 [11]. The use of a standardised definition framework in future studies of livestock-wildlife contacts would enable consistency in datasets, which could then be incorporated into models in a similar way to the retrospective data used in recent bovine tuberculosis transmission models [16, 44]. The generic unified framework proposed in this current paper will be useful in designing livestock-wildlife contact studies since defining the type of contact helps with the choice of observation method. The framework is also flexible and applicable to different contexts, species and diseases, and it is hoped it will broaden the range of future livestock-wildlife contact studies.

This review has identified the narrow scope of livestock-wildlife contact studies, with the majority of studies focusing 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 [45, 46]. That foot-and-mouth-disease was the most studied viral pathogen is likely explained by its broad geographical spread and high economic impact [47]. 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 [48]. There were, however, livestock-wildlife contact studies of high impact conservation importance such as mannheimiasis in bighorn sheep (*Ovis canadensis*) and pasteurellosis in saiga antelope [49-51]. 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.

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.

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 [52]. Preventing high-risk contacts may be more cost-effective than surveillance, but the effectiveness of prevention strategies will need to 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 [53]. 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 racoons [26]), and may identify livestock-wildlife contacts previously not considered (e.g., observing farm visits by foxes during a study focussing on badgers [54]). Identifying wildlife species that may be the origin of rapidly emerging human diseases such as COVID-19 is a priority to prevent future pandemics [55]. In situations where human infections are mediated by livestock, rapid implementation of observational methods to detect contacts between wildlife and livestock could improve the efficiency of identifying 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.

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 been of low power, particularly considering the relatively rare nature of certain types of direct contact.

Our study has some limitations which we summarise here. At present, our generic unified framework does not explicitly account for disease transmission via vectors (e.g. mosquitoes) or fomites (e.g. vehicle tyres), although the latter will to some extent be captured within our definition of indirect contact. We focussed on mammals so did not address diseases such as avian influenza. Small mammals (<5kg) were not included in this review despite bats and some rodents being hosts of pathogens that affect livestock such as Nipah virus, Hendra virus and leptospirosis. While the generic unified framework may be applicable to these types of wildlife, it is unclear whether the observational methods seen in this review would be applicable.

As human populations continue to expand and agriculture encroaches further on wildlife habitats, disease spill-over between wildlife, livestock and humans is becoming more frequent [1]. 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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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 (wildlife, livestock, contact term) 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.

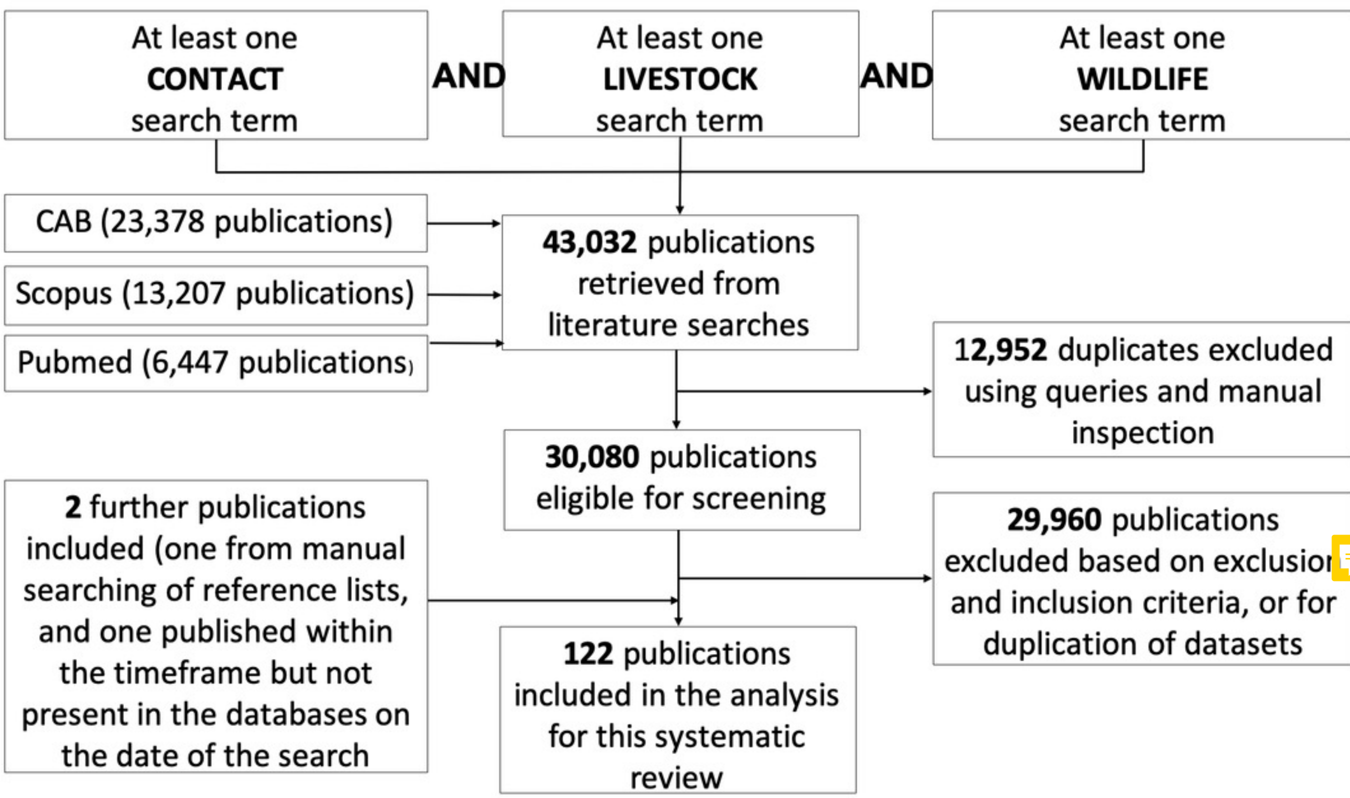

Figure 2

Distribution of the publication times of 122 papers included in the systematic review.

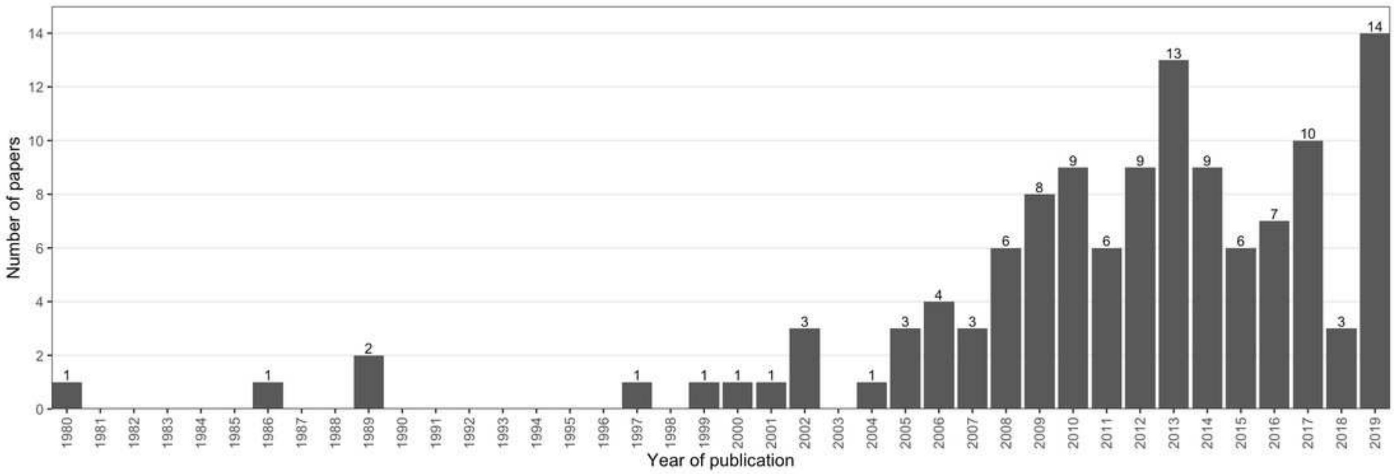

Figure 3

Methods used to monitor wildlife.

Data from 122 papers 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 numbers of studies exceed 100% for some groups.

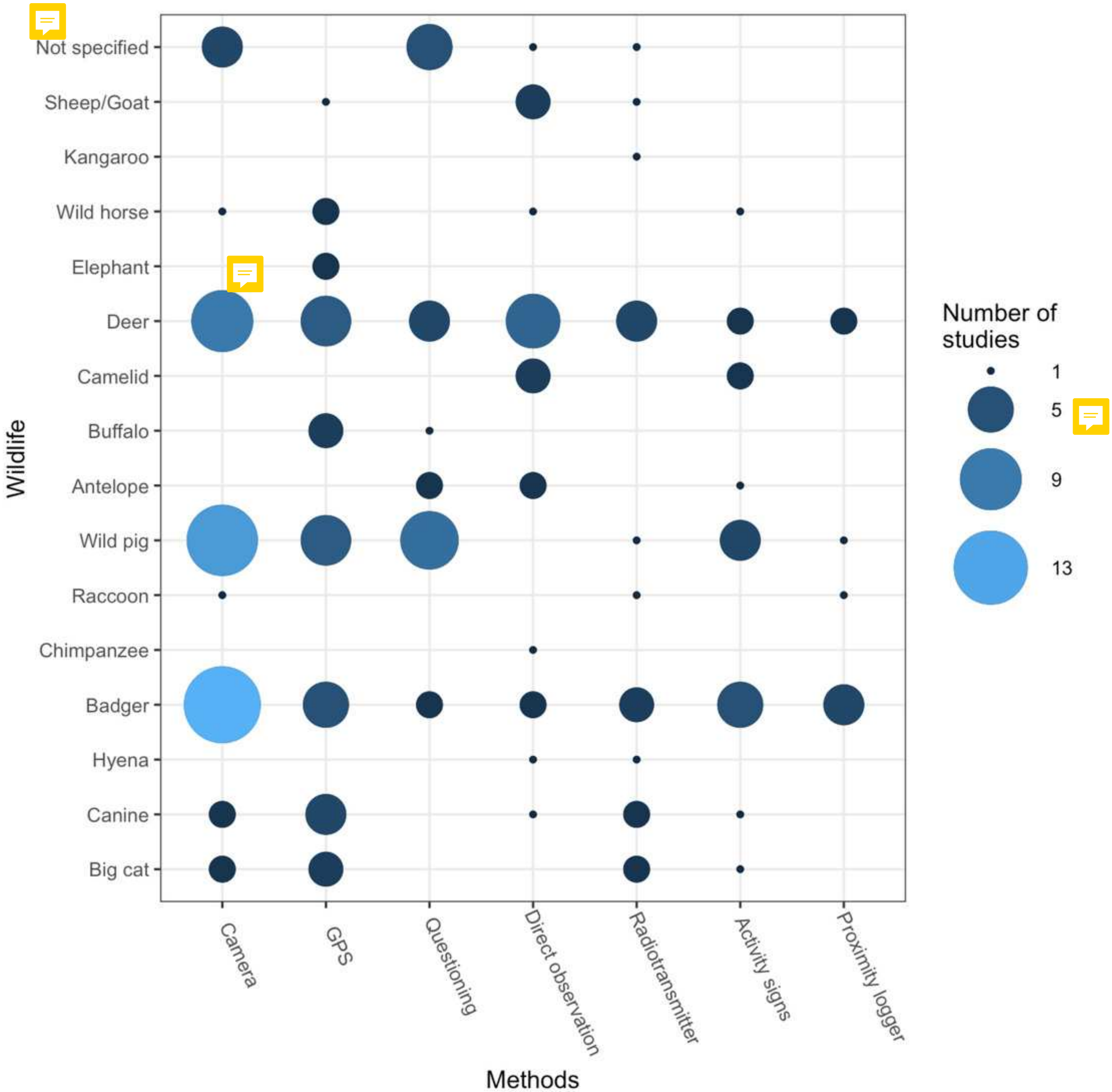
Not specified
Sheep/Goat
Kangaroo
Wild horse
Elephant
Deer
Camelid
Buffalo
Antelope
Wild pig
Raccoon
Chimpanzee
Badger
Hyena
Canine
Big cat
Wildlife
Camera
GPS
Questioning
Direct observation
Radiotransmitter
Activity signs
Proximity logger
Methods
Number of studies
1
5
9
13

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. The two key parameters are time and space: 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. Thus for a *direct contact* to occur, two or more individuals must be within a pre-specified critical space (distance or area: S_{C1}) within a pre-specified critical time window (T_{C1}). 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. Thus for an *indirect contact* to occur, two or more individuals must be within a pre-specified critical space (distance or area: S_{C2}) within a pre-specified critical time window (T_{C2}). Note that T_{C2} may be the same as T_{C1} (if S_{C2} is larger than S_{C1}: compare example A with example B) or T_{C2} may be different to 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). 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) or S_{C2} may be different to 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). The values of time or space which relate to being the *same*, *near* or *different* will vary by system and will depend on factors such as host behaviour and the survival time of an infectious dose of pathogen in the environment; 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. 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.

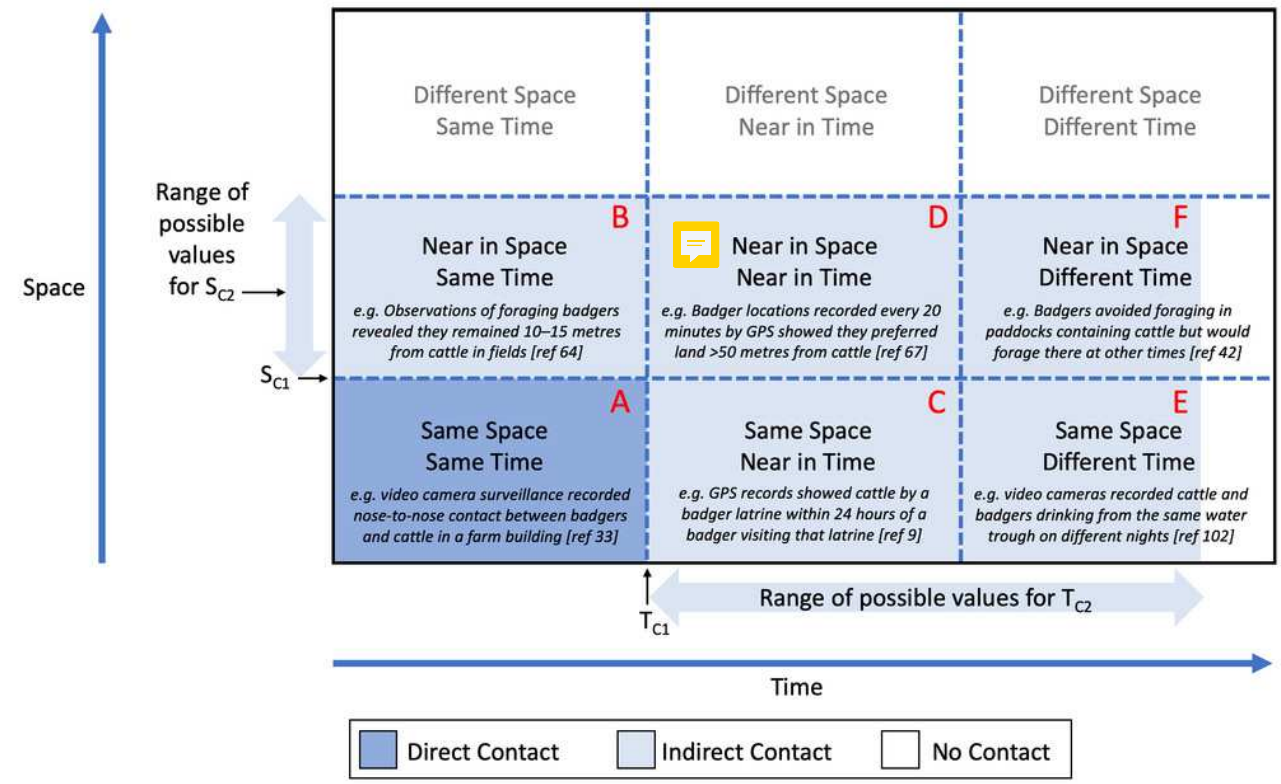

Table 1(on next page)

Exclusion and inclusion criteria to select studies for the systematic review of livestock and wildlife, and criteria used during data extraction to derive a ‘quality score’ for each study

Exclusion Criteria

1. Study does not involve a wild mammal species where adults are typically heavier than 5kg.
2. Study does not involve a farmed mammal species where adults are typically heavier than 5kg, 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.

Quality Appraisal Criteria

1. The study has clear aim(s) or objective(s)
2. One aim or objective is to investigate contact between livestock and wildlife
3. Direct or indirect contact is defined
4. Contacts are observable, not simply implied or alluded to
5. The power of the study is considered
6. Level of uncertainty of results are acknowledged
7. Conclusions are robust and are directly derived from the results

Table 2(on next page)

Definitions of direct contact from a systematic review of studies of livestock and wildlife.

Parameters are listed in ascending order of distance between animals. Definitions that have been used for both direct and indirect contacts are shaded grey.

'Direct Contact' definition	Number (%) of publications using this definition	% Cumulative	References
At least two individuals making physical contact	9 (16)	16	[33, 56-63]
Individuals close enough to inhale expired breath	1 (2)	17	[64]
Individuals within one metre of the same location within one second of each other	1 (2)	19	[15]
Individuals within two metres of each other	5 (9)	28	[9, 40, 65-67]
Individuals within five metres of each other	3 (5)	33	[8, 68, 69]
Individuals within the same camera image	5 (9)	42	[35, 70-73]
Individuals within 20 metres of each other	1 (2)	45	[74]
Individuals within 20 metres of the same location within 15 minutes of each other	1 (2)	47	[39]
Individuals within same farm building	1 (2)	48	[34]
Individuals within holding (farm) boundary	1 (2)	50	[75]
Individuals within 100 metres of each other	2 (4)	54	[76, 77]
Individuals within 120 metres of each other	1 (2)	56	[78]
Studies that reported the frequency of, types of, or risk factors for, direct contacts without first defining them	25 (44)	100	[13, 22, 25, 26, 29, 30, 41, 79-96]
Total	56 (100)		

Table 3(on next page)

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.

‘Indirect Contact’ definition	Number (%) of publications using this definition	% Cumulative	References
Individuals within the same camera image	2 (2)	2	[73, 97]
Two individuals photographed by the same camera trap within a specific time interval	1 (1)	3	[35]
Latrine (faecal pits) visits	5 (4)	7	[9, 65, 98-100]
Individuals visiting the same food and water sources at unspecified time intervals	13 (11)	18	[15, 27, 56, 63, 66, 68, 70, 89, 90, 101-104]
Individuals visiting the same food or water source at the same time	2 (2)	20	[25, 62]
Individuals in the same space at different times	3 (3)	22	[31, 58, 105]
Individuals in the same space at the same time	2 (2)	24	[106, 107]
Individuals in the same space at unspecified time interval	3 (3)	27	[10, 12, 69]
Individuals using the same food or water source within 6 hours	1 (1)	28	[40]
Individuals within 20 metres of the same location within 6 hours of each other	1 (1)	28	[39]
Individuals within 30 metres of livestock or feed	1 (1)	29	[108]
Presence in farm buildings at unspecified time interval	5 (4)	34	[26, 33, 59, 109, 110]
Individuals within 50 metres of each other	1 (1)	34	[85]
Individuals within 52 metres of the same location within one hour of each other	1 (1)	35	[111]
Individuals within 120m of each other	1 (1)	36	[28]
Individuals using the same space with 7 days of each other	2 (2)	38	[24, 72]
Individuals using the same space within	1 (1)	39	[74]

'Indirect Contact' definition	Number (%) of publications using this definition	% Cumulative	References
15 days of each other			
Presence on pasture at the same time	5 (4)	43	[49, 64, 91, 95, 96]
Presence on pasture at unspecified time interval	8 (7)	50	[30, 34, 36, 67, 112-115]
Presence on pasture at different times	1 (1)	51	[116]
At holding boundary and on pasture at unspecified time interval	1 (1)	52	[117]
Presence on farm at unspecified time interval	12 (10)	62	[42, 43, 50, 54, 88, 94, 118-123]
At holding (farm) boundary	3 (3)	65	[60, 61, 124]
Individuals within 120 metres of the same location at different times	1 (1)	66	[78]
Individuals within 300 metres of the same location within 15 days of each other	2 (2)	67	[125, 126]
Individuals within 500 metres of the same location within 6 weeks of each other	1 (1)	68	[93]
Individuals within 500m from holding (farm) boundary	2 (2)	70	[75, 76]
Individuals within 50 kilometres of the same location within 3 months of each other	1 (1)	71	[51]
Studies that reported the frequency of, types of, or risk factors for, indirect contacts without first defining them	34 (29)	100	[22, 23, 29, 32, 37, 41, 79-84, 89, 92, 127-146]
Total	116 (100)		

Table 4(on next page)

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

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
Camelid	Antelope	Multiple (d,k,q)	[51]	-	-	-	-	-	-	-	-	Shared space use
	Camelid	Direct observation	[79]	0	0	0	1	-	-	-	-	Mixed grazing and shared forage
		Multiple (a,d)	[130]									
Cattle	Antelope	Activity signs	[129]	0	0	0	1	6	6	6	1	Shared space use, grazing and water
		Direct observation	[145]									
		Model	[92]									
		Multiple (a,k,q)	[51]									
		Questioning	[93]									
	Badger	Activity signs	[98]	16.6	2.5	0-135	10	471.6	154	12-2099	17	Nose to nose contact, and being within two metres of each other. Cattle investigating or grazing at badger latrines and setts on pasture. Badgers visiting farms and farm buildings, and shared use of feed and water troughs.
		Camera	[54, 58, 73, 102, 104, 119, 146]									
		Direct observation	[64]									
		GPS	[42, 107, 114]									
		Model	[99, 100]									
		Multiple (a,c,m)	[66]									
		Multiple (a,c,r)	[109]									
		Multiple (a,q)	[12]									
		Multiple (a,c)	[43]									
		Multiple (d,c,r)	[124]									
		Multiple (c,g)	[33]									
		Multiple (c,q)	[94]									
		Multiple (c,r)	[67]									
		Multiple (c,l)	[110]									
		Proximity logger	[8, 9, 65]									
	Big cat	Camera	[127]	6	6	6	1	85	85	4-166	2	Predation
		GPS	[95, 121]									

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
Cattle		Multiple (a,c)	[96]									Visits to farm and pastures
	Buffalo	GPS	[125, 126, 144]	0	0	0	1	89	89	6-172	2	Young buffalo joining cattle herd Contact between cattle and buffalo Within 100m of each other Shared grazing and water source
		Model	[77]									
		Literature review	[135]									
		Questioning	[93]									
	Camelid	Activity signs	[128]	0	0	0	1	0	0	0	1	-
		Direct observation	[79, 86]									
		Multiple (a,d)	[130]									
	Canine	Camera	[59]	2.5	2.5	0-5	2	102.6	19	0-422	5	Within two metres of each other Excreting on stored feed, visits to pasture and buildings and hunting
		GPS	[82, 84, 115]									
		Multiple (a,d)	[117]									
		Radio-telemetry	[113, 120]									
	Deer	Activity signs	[138]	24.2	1	0-216	11	123	4545	0-40105	11	Aggression, being within five metres of cattle, being at water points at the same time. Sharing feed and
		Camera	[35, 73, 89, 90, 104]									
		Direct observation	[41, 69, 83, 91]									
		GPS	[32, 108, 123]									
		Literature review	[68]									
		Multiple (a,c)	[71]									

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
Cattle	Deer	Multiple (d,c)	[56]									water and salt licks and visiting feed stores and pasture at different times to cattle. Damage on farm. Licking cattle urine.
		Multiple (c,p)	[40]									
		Multiple (g,l)	[117]									
		Multiple (g,q)	[30, 136]									
		Proximity logger	[15]									
		Questioning	[101, 137]									
		Radio-telemetry	[131-133, 139]									
	Elephant	GPS	[31, 144]	-	-	-	-	-	-	-	-	Home range overlaps with cattle grazing. Using water sources when cattle not present
	Hyena	Multiple (d,r)	[81]	0	0	0	1	-	-	-	-	Foraging around bomas but not entering them. Predation events
	Kangaroo	Radio-telemetry	[122]	-	-	-	-	-	-	-	-	Presence on farms
	Not specified	Camera	[24, 26, 116]	28	28	0-55	2	200	90	21-600	4	Close contact with cattle. Sharing water
		Direct observation	[22]									
		Questioning	[25, 27-29, 106]									

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
Cattle	Not specified	Radio-telemetry	[23]									sources and grazing at the same and different times to cattle. Raccoon licking salt licks near cattle.
	Raccoon	Multiple (c,l,r)	[103]	-	-	-	-	284	284	284	1	Shared water, food and space
	Sheep/Goat	Direct observation	[74]	150	150	150	1	690	690	690	1	Close proximity. Shared pasture
		Multiple (g,m)	[49]									
	Wild horse	GPS	[31]	-	-	-	-	-	-	-	-	Home range overlaps with cattle grazing and feeding in close proximity. Using water sources.
		Multiple (a,d)	[142]									
	Wild pig	Activity signs	[36, 138]	29	1	0-216	9	327	213	6-992	8	Using feeders and water trough at the same and in close proximity. Predation. Using food and water sources at different times, in buildings and on pasture.
		Camera	[35, 70, 73, 89, 90, 104]									
		GPS	[10, 111]									
		Multiple (c,g)	[71]									
		Multiple (c,p)	[39]									
		Multiple (g,l)	[40]									
		Questioning	[88, 93]									
Farmed deer Farmed deer	Big cat	Radio-telemetry	[140]	-	-	-	-	-	-	-	-	

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
	Deer	Camera	[60, 61]	40	40	0-77	2	439	439	439	1	Sparring and moving together along fence line
Goat	Antelope	Multiple (d,k,q)	[51]				-				-	Shared space use
	Big cat	Camera	[127]	6	6	6	1	4	4	4	1	Predation
		Multiple (a,c)	[96]									Presence on pasture
	Camelid	Direct observation	[79, 86]	0	0	0	1	-	-	-	-	Mixed grazing and shared forage resources separated spatially and temporally
	Camelid	Multiple (a,d)	[130]									
	Canine	Radio-telemetry	[120]	-	-	-	-	22	22	22	1	-
	Chimpanzee	Direct observation	[57]	0	0	0	1	-	-	-	-	-
	Deer	Camera	[90]	0	0	0	1	-	-	-	-	-
	Hyena	Multiple (d,r)	[81]	-	-	-	-	-	-	-	-	Foraging around bomas but not entering them. Predation events
	Not specified	Camera	[112]	-	-	-	-	-	-	-	-	Presence on pasture
	Wild pig	Camera	[90]	0	0	0	1	-	-	-	-	-
		Questioning	[88]									
Not specified	Big cat	GPS	[37]	-	-	-	-	-	-	-	-	-
	Sheep/Goat	Direct observation	[143]	-	-	-	-	-	-	-	-	Shared space and food resources
	Wild horse	Multiple (c,g)	[97]	-	-	-	-	30	30	30	1	Within photographing distance

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
Pig	Canine	Camera	[34]	165	165	165	1	672	672	672	1	Approaching and entering farrowing huts and taking piglets Presence on pasture
	Deer	Camera	[35, 90]	75	8	0-216	3	352	352	80-624	2	Shared food and water
		Multiple (g,l)	[40]									
	Wild pig	Camera	[35, 90]	29	1	0-489	8	581	104	0-2907	11	Contact through fences, close proximity, mating, fighting and predation. Shared food and water resources, around farms and near fence lines. Shared space at different times.
		GPS	[141]									
		Multiple (a,c,g)	[105]									
		Multiple (a,c,q)	[118]									
		Multiple (c,m)	[72]									
		Multiple (c,q)	[40]									
		Multiple (g,l)	[134]									
		Multiple (m,q)	[75]									
		Multiple (p,r)	[76]									
		Questioning	[62, 63, 78, 88]									
Sheep	Antelope	Multiple (d,k,q)	[51]	-	-	-	-	-	-	-	-	Shared space use
	Badger	GPS	[42]	-	-	-	-	6	6	6	1	Farm visits
	Big cat	Radio-telemetry	[87, 140]	109	109	109	1	-	-	-	-	Predation
	Camelid	Direct observation	[79, 86]	0	0	0	1	-	-	-	-	Mixed grazing and shared forage resources separated

Livestock	Wildlife	Method(s)*	References	Reported frequency of Direct contacts#				Reported frequency of Indirect contacts#				Type of contact
				Mean	Median	Range	Number of Studies	Mean	Median	Range	Number of Studies	
		Multiple (a,d)	[130]									spatially and temporally
	Canine	GPS	[13]	0	0	0	1	22	22	22	1	Farm visits
		Radio-telemetry	[120]									
	Chimpanzee	Direct observation	[57]	0	0	0	1	-	-	-	-	-
	Deer	Camera	[90]	0	0	0	2	271	271	271	1	In close proximity
		Direct observation	[80]									
	Hyena	Multiple (d,r)	[81]	165	165	165	1	-	-	-	-	Foraging around bomas but not entering them. Predation events
	Kangaroo	Radio-telemetry	[122]	-	-	-	-	-	-	-	-	Farm visits
	Not specified	Camera	[112]	-	-	-	-	-	-	-	-	Presence on pasture
	Sheep/Goat	Direct observation	[74, 85]	90	90	30-150	2	690	690	690	1	Close proximity. Shared pasture
		Radio-telemetry	[50]									
	Wild pig	Activity signs	[36]	0	0	0	1	-	-	-	-	Rooting on pasture
		Camera	[90]									
		Questioning	[88]									

*Some studies used multiple methods combining variations of activity signs (a), cameras (c), direct observation (d), GPS (g), literature review and expert knowledge elicitation (k), models (m), pathogen monitoring (p), proximity loggers (l), questioning (q) and radio-telemetry (r).

#The average frequencies of direct and indirect livestock-wildlife contacts are displayed along with the number of studies reporting raw (un-extrapolated) data. Studies that only reported extrapolated data (e.g. annual rates) or summarised frequency values were excluded from the calculations in this table.

In some cases no data were reported (-).