

Global trends in infectious diseases at the wildlife–livestock interface

Anke K. Wiethoelter^a, Daniel Beltrán-Alcrudo^b, Richard Kock^c, and Siobhan M. Mor^{a,d,1}

^aFaculty of Veterinary Science, The University of Sydney, New South Wales 2006, Australia; ^bFood and Agriculture Organization of the United Nations (FAO), 00153 Rome, Italy; ^cDepartment of Pathology and Pathobiology, Royal Veterinary College, University of London, Hertfordshire AL9 7TA, United Kingdom; and ^dMarie Bashir Institute for Infectious Diseases and Biosecurity, The University of Sydney, New South Wales 2006, Australia

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The role and significance of wildlife–livestock interfaces in disease ecology has largely been neglected, despite recent interest in animals as origins of emerging diseases in humans. Scoping review methods were applied to objectively assess the relative interest by the scientific community in infectious diseases at interfaces between wildlife and livestock, to characterize animal species and regions involved, as well as to identify trends over time. An extensive literature search combining wildlife, livestock, disease, and geographical search terms yielded 78,861 publications, of which 15,998 were included in the analysis. Publications dated from 1912 to 2013 and showed a continuous increasing trend, including a shift from parasitic to viral diseases over time. In particular there was a significant increase in publications on the artiodactyls–cattle and bird–poultry interface after 2002 and 2003, respectively. These trends could be traced to key disease events that stimulated public interest and research funding. Among the top 10 diseases identified by this review, the majority were zoonoses. Prominent wildlife–livestock interfaces resulted largely from interaction between phylogenetically closely related and/or sympatric species. The bird–poultry interface was the most frequently cited wildlife–livestock interface worldwide with other interfaces reflecting regional circumstances. This review provides the most comprehensive overview of research on infectious diseases at the wildlife–livestock interface to date.

wildlife–livestock interface | infectious diseases | zoonoses | scoping review

Pathogen maintenance within wildlife populations and spillover to livestock has been reported as a precursor to disease emergence in humans (1–3). As such, there has been growing interest in applying knowledge synthesis methods to trace and quantify the zoonotic origins of human diseases (2–6). Though zoonoses can and do impact directly on human health (7), comparatively less research has been directed toward understanding the origins of animal diseases, particularly at the wildlife–livestock interface, as well as the associated impacts on each sector (8–10).

Globally, livestock constitutes on average 37% of the agricultural gross domestic product (11) and is one of the most important and rapidly expanding commercial agricultural sectors worldwide (12). Infectious diseases cause direct losses to this sector through increased mortality and reduced livestock productivity, as well as indirect losses associated with cost of control, loss of trade, decreased market values, and food insecurity (13). Diseases that are shared between species also represent a potential burden to the whole ecosystem, affecting biodiversity, changing behavior or composition of animal populations, and even relegating species to the fringe of extinction (14, 15).

Wildlife–livestock interfaces have traditionally been characterized according to the epidemiological role of wildlife—namely, as spillover/spillback, maintenance, or dead-end hosts (16, 17). This focus and categorization reflects to some extent the human bias placed on the importance of livestock, overemphasizing the role of wildlife in transmission while neglecting the manifold values of wildlife (18). More accurate in a biological sense, wildlife–livestock interfaces are dynamic and bidirectional with pathogens transmitted freely within and between wildlife and livestock species (16) as they

come into mostly indirect contact in a communal environment, through use of shared resources (e.g., pasture, water) and via vectors. Viewed this way, it can be seen that human-induced shifts in farming practices and land use changes—agricultural intensification, deforestation, and encroachment into pristine habitats, for instance—also influence observed epidemiological patterns (6, 19, 20).

Previous research on diseases at the wildlife–livestock interface has provided some insights. An inventory of known livestock pathogens revealed that 77% are capable of infecting multiple host species, including wildlife (5). Studies on certain wildlife–livestock interfaces have also identified several important diseases (16, 17, 21–25). However, no studies have characterized diseases and animal species involved on a global level.

The integration of findings from individual research studies on a given topic or question into the global knowledge base is referred to as “knowledge synthesis” (26). Of the different methodologies, scoping studies are most appropriate for mapping existing knowledge in research areas where comprehensive reviews are lacking (27). In this study, knowledge synthesis methodologies were refined to provide an overview of published research on infectious diseases at the wildlife–livestock interface. Specifically, the aim was to quantitatively characterize published literature with respect to the types of diseases, animal species involved, and temporal and regional patterns to identify where research on this topic has been focused.

Results

Overall, 15,998 publications were included in the analysis (Fig. 1), covering 113 of 118 diseases of interest. Approximately 17% of publications referred to more than one disease. Publications

Significance

Infectious diseases at the wildlife–livestock interface threaten the health and well-being of wildlife, livestock, and human populations, and contribute to significant economic losses to each sector. No studies have sought to characterize the diseases and animals involved on a global level. Using a scoping review framework we show that 10 diseases—mostly zoonoses—have accounted for half of the published research in this area over the past century. We show that relatively few interfaces can be considered important from a disease ecology perspective. These findings suggest that surveillance and research strategies that target specific wildlife–livestock interfaces may yield the greatest return in investment.

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¹To whom correspondence should be addressed. Email: siobhan.mor@sydney.edu.au.

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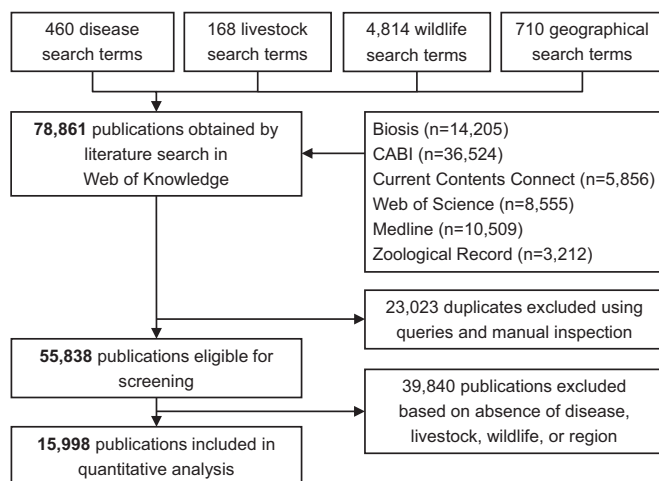


Fig. 1. Scoping review flowchart. All search categories (wildlife, livestock, disease, geographic region) were joined by the Boolean expression “AND,” resulting in the intersection used for analysis.

dated from 1912 to 2013 and showed a continuous increase over time (Fig. 2). Diseases cited were caused by viruses (60%), bacteria (40%), parasites (29%), and prions (2%). Fungal diseases were not represented. Whereas early publications predominantly described parasitic diseases, the majority from 1977 onward referred to viral diseases. The Top 10 diseases are shown in Table 1 (for full list, see Table S1). Together, these diseases constituted almost 50% of published research. This trend became apparent around 1960 and has remained relatively stable since (Fig. S1).

Fig. 3 shows the prominent wildlife–livestock interfaces reported in the scientific literature. Among wildlife, birds and members of the orders Carnivora (carnivorans), Artiodactyla (artiodactyls), Rodentia (rodents), and Chiroptera (bats) were the most frequently mentioned. Poultry, cattle, small ruminants, pigs, and equines formed the most cited livestock groups. Together the matrix combination of these five wildlife and five livestock groups accounted for 74% of all publications. In addition, only a few diseases were highlighted at each interface (Table 2). For example, 22% of all publications citing a bird–poultry interface were associated with only one disease [avian influenza (AI)], whereas 16% and 24% of all publications citing an artiodactyls–cattle or carnivorans–cattle interface, respectively, referred to bovine tuberculosis (bTB).

Table 3 shows the long-term publication trends on diseases at the top three wildlife–livestock interfaces. Between 2003 and 2013, publications referring to diseases at the bird–poultry interface increased at a rate of 10.8% per year (95% CI: 8.5, 13.1), compared with only 3.9% per year between 1912 and 2002 (95% CI: 3.6, 4.2; Davies’ test for slope change: $P < 0.001$). Similarly, publications on diseases at the artiodactyls–cattle interface increased significantly after 2002 (4.3% vs. 9.2% before and after 2002, respectively; $P < 0.001$). Time-series analysis of publications on AI and bTB revealed that the number of publications was highly positively correlated with media coverage and research funding for these specific diseases (Fig. 4).

Fig. 5 shows the geographic trends in diseases at the wildlife–livestock interface. The majority of publications were spatialized to Europe (38%), followed by Asia (30%), North America, including Caribbean and Central America (24%), Africa (18%), South America (8%), and Oceania (6%). The distribution of disease agents was similar across all continents, with viral diseases representing the largest fraction all over the world (Fig. 5A). The bird–poultry interface was the most frequently cited wildlife–livestock interface worldwide, ranking first in Asia,

Europe, and North America and second in Oceania, Africa, and South America (Fig. 5B). Other interfaces reflected regional circumstances, as illustrated by the marsupial–cattle interface in Oceania (mostly attributable to publications on transmission of bTB between brushtail possums (*Trichosurus vulpecula*) and cattle in New Zealand) as well as the artiodactyls–cattle interface in Africa (associated with theileriosis, foot and mouth disease, and malignant catarrhal fever).

Discussion

This study is, to our knowledge, the first to apply a scoping review framework to identify infectious diseases at the wildlife–livestock interface. Results suggest a growing interest by the scientific community in this area. In some cases (such as AI and bTB) these trends could be traced to key disease events that stimulated public interest and research funding. The findings indicate that animal disease dynamics at this interface are driven by interactions between only a few wildlife and livestock groups, differing to some extent based on geographic region; they also show that relatively few diseases are transmitted at these interfaces. Scientific interest appears to have been driven largely by the zoonotic aspects of some of these diseases, with comparatively less research directed to exclusive animal diseases that impact on livestock and/or wildlife health.

Ten diseases accounted for almost 50% of the published research on diseases at the wildlife–livestock interface. The fact that the majority of these were zoonoses reflects the importance of these diseases in human health (7) and/or how funding for infectious disease research is driven by human health. It is perhaps notable that rinderpest, the only animal disease to have been globally eradicated and which affected cattle and wild artiodactyls, only ranked 29 (Table S1) despite significant scientific and political investment in this disease within the agricultural sector. Although veterinary communities have long recognized that wildlife and livestock share diseases, the importance of wildlife health only came to prominence following work by Jones et al. (3) and others (5, 8) that implicated wildlife as the origins of more than half of the diseases that emerged in humans. Recent analysis showed, however, that disease emergence in wildlife is largely driven by exposure to domestic animals and/or human-induced activities (28).

The overall increase in publications referring to diseases at the wildlife–livestock interface since 1912 is congruent with findings of bibliometric studies on other infectious diseases (29–31). These studies attributed the growth to an increased production of research data and rising demand for publication over time—in particular, during the last decades driven by China, India, and Brazil—as well as to the introduction of new journals. Nevertheless, we note that rates of publication on diseases at the bird–poultry and artiodactyls–cattle interfaces have more than doubled in the past decade, and far exceed the average annual increase for all publications in Web of Knowledge (4.5% from 1991 to 2013). In particular, we observed a significant surge in publications on diseases at the bird–poultry interface from 2003 onward, consistent with widespread transmission of highly pathogenic AI (H5N1) in Southeast Asia during 2003/2004

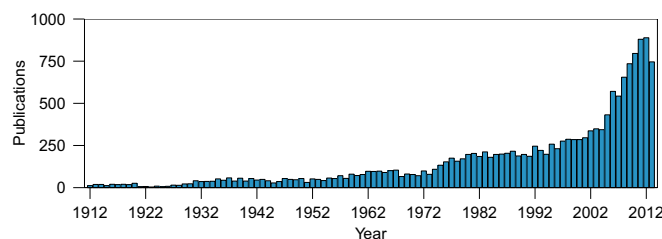


Fig. 2. Temporal trend of publications on diseases at the wildlife–livestock interface ($n = 15,998$).

Table 1. Top 10 diseases at the wildlife–livestock interface based on number of publications obtained

Publications (%)	Disease
1,590 (9.9%)	Avian influenza (low and highly pathogenic)
1,502 (9.4%)	Rabies
993 (6.2%)	Salmonellosis (<i>Salmonella enterica</i> excluding <i>Salmonella abortusovis</i>)*
913 (5.7%)	Bovine tuberculosis
795 (5%)	Trichinellosis
767 (4.8%)	Newcastle disease
666 (4.2%)	Brucellosis
651 (4.1%)	Leptospirosis*
609 (3.8%)	Echinococcosis
549 (3.4%)	Toxoplasmosis*

Overall, 118 diseases and 15,998 publications were included; for full presentation of all diseases, see [Table S1](#).

*Only listed by the OIE Working Group on Wildlife Diseases.

and resulting public interest and research investment in this disease. The decline in overall publications in 2013 probably relates to the fact that the final literature research was performed in early January 2014, when not all published literature of 2013 had been added to literature databases. However, other factors such as declines in research funding cannot be ruled out.

In our review, temporal trends in publication on AI and bTB correlated strongly with media interest in and research funding for these diseases, highlighting the influence of specific disease events and sociopolitical–economic drivers of research in this area. Although pandemic human influenza cannot be denied as a serious threat, many would argue that the international response to H5N1 (including wild bird surveillance) was not commensurate with the threat or scale of the problem (32) and has failed to be effective in some regions of the world (33). In fact, international interest and funding for H5N1 has now fallen despite ongoing outbreaks in poultry and sporadic spillover to humans (34), underscoring the transient influence of public interest on research on this interface. In the case of bTB, decades of funding has been largely ineffective in reducing the disease burden in the United Kingdom, which may explain to some extent the research focus on badgers (*Meles meles*) as the problem rather than any inherent changes in the livestock systems (35). These examples show that investments have largely been proportionate to the perceptions of disease at the wildlife–livestock interface, rather than actual costs associated with, e.g., animal and human morbidity, livestock production losses, and conservation impacts.

Interfaces between phylogenetically closely related and/or potentially cohabitant species (e.g., bird–poultry, artiodactyls–cattle) were most frequently identified in this review, consistent with the view that disease dynamics are determined by interaction between sympatric species (25). However, just because a certain wildlife–livestock interface is prominently reported in the scientific literature does not necessarily mean that actual transmission is frequently occurring at this interface. For most diseases, research into true interaction, contact networks, habitat overlap, and impacts of infection (e.g., clinical vs. subclinical) in animals is limited (9, 36). Avian influenza is an example where transmission at the wildlife–livestock interface is often implied, but a functional interface is seldom documented and proven (37, 38). In fact, global spread of H5N1 was facilitated by poultry movement and trade without any proximal role of wild birds in some countries (39).

Prominent livestock groups identified by this review represent the most frequent types of livestock worldwide (40). In biologic terms, the sheer abundance of these species may contribute to contact and therefore disease transmission. The finding that cattle appear in two of the top three interfaces may reflect the historical

and present day importance of the beef and dairy industries, with more substantial research and development funding in this sector (41). In recent decades, monogastric animals have risen to prominence, particularly in China (12, 41). Only 18% of the publications in this review addressed diseases at the wildlife–pig interface (vs. 33% and 25% for wildlife–cattle and wildlife–poultry interfaces, respectively), which may be an important knowledge gap considering the current trend in pig production.

Given the perceived importance of the order Chiroptera in emerging infectious diseases (42–44), we hypothesized that there would be an increase in publications exploring the bat–livestock interface. However, a relatively small number of publications referred to diseases at this interface. Emergence of viruses of proven/suspected bat origin, including Nipah (45) and Ebola Reston virus (46) in pigs and Middle East respiratory syndrome (MERS) coronavirus in camels (47), do however illustrate the potential importance of bat–livestock interfaces in emerging zoonotic diseases. The trend in agricultural expansion and intensification of the wildlife interface is particularly strong in recent decades in tropical systems, associated with external economic and development pressures and may drive spillover/emergence (48). These new diseases did not manifest strongly in findings presented here, most likely due to a lag in research and subsequent publication. Filovirus infections (e.g., Ebola) were included, but ranked 58 in this review ([Table S1](#)); coronaviruses were not considered because they are not listed diseases according to the World Organization for Animal Health (OIE), which represents an important gap in animal health surveillance, and likely reflects the limited understanding of the role of coronaviruses in wildlife and livestock disease.

There are several limitations to this study. Because this review is based on scientific publications, it is prone to publication bias influenced by country, language, institution, author career stage, study outcome, research topic, research sponsor, and timeline (49). Spatial bias also plays an important role as research and publication are linked to economic indices and therefore concentrate in developed countries, particularly in Europe and Northern America (31). As experience with H5N1 has shown (34), efficacy of disease surveillance and control measures are also largely dependent on resources available, which could be another reason for the spatial

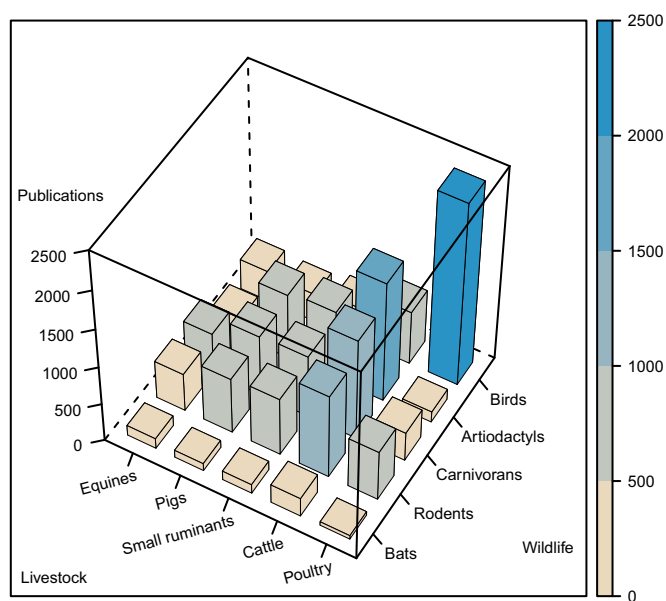


Fig. 3. Prominent wildlife–livestock interfaces reported in scientific literature. Shown are the five most frequently cited wildlife and livestock groups ([Dataset S1](#)); only publications with one disease ($n = 13,293$) were included.

Table 2. Top three wildlife–livestock interfaces including the five predominant diseases

Publications (%)	Wildlife	Livestock	Diseases
2,378 (17.9%)	Birds	Poultry	Avian influenza, Newcastle disease, salmonellosis, avian chlamydiosis, poxvirus infections
1,570 (11.8%)	Artiodactyls	Cattle	Bovine tuberculosis, brucellosis, malignant catarrhal fever, foot and mouth disease, theileriosis
1,324 (10%)	Carnivorans	Cattle	Rabies, bovine tuberculosis, echinococcosis, leptospirosis, salmonellosis

Only publications with one disease ($n = 13,293$) were included in analysis; diseases are listed in descending order. For full presentation of all interfaces depicted in Fig. 3, see [Table S2](#).

pattern observed here. Geographical biases stemming from underrepresentation of research on emerging diseases of wildlife, particularly in Africa and South America, have been noted previously (28); this may reflect limited regional capacity for wildlife surveillance in these areas. The fact that early literature primarily addressed parasitic diseases, whereas more contemporary publications focused on viral pathogens, is presumably a result of the availability of methods to study viral systems.

To keep the scope feasible, constraints related to diseases included in this review were inevitable. No attempt was made by the authors to quantify the importance of these diseases, in terms of health, economic, or conservation impacts; rather, we deferred to lists of livestock and wildlife diseases deemed important by the OIE and OIE Working Group on Wildlife Diseases, respectively. The latter includes all OIE-listed (notifiable) diseases that affect wild animals, as well as some nonlisted diseases that have particular relevance to wildlife health and conservation (e.g., filoviruses). Because admission to the OIE disease list is subject to several criteria, such as international spread and zoonotic potential, use of this list may have biased the findings toward diseases already known to be important. However, no other comprehensive lists for livestock or wildlife diseases exist. To keep this scoping review broad, all diseases listed in the 2013 OIE Terrestrial Animal Health Code were included regardless of whether any wildlife–livestock interface was known or suspected a priori. Not surprisingly, five diseases did not yield any publications following database extraction; these diseases are not known to involve a livestock (white-nose syndrome, elephant herpes virus, feline leukemia, immunodeficiency virus infections) or wildlife host (bovine genital/venereal campylobacteriosis) in their transmission cycle. Since its establishment in 1924, the OIE list has undergone major changes in 1963/1964 (raised from 9 to 49 diseases) and 1985/1986 (from 47 to 86 diseases). These changes were not temporally associated with a surge in publications in this review (Fig. 2).

The automatic search and indexing approach used here was advantageous in processing a large number of publications. However, identified interfaces may not necessarily occur in situ. For example, experimental work like infection trials, as well as serosurveys with negative results would return the same index pattern. Likewise, cell lines or laboratory reagents incorporating species names would result in findings. Additionally, the categorization of species into livestock and wildlife is already to some extent arbitrary and not straightforward. Given the constraints of the methodology, we could not distinguish between free-ranging, captive and semicaptive wildlife. In reality, this distinction can have profound implications on the interface and transmission (25).

In the light of these limitations, it should be emphasized that findings presented here reflect perceived interest by the scientific

community and should not be confused with incidence of diseases or absolute occurrence of interfaces. Likewise, high numbers should not be taken to mean high frequency of actual transmission at these interfaces as noted earlier for AI. Indeed, a good understanding of ecosystem dynamics for most multihost infectious diseases is still widely lacking (50). More basic research into these areas is needed, including specific quantitative research at the interface itself, to further elucidate the transmission pathways and specific role of wildlife and livestock species.

Our scoping review shows where research in this area has been focused over the past century. In the future, more detailed analyses using this database will focus on specific diseases, affected animal species, and geographic regions to deepen the knowledge of these interfaces and identify gaps as well as areas of knowledge saturation. These results will be useful to policymakers, donors, and other stakeholders, who require an understanding of global disease and research priorities to make informed investments in animal health programs. Combined with comprehensive field studies, more specific knowledge will help refine and adapt surveillance strategies to better monitor diseases at the wildlife–livestock interface.

Methods

Standardized definitions and guidelines—similar to ones available for systematic reviews (51, 52)—are lacking for scoping reviews (53). To ensure an objective and comprehensive approach, this scoping study was largely based on a framework encompassing an iterative rather than linear process (27); it was conducted in four main steps: defining the research question, literature search, screening of search results, and analysis.

Defining the Research Question. The review question was structured according to a modified population, interest, and context (PICO) principle and defined as “What is the current global state of knowledge based on published literature of infectious diseases at the wildlife–livestock interface?” Livestock was broadly defined as all nonaquatic, vertebrate animals (domestic as well as non-domestic) that are farmed in agricultural systems and holdings (40). Depending on the degree of human influence and supervision, wildlife can comprise feral domestic, captive wild, and wild animals (54). We did not differentiate between these groups; all feral and nondomestic animals—whether free-ranging, captive, or semicaptive—were included. Search terms for wildlife and livestock were derived from standard nomenclature volumes for mammals (55) and birds (56) and comprised the Latin genus or species name and the common genus name. In addition, generic terms such as “livestock” or “wildlife” were included to obtain publications that did not incorporate taxonomic nomenclature. This review focused on terrestrial mammals and birds; hence, fish, amphibians, reptiles, and invertebrates as well as infectious diseases thereof were excluded. Livestock diseases listed in the 2013 OIE Terrestrial Code (54) and diseases deemed important by the OIE Working Group on Wildlife Diseases (57) were included. Disease search terms comprised common and scientific names of pathogens including abbreviations. Terms for geographic regions were composed of United Nations’ sanctioned names of countries (58), continents, and geographical subregions (59) as well as ecological regions and

Table 3. Long-term trends in rates of publication on diseases at the top three wildlife–livestock interfaces

Interface	Changepoint year \pm SE	Intercept (95% CI)	β_1 (95% CI)	β_2 (95% CI)	<i>P</i> value for slope change
Bird–poultry	2003 \pm 1.28	−72.29 (−72.53, −67.05)	0.04 (0.04, 0.04)	0.10 (0.08, 0.12)	<0.001
Artiodactyls–cattle	2002 \pm 2.22	−81.41 (−88.23, −74.59)	0.04 (0.04, 0.05)	0.09 (0.06, 0.11)	<0.001
Carnivorans–cattle	1980 \pm 15.59	−74.91 (−86.53, −63.29)	0.04 (0.03, 0.05)	0.03 (0.03, 0.04)	0.121

Exponentiation of β_1 and β_2 yields the annual growth rate in publication before and after the changepoint, respectively. CI, confidence interval.

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