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What do we know about the epidemiology of infectious diseases and parasites of free-ranging Neotropical ungulates? Needs and priorities

Carlos E. Trillanes-Flores[1,2], Eduardo J. Naranjo[1], Neptali Ramírez-Marcial[1], Juan Carlos Pérez-Jiménez[3], José Gerardo Perera-Marín[4], Susana Rojas-Maya[4] and Carlos Chávez[5]

[1]Departamento de Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de Las Casas, CS, México; [2]Departamento de Ciencias de la Sustentabilidad, El Colegio de la Frontera Sur, Lerma, CM, México; [3]Departamento de Reproducción, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Coyoacan, CX, México; [4]Zoológico Regional Miguel Álvarez del Toro, Gobierno del Estado de Chiapas Secretaria de Medio Ambiente e Historia Natural, Tuxtla Gutierrez, CS, México and [5]Facultad de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Chiapas, Tuxtla Gutiérrez, CS, México

Review Article

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Corresponding author: Eduardo J. Naranjo; Email: enaranjo@ecosur.mx

Abstract

Our analysis covers 122 scientific publications about health issues in free-ranging Neotropical ungulates produced between 1990 and 2022, with an emphasis on the epidemiology of infectious diseases and parasites. Most studies focus on parasitology (43.4%) and bacteriology (15.6%), while body condition (0.8%), toxicology (1.6%), virology (6.6%), and health assessments (6.6%) are less studied. Brocket deer (*Mazama americana* and *M. gouazoubira*), followed by peccaries (*Pecari tajacu* and *Tayassu pecari*), and the lowland tapir (*Tapirus terrestris*) were the most frequent species surveyed (61.4% of all publications). We detected considerably higher numbers of studies and health topics covered in Brazil ($n = 64$; 52.5% of the total) compared to other Latin American countries. We emphasize the need for further research focused on poorly known health aspects of Neotropical ungulates that have received little attention in the past, especially the Chacoan peccary (*Catagonus wagneri*), taruca deer (*Hippocamelus antisensis*), Northern pudu (*Pudu mephistopheles*), and the least known *Mazama* species. Ecotoxicology and pathology studies are necessary to evaluate the impact of agrochemicals and other human disturbances on Neotropical ungulate populations in the wild. We encourage further research on the human impacts and trends of change in the epidemiology of infectious diseases, parasites, and health status of Neotropical wild ungulate populations.

Introduction

The health of ungulate populations may be affected by three main processes (Deem *et al.*, 2001): (1) landscape transformation, (2) shifts in population dynamics, and (3) changes in the ecology of diseases. The first is related to land-use change, which contributes to habitat fragmentation, habitat loss, macro- and microclimatic change, and environmental pollution. These factors favour interactions among humans, livestock, and wildlife, which in turn contribute to increased disease transmission across species (Daszak *et al.*, 2000; Harvell *et al.*, 2002). The indirect effects of land-use change consist of environmental changes related to human activities (e.g., temperature increase and shifts in precipitation regimes) and stress on wildlife populations, making them more vulnerable to either known or new diseases (Deem *et al.*, 2001; Harvell *et al.*, 2002).

The second process affecting the health of wildlife species consists of shifts in population dynamics due to human activities such as high hunting pressure, illegal trade, and translocation of animals (Cunningham *et al.*, 2003; Kruse *et al.*, 2004). Careless wild species translocations and releases of domestic animals (potential asymptomatic hosts) may help disseminate new pathogens and diseases in locations where native populations lack immunity. Wildlife markets constitute ideal scenarios for epidemic outbreaks because diverse animal species from multiple locations usually are kept in small and filthy cages, where secretions, excretions, food, water, and parasites are exchanged among them (Aguirre *et al.*, 2020; Galindo, 2022). The risk of zoonosis increases as animals are killed, sold, and transported from these markets to nearby cities and villages, as probably happened with the recent Covid-19 pandemic (Galindo, 2022). Another possibility is that the animals arriving in a new habitat may not have the natural defences against endemic diseases (Cunningham *et al.*, 2003; Daszak *et al.*, 2000; Kruse *et al.*, 2004). The third main process consists of changes in disease ecology occurring when the equilibrium among the host, the etiological agent, and their environment modifies. This can lead to 'endemic stability' loss, resulting in clinical disease (Deem *et al.*, 2001). The three processes described coupled with rapid human population growth, social inequality, deficient education, and weak environmental policies cause direct impacts on wildlife health and conservation (Valdez, 2014). These processes have synergic effects leading to increased poverty in rural communities, undervaluation, and higher demand for natural resources, resulting in higher impacts on wild populations, their habitats, and the environmental services they provide (Challenger and Dirzo, 2009).

The three families of Neotropical ungulates considered in this review (Cervidae, Tapiridae, and Tayassuidae) include 22 species, most of them frequently hunted for food and other purposes where they occur (Gallina, 2019). These species may be either recipients or transmitters of numerous parasitic, bacterial, and viral diseases with livestock, which could represent a conservation problem for wild populations (Kruse *et al.*, 2004; Romero *et al.*, 2008). The risk of global disease spread highlights the relevance of maintaining epidemiological vigilance and research on ungulate populations (Daszak *et al.*, 2000). This review aims to synthesize the state of knowledge on the epidemiology of infectious diseases, parasites, and health conditions of Neotropical ungulates. We offer evidence on information gaps and suggest directions for future research on their conservation.

Materials and methods

For this review, we compiled available information published on health aspects of Neotropical ungulate species between 1990 and 2022. We considered species distributed in the tropical areas of Mexico, Central America, South America, and the Antilles (Morrone, 2017). We excluded South American camelids (family Camelidae) from this analysis. We included papers in scientific journals, books and book chapters, theses and dissertations, proceedings of conferences and workshops, and technical reports. We also considered studies carried out in extensive Wildlife Conservation Units (UMA, in Spanish) and protected areas across Mexico. Our bibliographic searches were done using the resources available in the Web of Science, Scielo, Google Scholar, Research Gate, the National Consortium of Scientific and Technological Information (CONRICYT-Mexico), and the El Colegio de la Frontera Sur's library information system (SIBE-ECOSUR). The keywords used in our searches were: *Blastocerus, Catagonus, Dicotyles, Hippocamelus, Mazama, Neotropical, Odocoileus, Ozotoceros, Parachoerus, Pecari, Peccary, Pudu, Subulo, Tapirella, Tapirus, Tayassu*, and *Ungulates*. These keywords were linked through Boolean connectors (AND, OR, NOT) with the terms: *Body Condition, Conservation Medicine, Cortisol, Disease, Emerging Infectious Disease, Health Assessment, Microbiology, Parasite, Stress, Toxicology, Virus*, and their correspondent terms in Spanish and Portuguese.

We retrieved a total of 457 scientific publications, of which we discarded those focused on chemical contention, taxonomy, systematics, ecology (e.g., density, distribution, habitat use, and interactions, among others), papers in press or under review, and unfinished theses and dissertations. Although we considered publications including feral populations of domestic ungulates, we excluded studies done with captive animals or collection specimens unless they were very relevant to the discussion. After applying the above criteria, our final analyses consisted of 122 documents (see References and complementary list in Appendix S1).

The following data were retrieved from the documents reviewed: authors, year and type of publication, species, countries where the study took place, and topics covered. For studies carried out in Mexico, where both the Nearctic and the Neotropical regions converge, we only took those done in areas with Neotropical affinity (Morrone, 2014). The topics covered in publications were classified into seven categories: parasitology, bacteriology, virology, toxicology, pathology, body condition, and multi-themed studies. The publications titled 'health assessments' (those including hematic biometry, blood chemistry, and urine tests) were assigned to only one of the seven categories used. Studies including more than one topic (e.g., parasitology and bacteriology) were classified as 'multi-themed'. Our analysis incorporated studies documenting both the presence and absence of infectious agents. Finally, we discussed the needs and prospects for future research on health issues of Neotropical ungulates, with emphasis on cervids, peccaries, and tapirs.

Results

Of the 122 studies (1990–2022; see Table S1 in Supplementary material) on health issues of free-ranging Neotropical ungulates retrieved, 83 (68%) were published between 2011 and 2022, while 34 (27.9%) corresponded to the period 2001–2010, and only 5 (4.1%) were produced between 1990 and 2000 (see References and complementary list in Appendix S1). Most of the papers ($n = 101$; 55.5%) focused on deer species (Cervidae), while peccaries (Tayassuidae) and feral pigs (Suidae) were included in 45 studies (24.7%), and tapirs (Tapiridae) in 36 (19.8%). Two thirds ($n = 82$; 67.2%) of these publications covered more than one species, although only 15 (12.3%) covered more than one family. There were 19 ungulate species included in the studies reviewed, of which the red brocket deer (*Mazama americana,* $n = 27$; 14.8%), the brown brocket deer (*M. gouazoubira,* $n = 27$; 14.8%), the collared peccary (*Pecari tajacu,* $n = 20$; 11%), the lowland tapir (*Tapirus terrestris;* $n = 19$; 10.4%), and the white-lipped peccary (*Tayassu pecari,* $n = 19$; 10.4%) were the most frequent (Fig. 1).

Over a half of the published research on the health of free-ranging Neotropical ungulates between 1990 and 2022 was done in Brazil ($n = 64$; 52.5%), followed by Mexico ($n = 11$; 9%), Chile ($n = 9$; 7.4%), Argentina ($n = 7$; 5.7%), and Peru ($n = 7$; 5.7%). These five countries accounted for about 80% of all publications, while other eight countries (Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Trinidad, Uruguay, and Venezuela) and the territory of French Guiana produced the remainder (Fig. 2). No studies conducted in Belize, El Salvador, Guyana, Honduras, Nicaragua, Panama, Paraguay, Suriname, and the Antilles (except for Trinidad) were retrieved in our searches.

The majority (82.8%) of the reports were published in scientific journals, while dissertations and theses represented 8.2%. The remainder 9% was composed of book chapters, proceedings of conferences and workshops, and technical reports. The most frequent themes covered in the publications reviewed were parasitology ($n = 53$; 43.4%), bacteriology ($n = 19$; 15.6%), multi-themed studies ($n = 17$; 13.9%), and pathology ($n = 14$; 11.5%). Studies focused on health assessment, virology, toxicology, and body condition accounted for the remainder 15.5% (Table 1). The bacteria *Leptospira* spp. and *Brucella* spp., ticks, helminths, and bluetongue virus were the most frequently recorded organisms in Neotropical ungulates (Table 2, see References and complementary list in Appendix S1).

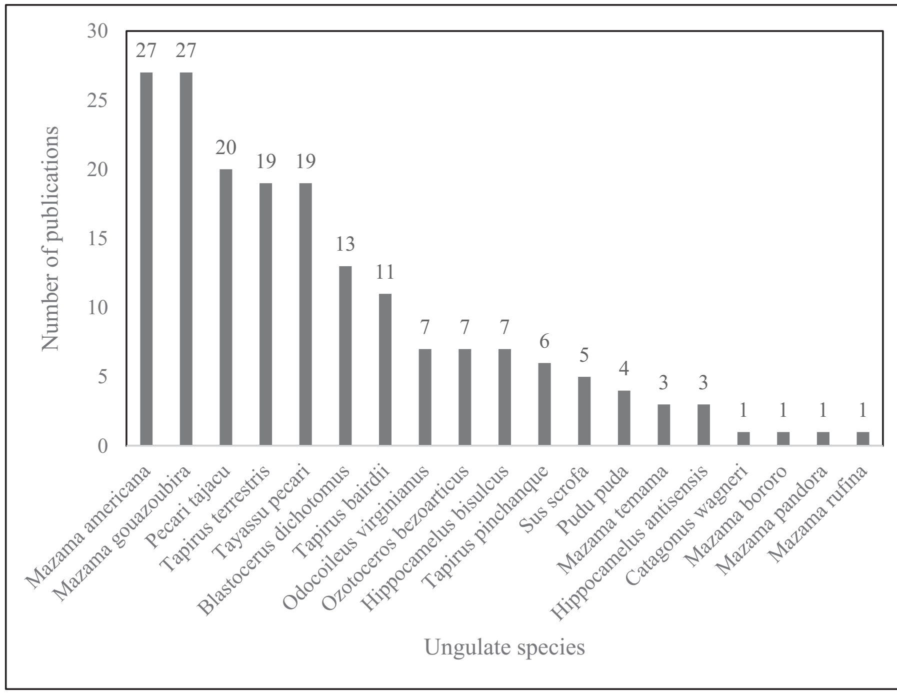

Figure 1. Number of publications on the health of free-ranging Neotropical ungulates in which each species appears ($N = 122$, 1990–2022). Most publications (67.2%) included more than one species.

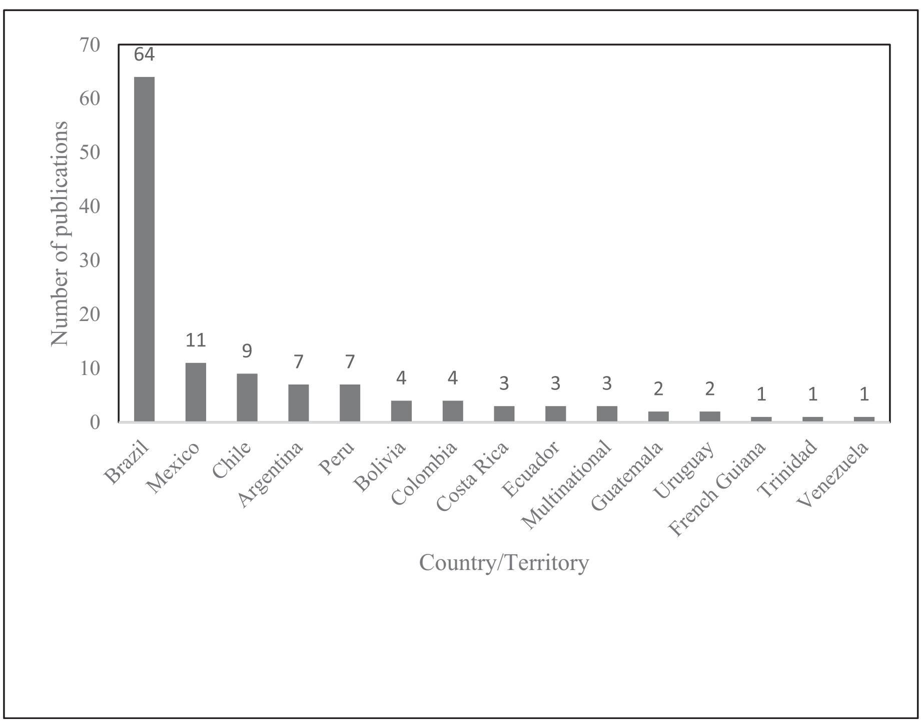

Figure 2. Number of publications on the health of free-ranging Neotropical ungulates by country/territory ($N = 122$, 1990–2022).

Tapirs (*Tapirus* spp.)

The lowland tapir (*T. terrestris*) has been widely surveyed across Brazil, including health assessments of free-ranging populations, the seroprevalence of infectious diseases (Fernandes *et al.*, 2020; May-Junior, 2011; Medici *et al.*, 2014), and parasite evaluations (Lima *et al.*, 2013; Malzoni *et al.*, 2010; May-Junior, 2011). At least two long-term surveys (1996–2021) have been conducted on tapirs in the Brazilian Atlantic Forest, the Cerrado, and the Pantanal (Labruna *et al.*, 2021; Medici *et al.*, 2014). Fernandes *et al.* (2020) compared the results of these surveys to their own obtained in the Brazilian Cerrado, showing that the tapirs of this region had more health problems than those of the Atlantic Forest and the Pantanal, probably due to a higher human disturbance present in the Cerrado. *Leptospira* spp., helminths (*Agriostomun* spp., *Parascaris spp., Strongyloides* spp., *Trichosrongylus* spp., *Strongylus* sp.), ticks (*Amblyomma* sp., *Haemapysalis* sp., *Rhipicephalus* sp.), bluetongue virus (Reoviridae), *Trypanosoma terrestris*, and *Toxoplasma gondii*

Table 1. Number of publications on the health of free-ranging Neotropical ungulates by theme (*N* = 122, 1990–2022)

Theme	*N*	%
Parasitology	53	43.4
Bacteriology	19	15.6
Multi-themed	17	13.9
Pathology	14	11.5
Health assessment	8	6.6
Virology	8	6.6
Toxicology	2	1.6
Body condition	1	0.8
Total	122	100

Table 2. Etiological agents and frequent diseases recorded in publications on the health of free-ranging Neotropical ungulates (1990–2022)

Etiological agent	*Cervidae*	*Tayassuidae*	*Suidae*	*Tapiridae*
Brucella sp.		x		
Leptospira sp.	x	x	x	x
Protozoans	x	x	x	x
Helminths	x	x	x	x
Ticks		x	x	x
AD		x		
BT				x
EEE				x
FMD	x			
IBR				x
PCT-2		x		
PP				x
VS		x		
WEE				x

AD = Aujeszky's disease; BT = bluetongue; EEE = East equine encephalitis; FMD = foot and mouth disease; IBR = infectious bovine rhinotracheitis; PCT-2 = porcine circovirus type 2; PP = porcine parvovirus; VS = vesicular stomatitis; WEE = West equine encephalitis.

have been the most frequently detected etiological agents in the lowland tapir (Malzoni *et al.*, 2010; May-Junior, 2011; Lima *et al.*, 2013; Navas *et al.*, 2019; Table 2).

The only published assessment of parasites present in free-ranging mountain tapirs (*T. pinchaque*) was done by Bernal *et al.* (2008) in the Nevados National Park in the Central Andes of Colombia. These authors collected blood samples for haematology and identified the ticks *Amblyoma multipunctum* and *Ixodes scapularis*. For Baird's tapirs (*T. bairdii*), parasitological evaluations have revealed the presence of the nematods *Lacandoria* sp., *Neomurshidia* sp., *Bunostonum* sp., *Agriostomum* sp., *Brachylumus* sp., *Strongylus* sp., *Trichostrongylus* sp., *Nematodirus* sp., *Tapironema* sp., *Trichonema* sp., *Tziminema unachi*, and the protozoans *Eimeria* sp. and *Balantidium* sp. (Cruz *et al.*, 2006; Güiris *et al.*, 2017; Méndez, 2017; Pérez-Flores *et al.*, 2019; Romero *et al.*, 2008).

There have been few pathology assessments describing diseases on free-ranging tapirs. Navas *et al.* (2019) published a study recording their findings on the pathology of 35 tapirs killed on roads of the Brazilian Cerrado. They found degeneration in adrenal glands, necrosis, and loss of fascicular and reticular cells with replacement by fibrosis and cortical atrophy, interstitial pneumonia, glossitis, lung anthracosis, colitis, cholangitis, and pericholangitis in several of the individuals examined. Intestinal parasitosis seems to be common in wild tapirs (Navas *et al.*, 2019). Tapirs killed in collisions along roads have also been subject of toxicological studies in Mato Grosso do Sul, Brazil (Fernandes *et al.*, 2018). Among the main toxic compounds detected in these ungulates are the organochlorines, organophosphates, pyrethroids, carbamates, and minerals such as lead, copper, manganese, and cadmium. In a second study, the same authors found pesticides and heavy metals linked to commercial farming in the Cerrado (Fernandes *et al.*, 2020). No other published surveys on this matter were found for tapirs across the Neotropics.

Peccaries (*Catagonus wagneri, Pecari tajacu*, and *Tayassu pecari*) and feral pigs (*Sus scrofa)*

Research on the epidemiology of peccary species has been done particularly in Brazil and other South American countries (see References and complementary list in Appendix S1). *Leptospira* spp., *Brucella* spp., helminths, and ticks have been the more frequently studied infectious agents in peccaries of Bolivia, Brazil, and Colombia (Ferreira, 2008; Karesh *et al.*, 1998; Montenegro *et al.*, 2018; Table 2). The seroprevalence of leptospirosis was reported in white-lipped peccaries of the Brazilian Pantanal, where these ungulates interacted with livestock (De Freitas *et al.*, 2010). Brucellosis has also been detected in white-lipped peccaries of the Pantanal (Real *et al.*, 2010) and Quedas do Iguaçu, Brazil (Mangini *et al.*, 2004). These surveys were focused not only on peccaries but also on feral pigs, cows (*Bos indicus*), dogs (*Canis lupus familiaris*), jaguars (*Panthera onca*), sheep (*Ovis aries*), horses (*Equus caballus*), and domestic pigs that tested positive to brucellosis and leptospirosis in Pontal do Paranapanema, Brazil (Ferreira, 2008).

Montenegro *et al.* (2018) detected leptospirosis in collared peccaries (prevalence = 78%) and feral pigs (prevalence = 100%) at several study sites in Colombia, while Lord and Lord (1991) isolated *Brucella* spp. from lymph nodes and spleens of collared peccaries from Venezuela. Other bacteria found in lung tissues of white-lipped peccaries and collared peccaries from Brazil were *Pasteurella multocida* and *Mycoplasma hyopneumonae* (Martins *et al.*, 2014). Regarding viral diseases, Montenegro *et al.* (2018) detected classic porcine fever, porcine circovirus type 2, and vesicular stomatitis in peccaries and feral pigs of Colombia. However, they did not find Aujesky's disease in their samples. In Brazil, Mangini *et al.* (2004), Paes *et al.* (2013), and Martins *et al.* (2014) found porcine circovirus type 2, porcine herpesvirus type 1, and Aujesky's disease in both peccaries and feral pigs.

In Bolivia, Karesh *et al.* (1998) examined the parasites and infectious diseases present in white-lipped peccaries at Noel Kempff National Park. They found evidence of *Leptospira* sp., *Mycoplasma hyorhinus*, Aujesky's disease, vesicular stomatitis, vesicular exanthema of the pig, and San Miguel's marine lion virus. All peccaries (both white-lipped and collared) sampled by Karesh *et al.* (1998), and by Rodríguez *et al.* (2019) in Bolivia were infested by ticks (*Amblyomma* sp.). A similar case was reported for the Chacoan peccary (*Catagonus wagneri*) in Salta, Argentina, where Nava *et al.* (2009) detected *Amblyomma boeroi* in 14 carcasses. Helminths in peccaries have only been reported by Carlos *et al.* (2008) in Peru, who identified *Ascaris* sp., Ancylostomatidae, spiruroid type, and the trematode *Paragonimus* sp.

In Mexico, Romero *et al.* (2008) detected the nematodes *Globocephalus usosubulatus, Parabronema pecariae*, and *Texicospirura turki*; the trematode *Paramphistomum* sp., and the cestode *Moniezia benedeni* in both collared peccaries and white-lipped peccaries of the Lacandon Forest. The only protozoans reported for wild peccaries, collared peccaries, and feral pigs in the Neotropics are *Trypanosoma cruzi* and *T. evansi*, which were identified by Herrera *et al.* (2008) in Brazil. These authors concluded that the parasitemia by *T. evansi* could have been due to the stress resulting from prolonged droughts and habitat loss. Being social species, peccaries and pigs may be good reservoirs of these parasites in both natural and humanized settings. Finally, the only survey to assess the presence of toxic compounds in peccaries was conducted by Karesh *et al.* (1998) in Bolivia, with negative results.

Cervids *(Blastocerus dichotomus, Hippocamelus* spp., *Mazama* spp., *Odocoileus virginianus, Ozotoceros bezoarticus*, and *Pudu* spp.)

Several epidemiological studies on free-ranging deer of South America were published between 1990 and 2022 (see References and complementary list in Appendix S1). Deem *et al.* (2004) reported the presence of *Amblyomma* spp. ticks, *Lipoptena mazamae* (Hippoboscidae) flies, and an unknown louse species in grey brocket deer (*Mazama guazoubira*) of Bolivia. These authors reported the presence of *Leptospira interrogans*, bovine respiratory syncytial virus, and probably, the epizootic haemorrhagic disease virus (EHDV). The nematodes, cestodes, and protozoans *Trichuris ovis, Paramphistommum* spp., *Schistosoma* sp., *Moniezia* sp., and *Eimeria* sp. have also been found in grey brocket deer of Bolivia (Beltrán *et al.*, 2009; Deem *et al.*, 2004). In Brazil, Szabó *et al.* (2003) found that the parasitic load and the number of tick species increased in pampas deer (*Ozotoceros bezoarticus*) after their habitat shrunk because of the flooding caused by the Puerto-Primavera dam. The nematodes *Physocephalus sexalatus, P. lassancei, Texicospirura turki*, and *Pygarginema verrucosa* have also been detected in brocket deer (*Mazama americana* and *M. gouazoubira*), and the pampas deer of the Brazilian Pantanal (Hoppe *et al.*, 2010; Silva *et al.*, 1999). Polymerase Chain Reaction (PCR) tests have allowed determining the incidence of *Theilerya* sp., *Babesia* sp., *Anaplasma* sp., *Brucella abortus* y *Leptospira interrogans* in wild brocket deer (*M. gouazoubira*), pampas deer, and swamp deer (*Blastocerus dichotomus*) in Brazil (Da Silveira *et al.*, 2011; Mathias *et al.*, 1999; Mongruel *et al.*, 2017). Regarding virology assessments, the bluetongue virus and the deer chronic wasting disease were detected in Brazil by Mazzoni *et al.* (2018), and Ribeiro *et al.* (2017). Similarly, pathological retrospective studies and clinical cases in free-ranging Brazilian cervids have been published by Cunha *et al.* (2014), Echenique *et al.* (2018), and Navas *et al.* (2019). No publications on the epidemiology or parasites of *Mazama bricenii, M. chunyi, and M. nana* were found in our searches.

Some studies have been done about parasites and diseases of the huemul deer and the taruca deer (*Hippocamelus* spp.). Analysing faeces of the Patagonian huemul deer (*Hippocamelus bisulcus*) collected in the Aysen and Magallanes regions of southern Chile, Hinojosa *et al.* (2019) found eggs of *Moniezia* sp., *Nematodirus* sp., *Eimeria* spp., and Strongyle-type nematods. In the same area and for the same deer species, Vila *et al.* (2019) observed foot disease probably caused by poxvirus, and Hernandez *et al.* (2019) isolated the bacteria *Echinococcus granulosus* from pulmonary tissue and found larvae of *Taenia hydatigena*. Previously, Hinojosa *et al.* (2014) observed in the same area a huemul female with numerous melanic tumours diagnosed as fibroma, while Morales *et al.* (2017) detected the presence of *Corynebacterium pseudotuberculosis* in abdominal abscesses of two huemul specimens. In southern Argentina, Reissig *et al.* (2020) identified the protozoan *Sarcocystis* sp., while Flueck and Smith-Flueck (2017) documented severe osteopathologies and muscle atrophy in seven huemul deer, probably due to a selenium and iodine-deficient diet. The only study retrieved about parasites of the taruca deer (*Hippocamelus antisensis*) was conducted by Gomez-Puerta *et al.* (2016) who identified the helminths *Trichostrongylus axei, Mazamastrongylus* sp., and *Taenia hydatigena* in a specimen from the southern Peruvian Andes.

Considerably fewer publications exist on the Southern pudu (*Pudu puda*). Oyarzun *et al.* (2018) found the nematode *Dictyocaulus eckerti* in lungs of pudu from southern Chile, while recently, Santodomingo *et al.* (2022) detected the protozoan *Babesia* sp. and the bacteria *Borrelia* sp. in pudus of Chiloé Island. In Argentina, Reissig *et al.* (2020) identified infection by the protozoan *Sarcocystis* sp. on pudus from the Patagonian National Parks. The only virological study on wild pudus was conducted by Hidalgo *et al.* (2022), who found caprine herpesvirus-2 present in samples of dead animals from southern Chile. No publications on the epidemiology or parasites of the Northern pudu (*Pudu mephistophiles*) were retrieved from our searches.

Several surveys on the infectious diseases and parasites of cervids have been done in Mexican extensive wildlife management units (UMA). González (2001) and Barranco (2016) detected protozoans and nematodes of the genus *Eimeria* sp., *Otertagia* spp., *Cooperia* spp., *Moniezia* spp., *Haemeonchus* spp., *Trichostrongylus* spp., *Trichuris* spp., and *Capillaria* spp. in white-tailed deer. Mukul *et al.* (2014) identified the presence of the nematode *Strongylus* sp., ticks (*Amblyomma cajennense*), fleas (*Pulex irritans*), lice (*Gliricola porcelli*), and flies (*Lipoptenena* sp.) in brocket deer (*M. temama*) and white-tailed deer of the Yucatan Peninsula. In the same region, Ojeda *et al.* (2019) detected *Ehrlichia chaffeensis, Anaplasma phagocytophilum, A. odocoilei, Amblyomma mixtum, A. parvum, A. cf. oblongoguttatum, Ixodes affinis, Ripicephalus microplus, R. sensu lato*, and *Haemaphysalis juxtakochi* in brocket deer and white-tailed deer.

Discussion

In the context of increasing demand to feed the global human population, interactions between wildlife and livestock are becoming more frequent, which heightens the risk of pathogen transmission among wild animals, livestock, and humans (Gordon IJ, 2018; Jones *et al.*, 2013). Effective biosecurity measures that are cost-effective are required to control various risks (Jori *et al.*, 2021). The emergence of virus-borne diseases such as AIDS, Ebola, Avian Influenza, and antibiotic-resistant bacteria during the twentieth century, and more recently, the COVID-19 pandemic highlight the need for cooperative work among physicians, veterinarians, economists, sociologists, anthropologists, environmentalists, and other specialists (Cook *et al.*, 2004; Daszak *et al.*, 2000). In 2004, the Wildlife Conservation Society (WCS) emphasized the relevance of understanding the ecology of emerging wildlife diseases under the 'One World-One Health' approach. This approach proposes the integration of medicine and ecosystem health through 12 'Manhattan Principles' seeking to prevent disease and maintain ecosystem health for the benefit of society, wildlife, and livestock (Gibbs, 2014). Neotropical wildlife species are food sources for rural societies throughout Latin America (e.g., Naranjo *et al.*, 2004; Ojasti, 2010); therefore, we need to understand the relationship between the health issues of wildlife, livestock, and people.

Although the majority (68%) of available publications on the epidemiology, parasites, and health conditions of Neotropical ungulates were produced in the last decade (2012–2022), knowledge is clearly uneven among topics, species, and countries. Out of the 33 countries in Latin America and the Antilles, research on the subjects of this review in free-ranging ungulates has been conducted in only 13 countries. Among these, Brazil, Mexico, Chile, Argentina, and Peru have produced 80% of all publications. The studies done in Brazil (52.5% of the total) have included parasitology, bacteriology, virology, and toxicology (Fernandes *et al.*, 2020, 2018; Lima *et al.*, 2013; Malzoni *et al.*, 2010; May-Junior, 2011; Medici *et al.*, 2014). Parasitology has been the most frequent field of study in Mexico (Cruz *et al.*, 2006; Güiris *et al.*, 2017; Romero *et al.*, 2008). In Argentina, Bolivia, Chile, and Colombia, researchers have covered a wider array of topics, such as general health assessments, bacteriology, virology, and parasitology in peccaries and deer (e.g., Bernal *et al.*, 2008; Deem *et al.*, 2004; Flueck and Smith-Flueck, 2017; Hinojosa *et al.*, 2019; Karesh *et al.*, 1998; Montenegro *et al.*, 2018; Rodríguez *et al.*, 2019; Suárez *et al.*, 2008).

It is unclear if the differences in government spending on healthcare and research explain the inequality in the number and thematic coverage of retrieved publications because each country recognizes different priorities (Arriagada *et al.*, 2005). In most countries, human health institutions are still separated from animal health agencies despite the potential benefits of the One Health approach (Gibbs, 2014; Zinsstag *et al.*, 2009). This makes it more difficult to determine if research funding for zoonotic diseases is sufficient.

Studies on free-ranging wildlife have logistic constrains (i.e., capture and handling of animals, hiring of specialized field guides, access to the study area, and sample collection and transport; De Thoisy *et al.*, 2003). Besides, epidemiologic monitoring of zoonotic diseases in wild host species may be difficult to apply in Neotropical countries because of the need for multidisciplinary task forces including veterinary doctors, ecologists, zoologists, epidemiologists, geographers, and mathematicians, among others (Gil and Samartino, 2001). The lack of continuity in political and financial incentives to train and update specialists makes it difficult for many Latin American countries to be self-sufficient in the generation of information about the health of their wildlife species (Schütz *et al.*, 2008). Considering the above, it looks pivotal to identify the drivers of emerging infectious diseases and establishing an epidemiological monitoring system on wildlife populations across the Neotropics.

Most research and publications on wild ungulates in Brazil have been done in public universities and research centres such as São Paulo University, Oswaldo Cruz Foundation, Institute of Ecological Research (IPE, in Portuguese), the Brazilian Institute of Conservation Medicine, and the IUCN Tapir Specialist Veterinary Group. Perhaps the outstanding biodiversity and large size of Brazil's tropical ecosystems (especially the Amazon) draw more interest and funding for research by national and international agencies, which favours higher scientific output. In other Latin American countries, almost all research on the health of ungulates has been done in public institutions. On the other side, remarkable differences in the distribution and density of Neotropical ungulate populations across species and habitats could be playing important roles in the amount of research devoted to assessing their epidemiology of infectious diseases, parasites, and general health conditions. This may help to explain why only four widely distributed species (red brocket deer, collared peccary, white-lipped peccary, and lowland tapir) have received more attention (54.7% of the publications reviewed) than the other 18 Neotropical ungulate species combined. After our review, we identified the following information gaps and needs for further studies on the health of Neotropical ungulates.

Tapirs

The environmental factors and the complex biological cycles determining the selective presence of certain pathogens in some wildlife species have not yet been fully understood. For example, there are places where peccaries and tapirs coexist with livestock. However, brucellosis has been detected in peccaries, but not in tapirs. Similarly, antibodies against diseases such as leptospirosis and toxoplasmosis have been found in coexisting tapirs and livestock (Malzoni *et al.*, 2010; Mangini *et al.*, 2012). Because of that, it is required that future epidemiological research initiatives consider the size of habitat fragments as well as ungulate and livestock population densities. This could help identifying why certain ungulate species are more prone than others to get infected by pathogens. For both Baird's and mountain tapirs, it will be needed to investigate the seroprevalence or isolation of infectious agents similarly to what has been done with the lowland tapir.

The priority diseases to be investigated in Neotropical ungulates should be those that are relevant for public health, the conservation of wild species, and those present in livestock at a regional scale (Quse and Fernandes, 2014). For example, leptospirosis is transmitted where livestock interacts with free-ranging ungulates and has been detected in tapirs of Brazil and Costa Rica (De Freitas *et al.*, 2010; Hernandez-Divers *et al.*, 2005). Thus, it should be a priority to assess the effects of these diseases in tapirs across Latin America. Other diseases potentially threatening tapir populations occurring nearby human settlements are encephalitis (i.e., Nile, East equine, and West equine), whose vector is present in southeastern Mexico and may affect equines and humans (Ulloa *et al.*, 2009). Horses have been used as sentinels of the Equine infectious anaemia in Guatemala and a potential threat for Baird's tapirs has been identified (Lepe *et al.*, 2018). Therefore, the search for antibodies against this disease in wild tapirs may constitute a good opportunity for doing research.

Few studies have focused on the analysis of the relationship between disease intensity and habitat features, for instance, the parasite composition on tapir faeces and their relationship with the vegetation cover (Alvarado, 2018). The environment can play a fundamental role in preserving certain parasites and commensals in tapir droppings (Güiris *et al.*, 2009). This is an opportunity to do relevant research for conserving these ungulates, especially in highly disturbed sites.

Peccaries and feral pigs

Feral pigs have received attention as potential disease vectors for livestock and wild ungulates in Brazil because many of them were introduced during the Paraguay War (Medici *et al.*, 2014; Paes *et al.*, 2013). Similarly, Montenegro *et al.* (2018) found evidence of transmission of leptospirosis between feral pigs and peccaries in Colombia. Nonetheless, no epidemiological studies have been done on feral pigs in Mexico, even though this species is already present in the southeastern part of the country (Hidalgo-Mihart *et al.*, 2014; Weber, 1995). In contrast, Mérida (2015) found presence of brucellosis (30% of the samples) and leptospirosis (34%) in white-lipped peccaries and feral pigs of Uaxactún, northern Guatemala. All feral pigs examined were heavily infested by ticks. The ecological and sanitary impact of these pigs on wild ungulate populations and their habitats across southern Mexico and Central America would constitute another research need to be attended to whenever possible.

Toxicological research on peccaries and feral pigs has been barely done in Latin America. Peccaries, tapirs, and deer sometimes feed on corn, soy, and other plantations across Latin America (Lima *et al.*, 2019; Romero *et al.*, 2006; Ruiz *et al.*, 2014; Serrano *et al.*, 2021), so they could be exposed to toxic compounds such as glyphosate and other pesticides. Therefore, there is a high probability to detect these toxic compounds in free-ranging ungulates across Colombia, where great amounts of herbicides were used since the mid-1980s to eradicate illegal crops (Idrovo, 2015). On the other side, analyses of hormones as stress indicators in ungulates have been applied in captive peccaries to assess the effects of density and space availability on their levels of cortisol (Mangini *et al.*, 2012; Montes *et al.*, 2009, 2012; Nogueira-Filho *et al.*, 2012). However, there are no published surveys of these hormones on peccaries in the wild.

Cervids

There have been evidences of ectoparasites, endoparasites, bacteria, and viruses, such as the bovine respiratory syncytial virus, and the EHDV in South American cervids (see Beltrán *et al.*, 2009; Da Silveira *et al.*, 2011; Deem *et al.*, 2004; Hoppe *et al.*, 2010; Mayor *et al.*, 2007; Mongruel *et al.*, 2017, and many other references in Appendix S1). Nevertheless, research describing shifts in the parasite composition after human disturbance, and pathological studies on Neotropical cervids are very scarce (Cunha *et al.*, 2014; Echenique *et al.*, 2018; Hinojosa *et al.*, 2014; Navas *et al.*, 2018; Szabó *et al.*, 2003).

In the case of Mexico, closeness to the United States, climatic conditions, and socio-economic factors impose remarkable differences in natural resource management between the north and the south of the country. While large numbers of private ranches and extensive UMAs (many with exotic ungulate species for sport hunting) prevail in the north, communal land ownership, subsistence hunting, and a complex sociocultural environment are more frequent in the south, which complicates the functioning of the UMA system originally designed for the north (Weber *et al.*, 2006). This disparity is mirrored in the body of published information about Mexican ungulates, where the white-tailed deer and the mule deer (*Odocoileus hemionus*) have been a lot more studied in northern Mexico than all wild ungulate species in the Neotropical portion of the country.

In northern Mexico, the bluetongue virus, *Boophilus* sp. ticks, EHDV, bovine diarrhoea virus, protozoans (*Theileria cervi*), and the bacteria *Borrelia burgdorferi, Brucella abortus, Brucella mellitensis*, and *Leptospira* sp. have been found in mule deer and white-tailed deer populations (Cantu *et al.*, 2008; Contreras *et al.*, 2007; Martinez *et al.*, 1999; Pavón *et al.*, 2020). Although the work by Cantu *et al.* (2008) on white-tailed deer was not done within the Neotropical region, it is one of the few in which some environmental factors were analysed as drivers of the host's response to an etiological agent.

In contrast, in central and southern Mexico, there have been a very few reports of ectoparasites, endoparasites, and rickettsiae in both free-ranging and UMA deer (Barranco, 2016; González, 2001; Mukul *et al.*, 2014; Ojeda *et al.*, 2019; Romero *et al.*, 2008). Hence, it is necessary to increase the quest for etiological agents that have already been described in the north of the country to create an epidemiological map of them.

Prospects for future research

While there have been many publications on health issues of Neotropical free-ranging ungulates, most of them have only focused on describing microorganisms or their seroprevalence. However, there are still important information gaps that need to be addressed, particularly in fields like environmental toxicology. Even diseases that are traditionally considered relevant for wildlife, livestock, and humans, such as rabies, require further study in this region. According to an epidemiological study based on official databases, only 2.6% of the 1,037 cases of rabies detected between 2001 and 2013 were found in white-tailed deer (Bárcenas *et al.*, 2015). However, these authors concluded that rabies had been under-registered and had spread to new areas. Castellanos and Venegas (2015) photographed a lowland tapir being bitten by false vampire bats (*Desmodus rotundus*) in Yasuni National Park, Ecuador, showing that wild ungulates may be exposed to rabies at any time.

Orta *et al.* (2018) discovered that red brocket deer, collared peccaries, and lowland tapirs consumed soil contaminated with oil in the Peruvian Amazon. Since these animals are hunted for food in the region, it is crucial to investigate whether geophagy could be a means through which humans are exposed to highly toxic substances such as heavy metals, radioactive isotopes, and hydrocarbons. Therefore, investigating the impact of the oil industry and pesticides on the health of wildlife and people in the Neotropics is highly relevant.

Accessing free-ranging ungulates for clinical examination and sampling is a primary challenge in their health research, leading to many surveys utilizing hunted specimens. (Deem *et al.*, 2004; Lord and Lord, 1991; Romero *et al.*, 2008). An alternative to this limitation would be studying livestock populations as models of infectious diseases in conditions like those of wild ungulates, considering the adaptability of the microorganisms to their hosts. In order to better understand the dynamics of diseases, nomadic and free-ranging livestock herds can serve as useful models for monitoring, as suggested by various studies (Abril-Galve *et al.*, 1994; Alberghini, 2019; Centelles *et al.*, 2021).

In southeastern Mexico, Díaz (2006) and Martínez-Mota *et al.* (2007) found higher cortisol levels in the faeces of black howler monkeys (*Alouatta pigra*), jaguars (*Panthera onca*), and pumas (*Puma concolor*) occupying disturbed habitats compared to those using pristine areas. These kinds of studies have not yet been done in Neotropical ungulates that require large tracts of tropical forest in relatively good condition (e.g., tapirs and white-lipped peccaries; Naranjo *et al.*, 2015). Further research is necessary to determine the impact of habitat variables and human disturbance on parasitic load and physiological stress in these species.

In this review, we found that most of the research published between 1990 and 2022 corresponded primarily to parasitological, bacteriological, multi-themed, and pathological surveys on deer, peccaries, and tapirs. We emphasize the need for further research focused on poorly known epidemiological aspects of Neotropical ungulates that have received little attention in the past, especially the Chacoan peccary, the taruca deer, pudus, the least known *Mazama* species (i.e., *M. bororo, M. bricenii, M. chunyi, M. nana*, and *M. rufina*) and wild camelids (i.e., *Lama guanicoe* and *Vicugna vicugna*). In particular, ecotoxicological and pathological studies are needed to assess the effects of agrochemicals and other human disturbances (e.g., feral species) on wild ungulate populations throughout the Neotropical region. It is also important to increase the reach and depth of epidemiological knowledge for wild ungulates out of Brazil. Funding for research and training of local specialists (especially virologists) will be essential for that purpose. Nonetheless, modest surveys on the parasitology, bacteriology, and haematology of local ungulate populations could be promoted in the short term in countries such as Belize, Cuba, Dominican Republic, El Salvador, Guyana, Honduras, Jamaica, Nicaragua, Panama, Paraguay, Puerto Rico, and Suriname, where some research groups and basic infrastructure already exist. Those studies would help to better understand the roles of ecological mechanisms and anthropic processes influencing the health of these mammals. Improving and expanding our knowledge on these elements, particularly in species and countries with the highest information gaps, should be a priority for their sustainable management and conservation.

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